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# Diet and trophic niche overlap of four syntopic species of *Physalaemus* (Anura: Leptodactylidae) in southern Brazil

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**Abstract.** Despite the current increase in studies on the diet of neotropical anurans, few of them take a comparative approach between syntopic species. The objective of this study was to compare the diet of four syntopic species of the genus *Physalaemus*. The collections occurred between November 2014 and January 2016 in a preserved area of the subtropical Atlantic Forest in southern Brazil. We compared the gastrointestinal content of 109 individuals distributed in the species *Physalaemus biligonigerus*, *P. cuvieri*, *P. gracilis* and *P. henselii*. We measured the Index of Relative Importance of each prey category and calculated trophic niche breadth using the Levins' index (Bsta) and trophic niche overlap using the Pianka's index (Ojk). We also applied compositional analysis to evaluate feeding specializations. Formicidae was the most important prey category for *P. biligonigerus* (IRI = 88.5%) and *P. gracilis* (IRI = 39.1%). For *P. henselii* and *P. cuvieri*, the most important category was Isopoda (IRI = 51.7% and 57.9%, respectively), followed by Formicidae (IRI = 34.9% and 24.8%). Isopoda was also important in the diet of *P. gracilis* (IIR = 28.6%), followed by Araneae (IIR = 22.6%). The trophic niche breadth of the four species was narrow, all smaller than 0.32, and the lowest was recorded for *P. biligonigerus* (0.04). The trophic niche overlap was higher between *P. biligonigerus* and *P. cuvieri* (96%), and between *P. gracilis* and *P. henselii* (95%). Only *P. gracilis* presented a significant level of feeding specialization. The differences in their diets suggest different uses of the resources, which could relate to different ways of exploring the microhabitat.

**Keywords.** Foraging, trophic niche, amphibians, behavior.

## INTRODUCTION

Resources can be shared by species in three different dimensions: temporal, trophic and spatial (Pianka, 1973). The different ways that species use resources can favor their coexistence and promote a reduction of competition between them (Pianka, 1974). These differences can be observed, for example, in the different ways the species use the microhabitat, in the variety and sizes of food items and their period of activity (Schoener, 1974; Duellman and Trueb, 1986). Thus, basic data gathering about the ecology of organisms brings a great contribution to the elaboration of hypotheses and premises regarding niche partitioning and general ecology.

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Although the divergence in feeding habits favors the coexistence of sympatric organisms, closely related species tend to use resources in a similar way (Pianka, 1973) since they are similar in physiology and often in morphology and behavior as well (Heyer et al., 1990). The number of studies on the diet of Neotropical anurans has increased in recent years (Siqueira et al., 2006, Dietl et al., 2009, Rodrigues and Santos-Costa, 2014, Moser et al. 2017; Oliveira et al. 2017, Dias et al. 2018, Farina et al. 2018, Moser et al. 2019, Protázio et al. 2019, Oliveira et al. 2021, Moser et al. 2022). However, few studies focus on a comparative approach to the species' diet (Oliveira et al., 2015, Moser et al., 2017).

Trophic relationships between species comprise one of the main aspects of their life history (Duellman and Trueb, 1986; Vitt and Caldwell, 2009). Information on resource partitioning among species can help us understand some parameters about community dynamics such as niche overlap and breadth (Lawor, 1980), which are essential data to describe part of their ecological niche (Sih and Christensen, 2001).

The genus *Physalaemus* (Leptodactylidae) has about 51species and is widely distributed in the Neotropical ecozone (Frost et al., 2006). Species of this genus are characterized by consuming predominantly ants, beetles and spiders, but having an opportunistic diet pattern (López et al., 2003; Becker et al., 2007; Santana and Juncá, 2007; Rodrigues and Santos-Costa, 2014; Oliveira et al., 2015; Moser et al., 2017; Farina et at., 2018). Possible variations in diet composition among species are generally associated with variations in prey availability since, in general, anurans have an opportunistic diet (López et al., 2003; Moser et al., 2017). Thus, the study of syntopic populations presents an excellent opportunity to evaluate differences in diet among species that have the same variety and amount of potential prey available. The objective of this study was to compare the diet of four species of *Physalaemus* (*P. biligonigerus*, *P. cuvieri*, *P. gracilis* and *P. henselii*) that occur in syntopy in a remnant of Atlantic Forest in southern Brazil.

