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Trophic ecology of juvenile amphibians: relative level of myrmecophagy in two anuran species

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ABSTRACT

Research on trophic niche dimensions is essential to understanding the role of species in ecosystems. In the case of amphibian conservation, it is particularly important to study juveniles, given the vulnerability of this life stage. Here, the diets consumed by juvenile *Rhinella arenarum* and *Odontophrynus* sp. were evaluated, with special attention paid to the incidence of ants. Diet composition was quantified by analyzing the amphibians' stomach contents. The representation of different taxonomic prey groups was determined, and the relationships between the amphibians' morphological traits and the characteristics of their prey were explored. Diet composition and diversity differed between juveniles of the two species. Juvenile *R. arenarum* occupied an intermediate position along the specialist-generalist spectrum. Their most commonly consumed prey were ants (mainly *Solenopsis* and *Linepithema*) followed by mites. Juvenile *Odontophrynus* sp. had a more generalist diet. Their most commonly consumed prey were Isopoda followed by Coleoptera and miscellaneous larvae. Snout-vent length (SVL) was greater for juvenile *Odontophrynus* sp. than for juvenile *R. arenarum*, but the latter consumed more prey. The results suggest that juveniles of *R. arenarum* tend to specialize more on ants than do juveniles of *Odontophrynus* sp.

Introduction

An important field in its own right, trophic ecology is a cornerstone of broader ecological research because it provides the foundation for work in other domains, including macroecology, evolution, and the environmental sciences (McCallen et al. 2019). A species' trophic ecology encompasses its physiological and behavioral features as well as the relationship it has with other organisms based on its feeding habits (Ings et al. 2009). In trophic webs, amphibians maintain the flow of nutrients between aquatic and terrestrial ecosystems. Because of their high densities and substantial biomass, amphibian eggs, tadpoles, and juveniles are preyed upon by aquatic and terrestrial predators alike. Amphibian larvae act as predators, incorporating terrestrial nutrients into aquatic ecosystems, such as when they consume mosquitoes (Schriever et al. 2014; Cortés-Gomez et al. 2015). Traditionally, it has been thought that amphibians fall along a trophic spectrum from specialist to generalist (Toft 1985, 1995). Generalist amphibians have diverse diets, while specialist amphibians have narrower diets and may feed upon very specific prey

(Bolnick et al. 2007), like ants. However, research suggests that the specialist-generalist spectrum might not be linear and could be influenced by diverse factors (Strüssmann et al. 1984; Bolnick et al. 2007; Nadaline et al. 2019). Indeed, amphibian feeding habits are closely associated not only with prey type and behavior, but also with amphibian foraging strategy, which can take the form of actively searching for versus ambushing prey (called active vs sit and wait foraging strategies; e.g. Glaudas et al. 2019).

Ants represent a large percentage of terrestrial biomass (Hölldobler & Wilson 1990; Schultheiss et al. 2022), provide a wide variety of ecological functions (e.g. seed dispersal, pollination), and act as agents of biological disturbance and control (Del Toro et al. 2012; Diamé et al. 2017; Elizalde et al. 2020). Ants are also the prey of several specialist predators (e.g. mammals, reptiles, and amphibians; Pough 1983; Mebs et al. 2010) against which they defend themselves using diverse strategies that are morphological, physiological, or behavioral in nature. Strategy complexity increases with the degree of social organization, from protecting themselves physically with their jaws to spraying

chemical compounds, most commonly alkaloids (Billen & Morgan 1998; Dornhaus & Powell 2010; Abbot 2022). Several anuran species mount their own defenses using the alkaloids obtained from the ants in their diet (Daly et al. 1996, 2008; Vences et al. 1998; Saporito et al. 2004; Clark et al. 2005; Mebs et al. 2010). Among the anuran taxa that feed mostly on ants (i.e. myrmecophagy) are Microhylidae (*Elachistocleis*: Solé et al. 2002; Berazategui et al. 2007), Bufonidae (*Melanophryniscus*: Bortolini et al. 2013; Hantak et al. 2013; *Rhinella*: da Rosa et al. 2006; Brandão et al. 2020; Maragno & Souza 2011), Hylidae (*Phyllodytes*: Solé & Loebmann 2017), and Dendrobatidae (*Ameerega*: Mebs et al. 2010). However, research on myrmecophagy in juvenile amphibians is scarce, although it is known that, in general, juveniles and adults differ in their diets (Lima & Moreira 1993; Giaretta et al. 1998; da Rosa et al. 2006). These ontogenetic patterns may be linked to morphological limitations (Hirai 2002), life-stage-related shifts in foraging and activity (Lima & Moreira 1993; Duellman & Trueb 1994), or different energy requirements (Pough 1983). The ability of juveniles to detect and capture prey may also play a significant role (Donnelly 1991; Simon & Toft 1991).

Against this backdrop, it is clear that more must be understood about the trophic ecology of juvenile amphibians in the hopes of better informing amphibian conservation strategies. Worldwide, amphibian populations are under threat and in decline (Stuart et al. 2004). Population persistence is greatly affected by juvenile survival because this life stage is an extremely vulnerable period of the life cycle (Werner 1986; Cabrera-Guzmán et al. 2013; Pittman et al. 2014), during which amphibians face predation, anthropogenic disturbances, and environmental stressors (Wells 2007; Petrovan & Schmidt 2019; Lowe et al. 2021). There are only a few studies that look exclusively at the trophic ecology of juvenile amphibians, including research exploring the relationship between the size of prey and two predators, *Chacophrys pierottii* and *Leptodactylus luctator* (Pueta & Perotti 2013; Lajmanovich 1996, respectively); selectivity and dietary changes in bufonids (Flowers & Graves 1995; Bull & Hayes 2009); and diet and microhabitat use in *Rhinella ornata* (Flynn et al. 2020). However, much remains to be explored, especially whether juveniles specialize on particular groups of prey, such as ants.

