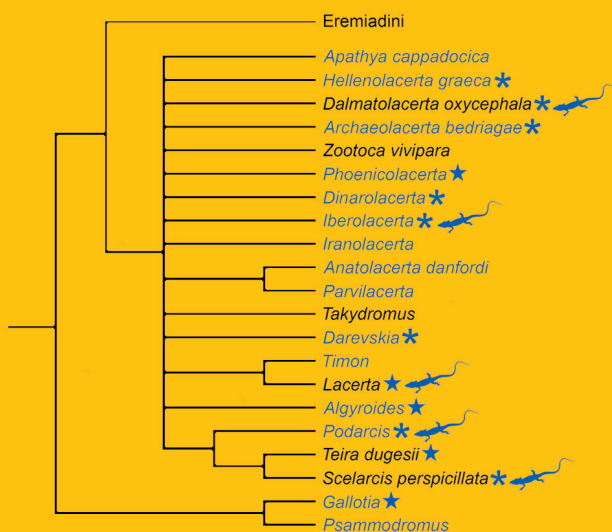


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Diet of anurans captured in forest remnants in southeastern Brazil

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Abstract: In this study we investigated, during one year of sampling, the diet of anurans captured in pitfalls installed in three forest remnants in northwestern São Paulo State, Brazil. Specimens were separated by age (juveniles and adults), and adults were separated according to sex. Of the ten species (231 individuals) captured in pitfalls, three species, *Eupemphix nattereri* (63), *Leptodactylus podicipinus* (50) and *Physalaemus cuvieri* (43), were abundant ($n > 40$). The diet of the species studied was, in general, similar to that reported in other localities in Brazil, suggesting that diet, within the niche breadth of each species, is a conservative characteristic. No difference was found between the diets of juvenile and adult *P. cuvieri*. *L. podicipinus*, a generalist, drastically changed its diet, juveniles consuming mainly small insects (Insecta larvae, Isoptera and Collembola) while adults consumed large insects (Blattodea and Coleoptera). On the other hand, juveniles of *E. nattereri* ate more Formicidae (which are smaller) than adults and adults ate more Isoptera (which are larger) than juveniles. Moreover, *E. nattereri* consumed more prey at the end of the rainy season suggesting that this species accumulates energy reserves to survive the dry season and prepare itself for a period of aestivation or inactivity until the next rainy season.

Key words: ontogeny, open-area anurans, semideciduous forest remnants.

Resumen: Dieta de anuros capturados en bosques remanentes en el sudeste de Brasil. – En el presente estudio se investiga la dieta de anuros en bosques remanentes en la parte noroeste del Estado de São Paulo, Brasil. Los anuros fueron capturados a lo largo de un año en trampas de caída instaladas en tres bosques remanentes. Se capturaron 231 individuos de 10 especies, y fueron separados en clases de edad (juveniles y adultos) y sexo (en el caso de los adultos). La muestra obtenida estuvo dominada por tres especies *Eupemphix nattereri*, *Leptodactylus podicipinus* y *Physalaemus cuvieri* ($n > 40$). La dieta de las especies estudiadas coincide con lo descrito en estudios publicados de otras localidades en Brasil, lo que sugiere que dentro de la amplitud de nicho de cada especie, la dieta es una característica conservadora. La dieta de los juveniles y adultos de *P. cuvieri* no presentó diferencias ontogenéticas. *L. podicipinus*, considerado generalista, mostró diferencias en la dieta, con los juveniles consumiendo principalmente pequeños insectos (larvas, Isoptera y Collembola) mientras que los adultos ingirieron presas de mayor tamaño. Por otra parte, los juveniles de *E. nattereri* consumieron más Formicidae que los ejemplares adultos, los cuales presentaron mayor abundancia de Isoptera (de mayor tamaño que los anteriores) en la dieta. Además, *E. nattereri* consumió una mayor cantidad de presas al final de la temporada de lluvias, lo que sugiere que esta especie acumula reservas de energía para sobrevivir al periodo de sequía pronunciada en la región, y prepararse para estar hasta la próxima temporada de lluvias.

Palabras clave: anuros de zonas abiertas, bosque estacional semi-decuido, ontogenia.