## MATERIAL AND METHODS

### *Study site*

The study was carried out in forest habitats inserted in the Atlantic Forest domain, located in a conservation unit (Reserva Biológica Lami José Lutzenberger - RBLJL), in Porto Alegre, state of Rio Grande do Sul (30°14'08"S; 51°05'42"W), southern Brazil. The local landscape corresponds to the transition region between forest formations and subtropical restinga, being one of the closest forest remnants to the southern boundary of the Atlantic Forest (Printes, 2002; Witt, 2013). The climate of the region is classified as subtropical humid, with an average temperature in the warmer month of 22 ºC and average annual temperature of 18 °C (Maluf, 2000).

### *Data collection*

In this study, we explored data from anurans available in herpetological collections. We had the opportunity to access a group of frogs collected accidentally by other colleagues when using pitfall traps (Campbell and Christman, 1982) for entomological sampling. As traps were constructed with 10-L buckets, they were large enough to capture small frogs. In addition, as the buckets were filled with an ethanol solution (70%), they preserved the gastrointestinal content of frogs. We had access to frogs captured from November 2014 to January 2016 and, according to Brazilian laws, since the captures were accidental, no collecting permits were needed. The accidentally caught anurans were donated to the Laboratory of Ecology of Terrestrial Vertebrates (LEVERT) by the management team of the biological reserve.

In the laboratory, the animals were dissected to remove the gastrointestinal contents (stomach and intestine), which were preserved in 70% ethanol and screened under a stereomicroscope. For each prey category, number, volume and frequency of occurrence were calculated. Volume was calculated by estimations of the area (mm²) occupied by each item with a graph paper support attached to the bottom of the Petri dish, where we evenly spread each item, maintaining a regular height of 1 mm (Hellawell and Abel, 1971). In order to calculate each item volume (V), the area value (mm²) was multiplied by its height (1 mm) (Oliveira et al., 2015). The set of prey present in each content (individual) was considered as a sample. Prey items were identified until the lowest possible taxonomic level based on Ribeiro-Costa and Rocha (2006). We were unable to reach the species level due to the high fragmentation in most of the prey items caused by the digestion process.

To improve our data interpretation, we added to our dataset data of *Physalaemus henselii* that had been previously published (Farina et al., 2018). We highlight that this non-novel dataset represents 16% of the amount of data of the current study. All analyzed individuals were collected in the same locality with the same trap model and in the same period of the year.

### *Data analysis*

We used the Index of Relative Importance (IRI), according to Pinkas et al. (1971) to calculate the importance of each category of prey using the following equation: IRI = (N% + V%) FO%, where N% is the relative abundance of each prey category in the diet, V% is the relative volumetric contribution of the prey in the diet, and FO% is its relative frequency of occurrence in the diet (Pinkas et al., 1971; Krebs, 1999). The higher the IRI value, the greater is the importance of a given prey category in the diet.

We constructed rarefaction curves using Past 4.03 software to estimate the sampling representativity of the prey set for each anuran species (Sanders, 1968). In this analysis, each gastrointestinal content was considered as a sample. Curves were based on Jackknife 1 estimator of species richness (Burnham and Overton, 1978, 1979) which could represent the studied populations.

The Levin's Standardized Niche Breadth Index ($B_{sta}$) (Krebs, 1999) ranges from 0 to 1 and is calculated according to the following equation: $B_{sta} = (B\text{-}1) / (n\text{-}1)$, where n is the number of resources registered in the diet (prey categories), and $B = 1 / \Sigma p_i^2$, p represents the proportion of individuals of a given prey category (i) found in the diet. Values near 0 indicate a specialist diet (narrow niche breadth), while values near 1 indicate a generalist diet (wide niche breadth). $B_{sta}$ was used to facilitate comparisons of trophic ecology between species.

To analyze the food overlap and/or degree of similarity between species diets, we used the Pianka's Trophic Niche Overlap Index ($O_{jk}$) (Pianka, 1973), defined by the following equation:

$$O_{jk} = \sum\nolimits_{n=1}^{o} p_{ij} \times p_{ik} \Big/ \sqrt{\sum\nolimits_{n=1}^{o} p_{ij}^2 \times \sum\nolimits_{n=1}^{o} p_{ik}^2}$$

where $O_{jk}$ is the niche overlap index between the species *j* and *k*; $p_{ij}$ is equivalent to the proportion of the resource type *i* relative to the total of resources used by the species *j*; $p_{ik}$ is the proportion of resource *i* relative to the total of resources used by the species *k*; and n is the total number of resource categories used by the species *j* and *k*. This index ranges from 0 to 1 when there is no overlap or a complete overlap between the species diets, respectively (Krebs, 1999). For this analysis, we used the program EcoSim v1.2d (Gotelli and Entsminger, 2000). Since we have samples from all species from all seasons, comparisons helped us in detect if and how feeding behavior differ between species. Possible prey preferences were evaluated by Compositional Analysis (Aebischer et al., 1993) using the R package 'adehabitatHS' (Calenge, 2013). This analysis is based on a comparison between the matrix of consumed prey and the mean frequencies of components used by all individuals of the sampled species (Sacchi et al., 2013). The analysis use randomization tests (number of permutations = 500) to assess the significance of the ranking matrices (Aebischer et al., 1993).

