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Seasonal and ontogenetic variation in diet composition of *Leptodactylus podicipinus* (Anura, Leptodactylidae) in the southern Pantanal, Brazil

DOMINGOS DE J. RODRIGUES,[1] MASAO UETANABARO [1] & CYNTHIA P.A. PRADO,[1, 2]

[1] *Departamento de Biologia, Universidade Federal de Mato Grosso do Sul, Caixa Postal 549, 79070-900, Campo Grande, MS, Brazil (e-mail: poxo@inpa.gov.br)*

[2] *Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil*

Abstract: The foraging strategies of amphibians allow them to capture a wide variety of prey, diet variation being generally associated with morphological, physiological, and behavioral traits that facilitate the location, identification, and digestion of food items. Herein we present the diet composition of *L. podicipinus* and variations regarding the number and type of prey consumed by juveniles, males and females during the wet and dry seasons, in the southern Pantanal, Brazil. Sampling was conducted at three different times during the dry season, and three different times during the wet season between June 1998 and May 1999. The quantitative analysis showed that the diet of *L. podicipinus* is composed mainly by Coleoptera (51.0%), Hymenoptera (9.1%), Diptera (8.7%), Aranae (5.3%), and Orthoptera (4.7%). In the wet season, males captured more prey than juveniles and females, but in the dry season there were no differences. Males and females ingested larger prey compared to juveniles. The frog *L. podicipinus* is an opportunist and generalist predator, and the availability of prey in the environment may be an important factor determining its diet composition in the Pantanal.

Key words: diet, *Leptodactylus podicipinus*, ontogenetic diet shift, Pantanal, seasonality.

Resumen: Variación estacional y ontogenética en la composición de la dieta de *Leptodactylus podicipinus* (Anura, Leptodactylidae) en el sur del Pantanal, Brasil. – Las estrategias de forrajeo de los anfibios les permiten capturar una amplia variedad de presas, y las variaciones en su dieta están en general relacionadas con caracteres morfológicos, fisiológicos y de comportamiento que les facilitan la localización, identificación y digestión del alimento. Aquí presentamos datos sobre la composición de la dieta en *L. podicipinus* y las variaciones en el número y tipo de presas que consumen los juveniles, los machos y las hembras durante las estaciones seca y húmeda en el sur del Pantanal, Brasil. Se obtuvieron muestras en tres momentos distintos durante la estación seca y otros tres durnate la estación húmeda entre junio de 1998 y mayo de 1999. El análisis cuantitativo demostró que la dieta de *L. podicipinus* está compuesta fundamentalmente por Coleoptera (51.0%), Hymenoptera (9.1%), Diptera (8.7%), Aranae (5.3%) y Orthoptera (4.7%). Durante la estación húmeda, los machos capturaron más presas que los juveniles y que las hembras, pero no se observaron diferencias durante la estación seca. Los machos y las hembras ingirieron presas de mayor tamaño que los juveniles. La rana *L. podicipinus* es un depredador oportunista y generalista, y la disponibilidad de presas en su ambiente puede ser un factor determinante de la composición de su dieta en el Pantanal.

Palabras clave: cambio ontogenético de dieta, dieta, estacionalidad, *Leptodactylus podicipinus*, Pantanal.

INTRODUCTION

The foraging strategies of amphibians allow them to capture a wide variety of prey (STEBBINS & COHEN, 1995). Studies on the diet of anurans through the analysis of stomach contents demonstrate that most species feed on arthropods, being considered generalists (e.g. TOFT, 1980b; WERNER *et al.*, 1995; VAN SLUYS & ROCHA, 1998). Nevertheless, some species consume small vertebrates (DUELLMAN & TRUEB, 1986), whereas others are considered herbivores (e.g. SILVA *et al.*, 1989; DAS, 1996). In general, their diet is associated with morphological, physiological, and behavioral traits that facilitate the location, identification, and digestion of food items (e.g. MEDDEB & CHENITI, 1998; CALDWELL & VITT, 1999; BELLOCQ *et al.*, 2000).

