

# Food selection strategy during the reproductive period in three syntopic hylid species from a subtropical wetland of north-east Argentina

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*Dendropsophus nanus*, *D. sanborni* and *Lysapsus limellum* are three hylid species, similar in body size and frequently coexisting at the same reproductive sites. To determine whether food partitioning occurred during the reproductive phase, both numerical and volumetric analyses of stomach contents were performed on syntopic populations inhabiting a wetland system in Corrientes Province, north-east Argentina. The analyses showed a marked specialization towards Diptera prey in *Dendropsophus* species, particularly in *D. sanborni*, and a more generalist habit in *L. limellum*. The three study species exhibited different foraging modes, with *L. limellum* belonging to the sit-and-wait predator type, *D. sanborni* to the forager predator type, and *D. nanus* exhibiting a mixed foraging mode. The comparison of the feeding strategies adopted by the various species in different habitat types and condition of syntopy showed a noteworthy plasticity. According to Schoener's food size selection strategy model for a syntopic predator species system, the larger species (*L. limellum*) selected prey bigger in size and the smaller (*D. sanborni*) ate a larger number of prey specimens, whereas *D. nanus* showed an intermediate trophic strategy. Although the degree of trophic niche overlap was higher than expected, the study species did not show a clear segregation in terms of use of space, hence the coexistence mechanism during the reproductive period should not be related to competition processes for food resources.

*Key words:* Amphibia, *Dendropsophus*, diet, *Lysapsus*, resource partitioning

## INTRODUCTION

The competitive exclusion between species sharing the same resources is one of the basic principles of community ecology (Vandermeer, 1972; Pianka, 1973, 1974; Pianka & Huey, 1978). In amphibians, sympatric species may differ in terms of microhabitat selection (Griffiths & Mylotte, 1987; Brodman et al., 2003; Martinez-Solano et al., 2003; Vignoli et al., 2007c), seasonal activity (Semlitsch & Pechmann, 1985; Morin et al., 1990; Lawler & Morin, 1993; Semlitsch et al., 1993, 1996; Jakob et al., 2003; Vignoli et al., 2007b), or diet (Toft, 1981; Jones, 1982; Griffiths, 1986; Fasola & Canova, 1992; Joly & Giacoma, 1992; Das, 1996; Parmelee, 1999; Eniang et al., 2003), and in many cases sympatric species differ for a combination of these three dimensions (Toft, 1985; Dolmen, 1988; Denton & Beebe, 1994; Kuzmin, 1995; Vignoli, 2003).

Ecological studies on neotropical amphibian assemblages are still scarce compared to their high taxonomical diversity (but see Parmelee, 1999; Eterovick & Sazima, 2000; Neckel-Oliveira et al., 2000). In particular, dietary investigations of neotropical hylids are mainly descriptive, mostly involving one or two species (Toft, 1981; Del Grande & Moura, 1997; Duré, 1999; Peltzer & Lajmanovich, 1999; Peltzer & Lajmanovich, 2000; Duré & Kehr, 2001; Menin et al., 2005).

In Argentina, hylids often occur syntopically and form assemblages in permanent and temporary water bodies (Ceï, 1983). These assemblages constitute predator species-systems well suited for studies aimed at investigating competition phenomena. *Dendropsophus*

*nanus* (Boulenger, 1889), *Dendropsophus sanborni* (Schmidt, 1944) and *Lysapsus limellum* (Cope, 1862) are often recorded sharing the same water bodies (Ceï, 1983; Macale & Carpaneto, unpublished data). These three species occur in either permanent or temporary water basins and are sympatric over a large portion of their geographic range, extending from the eastern provinces of Argentina (Paraná delta, Buenos Aires, Corrientes, Santa Fe and Entre Ríos provinces), to south-east Brazil (São Paulo state) and northern Uruguay (Contreras & de Contreras, 1982; Basso et al., 1985; Langone & Basso, 1987; Langone, 1994; Alvarez et al., 1996; Prado et al., 2005).

*Dendropsophus nanus* and *D. sanborni*, recently removed from the genus *Hyla* by Faivovich et al. (2005), are among the smallest tree frogs of South America. In the past, some authors considered *D. sanborni* as a subspecies of *D. nanus* (Gallardo, 1974; Ceï, 1983), but these were later recognized as two distinct species, based on the marked difference in both morphology and call voice (Cardoso, 1981; Basso et al., 1985; Langone & Basso, 1987; Skuk & Langone, 1992; Martins & Jim, 2003). *Lysapsus limellum* is a well-investigated species as concerns reproductive aspects (Kehr & Basso, 1990; Bosch et al., 1996; Marangoni & Kehr, 2000; Prado & Uetanabaro, 2000), but whose dietary spectrum has been only preliminarily described by Duré & Kehr (2001) and by Peltzer & Lajmanovich (2002).

*Dendropsophus* species mainly forage on the low vegetation surrounding the ponds (Ceï, 1983; Peltzer & Lajmanovich, 2000; Menin et al., 2005), whereas *L. limellum* is a more aquatic species, usually stationing it-

self on floating plants or directly on the water surface (Peltzer & Lajmanovich, 2002).