Rhinella arenarum (Hensel 1867) is a member of the Bufonidae family and inhabits coastal areas, grasslands, and anthropogenic habitats. In adults, snout-to-vent length (SVL) can reach approximately 100 mm (Quiroga et al. 2009), and this species engages in explosive breeding, usually between August and March (Maneyro & Carreira 2012). The species is found throughout South America, with a distribution that spans from Bolivia to coastal southern Brazil, the southern province of Chubut in Argentina, southern and southeastern Uruguay, and perhaps even Paraguay (Frost 2023). The International Union for Conservation of Nature (IUCN) has categorized it as a species of least concern (Kwet et al. 2004; Carreira & Maneyro 2015).

The genus *Odontophrynus* belongs to the family Odontophrynidae and is represented by two species in Uruguay: *Odontophrynus americanus* and *Odontophrynus maisuma*. Both are fossorial; inhabitants of meadows, marshes, and areas near urban zones; and explosive breeders (Maneyro & Carreira 2012). In adults, SVL ranges from 38 to 44 mm (Rosset 2008). *Odontophrynus americanus* breeds throughout the year, except during the winter (Valdez & Maneyro 2016). Its range extends from Brazil to Bolivia, southern Paraguay, Argentina, and Uruguay (Frost 2023). It is categorized as a species of least concern (Aquino et al. 2010; Carreira & Maneyro 2015). In contrast, *Odontophrynus maisuma* is predominantly found in coastal regions from Santa Catarina, Brazil, to southern Uruguay, and its conservation status is unknown (Carreira & Maneyro 2015).

Rhinella arenarum (Hensel 1867) and the species belonging to genus *Odontophrynus* Reinhardt & Lütken 1862 mentioned above (hereafter *Odontophrynus* sp.) seem to differ in their degree of myrmecophagy, but little is actually known about the diets of juveniles in these species. Adults of *R. arenarum* consume a diet containing a large proportion of ants and are considered to occupy an intermediate position along the specialist-generalist spectrum (Quiroga et al. 2009; Cossovich et al. 2011). Quiroga et al. (2009) also found that ants were prominent in the diets of juvenile *R. arenarum*. Adult *Odontophrynus* sp. are considered to be generalists, and ants likely contribute little to their diets (Achaval-Coppes 2011; Cossovich et al. 2011; Maneyro & Carreira 2012). Although juvenile *Odontophrynus* sp. do not primarily consume ants, they do eat more ants than do adults (Achaval-Coppes 2011). To better understand the diets of juvenile *R. arenarum* and *Odontophrynus* sp., we examined their stomach contents, paying particular attention to the incidence of ants.

Materials and methods

Sampling methods

Twenty-five juveniles of each species were collected for this study. Most individuals, 21 *R. arenarum* and 22

Odontophrynus sp., were selected at random from large storage jars in the zoology vertebrate collection (ZVCB) at the Faculty of Sciences in Montevideo, Uruguay (Appendix A Table A1). They were sampled across various seasons, likely during postreproduction periods, when juvenile abundance is greatest (see Table A1).

The remaining individuals, 3 *R. arenarum* and 4 *Odontophrynus* sp., came from pitfall traps. Sampling occurred in Shangrilá (34°52'S, 56°0'W) and El Pinar (34°48'S, 55°54'W), in the coastal zone of the Canelones Department, Uruguay. Both locations are characterized by sandy dune ecosystems and are found in close proximity to urban areas. During the sampling month, November 2017, mean temperature and rainfall were 18.3°C and $31.9 \, l/m^2$, respectively (Instituto Nacional de Estadística 2018). Ten pitfall traps (250-mL plastic cups) were run for 3 days. Upon collection, the individuals were preserved in 70% ethanol and deposited in the ZVCB.

Individuals were confirmed to be juveniles through gonadal examinations. SVL and jaw width (JW) was measured (±0.1 mm) for all the amphibians. Their digestive tracts were completely removed (Schoener 1989). The contents were placed in alcohol (70%) and were later sorted out. The taxonomic identity and size (maximum length and width, ±0.01 mm) of each prey item therein was determined using a binocular stereoscope. Individuals without stomach contents were excluded from the analyses (one *R. arenarum* and four *Odontophrynus* sp.).

Prey were identified to order, except in the case of species in Diplopoda and Chilopoda, which were identified to class. Bentancourt et al. (2009) was used to classify the prey overall, and Fernández (2003) was employed specifically for ants. Due to their morphological similarity, all larvae were simply categorized as 'larvae.' Ants (family: Formicidae) were treated independently from other insects in the order Hymenoptera; when possible, they were identified to genus and species (Appendix B Figure B1).

