JOURNAL OF NATURAL HISTORY
2026, VOL. 60, NOS. 21–24, 1223–1232
https://doi.org/10.1080/00222933.2026.2658802

Taylor & Francis
by informa

Check for updates

# Trophic ecology of tropical frogs (*Leptodactylus*) assemblage during a drastic drought in Southern Pantanal

Diego G. Cavalheri[a,b,c*], Bruna E. Bolochio[c*], Márcia Marrie Pinheiro Müller[c,d], Patrícia Dos Santos Sousa[c], Sean Keuroghlian-Eaton[c,d], Karoline Ceron[e] and Diego J. Santana[c,d,f]

[a]Centro de Pesquisa e Inovação Itaqui, Instituto Itaqui, Itapevi, Brazil; [b]Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, São Bernardo do Campo, Brazil; [c]Programa de Pós-Graduação em Biodiversidade, Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista 'Júlio de Mesquita Filho', São José do Rio Preto, Brazil; [d]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil; [e]Departamento de Biologia, Universidade Federal Ceara, Fortaleza, Brazil; [f]Negaunee Integrative Research Center and Keller Science Action Center, Field Museum of Natural History, Chicago, Illinois, USA

**ABSTRACT**

Extreme environmental events such as prolonged droughts can drastically alter trophic dynamics in freshwater ecosystems. Amphibians, due to their permeable skin and dual life cycle, are particularly sensitive to such disturbances. The Pantanal, one of the largest floodplains in the world, has recently experienced unprecedented drought and fire events, yet the ecological consequences for the local amphibian fauna remain poorly understood. Here, we investigate the trophic ecology of a *Leptodactylus* assemblage during a severe drought in the southern Pantanal, Brazil. We sampled 84 individuals belonging to three *Leptodactylus* species from a temporary pond over two nights at the end of 2021, examined their stomach contents, and assessed prey availability using pitfall traps. Coleoptera was the most important prey category for *L. fuscus* and *L. podicipinus*, whereas *L. macrosternum* was dominated by Blattaria and Araneae. Electivity analysis revealed active selection for Hemiptera and avoidance of highly abundant taxa such as Collembola and Formicidae, indicating nonrandom foraging under environmental stress. *Leptodactylus macrosternum* and *L. podicipinus* also consumed unidentified tadpoles, representing a novel record of anurophagy involving larval forms in these species. Morphometric ordinations showed broad interspecific differentiation with partial overlap among individuals, consistent with shared morphospace among sympatric species. Our findings suggest that extreme drought promotes short-term trophic compression driven by habitat contraction, characterised by convergent prey selection for Hemiptera, reduced prey heterogeneity, maintenance of generalist feeding patterns, and occasional opportunistic predation on tadpoles.

**ARTICLE HISTORY**
Received 25 September 2025
Accepted 7 April 2026

**KEYWORDS**
Amphibian diet; anurophagy; drought impacts; floodplain ecosystems

## Introduction

Dietary studies are the starting point for answering many questions about organisms' interactions and understanding the flow of energy in the ecosystem (Duellman and Trueb 1994). Additionally, amphibian dietary analyses can examine interactions in both aquatic and terrestrial ecosystems, as many amphibians use both environments (Duré *et al*. 2009; Machado *et al*. 2021). Anurans are considered generalist predators, and feed mainly on arthropods (Santos *et al*. 2004; Caldart *et al*. 2012), although some families specialise in some type of invertebrate (Santana and Juncá 2007; Forti *et al*. 2011; Ceron *et al*. 2019). Anuran diet is influenced by body size, where a positive relationship between frog size and prey size is expected (Sanabria *et al*. 2005; López *et al*. 2007; Ceron *et al*. 2023; Machado *et al*. 2025). Another factor that influences anuran diet is prey availability (López *et al*. 2007; Michelin *et al*. 2020), and therefore, different conspecific populations may have different diets depending on the region or season.

One of the factors that can change prey availability, and consequently the diet of frog species, is changes in their habitat, especially due to anthropogenic impacts (Piatti and Souza 2011; Santana *et al*. 2019). The Pantanal is the largest temporary floodplain in the world, and it has undergone major anthropic changes

**CONTACT** Diego J. Santana dsantana@fieldmuseum.org
*These authors contributed equally to this work

© 2026 Informa UK Limited, trading as Taylor & Francis Group

Published online 11 May 2026

over the last few years (da Silva *et al*. 2011; Alho *et al*. 2019). This ecoregion is located in the upper Paraguay River basin in South America, extending across Bolivia, Paraguay and Brazil, with 78% of its extension located in Brazil. The Pantanal is increasingly affected by drought, driven by both climatic and human factors (Thielen *et al*. 2021; Kumar *et al*. 2022; Costa *et al*. 2024). The region's primary economic activity, cattle ranching, has generated large amounts of deforestation (Da Silva and Girard 2004; Alho *et al*. 2019). Fire is one of the main tools in this deforestation and although fire is a natural process in the Pantanal, nowadays it is predominantly associated with human activities to clear land for ranching (Alho and Silva 2012; Marengo *et al*. 2021). This widespread, human-induced burning has led to some of the most extensive uncontrolled fires in the region's history, resulting in severe biodiversity loss (Alho *et al*. 2019; Marengo *et al*. 2021; Tomas *et al*. 2021).

At the peak of one of the worst droughts of the century, in 2021, we sampled frogs in a drying pond, one of the few remaining water bodies in the region, and found a community composed of three *Leptodactylus* species: *Leptodactylus fuscus*, *L. macrosternum* and *L. podicipinus*. These three species are common and widely distributed across South America (Frost 2024). Neotropical foam-nesting frogs differ markedly in reproductive strategies, including subterranean nesting in burrows, foam nests deposited in marginal basins, and aquatic foam nests associated with exotrophic tadpoles (Carrillo *et al*. 2023). They also differ substantially in body size, with *L. podicipinus* being the smallest, *L. fuscus* of intermediate size and *L. macrosternum* the largest. The diet of these species is considered to be generalist, although there are some differences among populations (Sugai *et al*. 2012; Ceron *et al*. 2018; Santana *et al*. 2019). The most frequent prey is within the order Coleoptera (Sugai *et al*. 2012; Ceron *et al*. 2018; Santana *et al*. 2019). Given the frogs' differences in size and biology, and the fact that they were concentrated in a single shrinking pond during this severe drought, we expected shifts in diet composition and prey availability compared to previous studies, potentially reflecting both interspecific differences and the influence of altered prey availability under extreme environmental conditions.

