Bol. Soc. Zool. Uruguay,
2ª época, 2002. 13: 12-20

[2002

DIET OF FOUR SYMPATRIC ANURAN SPECIES IN A TEMPERATE ENVIRONMENT

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RESUMEN

Se estudió la dieta de cuatro especies simpátricas de anuros, desde Octubre de 1998 a Noviembre de 1999, en un ambiente Neotropical templado (Arroyo Espinas, Maldonado, Uruguay). Un total de 387 individuos fueron colectados y su contenido estomacal, examinado (186 *Physalaemus gracilis,* 88 *Leptodactylus ocellatus*, 96 *Hyla p. pulchella* y 17 *Bufo* gr*. granulosus*). Los principales ítems presa fueron: coleópteros, arañas y ácaros para *L. ocellatus*; dípteros, arañas, coleópteros, hemípteros y ácaros para *H. p. pulchella*; formícidos para *B.* gr*. granulosus*; y colémbolos, ácaros y formícidos para *P. gracilis*. *Leptodactylus ocellatus* e *H. p. pulchella* mostraron los valores más altos de amplitud trófica, *P. gracilis* ocupó una posición intermedia, y *B*. gr. *granulosus* presentó los valores más bajos. De acuerdo a las características de las presas consumidas, se propone una estrategia de forrageo de tipo "sit-and-wait" para *L. ocellatus* e *H. p. pulchella*, y una estrategia de tipo activa para *B.* gr. *granulosus*. El análisis de los cambios estacionales indicó que, salvo *P. gracilis*, las demás especies incrementaron la amplitud trófica durante la estación fría, principalmente por inclusión de nuevas presas por cada depredador. Este aumento, probablemente relacionado con un cambio en la oferta de presas, indicaría que las especies no ocupan lugares estancos sobre un continuo con extremos "generalista" y "especialista".

ABSTRACT

The diet of four sympatric anurans species was studied, from October 1998 to November 1999, in a temperate Neotropical environment (Espinas Stream, Maldonado, Uruguay). A total of 387 individuals were collected and their stomach prey content, examined (186 *Physalaemus gracilis,* 88 *Leptodactylus ocellatus*, 96 *Hyla p. pulchella* and 17 *Bufo* gr. *granulosus*). The main prey items were: coleopterans, spiders and acari for *L.ocellatus*; dipterans, spiders, coleopterans, hemipterans, and acari for *H. p. pulchella*; formicids for *B.* gr. *granulosus*; and collembolans, acari and formicids for *P. gracilis*. *Leptodactylus ocellatus and H. p. pulchella* showed the highest diet amplitude, *P. gracilis* occupied a middle position, and *B.* gr. *granulosus* presented the lowest diet amplitude value. According to prey items attributes, a sit-and-wait foraging strategy is proposed for *L. ocellatus* and *H. p. pulchella*, and an active capture strategy for *B.* gr. *granulosus*. Seasonal analysis indicated that, except for *P. gracilis*, all the other predator species increased their diet richness during the cold season, mainly because each predator included new preys. This result, probably related to seasonal changes in prey availability, may indicate that species trophic behavior change along the year, and so, do not allow to locate a species in fixed place between generalist and specialist extremes.

INTRODUCTION

The study of trophic niche allows to make characterizations at the population level and to postulate guild structure, since this dimension includes, among others factors, the diet composition and the species requirements (Schoener, 1974). Regarding to amphibians, the trophic niche plays a relevant role in the population dynamics and in the interspecific relationships, and has been shown as an important factor structuring communities (Peltzer and Lajmanovich, 1999).

Species trophic niche depends on intrinsic and extrinsic factors, like ontogenic development, predator vagility, diet plasticity, changes in resources availability and resources spatial distribution (Jaksic *et al.*, 1993). Changes in these factors may affect the predator location on a resources axis and its trophic amplitude. These facts influence on coexistence patterns among populations (Jaksic, 2001). In amphibians many studies indicate that preys availability and diet, are used to exhibit spatial and temporal variations (Toft, 1980; Mac Nally, 1983; Donnelly, 1991; Maneyro, 2000). However, studies about this topic on amphibians from to temperate Neotropical region are still scarce (e.g., Basso, 1990; Guix, 1993; Lajmanovich, 1996; Duré, 1999; Texeira *et al.*, 1999).

