Herpetological Review, 2003, 34(4), 336–341.

Ecological Aspects of Parasitism in the Tadpole of *Pseudis paradoxa* from Argentina

ARTURO I. KEHR
CECOAL-CONICET
C.C. 140, (3400) Corrientes, Argentina
e-mail: kehr@arnet.com.ar

and
MONIKA I. HAMANN
CECOAL-CONICET
C.C. 291, (3400) Corrientes, Argentina
e-mail: monika_hamann@yahoo.com

Tadpoles act as intermediate hosts for a great number of parasitic helminth species. The metamorphosing tadpole can serve as an efficient link between aquatic and terrestrial ecosystems by transporting larvae of helminths to terrestrial vertebrates. According to Alford (1999), parasites and commensals of tadpoles have not been studied extensively. Until recently, few studies have addressed parasites of different larval stages of amphibians in South America (Hamann and Kehr 1997, 1999; Kehr and Hamann 1995). In North America, to determine the effects of parasitism on performance of amphibians (growth, survival, locomotion), studies have been carried out under experimental conditions. These studies have addressed parasitic infection in different amphibian larval stages, juveniles, and adults (Goater 1994; Goater and Vandenbos 1997; Johnson et al. 1999).

There are very few ecological studies that examine the interaction between parasitism and other environmental factors in anurans. Parasitism may affect an individual's growth and survival. Indeed, ecologists have become increasingly interested in determining the effects of parasitism on their hosts (Minchella and Scott 1991), especially since theoreticians have shown that parasites can regulate host population size (Anderson and May 1979; May and Anderson 1979; Thiemann and Wassersug 2000a, b).

We were interested in examining the interaction of parasitism + environment on a model anuran species, *Pseudis paradoxa*, from the family Pseudidae. This species is endemic to South America, and in Argentina the family is represented by three species: *Lysapsus limellus* Cope 1862, *Pseudis minuta* Gunther, 1859 "1858," and *Pseudis paradoxa* (Linnaeus 1758) (Kehr and Basso 1990). The three species are largely sympatric in the northern provinces of Formosa, Chaco, Santa Fé, Corrientes, and Entre Ríos (24°00'S – 33°00'S; and 56°00'W – 62°00'W) (Cei 1980; Gallardo 1987). *Pseudis paradoxa* uses permanent ponds with floating vegetation (Duré and Kehr 2001). The tadpole of *P. paradoxa* is characterized by its large size (maximum length = 230 mm; Kenny 1969) particularly compared to the size of the metamorphosed adult. This gigantism appears to be the result of extended exposure to prolactin in the tadpoles (e.g., during overwintering) (Emerson 1988). Size variability in *P. paradoxa* tadpoles from Argentinean populations has been reported by Dixon et al. (1995).

The main goals of this study were: 1) to record and analyze morphological measurements of tadpoles for different stages; 2) to determine how many helminth taxa infest *P. paradoxa* tadpoles under natural conditions; and 3) to examine the co-occurrence of parasite taxa, and the relationship between co-occurrence and tadpole morphology.

Materials and Methods.—The tadpoles studied were collected in two ponds located ca. 25 km from Corrientes City, Corrientes province, Argentina (27°30'S, 58°45'W). The distance between the ponds was 5 km. Pond 1 is a semi-permanent circular pond, ca. 60 m diameter, with a maximum depth at center of ca. 1.5 m. During the study period, the dominant vegetation was *Cyperus* spp., *Salvinia* sp., *Ludwigia peploides*, *Nymphoides* sp., and *Paspalum* sp. Pond surface vegetative cover was 20–30%. Pond 2 is a permanent circular pond, ca. 110 m diameter, with a maximum depth at center of 2 m. During the study period the dominant vegetation was *Salvinia rotundifolia*, *Pistia stratiotes*, and *Eichornia crassipes*. The pond contained a wide range of aquatic invertebrate organisms including abundant snails belonging to the family Planorbidae.