In this paper, a detailed study of the food habits of these three syntopic hylid species in a marshland system is presented. Our aim was to test if the study species exhibit segregation in diet, revealing patterns of potential resource partitioning. Because these hylid species are closely related to one another and have similar morphological and/or ecological traits, they may provide a great opportunity for revealing the potential role of resource partitioning in maintaining the structure of amphibian assemblages.

## MATERIALS AND METHODS

### Study area

The fieldwork was carried out in the Ibera Lake (28°30'S, 57°10'W), one of the most important waterbasins (52 km<sup>2</sup>) of the “Esteros del Iberá”, a large wetland system situated in Corrientes Province, north-east Argentina (Ramsar site no. 1162). It is a wide, flat area measuring about 1,200,000 ha, including a complex mosaic of lentic and lotic habitats.

Two special environments for amphibian populations are the “bañados” (semi-permanent water courses) and “malezales” (marshes with a strong water level fluctuation). These are interphasic habitats (ecotones), highly unstable for water availability and biochemical cycles. The climate is subtropical with an annual average temperature of 21 °C and a monthly average temperature ranging from 16 °C in June–July (austral winter) to 27 °C in January–February (austral summer). The absolute maximum temperature reaches 44 °C while the absolute minimum is –2 °C. The relative humidity is high, and annual precipitation ranges from 1200 to 1500 mm (Neiff, 1977).

The research was carried out during the wet season, from December 2000 to February 2001, for a total of 74 nocturnal samplings. Specimens were collected from five sampling sites, all situated near Colonia Carlos Pellegrini (28°31'60"S, 57°10'00"W). During the wet season the species occur syntopically in the satellite permanent and temporary ponds near Iberá Lake. The pond hydroperiod is strongly influenced by waterfalls and periodical lake flooding. The ponds surveyed were rich in floating and emergent or marshy aquatic vegetation (e.g. *Azolla*, *Carex*, *Juncus*, *Lemna*, *Sagittaria*, *Salvinia*).

### Sampling methods

*Dendropsophus nanus* (Dn), *D. sanborni* (Ds) and *Lysapsus limellum* (Ll) individuals were located using a visual encounter survey technique and by their vocalizations and captured by hand. We decided to sacrifice frogs instead of performing stomach flushing for three main reasons: 1) their extremely small body size (species MCL: mean = 19.04 mm, SD = 2.08 mm, min = 14.0 mm, max = 25.3 mm) and fragility; 2) to obtain the entire digestive tract and greatly increase prey sample size (especially important when few specimens were available – *L. limellum* in our case) (Schoener, 1989); and 3) to collect prey in the intestine avoiding the overestimate of larger

prey versus smaller ones (especially important in comparisons by volume, as in our case) (Schoener, 1989). Frogs were sacrificed within two hours of capture by immersing the animals in an anaesthetic solution (10% ethanol) for 5 min (ASIH, 2004), following one of the procedures advised by the Institutional Animal Care and Use Committee (IACUC). For an agreement with the Museum of Natural Sciences “Bernardino Rivadavia” of Buenos Aires, a relevant part of the examined material has been donated to the Museum, to improve its scientific collection.

Frogs were observed on the vegetation and the height from the water surface of the first sighting was recorded. In order to preserve the food contents, the entire digestive tract was removed and placed in 70% ethanol. Taxonomic identification of stomach contents was made using a stereomicroscope. Food items were identified to the lowest taxonomical level reachable, then photographed with a digital camera. Pictures of items were analysed by Image Tool 3.00 software (University of Texas Health Science Center, San Antonio) and measured. Prey volume was estimated using the volume of a prolate spheroid [ $V = 4/3\pi$  (prey length/2)·(prey width/2)<sup>2</sup>] (used for most adult insects and other arthropods) or of a cylinder [ $V = 2\pi r$  (prey length)] (used for insect larvae). Specimens whose stomach was empty were not considered in the diet analysis.

### Data analysis

Cumulative diversity curves (prey diversity plotted against the number of stomachs) were produced for each species to test whether the data collected were representative of the dietary spectrum and to avoid sample size bias in intraspecific comparisons (Kovács & Török, 1997). The index of vacuity, calculated as the percentage of empty stomachs out of the total analysed, was estimated for the three species. Prey items are reported by frequency of occurrence (FO: number of stomachs containing one item divided by the total number of stomachs containing food) and relative abundance (RA: number of individuals belonging to a single prey item divided by the total number of individuals belonging to all prey items).

