HERPETOLOGICAL JOURNAL, Vol. 16, pp. 387-394 (2006)

TROPHIC, REPRODUCTIVE AND PARASITOLOGICAL ASPECTS OF THE ECOLOGY OF *LEPTODACTYLUS CHAQUENSIS* (ANURA: LEPTODACTYLIDAE) IN ARGENTINA

EDUARDO F. SCHAEFER, MONIKA I. HAMANN, ARTURO I. KEHR, CYNTHYA E. GONZÁLEZ AND MARTA I. DURÉ

CECOAL-CONICET, C.C. 140, (3400) Corrientes, Argentina

We studied the trophic and reproductive ecology and document the helminth fauna of the Cei's white-lipped frog, *Leptodactylus chaquensis*, from north-eastern Argentina. This frog is a generalist predator, using an intermediate strategy between active foraging and sit and wait predation. The diet consisted of 17 types of prey and was dominated numerically and volumetrically by coleopterans. The number of mature ova per female (ovarian complement) ranged from 3113 to 16234, and the ovum diameter varied from 0.4 to 1.2 mm. The testes mass ranged from 0.32 to 1.54 g, and the species has an explosive reproductive pattern. The parasite fauna was rich, consisting of 20 species of helminths (twelve trematodes, one cestodes, six nematodes and one acanthocephalan), the kidneys, lungs and large intestine being the organs most infected. The trophic niche breadth and the habitats where this species is living structured the parasite community.

Key words: diet, frog, helminths, parasites, reproduction

INTRODUCTION

The Argentinean members of the *Leptodactylus ocellatus* group are represented by *L. ocellatus* (Linnaeus, 1758) and *L. chaquensis* Cei, 1950. Both species are sympatric in the Argentinean provinces of Corrientes, Entre Ríos and Santa Fé (Cei, 1980). In Corrientes Province, both species are syntopic. The distribution area of *L. chaquensis* in South America encompasses northern Argentina, eastern Bolivia, Paraguay, northern Uruguay, and Brazil (Mato Grosso do Sul) (Frost, 2004). *Leptodactylus ocellatus* has been studied mainly because of its complex reproductive behaviour (Vaz-Ferreira & Gerhau, 1975, 1986), while Gallardo (1964) and Basso (1990) gave data about the adult diet for several Argentinean populations.

Until now, the diet and trophic patterns of Argentinean *L. chaquensis* have never been studied. Some reproductive characteristics of populations from north-western Argentina were analyzed by Perotti (1994, 1997). The parasitic helminths of this frog have been poorly studied with some parasitic nematodes recorded for Paraguayan populations (Baker, 1987). The helminths of the Argentinian populations are unknown.

The main goals of this study of an Argentinian population of *Leptodactylus chaquensis*, were: (1) to describe its diet, the width of its trophic niche and its foraging pattern; (2) to analyse its reproductive characteristics (ovum diameter and ovum numbers); and (3) to determine the number of helminth taxa infecting this frog under natural conditions.

Correspondence: E. F. Schafer, CECOAL-CONICET, C.C. 140, (3400) Corrientes, Argentina. *E-mail*: eclschaefer247@yahoo.com.ar

MATERIALS AND METHODS

The study area was demarcated by a maximum distance of approximately 40 km towards the east and south of the city of Corrientes (27º 30' S, 58º 45' W), while the Paraná River defined its western and northern limits. Data were collected monthly from 1996 to 2004. Adults of *L. chaquensis* were hand-captured preferentially between 1800 to 2300 hours, using the sampling technique defined as "visual encounters survey" (Crump & Scott Jr., 1994). Data were collected monthly from 1996 to 2004, with a minimum of two samples per month in the field. The study area is characterized by its wide variety of habitats, including numerous temporary, semipermanent and permanent ponds. The predominant vegetation is the forest, with herbaceous strata composed of grasses, numerous cacti and terrestrial bromeliads.

Specimens for diet and reproductive study were captured, humanely euthanased and fixed in 10% formalin and deposited in the Centro de Ecología del Litoral (CECOAL-CONICET) collection. For the parasitological study, a separate sample of frogs was kept alive until needed for later analysis.