Eight tadpole samples (four per pond) were taken between 28 February and 20 March 1997. The tadpoles were captured with a 45 cm diameter dip net and maintained alive in the laboratory until they were studied (for up to two days after capture). All tadpoles were anesthetized with ether for study. The developmental stages (Gosner 1960), body length (i.e., distances from the oral disc to the beginning of the cloacal tube), oral disc width, intestine length, maximum body height, maximum tail height, maximum tail muscle height, and maximum body width were recorded for each tadpole.

TABLE 1. Tadpole measurements for each stage (Gosner 1960) captured in each pond type and, number of helminth parasites by taxa. N= number of tadpoles; when more than one tadpole was obtained the measurement for each stage is the mean and in parenthesis is the deviation standard (1s). Parasites species: Trematodes: 1) Diplostomidae gen. sp. 1; 2) Diplostomidae gen. sp. 2; 3) Diplostomidae gen. sp. 3; 4) Digenea gen. sp. 1; 5) Strigeoidea gen. sp.; 6) Digenea gen. sp. 2; 7) Echinostomatidae gen. sp.; 8) *Glypthelmins* sp.; 9) *Catadiscus* sp.; Nematodes: 10) *Gyrinicola* sp.

Pond 1 (N = 14)		Tadpole measurements (mm)					Helminth parasites									
Stages	N	Total length	Body length	Oral disc width	Body height	Tail height	Tail muscle height	1	2	3	4	5	6	7	8	9	10	TOTAL PAR.
28	1	85.50	30.50	4.20	18.80	22.50	8.40	5	-	1	-	-	-	-	-	-	24	30
34	1	123.00	42.20	5.60	29.80	32.20	10.60	-	1	-	-	-	-	-	-	-	73	74
35	3	117.26 (31.28)	47.40 (14.74)	6.70 (2.04)	31.26 (11.20)	35.50 (14.15)	11.26 (3.20)	8	19	-	-	-	-	-	-	-	319	346
40	1	154.40	53.60	6.60	48.70	52.00	17.90	19	-	-	-	-	-	-	-	-	3	22
42	3	157.50 (10.82)	53.76 (6.18)	7.80 (0.50)	38.36 (5.09)	47.66 (2.50)	11.10 (7.75)	12	33	-	-	-	-	-	-	-	662	707
45	5	112.80 (20.56)	34.86 (3.24)	13.08 (1.29)	16.72 (0.99)	21.52 (6.80)	13.46 (2.66)	9	-	-	-	-	1	10	-	1	21	
TOTAL	14							53	53	1	-	-	1	10	-	1082	1200	
Pond 2 (N = 13)																		
25	2	66.50 (34.36)	24.55 (7.70)	3.50 (1.69)	15.55 (4.45)	17.40 (4.38)	6.65 (3.60)	7	1	-	-	-	-	-	56	73	137	
26	1	57.00	20.70	2.70	11.70	10.50	4.20	-	-	-	-	-	-	-	-	2	2	
29	1	114.60	38.20	5.90	27.30	32.30	10.70	-	-	-	-	-	-	-	67	2	69	
32	1	129.30	46.40	5.20	30.50	37.40	11.70	4	1	-	-	-	-	-	69	222	296	
37	3	101.36 (54.55)	48.13 (4.44)	7.10 (0.60)	36.43 (4.71)	37.03 (3.52)	13.06 (1.10)	3	3	-	-	2	-	1	227	321	557	
38	1	157.00	58.30	8.30	45.30	42.30	14.40	-	-	-	-	-	-	-	162	226	388	
39	1	111.00	41.00	5.70	30.50	32.30	11.20	-	-	-	-	3	-	-	56	232	291	
42	1	167.90	57.00	17.80	43.70	41.50	15.70	-	-	-	-	-	-	-	94	142	236	
45	2	127.95 (2.05)	38.10 (1.97)	14.40 (1.13)	15.15 (1.06)	15.80 (3.53)	11.75 (0.49)	-	-	1	1	-	-	12	74	-	88	
TOTAL	13							14	5	-	1	1	5	-	13	805	1220	2064

The intestine, kidney, coelomic cavity, musculature, integument, brain, and eyes of each tadpole were examined for parasites by dissection. Metacercariae were observed *in vivo* after anesthetizing the tadpoles. Parametric tests were used to establish the relationship between the morphological variables and parasite presence (Kehr 1994; Zar 1996).