Food categories were represented with a graphic technique first used by ichthyologists (Costello, 1990; Amundsen et al., 1996) and later by herpetologists (Vignoli, 2003; Vignoli et al., 2006, 2007a) that explains the feeding attitude of a predator. This graphical technique is used to represent the feeding strategy of the species analysed, as well as intra- and interindividual shifts in niche utilization. This method enables researchers to interpret graphically the importance of dietary items (the first diagonal, /, represents abundance increase along with prey importance), the types of feeding specializations (the vertical axis, ↓, represents predator strategy going from generalist to specialist), and the dietary niche-width of the forms analysed. The second diagonal, \, represents resource use changing from BPC (Between Phenotype Component, among individuals of population) to WPC (Within Phenotype Component – tending towards the same resource use), by dividing the diet into its constituent components (Amundsen et al., 1996). These

components are then graphed, plotting frequency of occurrence (%) on the x-axis and prey-specific abundance on the y-axis. Prey-specific abundance ( $P_i$ ) was calculated as the number of prey  $i$  divided by the total number of prey in the stomach that contained the prey  $i$  (Amundsen et al., 1996). Prey-specific abundance is calculated as follows:

$$P_i = (\sum S_i / \sum S_{ji}) 100$$

where  $P_i$  equals prey-specific abundance of prey  $i$ ,  $S_i$  equals the abundance of prey  $i$  in stomachs and  $S_{ji}$  equals the total abundance of prey in specimens that contain prey  $i$ . This index was calculated using both number and volume of prey.

Food niche breadth was estimated using Levin's (1968) index,  $B$ , and its standardised form,  $B_A$  (Hurlbert, 1978):

$$B = \frac{1}{\left[ \sum_i^n P_{ji}^2 \right]}$$

$$B_A = \frac{(B-1)}{(n-1)}$$

where  $p_{ji}$  is the proportion of species  $j$  using prey  $i$  and  $n$  is the number of food categories found.

Prey niche overlap was calculated by applying 1) Czechanowski's (Feinsinger et al., 1981) and 2) Pianka's (1973) indices:

$$1) C = 1 - 0.5 \left( \sum_i |p_{xi} - p_{yi}| \right)$$

$$2) O_{xy} = \frac{\sum_{i=1}^n p_{xi} p_{yi}}{\left( \sum_{i=1}^n p_{xi}^2 \sum_{i=1}^n p_{yi}^2 \right)^{1/2}}$$

where  $p_{xi}$  is the proportional utilization of prey  $i$  by form  $x$  and  $p_{yi}$  the proportional utilization of prey  $i$  by form  $y$ . Both indices range from 0 (no prey in common in the diet spectrum) to 1 (same diet spectrum).

Because the evaluation and comparison of niche overlap indices are affected by the limitation of arbitrary cut-offs (Feinsinger et al., 1981), we compared the observed overlap values to an appropriate null model. The distribution of the null model was created using Ecosim software (version 7.0; Gotelli & Entsminger, 2001, 2004) running two simulations each with 1000 randomized replications of the data set. The simulations were generated using two randomization algorithms: RA2 (niche breadth relaxed/zero states retained) whereby every cell in the matrix is replaced with a randomly chosen, uniforming number between zero and one but maintaining the zero structure in the matrix; and RA3 (the "scrambled-zeros" randomization algorithm proposed by Winemiller & Pianka, 1990), whereby the entries in each row of the utilization matrix were randomly reshuffled for each iteration retaining the niche breadth of each species but

randomizing which particular resource states are utilized. Due to the objective limits in assessing food availability in a complex environment, resource availability was assumed to be equiprobable. Statistical significance was determined by comparing the observed overlap value to the null distribution; an observed value greater than 95% of the simulated values indicates significant overlap at the  $P < 0.05$  level (Winemiller & Pianka, 1990).

Statistical analyses were performed to compare food habits among the three hylid species. We used parametric tests when the data fitted a normal distribution, and non-parametric tests when the data did not fit a normal distribution even after logarithmic and arcsin transformations): 1) Kruskal–Wallis ANOVA to compare the average stomach content volume and the average number of prey found in non-empty stomachs in the study species; 2) Factorial Analysis of Correspondence (FAC) to evaluate how the three species exploit the food resources; 3) Multi Response Permutation Procedure (MRPP) to evaluate the significance of interspecific differences generated by means of FAC. The strategy of MRPP is to compare the observed intra-group average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis. In the Costello graphic representation and in the Factorial Analysis of Correspondence, food items were grouped in homogeneous assemblages based on taxonomy and ecological characteristics, in order to optimize the analyses.

In order to correlate average stomach content and food item volume with the mean body size of the species, each specimen was measured using an electronic calliper (0.01 mm). Both snout–vent length (SVL) and mouth width (MW) were measured. Because the two biometric measures were highly correlated (normal distribution data;  $R_{DN=36} = 0.807$ ,  $P < 0.001$ ;  $R_{DS=67} = 0.669$ ,  $P < 0.001$ ;  $R_{LL17} = 0.894$ ,  $P < 0.001$ ; linear regression), we analysed interspecific differences using the MW measure.

## RESULTS

During the reproductive period, *Dendropsophus nanus*, *D. sanborni* and *Lysapsus limellum* frequently used both temporary and permanent small water basins. Both *Dendropsophus* species foraged on the vegetation surrounding the shoreline and were observed on hygrophilous plants over the water surface (the vertical distribution of both these species largely overlapped and ranged from about 20 to 2 m in height), whereas *L. limellum* was found only on the floating leaves of the aquatic fern *Azolla* sp. In the five different sites investigated, the three species always occurred together. Individuals were found only along an approximately 20 m belt along the shore, covered by emergent or marshy aquatic vegetation. All the species analysed were observed on aquatic and marsh plants growing on flooded soils but never on the ground surface.