Most amphibians are generalists and opportunists, and prey availability is the dominant factor determining their diet, along with the constraints provided by the prey/predator size relationship (e.g. MACNAMARA, 1977; POUGH *et al.*, 1998). There are, however, some species of amphibians that can be considered specialists, selecting the prey items to be consumed (e.g. LIEBERMAN, 1986; SIMON & TOFT, 1991; DAS, 1996).

Generally, anurans are classified into two groups depending on the foraging strategy adopted (e.g. TOFT, 1981; STRÜSSMANN *et al.*, 1984; LIMA & MOREIRA, 1993): widely foragers, and sit-and-wait foragers. Active foragers usually feed on small, aggregated prey (ants and termites), and are considered specialists, whereas the sedentary foragers feed upon larger prey, and have a more generalist and opportunistic diet (LIMA & MOREIRA, 1993).

Variation in the diet of anurans also occurs due to ontogenetic changes (POUGH *et al.*, 1998), mainly regarding the type and size of prey (e.g. WOOLBRIGHT & STEWART, 1987; WIGGINS, 1992; LIMA & MOREIRA, 1993). The mechanisms responsible for this ontogenetic variation have not yet been elucidated, but an important part of the differences regarding type and size of prey chosen by adult amphibians when compared to juveniles reflects changes in foraging methods (e.g. TOFT, 1981; OVASKA, 1991), as well as changes in predator size (e.g. STRÜSSMANN *et al.*, 1984; LIMA & MOREIRA, 1993).

The Pantanal is a floodplain that possesses a variable precipitation regime, leading to a regular cycle of rising and lowering of the water level (LOURIVAL *et al.*, 2000). The annual floods allow some lotic habitats to mix regularly, while some microhabitats remain isolated for up to 50-100 years, developing peculiar characteristics until a great flood mixes them again. This makes the Pantanal an ideal region for conducting research on diets, especially associated to the variations on the availability of prey related to the local seasonality.

Studies on anuran diets in the Pantanal are nonexistent, and the few studies that do exist refer to preliminary species lists, taxonomic comments, and studies on the biology and reproductive strategies (e.g. PRADO & UETANABARO, 2000; PRADO *et al.*, 2000, 2002; STRÜSSMANN *et al.*, 2000). *Leptodactylus podicipinus* is a nocturnal, medium-sized frog, widely distributed in open formations of Brazil, Bolivia, Paraguay and Argentina (HEYER, 1994), and is very common at the study site. Reproduction occurs throughout the year in the southern Pantanal, associated with the margins of permanent and temporary lagoons, where the males build small depressions destined for egg-laying (PRADO *et al.*, 2002). The present work studied the diet composition of *L. podicipinus* in the southern Pantanal, State of Mato Grosso do Sul, Brazil,

and analyzed the variation in size and number of prey consumed by juveniles, males, and females. These comparisons took into account the seasonal climate of the region, considering the dry and wet seasons separately.

MATERIALS AND METHODS

Study area

The Pantanal can be divided into at least 10 different subregions, each with its own physiognomy resulting from a unique interaction of edaphic, hydrological, and biogeographical factors (LOURIVAL *et al*., 2000). Herein we follow ADÁMOLI (1982), who proposed 10 subregions for the Pantanal: Cáceres, Poconé, Barão de Melgaço, Paiaguás, Nhecolândia, Aquidauna, Paraguai, Miranda, Nabileque, and Abobral. According to TARIFA (1986), the mean monthly temperatures range from 19.9ºC (July) to 27.4ºC (December), with frequent chills reaching 10ºC that last 2-3 days, usually between April and September. Rainfall is considered low in the region, with an annual mean of 972 mm. Floods are common between January and April, and are not related to local rainfall but are associated with reduced drainage (AMARAL FILHO, 1986). The plant cover of the site is represented by native grassy fields, semideciduous forest patches ("capões" and "cordilheiras"), riparian forests, and monospecific formations of *Tabebuia aurea* ("paratudal"; Bignoniaceae) or *Copernicia australis* ("carandazal"; Palmae).