INTRODUCTION

Recent studies of the anuran diet demonstrate that many species show some degree of diet specialization (SIMON & TOFT, 1991; TOFT, 1995; SANTANA & JUNCÁ, 2007), which is contrary to the idea that frogs are opportunistic and generalist in their diet (DUELLMAN & TRUEB, 1986; SANTOS *et al.*, 2004). In a study with an open-area anuran community, ROSSA-FERES (1997) found that the niche overlap of adult anurans was small for most species, and identified three functional groups: species that feed on Isoptera, on Formicidae, and on Diptera and Homoptera.

Although anurans can exist in a habitat with a wide variety of potential food items, their diet is influenced by the size, mobility, palatability, nutritional value, availability, foraging activity and abundance of prey (TOFT, 1980; DUELLMAN & TRUEB, 1986; STEBBINS & COHEN, 1995; LIMA & MAGNUSSON, 1998; POUGH *et al.*, 1998). Information about diet is necessary to understand patterns of life history, population fluctuations and effects of habitat modifications on anurans (TOFT, 1981; BEEBEE, 1996), which vary depending on the population studied, local environmental conditions, and climatic seasonality. For a thorough understanding of a species' diet, both temporal and geographic variation need to be considered. Such data are lacking for most tropical anurans, which precludes generalizations and makes comparative analysis difficult (GARDA *et al.*, 2006).

Despite having the greatest anuran richness in the world, with 825 species (SBH, 2007) and an endemism rate of 64% (IUCN, 2004), few studies provide information about the diet of Brazilian anurans (e.g., ROSSA-FERES, 1997; VAN SLUYS & ROCHA, 1998; RODRIGUES *et al.*,

2004; SANTANA & JUNCÁ, 2007). Thirty-one anuran species have been recorded from northwestern São Paulo State (VIZOTTO, 1967; BERNARDE & KOKUBUM, 1999; ROSSA-FERES & JIM, 2001; VASCONCELOS & ROSSA-FERES, 2005; SANTOS *et al.*, 2007), but only one study (ROSSA-FERES, 1997) describes and analyzes overlap in the diet of these species. Climate in this region is characterized by a pronounced dry season (BARCHA & ARID, 1971; ROSSA-FERES & JIM, 2001), which limits the reproductive period of about 90% of species to the rainy season (ROSSA-FERES & JIM, 2001; VASCONCELOS & ROSSA-FERES, 2005; SANTOS *et al.*, 2007). Inland São Paulo State, southeastern Brazil, is characterized as mesophytic semi-deciduous forest and savanna. In recent decades, this region has undergone an intense process of fragmentation which has reduced the forest area to 4% of its former size (SMA/IF, 2005). According to CUSHMAN (2006), habitat loss and fragmentation are among the biggest threats to world amphibian populations. Most diet studies are conducted by sampling individuals from water bodies during the breeding period. Very little is known about the activities and places occupied by anurans when not breeding, especially those which breed in open areas. SILVA & ROSSA-FERES (2007) verified that anurans of this region may use the forest fragments as daytime shelter, shelter areas during the dry season, and possibly as foraging areas.

In order to understand the influence of the regional climate and the fragmentation process on anuran biology, we analyzed the diet of anurans by employing pitfall sampling in forest remnants. We sought to answer the following questions: which food resources are used by the species? Does diet vary according to sex and age in different species? Does diet vary according to season?

MATERIALS AND METHODS

This study was carried out from November 2004 to August 2005 in Icém (20° 20' 25" S, 49° 11' 52" W), a municipality located in northwestern São Paulo State, southeastern Brazil (Fig. 1). The climate of this region is tropical seasonal (Aw according to Köppen), characterized by two seasons (Fig. 2): the rainy season, between October and March, and a pronounced dry season, between April and September, which receives only 15% of the total annual rainfall (VASCONCELOS & ROSSA-FERES, 2005; SANTOS *et al.*, 2007).

Anurans were caught in pitfall traps in three mesophytic semideciduous forest remnants located in a pasture matrix. Each remnant was 0.4 - 4.6 km from its nearest neighbor (Fig. 1). Forest remnant 1 (FR1) (7 ha) has a stream running through it and a large amount of litter on the soil. It is separated, at its extremes, from two other fragments (2 and 40 ha respectively) by dirt roads 10 and 12 m wide, respectively. Forest remnant 2 (FR2) (1 ha) has many vines and bare soil, and is separated from a larger fragment (67 ha) by a pasture area 20 m wide. Forest remnant 3 (FR3) (2 ha) also has many vines, dry rocky soil and the trees are more widely spaced than in the other remnants. It is separated from two fragments (22 and 6 ha respectively) by a dirt road 8 m wide and a pasture area 40 m wide.