The biometric analyses showed that the species differed significantly in mouth width, with *L. limellum* larger than *D. nanus* and the latter larger than *D. sanborni* (mean<sub>DN=36</sub> = 5.94 mm, SD<sub>Dn</sub> = 0.55; mean<sub>DS=67</sub> = 4.52 mm, SD<sub>Ds</sub> = 0.44; mean<sub>LL=17</sub> = 6.65 mm, SD<sub>Ll</sub> = 0.41;  $F_{2,177} = 194.20$ ,

**Table I.** Number and volume of 33 prey taxa found in the 138 analysed stomachs (47 of *Dendropsophus nanus*, 76 of *D. sanborni* and 15 of *Lysapsus limellum*). Frequency of occurrence and relative abundance of preys are shown based on numeric (N) and volumetric (V) data. Main taxonomic categories in *italic*. n.d. = undetermined

Prey items	Frequency of occurrence (%)			Relative abundance (N)			Relative abundance (V)		
	<i>Dn</i>	<i>Ds</i>	<i>Ll</i>	<i>Dn</i>	<i>Ds</i>	<i>Ll</i>	<i>Dn</i>	<i>Ds</i>	<i>Ll</i>
<i>Isopoda</i>	-	2.00		-	0.21	-	-	2.64	-
<i>Acarina</i>	3.23	11.48		2.95	1.45	-	0.04	0.16	-
Oribatei	3.23	1.64		0.42	-	-	0.04	0.09	-
Mesostigmata	-	4.92		1.26	1.45	-	-	0.02	-
<i>Acarina n.d.</i>	-	4.92		1.26	-	-	-	0.05	-
<i>Araneae</i>	38.71	13.11	20.00	17.39	3.36	8.82	22.70	2.52	4.30
Labidognatha	29.03	13.11	-	13.04	3.36	-	20.70	2.52	-
<i>Araneae n.d.</i>	9.68	-	20.00	4.35	-	8.82	2.00	-	4.30
<i>Collembola</i>	-	1.64	6.67	-	0.42	2.96	-	0.09	0.20
Symphyleona	-	1.64	6.67	-	0.42	2.96	-	0.09	0.20
<i>Anisoptera</i>	-	-	13.30	-	-	5.88	-	-	9.60
<i>Zygoptera</i>	-	-	20.00	-	-	8.82	-	-	14.70
<i>Ephemeroptera</i>	3.23	-	6.67	1.45	-	2.94	3.50	-	4.30
<i>Orthoptera</i>	6.46	-	13.30	2.90	-	5.88	17.70	-	22.30
Tettigonidae	3.23	-	-	1.45	-	-	8.80	-	-
<i>Orthoptera n.d.</i>	3.23	-	13.30	1.45	-	5.88	8.90	-	22.30
<i>Heteroptera</i>	-	6.56	13.30	-	2.11	8.82	-	2.72	2.40
<i>Homoptera</i>	3.23	8.20	6.67	1.45	3.80	2.94	1.7	17.8	3.6
Aphididae	-	4.92	6.67	-	0.84	2.94	-	1.29	3.6
Cicadodea	3.23	3.28	-	1.45	1.26	-	1.7	15.17	-
Fulgoroidea	-	1.64	-	-	0.42	-	-	0.05	-
Sternorrhyncha	-	1.64	-	-	1.26	-	-	0.16	-
<i>Isoptera</i>	3.23	-	-	1.45	-	-	0.30	-	-
<i>Psocoptera</i>	6.45	1.64	-	10.14	0.42	-	0.50	0.02	-
<i>Trichoptera</i>	-	3.28	-	-	0.84	-	-	0.39	-
<i>Lepidoptera</i>	3.23	-	-	1.45	-	-	3.90	-	-
<i>Coleoptera</i>	3.23	-	6.67	1.45	-	2.94	2.72	-	3.40
Chrysomelidae Cryptocephalinae	3.23	-	6.67	1.45	-	2.94	2.72	-	3.40
<i>Hymenoptera</i>	6.45	4.92	6.67	2.90	1.69	2.94	0.20	0.23	0.10
Formicidae	6.45	4.92	6.67	2.90	1.69	2.94	0.20	0.23	0.10
<i>Diptera Nematocera</i>	58.06	91.8	26.7	57.97	78.90	32.35	46.80	69.80	30.20
Ceratopogonidae	12.9	4.9	-	14.49	2.52	-	3.07	0.51	-
Chironomidae	25.81	52.46	13.30	18.84	34.87	18.20	24.85	60.70	14.1
Culicidae	-	4.90	-	-	1.68	-	-	0.23	-
Culicomorpha (not Culicidae)	3.22	9.84	-	1.45	3.36	-	0.28	1.55	-
Sciaroidea	-	9.84	-	-	6.30	-	-	1.04	-
<i>Nematocera n.d.</i>	25.81	41	13.4	23.19	29.83	14.15	17.59	5.40	16.1
<i>Diptera Brachycera</i>	-	11.48	33.3	-	5.48	14.71	-	3.07	4.70
Acalyptrata	-	3.28	-	-	0.84	-	-	0.84	-
Dolicopodidae	-	3.28	-	-	1.68	-	-	0.15	-
Empididae	-	1.64	-	-	0.43	-	-	1.12	-
Ephydroidea	-	3.28	-	-	1.26	-	-	0.27	-
<i>Brachicera n.d.</i>	-	3.28	33.3	-	1.26	14.71	-	0.68	4.7