Data collection

The study was conducted in the Pantanal of Abobral, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19º 34' S, 57º 00' W). Individuals were captured at the margins of water bodies, flooded fields, and "borrowing boxes" (depressions formed by soil removal for construction purposes).

Three samples were obtained during the dry season (September, October and November 1999) and three during the wet season (June and July 1998, and May 1999). Collecting always started two hours after sunset, and was done with the aid of an electric flashlight. Collecting effort of 2h remained constant. Specimens were collected at random, fixed in 10% formalin while still in the field for immediate cessation of digestion, and later preserved in 70% ethanol. The material was deposited in the Coleção Zoológica of the Universidade Federal de Mato Grosso do Sul.

The snout-vent length (SVL) of individuals was measured with precision calipers to the nearest 0.1 mm. For the study of diet variation, specimens were separated in classes: juveniles, males and females. Due to sexual size dimorphism (PRADO *et al.*, 2000), males smaller than 26 mm and females smaller than 32 mm were considered as juveniles. Adults were sexed by examination of the external morphology (presence of vocal sacs and nuptial spines in males) and gonads.

Stomachs were removed through a longitudinal abdominal incision and preserved in 70% ethanol. Stomach contents were analyzed separately for sex and size classes under a stereomicroscope. Items were quantified, measured (length) with precision calipers, and identified up to Order level. We tested for variations in number and size of prey between seasons (dry / wet) and size classes (juvenile, male, and female) using a two way ANOVA ($\alpha = 0.05$). If differences were detected by ANOVA, a Tukey test was then conducted. The number and size of prey per stomach were log-transformed in order to homogenize the variances.

RESULTS

Of 189 stomachs analyzed, 155 contained food items, while only 34 were empty (19 juveniles and 15 adults). Food items in an advanced stage of digestion were found in 31 stomachs and were not identified. The mean SVL of juveniles was 22.4 ± 4.4 mm (N = 81; range = 11.5-31.8), that of males was 32.2 ± 3.4 mm (N = 55; range = 26.0-39.0), and females averaged 38.0 ± 3.7 mm (N = 53; range = 32.0-47.0). The quantitative analysis of the diet of *L. podicipinus* revealed that it was composed mainly by arthropods (Table 1). The most frequent prey group was Coleoptera (51%), followed by Hymenoptera (9.1%), Diptera (8.7%), Aranae (5.3%), and Orthoptera (4.7%; Fig. 1). Chilopoda (3), Diplopoda (1), Isopoda (1), Lepidoptera (1), Mollusca (1), and Odonata larvae (2) occurred in low frequencies in the stomachs analyzed.

The number of prey consumed by *L. podicipinus* differed significantly among size classes (ANOVA: $F_{2,158} = 3.51$, p = 0.030). There was a significant interaction between period and size classes (ANOVA: $F_{2,158} = 3.33$, p = 0.039), but there were no significant differences between periods (ANOVA: $F_{1,158} = 0.72$, p = 0.39). Males consumed, on average, more items than females (Tukey = 0.318, p = 0.031) and juveniles (Tukey = 0.271, p = 0.022; Fig. 2) during the wet season (Table 2).

Prey size also differed among size classes (ANOVA: $F_{2,120} = 10.86$, p < 0.001), but there were no significant differences between periods (ANOVA: $F_{1,120} = 2.231$, p = 0.001). Females consumed larger prey items than juveniles in the dry season (Tukey = 0.517, p = 0.003), and in the wet season males and females consumed larger items than juveniles (Tukey = 0.467, p = 0.010 and Tukey = 0.575, p = 0.000, respectively; Fig. 3).

TABLE 1. Total occurrence (TO) and frequency (Fr) of prey items recorded (phylum, class and order) in the stomachs of *L. podicipinus* in the southern Pantanal during dry and wet seasons. N = nymphs, L = larvae.