The objective of this work was to describe the diet of four sympatric anuran species, and to analyze trophic interactions and diet seasonal changes. The chosen species were *Physalaemus gracilis*, *Leptodactylus ocellatus, Hyla pulchella pulchella*, and *Bufo* gr. *granulosus*, which are common and widely distributed in Uruguay.

MATERIAL AND METHODS

The survey was conducted in the Espinas stream, Departamento de Maldonado, Uruguay (34° 47´ S, 55° 22´ W) (Fig. 1). This stream is interrupted by an artificial dam that avoids the mixture of its waters with the Rio de la Plata estuary; this fact determined the existence of an artificial lentic ecosystem. Fieldwork took place monthly from October 1998 to November 1999. For the seasonal analysis, data were grouped in two periods: a warm season (October - March) and a cold season (April - September). Animals were caught with nine pitfall traps (volume = 20 l). The survey was complemented by hand catched animals, collected during the night. In both cases specimens were immediately fixed with formaline solution.

A total of 387 individuals were collected: 186 *P. gracilis*, 88 *L. ocellatus*, 96 *H. p. pulchella*, and 17 *B.* gr. *granulosus*. All these individuals were ventrally dissected and its digestive tract removed. The content of the stomach and first intestine portion was extracted following Schoener (1989) and analyzed under Carl Zeiss Binocular lens (4x and 16x). To describe predators diets, the percentual number of individuals (PNI) was calculated for each prey item as follows: PNI_i = 100* (number of individuals in the "i" item category / total number of prey individuals in the sample). The prey items whose PNI comprised less than 5% in the four predator species, were not considered in the data analysis. Unidentified preys did not exceed 5% of the overall sample.

Since species richness is strongly associated to the number of observations (Gotelli and Graves, 1996) the comparison of species diet diversity was evaluated through a "rarefaction" null model (Magurran, 1988; Krebs, 1989):

$$\text{Expected Richness} = \sum_{1}^{S} \left(1 - \frac{\binom{N - m_i}{n}}{\binom{N}{n}} \right)$$

Where S is the observed item prey, N is the total number of prey individuals, m_i is the total of individuals in category i, and n is the number of preys whose expected richness is being evaluated.

Diet overlap between species was estimated by Pianka´s Symmetric Overlap Index (Krebs, 1989), which run from 0 (no overlap) to 1 (total overlap):

$$\text{Pianka´s Index} = \frac{\sum Pij * Pik}{\left[\sum(Pij^2) * \sum(Pik^2)\right]^{0.5}}$$

Where Pij y Pik are i resource proportions used by j and k species.

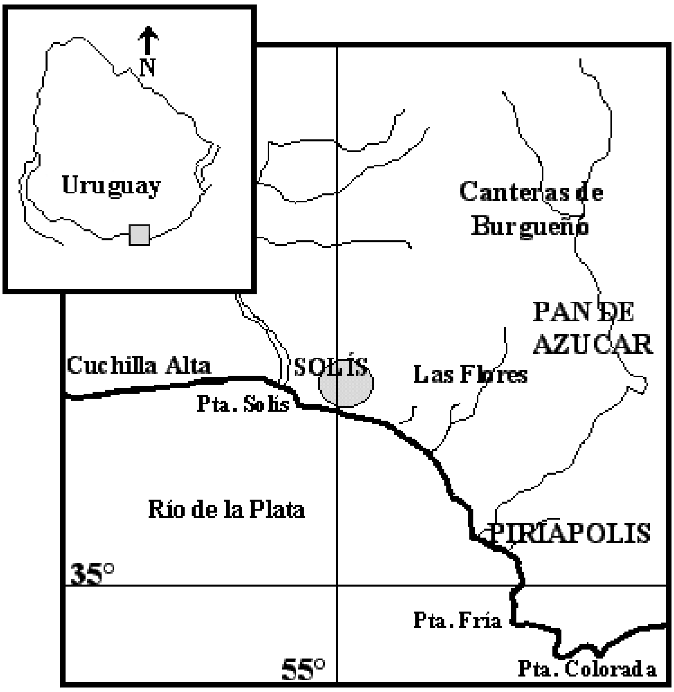

Fig. 1. Map of the study area, showing trough a grey circle the location of Espinas stream, Departamento de Maldonado, Uruguay.

A Correspondence Analysis (AC) was conducted in order to analyze predator species and prey items association. This statistic method allows to make a graphic representation of the existent information in a contingency Table (ter Braak, 1987). For that purpose, a matrix was built with the individuals number in each consumed prey category by each predator species.