TROPHIC STUDY

Sex (determined by examination of gonads and external nuptial features), body length (mm), and maximum mouth width (mm) were recorded for each individual. Diets were analyzed by removing the complete alimentary canal, as recommended by Schoener (1989). We only included prey that had at least 70% of their body undigested. Prey items were identified to the order level using the keys of Brewer & Arguello (1980) and Coronado Padilla & Márquez Delgado (1978). The number of prey items per stomach for each prey category and the individual volume of each prey item were recorded. All measurements were taken with caliper to the nearest 0.1 mm. The volume of each prey item was estimated using the formula for an ellipsoid (Dunham, 1983; Duré & Kehr, 2004). The diversity index used was the Shannon index (*H*') (Shannon & Weaver, 1949) using decimal logarithm (log_{10}). The niche breadth was calculated using Levins' index (Levins, 1968). We also calculated the standardized niche breadth by expressing it on a scale from 0 to 1. Hurlbert (1978) suggest the following measure for standardized niche breadth, where B_A = Levin's standardized niche breadth; *B* = Levins's measure of niche breadth; and *n*= number of food items.

Parametric and non-parametric tests were used in order to establish the relationship between the predator morphology and the prey volume (Kehr, 1994; Zar, 1996).

Reproductive Study

The morphometric variables considered for both sexes were: snout-vent length (SVL) (mm), body mass (g) and net weight (g) (total body mass without gonad mass) (for females only; Prado *et al*., 2000). The reproductive variables recorded for each individual were: ovary mass, mature ova number (ovarian complement), mature ovum diameter, mature ovum coloration and testes weight, coloration and form. All variables were registered on individuals fixed in formaldehyde (10.0%). Body length and ovum diameter (estimated from 100 randomly selected mature ova/female) were determined to the nearest 0.1 mm by caliper. Body and testes mass was measured in the laboratory after the individuals were blotted to remove excess liquid. For that an electronic balance to the nearest 0.01 g was used. Male maturity was determined by testes size and presence of nuptial excrescences. The maturity of the ova was determined by degree of pigmentation (Crump, 1974; Basso, 1990; Perotti, 1994, 1997). Once the ovarian complement for each female had been recorded, 100 mature ova were selected randomly to obtain the mean ovum diameter. The reproductive effort (RE) for both sexes was measured as a percentage of mature gonad mass relative to body mass (Kuramoto, 1978; Perotti, 1994, 1997; Prado *et al*., 2000). Net weight of female and male body (total body mass without gonad mass) was used for correlation and comparative analysis.

Parasitological Study

Frogs were transported to the laboratory, humanely ethanased and their snout-vent length (SVL) and weight recorded. At necropsy, hosts were sexed and the alimentary canal, lungs, liver, gall bladder, kidneys, body cavity, musculature, integument and brain examined for parasites by dissection. Helminths were observed *in vivo*, counted and killed in hot distilled water before being fixed in 70% ethyl alcohol. Digeneans, cestodes and acanthocephalans were stained with carmine hydrochloride, cleared in creosote and mounted in Canada balsam. Nematodes were cleared in glycerin or lactophenol and examined as temporary mounts. The systematic determination of the helminth was carried out following the approaches given by Anderson (2000), Anderson *et al*. (1974), Baker (1987), Gibson *et al*. (2002) and Yamaguti (1961; 1963; 1971; 1973). The infection prevalence, intensity and abundance were calculated according to Bush *et al*. (1997). Parasite community analysis was determined from richness, abundance, diversity (Shannon index, *H´*) (Shannon & Weaver, 1949) and evenness ($J' = H' / H'_{max}$) (Pielou, 1966; Zar, 1996). All indices were used with decimal logarithms (log_{10}). Chi-square test with Yates' correction for continuity was used for sex proportion comparisons.

RESULTS

Trophic Study

Fifty-seven individuals with identifiable stomach content (37 males and 20 females; 56.0% of all animals captured) were collected during two periods, January 1998 to May 1999 and January 2002 to August 2003.

The diet consisted of 17 types of prey (Table 1) and was dominated numerically (24.9%) and volumetrically (24.80%) by coleopterans. The orthopterans were also important volumetrically (22.0%). Coleopterans were the most frequently represented prey in 30 individuals (53.0% of adults). Other numerically important items were Formicidae, Araneida and Orthoptera. Prey diversity was 0.94. Niche breadth was 6.63 and the standardized niche breadth was 0.35.

Leptodactylus chaquensis showed a positive and significant relatonship between body length and mouth width (ln *y* = -1.33 + 1.03 ln *x*, *n*=57, *r*=0.91, $F_{1,55}$ =274.0; *P*<0.0001). Another positive and significant relationship was observed between mouth width and the mean prey volume by stomach (ln *y* = -6.41 + 3.71 ln *x*, *n*=57, *r*=0.40; $F_{1,55}$=10.3, *P*=0.002).