## RESULTS

We analyzed the gastrointestinal contents of 109 individuals (Table 1). Of these, eight were *Physalaemus biligonigerus* (containing 190 food items distributed in 11 prey categories), nine *P. cuvieri* (221 items, 13 categories), 74 *P. gracilis* (529 items, 19 categories) and 18 *P. henselii* (154 items, 10 categories) (Table 1). Only one individual of *P. cuvieri* and 10 of *P. gracilis* had no gastrointestinal content. Even though some species, such as *P. biligonigerus* (8) and *P. cuvieri* (9), had a small sample size, we recorded 11 and 13 prey categories for them, respectively. Furthermore, an estimate of 9,81 for *P. biligonigerus*, 8 for *P. cuvieri*, 74,4 *P. gracilis* and 18,9 *P. henselii* was obtained using the Jackknife 1 estimator, which indicates that even with a small N (*P. biligonigerus* and *P. cuvieri*) the samples were sufficient to represent the populations, in the same way as for *P. henselii*. However, the rarefaction curves (Fig. 1) did not stabilize, suggesting that, by adding new samples (more frogs), other prey taxa were expected to be recorded. Based on this, results must be evaluated with caution.

Formicidae was the most important prey category for *P. biligonigerus* (IRI = 88.5%) and *P. gracilis* (IRI = 39.1%). For *P. henselii* and *P. cuvieri*, the most important category in the diet was Isopoda (IRI = 51.7% and 57.9%, respectively), followed by Formicidae (IRI = 34.9% and 24.8%). Isopoda was also important in the diet of *P. gracilis* (IRI = 28.6%), followed by Araneae (IRI = 22.6%) (Table 1). The trophic niche breadth was higher for *P. henselii* ($B_{sta} = 0.32$) followed by *P. gracilis* ($B_{sta} = 0.23$). The lowest values of niche breadth were recorded for *P. biligonigerus* ($B_{sta} = 0.04$) and *P. cuvieri* ($B_{sta} = 0.13$). The overlap of trophic niche (Ojk) was 96% between *P. biligonigerus* and *P. cuvieri*, 95% between *P. gracilis* and *P. henselii*, 91% between *P. cuvieri* and *P. gracilis*, 83% between *P. cuvieri* and *P. henselii*, 83% between *P. biligonigerus* and *P. gracilis*, and 71% between *P. biligonigerus* and *P. henselii.*

Results from Compositional Analysis pointed out that only *Physalaemus gracilis* has a certain degree of feeding specialization (lambda = 0.108; P < 0.001; Table 1), preying upon Araneae, Coleoptera larvae, Isopoda, Formicidae and Hymenoptera in a higher frequency than expected by chance.

**Table 1.** Prey categories found in the gastrointestinal contents of *Physalaemus biligonigerus*, *P. cuvieri*, *P. gracilis* and *P. henselii*. N = number of individuals, V% = total volume (in mm$^3$) occupied by prey category, FO% = frequency of occurrence of prey category, IRI% = Index of Relative Importance.

