PARASITE AND REPRODUCTIVE FEATURES OF *Scinax nasicus* (Anura: Hylidae) FROM A SOUTH AMERICAN SUBTROPICAL AREA

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SUMMARY

From February 2002 to December 2004, the helminth parasite fauna and reproductive features of the frog Scinax nasicus *were studied from Corrientes city, Province of Corrientes, Argentina. The parasite richness was 15 species of helminths (larval and adult) including trematodes (73%), nematodes (20%) and acanthocephalans (7%).* Opisthogonimus *sp. showed the highest prevalence (41%). The definitive hosts of these larval trematodes are probably snakes;* S. nasicus *acts as second intermediate host, and become infected by direct penetration of cercariae. The number of mature ova per female ranged from 413 to 3922, and the mean mature ovum diameter was 0.76 ±0.17mm. This species has a prolonged reproductive pattern.*

PARÁSITOS DE *Scinax nasicus* (Anura: Hylidae) DE UN ÁREA SUBTROPICAL DE AMÉRICA DEL SUR Y SUS RASGOS REPRODUCTIVOS

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RESUMEN

Desde febrero de 2002 a diciembre de 2004, se analizó la fauna de helmintos parásitos y las características reproductivas de Scinax nasicus *en un área cercana a la ciudad de Corrientes, Argentina. La fauna de parásitos helmintos estuvo conformada por 15 especies de helmintos (larvas y adultos) incluyendo trematodes (73%), nematodes (20%) y acantocéfalos (7%). La especie* Opisthogonimus *sp. presentó la mayor prevalencia (41%) de infección. Los hospedadores definitivos de esta metacercaria son probablemente las serpientes.* Scinax nasicus*, interviene como segundo hospedador intermediario, infectándose por la penetración directa de cercarias. El número de óvulos maduros por hembra (complemento ovárico) osciló entre 413-3922, mientras que el diámetro medio de los óvulos fue de 0,76 ±0,17mm. Esta especie posee un patrón reproductivo prolongado.*

Introduction

The genus *Scinax* is distributed from eastern and nouthern Mexico to Argentina and Uruguay, as well as in Trinidad and Tobago, and St. Lucia (Frost, 2007). *Scinax nasicus* can be found in Paraguay, Northern Argentina (provinces of Corrientes, Córdoba, Chaco, Formosa, Entre Ríos, Jujuy, Salta, Santa Fe, Santiago del Estero, Tucumán, Misiones and Buenos Aires), Uruguay (Artigas, Paysandú, Río Negro and Salto), eastern Bolivia (Beni, Chuquisaca, Santa Cruz, Tarija), and southwestern Brazil to Rio Grande do Sul State, being found up to 1000masl (Lavilla *et al*., 2000, Frost, 2007).

In the province of Corrientes, Argentina, *S. nasicus* is very abundant, and its conservation status is "not threatened" (equivalent to "Least Concern for Red List Category") according to Lavilla *et al.* (2000). In contrast, Uruguayan populations are listed as "threatened" by Maneyro and Langone (2001). This species of *Scinax* lives in sympatry with *S. acuminatus*, occurs in forests, shrublands and grasslands, and is very well adapted to anthropogenic areas (Duré 1999, 2004, Schaefer, 2007).

The presence of the nematode genus *Gyrinicola* (Pharyngodonidae) in tadpoles of *S. nasicus* was recorded by González and Hamann (2005) for the Corrientes' populations. The parasitic fauna of this frog, which consists mainly of nematodes, has also been studied to some extent by Baker and Vaucher (1984) in Paraguayan populations. Some reproductive characteristics of *S. nasicus* from north-western Argentina have been analyzed by Perotti (1995) and Prado *et al.* (2005) from populations living at least 800km away from the present work study area. However, integrated studies are necessary for a better understanding of the ecology of this species. Studies carried out without basic information on the natural history of this particular frog run the risk of producing irrelevant results. In fact, conceptually-based questions must be asked within the framework of the ecology of the individual species if

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PARASITOS DE *Scinax nasicus* (Anura: Hylidae) DE UMA ÁREA SUBTROPICAL SUL AMERICANA E SEUS RASGOS REPRODUTIVOS