TABLA 1. Ocurrencia total (TO) y frecuencia (Fr) de las presas registradas (phylum, clase y orden) en los estómagos de *L. podicipinus* en el sur del Pantanal durante las estaciones seca y húmeda. N = ninfas, L = larvas.

	Dry	Wet	TO	Fr (%)
Annelida				
Oligochaeta	1	1	2	0.41
Arthropoda				
Arachnida				
Acarina	1	–	1	0.20
Araneida	10	16	26	5.30
Crustacea				
Decapoda	12	–	12	2.45
Isopoda	1	–	1	0.20
Insecta				
Blattodea	5	–	5	1.01
Blattodea (N)	1	–	1	0.20
Dermaptera	3	–	3	0.62
Dermaptera (N)	–	1	1	0.20
Ephemeroptera	–	1	1	0.20
Lepidoptera	1	–	1	0.20
Lepidoptera (L)	9	2	11	2.20
Orthoptera	13	10	23	4.65
Orthoptera (N)	2	–	2	0.41
Odonata (L)	–	2	2	0.41
Diptera	16	27	43	8.70
Coleoptera	127	125	252	51.00
Coleoptera (L)	4	3	7	1.41
Hemiptera	4	3	7	1.41
Homoptera	4	8	12	2.41
Hymenoptera	26	19	45	9.10
Miriapoda				
Diplopoda	1	–	1	0.20
Chilopoda	2	1	3	0.61
Mollusca	–	1	1	0.20
Undetermined	24	7	31	6.30
Total			494	100

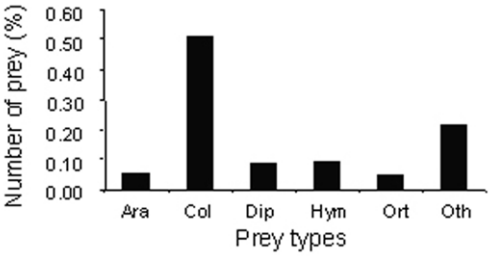

FIGURE 1. Number of prey items (%) in the diet of *L. podicipinus* in the southern Pantanal, Brazil. Ara: Aranae, Col: Coleoptera, Dip: Diptera, Hym: Hymenoptera, Ort: Orthoptera, Oth: other.

FIGURA 1. Número de presas (%) en la dieta de *L. podicipinus* en el sur del Pantanal, Brasil. Ara: Aranae, Col: Coleoptera, Dip: Diptera, Hym: Hymenoptera, Ort: Orthoptera, Oth: otras.

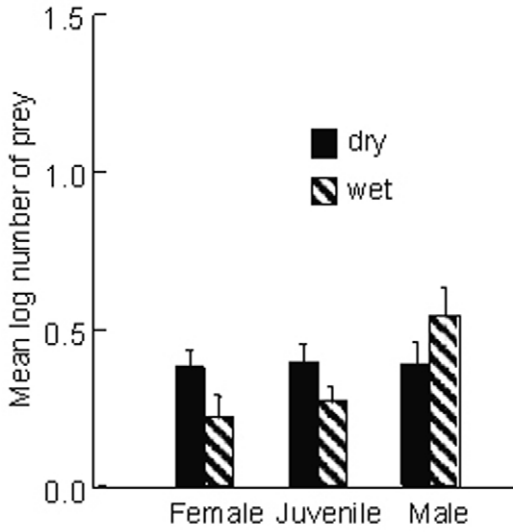

FIGURE 2. Mean ± SE of log of number of prey by stomach consumed by juveniles (63), females (49), and males (46) of *L. podicipinus* during the dry and wet seasons in the southern Pantanal, Brazil.

FIGURA 2. Media ± SE del logaritmo del número de presas por estómago ingeridas por juveniles (63), hembras (49), y machos (46) de *L. podicipinus* durante las estaciones seca y húmeda en el sur del Pantanal, Brasil.

Coleoptera appeared in larger quantities in the stomachs during both seasons (Table 1). However, some food items, such as mites, crustaceans, diplopods, and isopods, appeared in only one season (Table 1). Ingestion of plant material and sand was also recorded.