FIGURE 1. Aerial photograph (Google Earth 2007) showing the study area with highlighting in the three forest remnants where pitfalls were installed.

FIGURA 1. Fotografía aérea (Google Earth 2007) del área de estudio, en la que se indican los tres bosques remanentes donde se efectuó el estudio.

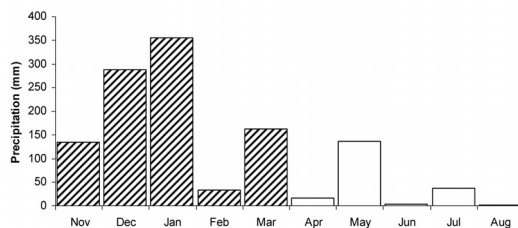


FIGURE 2. Rainfall (mm) in northwestern São Paulo state, Brazil, in the period from November 2004 to August 2005. Rainy season (hatched bars) with total rainfall of 973.7 mm (83.2 %) and dry season (blank bars) with 196.7 mm (16.8 %). FIGURA 2. Precipitación (mm) en el noroeste del estado de São Paulo, Brasil, durante el período comprendido entre noviembre de 2004 y agosto de 2005. Temporada de lluvias (barras rayadas) con precipitación total de 973.7 mm (83.2 %) y estación seca (barras blancas), con 196.7 mm (16.8 %).

In each forest remnant we placed two parallel 20 m long transects of pitfall traps, with 10 m separating the two transects. Every 5 m we buried five plastic buckets (3 L) filled with 10% formaldehyde solution. The farm owners of the study sites did not give permission to install larger buckets (100 L). As a result, we were forced to install 3 L buckets, which are not appropriate for anurans as they can easily jump out of the bucket. On the other hand, the use of formalin paralyzes the digestive process by immediately fixing the stomach's contents, ensuring that they do not contain prey that might have fallen into the buckets. The plastic buckets were checked for anurans once every two weeks from November 2004 to August 2005.

Animals captured in the pitfalls had their stomachs removed through a longitudinal abdominal incision and the contents were preserved in a 70% alcohol solution. Food items were identified to order according to taxonomic keys and characterization as per BUZZI & MIYAZAKI (1993) and COSTA *et al.* (2006).

Of the ten species captured in the pitfalls, only *Eupemphix nattereri*, *Physalaemus cuvieri* and *Leptodactylus podicipinus*

provided a large enough number ($n > 40$) of captured individuals to conduct a comparative analysis of the diet between adults and juveniles. We investigated diet variation between the sexes and age classes (juveniles and adults). Adults were sexed by examination of the external morphology (presence of vocal sac and nuptial spines in males) and the gonads. Adults and juveniles were separated based on examination of the gonads (individuals were considered adults when reproductively mature) and snout-vent length (SVL) (HEYER *et al.*, 1990; ETEROVICK & SAZIMA, 2004; BRASILEIRO *et al.*, 2005; RIBEIRO *et al.*, 2005; SILVA *et al.*, 2008; UETANABARO *et al.*, 2008; CAMPIÃO *et al.*, 2009). The following criteria were used to classify individuals according to age class: juveniles of *E. nattereri* were smaller than 23.0 mm and adults were larger than 29.0 mm; juveniles of *P. cuvieri* were smaller than 18.6 mm and adults larger than 20.7 mm, and juveniles of *L. podicipinus* were smaller than 19.8 mm and adults larger than 21.9 mm. Furthermore, for the study of seasonal variation in the diet of adults and juveniles we considered a rainy season, from November to March (mean monthly rainfall = 194.4 mm) and a dry season, from April to August (mean monthly rainfall = 39.3 mm).

Frequency of occurrence (GELWICK & MATTHEWS, 1996) and dominance (FROST & WENT, 1940) were calculated for each food item. Niche breadth (B_A) was determined by using a standardized Levins index (KREBS, 1999). Food niche overlap (Φ) between sexes and between adults and juveniles of each species was calculated by the symmetrical overlap index (PIANKA, 1973). This index measures the degree to which two species share a number of features, on a scale ranging from zero to one. A zero value indicates that two species are quite dissimilar, while a value of one indicates complete overlap.

The abundance of food items consumed by males, females and juveniles were compared by one-way ANOVA followed by Tukey *a posteriori* tests, with $\alpha = 0.05$. To compare the effects from different seasons (rainy and dry season) on the abundance of food items consumed by males, females and juveniles, we used t-tests. For both analyses, data were \log_{10} transformed for normalization and homogenization of the variances (SOKAL & ROHLF, 1995). Statistical analyses were done with STATSOFT (2004).