$P < 0.001$ , one-way ANOVA) ( $P < 0.001$ ; Tukey post-hoc test). The body size, expressed as snout–vent length (SVL), was strongly correlated with MW (see Methods).

A total of 145 stomachs was analysed: 47 from *D. nanus*, 76 from *D. sanborni* and 22 from *L. limellum*. The index of vacuity was nearly 34% ( $n=16$ ) in *D. nanus*, 18.4% ( $n=14$ ) in *D. sanborni* and 32% ( $n=7$ ) in *L. limellum*. A total of 629 prey items, belonging to 33 taxonomic groups, was identified and classified into 18 main taxonomic cat-

egories (Table I). For the three hylid species, the cumulative diversity curves reached a plateau, evidence that prey composition was reliably assessed (Fig. 1). Considering the prey types with frequency of occurrence greater than 5%, *D. nanus* and *D. sanborni* shared 71.4% (5/7) of prey types, and both *Dendropsophus* species shared 53.8% (7/13) of prey types with *L. limellum*.

The species studied (particularly *Dendropsophus* spp.) showed a food spectrum characterized by a clear



preference for nematocerans (Diptera, Nematocera), which represented the most important food category for both FO and RA in terms of number and volume of prey ( $D_n$ : FO=58%, RA<sub>num</sub>=58%, RA<sub>vol</sub>=47%;  $D_s$ : FO=92%, RA<sub>num</sub>=79%, RA<sub>vol</sub>=70%;  $L_l$ : FO 27%; RA<sub>num</sub>=32%, RA<sub>vol</sub>=30%).

In terms of prey number per stomach, the three species showed significant differences (mean <sub>$D_n=31$</sub> =2.23, SD <sub>$D_n$</sub> =1.91; mean <sub>$D_s=61$</sub> =3.88, SD <sub>$D_s$</sub> =3.72; mean <sub>$L_l=17$</sub> =2.31, SD <sub>$L_l$</sub> =1.48;  $H_{2,107}$ =11.38;  $P<0.01$ , Kruskal-Wallis test). *D. sanborni* contained a higher number of prey items per stomach than the other two species, with a marked difference only compared to *D. nanus* ( $P<0.01$ , Tukey HSD post-hoc test performed on ranked data).

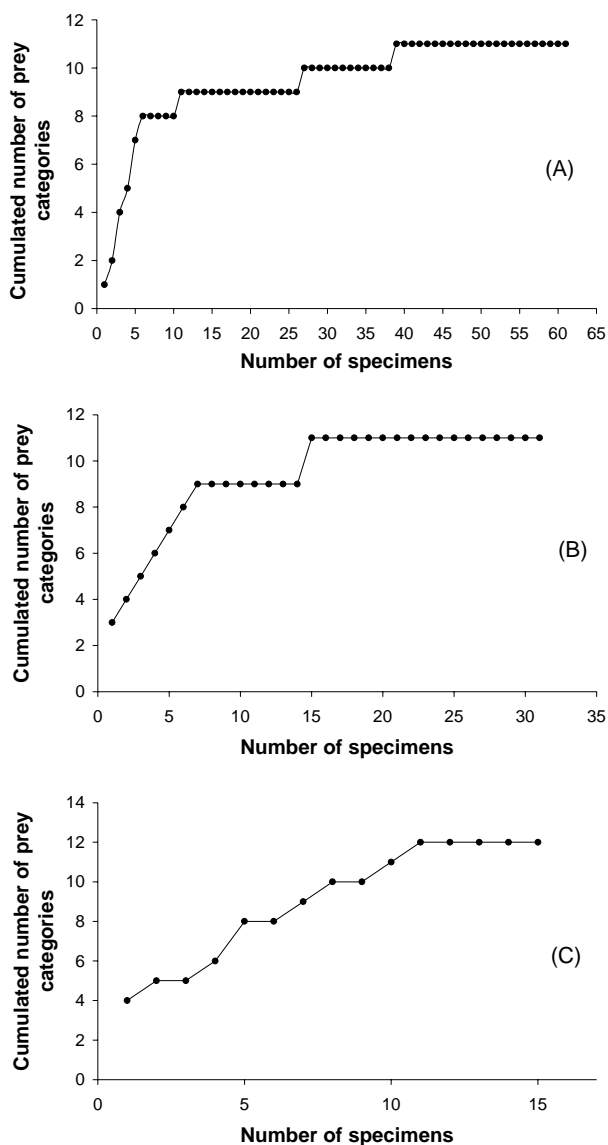
In terms of prey volume, the species showed a marked discrepancy in prey selection (mean <sub>$D_n=44$</sub> =29.94 mm<sup>3</sup>,