No relationship was found between the body length and the number of prey found in stomachs (ln *y* = -0.25 + 0.28 ln *x*, *n*=57, *r*=0.06, $F_{1,55}$=0.20, *P*=0.65).

Reproductive Study

Reproductive characteristics of *L. chaquensis* were determined from thirty five individuals captured during the breeding season between 1996 and 2003 (fourteen females and twenty one males). Thirteen gravid females were collected during the following seasons and year: seven during spring (October and November), five in summer (January and February), and one in autumn (April). Twenty one mature males were collected in the following seasons and year: sixteen during spring (September-December), and five in summer (January and February). All meristic and reproductive data are summarized in Table 2. For females, no significant correlation was found between body length and ovarian complement (r_s=0.41, *n*=13, *P*=0.17), ovary mass

TABLE 1. Types of prey in the diet of *Leptodactylus chaquensis* (*n*=57) from Corrientes, Argentina. Volume in mm^3; Freq.: number of frogs eaten each prey.

Prey type	Number	%	Volume (mm^3)	%	Frequency
INSECTA					
Coleoptera	46	24.9	4806.9	24.8	30
Hemiptera	13	7.0	3276.5	16.9	11
Hymenoptera (Formicidae)	30	16.2	302.5	1.6	20
Hymenoptera (No Formicidae)	3	1.6	72.6	0.4	3
Diptera	2	1.1	6.3	0.03	2
Homoptera	9	4.9	346.1	1.8	7
Orthoptera	12	6.5	4271.8	22.0	9
Odonata	2	1.1	250.3	1.3	2
Phasmantodea	3	1.6	774.0	4.0	3
Mantodea	1	0.5	5.1	0.03	1
Dictioptera	2	1.1	2478.9	12.8	2
Insect larvae	22	11.9	1363.3	7.0	14
ARACHNIDA					
Araneida	35	18.9	1015.1	5.2	16
Phalangida	1	0.5	24.2	0.1	1
MOLLUSCA					
Gastropoda	1	0.5	20.6	0.1	1
MYRIAPODA					
Diplopoda	2	1.1	194.0	1.0	2
CRUSTACEAE					
Decapoda	1	0.5	171.6	0.9	1
TOTAL	185	100.0	19375.1	100.0	

(r_s=0.32, *n*=13, *P*=0.30) or reproductive effort (r_s=0.02, *n*=13, *P*=0.94). For males, a significant correlation was observed between body mass (net weight) and testis mass (r_s=0.64, *n*=21, *P*<0.01), but not between body mass (net weight) and reproductive effort (RE) (r_s=-0.19, *n*=21, *P*>0.05). A significant positive correlation was also found between body length and testes mass (r_s=0.55, *n*=21, *P*<0.05) , but not between body length and reproductive effort (r_s=-0.26, *n*=21, *P*>0.05).

No significant differences were observed between sexes for body length and body mass (net weight) (body length: Mann-Whitney *U*-test = 117, *P*=0.31, n_1=14, n_2=21); (body mass: Mann-Whitney *U*-test = 163, *P*=0.59, n_1=14, n_2=21).

Each ovum was half dark grey or black and half white. The testes were white and bean-shaped.

The adults showed preferences for either humid or dry earth, and were also found in mud, near the shore of temporary, semipermanent and permanent ponds, and in flooded high grass (approximately 1m high). Foam nests containing eggs, were observed partially hidden among the flooded vegetation, in areas with water deeper than 20 cm.

TABLE 2. Mean ± SD body length (SVL); body mass (BM); net body mass (total body mass - gonad mass) (NBM); ovarian complement (OC, total mature ova count number per female); gonad mass (GM); reproductive effort (RE, percentage of gonad mass relative to net body mass) and ova diameter (OD), for females and males of *Leptodactylus chaquensis* from Corrientes, Argentina. Range and sample size in parentheses.

Variables	Females	Males
SVL (mm)	65.3±7.82 (54.80-81.50; *n*=14)	62.9±5.43 (54.50-75.17; *n*=21)
BM (g)	33.9±11.31 (19.53-62.11; *n*=14)	33.9±10.43 (16.01-54.17; *n*=21)
NBM (g)	30.6±9.62 (18.41-52.24; *n*=13)	33.0±10.16 (15.56-52.63; *n*=21)
OC	4401.2±2231.10 (750-7812; *n*=13)	—
GM (g)	3.4±2.47 (0.90-9.87; *n*=13)	0.90±0.39 (0.32-1.94; *n*=21)
RE (%)	10.7±5.74 (3.35-20.62; *n*=13)	2.8±0.86 (1.00-4.41; *n*=21)
OD (mm)	0.8±0.14 (0.40-1.20; *n*=1100)	—

TABLE 3. Summary of helminth taxa, number of parasites prevalence (%), mean abundance, mean intensity, stage and site of infection in *Leptodactylus chaquensis* from Corrientes, Argentina. Number of collection is cited below each taxa.