Specimens were deposited in the Amphibian Collection (DZSJRP 10093 to 10322) of the Departamento de Zoologia e Botânica, Universidade Estadual Paulista, São Paulo State, Brazil (<http://spling.cria.org.br/manager/detail?resource=DZSJRP-Amphibia-adults&setlang=pt>).

RESULTS

The pitfall traps captured 231 individuals from ten species belonging to four families: Bufonidae, *Rhinella schneideri* (11); Leuperidae, *Eupemphix nattereri* (92), *Physalaemus cuvieri* (59) and *Pseudopaludicola* aff. *falcipes* (5); Leptodactylidae, *Leptodactylus fuscus* (4), *L. labyrinthicus* (1), *L. mystacinus* (2) and *L. podicipinus* (53); Microhylidae, *Dermatonotus muelleri* (3) and *Elachistocleis* sp. (1). Only 173 (74.8%) individuals from seven species had stomach contents. The diet of adult *Leptodactylus podicipinus* was the most varied ($B_A = 0.4$), including invertebrates belonging to 17 taxonomic orders (Table 1), while *Eupemphix nattereri* was the most specialist ($B_A = 0$), having consumed almost exclusively Isoptera (Table 2, Fig. 3), followed by *Physalaemus cuvieri* ($B_A = 0.07$) which had consumed mainly Formicidae (Table 3, Fig. 4).

TABLE 1. Seasonal and ontogenetic variation in the frequency of occurrence (F) and dominance (D) of the food items consumed by males, females and juveniles of *Leptodactylus podicipinus* captured in the pitfalls installed in three forest remnants in northwestern São Paulo state, Brazil, during rainy season (RS) and dry season (DS). Juveniles were not collected in the dry season.

TABLE 1. Variación estacional y ontogenética en la frecuencia de ocurrencia (F) y dominancia (D) de los alimentos consumidos por los machos, hembras y juveniles de *Leptodactylus podicipinus* capturados en las trampas de caídas instaladas en tres bosques remanentes en el noroeste parte del estado de Sao Paulo, Brasil, durante la temporada de lluvias (RS) y la estación seca (DS). No se capturaron juveniles durante la estación seca.

	Males				Females				Juveniles	
	RS (n = 25)		DS (n = 5)		RS (n = 6)		DS (n = 6)		RS (n = 7)	
	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)
Annelida										
Oligochaeta					16.6					
Arthropoda										
Araneida	20	4			33.3		16.6			
Crustacea										
Isopoda	4	4								
Hexapoda										
Blattodea	48	20	80		33.3	16.6	50	33.3		
Collembola	12	4							28.6	
Dermaptera	20									
Lepidoptera							16.6			
Orthoptera	8				16.6					
Odonata	4									
Diptera									14.3	14.3
Coleoptera	48	4	40		33.3		16.6		28.6	14.3
Hemiptera	8				16.6		33.3			
Hymenoptera										
Formicidae	16		40	20	33.3		50	16.6	14.3	14.3
Vespidae	4						16.6			
Isoptera	12		20	20			33.3		28.6	14.3
Plecoptera	4									
Protura							16.6			
Insect larvae	20	4			16.6	16.6			42.8	28.6
Mollusca			20	20						
Richness		14		5		8		9		4
N. ^o of items consumed		60		12		19		19		6
Individual consume		2.4		2.4		3.16		3.16		1.5

Ontogenetic variation

In *Eupemphix nattereri*, the food niche overlap was low between adults and juveniles ($\Phi = 0.32$), but completely overlapped between males and females ($\Phi = 1.00$). Isoptera was the most frequent and dominant item in the diet of males and females of *E. nattereri* (Fig. 3). Compared to the adults, *E.*

nattereri juveniles consumed Formicidae at a higher frequency (100%) and dominance (50%) (Fig. 3). The mean type of prey consumed differed between males (ANOVA: $F_{4,140} = 88.46$, $p < 0.001$), and females (ANOVA: $F_{2,28} = 6.14$, $p < 0.006$) of *E. nattereri* while in juveniles it did not (ANOVA: $F_{2,32} = 2.17$, $p < 0.13$) (Fig. 3).