DISCUSSION

Leptodactylids are considered sit-and-wait generalist predators, and thus more efficient in the capture of prey such as Orthoptera and Coleoptera (e.g. TOFT, 1980a, 1981; PERRY *et al.*, 1990; LIMA & MOREIRA, 1993; POUGH *et al.*, 1998). In the present study, *Leptodactylus podicipinus* seems to be a generalist predator, because its diet is composed by different food items, mainly arthropods. GALATTI (1992) and TOFT (1981, 1995) showed that consumption of some prey types by *L. pentadactylus* and *Epipedobates femoralis* was directly proportional to their availability in the environment, which could explain the large occurrence of Coleoptera in the diet of *L. podicipinus*. This order is the most abundant among the insects and is easily found in almost all habitats (BORROR & DELONG, 1969). The ingestion of large fleshy items, such as larvae of Odonata (27 mm) and Lepidoptera (27 mm), likewise suggests opportunism in *L. podicipinus*. However, since we did not estimate the availability of prey in the environment, and considering that more than 50% of the diet of *L. podicipinus* was composed by Coleoptera, we should be cautious in stating that this species is totally generalist. The results obtained could be due to prey selection, or could be due to behavior and microhabitat use (mainly lagoon margins) facilitating the encounter with this type of prey.

Ontogenetic changes in the diet of anurans occur regarding type and size of prey, mainly due to an increase in predator size (e.g. STRÜSSMANN *et al.*, 1984; WOOLBRIGHT &

TABLE 2. Mean ± SE number of prey and prey size in the stomachs of *L. podicipinus* during dry and wet seasons in the southern Pantanal, Brazil. N = number of stomachs analyzed.

TABLA 2. Media ± SE del número y tamaño de las presas en los estómagos de *L. podicipinus* durante las estaciones seca y húmeda en el sur del Pantanal, Brasil. N = número de estómagos analizados.

	Number of prey				Prey size			
	Dry		Wet		Dry		Wet	
	N	$\bar{x}$ ± SE	N	$\bar{x}$ ± SE	N	$\bar{x}$ ± SE	N	$\bar{x}$ ± SE
Females	33	3.30 ± 0.62	16	2.00 ± 0.34	29	6.69 ± 0.61	11	5.55 ± 0.76
Males	26	3.35 ± 0.58	20	5.15 ± 1.08	20	5.85 ± 0.61	17	5.12 ± 0.46
Juveniles	24	2.96 ± 0.33	39	2.41 ± 0.38	18	4.33 ± 0.86	25	3.76 ± 0.33

STEWART, 1987; OVASKA, 1991; WIGGINS, 1992; LIMA & MOREIRA, 1993). BRYUN *et al.* (1996) observed ontogenetic changes in type and size of prey of *Xenopus fraseri*, and such changes were also observed in *Colostethus stepheni* (LIMA & MOREIRA, 1993) and *Eleutherodactylus johnstoni* (OVASKA, 1991). TOFT (1981), studying the foraging method of anurans in Panama and Peru, noted that body size is highly correlated with prey size in 20 species of litter frogs. WOOLBRIGHT & STEWART (1987), studying *Eleutherodactylus coqui,* and DONNELY (1991), studying *Dendrobates pumilio*, found the same relationship. VAN SLUYS *et al.* (2001) found a significant positive relationship between mouth size and number of prey consumed by the litter frog *Zachaenus parvulus* in the Atlantic Forest, southeastern Brazil. Ontogenetic changes were also observed for *L. podicipinus* in the present study, since males and females consumed more and larger prey than juveniles. However, other factors such as the foraging method adopted (DUELMANN & TRUEB, 1986), change of substrate (TOFT, 1980b), capture efficiency, and seasonal variation in composition and abundance of prey (DONELLY, 1991; STEBBINS & COHEN, 1995) could also explain the occurrence of ontogenetic changes in anuran diets.