Helminths	No.	%	Mean abundance	Mean intensity (min-max)	Stage in frog	Site of infection
TREMATODA						
Haematoloechus longiplexus CECOAL 03111804	92	40.0	2.04±3.77	6.38 (1-23)	Adult	Lung
Gorgoderina parvicava CECOAL 03032702	29	20.0	0.64±1.99	3.22 (1-12)	Adult	Urinary bladder
Glypthelmins repandum CECOAL 03032704	49	27.0	1.08±2.39	4.08 (1-9)	Adult	Small intestine
Glypthelmins palmipedis CECOAL 03042807	70	62.0	1.55±2.22	2.50 (1-10)	Adult	Small intestine
Catadiscus sp. CECOAL 01032802	160	58.0	3.55±6.98	6.15 (1-39)	Adult	Large intestine
Travtrema sp. CECOAL 03012905	34	24.0	0.75±2.24	3.09 (1-13)	Metacerc.	Muscle, mesenteries, body cavity , pharyngeal zone
Bursotrema sp. CECOAL 03051607	3331	69.0	74.02±297.60	107.45 (1-2000)	Metacerc.	Kidney
Strigeidae gen. sp. 1 CECOAL 03052702	15	9.0	0.33±1.55	3.75 (1-10)	Metacerc.	Body cavity
Strigeidae gen. sp. 2 CECOAL 03042806	13	2.0	0.02±0.14	13	Metacerc.	Liver
Diplostomidae gen. sp. CECOAL 03042804	3	4.0	5.15±33.97	1.50 (1-2)	Metacerc.	Body cavity
Plagiorchiata gen. sp. 1 CECOAL 03012105	41	13.0	0.91±3.85	6.83 (1-24)	Metacerc.	Muscle mesenteries, body cavity pharyngeal zone
Plagiorchiata gen. sp. 2 CECOAL 03051605	53	7.0	1.17±6.51	17.66 (1-43)	Metacerc.	Kidney, muscle
NEMATODA						
Cosmocerca podicipinus CECOAL 03012903	81	62.0	1.80±2.58	2.89 (1-12)	Adult	Lung, large intestine
Cosmocerca parva CECOAL 03031001	10	7.0	0.22±0.95	3.33 (1-5)	Adult	Large intestine
Aplectana delirae CECOAL 03092418	2	2.0	0.04±0.29	2	Adult	Large intestine
Aplectana sp. CECOAL 02112902	5	2.0	0.11±0.74	5	Adult	Large intestine
Porrocoecum sp. CECOAL 03092418	1	2.0	0.02±0.14	1	Larvae	Serous of stomach
Camallanus sp. CECOAL 03042804	1	2.0	0.02±0.14	1	Larvae	Small intestine
ACANTHOCEPHALA						
Centrorhynchus sp. CECOAL 03012105	11	16.0	0.24±0.64	1.57 (1-3)	Larvae	Serous of stomach, mesenteries
CESTODA						
Unidentified metacestodes CECOAL 03041001	13	2.0	0.28±1.93	13		Larvae mesenteries

Parasitological Study

A total of 45 frogs were captured between 2001 and 2003. Five were collected between March and June 2001; four between September and November 2002 and 36 between January and November 2003. Parasite prevalence was 100% in both sexes and there was no significant difference between females (26) and males (19) (χ^2 with Yates correction for continuity = 1.11, df=1, P>0.05).

The component community consisted of twenty helminth parasite taxa (larvae and adults), including twelve trematodes, one cestode, six nematodes and one acanthocephalan. The prevalence, mean abundance and intensity, minimum and maximum parasite numbers, stage and localization are detailed in Table 3. Helminth species diversity (H' = 0. 38) and evenness (J' = 0.29) were low with few species being well represented. The mean helminth species richness was 4.56±1.85 (maximum = 8) species per frog infected. Multiple species infections were common with 1, 2, 3, 4, 5, 6, 7 and 8 species occurring in 4, 3, 4, 10, 10, 7, 5 and 2 individuals respectively of *L. chaquensis*.