RESULTS

Overall Diets

The PNI of each prey item is shown for each predator species in Table 1. From 88 *L. ocellatus* specimens analyzed a total 235 individual preys, belonging to 12 prey items, were identified. *Leptodactylus ocellatus* diet was dominated by coleopterans, spiders, and acari. In 96 *H. p. pulchella* stomachs analyzed, 184 individual preys were identify from 11 prey categories. Dipterans, spiders, coleopterans, hemipterans, and acari were the main prey items in this species diet. In the 17 stomaches of *B.* gr. *granulosus* examined, 432 individual preys were identified. Although 8 prey items were identified in the diet of this toad, formicids comprised 79% of the total diet. This prey item was followed in importance by colleopterans and acari. From 186 *P. gracilis* specimens analyzed a total of 1509 individual preys and ten prey items were

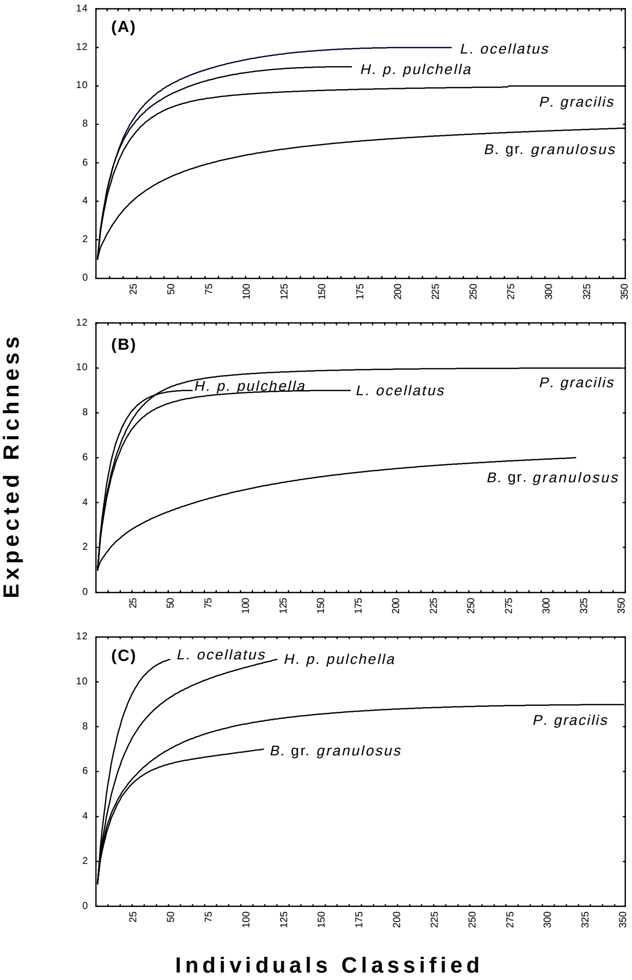

Fig. 2. Rarefaction curves for each predator species: (A) Overall Sample, (B) Warm Season, (C) Cold Season.

recorded. The most important prey items for this species were colembolans, acari, and formicids.

Rarefaction curves are in agreement with the observed diet absolute richness, and indicate that *L. ocellatus* and *H. p. pulchella* show the highest diet amplitude, *P. gracilis* occupies a middle position, and *B.* gr. *granulosus* has the lowest amplitude value (Fig. 2a). Conversely, the mean number of individual preys per stomach reached highest values for *B.* gr. *granulosus*, middle for *P. gracilis*, and lowest for *L. ocellatus* and *H. p. pulchella* (Table 2).

Seasonal Changes

During the warm season, *P. gracilis* consumed a total of ten prey items, *L. ocellatus* and *H. p. pulchella* nine, and *B.* gr. *granulosus* only six (Fig. 2b). Coleopterans, collembolans, and formicids were the dominant prey item found in *L. ocellatus*, *P. gracilis* and *B.* gr. *granulosus*, respectively (Table 1). This last species showed the greatest number of preys per stomach, and the lowest trophic niche amplitude. The highest overlap was observed between *H. p. pulchella* and *L. ocellatus*, while the lowest were between *B.* gr. *granulosus* and the other three species (Table 3). Correspondence Analysis ordination (Fig. 3a) was in agreement with the overlap results. The prey items that most contributed to generate AC axes were formicids and collembolans for the dimension 1, and coleopterans, and collembolans for the dimension 2 (Table 4). Dimension 1 clearly separates *B.* gr. *granulosus* (mainly related with formicids) from the other predator species, while dimension 2 separates *H. p. pulchella* and *L. ocellatus* (mainly related with coleopterans) from *B.* gr. *granulosus* and *P. gracilis* (mainly related with collembolans).