Females of *L. podicipinus* were larger than males, which is common in anurans (CRUMP, 1974; SHINE, 1979). However, females did not consume larger prey or in greater amounts than males and, in contrast, males of *L. podicipinus* consumed more prey during the

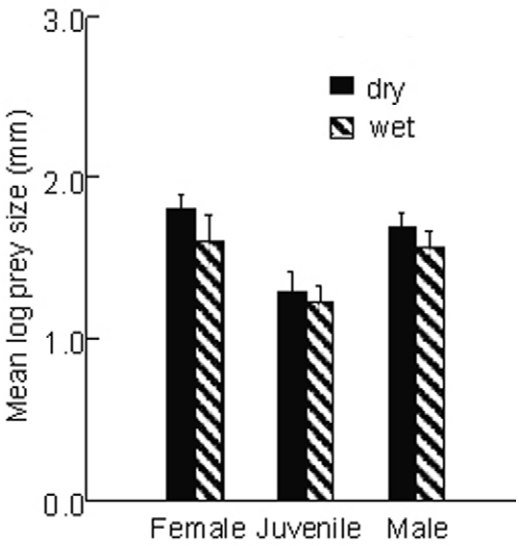

FIGURE 3. Mean ± SE of log of prey size by stomach consumed by juveniles (43), females (37), and males (40) of *L. podicipinus* during the dry and wet seasons in the southern Pantanal, Brazil.

FIGURA 3. Media ± SE del logaritmo del tamaño de las presas por estómago ingeridas por juveniles (43), hembras (37), y machos (40) de *L. podicipinus* durante las estaciones seca y húmeda en el sur del Pantanal, Brasil.

wet season. Possibly, the differences recorded herein may be related to the behavior of *L. podicipinus*, particularly reproduction and habitat use as was observed for the myobratrachid *Adelotus brevis* (KATSIKAROS & SHINE, 1997). Peak breeding activity in *L. podicipinus* occurs in the wet season, and females exhibit parental care of eggs and tadpoles (PRADO *et al.*, 2000, 2002), probably reducing the time available for foraging. Another consequence of the maternal care of tadpoles is that males and guarding females occupy different portions of the water bodies, which may also explain divergences in food consumption; females are often in places deeper than males, the latter occurring mainly in the margins (C.P.A. Prado, unpublished data). Furthermore, gravid females may also be restricted in their prey consumption due to lack of free space in the abdomen, which becomes almost totally filled by the ovaries. Finally, it is possible that during the wet season, when an increase in prey availability is expected, males feed more, stocking up energy to continue reproducing during the dry season.

Various prey items exhibited low capture rates, some due to their behavior, others due to their life cycle which limits their availability to one period of the year, and others were considered accidental ingestions. One moth was found as a prey item in the diet of *L. podicipinus.* Even though they are nocturnal, lepidopterans are not frequently found in stomach contents of amphibians, probably due to their rapid movements and flight (BLACKITH & SPEIGHT, 1974). The Acarina item, represented by a sole small mite, was considered an accidental ingestion. Herbivory has been documented for some anuran species, such as *Xenohyla truncata* (referred as *Hyla truncata* by SILVA *et al.*, 1989), *Rana hexadactyla* (DAS, 1996), and *Zachaenus parvulus* (VAN SLUYS *et al.*, 2001). The occurrence of plant material in the stomachs of *L. podicipinus* was also considered accidental ingestion, as in *Bufo marinus* (EVANS & LAMPO, 1996).

GALATTI (1992) stated that the consumption of prey items is directly related to their availability. In this study, differences in the wet and dry seasons were observed concerning prey types consumed. Some prey types were captured during the wet season (Diplopoda, Mollusca, Dermaptera nymphs, Odonata larvae), while others during the dry season (Blattodea and Orthoptera nymphs). Since the Pantanal exhibits an unpredictable seasonal climate, which can influence the availability of certain prey items, seasonal variations are expected to occur in the organisms diets, as observed for *L. podicipinus* in the Pantanal in the present study.

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