TABLE 2. Seasonal and ontogenetic variation in the frequency of occurrence (F) and dominance (D) of the food items consumed by males, females and juveniles of *Eupemphix nattereri* captured in the pitfalls installed in three forest remnants in northwestern São Paulo state, Brazil, during rainy season (RS) and dry season (DS). Juveniles were not collected in the dry season.

TABLE 2. Variación estacional y ontogenética en la frecuencia de ocurrencia (F) y dominancia (D) de los alimentos consumidos por los machos, hembras y juveniles de *Eupemphix nattereri* capturados en las trampas de caídas instaladas en tres bosques remanentes en el noroeste parte del estado de Sao Paulo, Brasil, durante la temporada de lluvias (RS) y la estación seca (DS). No se capturaron juveniles durante la estación seca.

	Males				Females				Juveniles	
	RS (n = 30)		DS (n = 6)		RS (n = 11)		DS (n = 3)		RS (n = 8)	
	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)
Arthropoda										
Araneida			16.6		7.1					
Hexapoda										
Collembola									12.5	
Coleoptera	3.3	3.3								
Hymenoptera										
Formicidae	13.3	10	33.3	16.6	14.3				100	50
Isoptera	93.3	86.6	83.3	83.3	100	100	100	100	50	37.5
Richness		3		3		3		1		3
N. ^o of items consumed		1269		550		608		79		54
Individual consume		42.3		91.6		55.3		26.3		6.75

The food niche overlap of *Physalaemus cuvieri* was high for both males and females ($\Phi = 0.87$) and adults and juveniles ($\Phi = 0.81$). Formicidae was the most frequent and dominant food item in the diet of this species (Table 3, Fig. 4). The mean type of prey consumed differed between males (ANOVA: $F_{5,45} = 6.59$, $p < 0.001$), females (ANOVA: $F_{5,45} = 4.44$, $p < 0.002$) and juveniles (ANOVA: $F_{8,152} = 28.3$, $p < 0.001$) of *P. cuvieri* (Fig. 4).

Leptodactylus podicipinus presented the most varied diet and the food niche overlap was lower between adults and juveniles ($\Phi = 0.48$) than between males and females ($\Phi = 0.84$). Blattodea was the most frequent and dominant food item among males (Fig. 5). Blattodea and Formicidae were the most frequent and dominant items among females (Fig. 5), while for juveniles, Insecta larvae were the most frequent and dominant food

items (Fig. 5). The mean types of prey consumed differed between males (ANOVA: $F_{14,435} = 6.43$, $p < 0.001$), but not between females (ANOVA: $F_{13,143} = 1.53$, $p = 0.11$) and juveniles (ANOVA: $F_{5,30} = 0.31$, $p = 0.9$) of *L. podicipinus* (Fig. 5).

Seasonal variation in the diet

Adults of *Eupemphix nattereri* consumed Isoptera, which was the most frequent and dominant item in their diet during the studied period (Table 2). We did not collect juveniles of *E. nattereri* during the dry season. Males (t-test, $t = -0.51$, $df = 34$, $p = 0.61$) and females (t-test, $t = 0.14$, $df = 12$, $p = 0.88$) of *E. nattereri* did not differ in the quantity of prey consumed between rainy and dry seasons (Table 2).

Both adult and juvenile *Physalaemus cuvieri* presented no seasonal diet variation,