We used Principal Component Analysis to 1) examine the relationship between the tadpoles' morphometric variables and the variation explained by the different combinations of them (principal components); and 2) to analyze the association among parasite taxa through a correlation matrix based on the parasite counts. Relationships between two sets of variables were investigated by performing a Canonical Correlation Analysis, one independent set composed of tadpole morphological measurements and other dependent set formed by abundance of parasites by taxa.

Statistical tests were carried out using SYSTAT 7.0 software. In order for all variables to have the same influence on the distance calculation, the variables were standardized, subtracting the variable's sample mean from each value and dividing the difference by the sample standard deviation. The standardized values have a mean of 0 and a variance of 1.

We defined parasite prevalence as the number of hosts infected with one or more parasite taxa divided by the total number of hosts examined and expressed as a percentage. Mean intensity was defined as the average intensity of a parasite taxon in the host infected with that parasite. Bush et al. (1997) detailed more information on these and other aspects of parasite terminology. The relation of variance/mean was used for determining the spatial distribution of parasites inside the host.

Results.—Twenty-seven tadpoles were collected (Pond 1: N = 14; Pond 2: N = 13). The total length of tadpoles ranged from 26.5 to 167.9 mm. Maximum body length recorded (58.3 mm) was for a stage 38 tadpole captured in Pond 2 (Table 1).

The principal components and the percentages of variation accounted for by the morphometric variables are shown in Table 2. All tadpoles collected (N = 27) were included in this analysis. The first component mainly reflects the sum of body length, body height, body width, and tail height. The second component mainly reflects the influence of oral disc width variation and the tail muscle height. The third component mainly reflects a contrast between the total length and tail muscle height.

Ten helminth parasite taxa (larvae and adults) were recorded—nine trematodes and one nematode (Table 1). The prevalence, mean intensity, minimum and maximum parasite numbers, and localization are detailed in Table 3 and 4. In pond 1 (low

TABLE 2. Results of a principal component analysis of morphometric variables of *Pseudis paradoxa* tadpoles (N = 27): coefficients of standardized measurements (each variable: mean = 0 and $s^2 = 1$), and the percentage of variation explained. Tadpoles analyzed from pond 1 + pond 2 pooled.

Coefficients	PC1	PC2	PC3
Total length	0.726	-0.180	-0.625
Body length	0.959	0.022	0.072
Oral disc width	0.169	-0.923	-0.057
Body height	0.945	0.262	0.082
Body width	0.950	0.131	0.114
Tail height	0.945	0.241	-0.005
Tail muscle height	0.596	-0.561	0.359
Percent of total variance explained	64.567	19.195	7.831
Cumulative	64.567	83.762	91.593

snail abundance, pers. obs.) the more representative helminth taxa infecting the tadpoles, in decreasing order, were: 1) *Gyrinicola* sp. (localized in the intestine), 2) Diplostomidae gen. sp. 2 (localized in the kidneys) and, 3) Diplostomidae gen. sp. 1 (localized in the kidneys). In pond 2 (high snail abundance, pers. obs.) the helminth taxa more numerous, in decreasing order, were: 1) *Gyrinicola* sp. (localized in the intestine), 2) *Catadiscus* sp. (localized in the intestine) and, 3) Diplostomidae gen. sp. 1 (localized in the kidneys).

The *P. paradoxa* tadpoles of the two ponds shared four of the ten parasite taxa recorded. In the kidneys of tadpoles three taxa of trematodes were recorded from both ponds (Diplostomidae sp. 1, 2 and Digenea gen. sp. 2), and one taxon was observed in the intestine of tadpoles in the two ponds (*Glypthelmins* sp.). The nematode, *Gyrinicola* sp. was recorded from the intestine of tadpoles from both ponds.

