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SPECIES AFFINITY AND INFRACOMMUNITY ORDINATION OF HELMINTHS OF *LEPTODACTYLUS CHAQUENSIS* (ANURA: LEPTODACTYLIDAE) IN TWO CONTRASTING ENVIRONMENTS FROM NORTHEASTERN ARGENTINA

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ABSTRACT: One hundred seventy-two frogs (*Leptodactylus chaquensis*) were collected from November 2002 to November 2003, in agricultural (n = 132) and nonagricultural (n = 40) areas. Both sites are near the city of Corrientes, Argentina. The main goals of this study were as follows: (1) to determine the helminth parasite community in agricultural and nonagricultural habitats; (2) to analyze the relationships between helminth parasites and site of infection, frog body size, and gender; (3) to identify and examine covariation and association of helminth communities; and (4) to determine the mean richness and diversity of parasite communities. The helminth compound community of this amphibian species consisted of 24 species: 19 in agricultural habitats and 18 in nonagricultural habitats. The mean richness, mean diversity, and evenness of helminths were significantly different between the habitats ($P < 0.05$). The body size of the host was the important factor in determining parasite richness. Both habitats exhibited differences in community ordination. The helminth species in the 2 habitats exhibited the same interspecific relationships, although differences were observed in the intensity of infection.

Many processes have been reported to influence the structure of amphibian parasite communities, including host size, gender, diet, site of infection, species, and behavior (Tucker and Joy, 1996; Yoder and Coggins, 1996; McAlpine, 1997; Joy and Pennington, 1998; Bursey et al., 2001; Goldberg and Bursey, 2002; Bolek and Coggins, 2003). In addition, the host's characteristic habitat (Wetzel and Esch, 1997; McAlpine and Burt, 1998; Zelmer et al., 1999; Kehr et al., 2000; Muzzall et al., 2001; Zelmer et al., 2004; Goater et al., 2005) is also a key factor in the colonization probabilities of parasites.

Interspecific interactions have been clearly demonstrated in experimental studies of helminth species in their definitive hosts. In such experiments, the species that share the same organ and host are typically established in different regions (niche segregation). In other studies, the abundance of 1 species is lower when other species are present in the same organ in a host. Although this type of evidence is convincing, it is not easily reconciled with field data (Poulin, 2001). In natural conditions, there may be several potentially interacting species involving direct and indirect effects. For competition, which is a negative direct effect, the resource must be scarce, and according to Poulin (2005), the interpretation of competition between species through a matrix of correlation coefficients must be considered with caution. Association between 2 species can exist because (1) both species select or avoid the same habitat or habitat factors; (2) they have the same general biotic and abiotic environmental requirements; or (3) both species have an affinity for the other, which can be positive or negative (Hubalek, 1982). Covariation in abundance data between 2 species can be observed through correlation coefficients. A positive correlation implies that for a given increase in abundance of 1 species, there is a corresponding increase in the other species. For negative correlation, an increase in one implies a decrease in the other. Of course, establishing the existence of a correlation does not imply causality (Ludwig and Reynolds, 1988).

The helminth parasites of Argentinean amphibians have been analyzed mainly at the infrapopulation level. These studies have reported levels of prevalence, abundance, intensity of infection, and seasonal fluctuations related to body size, gender, and diet (Hamann and Kehr, 1997, 1998, 1999; Duré et al., 2004; Hamann, 2004) in select Argentinean amphibians. The few studies at the compound community level provide information relative to the influence of habitat and intermediate host availability on helminth species richness, diversity, and relative abundance of Argentinean amphibian parasites (Kehr et al., 2000; Kehr and Hamann, 2003; Hamann, 2004). To gain a better understanding of these phenomena, further examination of amphibian hosts exhibiting a wider array of life history strategies is required.

The present study analyzed the interspecific relationships and infracommunity ordination of helminth parasite in the frog, *Leptodactylus chaquensis*, from 2 contrasting areas in northeast Argentina. One area supports an intensive agricultural activity (rice field). This habitat is characterized by its instability (i.e., water levels in the rice field fluctuate due to farming practices involved in growing rice). Even though it is relatively unstable, the habitat is nonetheless homogeneous. The second area is nonagricultural and more stable, with minor fluctuations in water levels; it is characterized by habitat heterogeneity.