Data analysis

The abundance (n) of each taxonomic prey group was calculated for the two amphibian species. When dismembered prey were observed and could be identified, the most abundant part was counted (e.g. head, thorax), making the assumption that the entire individual had been ingested. Prey volume was calculated using the formula for an ellipsoid ($V = 4/3*\pi*$ [length/$2]*[width/2]^2$) to estimate the total volume of each taxonomic prey group for the two amphibians. When large numbers of dismembered ants were observed within the stomach contents, a per-ant volume was defined – a mean value based on all the ants found in one piece (Alvarez-Blanco et al. 2017). To estimate ant number, the same approach was used as above: the most abundant part was counted (i.e. head, mesosoma, or gaster). Relative abundance (%Ab), relative occurrence (%FO), and percent volume (%V) were calculated for each taxonomic prey group. An index of relative importance (Pinkas et al. 1971) was also calculated (IRI = %FO*[%Ab + %V]). The prey group Formicidae was compared to all the other prey groups in terms of %V, %Ab, and %FO. We also estimated richness, abundance, volume, %Ab, %V, %FO, and IRI for the ants at genus level.

Trophic niche breadth was characterized using the standardized Shannon-Weaver index:

$$J = H/\log(s), \text{where } H = -\sum(pi * \log[pi])$$

where pi is the proportion of a given taxonomic prey group in the sample, and *s* is the total number of taxonomic prey groups (Weaver & Shannon 1949). A rarefaction curve was constructed using PAST (Hammer et al. 2001, v. 3.24) to compare expected prey richness for the two amphibian species. To describe niche overlap (O), the Pianka index (1973) was calculated. To assess similarities in complete dietary composition, a community analysis was carried out utilizing non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance matrix (*vegan* package, Oksanen et al. 2017; R Core Team 2017). NMDS objectively represents the raw data with the smallest possible deviation, which reveals certain community properties of interest (Gauch 1982).

Using a generalized linear model (binomial with logit link function; Proc Genmod, SAS v. 9.4; SAS Institute Inc 2023), we determined whether the two amphibian species (dependent variable) differed in prey abundance per stomach, total prey volume per stomach, maximum prey volume per stomach, amphibian SVL, and amphibian JW (independent variables).

Using generalized linear models (Proc Genmod, SAS v. 9.4; SAS Institute Inc 2023), we examined the relationships between amphibian JW (dependent variable) and prey abundance per stomach, total prey volume per stomach, and maximum prey volume per stomach (independent variables). We carried out separate analyses for each amphibian species via the *by* option in Proc Genmod (SAS software v. 9.4; SAS Institute Inc 2023). We also examined the relationship between SVL and volume of prey per stomach for each amphibian using generalized linear models and the *by* option

(Proc Genmod, SAS software v.9.4, SAS Institute Inc 2023). In both sets of analyses, we employed the error distribution that minimized model deviance as well as the AIC value.

Results

Diet

A total of 628 and 117 prey were identified in the stomach contents of juvenile *R. arenarum* and *Odontophrynus* sp., respectively. The former occupied a volume of 392 mm³, and the latter occupied a volume of 2,745 mm³. In juvenile *R. arenarum*, 11 different taxonomic prey groups were identified, while 15 taxonomic prey groups were identified in juvenile *Odontophrynus* sp. (Table 1).

Trophic niche breadth was wider for juvenile *Odontophrynus* sp. (J = 0.79) than for juvenile *R. arenarum* (J = 0.46); the former's trophic niche was also more diverse (Figure 1). Trophic niche overlap between the species was low (O = 0.35), and the NMDS analysis indicated that the two species differed significantly in overall diet composition (F = 9.76, $p <$ 0.001; Figure 2).

In juvenile *R. arenarum*, Formicidae was the predominant taxonomic prey group, with the highest %FO (>75%) and IRI values (Table 1), followed by Coleoptera and Acari. Percent volume was higher for Coleoptera and Formicidae (Table 1), whereas relative abundance was higher for Formicidae and Acari (Figure 3). In juvenile *Odontophrynus* sp., the groups Isopoda, Coleoptera, and larvae displayed high IRI values and large relative abundance (Figure 3). According to the %FO values, Coleoptera, Isopoda,

and Formicidae were most common, while Isopoda had the highest percent volume (Table 1).

Formicidae occurrence, abundance, and volume were greater in juvenile *R. arenarum* than in juvenile *Odontophrynus* sp. In juvenile *R. arenarum*, ants were the most abundant and commonly occurring prey and ranked second in terms of volume (Table 1). A total of 325 ants were present in the stomach contents of both species. Of this, 94 were identified and belonged to seven genera. In juvenile *R. arenarum*, 89 ants from 7 genera were found across 10 stomachs (Table 2). In juvenile *Odontophrynus* sp., 5 ants, each from a different genus, were found across 4 stomachs (Table 2, Figure 3).
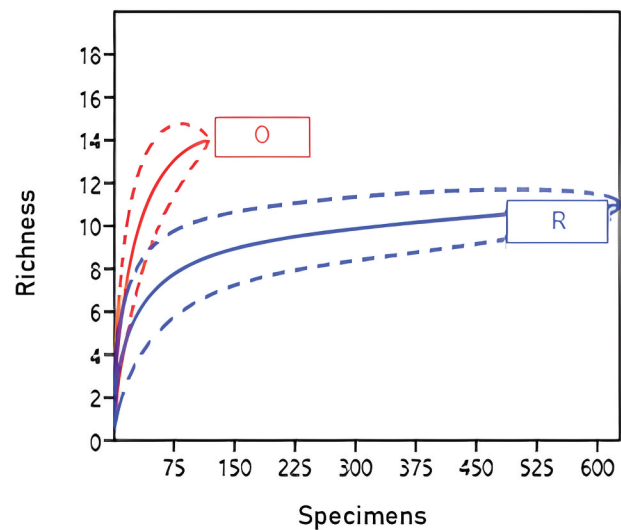

Figure 1. Rarefaction curve for diet richness in juvenile *Odontophrynus* sp. (O, red) and *R. arenarum* (R, blue) (dashed line = 95% confidence interval).