Herein, we analysed the diet of *L. fuscus*, *L. macrosternum* and *L. podicipinus* during this extreme drought in the Pantanal, while simultaneously assessing the availability of prey in the environment. Given that anthropogenic habitat modification alters prey availability, we hypothesised that *Leptodactylus* populations would exhibit shifts in dietary breadth and dominant prey items compared to previous studies. With the recent anthropogenic changes in the Pantanal, studies observing the diet of these animals can provide valuable perspectives on shifts in ecological interactions, which can directly contribute to our understanding of changes in ecosystem functioning.

## Material and methods

### *Study area*

We worked along the Estrada Parque do Pantanal, located in the Southern Pantanal, in the state of Mato Grosso do Sul, Brazil. The average rainfall is 1000 mm per year, with a dry season from April to October and a rainy season from November to March (Ivory *et al*. 2019). We collected all observed *Leptodactylus* species (*L. fuscus, L. macrosternum*, and *L. podicipinus*) at a pond for two consecutive nights (30 November and 1 December 2021) from 7.00pm to 9.00pm. The pond is a temporary pond (19.47703°S, 57.04382°W) located along the Estrada Parque do Pantanal. After two years of drastic dry seasons in the Pantanal, the pond showed little to no water. Its soil was composed of sand and clay, surrounded by herbaceous vegetation. All individuals were captured manually. Frogs were killed using lidocaine 5% immediately after collection. This research was conducted under licence number SISBIO 49080, provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). To measure the availability of potential prey, we installed 15 pitfall traps around the pond, spaced at least 2 m apart, in the same habitat where we sampled the frogs. Pitfalls consisted of 500 mL plastic containers (diameter: 12 cm) filled with 50 mL of 70% ethanol and some detergent drops, open for 12 h from 7.00pm to 7.00am, during the two nights we collected anurans.

### *Measurements*

We measured the snout–vent length (SVL), head length (HL), head width (HW), internarial distance (IND), eye-to-nostril distance (END), eye diameter (ED), upper eyelid width (UEW), interorbital distance (IOD), hand

length (HAL), thigh length (THL), tibia length (TL), and foot length (FL) of each captured individual, using digital callipers with 0.01 mm precision. These morphometric variables, particularly SVL, were later used to classify individuals by size using a K-means clustering method. We removed stomachs through a small abdominal incision and stored the contents in separate vials for dietary analysis.

### *Statistical analysis*

To establish the species groupings based on morphometric data (specifically SVL), we employed K-means clustering (Legendre and Legendre 2012). The ideal number of clusters was identified using the statistical gap method (Tibshirani *et al*. 2001). The K-means analysis was performed using the factoextra package (Kassambara and Mundt 2016) within the R programming environment (R Core Team 2022).

We visualised the results of the clustering analysis using two graphical approaches: (1) a scatter plot of snout–vent length (SVL) versus head length (HL), colour-coded by cluster (Figure 1); and (2) a principal component analysis (PCA) plot based on all morphometric variables (Figure 2). Because clustering was