| Prey categories | *P. biligonigerus* (N = 8) | | | | *P. cuvieri* (N = 8) | | | | *P. gracilis* (N = 64) | | | | *P. henselii* (N = 18) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N% | V% | FO% | IRI% | N% | V% | FO% | IRI% | N% | V% | FO% | IRI% | N% | V% | FO% | IRI% |
| Acarina | 1.1 | 0.2 | 12.5 | 0.1 | 2.7 | 0.5 | 22.2 | 0.3 | 5.7 | 0.8 | 18.9 | 1.6 | 11.0 | 2.0 | 50.0 | 6.7 |
| Amphipoda | 1.1 | 0.7 | 25.0 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 0.7 | 4.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| Araneae | 1.6 | 1.0 | 37.5 | 0.6 | 5.0 | 4.1 | 55.6 | 2.2 | 18.0 | 13.4 | 55.4 | 22.6 | 5.2 | 3.6 | 22.2 | 2.0 |
| Blattodea | 0.0 | 0.0 | 0.0 | 0.0 | 1.8 | 6.1 | 44.4 | 8.7 | 0.6 | 0.6 | 4.1 | 0.1 | 3.9 | 8.4 | 16.7 | 2.1 |
| Coleoptera | 2.1 | 3.0 | 25.0 | 0.8 | 3.6 | 5.8 | 44.4 | 1.8 | 2.3 | 4.7 | 13.5 | 1.2 | 5.2 | 2.0 | 16.7 | 1.2 |
| Coleoptera (larva) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 8.5 | 14.9 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| Collembola | 0.0 | 0.0 | 0.0 | 0.0 | 1.8 | 0.8 | 22.2 | 0.6 | 1.0 | 0.1 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Dermaptera | 0.5 | 0.1 | 12.5 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diptera | 1.6 | 1.5 | 25.0 | 0.5 | 2.3 | 1.0 | 22.2 | 0.7 | 1.3 | 0.6 | 8.1 | 0.2 | 2.6 | 0.5 | 16.7 | 0.5 |
| Diptera (larva) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 1.2 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Formicidae | 83.7 | 52.1 | 100.0 | 88.5 | 57.5 | 15.8 | 77.8 | 24.8 | 32.5 | 12.0 | 67.6 | 39.1 | 35.1 | 12.1 | 72.2 | 34.9 |
| Gastropoda | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.2 | 5.6 | 18.9 | 2.4 | 0.7 | 0.3 | 5.6 | 0.1 |
| Hemiptera | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.4 | 11.1 | 0.0 | 1.5 | 1.6 | 9.5 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Heteroptero | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Hymenoptera | 0.5 | 1.0 | 12.5 | 0.1 | 0.5 | 0.4 | 11.1 | 0.0 | 3.4 | 1.7 | 14.9 | 1.0 | 2.0 | 1.4 | 16.7 | 0.6 |
| Isopoda | 1.1 | 2.2 | 25.0 | 0.5 | 13.1 | 28.3 | 66.7 | 57.9 | 20.4 | 29.0 | 44.6 | 28.6 | 33.1 | 36.7 | 72.2 | 51.7 |
| Isoptera | 0.0 | 0.0 | 0.0 | 0.0 | 9.5 | 7.8 | 11.1 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Lepidoptera (larva) | 4.7 | 24.5 | 37.5 | 7.4 | 0.9 | 0.7 | 22.2 | 0.2 | 0.6 | 1.1 | 4.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Odonata | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.6 | 2.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Opilionida | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.6 | 11.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Orthoptera | 2.1 | 2.3 | 37.5 | 1.1 | 0.5 | 0.1 | 11.1 | 0.0 | 1.0 | 1.6 | 6.8 | 0.2 | 1.3 | 0.6 | 11.1 | 0.2 |
| Pseudoescorpionidae | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.5 | 4.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Other | -- | 11.4 | -- | -- | -- | 27.7 | -- | -- | -- | 15.8 | -- | -- | -- | 32.4 | -- | -- |
| Niche breadth | 0.04 | | | | 0.13 | | | | 0.23 | | | | 0.32 | | | |

## DISCUSSION

The species of this study exhibited a similar prey composition in their diets. In all of them, Formicidae and/or Isopoda were the predominant prey categories. The high relevance of ants was also recorded for other populations of *Physalaemus biligonigerus*, *P. cuvieri* and *P. gracilis* in studies of restinga habitats in southern Brazil (Oliveira et al., 2015), Atlantic Forest biome in northern Brazil (Santos et al., 2004) and Araucaria forest in southern Brazil (Moser et al., 2017). Formicidae had high importance in the diet of *P. biligonigerus*, reaching IRI values of 88.47%, while IRI of the second most important prey category was less than 8% (Lepidoptera larvae). Based on this, we argue that *P. biligonigerus* is locally a "Formicidae specialist". Large consume of Formicidae has been previously reported in *P. biligonigerus* (Oliveira et al., 2021) as well in other *Physalaemus* (Santana and Juncá, 2007). Is hard to list environmental components that favored the dominance of ants in contents. On the other hand, high consumption of ants involves physiological adaptations to the digestion due to the presence of formic acid, resulting in a high energy cost (Hirai and Matsui, 2002). Then, the ability to feed on ants would increase the advantages in explore the food resources in the habitat. Our sampling design did not make us able for a deeper discuss among diet specialization, niche partitioning and competition. We believe that specialization on ant consumption is a topic that deserves new studies.

Ants were also important food items for other species of the genus in different Brazilian locations, such as the Atlantic and Amazon Forests for *P. lisei* (Moser et al., 2017) and *P. ephippifer* (Rodrigues and Santos-Costa, 2014), Caatinga (Protázio et al. 2019; Oliveira et al. 2021) and in Argentina for *P. riograndensis* (López et al., 2003) and *P. albonotatus* (Falico et al., 2012).