Table 1. Taxonomic prey groups found in the stomach contents of juvenile *Odontophrynus* sp. (O, 21 individuals) and *R. arenarum* (R, 24 individuals). Abbreviations: n = number of prey; %FO = relative prey occurrence; %V = percent prey volume; IRI = index of relative dietary importance.

| Taxonomic prey group	n		%V		%FO		IRI	
	O	R	O	R	O	R	O	R
Acari	6	147	0.04	2.44	23.81	41.67	122.98	1076.82
Araneae	6	8	1.22	0.70	28.57	12.50	181.27	24.64
Blattaria	2	–	0.00	–	4.76	0.00	8.16	–
Chilopoda	1	–	0.19	–	4.76	0.00	4.96	–
Coleoptera	28	72	18.83	55.73	57.14	58.33	2443.27	3919.64
Collembola	2	32	0.07	0.46	4.76	20.83	8.49	115.72
Diplopoda	–	1	–	0.00	–	4.17	–	0.66
Diptera	4	22	0.40	1.42	19.05	12.50	72.78	61.49
Formicidae	**8**	**317**	**7.19**	**29.40**	**33.33**	**79.17**	**467.48**	**6323.85**
Hemiptera	6	4	0.67	0.09	23.81	12.50	138.11	9.03
Hymenoptera (non Formicidae)	2	–	0.05	–	4.76	0.00	8.38	–
Isopoda	30	–	44.44	–	38.10	0.00	2669.69	–
Isoptera	3	–	2.70	–	4.76	0.00	25.07	–
Larvae	17	14	19.81	1.44	19.05	16.67	654.16	61.12
Orthoptera	2	10	4.40	8.32	9.52	16.67	58.15	165.15
Thysanoptera	–	1	–	0.02	–	4.17	–	0.75
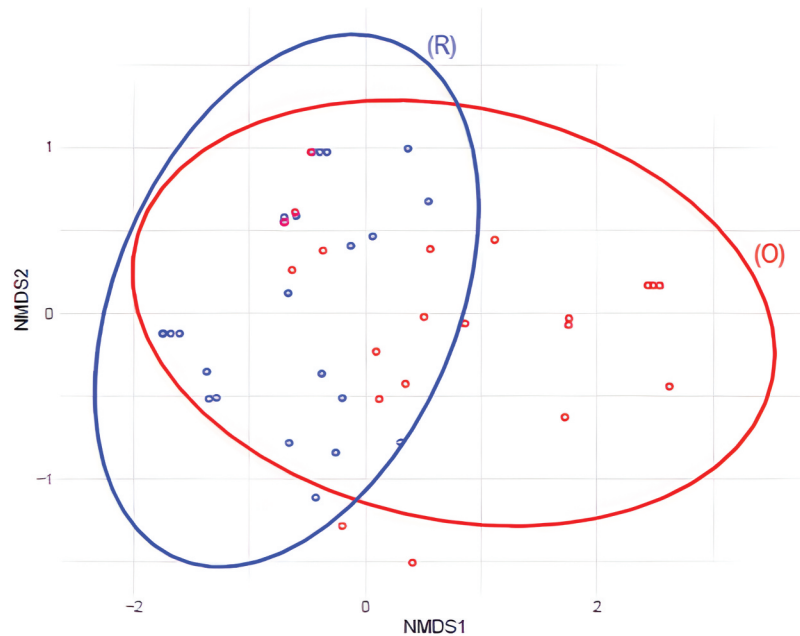
Figure 2. Spatial representation of the non-metric multidimensional scaling (NMDS) analysis with a Bray-Curtis distance matrix, which compared dietary similarity between juvenile *Odontophrynus* sp. (O, red) and *R. arenarum* (R, blue). All the taxonomic prey groups were included in the analysis. The ovals represent the grouped data for each amphibian species. The individual amphibians are represented by small circles (*Odontophrynus* sp. = red and *R. arenarum* = blue).
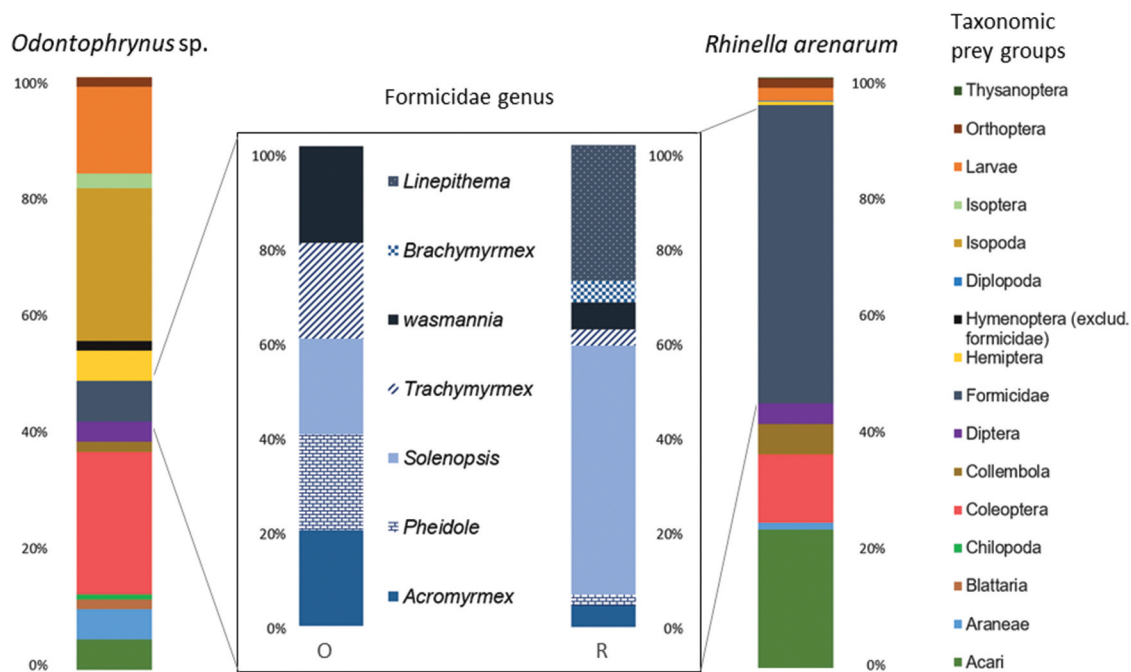