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RESUMO

Desde fevereiro de 2002 a dezembro de 2004, se analisou a fauna de helmintos parasitos e as características reprodutivas de Scinax nasicus *em uma área perto da cidade de Corrientes, Argentina. A fauna de parasitos helmintos esteve conformada por 15 espécies de helmintos (larvas e adultos) incluindo trematodes (73%), nematodes (20%) e acantocéfalos (7%). A espécie* Opisthogonimus *sp. apresentou a maior prevalência (41%) de infecção. Os hospedadores definitivos desta metacercária são provavelmente as serpentes.* Scinax nasicus*, intervem como segundo hospedador intermediario, infectando-se pela penetração direta de cercarias. O número de óvulos maduros por fêmea (complemento ovárico) oscilou entre 413-3922, enquanto que o diâmetro médio dos óvulos foi de 0,76 ±0,17mm. Esta espécie possui um padrão reprodutivo prolongado.*

they are to be examined and interpreted correctly (Greene, 1986, Vitt *et al*., 2002).

The main goals of this study of a northeastern Argentinian population of *S. nasicus* were 1) to determine the number of helminth taxa infecting this frog under natural conditions, and 2) to analyze the reproductive characteristics (number and diameter of mature ova, reproductive effort).

Materials and Methods

The study area was established within a maximum distance of approximately 40km towards the east and south of the city of Corrientes (27º30'S, 58º45'W) and the Paraná River established its western and northern limit. As in Schaefer *et al*. (2006), adults of *S. nasicus* were hand-captured preferentially between 19:00 and 24:00, using the sampling technique defined as visual encounters survey (Crump and Scott, 1994). The study area is distinguished by its large diversity of habitats, containing numerous temporary, semi-permanent and permanent ponds, with herbaceous strata composed of gramineous species, cacti and terrestrial bromeliads, where the forest is the dominant vegetation. In the present study, all the regulations and ethical and legal considerations for the capture and use of animals established by the *Centro de Ecología Aplicada del Litoral* (CECOAL-CONICET), Argentina, have been followed.

Parasite study

Frogs for the parasite study (21 females and 28 males) were caught from March 2003 to December 2004. Specimens were transported to the laboratory, placed in a chloroform ($CHCL_3$) solution and their snout-vent length (SVL) measured, and then weighed. At necropsy, hosts were sexed and the alimentary canal, lungs, liver and gall bladder, kidneys, body cavity, musculature, integument and brain were examined for parasites by dissection. Helminths were observed *in vivo*, counted and killed in hot distilled water and fixed in 70% ethyl alcohol. Digeneans and acanthocephalans were stained with hydrochloric carmine, cleared in creosota and mounted in Canada balsam. Nematodes were cleared in glycerin or lactofenol and examined as temporary mounts. The systematic determination of the helminths was carried out following the guidelines given by Yamaguti (1961, 1963, 1971, 1975), Anderson *et al*. (1974), Baker (1987), Anderson (2000), Gibson *et al*. (2002), and Jones *et al*. (2005). The infection prevalence, intensity and abundance were calculated for helminth species according to Bush *et al*. (1997). Species richness is the number of helminth species, and mean helminth species richness is the sum of helminth species, per individual frog, divided by the total number of infected individuals**.** The diversity was calculated with the Shannon index (H'; Shannon and Weaver 1949) using decimal logarithms. The chi-square test, with Yates correction for continuity, was used for comparing the sex ratio of the frogs. A 2×2 contingency table was used for comparing the infection between the sexes.