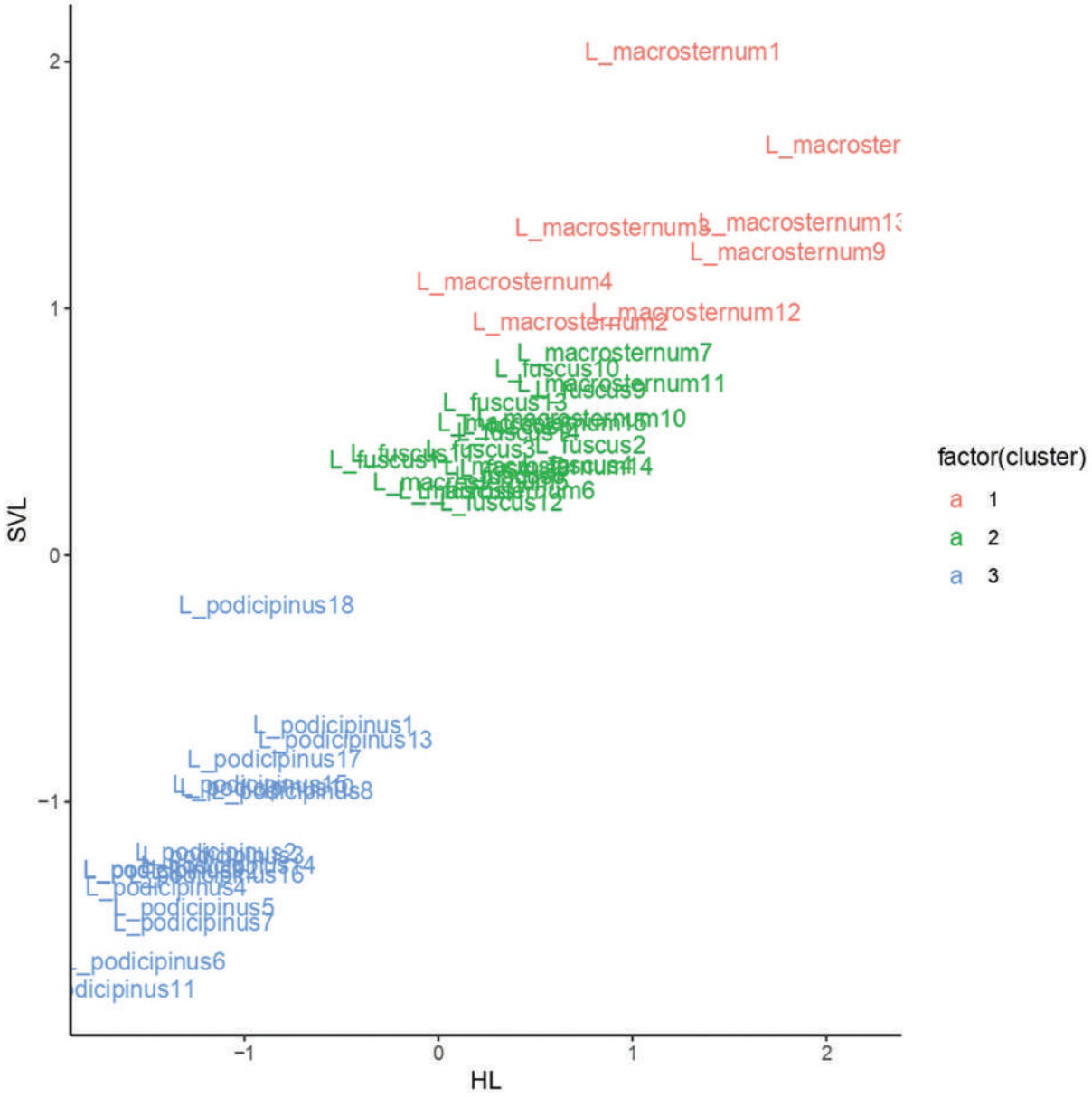


**Figure 1.** Cluster analysis based on morphological measurements (snout–vent length - SVL and head length - HL) for individuals of the three *Leptodactylus* species, using k-means clustering. Colours represent the groups identified by the clustering analysis.

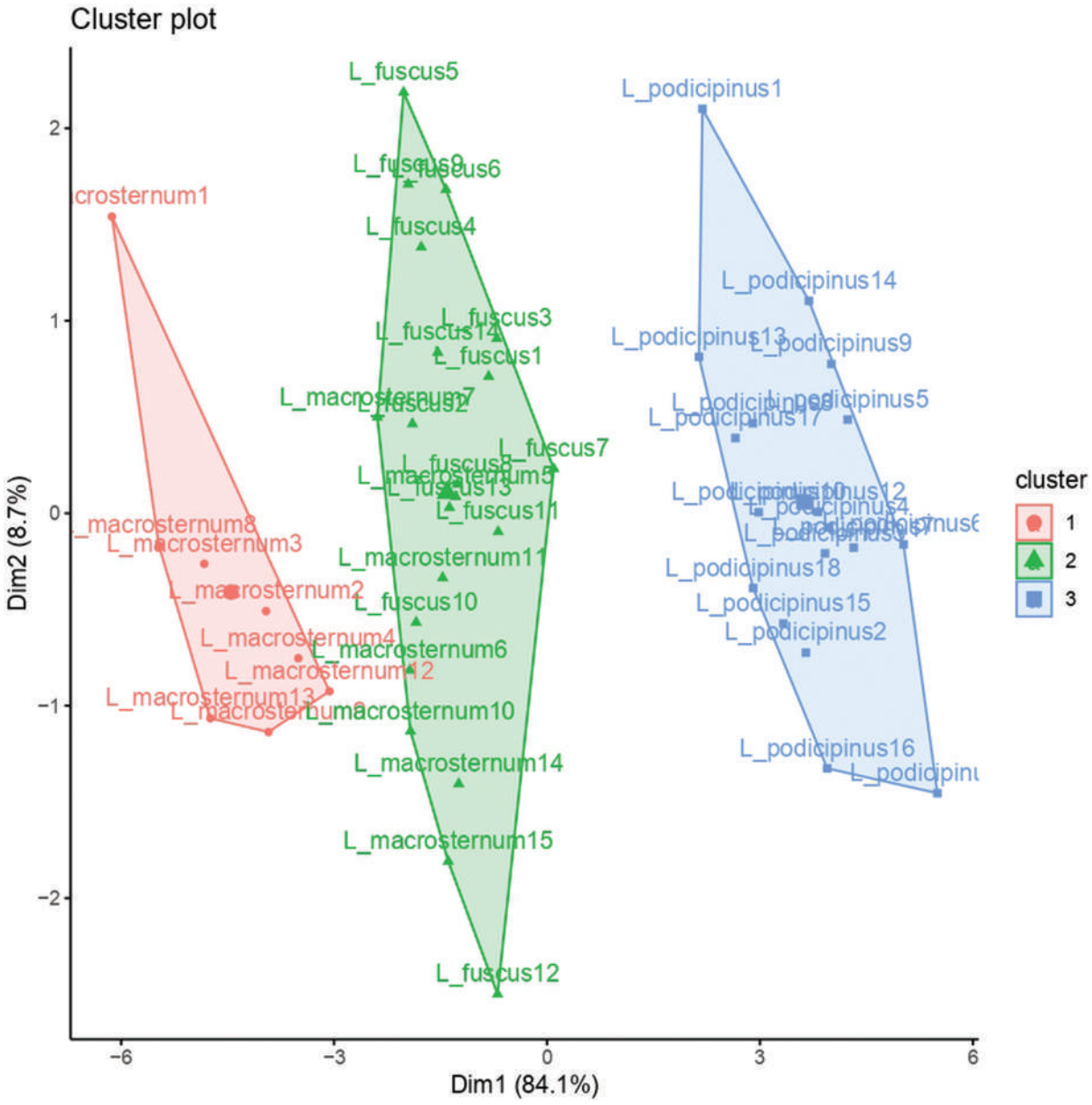


**Figure 2.** Two-dimensional representation of the k-means cluster analysis based on principal component analysis (PCA) of morphometric variables. Each point represents an individual, and colour-coded groups correspond to the three main clusters consistent with the three analysed species.

unsupervised, cluster membership was interpreted as a pattern of morphometric similarity rather than as a taxonomic reassignment. Overall, the ordinations showed broad separation among groups consistent with the three species, while also indicating partial overlap between *L. macrosternum* and *L. fuscus* for some individuals.