In general, ants are considered unpalatable for several predators (Hirai and Matsui, 2000) but species of *Physalaemus* consume ants with considerable frequency (Moser et al., 2017). For some amphibians, the seques-

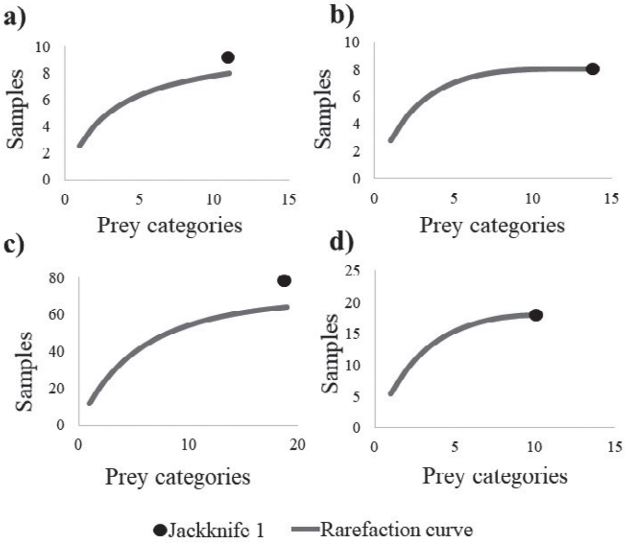

**Fig. 1.** Rarefaction Curves and the Jackknife 1 estimator of prey-species richness according to the number of samples (anurans): a) *Physalaemus biligonigerus*, b) *Physalaemus cuvieri*, c) *Physalaemus gracilis* and d) *Physalaemus henselii.*

tration of alkaloids is associated with the consumption of ants (Saporito et al., 2004), but no studies prove the ingestion for this purpose by *Physalaemus*. The high consumption of Formicidae may be associated with the abundance and displacement capacity of these invertebrates in the environment (Baretta, 2007), thus characterizing an opportunistic feeding behavior by the anurans. This behavior may minimize the potential competition between species, favoring their coexistence.

Also, Isopoda was one of the most important prey categories for three of the four species (*P. cuvieri*, *P. gracilis* and *P. henselii*). The relevance of Isopoda to the diet of *Physalaemus* species was poorly reported. Although the group is part of the genus' diet (Rodrigues and Santos-Costa, 2014; Moser et al., 2017), it is not frequently consumed. In the study by Leivas et al. (2018), Isopoda were not found in the diet of *P. cuvieri*, which may be associated with prey availability. We observed feed specialization for two prey groups: ants and isopoda. Both of them are social insects. Their nests offer a large number of preys which cold leads for their high density in contents of frogs that are able to eat them.

The trophic niche breadth for *P. biligonigerus*, *P. cuvieri* and *P. gracilis* was equal to or similar to results found in other studies of the same species (Santos et al., 2004, Moser et al. 2017). In contrast, for *P. henselii* ($B_{sta}$ = 0.32, Farina et al., 2018), trophic niche breadth was higher than for other species of this study and also of the literature, such as *P. gracilis* and *P. lisei* ($B_{sta}$ = 0.15 and $B_{sta}$ = 0.11 respectively, Moser et al., 2017), *P. ephippifer* ($B_{sta}$ = 0.19, Rodrigues and Santos-Costa, 2014) and *P. biligonigerus* ($B_{sta}$ = 0.04, Oliveira et al., 2015), suggesting a more generalist behavior in relation to its congeners (Farina et al., 2018). In general, leptodactylids have narrower niches when compared to other families, such as hylids (Sabagh et al., 2010; Barbosa et al., 2014), revealing a great abundance of local resources that favors coexistence and high trophic niche overlap. Despite of little speculative our data suggests a reasonable degree of food specialization in for *P. biligonigerus* and *P. cuvieri*.

The predominant consumption of ants is one of the reasons for the high trophic niche overlap between the species. The phylogenetic proximity of the species may also relate to their high niche overlap (Lourenço et al., 2015), besides indicating a great prey availability in the environment, which is evidenced by the niche breadth. Also, species may be foraging in similar places, considering that species that share the same habitat tend to have a similar diet (Duellman and Trueb 1986, Guidali et al., 2000, Sabagh et al., 2010). Compositional Analysis pointed out that differently from other species, *P. gracilis* exhibited a considerable level of selectivity in its diet, preying on Araneae, Coleoptera larvae, Isopoda, Formicidae and Hymenoptera more frequently than their expected availability in the habitat. This result brings some light to the relevance of studying syntopic species to elucidate feeding adaptations.

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