Reproductive study

Frogs for the reproductive study (13 gravid females and 12 males) were caught from February 2002 to April 2004. The specimens were placed in chloroform ($CHCL_3$) solution, fixed in 10% formalin and deposited in the *Centro de Ecología Aplicada del Litoral* (CECOAL-CONICET) collection. The morphometric variables considered for both sexes were body length (SVL_{mm}) and body mass (BM_g). For females the net body mass (total body mass - ovary mass) was used. The reproductive variables analyzed for each individual were gonad mass (GM_g= ovary mass for females and testes mass for males), total mature ova count number per female (ovarian complement= OC), mature ova diameter (OD_{mm}), reproductive effort (RE), mature ova coloration and testes coloration and form. All variables were registered on individuals fixed in formaldehyde (10%). Body length and ova diameter were determined to the nearest 0.1mm with a caliper. Body, ovary and testes masses were measured in the laboratory after the individuals and gonads were blotted dry to remove excess liquid, using an electronic balance to the nearest 0.01g. Ova maturity was determined by the degree of pigmentation (Basso 1990, Perotti 1994, 1997). Once the ovarian complement for each female had been calculated, 100 mature ova were separated randomly and measured for obtaining the mean diameter and the standard deviation. Reproductive effort (RE) was measured as the percentage of ovary mass relative to net body mass (Prado *et al*., 2000, Prado and Hadad, 2005).

Results

Parasite study

Out of a total of 48 individuals analyzed, 37 (76%) were found infected with helminths. There was no significant difference (χ^2-Yates correction for continuity= 0.19; *df* = 1; P>0.05)in the number of infected females (17) and males (20).

The component community consisted of 15 helminth taxa (larvae and adults), including trematodes (73%), nematodes (20%) and acanthocephalans (7%). Helminth species diversity (H'= 0.83) and evenness (J'= 0.70) were high. At the infracommunity level the mean helminth intensity was 1.48 ±2.56 (maximum= 110) worms per frog. Mean helminth species richness was 2.47 ±1.31 (maximum= 6) species per infected frog. Multiple infections were common, with 1, 2, 3, 4, 5 and 6 species simultaneously present in 9, 15, 6, 4, 3, and 1 frogs, respectively.

Larval digeneans dominated numerically and taxonomically the helminth infracommunity, with prevalence ranging from 41% for *Opisthogonimus* sp. (located in body cavity, liver, muscle and pharyngeal zone) to a low of 2% for unknown echinostomatid species (located in kidney) and *Apharingostrigea* sp. (located in body cavity). The cistacanth (*Centrorhynchus* sp.) found in the liver and in the mesentery presented an infection prevalence >15%, whereas adult trematodes and nematodes located in the intestinal tract presented infection prevalences <15% (Table I).

Reproductive study

Meristics and reproductive data of males and females are summarized in Table II. For females, significant correlations were found between SVL and the variables OC (r_s= 0.54, P=0.05, n=13), $GM_{(ovary\ mass)}$ (r_s= 0.75, P=0.003, n=13), RE (r_s= 0.64, P=0.03, n=13), and OD (r_s= 0.71, P=0.006, n=13). The $BM_{(net\ body\ mass)}$ of females was significantly correlated with OC (r_s= 0.85, P=0.0003, n=13), $GM_{(ovary\ mass)}$ (r_s= 0.89, P=0.0001, n=13), RE (r_s= 0.76, P=0.003, n=13) and OD (r_s= 0.57, P=0.04, n=13).

No significant sexual dimorphisms were observed for SVL (Mann-Whitney *U*-Test= 0.30, P=0.57; $n_{♂}$= 12, $n_{♀}$= 13); and BM (Mann-Whitney U-Test= 0.15, P= 0.99, $n_{♂}$= 12, $n_{♀}$= 13).

The coloration of each ovum was 50% dark brown and 50% white, with the animal and vegetable poles well differentiated. The color of the oval shaped testes was white. For their reproduction, the adults showed preference for flooded vegetation near the shore or inside temporary, semi-permanent and permanent ponds, as well as for flooded high grass (normally no more than 2m in height). It is interesting to remark that in the present study area, *S. nasicus* is the most common anuran species that inhabits human buildings. Tadpoles were observed in different developmental stage and continuously throughout most of the year in temporary, semi-permanent and permanent ponds.