### *Dietary analysis*

We observed the stomach contents of each frog under a stereomicroscope. We classified the stomach food items and arthropods from our pitfall traps to the order level, with exception of Formicidae, which was identified at the family level. Identifications were based on a specialised key (Rafael *et al*. 2024). The width and length of each prey was measured with a digital calliper (0.01 mm resolution), and we estimated the volume of the contents of each stomach using the ellipsoid formula $V = \frac{4\pi}{3} * \frac{l}{2} * \left(\frac{w}{2}\right)^2$, where *w* corresponds to item width and *l* is the item length (Magnusson *et al*. 2003). Total prey volume per species was calculated

as the sum of the volumes of all prey items consumed by all individuals of that species. We determined the number, frequency and volume of each stomach item and calculated its significance value using the index of relative importance: $IRI = \frac{(F\%+N\%+V\%)}{3}$, where F% represents the frequency proportion, N% the numeric proportion and V% the volumetric proportion (Biavati *et al*. 2004; Marques-Pinto *et al*. 2019).

Electivity was quantified using Vanderploeg and Scavia's relativised electivity index (E*), which compares the proportional contribution of each prey category in the diet (r) to its proportional availability in the environment (p). Positive values indicate selection, values near zero indicate consumption proportional to availability and negative values indicate avoidance.

We calculated the niche breadth for prey abundance for each species using the inverse of the Simpson index: $B = 1/\Sigma^{(pi2)}$, where *i* is the resource category and *p* is the resource *i* category proportion (Simpson 1949). Pairwise niche overlap was calculated using the Pianka index: $\alpha = \frac{U1j*U2j}{(U1j)*(U2j)*\alpha^2}$ where *U1j* is the proportion of resource *j* used by species *1* and *U2 j* refers to the proportion of resource *j* used by species 2 (Pianka 1973).

## Results

We collected 84 individuals of *Leptodactylus*: 19 *L. fuscus*, 31 *L. macrosternum* and 34 *L. podicipinus*. Of the stomachs analysed, seven were empty (five *L. fuscus*, one *L. macrosternum* and one *L. podicipinus*). For *L. fuscus*, we recorded 18 prey items distributed across six categories (Araneae, Coleoptera, Formicidae, Hemiptera, Lepidoptera and not identified [NI]), in addition to two seeds (Table 1). For *L. macrosternum*, we recorded 298 prey items distributed across nine categories (Anura [tadpole], Araneae, Blattaria, Coleoptera, Diptera, Formicidae, Hemiptera, Hymenoptera and Lepidoptera) (Table 1). For *L. podicipinus*, we recorded 43 prey items distributed across 10 categories (Anura [tadpole], Araneae, Coleoptera, Diplopoda, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera and NI), in addition to one seed (Table 1). The most important prey categories based on IRI% were Coleoptera for *L. fuscus* (IRI% = 47.2) and *L. podicipinus* (IRI% = 79.05), and Blattaria for *L. macrosternum* (IRI% = 71.15) (Table 1).

**Table 1:** Diet of three species of *Leptodactylus* (*L. fuscus, L. macrosternum*, and *L. podicipinus*) at Estrada Parque do Pantanal, located in the state of Mato Grosso do Sul, Brazil during a drastic drought. V = volume, N = number of preys, F = frequency, IRI = important relative index, NI = Not indentified.

| Species | V ($mm^3$) | V% | N | N% | F | F% | IRI | IRI% |
|---|---|---|---|---|---|---|---|---|
| ***L. fuscus* (19)** | | | | | | | | |
| Aranae | 114.15 | 3.20 | 2 | 11.11 | 2.00 | 22.22 | 317.97 | 5.57 |
| Coleoptera | 575.22 | 16.15 | 8 | 44.44 | 4.00 | 44.44 | 2692.62 | 47.20 |
| Formicidae | 558.55 | 15.68 | 2 | 11.11 | 2.00 | 22.22 | 595.27 | 10.43 |
| Hemiptera | 597.25 | 16.77 | 3 | 16.67 | 2.00 | 22.22 | 743.04 | 13.02 |
| NI | 76.19 | 2.14 | 1 | 5.56 | 1.00 | 11.11 | 85.55 | 1.50 |
| Lepidoptera | 1640.66 | 46.06 | 2 | 11.11 | 2.00 | 22.22 | 1270.32 | 22.27 |
| ***L. macrosternum* (31)** | | | | | | | | |
| Anura | 195.32 | 1.11 | 3 | 1.01 | 3.00 | 21.43 | 45.43 | 0.45 |
| Aranae | 9188.66 | 52.27 | 117 | 39.26 | 4.00 | 28.57 | 2615.01 | 25.70 |
| Blattaria | 6526.00 | 37.12 | 164 | 55.03 | 11.00 | 78.57 | 7240.23 | 71.15 |
| Coleoptera | 90.43 | 0.51 | 1 | 0.34 | 1.00 | 7.14 | 6.07 | 0.06 |
| Diptera | 542.78 | 3.09 | 7 | 2.35 | 5.00 | 35.71 | 194.26 | 1.91 |
| Formicidae | 64.05 | 0.36 | 1 | 0.34 | 1.00 | 7.14 | 5.00 | 0.05 |
| Hemiptera | 751.80 | 4.28 | 1 | 0.34 | 1.00 | 7.14 | 32.99 | 0.32 |
| Hymenoptera | 105.16 | 0.60 | 2 | 0.67 | 2.00 | 14.29 | 18.15 | 0.18 |
| Lepidoptera | 114.92 | 0.65 | 2 | 0.67 | 2.00 | 14.29 | 18.86 | 0.19 |
| ***L. podicipinus* (34)** | | | | | | | | |
| Anura | 95.07 | 7.89 | 4 | 9.30 | 4.00 | 23.53 | 404.48 | 5.16 |
| Aranae | 139.27 | 11.55 | 2 | 4.65 | 1.00 | 5.88 | 95.26 | 1.21 |
| Coleoptera | 498.42 | 41.35 | 20 | 46.51 | 12.00 | 70.59 | 6202.04 | 79.05 |
| Diplopoda | 29.54 | 2.45 | 2 | 4.65 | 1.00 | 5.88 | 41.75 | 0.53 |
| Diptera | 82.36 | 6.83 | 4 | 9.30 | 3.00 | 17.65 | 284.69 | 3.63 |
| Hemiptera | 51.63 | 4.28 | 2 | 4.65 | 2.00 | 11.76 | 105.02 | 1.34 |
| Hymenoptera | 128.68 | 10.67 | 1 | 2.33 | 1.00 | 5.88 | 76.44 | 0.97 |
| Lepidoptera | 10.66 | 0.88 | 2 | 4.65 | 2.00 | 11.76 | 65.03 | 0.83 |
| Orthoptera | 134.77 | 11.18 | 4 | 9.30 | 4.00 | 23.53 | 481.89 | 6.14 |
| NI | 35.05 | 2.91 | 2 | 4.65 | 2.00 | 11.76 | 88.91 | 1.13 |