SD <sub>$D_n$</sub> =33.05; mean <sub>$D_s=111$</sub> =16.44 mm<sup>3</sup>, SD <sub>$D_s$</sub> =43.41; mean <sub>$L_l=34$</sub> =69.79 mm<sup>3</sup>, SD <sub>$L_l$</sub> =50.44;  $H_{2,188}$ =25.99;  $P<0.0001$ , Kruskal-Wallis test). *L. limellum* exhibited a clear selection towards larger prey (highest mean prey volume and relative low SD) than *D. nanus* ( $P<0.05$ ) and *D. sanborni* ( $P<0.0001$ ), whereas between *Dendropsophus* species the former selected prey significant larger than the latter ( $P<0.05$ ) (Tukey post-hoc tests performed on ranked data). The high values of SD in both *Dendropsophus* species indicated a selection towards both very small and large prey. The analysis performed on the volume of Nematocera (i.e. the commonest shared prey) revealed significant divergence among species ( $H_{2,78}$ =13.755;  $P<0.001$ ; Kruskal-Wallis test), with *L. limellum* preying on nematocerans significantly bigger in size than those selected by the other species ( $P<0.05$ , Tukey post-hoc test performed on ranked data).

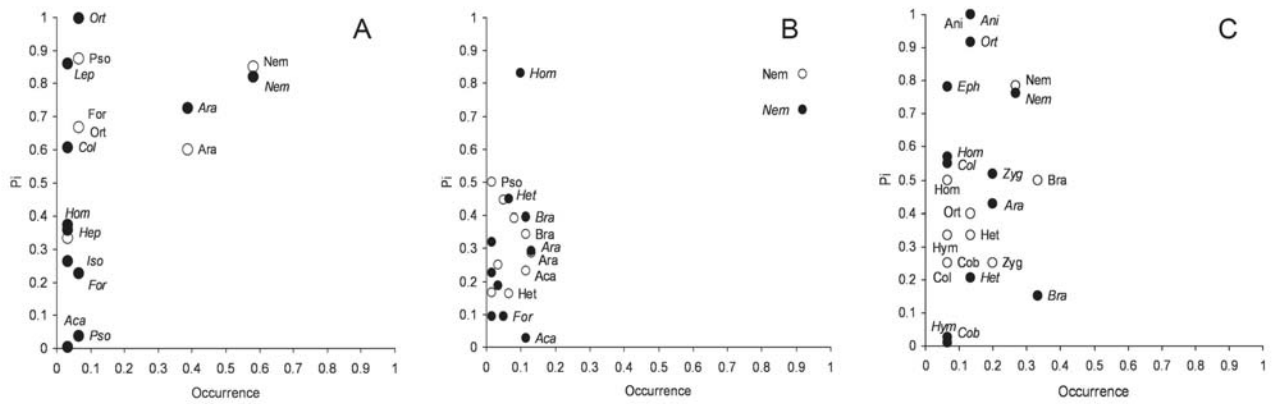
All the species showed significant differences in stomach content volume (mean <sub>$D_n=61$</sub> =42.5 mm<sup>3</sup>, SD <sub>$D_n$</sub> =50.92; mean <sub>$D_s=31$</sub> =30.67 mm<sup>3</sup>, SD <sub>$D_s$</sub> =44.59; mean <sub>$L_l=17$</sub> =69.79 mm<sup>3</sup>, SD <sub>$L_l$</sub> =50.44;  $H_{2,109}$ =10.87;  $P<0.01$ ; Kruskal-Wallis test). *L. limellum* stomach contents were significantly larger than those of *D. sanborni* ( $P<0.01$ , Tukey HSD post-hoc test performed on ranked data).

The analysis of Costello graphics (based on numeric and volumetric data; Fig. 2) highlighted different prey distribution patterns for the study species. *D. nanus* (Fig. 2A) showed a mixed feeding strategy characterized by a slight specialization towards nematoceran flies (Diptera, Nematocera) and spiders (Araneae) with low within-phenotype contribution to the niche width but a relatively high between-phenotype component. *D. sanborni* (Fig. 2B) showed a restricted niche breadth (neither within- nor between-phenotype components were high), being a strong specialist predator of nematoceran flies (FO: 0.91;  $P_i$ : 0.83 in number and 0.72 in volume), with small proportions of other prey types included occasionally in the diet of some individuals. *L. limellum* (Fig. 2C) showed a high between-phenotype contribution to the niche width, with most of the prey types positioned in the upper left corner; each food category had been consumed by only a limited proportion of the individuals, being specialized on different prey types. Spiders represented an additional main prey category for *D. nanus* (FO: 0.39;  $P_i$ : 0.60 in number and 0.72 in volume) and *L. limellum* (FO: 0.20;  $P_i$ : 0.42 in number and volume) (particularly for the former), but only a small fraction of the diet of *D. sanborni* (FO: 0.13;  $P_i$ : 0.29 in number and volume).