Of all metacercaria found in different organs, the most common taxon (with a prevalence > 50.0%) was *Bursotrema* sp. (located in the kidney). The adult trematodes recorded in the small intestine (*Glypthelmins palmipedis*), in the large intestine (*Catadiscus* sp.) and in the lungs (*Haematoloechus longiplexus*) presented an infection prevalence >40%. The nematodes (*Cosmocerca podicipinus*) found in the large intestine and in the lungs presented an infection prevalence >50%. Cestodes and acanthocephalans presented infection prevalence <20%.

DISCUSSION

Trophic Characteristics

According to the type and prey proportion, *L. chaquensis* appears to be a generalist with a foraging strategy considered as intermediate between a pure sit-and-wait and an actively foraging predator. The prey of a conventional sit-and-wait predator are active, the encounter rate with prey is low, niche breadth is wide, and the sensory mode is visual (Perry & Pianka, 1997; Duré & Kehr, 2004). Coleopterans and hymenopterans (ants) were important prey for this species. They are relatively mobile prey. Nevertheless, *L. chaquensis* also selected relatively sedentary prey (insect larvae and spiders), which suggests a change from sit-and-wait behavior to actively foraging. The same behaviour was observed in *Leptodactylus latinasus* and *L. bufonius* (Duré & Kehr, 2004). Our results indicate that as the mouth size of *L. chaquensis* increases (proportionally to body size) they consume larger prey items (> volume). On the other hand, the largest frogs did not show an increase in the number of prey items ingested. Similar results on diet composition have been reported by Duré (1999).

Basso (1990) also recorded coleopterans (mobile prey) and insect larvae (sedentary prey) as the most important prey items for the sister species *L. ocellatus* in an Argentinian population, and Maneyro *et al.* (2004) also recorded coleopterans, arachnids and larvae as important items in the diet of *L. ocellatus* in Uruguay. The number of the prey items was also similar between the two species. Presumably, the foraging strategy of *L. ocellatus* is similar to that observed in *L. chaquensis* in being intermediate between sit and wait and an actively foraging, depending of availability of prey.

Leptodactylus chaquensis behaves as a non-selective predator, which optimizes the ingestion of nutrients by consuming increasingly larger volume prey as their mouth width increases. Nevertheless, when only small prey are available, they are ingested in large numbers, independently of frog body size.

Reproductive Ecology

Reproduction in *L. chaquensis* occurs between October and February. Within this period, reproduction can be considered to be explosive and dependent on the amount of rainfall. This means that breeding activity is intense for one or more days, with the synchronous arrival of both sexes at the breeding sites (Wells, 1977). Our results are consistent with those reported by Prado *et al*. (2005), who classified the reproductive mode of *L. chaquensis* from the southern Pantanal (Brazil) as number 8 (i.e., with foam nest and exotrophic tadpoles in lenitic waters) and the reproductive activity pattern as explosive. Prado *et al.* (2002) also classified the reproductive mode of this species as mode 1 (similar definition to mode 8 described above).

The mean reproductive effort of females (RE = 10.70±5.74%.) was lower than that recorded by Prado *et al.* (2000) and Prado & Haddad (2005) in populations from the Pantanal (Brazil). The reproductive effort of males (RE = 2.78±0.86%.) was also lower than in the Pantanal (4.13% - Prado & Haddad, 2003). The testis mass relative to body mass in species of the family Leptodactylidae ranges from 0.04 to 4.13%, with the testes of *L. chaquensis* (4.13%) and *L. podicipinus* (0.75%) being larger than those of other leptodactylids from the Pantanal (Prado & Haddad, 2003).

Leptodactylus chaquensis, *Chiromantis xerampelina* and *Rhacophorus arboreus* have much larger testes than other anuran species, including rhacophorids and leptodactylids (Prado & Haddad, 2003). *Leptodactylus chaquensis*, *L. macrosternum* and *L. ocellatus*, all belong to the ''*ocellatus*'' group (Heyer, 1969), and deposit their eggs in foam nests on the water surface. Testis size does not appear to be related to the species group, at least in the ''*ocellatus*'' group, with *L. chaquensis* exhibiting a much greater testis mass than the other two species from the same group.

Recently, Prado & Haddad (2003) reported multimale spawning in *L. chaquensis*. In species having external fertilization, the strategies available to males to increase their fertilization success include: (1) increasing the number of sperms released and (2) maintaining their proximity to females (Gross, 1985; Jennions &

Passmore, 1993). Therefore, selection would favour males with high sperm production, and hence with large testes (Jennions & Passmore, 1993). Large testes size in frogs with multimale spawning supports the sperm competition hypothesis.