**Table 2.** Absolute prey availability recorded in the sampling areas. For each prey category, we report the number of samples in which the item was detected (N), the total number of individuals collected (N total), mean prey length and width (mm), and the estimated prey volume calculated using the ellipsoid approximation ($mm^3$).

| Prey category | N total | Length | Width | Volume ellipsoid |
|---|---|---|---|---|
| Coleoptera | 274 | 17.84 | 6.05 | 276,104.9 |
| Arachnids | 36 | 7.3 | 2.19 | 2,198.72 |
| Orthoptera | 25 | 5.15 | 1.42 | 492.74 |
| Hemiptera | 7 | 9.58 | 2.32 | 780 |
| Collembola | 3,840 | 0.151 | 0.023 | 1.054 |
| Plecoptera | 1 | 15.27 | 2.79 | 340.46 |
| Diptera | 108 | 2.54 | 0.89 | 324.53 |
| Formicidae | 835 | 2.88 | 0.79 | 2,160.04 |

**Table 3.** Vanderploeg and Scavia's relativised electivity index.

| Electivity index | *L. fuscus* | *L. macrosternum* | *L. podicipinus* |
|---|---|---|---|
| Anura | NA | NA | NA |
| Aranae | 0.17 | −0.22 | 0.26 |
| Blattaria | NA | NA | NA |
| Coleoptera | −0.16 | 0.64 | 0.04 |
| Collembola | −1 | −1 | −1 |
| Diplopoda | NA | NA | NA |
| Diptera | −1 | −0.87 | −0.56 |
| Formicidae | −0.89 | −0.96 | −1 |
| Hemiptera | 0.83 | 0.77 | 0.79 |
| Hymenoptera | NA | NA | NA |
| Lepidoptera | NA | NA | NA |
| Orthoptera | −1 | −1 | 0.10 |
| Plecoptera | −1 | −1 | −1 |

Regarding the availability of prey in the environment, we found eight categories: Coleoptera, Aranae, Orthoptera, Hemiptera, Collembola, Plecoptera, Diptera and Formicidae (Tables 2 and 3). The most frequently available food item was Colembola (3840 individuals), followed by Formicidae (835 individuals) and Coleoptera (274 individuals) (Table 2). However, the prey with the largest volume was Coleoptera (276,104 $mm^3$), followed by Formicidae (2267 $mm^3$) and Aranae (2198 $mm^3$). Five prey types did not fall into our pitfall traps, but were consumed by frogs: Lepidoptera, Blattaria, other categories of Hymenoptera, Diplopoda and Anura.

Morphometric clustering using K-means revealed three distinct groups consistent with the taxonomic identification of *L. fuscus, L. macrosternum* and *L. podicipinus*. The scatter plot of SVL vs. HL (Figure 1) clearly showed the separation of individuals by size and species. The PCA-based cluster plot (Figure 2) further supported this differentiation, with individuals forming three cohesive groups along the first two dimensions, which explained over 90% of the total variance. Additionally, electivity analysis using the Vanderploeg and Scavia index (Table 3; Figure 3) revealed prey selection patterns relative to environmental availability (Table 2). All species positively selected Hemiptera and avoided Collembola and Formicidae, despite the high numerical abundance of the latter in the environment. The butter-frog (*L. macrosternum*) also showed positive electivity for Coleoptera.

Niche breadth based on prey abundance (inverse Simpson's B) was highest for *L. podicipinus* (B = 3.94), followed by *L. fuscus* (B = 3.77), and lowest for *L. macrosternum* (B = 2.18). Pianka's niche overlap was high between *L. fuscus* and *L. podicipinus* (O = 0.876) and low for pairs involving *L. macrosternum* (*L. fuscus* × *L. macrosternum*: O = 0.134; *L. macrosternum* × *L. podicipinus*: O = 0.069).

## Discussion

*Leptodactylus fuscus* and *L. podicipinus* showed Coleoptera as the most important prey category in terms of IRI% (Table 1), a pattern commonly reported for anurans (Ceron *et al.* 2019) and consistent with the high availability of Coleoptera in our environmental samples (Table 2). In general, species of *Leptodactylus* have been described as sit-and-wait foragers that often capture relatively large and mobile prey (Solé and Rödder 2009). We also recorded Anura (tadpoles) in the stomach contents of *L. macrosternum* and *L. podicipinus* (Table 1). Anurophagy involving adult anurans as prey has been documented in leptodactylid frogs, whereas