Figure 3. Relative abundance (%Ab) of the taxonomic prey groups (exterior) and ant genera (Formicidae, center) consumed by juvenile *Odontophrynus* sp. (O) and *R. arenarum* (R).

In juvenile *R. arenarum*, the ant genus *Solenopsis* predominated; it had the greatest IRI values, relative abundance, and occurrence. *Linepithema* was also important, displaying high levels of abundance (Figure 3) and occurrence. *Solenopsis* had the greatest percent volume, followed by *Acromyrmex*, *Trachymyrmex*, and *Linepithema* (Table 2). In juvenile *Odontophrynus* sp., the genus *Acromyrmex* presented a higher proportion of volume, followed by *Trachymyrmex* and *Solenopsis* (Table 2).

Table 2. Formicidae subfamilies and genera identified in the stomach contents of juvenile *Odontophrynus* sp. (O) and *R. arenarum* (R). Abbreviations: n = number of individuals; FO = frequency of prey occurrence; V = total prey volume (mm^3); %V = percent prey volume; IRI = index of relative dietary importance.

Subfamily	Genus	n O	n R	FO O	FO R	V O	V R	%V O	%V R	IRI O	IRI R
Myrmicinae	*Solenopsis*	1	46	1	5	1.47	67.43	0.75	50.61	518.68	5114.80
	Wasmannia	1	5	1	2	0.13	0.66	0.07	0.50	501.69	122.33
	Acromyrmex	1	4	1	2	188.01	28.48	95.85	21.38	2896.22	517.45
	Trachymyrmex	1	3	1	1	5.61	16.84	2.86	12.64	571.56	160.13
	Pheidole	1	2	1	1	0.93	1.86	0.47	1.40	511.85	36.43
Dolichoderinae	*Linepithema*	–	25	–	5	–	16.82	–	12.62	–	2035.68
Formicinae	*Brachymyrmex*	–	4	–	1	–	1.13	–	0.85	–	53.46

Table 3. Differences between juvenile *Odontophrynus* sp. and *R. arenarum* in (a) prey characteristics and amphibian morphology. Relationship between prey characteristics and (b) amphibian jaw width (JW) and (c) amphibian snout-vent length (SVL). Statistically significant variables are in bold.

Variables	DF	X^2	P	DF	X^2	P
a) Interspecific differences						
Prey abundance	**1,33**	**11.66**	**<.001**			
Total prey volume	1,33	1.40	.237			
Maximum prey volume	1,33	1.57	.211			
JW	**1,33**	**27.52**	**<.001**			
SVL	**1,33**	**6.40**	**.011**			
b) Relationship with JW		*Rhinella arenarum*			*Odontophrynus* sp.	
Number of prey	1, 15	2.01	.157	1, 16	0.46	.497
Maximum prey width	1, 15	0.21	.649	1, 16	1.24	.265
Maximum prey length	1, 15	1.67	.196	1, 16	0.00	.963
c) Relationship with SLV		*Rhinella arenarum*			*Odontophrynus* sp.	
Total prey volume	**1, 22**	**8.57**	**.003**	1, 19	3.52	.061

Relationship between amphibian traits and prey consumed

Juvenile *Odontophrynus* sp. had significantly larger SVL and JW values (mean ± SE: 23.3 ± 0.6 and 11.34 ± 0.6, respectively) than did juvenile *R. arenarum* (mean ± SE: 17.9 ± 0.5 and 6.01 ± 0.2, respectively) (Table 3). Prey abundance per stomach was significantly higher for juvenile *R. arenarum* than for juvenile *Odontophrynus* sp. (mean ± SE: 26.17 ± 6.5 and 5.57 ± 0.8, respectively). However, there was no difference in prey volume per stomach (Table 3). JW was not correlated with prey richness, maximum prey width, or maximum prey length (Table 3). The relationship between SVL and total prey volume per stomach was significant for juvenile *R. arenarum* but not for juvenile *Odontophrynus* sp.