Discussion

Parasite ecology

Previous studies of amphibian helminth infracommunities (McAlpine and Burt, 1998; Muzzall *et al*., 2001; Bolek and Coggins, 2003; Hamann *et al*., 2006a, b) suggest that numerous vacant niches exist within these hosts. The analysis presented here has shown that *S. nasicus* has ac-

TABLE I
INFECTION PARAMETERS, STAGE AND MICROHABITAT OF HELMINTH SPECIES PARASITIZING *Scinax nasicus* FROM CORRIENTES, ARGENTINA

Helminths	#	%	Mean abundance	MI (range)	Stage in frog	Micro-habitat **
Trematoda						
Bursotrema tetracotyloides CECOAL 03120202	265	20	5.40 ±18.80	26.50 (1-110)	Metacerc.	K
Unknown diplostomid species CECOAL 04121322	21	8	0.42 ±1.62	5.25 (3-9)	Mesocerc.	K
Travtrema aff. *stenocotyle* CECOAL 04012008	190	30	3.87 ±15.09	12.66 (1-101)	Metacerc.	B-P-Mu
Styphlodora sp. CECOAL 04012003	23	16	0.46 ±1.67	2.87 (1-10)	Metacerc.	K-Mu-L
Lophosyciadiplostomun aff. *nephrocystis* CECOAL 04050347	14	6	0.28 ±1.39	4.66 (1-9)	Metacerc.	K
Apharingostrigea sp. CECOAL 04121324	1	2	0.02 ±0.14	1	Metacerc.	B
Opisthogonimus sp. CECOAL 04092904	226	41	4.61 ±13.26	11.30 (1-69)	Metacerc.	B-Mu-P-L
Unknown echinostomatid species #1 CECOAL 04012014	78	24	1.59 ±4.28	6.50 (1-22)	Metacerc.	K-B-P
Unknown echinostomatid species #2 CECOAL 04121318	1	2	0.02 ±0.14	1	Metacerc.	K
Catadiscus inopinatus CECOAL 04121330	7	10	0.14 ±0.45	1.40 (1-2)	Adult	Li
Glypthelmins sp. CECOAL 04092904	2	2	0.04 ±0.28	2	Adult	Si
Nematoda						
Oxyascaris caudacutus CECOAL 03120202	1	2	0.02 ±0.14	1	Adult	Si
Cosmocerca parva CECOAL 04121316	1	2	0.02 ±0.14	1	Adult	Li
Unknown rhabdochonid species CECOAL 04101102	10	6	0.20 ±0.91	3.33 (1-5)	Larvae	S
Acanthocephala						
Centrorhynchus sp. CECOAL 04092904	91	16	1.85 ±7.15	1.37 (1-44)	Cystacanth.	L-Me-S

#: number of parasites, %: prevalence.
** Site of infection is K: kidneys, B: body cavity, P: pharyngeal zone, Si: small intestine, Li: large intestine, S: serous layer of the stomach, Mu: muscle, and Me: mesenteries. L: liver.

TABLE II
MEAN ±1 SD OF REPRODUCTIVE AND MORPHOLOGICAL VARIABLES FOR FEMALES AND MALES OF *Scinax nasicus* FROM CORRIENTES, ARGENTINA

Variables	Females	Males
SVL_{mm}	29.94 ±1.97 (27.20-33.30; 6.60%; 13)	30.07 ±1.44 (27.50-32.15; 4.78%; 12)
BM_g	2.59 ±0.70 (1.67-4.14; 26.00%; 13)	2.56 ±0.66 (1.54-3.84; 25.64%; 12)
OC	1628.54 ±1019.52 (413-3922;62.60%; 13)	—
$GM_{g\ (ovary/testes)}$	0.54 ±0.32 (0.11-1.13; 59.94%; 13)	<0.01 (12)
$RE_{\%}$	19.47 ±9.25 (6.59-33.24; 47.49%; 13)	ND
OD_{mm}	0.76 ±0.17 (0.43-1.07; 22.15%; $1800_{mature\ ova}$)	—

SVL: body length, BM: net body mass for females, OC: total mature ova count number per female, GM: ovary or testes mass, RE: percentage of gonad mass relative to net body mass= GM/net body mass (specified only for females), OD: ova diameter. In parenthesis: minimum-maximum; mean variation coefficient (expressed as percentage); sample size. ND: not determined.

quired a great richness (15 species) of helminths (larval and adult), with a maximum of six species per frog and high values of diversity and evenness, but no core species (<50% of infections). Adult helminths were very low in number in the digestive tracts, but larval trematodes were the primary members of this amphibian's helminth infracommunity. These results indicate that *S. nasicus* is infected by direct penetration of cercariae in the tadpole stage or when entering the water for a short period to breed, and it acts as intermediate hosts of these parasites.