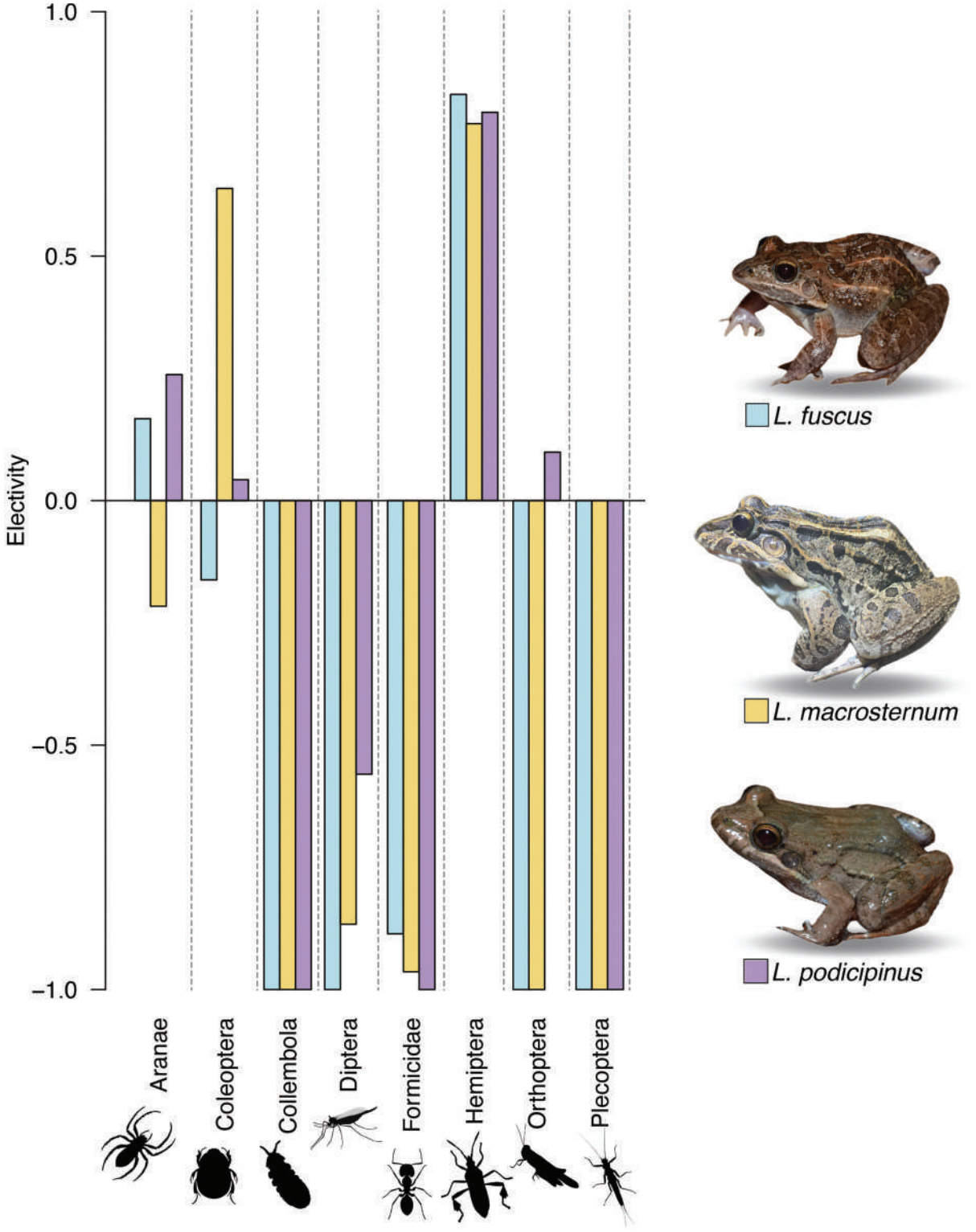


**Figure 3.** Vanderploeg and Scavia electivity index for food items consumed by three *Leptodactylus* species (*L. fuscus, L. macrosternum* and *L. podicipinus*) during a severe drought in the southern Pantanal, Brazil. Positive values indicate active selection, values near zero indicate consumption in proportion to environmental availability, and negative values indicate avoidance.

predation on tadpoles remains rarely reported (see Cavalheri *et al*. 2022). Given the low frequency of these records in our sample, we interpret tadpole consumption as an opportunistic event under the studied conditions rather than evidence of consistent anurophagy in these species.

The Pantanal experienced a prolonged drought period followed by severe fires between 2019 and 2021, causing unprecedented impacts on regional fauna and flora (Marengo *et al*. 2021; Ferreira Barbosa *et al*. 2022; Silva *et al*. 2024). Such extreme events can alter trophic interactions and resource pathways, and may change amphibian feeding patterns and resource use (eg Carreira *et al*. 2016; Chang *et al*. 2016). Therefore, understanding how amphibians adjust trophic strategies during extreme climatic events is essential for predicting their persistence under future climate scenarios. In this context, the convergent positive electivity for Hemiptera observed among species with distinct body sizes and life-history traits suggests short-term trophic compression driven by environmental constraints rather than intrinsic feeding preferences. Similar species studied under typical Pantanal hydrological regimes show broader prey representation associated with floodplain heterogeneity (Rodrigues *et al*. 2004; Sugai *et al*. 2012), reinforcing the role of drought-driven habitat contraction in shaping trophic interactions in the present study. In increasingly drought- and fire-prone floodplains such as the Pantanal, these disturbances may temporarily reshape trophic interactions and energy pathways rather than producing persistent shifts in community structure.

Although electivity indicated convergence in the positive selection of Hemiptera, niche metrics based on prey abundance suggested that overlap was not uniform across species. Pianka's index revealed high overlap between *L. fuscus* and *L. podicipinus*, but low overlap for pairs involving *L. macrosternum*, indicating partial trophic differentiation despite shared selection for a key prey group (Pianka 1973). Niche breadth indicated broader prey use in *L. fuscus* and *L. podicipinus* than in *L. macrosternum* (Simpson 1949).

Furthermore, our morphometric analyses revealed clear species-level differentiation, reinforcing the idea that morphological variation is often associated with differences in resource use and foraging ecology (Santana and Juncá 2007; Sugai *et al*. 2012; Ceron *et al*. 2018; Machado *et al*. 2025). The three sympatric species differ markedly in body size, with *L. podicipinus* being the smallest, *L. fuscus* intermediate and *L. macrosternum* the largest. Despite extreme drought, we observed significant trophic convergence in the positive selection of Hemiptera. However, interspecific differences in secondary prey categories and total consumption volume suggest that morphological constraints (eg gape limitation and handling capacity) continue to influence the range of prey exploited, particularly for the largest species. Nevertheless, additional quantitative analyses will be necessary to formally test the role of body size in this assemblage, such as analyses relating body size or gape limitation to prey size distribution and consumption volume across species (eg Moroti *et al*. 2021; Ceron *et al*. 2023; Machado *et al*. 2025).