Discussion

We studied the stomach contents of juvenile *R. arenarum* and *Odontophrynus* sp. to better understand their diets and, particularly, their ant consumption. Our results suggest that juvenile *Odontophrynus* sp. have a more generalist diet than do juvenile *R. arenarum*. Achaval-Coppes (2011) classified juvenile *Odontophrynus americanus* as generalist amphibians. Many other researchers have also classified adults of this genus as generalists (Isacch & Barg 2002; Peltzer et al. 2010; Brito et al. 2012; Nieva Cocilio 2019; but see; Cossovich et al. 2011).

In the stomach contents of juvenile *R. arenarum*, Formicidae was the dominant prey. Coleoptera was also strongly represented, in terms of volume and occurrence, and mites were highly abundant. This result concurs with previous work (Quiroga et al. 2009; Nieva Cocilio 2019) showing that ants were the main taxonomic prey group consumed by juvenile *R. arenarum*. Some research has shown that Formicidae was still the primary prey group in adult *R. arenarum*, with other prey, such as Coleoptera, coming in second (Quiroga et al. 2009; Cossovich et al. 2011; Nieva Cocilio 2019). That said, de Oliveira et al. (2017) noted that Coleoptera was the predominant prey.

The IRI values demonstrated that Isopoda was the most important taxonomic group in the diet of juvenile *Odontophrynus* sp.; it was followed by Coleoptera and miscellaneous larvae. The same was seen by Machado et al. (2019) for *O. americanus* in the Atlantic Forest of Brazil and by Achaval-Coppes (2011), in part, for juveniles in Uruguayan forest plantations. However,

Cossovich et al. (2011) observed that Isopoda was fundamental in the diet of adult *O. americanus* in Argentinian grasslands. These differences suggest that *Odontophrynus'* diet might differ across different environments (Peltzer et al. 2010; Machado et al. 2019).

The niche overlap index and the dietary similarity analysis indicated that juvenile *R. arenarum* and *Odontophrynus* sp. differed in diet composition, as was seen for adults by Isacch and Barg (2002) and Cossovich et al. (2011), whose work included other *Rhinella* species. These dissimilarities may be due to differences in daily foraging periods or feeding habits (Pough 1983; Achaval-Coppes 2011; Brito et al. 2012). It has been hypothesized that adult *O. americanus* exhibit nocturnal behavior (Achaval-Coppes 2011; Brito et al. 2012), and juvenile *Odontophrynus* sp. have been seen to primarily display nocturnal activity in captivity (pers. obs.). In contrast, juvenile *R. arenarum* display diurnal activity patterns at emergence sites (Pough 1983), both in captivity and in the wild (pers. obs.).

While juvenile *R. arenarum* consumed a greater abundance of prey than juvenile *Odontophrynus* sp., the two had similar prey volumes. This result could be explained by differences in prey size: juvenile *R. arenarum* ate a substantial number of smaller prey, like ants and mites, whereas juvenile *Odontophrynus* sp. ate larger prey. Maragno and Souza (2011) observed that juvenile and adult *Rhinella scitula* of larger sizes fed upon larger prey, even if they could also consume smaller prey. Here, we found that larger juvenile *R. arenarum* had larger dietary volumes, which was not the case for larger juvenile *Odontophrynus* sp. This pattern could be linked to the energy demands of juvenile *R. arenarum*—ants, their predominant prey group, have a low energy content (Parmelee 1999; Quiroga et al. 2009). Thus, to satisfy their energy requirements, juveniles may need to increase overall food intake as they grow, either by consuming more ants or by eating larger prey, such as coleopterans. Our analyses revealed that JW was not related to prey richness, prey width, prey length, or maximum prey length in either species, which is similar to what was found by Pueta and Perotti (2013). It may be that our samples displayed limited variability in JW, given that most studies have seen such a relationship in juveniles and adults when samples contained a broad range of JW values (Hirai & Matsui 1999; Parmelee 1999; Maneyro et al. 2004) or when they included juveniles of two well-differentiated size classes (Lajmanovich 1996).

The question remains as to whether the dietary composition seen in the stomach contents was influenced by prey availability, or whether it was characteristic of juvenile feeding habits. More research is needed in which sampling takes place over broader spatial and temporal scales and also takes into account both daily and seasonal fluctuations in predator and prey activity.

It would seem that juvenile *R. arenarum* display a certain degree of specialization, based on two findings: the large abundances and high IRI values of Formicidae and Acari (Table 1, Figure 3) and the species' intermediate diversity index value (J = 0.46). These results are consistent with those of Quiroga et al. (2009) for juveniles of this species and with those of studies on adults of *Rhinella* species (Quiroga et al. 2009; Peltzer et al. 2010; Cossovich et al. 2011; Brandão et al. 2020). Additionally, in juvenile *R. arenarum*, ant genus and subfamily diversity and frequency of occurrence were greater than in *Odontophrynus* sp. The dietary specialization of juvenile *R. arenarum* on ants and mites may have an evolutionary origin, such as co-evolution with other species (Toft 1980) or the sequestration of dietary alkaloids for defense (Caldwell 1996; Vences et al. 1998). However, there is no evidence that the genus *Rhinella* utilizes alkaloid-based chemical defenses, and, indeed, some taxa are known to produce their own toxins (Lyttle et al. 1996), such as bufadienolides and indolealkylamines (Mebs et al. 2007; Rodriguez et al. 2021). In this instance, other factors may be at play, including morphological limitations (Simon & Toft 1991; Hirai 2002; Isacch & Barg 2002; Duré et al. 2009; Lopes et al. 2017), energy requirements (Pough 1983), prey availability (Donnelly 1991; Simon & Toft 1991), or prey size and texture (McElroy & Donoso 2019).