PARASITES

Of all the helminth groups, trematodes with an aquatic life cycle presented a high species richness, both as adult and larval stages. They were primarily represented by the metacercariae of *Bursotrema* sp., which had the greatest infection intensity and prevalence. Our results are similar to those reported by Duré *et al.* (2004) for *Pseudopaludicola boliviana*, captured in the same area. It must be pointed out that both hosts (*L. chaquensis* and *P. boliviana*) use the same microhabitat, along the edge of water bodies, which favours their infection with these metacercariae. The highest occurrence (> 40.0%) among adult trematodes corresponded to species found in the lungs (*H. longiplexus*), small intestine (*G. palmipedis*), and in the large intestine (*Catadiscus* sp.), all of them with indirect life cycles. For *H. longiplexus*, hosts acquire infection by feeding on aquatic and terrestrial insects. These possible intermediate hosts (e. g. Odonata and other insect larvae) were part of the diet of *L. chaquensis*. For *G. palmipedis* and *Catadiscus* sp., amphibians become infected when they ingest their own skin or eat other frogs (Grabda-Kazubska, 1976; Smyth & Smyth, 1980). The life cycle of *Catadiscus* species are unknown, but in general it may resemble that of other amphibian paramphistomes (e.g. genus *Megalodiscus*), their metacercariae encyst on the frog's skin (Smyth & Smyth, 1980). G*lypthelmins palmipedis* may resemble the life cycle of *G. quieta*, their metacercariae encysting in the skin of tadpoles and frogs (Leigh, 1946).

Nematodes with terrestrial and direct life cycles were the second most abundant group of helminths, *C. podicipinus* being the dominant species. Their larvae penetrate the skin of the host and, after migrating to the lungs to complete their development, they are located in the large intestine (Anderson, 2000). On the other hand, *L. chaquensis* was found to be the paratenic host of *Centrorhynchus* sp. (cystacanths), birds being their definitive host (e.g., falconiformes, strigiformes). The possible intermediary hosts of this taxon (i.e., coleopterans and orthopterans) were predominant food items of *L. chaquensis* (infection prevalence 16.0 %).

As a generalisation, terrestrial frogs are more infected with nematodes (Bolek & Coggins, 2000; 2003) and aquatic amphibians are more commonly infected with trematodes (Hamann & Kehr, 1998; 1999; McAlpine & Burt, 1998; Kehr *et al.*, 2000; Bolek & Coggins, 2001; Muzzall *et al.*, 2001; Kehr & Hamann, 2003; Hamann, 2004). The data suggest that *L. chaquensis* show a wide variation in the helminths they harbour, acquiring helminths characteristic of both aquatic and terrestrial frogs, due to habitat variability or feeding strategy, or to both factors.

ACKNOWLEDGEMENTS

This project was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas – CONICET – from Argentina, through grants PIP 2766 and 2945 to A.I. Kehr and M.I. Hamann respectively.

REFERENCES

Anderson, R. C. (2000). *Nematode Parasites of Vertebrates: Their Development and Transmission*. Wallingford, Oxon: CABI Publishing.

Anderson, R. C., Chabaud, A. G. & Willmont, S. (1974). *CIH. Keys the nematodes parasites of vertebrates*. Farnham Royal: Common Wealth Agricultural Bureaux.

Baker, M. R. (1987). Synopsis of the nematoda parasitic in amphibians and reptiles. *Occasional Papers in Biology University of Guelph, Canada* **11**, 1–325.

Basso, N. G. (1990). Estrategias adaptativas en una comunidad subtropical de anuros. *Cuadernos de Herpetología A.H.A., Serie Monografías* **1**, 1–72.

Bolek, M. G. & Coggins, J. R. (2000). Seasonal occurrence and community structure of helminth parasites from the eastern American toad, *Bufo americanus americanus*, from southeastern Wisconsin, U.S.A. *Comparative Parasitology* **67**, 202–209.

Bolek, M. G. & Coggins, J. R. (2001). Seasonal occurrence and community structure of helminth parasites in green frogs, *Rana clamintans melanota*, from southeastern Wisconsin, U.S.A. *Comparative Parasitology* **68**, 164–172.

Bolek, M. G. & Coggins, J. R. (2003). Helminth community structure of sympatric eastern American toad, *Bufo americanus*, northern leopard frog, *Rana pipiens*, and blue-spotted salamander, *Ambystoma laterale*, from southeastern Wisconsin. *Journal of Parasitology* **89**, 673–680.

Brewer, M. & Arguello, N. (1980). Guía ilustrada de insectos comunes de la Argentina. *Miscelanea Nº 67. Fundación Miguel Lillo 131*.