During the cold season, the diet of *L. ocellatus* comprised 11 prey items, *P. gracilis* eight, *H. p. pulchella* eleven, and *B.* gr. *granulosus* seven (Fig. 2c). Dipterans were the dominant item in the diet of *H. p. pulchella* during this season; in the other predator species no seasonal

Table 1. Percentual number of individuals (PNI) consumed for each predator species during the warm season (WS), cold season (CS) and overall sample (T). N = number of stomachs analyzed, NE = number of empty stomachs, NIP = number of individual preys.

	L. ocellatus			*H.p. pulchella*			*B.* gr. *granulosus*			*P. gracilis*		
	WS	CS	T	WS	CS	T	WS	CS	T	WS	CS	T
Aranae	15.6	14.3	15.3	23.4	8.3	13.6	0.9	4.5	1.9	7.0	2.7	5.8
Acarina	9.7	4.1	8.5	6.3	10.8	9.2	2.2	15.3	5.6	19.2	15.9	18.2
Collembola	0	0	0	0	2.5	1.6	0.3	9.9	2.8	36.7	47.8	40.0
Coleoptera	40.9	26.5	37.9	20.3	6.7	11.4	9.0	6.3	8.3	6.4	5.7	6.2
Orthoptera	4.3	8.2	5.1	6.3	0.8	2.7	0	0	0	1.3	0	0.9
NFH *	1.6	4.1	2.1	9.4	4.2	6.0	0	5.4	1.4	7.2	2.3	5.8
Formicidae	6.5	8.2	6.8	3.1	0.8	1.6	86.6	57.7	79.2	6.5	20.0	10.5
Diptera	8.1	2.0	6.8	10.9	41.7	31.0	0	0.9	0.2	6.4	1.1	4.9
Hemiptera	5.4	14.3	7.2	14.1	10.0	11.4	0.9	0	0.7	4.3	3.6	4.1
Larvae	8.1	0	6.4	6.3	5.8	6.0	0	0	0	4.9	0.7	3.6
Odonata	0	6.1	1.3	0	8.3	5.4	0	0	0	0	0	0
Isopoda	0	6.1	1.3	0	0	0	0	0	0	0	0	0
Chilopoda	0	6.1	1.3	0	0	0	0	0	0	0	0	0
N	54	34	88	54	42	96	9	8	17	147	39	186
NE	14	13	27	25	13	28	0	0	0	30	1	31
NIP	186	49	235	64	120	184	1070	439	432	321	111	1509

* NFH = non formicids himenopterans

Table 2. Number of individual preys per stomach (mean ± 1 sd), for each predator species and season. WS = warm season, CS = cold season, T = overall sample.

	WS	CS	T
L. ocellatus	3.5 (4.68)	1.4 (1.94)	2.7 (3.96)
H. p. pulchella	1.2 (1.58)	4.9 (13.97)	2.8 (9.48)
B. gr. *granulosus*	35.7 (22.95)	13.9 (11.98)	25.4 (21.26)
P. gracilis	7.3 (12.54)	11.3 (10.93)	8.1 (12.30)