All the ants consumed by juvenile *Odontophrynus* sp. were myrmicines (i.e. belonged to the subfamily Myrmicinae). In juvenile *R. arenarum*, myrmicines were the most diverse and abundant ants found. These results could indicate a predilection of juveniles of both species for Myrmicinae; this subfamily is also preferred by several myrmecophagous amphibians, such as *Melanophryniscus devincenzii* (Bortolini et al. 2013), *Elachistocleis bicolor* (Solé et al. 2002; Berazategui et al. 2007), *Chiasmocleis leucosticta* (Lopes et al. 2017), and other *Rhinella* species (Sabagh & Carvalho-E-Silva 2008). Although myrmicine ants accumulate certain alkaloids for use in defense (Daly et al. 1996; Clark et al. 2005), the amphibian species in this study are not known to sequester dietary alkaloids. It may be that this subfamily of ants is consumed in large quantities because myrmicine species are diverse and broadly occur in temperate regions (Fernández 2003).

In summary, juvenile *Odontophrynus* sp. and *R. arenarum* exhibited differences in diet

composition. Juvenile *Odontophrynus* sp. appeared to be more generalist in their feeding habits and tended to consume longer prey. The ants and mites in their diet may be the result of opportunistic foraging behavior, such as the use of a 'sit and wait' strategy. In contrast, following Toft (1985, 1995) theory, juvenile *R. arenarum* occupied an intermediate position along the specialist-generalist spectrum. Ants were the primary prey they consumed, followed by mites. These ants were largely myrmicines, among which the genera *Solenopsis* (Myrmicinae) and *Linepithema* (Dolichoderinae) were highly represented. It seems likely that *R. arenarum* utilizes active searching, as these types of prey typically occur in groups or trails rather than individually.

Most amphibian species are endangered, and their populations are in decline (Stuart et al. 2004). However, little research has looked at juveniles, even though they represent the most vulnerable stage in the amphibian life cycle (Werner 1986; Cabrera-Guzmán et al. 2013; Pittman et al. 2014; Petrovan & Schmidt 2019). While the species studied here remain common in Uruguay and have been classified as being of least concern by the IUCN, they are facing increasing conservation issues at the population level (Nicholls et al. 2017). They live in habitats where urbanization is an increasing threat (e.g. the sites where our samples were collected), and there may be future impacts on both their diets (Santana et al. 2019) and their reproductive cycles (Montezol et al. 2018). Future work should focus on the direct and indirect consequences of habitat modifications on the trophic ecology and conservation of these amphibians.

Data availability statement

The data obtained in this study are provided in the Supplementary Materials (Appendices 1–2).

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Appendix A. Amphibian data

Table A1. Descriptive information for the specimens of juvenile *Odontophrynus* sp. and *R. arenarum* used in this study. Provided below are the identification code (ID) for each specimen, the specimen's source (origin: pitfall trap or zoological collection at the Faculty of Sciences in Montevideo [ZVCB]); and the place (location), environment (habitat); and time of year (season) associated with the specimen's initial capture.

ID	Origin	Location	Habitat	Season
Odontophrynus sp.				
O1	Pitfall trap	El Pinar	Coastal-urban	Spring
O2	Pitfall trap	Shangrilá	Coastal-urban	Spring
O3	Pitfall trap	Shangrilá	Coastal-urban	Spring
O4	Pitfall trap	Shangrilá	Coastal-urban	Spring
O5	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O6	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O7	ZVCB	Cuchilla del Rincón	Grasslands	Winter
O8	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O9	ZVCB	Cuchilla del Rincón	Grasslands	Winter
O10	ZVCB	Cuchilla del Rincón	Grasslands	Winter
O11	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O12	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O13	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O14	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O15	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O16	ZVCB	Cuchilla del Rincón	Grasslands	Spring
O17	ZVCB	Cuchilla del Rincón	Grasslands	Autumn/Winter
O18	ZVCB	Cuchilla del Rincón	Grasslands	Autumn
O19	ZVCB	Cuchilla del Rincón	Grasslands	Autumn
O20	ZVCB	Cuchilla del Rincón	Grasslands	Autumn
O21	ZVCB	Cuchilla del Rincón	Grasslands	Summer
O22	ZVCB	Cuchilla del Rincón	Grasslands	Summer
O23	ZVCB	Cuchilla del Rincón	Grasslands	Winter
O24	ZVCB	Cuchilla del Rincón	Grasslands	Winter
O25	ZVCB	Cuchilla del Rincón	Grasslands	Winter
Rhinella arenarum				
R1	Pitfall trap	Shangrilá	Coastal-urban	Spring
R2	Pitfall trap	Shangrilá	Coastal-urban	Spring
R3	Pitfall trap	Shangrilá	Coastal-urban	Spring
R4	ZVCB	Parque del Plata	Coastal-urban	Summer
R5	ZVCB	Parque del Plata	Coastal-urban	Summer
R6	ZVCB	Parque del Plata	Coastal-urban	Summer
R7	ZVCB	Parque del Plata	Coastal-urban	Summer
R8	ZVCB	Cabo Polonio	Coastal	Summer
R9	ZVCB	Cabo Polonio	Coastal	Summer
R10	ZVCB	Cabo Polonio	Coastal	Summer
R11	ZVCB	Cabo Polonio	Coastal	Summer
R12	ZVCB	Cabo Polonio	Coastal	Summer
R13	ZVCB	Cabo Polonio	Coastal	Summer
R14	ZVCB	Costa Azul	Coastal-urban	Summer
R15	ZVCB	Costa Azul	Coastal-urban	Summer
R16	ZVCB	Costa Azul	Coastal-urban	Summer
R17	ZVCB	Costa Azul	Coastal-urban	Summer
R18	ZVCB	Costa Azul	Coastal-urban	Summer
R19	ZVCB	Costa Azul	Coastal-urban	Summer
R20	ZVCB	Arroyo Carrasco	Riparian-urban	Spring
R21	ZVCB	Arroyo Carrasco	Riparian-urban	Spring
R22	ZVCB	Arroyo Carrasco	Riparian-urban	Spring
R23	ZVCB	Arroyo Carrasco	Riparian-urban	Spring
R24	ZVCB	Arroyo Carrasco	Riparian-urban	Spring
R25	ZVCB	Arroyo Carrasco	Riparian-urban	Spring