The factorial analysis of the correspondences applied to volumetric data of five comprehensive food categories (excluding prey with frequency of occurrence <5%), based on the first two factors (60% of the explained variance; Fig. 3), showed a different spatial arrangement of the three species due to the differential use of some food categories: the plot distributions of *D. nanus* and *L. limellum* significantly overlapped ( $\delta_{obs}$ =1.395,  $\delta_{exp}$ =1.390,  $P=0.41$ ; MRPP analysis) and were influenced predominantly by spiders and a varied assemblage of winged insects (Ephemeroptera, Orthoptera, Isoptera, Trichoptera and Lepidoptera), whereas *D. sanborni*'s plot distribution clearly segregated from the others



**Fig. 1.** Number of frog specimens analysed (counted randomly) against cumulative number of prey categories found in their stomachs. Note that for all three plots a plateau was reached. A = *Dendropsophus sanborni*; B = *D. nanus*; C = *Lysapsus limellum*.



**Fig. 2.** Costello (modified by Amundsen et al., 1996) graphic visualization showing trophic strategies of *Dendropsophus nanus* (A), *D. sanborni* (B) and *Lysapsus limellum* (C), based on numeric (empty circles, regular) and volumetric (black circles, italic) data. See Methods for interpretation. Pi = prey specific abundance. Ara = Araneae; Aca = Acarina; Ani = Anisoptera nymph; Bra = Diptera, Brachicera; Cob = Collembola; Col = Coleoptera; Eph = Ephemeroptera; For = Formicidae; Het = Heteroptera; Hom = Homoptera; Iso = Isoptera; Isp = Isopoda; Lep = Lepidoptera; Nem = Diptera, Nematocera; Ort = Orthoptera; Pso = Psocoptera; Tri = Trichoptera; Zyg = Zygoptera. For clarity, some food categories are not labelled.

( $\delta_{obs}=1.037$ ,  $\delta_{exp}=1.192$ ,  $P<0.001$ ; MRPP analysis) with hemipterans (Hemiptera) representing an almost exclusive food category. Diptera (Nematocera and Brachycera) were the main prey shared by the three species.

Niche breadth ( $B_A$ ) for both numerical and volumetric data was greater in *L. limellum* than in *Dendropsophus* species ( $Dn_{num}=0.09$ ,  $Dn_{vol}=0.13$ ;  $Ds_{num}=0.03$ ,  $Ds_{vol}=0.05$ ;  $Ll_{num}=0.29$ ,  $Ll_{vol}=0.25$ ). The application of Pianka's and Czekanowski's indices showed a diffuse overlap among the study species in the diet spectrum for both numeric and volumetric data (Table 2).

The application of an appropriate null model revealed that the observed degrees of overlap were significantly higher than the mean values obtained from simulations using both the RA2 and RA3 randomization algorithms performed on numeric and volumetric data (for all tests  $P<0.01$ ).

**Table 2.** Diet spectrum overlap degree among the study species calculated on numeric (N) and volumetric (V) data. Values of Pianka's (above diagonal - 1973) and Czekanowski's (below diagonal - Feinsinger et al., 1981) indices are shown.

Species	<i>D. nanus</i>		<i>D. sanborni</i>		<i>L. limellum</i>	
		N	V	N	V	
<i>D. nanus</i>	–	0.95	0.84	0.84	0.82	
<i>D. sanborni</i>	N	0.66	–	0.85	0.72	
	V	0.51	–			
<i>L. limellum</i>	N	0.51	0.48	–		
	V	0.43	0.60		–	

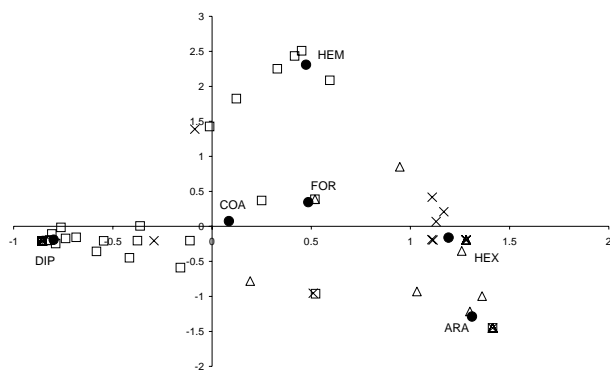
## DISCUSSION

*Dendropsophus nanus*, *D. sanborni* and *Lysapsus limellum* were found syntopically in semi-permanent ponds characterized by dense surrounding hygrophilous vegetation and a water surface largely covered by floating plants. With regard to microhabitat use, *Dendropsophus* spp. exploited the vertical vegetational component with considerable overlap in spatial resource use, whereas *L. limellum* was limited to the floating vegetation on the water surface.