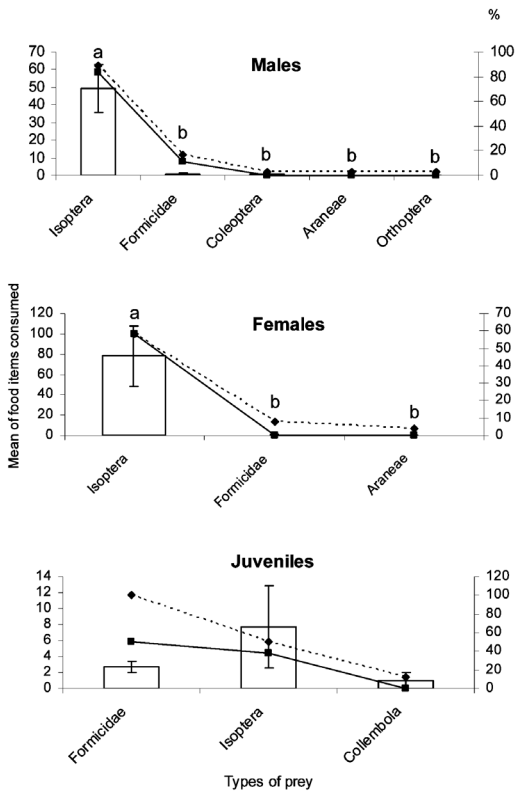


FIGURE 3. Mean consumed, frequency of occurrence (diamonds, dashed line) and dominance (square, continuous line) of the food items found in the stomachs of males ($n = 36$), females ($n = 14$) and juveniles ($n = 8$) of *Eupemphix nattereri* in northwestern São Paulo state, in the period from November 2004 to August 2005. Different letters indicate a difference between mean consumed amounts of types of prey ($p < 0.05$). Error bars = ± 1 SEM.

FIGURA 3. Consumo promedio, frecuencia de ocurrencia (diamantes, línea discontinua) y dominancia (cuadrados, línea continua) de las presas encontradas en estómagos de machos ($n = 36$), hembras ($n = 14$) y juveniles ($n = 8$), de *Eupemphix nattereri* en el noroeste del estado de Sao Paulo, en el período comprendido entre noviembre de 2004 y agosto de 2005. Las diferentes letras indican diferencias significativas entre las medias de los tipos de presa consumidos ($p < 0.05$). Barras de error = ± 1 SEM.

and Formicidae was the dominant food item in their diet during the study period (Table 3). Females consumed a greater abundance of

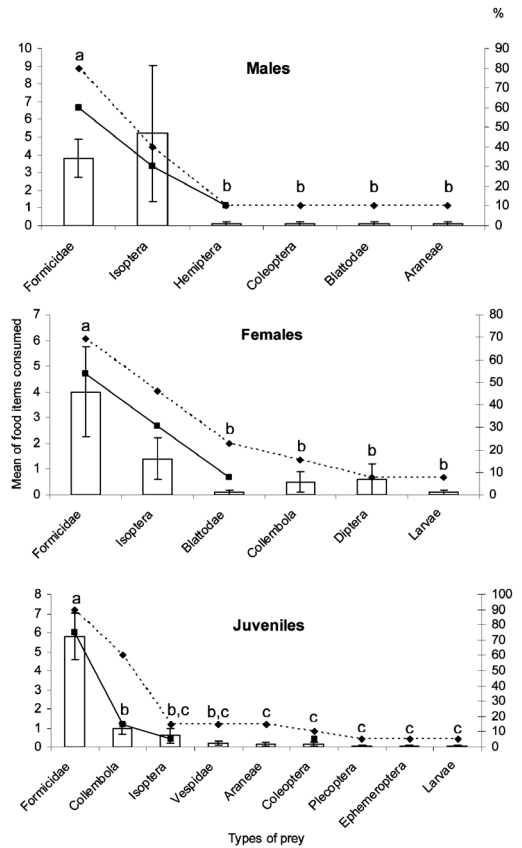


FIGURE 4. Mean consumed, frequency of occurrence (diamonds, dashed line) and dominance (square, continuous line) of the food items found in the stomachs of males ($n = 10$), females ($n = 13$) and juveniles ($n = 20$) of *Physalaemus cuvieri* in northwestern São Paulo state, in the period from November 2004 to August 2005. Different letters indicate a difference between mean consumed amounts of types of prey ($p < 0.05$). Error bars = ± 1 SEM.

FIGURA 4. Consumo promedio (bars ± 1 DE), frecuencia de ocurrencia (diamantes, línea discontinua) y dominancia (cuadrados, línea continua) de las presas encontradas en estómagos de machos ($n = 10$), hembras ($n = 13$) y juveniles ($n = 20$), de *Physalaemus cuvieri* del noroeste del estado de Sao Paulo, en el período comprendido entre noviembre de 2004 y agosto de 2005. Las diferentes letras indican diferencias significativas entre las medias de los tipos de presa consumidos ($p < 0.05$). Barras de error = ± 1 SEM.

food items in the dry season than in the rainy season (t-test: $t = -5.78$, $df = 9.24$, $p < 0.0002$, Table 3), juveniles (t-test, $t = -0.37$, $df = 18$,

TABLE 3. Seasonal and ontogenetic variation in the frequency of occurrence (F) and dominance (D) of the food items consumed by males, females and juveniles of *Physalaemus cuvieri* captured in the pitfalls installed in three forest remnants in northwestern São Paulo state, Brazil, during rainy season (RS) and dry season (DS).