The principal components and the percentages of variation accounted for by the totality of helminths (pond 1 + pond 2) are shown in Table 5. The first component mainly reflects a contrast among the counts of *Glypthelmins* sp. against the sum of the counts of Diplostomidae gen. sp. 1, Diplostomidae gen. sp. 2 and *Gyrinicola* sp. The second component is mainly a contrast between the sum of the counts of *Catadiscus* sp. and *Gyrinicola* sp. against *Glypthelmins* sp. The third component mainly reflects the contrast between the counts of Digenea gen. sp. 2. against *Catadiscus* sp. The fourth component is mainly the sum of the counts of *Glypthelmins* sp. and *Gyrinicola* sp. The fifth component is mainly the sum of the counts of Diplostomidae gen. sp. 2 and *Catadiscus* sp.

Canonical correlation analysis (CCA) showed a very strong association between the two data sets, one set formed by parasite taxa (dependent variables) and another by tadpoles morphometric variables (independent variables) (R^2= 0.977; RAO F= 2.027, df= 42, 69.1, P= 0.004; Table 6). In Table 6, are summarized the canonical correlations and the Bartlett test of residual correlations. The two first canonical correlations were significant, demonstrating the good associations between the two variables sets.

TABLE 3. Prevalence, mean intensity, and s^2/mean relation of helminths recorded from *Pseudis paradoxa* tadpoles at two ponds from Corrientes, Argentina, and numbers of tadpoles parasitized.

	Pond 1 (N = 14)				**Pond 2 (N = 13)**			
	Mean Intensity (min.–max.)	Prevalence %	S^2/Mean	Tadpoles parasitized	Mean Intensity (min.–max.)	Prevalence %	S^2/Mean	Tadpoles parasitized
Trematodes								
Diplostomidae gen. sp. 1	9.00 (1–19)	35.71	10.15	5	14.00 (3–7)	23.07	4.55	3
Diplostomidae gen. sp. 2	9.10 (1–32)	50.00	18.70	7	5.00 (1–3)	23.07	1.96	3
Diplostomidae gen. sp. 3	(1)	7.14	–	1	–	–	–	–
Digenea gen. sp. 1	–	–	–	–	(1)	7.69	–	1
Strigeoidea gen. sp.	–	–	–	–	(1)	7.69	–	1
Digenea gen. sp. 2	–	–	–	–	2.50 (2–3)	15.38	2.42	2
Echinostomatidae gen. sp.	(1)	7.14	–	1	–	–	–	–
Glypthelmins sp.	1.50 (1–3)	28.57	1.69	4	4.50 (1–8)	15.38	7.07	2
Catadiscus sp.	–	–	–	–	73.20 (3–162)	84.61	40.06	11
Nematodes								
Gyrinicola sp.	155.60 (24–323)	64.28	125.35	9	110.40 (2–232)	84.61	103.86	11

Discussion.—Our data agree with the observation of Dixon et al. (1995) that populations of *P. paradoxa* tadpoles are highly polymorphic. In our tadpole samples we also recorded great variability in the measurements. About 65% of the variation observed in the tadpoles morphological features were mainly related to body features differences. Approximately 19% of the tadpole variation was produced mainly by the oral disc width. Nevertheless, only about 8% of the variation was attributed to tadpole total length.

Overall, *Gyrinicola* sp. (Nematodes) and *Catadiscus* sp. (Trematodes) showed the highest abundance and a constant frequency and, in both cases, infecting the intestine. Amphibians are the definitive host for these parasites (Baker 1987; Prudhoe and Bray 1982). For both cases, the infection depends directly upon tadpole feeding behavior because the transmission is through oral ingestion of eggs and larvae for the first taxon and metacercariae for the second. A positive correlation with the tadpole body characteristics was observed for both taxa (Table 6), probably because it is related to intestine length.

Gyrinicola sp. had the greatest infestation intensity, prevalence, and formed big nematode schools in the intestine of tadpoles in both ponds. These were the only adult helminth parasites encountered because tadpoles are their definitive host. The oxyurids (*Gyrinicola* sp.) belong to a group of parasites with simple life cycles (SLC) because they require a single host individual for their development (i.e., the eggs are directly infective to the host). Oxyurids are the only nematodes found in both vertebrates and invertebrates (Baker 1987). They commonly parasitize fishes, amphibians and reptiles.