S. nasicus occupies an intermediate position in the food web, being a prey only for terrestrial animals. In this respect, possibly the definitive hosts of these larval trematodes are mammals (*Bursotrema tetracotyloides*) and snakes (*Travtrema* aff. *stenocotyle* and *Styphlodora* sp.). On the other hand, host feeding habitats were an important factor in determining the adult helminth faunal composition in *S. nasicus*. Thus, the lower prevalence of infection and poorer species richness of adult digeneans suggest that intermediate hosts of this helminth may not be an important item in this amphibian's diet. The relative high intensity of infection found for cystascanth (*Centrorhynchus* sp.) may be explained by the predominant coleopterans in the alimentary items of *S. nasicus* (Duré, 1999, 2004). The life cycle of *Centrorhynchus* sp. depends on terrestrial intermediates (e.g., coleopterans). The results indicate the importance of local factors associated with aquatics and terrestrial habitat use by the host. Thus, the combination of these factors with the diet, body size, and reproductive behavior of the host (Hamann and Kehr, 1998, 1999a,b, Kehr *et al*., 2000, Hamann, 2004, 2006, Hamann *et al*., 2006a,b) and the behavioral ecology of intermediate hosts, in combination with transmission strategies of parasites (Esch *et al*., 2002), may be regulating the stability of this host-parasite system.

Reproductive ecology

Reproductive activity (gravid females and calling males) in *S. nasicus* occurs for most of the year except in June and July, the winter months with the lowest temperatures, thus establishing *S. nasicus* as a prolonged breeder (Wells, 1977). Prado *et al.* (2005) however, suggest for populations of this species in El Pantanal, Brazil, that *S. nasicus* has an explosive reproductive pattern. Perotti´s (1995) observations in Salta, Argentina, on the other hand, are consistent with the present study since this author also classified the species as a prolonged breeder.

For the reproductive mode, Perotti (1994) and Prado *et al.* (2005) classified this species as Mode 1 according to Duellman and Trueb (1986), consisting in eggs and exotrophic tadpoles in lentic water. We also use mode 6, proposed by Lavilla and Rougés (1992), which is more precise according to our observations and implies eggs laid in a spherical jellied mass that adheres to submerged objects. The embryonic and tadpole development occur in the same water body in which the eggs are laid.

Of 27 species (5 Bufonidae; 1 Cycloramphidae; 6 Leptodactylidae; 4 Leiuperidae; 10 Hylidae and 1 Microhylidae) studied in the area (Schaefer, 2007) females of *S. nasicus* are those presenting bigger values of reproductive effort (18.00 ±8.92%), being only overcome by females of *Pseudopaludicola falcipes* (22.83 ±11.96%).

Comparing the present results with those obtained by Perotti (1994, 1995) for populations from Salta, in northwest Argentina, the values are similar regarding mean body length, mean body mass, mean ovarian complement and mean ova diameter. However, the mean ovary mass (0.48 ±8.92g) and mean female reproductive effort (18.00 ±8.92%) that we observed was lower than observed by Perotti (1994, 1995). These differences could be simply due to peculiarities of two populations that inhabit totally different environments, the season in which samples were collected or even the great variability normally presented by *S. nasicus*. Males and females did not present significant differences for SVL and BM. Females with higher SVL and net BM had significantly higher values of $GM_{ovary\ mass}$, OC, RE and OD, probably due to the presence of breeding females of different ages or that females that were able to feed better before the reproductive season had better conditions for increased egg production. These are only, for the moment, hypotheses that require further research to be tested.

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REFERENCES

Anderson RC (2000) *Nematode Parasites of Vertebrates: Their Development and Transmission*. 2nd ed. CABI. Wallingford, UK. 650 pp.