## Author contributions

CRediT: **Diego G. Cavalheri:** Conceptualization, Data curation, Methodology, Writing – original draft, Writing – review & editing; **Bruna E. Bolochio:** Data curation, Formal analysis, Methodology, Project administration, Writing – original draft; **Márcia Marrie Pinheiro Müller:** Data curation, Methodology; **Sean Keuroghlian-Eaton:** Data curation, Methodology; **Karoline Ceron:** Methodology, Software, Writing – original draft; **Diego J. Santana:** Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

## Disclosure statement

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

## Funding

DGC, BEB, MPM, PSS, SKE thank Coordenacão de Aperfeiçoamento de Pessoal de Nıvel Superior – Brasil (CAPES) Funding code 001. DGC also thanks Centro de Pesquisas e Inovação Itaqui for financial support. DJS thanks Conselho Nacional de Desenvolvimento Cientıfico e Tecnologico [CNPq processes 404239/2021-8, 402519/2016-7, 309420/2020-2] and Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul [FUNDECT process 054/2017] for financial support. KC thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research fellowship (#444240/2024-1).

## References


Alho CJR, Mamede SB, Benites M, Andrade BS, Sepúlveda JJO. 2019. Threats to the biodiversity the Brazilian Pantanal due to land use and occupation. Ambiente Soc. 22:e01891. https://doi.org/10.1590/1809-4422asoc201701891vu2019l3ao

Alho CJR, Silva JSV. 2012. Effects of severe floods and droughts on wildlife of the Pantanal wetland (Brazil)—a review. Animals. 2(4):591–610. https://doi.org/10.3390/ani2040591

Biavati GM, Wiederhecker HC, Colli GR. 2004. Diet of Epipedobates flavopictus (Anura: Dendrobatidae) in a neotropical savanna. J Herpetol. 38(4):510–518. https://doi.org/10.1670/30-04A

Caldart VM, Iop S, Bertaso TRN, Zanini S. 2012. Feeding ecology of Crossodactylus schmidti (Anura: Hylodidae) in southern Brazil. Zool Stud. 51(4):484–493.

Carreira BM et al. 2016. Warm vegetarians? Heat waves and diet shifts in tadpoles. Ecology. 97(11):2964–2974. https://doi.org/10.1002/ecy.1541

Carrillo JFC, Santana DJ, Prado CPA. 2023. An overview of parental care in the foam-nesting frogs of the genus Leptodactylus (Anura: leptodactylidae): current knowledge and future directions. Amphibia-Reptilia. 44(3):1–10. https://doi.org/10.1163/15685381-bja10140

Cavalheri DG, Cuestas Carrillo JF, Dos Santos Souza V, Santana DJ. 2022. Two records of anurophagy in Leptodactylus macrosternum from Cerrado, Brazil, with a review list of cases for the genus Leptodactylus (Anura: Leptodactylidae). Caldasia. 45(1):136–150. https://doi.org/10.15446/caldasia.v45n1.96789

Ceron K et al. 2018. Diet and first report of batracophagy in Leptodactylus podicipinus (Anura: Leptodactylidae). Neotrop Biodivers. 4(1):70–74. https://doi.org/10.1080/23766808.2018.1467173

Ceron K et al. 2019. Global patterns in anuran–prey networks: structure mediated by latitude. Oikos. 128(11):1537–1548. https://doi.org/10.1111/oik.06621

Ceron K et al. 2023. Trophic ecology of small to large hylids from an Amazonia-Cerrado transitional zone in Brazil. Food Webs. 36(e00295):1–7. https://doi.org/10.1016/j.fooweb.2023.e00295

Chang C-W, Huang B-H, Lin S-M, Huang C-L, Liao P-C. 2016. Changes of diet and dominant intestinal microbes in farmland frogs. BMC Microbiol. 16(1):33. https://doi.org/10.1186/s12866-016-0660-4

Costa MC, Marengo JA, Alves LM, Cunha AP. 2024. Multiscale analysis of drought, heatwaves, and compound events in the Brazilian Pantanal in 2019–2021. Theor Appl Climatol. 155(1):661–677. https://doi.org/10.1007/s00704-023-04655-2

Da Silva CJ, Girard P. 2004. New challenges in the management of the Brazilian Pantanal and catchment area. Wetlands Ecol Manag. 12(6):553–561. https://doi.org/10.1007/s11273-005-1755-0

da Silva JDSV, Abdon MDM, da Silva SMA, de Moraes JA. 2011. Evolution of deforestation in the Brazilian Pantanal and surroundings in the timeframe 1976 – 2008. Geografia. 36:35–55.

Duellman WE, Trueb L. 1994. Biology of amphibians. Baltimore: Johns Hopkins University Press.

Duré MI, Kehr AI, Schaefer EF. 2009. Sobreposição de nicho e partilha de recursos entre cinco espécies simpátricas de bufonídeos (anura, bufonidae) do nordeste da Argentina. Phyllomedusa J Herpetol. 8(1):27. https://doi.org/10.11606/.2316-9079.v8i1p27-39

Ferreira Barbosa ML et al. 2022. Compound impact of land use and extreme climate on the 2020 fire record of the Brazilian Pantanal. Glob Ecol Biogeogr. 31(10):1960–1975. https://doi.org/10.1111/geb.13563

Forti L, Tissiani A, Mott T, Strüssmann C. 2011. Diet of Ameerega braccata (Steindachner, 1864) (Anura: Dendrobatidae) from Chapada dos Guimarães and Cuiabá, Mato Grosso State, Brazil. Braz J Biol. 71(1):189–196. https://doi.org/10.1590/S1519-69842011000100027

Frost DR (2024) Amphibian species of the world: an online reference.