Bush, A. J., Lafferty, K. D., Lotz, J. M. & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.

Cei, J. M. (1980). Amphibians of Argentina. *Monitore Zoologico Italiano (N.S.). Monografías* **2**, XII.

Coronado Padilla, R. & Márquez Delgado, A. (1978). *Introducción a la entomología – morfología y taxonomía de los insectos*. México: Editorial Limusa.

Crump, M. L. (1974). Reproductive strategies in a tropical anuran community. *Miscellaneous Publication of Museum of Natural History, University of Kansas* **61**, 1–68.

Crump, M. L. & Scott Jr., N. J. (1994). Visual Encounter Surveys. In *Measuring and Monitoring Biological Diversity – standard methods for amphibians*, 84–91. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek & M. S. Foster (Eds.). Washington: Washington Smithsonian Institution Press.

Dunham, A. E. (1983). Realized niche overlap, resource abundance and intensity of interspecific competition. In: *Lizard Ecology*, 261–280. Huey D., Pianka E. R. and Schoener, T. W. (Eds.). Massachussetts: Harvard University Press.

Duré, M. I. (1999). *Leptodactylus chaquensis* (NCN). Diet. *Herpetological Review* **30,** 92.

Duré, M. I. & Kehr, A. I. (2004). Influence of microhábitat on the trophic ecology of two leptodactylids from northeastern Argentina. *Herpetologica* **60,** 295–603.

Duré, M. I., Schaefer, E. F., Hamann, M. I. & Kehr, A. I. (2004). Consideraciones ecológicas sobre la dieta, reproducción y el parasitismo de *Pseudopaludicola boliviana* (Anura: Leptodactylidae) de Corrientes, Argentina. *Phyllomedusa* **3,** 121–131.

Frost, D. R. (2004). *Amphibian Species of the World: an Online Reference*. Version 3.0 (22 August, 2004). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Gallardo, J. M. (1964). *Anfibios de los alrededores de Buenos Aires*. Buenos Aires: Editorial Universitaria de Buenos Aires.

Gibson, D. I., Jones, A. & Bray, R. A. (2002). *Keys niche overlap, resource abundance and intensity of interspecific competition to the Trematoda*. London: CABI Publishing & The Natural History Museum.

Grabda-Kazubska, B. (1976). Abbreviation of the life cycles of plagiorchid trematodes. General remarks. *Acta Parasitologica Polonica* **24**, 125–141.

Gross, M. R. (1985). Disruptive selection for alternative life histories in salmon. *Nature* **313**, 47–48.

Hamann, M. I. (2004). Seasonal maturation of *Catadiscus propinquus* (Digenea: Diplodiscidae) in *Lysapsus limellus* (Anura: Pseudidae) from an Argentinean subtropical permanent pond. *Physis* **59,** 29–36.

Hamann, M. I. & Kehr, A. I. (1998). Variación espacio temporal en infrapoblaciones de helmintos y su relación con las fluctuaciones poblacionales de *Hyla nana* (Anura, Hylidae). *Cuadernos de Herpetología. A.H.A.* **12,** 23–33.

Hamann, M. I. & Kehr, A. I. (1999). Populational dynamics and ecological relationships between *Glypthelmins vitellinophilum* Dobbin, 1958 (Trematoda, Macroderoididae) and the host *Lysapsus limellus* Cope, 1882 (Anura, Pseudidae) in a semipermanent pond of Argentina. *Physis* **57**, 17–24.

Heyer, W. R. (1969). The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia: Leptodactylidae). *Evolution* **23**, 421–428.

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77.

Jennions, M. D. & Passmore, N. I. (1993). Sperm competition in frogs: testis size and a “sterile male” experiment on *Chiromantis xerampelina* (Rhacophoridae). *Biological Journal of the Linnean Society* **50,** 211–220.

Kehr, A. I. (1994). Usos y abusos de las correlaciones en biología. *Cuadernos de Herpetología. A.H.A.* **8**, 225–228.

Kehr, A. I., Manly, B. F. J. & Hamann, M. I. (2000). Coexistence of helminth species in *Lysapsus limellus* (Anura: Pseudidae) from an Argentinean subtropical area: influence of biotic and abiotic factors. *Oecologia* **125**, 549–558. DOI 10.1007/s004420000480.

Kehr, A. I. & Hamann, M. I. (2003). Ecological aspects of parasitism in the tadpole of *Pseudis paradoxa* from Argentina. *Herpetological Review* **34,** 336–341.