Catadiscus sp. were only recorded in the tadpoles captured in the pond that possessed a great abundance of snails (Planorbidae) because snails are the intermediary host. Their metacercariae encyst on the substrate (e.g., roots, aquatic vegetation) and they are ingested when the tadpoles eat. According to Yamaguti (1973) the life cycle of *Catadiscus* sp. resembles that of trematodes in the genus *Megalodiscus.* The life cycles of *Catadiscus* sp. can be considered autogenic because they complete their cycles within the pond and use definitive hosts which are almost permanently restricted to the pond (e.g., frogs, turtles, snakes). This life cycle is also simple (SLC).

Two other taxa well represented in abundance in both of the ponds studied were Diplostomidae gen sp. 1 and Diplostomidae gen sp. 2. These taxa were not as well represented as *Gyrinicola* sp. and *Catadiscus* sp. For Diplostomidae gen sp. 1 and sp. 2 birds and mammals are the definitive host and inside tadpoles they are localized in the kidney (Table 4). In both parasite taxa the infection depends upon either tadpole feeding behavior and cercariae activity. The parasite penetration is through the skin and cloacae of tadpoles. The abundance of Diplostomidae gen sp. 1 and sp. 2 was positively correlated with variables related to the tail of tadpoles (swimming features) (Table 6).

The results suggest that in *P. paradoxa* tadpoles parasite infestation may be either constant or sporadic in occurrence. These results agree with Aho (1990) who suggests that communities of amphibian parasites are generally poor either from the standpoint of number of species or density of individuals that compose them. In our study the influence of pond type and tadpole morphometric features were both important factors regulating the helminth infracommunity. *Catadiscus* sp., one dominant species, was only

TABLE 4. Summary of helminth taxa, parasite stages, position, transmission and definitive host of parasites in the giant tadpoles of *Pseudis paradoxa* tadpoles from Corrientes, Argentina.

Helminths	Stage in tadpole	Position in tadpole	Transmission	Definitive host
Trematodes				
Diplostomidae gen. sp. 1	Metacerc.	Kidney	Skin and cloaca penetration by cercariae	Bird and mammal
Diplostomidae gen. sp. 2	Metacerc.	Kidney	Skin and cloaca penetration by cercariae	Bird and mammal
Diplostomidae gen. sp. 3	Metacerc.	Kidney	Skin and cloaca penetration by cercariae	Bird and mammal
Digenea gen. sp. 1	Metacerc.	Kidney	?	?
Strigeoidea gen. sp.	Metacerc.	Kidney	Skin and cloaca penetration by cercariae	Reptiles, bird and mammal
Digenea gen. sp. 2	Metacerc.	Kidney	?	?
Echinostomatidae gen. sp.	Metacerc.	Manicotto outside	Oral ingestion by cercariae	Bird
Glyphelmins sp.	Juvenile	Intestine	Skin and cloaca penetration by cercariae	Amphibian
Catadiscus sp.	Juvenile	Intestine	Oral ingestion by metacercariae	Amphibian
Nematodes				
Gyrinicola sp.	Adult	Intestine	Oral ingestion by eggs and larvae	Amphibian

TABLE 5. Results of a principal component analysis of helminth parasites: coefficients of parasites numbers standardized (each variable: mean= 0 and s^2= 1), and the percentage of variation explained. Hosts species: tadpoles of *Pseudis paradoxa* (N= 27) from pond 1 + pond 2 pooled. The only taxa considered were those with more than 1 parasite in total.