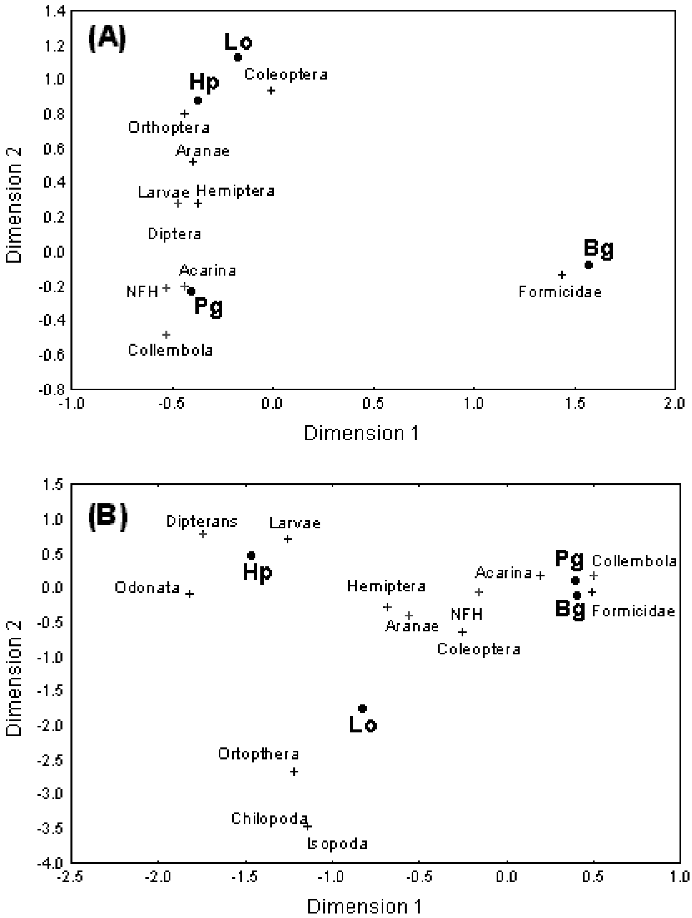

Fig. 3. Plots of species predators and prey items scores in the first two dimensions: (A) Warm Season CA, (B) Cold Season CA. Lo = *L. ocellauts*, Hp = *H. p. pulchella*, Bg = *B.* gr. *granulosus*, Pg = *P. gracilis*.

change in dominant items were recorded (Table 1). During the cold period a decrement in the total number of preys per stomach was observed (Table 2). The feeding behavior of the four species appears to be more generalist than in the warm one. The overlap (Table 3) between the pairs *H. p. pulchella* - *L. ocellatus* and *H. p. pulchella* – *P. gracilis* were lower than in the warm season. On the other hand, the overlap between *B.* gr. *granulosus* – *P. gracilis* was higher. This fact may be a consequence of the increment in ants consumption by *P. gracilis*. Correspondence Analysis (Fig. 3b, Table 4) indicated that *P. gracilis* and *B.* gr. *granulosus* were closely grouped, which may be related to the high consumption of collembolans and formicids, and the low consumption of isopodans, chilopodans, ortopterans and coleopterans. *H. p. pulchella* also showed a low consumption of these last prey items, but presented a high predation frecuency over dipterans; then this species only segregated from *P. gracilis* and *B.* gr. *granulosus* in the dimension 1. Finally, *L. ocellatus* was more distant from the other predator species in both analysis axes, being mainly related with ortopternas, chilopodans, and isopods.

DISCUSSION

Since the energetic profit that a predator obtains from a prey is strongly affected by prey biomass, some authors recommend to consider volume measures as diet descriptors (Caldwell, 1996; Guix, 1993). However, at least in some cases, the numeric frequencies are more closely related with general diet descriptors and trophic behavior than volumetric ones (Basso, 1990; Mangusson and da Silva, 1993), we used numeric data in our analysis. In the present study, preys

Table 3. Diet Similarity Matrix (Pianka´s Overlap Index) for each season. *L.o.* = *L. ocellatus*, *H.p.* = *H. p. pulchella*, *B.g.* = *B.* gr. *granulosus*, *P.g.* = *P. gracilis*.

	Warm Season				Cold Season		
	L.o.	H.p.	P.g.		L.o.	H.p.	P.g.
H.p.	0.84	—	—	*H.p.*	0.37	—	—-
P.g.	0.35	0.39	—	*P.g.*	0.24	0.18	—-
B.g.	0.24	0.15	0.18	*B.g.*	0.34	0.13	0.58

Table 4. Factors scores of each prey item for the first two axes. D1 = Dimension 1, D2 = Dimension 2, Coor. = Coordinate, Iner. = Inertia, EV = Eigenvalues, %I = Percent of Inertia.