Anderson RC, Chabaud AG, Willmont S (1974) *CHI. Keys to the Nematode Parasites of Vertebrates*. Commonwealth Agricultural Bureaux. Farnham Royal, Bucks, UK. 170 pp.

Baker MR (1987) *Synopsis of the Nematode Parasitic in Amphibians and Reptiles*. Occasional Papers in Biology. University of Guelph. Canada. 325 pp.

Baker MR, Vaucher C (1984) Parasitic helminths from Paraguay VII: Systematic position of *Oxyascaris* Travassos, 1920 (Nematoda: Cosmocercoidea). *Rev. Suisse Zool. 92*: 303-310.

Basso NG (1990) Estrategias adaptativas en una comunidad subtropical de anuros. *Cuad. Herpetol. Ser. Monog.1*: 1-72.

Bolek MG, Coggins JR (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. *J. Parasitol. 89*: 673-680.

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol. 83*: 575-583.

Crump ML, Scott NJJr (1994) Visual encounters surveys. In Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS (Eds.) *Measuring and Monitoring Biological Diversity - Standard Methods for Amphibians*. Smithsonian Institution Press. Washington DC, EEUU. pp. 84-91.

Duellman WE, Trueb L (1986) *Biology of the Amphibians*. McGraw Hill. New York, NY, USA. 670 pp.

Duré MI (1999) Interrelaciones en los nichos tróficos de dos especies sintópicas de la familia Hylidae (Anura) en un área subtropical de Argentina. *Cuad. Herpetol. 13*: 11-18.

Duré MI (2004) *Estructura Trófica y Aspectos Ecológicos de los Gremios de una Comunidad de Anfibios de la Provincia de Corrientes*. Tesis. Universidad Nacional de La Plata. Buenos Aires, Argentina. 210 pp.

Esch GW, Barger MA, Fellis KJ (2002) The transmission of digenetic trematodes: style, elegance, complexity. *Integr. Comp. Biol. 42*: 304-312.

Frost D (2007) *Amphibian Species of the World: an Online Reference*. Version 5.0 American Museum of Natural History, New York, NY, USA. http://research.amnh.org/ herpetology/amphibia/index.php (Cons. Febr. 2007).

Gibson DI, Jones A, Bray RA (2002) *Keys to the Trematoda. Vol 1.* CABI / The Natural History Museum. London, UK. 521 pp.

González CE, Hamann MI (2005) *Gyrinicola chabaudi* Araujo & Artigas, 1982 (Nematoda: Pharyngodonidae) in tadpoles of *Scinax nasicus* (Cope, 1862) (Anura: Hylidae) from Corrientes, Argentina. *Facena 21*: 145-148.

Green HW (1986) Natural history and evolutionary biology. In Feder ME, Lauder GV(Eds.) *Perspectives and Approaches from the Study of Lower Verte-*

brates. Predator-Prey Relationships. University of Chicago Press. Chicago, IL, USA.: pp. 99-108.

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

Hamann MI (2006) Seasonal maturation of *Glypthelmins vitellinophilum* (Trematoda: Digenea) in *Lysapsus limellus* (Anura: Pseudidae) from an Argentinean subtropical permanent pond. *Braz. J. Biol. 66*: 85-93.

Hamann MI, Kehr AI (1998) Variación espacio temporal en infrapoblaciones de helmintos y su relación con las fluctuaciones poblacionales de *Hyla nana* (Anura, Hylidae). *Cuad. Herpetol. 12*: 23-33.

Hamann MI, Kehr AI (1999a) Relaciones ecológicas entre metacercarias de *Lophosicya-diplostomum* sp. (Trematoda, Diplostomidae) y *Lysapsus limellus* Cope, 1862 (Anura, Pseudidae) en una población local del nordeste argentino. *Facena 15*: 39-46.

Hamann MI, Kehr AI (1999b). 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.

Hamann MI, Kehr AI, González CE (2006a) Species affinity and infracommunity ordination of helminths of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in two contrasting environments from northeastern Argentina. *J. Parasitol. 92*: 1171-1179.