Ivory SJ, McGlue MM, Spera S, Silva A, Bergier I. 2019. Vegetation, rainfall, and pulsing hydrology in the Pantanal, the world's largest tropical wetland. Environ Res Lett. 14(12):124017. https://doi.org/10.1088/1748-9326/ab4ffe

Kassambara A, Mundt F (2016) Factoextra: extract and visualize the results of multivariate data analyses. 1.0.7.

Kumar S et al. 2022. Changes in land use enhance the sensitivity of tropical ecosystems to fire-climate extremes. Sci Rep. 12(1):964. https://doi.org/10.1038/s41598-022-05130-0

Legendre P, Legendre L. 2012. Numerical ecology. 3d English ed. Amsterdam: Elsevier.

López JA, Ghirardi R, Scarabotti PA, Medrano MC. 2007. Feeding ecology of Elachistocleis bicolor in a riparian locality of the middle Paraná River. Herpetol J. 17(1):48–53.

Machado HTS, Araújo KC, Benício RA, Ávila RW. 2021. Feeding habits of Dermatonotus muelleri (Anura, Microhylidae) from a semiarid region in Pernambuco state, northeastern Brazil. Braz J Biol. 81(4):1120–1121. https://doi.org/10.1590/1519-6984.230774

Machado RR et al. 2025. Trophic ecology of a Pantanal treefrog assemblage during a severe drought. Stud Neotropical Fauna Environ. 60(3):1–10. https://doi.org/10.1080/01650521.2025.2507368

Magnusson WE, Lima AP, Silva WA, Araújo MC 2003. Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. Copeia. 2003(1):13–19.

Marengo JA et al. 2021. Extreme drought in the Brazilian Pantanal in 2019–2020: characterization, causes, and impacts. Front Water. 3:639204. https://doi.org/10.3389/frwa.2021.639204

Marques-Pinto T, Barreto-Lima AF, Bradão RA. 2019. Dietary resource use by an assemblage of terrestrial frogs from the Brazilian cerrado. North West J Zool. 15(2):135–146.

Michelin G, Ceron K, Santana DJ. 2020. Prey availability influences the diet of Scinax fuscomarginatus in a cerrado area, central Brazil. Anim Biodivers Conserv. 169–175. https://doi.org/10.32800/abc.2020.43.0169

Moroti MT, Soares PT, Pedrozo M, Provete DB, Santana DJ. 2021. The effects of prey availability, phylogeny, and morphology on trophic resource partitioning in an anuran community. Basic Appl Ecol. 50:181–191. https://doi.org/10.1016/j.baae.2020.11.005.

Pianka ER. 1973. The structure of lizard communities. Annu Rev Ecol Syst. 4(1):53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Piatti L, Souza F. 2011. Diet and resource partitioning among anurans in irrigated rice fields in Pantanal, Brazil. Braz J Biol. 71(3):653–661. https://doi.org/10.1590/S1519-69842011000400009

Rafael JA, Melo GAR, Carvalho CJB, Cesari SA, Constatino R. 2024. Insetos do Brasil: diversidade e taxonomia. 2nd ed. Manaus (AM): Editora INPA.

R CORE TEAM. 2022. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org

Rodrigues DJ, Uetanabaro M, Lopes FS. 2004. Diet of *Leptodactylus podicipinus* (Anura: Leptodactylidae) in the southern Pantanal, Brazil. Stud neotropical fauna environ. 39(3):243–247. https://doi.org/10.1080/01650520400025759

Sanabria EA, Quiroga LB, Acosta JC. 2005. Dieta de Leptodactylus ocellatus (Linnaeus, 1758) (Anura:Leptodactylidae) en un humedal del oeste de Argentina. Rev Peru Biol. 12(3):472–477. https://doi.org/10.15381/rpb.v12i3.2424

Santana A, Juncá F. 2007. Diet of Physalaemus cf. cicada (Leptodactylidae) and Bufo granulosus (Bufonidae) in a semideciduous forest. Braz J Biol. 67(1):125–131. https://doi.org/10.1590/S1519-69842007000100017

Santana DJ, Ferreira VG, Crestani GN, Neves MO. 2019. Diet of the rufous frog Leptodactylus fuscus (Anura, Leptodactylidae) from two contrasting environments. Herpetozoa. 32:1–6. https://doi.org/10.3897/herpetozoa.32.e35623

Santos EM, Almeida AV, Vasconcelos SD. 2004. Feeding habits of six anuran (Amphibia: anura) species in a rainforest fragment in northeastern Brazil. Iheringia Ser Zool. 94(4):433–438. https://doi.org/10.1590/S0073-47212004000400014

Silva PS et al. 2024. Joining forces to fight wildfires: science and management in a protected area of Pantanal, Brazil. Environ Sci Policy. 159:103818. https://doi.org/10.1016/j.envsci.2024.103818

Simpson EH. 1949. Measurement of Diversity. Nature. 163(4148):688. https://doi.org/10.1038/163688a0

Solé M, Rödder D. 2009. Dietary assessments of adult amphibians. In: Dodd CK, editor. Amphibian ecology and conservation. Oxford: Oxford University Press. p 167–184.

Sugai JLMM, Terra JDS, Ferreira VL. 2012. Diet of Leptodactylus fuscus (Amphibia: anura: Leptodactylidae) in the Pantanal of Miranda River, Brazil. Biota Neotrop. 12(1):99–104. https://doi.org/10.1590/S1676-06032012000100008

Thielen D et al. 2021. The Pantanal under Siege—On the origin, dynamics and forecast of the megadrought severely affecting the largest wetland in the world. Water. 13(21):3034. https://doi.org/10.3390/w13213034

Tibshirani R, Walther G, Hastie T. 2001. Estimating the number of clusters in a data set via the gap statistic. J R Stat Soc Ser B Stat Methodol. 63(2):411–423. https://doi.org/10.1111/1467-9868.00293

Tomas WM et al. 2021. Distance sampling surveys reveal 17 million vertebrates directly killed by the 2020's wildfires in the Pantanal, Brazil. Sci Rep. 11(1):23547. https://doi.org/10.1038/s41598-021-02844-5