	Warm Season				Cold Season			
	D1		D2		D1		D2	
	Coor.	Iner.	Coor.	Iner.	Coor.	Iner.	Coor.	Iner.
Aranae	-0.39	0.02	0.52	0.10	-0.56	0.03	-0.41	0.03
Acarina	-0.44	0.04	-0.21	0.03	0.18	0.01	0.14	0.01
Collembola	-0.53	0.11	-0.49	0.28	0.51	0.15	0.18	0.04
Coleoptera	-0.01	0.00	0.93	0.47	-0.26	0.01	-0.65	0.12
Orthoptera	-0.43	0.00	0.79	0.05	-1.32	0.02	-2.60	0.18
NFH *	-0.52	0.02	-0.22	0.01	-0.16	0.00	-0.07	0.00
Formicidea	1.44	0.75	-0.14	0.02	0.49	0.10	-0.06	0.00
Diptera	-0.48	0.02	0.18	0.01	-1.74	0.46	0.77	0.18
Hemiptera	-0.37	0.01	0.28	0.02	-0.68	0.04	-0.29	0.02
Larvae	-0.47	0.02	0.27	0.02	-1.26	0.04	0.71	0.03
Odonata	——	——	——	——	-1.82	0.11	-0.09	0.00
Isopoda	——	——	——	——	-1.14	0.01	-3.49	0.20
Chilopoda	——	——	——	——	-1.14	0.01	-3.49	0.20
EV	0.61		0.21		0.52		0.26	
%I	72.66		24.85		56.57		28.00	

* NFH = non formicids hymenopterans

were indentified to ordinal level, then a understimation in niche amplitude and an overstimation in niche overlap between predators may occur (Green and Jaksic, 1983). However, niche overlap among the four studied species, was low, and thus these misestimating may not be considered significant. The taxonomic resolution level may convey other restrictions, like inferences about the biological significance of Correspondence Analysis factors. Since many preys attributes changes markedly within each taxonomic order (eg., size, habitat use, activity times) association between these attributes and predator consumption can not be directly detected.

Taking into account the number of items consumed and the contribution of each prey item to the overall diet, the predators that were analyzed could be ordinate in a feeding behavior gradient, from generalist to specialist. In this sense, we consider that *L. ocellatus*, *H. p. pulchella* and *P. gracilis* are more generalist than *B.* gr. *granulosus*. Although the number of stomach analyzed for *B.* gr. *granulosus* was markedly lower than for the other three species, the specialist behavior of the former species is in agreement with other works (Basso, 1990; Lajmanovich, 1996), this justifies the small sample size.

The "prey selection" theory is based on the paradigm that predators can discriminate among prey items (Freed, 1980). Although amphibians were historically considered opportunistic predators (Duellman and Trueb, 1994), field and laboratory works have shown that several species are selective predators, with a close relationship between predators and prey types (Low and Török, 1988). In this sense, it was proposed that very active preys would be caught by sit-and-wait predators, while prey with sedentary habits would be caught by active predators (Huey and Pianka, 1981; Freed, 1980). In the present study, the diets of *H. p. pulchella* and *L. ocellatus* were characterized by consumption of active prey (e.g, coleopterans and dipterans), indicating a sit-and-wait foraging mode. On the other hand, *B.* gr. *granulosus* is an ant specialist, and so, an active capture strategy could be proposed for this species. The diet of *P. gracilis* did not allow its location in any of these two extremes.

Diet composition and associated foraging strategies respond to many factors, like physiological restrictions, interactions among trophic levels, prey availability, and physical or environmental changes (Huey and Pianka, 1981). Niche overlarp hypothesis predicts that if preys availability decrease, then niche overlap must also decrease through trophic amplitude reduction or changes in location on the resources axis (Jacksic, 2001). In reference to the trophic dimension, each species specialists diminishing the number of prey items (amplitude reduction) or changing prey items type (location changes). In this study, a decrease in overlap was observed in three of the four predators during the cold seasons, when preys' availability is expected to be lower. Taking into account this, except for *P. gracilis*, all the other predator species increased their diet richness. The overlap reduction mentioned is a result of displacements on the trophic resources axis (incorporating new items prey by each predator). A similar pattern of diet seasonal variation in relation to prey offer was previously observed in other Uruguayan anuran assemblage (Maneyro, 2000). Additionally, these results may indicate that species trophic behavior has enough plasticity to change along the annual cycle. Then, species could not be located in fixed places, but on a continuos and dynamic one, between generalist and specialist extremes.

ACKNOWLEDGMENTS

We would like to thank D. Nuñez and L. Ziegler for their help during the field work, A. Jauri for logistic support in the study area, M. Arim for their contributions during the course of the study, P. Vaz and M. Loureiro for language corrections. D. E. Naya is supported by a fellowship from PEDECIBA, Uruguay.

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