TABLA 3. Variación estacional y ontogenética en la frecuencia de ocurrencia (F) y dominancia (D) de los alimentos consumidos por los machos, hembras y juveniles de *Physalaemus cuvieri* capturados en las trampas de caídas instaladas en tres bosques remanentes en el noroeste parte del estado de Sao Paulo, Brasil, durante la temporada de lluvias (RS) y la estación seca (DS).

	Males				Females				Juveniles			
	RS (n = 8)		DS (n = 2)		RS (n = 5)		DS (n = 7)		RS (n = 15)		DS (n = 5)	
	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)	F (%)	D (%)
Arthropoda												
Araneida			50						20			
Hexapoda												
Blattodea	13				20	20	28.6					
Collembola					20		14.3		60	13.3	60	
Ephemeroptera									6.6			
Diptera							14.3		6.6			
Coleoptera	13								6.6	6.6	20	
Hemiptera	13	13										
Hymenoptera												
Formicidae	75	63	100	50	60	40	71.4	57.1	86.6	66.6	100	100
Vespidae									13.3		20	
Isoptera	38	25	50	50	20	20	71.4	42.8	20	6.6		
Plecoptera									6.6			
Insect larvae							14.3		13.3			
Richness	5		3		4		6		10		4	
N.º of items consumed	45		49		7		79		124		36	
Individual consume	5.6		24.5		1.4		11.3		8.3		7.2	

$p = 0.7$) did not differ in the abundance of items consumed between the seasons and males did not have enough samples for analyses (Table 3).

In the rainy season, Blattodea and Coleoptera were the most frequent item in the diet of males and Insecta larvae in the diet of juveniles of *L. podicipinus*. Blattodea and Formicidae were the most frequent and dominant food items in the diet of females during the study period (Table 1). The abundance of consumed items in the different seasons did not differ in males (t-test, $t = -0.2$, $df = 20$, $p = 0.83$) and females (t-test, $t = 0.3$, $df = 10$, $p = 0.76$, Table 1). Juveniles were not collected in the dry season.

DISCUSSION

The diet of the species studied was, in general, similar to that reported in other localities in Brazil (MOREIRA & BARRETO, 1996; ROSSA-FERES, 1997; VAN SLUYS & ROCHA, 1998; RODRIGUES *et al.*, 2004, SANTOS *et al.*, 2004), suggesting that diet, within the niche breadth of each species, is a conservative characteristic. Of the three abundant species studied, *Physalaemus cuvieri* and *Eupemphix nattereri* were diet specialists, consuming mainly Formicidae and Isoptera respectively. *Leptodactylus podicipinus* was a generalist, consuming a greater variety of food items. Our results are

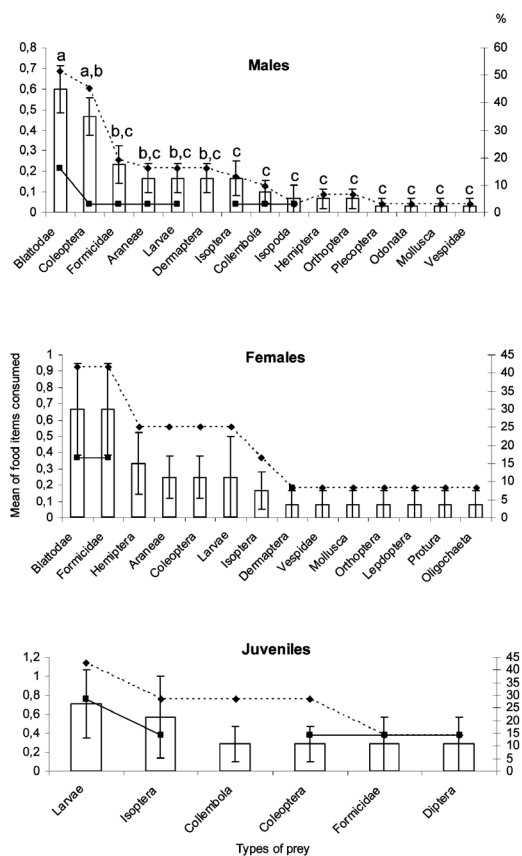


FIGURE 5. Mean consumed, frequency of occurrence (diamonds, dashed line) and dominance (square, continuous line) of the food items found in the stomachs of males ($n = 31$), females ($n = 12$) and juveniles ($n = 7$) of *Leptodactylus podicipinus* in northwestern São Paulo state, in the period from November 2004 to August 2005. Different letters indicate a difference between mean consumed amounts of types of prey ($p < 0.05$). Error bars = ± 1 SEM.