Table A2. Morphological data for the specimens (ID) of juvenile *Odontophrynus* sp. and *R. arenarum* used in this study. Abbreviations: JW, jaw width; W. max, maximum prey width; and L. max, maximum prey length.

ID	JW (mm)	W. max (mm)	L. max (mm)
Odontophrynus sp.			
O1	6	0.85	3.6
O6	7.5	2.5	5.3
O2	7.9	1.2	6.8
O5	10.5	4.4	9
O25	10.5	1.75	10.6
O8	11	1.55	4.2
O16	11	2.8	5.8
O19	11	4.3	10
O23	11	3.1	9
O4	12	5.6	11.45
O12	12	0.95	3.05
O13	12	2.25	3.75
O20	12	3.3	7.1
O24	12	3.3	7.3
O18	12.5	5	29.5
O7	13	2.05	11
O9	13	1.85	4.5
O11	13	1.45	5.1
O14	13	4.3	9
O15	14	2.6	6.4
Rhinella arenarum			
R2	3.8	0.75	3.35
R3	3.9	0.575	2.6
R1	4	1.2	2.5
R20	5.5	0.32	0.5
R10	5.7	1.17	3.6
R5	5.8	1.8	0.75
R23	5.8	0.57	0.81
R8	6	2.9	6
R6	6.1	1.47	8.5
R19	6.3	1.75	5.35
R18	6.6	2.2	5
R11	6.7	2	6.3
R12	6.7	1.4	3.35
R16	6.7	2.5	5.6
R7	7.1	0.6	2.7
R13	7.2	0.7	3.5
R15	7.2	2.5	6
R4	7.4	0.375	1.44
R9	7.4	1.7	5

Appendix B. Ant species identified from stomach contents

Figure B1. *Linepithema micans*. Found in *R. arenarum*.

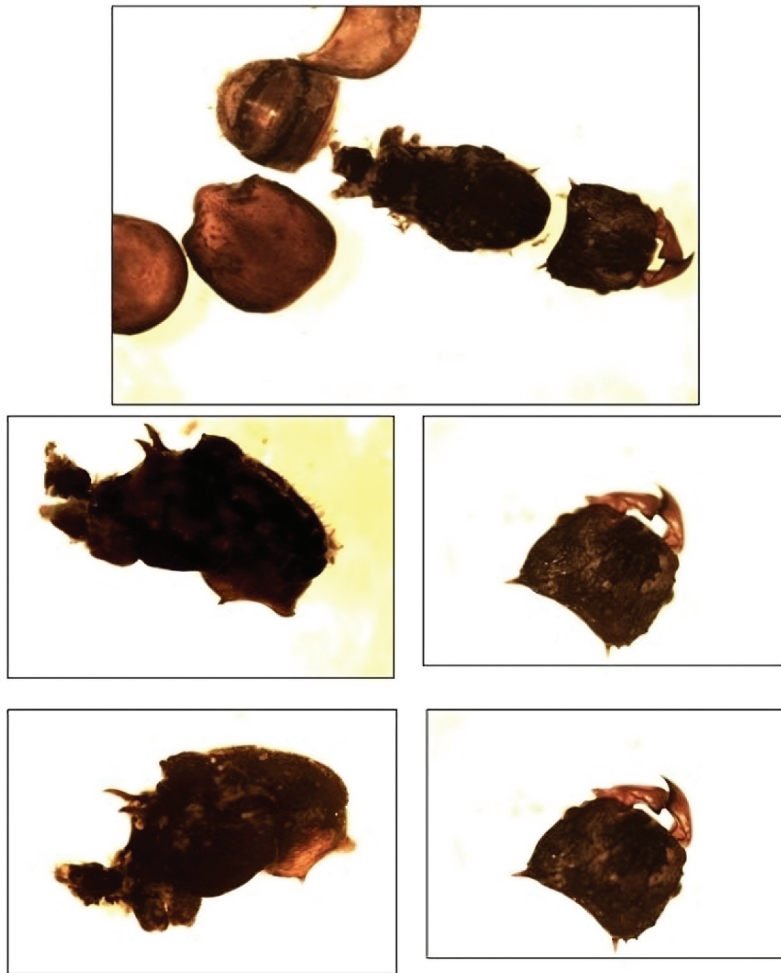**Figure B2.** Possible *Linepithema humile*. Found in *R. arenarum*.

Figure B3. *Acromyrmex striatus* (queen). Found in *Odontophrynus sp*.

Figure B4. *Acromyrex lundii*. Found in *R. arenarum*.