Coefficients	PC1	PC2	PC3	PC4	PC5
Diplostomidae gen. sp. 1	-0.798	-0.354	-0.012	0.159	0.238
Diplostomidae gen. sp. 2	-0.672	-0.377	0.188	-0.046	-0.594
Digenea gen. sp. 2	0.051	0.396	0.909	-0.038	0.030
Glypthelmins sp.	0.526	-0.484	0.153	0.674	-0.103
Catadiscus sp.	0.039	0.814	-0.269	0.215	-0.383
Gyrinicola sp.	-0.655	0.508	-0.000	0.405	0.217
Percent of total variance explained	29.962	26.315	15.965	11.559	10.239
Cumulative	29.965	56.277	72.242	83.801	94.040

TABLE 6. Results of a canonical correlation analysis between two sets of variables: one set formed by six parasite taxa (dependent variables: Y) and the other set formed by seven tadpole morphometric variables (independent variables: X). Variables of the two sets were standardized (each variable: mean = 0 and s^2 = 1). The *Pseudis paradoxa* tadpoles considered (N = 27) were pooled (Pond 1 + Pond 2). The only taxa considered were those with more than 1 parasite in total. Parasite's names: Dipl. 1: Diplostomidae gen. sp. 1; Dipl. 2: Diplostomidae gen. sp. 2; Dig. 2: Digenea gen. sp. 2; Glypt.: *Glypthelmins* sp.; Catad.: *Catadiscus* sp., and Gyrin.: *Gyrinicola* sp.

	Parasite taxa					
Tadpole variables	Dipl. 1	Dipl. 2	Dig. 2	Glypt.	Catad.	Gyrin.
Total length	0.136	0.142	0.020	-0.390	0.004	0.288
Body length	0.078	0.120	-0.006	-0.149	0.337	0.651
Oral disc width	-0.198	-0.123	-0.167	0.487	0.038	-0.245
Body maximum height	0.242	0.170	0.071	-0.368	0.400	0.770
Body maximum width	0.116	0.057	0.043	-0.256	0.439	0.702
Tail maximum height	0.312	0.260	0.044	-0.411	0.212	0.731
Tail maximum muscle height	0.353	0.333	-0.011	0.044	0.225	0.156

Overall association: R^2 = 0.977; RAO F = 2.027, df = 42, 69.1; P = 0.004

Canonical correlations	1	2	3	4	5	6
	0.867	0.802	0.752	0.581	0.297	0.074

Bartlett test of residual correlations

Correlations 1 through 6:	χ^2 = 71.551	df = 42	prob = 0.003 *
Correlations 2 through 6:	χ^2 = 45.091	df = 30	prob = 0.038 *
Correlations 3 through 6:	χ^2 = 25.551	df = 20	prob = 0.181
Correlations 4 through 6:	χ^2 = 9.698	df = 12	prob = 0.642
Correlations 5 through 6:	χ^2 = 1.861	df = 6	prob = 0.932
Correlations 6 through 6:	χ^2 = 0.105	df = 2	prob = 0.949

* Significant (P < 0.05)

present in the pond where snails were abundant. Recently, Kehr et al. (2000) demonstrated the relationship between biotic (parasite coexistence) and abiotic factors (pond type) on helminth infracommunity structure in populations of the frog *Lysapsus limellus*. The rate at which the host can be infected and the persistence of infection depends strongly on habitat variation, host size, and diet (Kehr et al. 2000).

Johnson et. al. (1999, 2001), under field and experimental conditions, identified a trematode parasite (*Ribeiroia ondatrae*) as the probable cause of malformations in some species of frog from North America. In our study, we did not see malformations or abnormalities in the *P. paradoxa* tadpoles.

Acknowledgments.—We are extremely grateful to M. L. Crump, R. W. Wassersug, and F. R. Hensley for helpful comments made on an earlier version of this manuscript which greatly improved it. Furthermore, we are especially indebted to M. I. Duré and F. Marangoni for helping in the laboratory and fieldwork.

Literature Cited

Aho, J. M. 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. *In* G. W. Esch, A. O. Bush, and J. M. Aho (eds.), Parasite Communities: Patterns and Processes, pp. 157–195. Chapman and Hall, London, New York.

Alford, R. A. 1999. Ecology: resource use, competition, and predation. *In* R. W. McDiarmid and R. Altig (eds.), Tadpoles: the Biology of Anuran Larvae, pp. 240–278. The University of Chicago Press, Chicago.