FIGURA 5. Consumo promedio, frecuencia de ocurrencia (diamantes, línea discontinua) y dominancia (cuadrados, línea continua) de las presas encontradas en estómagos de machos ($n = 31$), hembras ($n = 12$) y juveniles ($n = 7$), de *Leptodactylus podicipinus* del noroeste del estado de Sao Paulo, en el período comprendido entre noviembre de 2004 y agosto de 2005. Las diferentes letras indican diferencias significativas entre las medias de los tipos de presa consumidos ($p < 0.05$). Barras de error = ± 1 SEM.

in agreement with the hypothesis that specialization should be found in species that feed on constant or abundant resources (PYKE, 1984).

SILVA & ROSSA-FERES (2007) observed an individual of *Leptodactylus podicipinus* eating an individual of Blattodea in an artificial shelter installed in forest remnants, suggesting that forest remnants are important areas for foraging. GOEHRING *et al.* (2002), in a study of the distribution of arthropods in forests and agricultural areas in Costa Rica, found that insects of four orders (Blattaria, Coleptera, Diptera and Orthoptera) were more abundant in forest remnants than in agricultural landscapes. In this study, *Leptodactylus podicipinus* consumed mainly insects belonging to these taxonomic groups, suggesting that it may use the fragments as areas for foraging.

Variation in diet during ontogeny is often as great or greater than differences among species (LIMA & MAGNUSSON, 1998), mainly due to the increase in size of the anuran and prey type consumed (WOOLBRIGHT & STEWART, 1987; LIMA & MOREIRA, 1993; RIBEIRO, 2006). Ontogenetic diet changes have been observed in *Eleutherodactylus johnstonei* (OVASKA, 1991), *Anomaloglossus stepheni* (LIMA & MOREIRA, 1993), *Rhinella marina* (EVANS & LAMPOS, 1996), *Xenopus fraseri* (DE BRYUN *et al.*, 1996) and *Proceratophrys boiei* (GIARETTA *et al.*, 1998). In our study, the generalist *L. podicipinus* underwent a drastic ontogenetic diet change: juveniles consumed mainly small insects (Insecta larvae, Isoptera and Collembola), while adults consumed large insects (Blattodea and Coleoptera). On the other hand, juvenile *E. nattereri* ate more Formicidae (which are smaller) and adults ate more Isoptera (which are larger). Factors such as foraging method (DUELLMAN & TRUEB, 1986), changes in the type of substrate (TOFT, 1980), efficiency of capture, and seasonal variation in the composition and abundance of prey (GALATTI, 1992; STEBBINS & COHEN, 1995), could explain the occurrence of

ontogenetic changes in the diet of these frogs (RODRIGUES *et al.*, 2004).

In natural assemblages of amphibians, food competition appears to be an unusual event, which plays a minor, or insignificant, role in the structure and dynamics of the assemblage (KUZMIN, 1995; MENIN *et al.*, 2005). Therefore, a high niche overlap index between males and females does not necessarily indicate competition, because if resources are not in short supply, two organisms can share them without detriment to one another (PIANKA, 1974). The species analyzed in the present study feed mainly on constant or abundant resources; for that reason, we believe that the low values of niche overlap found between adults and juveniles of *E. nattereri* and *L. podicipinus* are probably more influenced by the prey size that juveniles can eat than by competition between adults and juveniles or with juveniles of other species. Other studies have found low overlap in food resource use among anurans (CARAMASCHI, 1981; ROSSA-FERES, 1997; SANTANA & JUNCÁ, 2007) and this low overlap seems to be a consequence of a prevalence of species with specialized food habits. In this study, *E. nattereri* and *P. cuvieri* were specialists while *L. podicipinus* was a generalist. Therefore, in agreement with previous studies, the prevalence of specialist species may be a major factor contributing to the low niche overlap between species.

The reduction in the number of prey items found in anuran stomachs during the dry season is probably due to a reduction in foraging during this period of the year (SILVA & ROSSA-FERES, 2007). *Eupemphix nattereri* females and juveniles consumed a greater number of prey items at the end of the rainy season. Therefore, the end of the rainy season seems to be the period when this species consumes the greatest quantity of food, accumulating reserves of energy to survive during the dry season, which

is pronounced in the region, and preparing for a period of aestivation or inactivity until the next rainy season.

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