Kuramoto, M. (1978). Correlations of quantitative parameters of fecundity in amphibians. *Evolution* **32**, 287–296.

Leigh, W. H. (1946). Experimental study on the life cycle of *Glypthelmins quieta* (Stafford, 1900), a trematode of frogs. *American Midland Naturalist* **35**, 460–483.

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. New Jersey: Princeton University Press.

Maneyro, R., Naya, D. E., da Rosa, I., Canavero, A. & Camargo, A. (2004). Diet of the South American frog *Leptodactylus ocellatus* (Anura, Leptodactylidae) in Uruguay. *Iheringia (Zoologia)* **94**, 57–61.

McAlpine, D. F. & Burt, D. B. (1998). Helminths of Bullfrogs, *Rana catesbeiana*, Green frogs, *R. clamitans*, and Leopard frogs, *R. pipiens* in New Brunswick. *Canadian Field-Naturalist* **112**, 50–68.

Muzzall, P. M., Gillillant, M. G, Summer, C. S. & Mehne, C. J. (2001). Helminth communities of green frogs *Rana clamitans* Latreille, from southwestern Michigan. *Journal of Parasitology* **87**, 962–968.

Perotti, M. G. (1994). Aportes preliminares sobre la reproducción en una comunidad de anuros chaqueños en Argentina. *Cuadernos de Herpetología A.H.A.* **8,** 39–50.

Perotti, M. G. (1997). Modos reproductivos y variables reproductivas cuantitativas de un ensamble de anuros del Chaco semiárido, Salta, Argentina. *Revista Chilena de Historia Natural* **70**, 277–288.

Perry, G & Pianka, E. R. (1997). Animal foraging: past, present and future. *Trends in Ecology & Evolution* **12**, 360–363.

Pielou, E. C. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13,** 131–144.

Prado, C. P. A. & Haddad, C. F. B. (2003). Testes size in Leptodactylid frogs and occurrence of multimale spawning in the genus *Leptodactylus* in Brazil. *Journal of Herpetology* **37**, 354–362.

Prado, C. P. A. & Haddad, C. F. B. (2005). Size-fecundity relationships and reproductive investment in female frogs in the Pantanal, south-western Brazil. *Herpetological Journal* **15,** 181–189.

Prado, C. P. A., Uetanabaro, M. & Haddad, C. F. B. (2002). Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of the reproductive specialization toward terrestriality in the genus. *Copeia* **2002**, 1128–1133.

Prado, C. P. A., Uetanabaro, M. & Haddad, C. F. B. (2005). Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia* **26,** 211–221.

Prado, C. P. A., Uetanabaro, M. & Lopes, F. S. (2000). Reproductive strategies of *Leptodactylus chaquensis* and *L. podicipinus* in the Pantanal, Brazil. *Journal of Herpetology* **34,** 135–139.

Schoener, T. W. (1989). Should hindgut contents be included in lizard dietary compilations? *Journal of Herpetology* **23,** 455–458.

Shannon, C. E. & Weaver, W. (1949). *The mathematical theory of communication*. Urbana: Illinois Press

Smyth, J. D. & Smyth, M. M. (1980). *Frogs as host-parasite systems. I. An introduction to parasitology through the parasites of Rana temporaria, R. esculenta and R. pipiens*. New York: MacMillan.

Vaz-Ferreira, R. & Gerhau, A. (1975). Comportamiento epimelético de la rana común *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae) I. Atención de la cría y actividades alimentarias y agresivas relacionadas. *Physis* **34,** 1–14.

Vaz-Ferreira, R. & Gerhau, A. (1986). *Comportamiento de los renacuajos gregarios de Leptodactylus ocellatus.* Montevideo: Dirección General de Extensión Universitaria, División Publicaciones y Ediciones.

Wells, K. D. (1977). The social behavior of anuran amphibians. *Animal Behaviour* **25,** 666–693.

Yamaguti, S. (1961). *Systema Heminthum. The Nematodes of Vertebrate. 3.* New York: Interscience.

Yamaguti, S. (1963). *Systema Heminthum. The Acantocephala of Vertebrates. 5.* New York: Interscience.

Yamaguti, S. (1971). *Synopsis of the Digenetic Trematodes of Vertebrates. 1.* Tokyo: Keigaku Publishing Company.

Yamaguti, S. (1973). *A Synoptical Review of life histories of Digenetic of Trematodes of Vertebrates.* Tokyo: Keigaku Publishing Company.

Zar, J. H. (1996). *Biostatistical Analysis*. New Jersey: Prentice Hall.

Accepted: 13.3.06