Anderson, R. M., and R. M. May. 1979. Population biology of infectious diseases: part I. Nature 280: 361-367.

Baker, M. R. 1987. Synopsis of the Nematoda Parasitic in Amphibians and Reptiles. Memorial University of Newfoundland Occas. Pap. Biol. No. 11, 325 pp.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83:575–583.

Cei, J. M. 1980. Amphibians of Argentina. Monitore Zool. Ital. (n.s.) Monog. 2: 609 pp.

Dixon, J. R., C. Mercolli, and A. A. Yanosky. 1995. Some aspects of the ecology of *Pseudis paradoxa* from northeastern Argentina. Herpetol. Rev. 26:183–185.

Duré, M. I., and A. I. Kehr. 2001. Differential exploitation of the trophic resources in two species of Pseudidae from Corrientes, Argentina. J. Herpetol. 35:340–343.

Emerson, S. B. 1988. The giant tadpole of *Pseudis paradoxa*. Biol. J. Linn. Soc. 34:93–104.

Gallardo, J. M. 1987. Anfibios Argentinos. Biblioteca Mosaico, Buenos Aires, 98 pp.

Goater, C. P. 1994. Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. Ecology 75:2264–2274.

———, and R. E. Vandenbos. 1997. Effects of larval history and lungworm infection on the growth and survival of juvenile wood frogs (*Rana sylvatica*). Herpetologica 53:331–338.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190.

Hamann, M. I., and A. I. Kehr. 1997. *Lysapsus limellus* (NCN). Parasitism. Herpetol. Rev. 28:85.

———, and ———. 1999. Population dynamics and ecological relationships between *Glypthelmins vitellinophilum* Dobbin, 1958 (Trematoda, Macroderoididae) and the host *Lysapsus limellus* Cope, 1862 (Anura, Pseudidae) in a semipermanent pond of Corrientes, Argentina. Physis 57:17–24.

Johnson, P. T. J., K. B. Lunde, E. G. Ritchie, and A. E. Launer. 1999. The effect of trematode infection on amphibian limb development and survivorship. Science 284:802–804.

———, ———, R. W. Haight, J. Bowerman, and A. R. Blaustein. 2001. *Ribeiroia ondatrae* (Trematoda: Digenea) infection induces severe limb malformations in western toads (*Bufo boreas*). Can. J. Zool. 79:370–379.

Kehr, A. I. 1994. Usos y abusos de las correlaciones en biología. Cuad. Herp. 8:225–228.

———, and N. G. Basso. 1990. Description of the tadpoles of *Lysapsus limellus* (Anura: Pseudidae) and some considerations of its biology. Copeia 1990:573–575.

———, and M. I. Hamann. 1995. Estado actual de la teoría de la competencia como un factor organizador de las comunidades parasitarias de helmintos. Facena 11:115–122.

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

Kenny, J. S. 1969. The Amphibia of Trinidad. Stud. Fauna Curacao Caribb. Isl. 108:1–78.

May, R. M., and R. M. Anderson. 1979. Population biology of infectious diseases: part II. Nature 280:455–461.

Minchella, D. J., and M. E. Scott. 1991. Parasitism: A cryptic determinant of animal community structure. Trends Ecol. Evol. 6:250–253.

Prudhoe, S. O. B. E., and R. A. Bray. 1982. Platyhelminth Parasites of the Amphibia. British Museum (Natural History). Oxford University Press, London. 217 pp.

Thiemann, G. W., and R. J. Wassersug. 2000a. Patterns and consequences of behavioural responses to predators and parasites in *Rana* tadpoles. Biol. J. Linn. Soc. 71:513–528.

———, and ———. 2000b. Biased distribution of trematode metacercariae in the nephric system of *Rana* tadpoles. J. Zool. Lond. 252:534–538.

Yamaguti, S. 1973. A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates. Kyoto, Japan. 590 pp.

Zar, J. H. 1996. Biostastistical Analysis. Third Edition. Prentice Hall. New Jersey. 662 pp.