Hamann MI, González CE, Kehr AI (2006b) Helminth community structure of the oven frog *Leptodactylus latinasus* (Anura, Leptodactylidae) from Corrientes, Argentina. *Acta Parasitol. 51*: 294-299.

Jones AR, Bray A, Gibson DI (2005) *Keys to the Trematoda. Vol 2*. CABI / The Natural History Museum. London, UK. 745 pp.

Kehr AI, Manly BFJ, Hamann MI (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.

Lavilla EO, Rougés M (1992) Reproducción y desarrollo de anuros argentinos. Asociación Herpetológica Argentina. *Serie de Divulgación 5*: 1-66.

Lavilla EO, Richard E, Scrocchi GJ (2000) *Categorización de los Anfibios y Reptiles de la República Argentina*. Edición Especial Asociación Herpetológica Argentina. Argentina. 97 pp.

Maneyro R, Langone JA (2001) Categorización de los anfibios del Uruguay. *Cuad. Herpetol. 15*: 107-118.

McAlpine DF, Burt MDB (1998) Helminths of bullfrogs, *Rana catesbeiana*, green frogs, *R. clamitans*, and leopard frogs, *R. pipiens* in New Brunswick. *Can. Field-Nat. 112*: 50-68.

Muzzall PM, Gillillant MG, Summer CS, Mehne CJ (2001) Helminth communities of green frogs *Rana clamitans* Latreille, from southwestern Michigan. *J. Parasitol. 87*: 962-968.

Perotti MG (1994) Aportes preliminares sobre la reproducción en una comunidad de anuros chaqueños en Argentina. *Cuad. Herpetol. 8*: 39-50.

Perotti MG (1995) *Biología y Reproducción de Anuros Chaqueños*. Tesis. Universidad Nacional de Tucumán. 114 pp.

Perotti MG (1997) Modos reproductivos y variables reproductivas cuantitativas de un ensamble de anuros del Chaco semiárido, Salta, Argentina. *Rev. Chil. Hist. Nat. 70*: 277-288.

Prado CPA, Haddad CFB (2005) Size-fecundity relationships and reproductive investment in female frogs in the Pantanal, South-Western Brazil. *Herpetol. J. 15*: 181-189.

Prado CPA, Uetanabaro M, López FS (2000) Reproductive strategies of *Leptodactylus chaquensis* and *L. podicipinus* in the Pantanal, Brazilian. *J. Herpetol. 34*: 135-139.

Prado CPA, Uetanabaro M., Haddad CFB (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.

Schaefer EF (2007) *Restricciones Cuantitativas Asociadas con los Modos Reproductivos de los Anfibios en Áreas de Impacto por la Actividad Arrocera en la Provincia de Corrientes*. Tesis. Universidad Nacional de La Plata. 233 pp.

Schaefer EF, Hamann MI, Kehr AI, González CE, Duré MI (2006) Trophic, reproductive and parasitological aspects of the ecology of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in Argentina. *Herpetol. J. 16*: 387-394.

Shannon CE, Weaver W (1949) *The Mathematical Theory of Communication*. University of Illinois Press. Urbana, IL, USA. 144 pp.

Vitt JL, Ávila-Pires TCS, Zani PA, Esposito MC (2002) Life in shade: the ecology of *Anolis trachyderma* (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar Anoles. *Copeia 2002*: 275-286.

Wells KD (1977) The social behavior of anuran amphibians. *Anim. Behav. 25*: 666-693.

Yamaguti S (1961) *Systema Heminthum. The Nematodes of Vertebrate*. Vol. 3. Wiley. New York, NY, USA. 679 pp.

Yamaguti S (1963) *Systema Heminthum. The Acantocephala of Vertebrates*. Vol. 5. Wiley. New York, NY, USA. 423 pp.

Yamaguti S (1971) *Synopsis of the Digenetic Trematodes of Vertebrates*. Vol. 1. Keigaku. Tokyo, Japan. 1074 pp.

Yamaguti S (1975) *A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates*. Keigaku. Tokyo, Japan. 590 pp.