The diets of *D. nanus*, *D. sanborni* and *L. limellum* were grossly similar in composition. Nematocerans were the elective prey in the diet spectrum of both *Dendropsophus* species, particularly of *D. sanborni*, in agreement with the results of Menin et al. (2005). For *D. nanus*, as also reported in previous studies (Basso, 1990; Menin et al., 2005), a significant portion of the food spectrum consisted of spiders. Moreover, spiders constituted the main prey category shared by *D. nanus* and *L. limellum*. The vacuity index values, being similar for each species, demonstrated a shared feeding rate.

Menin et al. (2005) studied the diet of the two *Dendropsophus* species in Brazil and considered them to be generalists, with a low niche overlap and wide niche breadth. In the present study, the two species showed a clear specialization towards nematocerans with a narrow niche breadth. However, Menin et al. (2005) did not pool their data for analysis despite small sample sizes, and their analysis is somewhat inappropriate on occasion (for instance the prey subgroups used for overlap analysis were too narrow in comparison to the sample size examined, thus introducing potential biases in the results). Hence, their conclusions are not comparable with ours.

*Dendropsophus nanus* exhibited higher overall prey diversity but fewer prey items per stomach than *D. sanborni*. The wider niche breadth of *L. limellum* is due to its behavioural feeding strategy: this species stayed at the water surface on the leaves of the floating vegetation



**Fig. 3.** CFA analysis on the first two factors ordinating the species on the basis of their trophic spectrum (volumetric data). Symbols: ARA = Araneae; COA = Collembola and Acarina; DIP = Diptera; FOR = Hymenoptera Formicidae; HEM = Hemiptera; HEX = Ephemeroptera, Orthoptera, Isoptera, Trichoptera and Lepidoptera; black circles = food categories; triangles = *Dendropsophus nanus*; squares = *D. sanborni*; crosses = *Lysapsus limellum*.

and did not actively look for prey, selecting a large variety of prey types dwelling near floating plants, without evident specialization towards any food category. In this anuran assemblage, *L. limellum* is the only predator that also feeds on aquatic prey (dragonfly larvae), whereas *Dendropsophus* species fed exclusively on terrestrial prey. The food spectrum composition, evidenced by the factorial analysis of the correspondences, indicated a preference towards prey of large average size (Araneae and Hexapoda assemblage) for *L. limellum* and *D. nanus*, whereas *D. sanborni* was clearly linked with small-sized prey (particularly various species of flies).

A cline in prey size selection was observed among the study species, with *L. limellum* feeding on prey larger than *D. nanus*, which in turn selected larger prey than *D. sanborni*. When limiting our comparisons to the size of the most common prey that was shared among study species (i.e. nematoceraans), the same apparent trend was supported. According to other studies on anuran assemblages (Toft, 1981), the discrepancy in prey size selection is probably related to the body size of the predators, with *L. limellum* > *D. nanus* > *D. sanborni* in terms of both SVL and MW. Our findings on hylids, as well as those reported in other studies on amphibians such as plethodontid salamanders (Lynch, 1985) and newts (Joly & Giacoma, 1992), are in agreement with the food size selection strategy model proposed by Schoener (1969): in a syntopic predator species system, where food availability is abundant, prey diversity should be higher for the larger ones, but the stomach of the small ones should contain a higher number of prey items.

The three study species exhibited different foraging modes (*sensu* Toft, 1981), at least if we consider number, size, difficulty of capture and digestibility of prey as elements of foraging mode. *Lysapsus limellum* was a sit-and-wait predator, this being shown by the average size of prey items and their occurrence in low numbers in

stomachs. *Dendropsophus sanborni* was a forager predator, with a higher frequency of occurrence and number per stomach of small prey and a narrower niche breadth, indicating a clear specialization towards prey that were actively selected. *Dendropsophus nanus* exhibited a mixed foraging mode in terms of both prey size and niche breadth, having trophic behavioural traits intermediate between the other two species. The comparison of the feeding strategies adopted by the various species in different habitat types and condition of syntopy (different number of species and composition of the amphibian assemblages) showed a noteworthy plasticity. *Dendropsophus nanus* and *D. sanborni*, studied in syntopy in Brazil by Menin et al. (2005), had the same feeding strategy (similar number of prey per stomach), with the former species feeding on larger prey. In preliminary descriptive studies *L. limellum* was defined as both generalist forager and sit-and-wait predator in a permanent pond (province of Corrientes, Argentina), where it lived in syntopy with *Pseudis paradoxa* (Duré & Kehr, 2001) and in temporary ponds of Paraná River (province of Entre Ríos, Argentina) where it was studied alone (Peltzer & Lajmanovich, 2002).

The observed overlap values compared to the appropriate null model suggested that the degree of trophic niche overlap was higher than expected by chance. For species assemblages with high resource overlap (food in the case of this study), segregation is expected along other niche aspects (i.e. spatial) if competition is a strong community structuring force (Hofer et al., 2004). Despite the high degree of trophic niche overlap, *D. nanus*, *D. sanborni* and *L. limellum* did not show a clear segregation in spatial use, hence the coexistence mechanism should not be related to competition. However, overlap indices on their own are not a direct measure of interspecific competition because they can be interpreted as evidence both for and against competition (Colwell & Futuyma, 1971).

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