Adult *L. chaquensis* can survive in both dry and moist substrata (i.e., near to the shore of temporary, semipermanent, and permanent ponds), and in flooded grass. It has a generalist diet, with a foraging strategy intermediate between that of an ambush predator and an actively foraging predator (A. I. Kehr, pers. comm.). In South America, its habitat distribution includes northern Argentina, eastern Bolivia, Paraguay, northern Uruguay, and Mato Grosso do Sul, Brazil (Frost, 2004).

Given these contrasting environments, the main goals of the present study were as follows: (1) to determine the helminth parasite community structure in the agricultural and nonagricultural habitats; (2) to analyze the relationships between helminth parasites and site of infection, frog body size, and gender; (3) to identify and examine covariation and association of helminth communities; and (4) to determine the mean species richness and diversity of parasite communities.

MATERIALS AND METHODS

Study area

Study areas are located in a northwestern part of Corrientes Province, Argentina. The 2 areas are situated at 27°36′S, 58°48′W (agricultural area) and 27°27′S, 58°47′W (nonagricultural area). The agricultural habitat of 300 ha is characterized by rice cultivation and discrete, extended

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TABLE I. Helminth record of *Leptodactylus chaquensis* from agricultural and nonagricultural area from Corrientes, Argentina.

Helminth site of infection†	Agricultural area‡			Nonagricultural area‡				
	%	#	MI/SD	%	#	MI/SD	*Z*	χ^2
Trematoda								
Haematoloechus longiplexus§ Lung	14.4	44	2.3/1.9	35.0	101	7.2/6.3	*2.90	*22.41
Gorgoderina parvicava§ Uri-Bla	9.1	35	2.9/2.7	20.0	26	3.3/3.5	1.91	1.34
Gorgoderina rocholimai§ Uri-Bla	Absent	Absent	Absent	2.5	3	—	—	—
Glypthelmins repandum§ Ant-Int/Mid-Int	1.5	2	1.0	32.5	44	3.5/3.0	**6.09	*38.37
Glypthelmins palmipedis§ Ant-Int/Mid-Int	7.6	16	1.5/0.9	57.5	52	2.2/1.9	**7.02	*19.07
Catadiscus inopinatus§ Lar-Int	Absent	Absent	Absent	55.0	133	6.0/ 8.8	—	—
Catadiscus propinquus§ Lar-Int	5.3	35	5.0/5.5	Absent	Absent	Absent	—	—
Bursotrema aff. *tetracotyloides*‖ Kidney	5.0	500	83.3/81.7	75.0	3,323	110.7/354.7	**9.48	*2084.57
Heterodiplostomum sp.‖ Bod-Cav	Absent	Absent	Absent	5.0	3	1.5/0.5	—	—
Styphlodora sp.‖ Muscle/Kidney	Absent	Absent	Absent	25.0	85	8.7/10.8	—	—
Travtrema aff. *stenocotyle*‖ Muscle/Mesentery/Bod-Cav/Pha-Zon	0.8	2	—	27.5	41	3.7/4.7	**3.26	*35.40
Echinoparyphium sp.‖ Kidney	0.8	2	—	Absent	Absent	Absent	—	—
Nephrostomum sp.‖ Kidney	2.3	13	4.3/4.0	Absent	Absent	Absent	—	—
Unknown strigeid species No. 1‖ Muscle/Mesentery/Bod-Cav/	12.1	80	5.1/7.6	12.5	17	3.4/3.4	0.07	*40.93
Unknown strigeid species No. 2‖ Liver	5.0	1002	167.0/137.0	2.5	13	—	0.67	*963.67
Unknown opisthogonimid sp.‖ Muscle/Mesentery/Bod-Cav/Pha-Zon	Absent	Absent	Absent	25.0	19	3.1/2.3	—	—
Cestoda								
Unknown cestoda species‖ Mesentery	2.3	8	0.1/0.5	Absent	Absent	Absent	—	—
Cylindrotaenia sp.§ Ant-Int/Mid-Int	5.3	33	4.7/3.9	Absent	Absent	Absent	—	—
Nematoda								
Cosmocerca podicipinus§ Lung/Lar-Int	59.1	473	6.0/6.5	65.0	72	2.8/2.6	0.68	*295.05
Cosmocerca parva§ Lar-Int	5.0	21	3.5/3.4	7.5	11	3.7/1.9	0.60	3.16
Aplectana hylambatis§ Mid-Int/Lar-Int	2.3	37	12.3/13.9	2.5	5	—	0.07	*24.40
Porrocoecum sp.‖ Liver/Mesentery	1.5	19	9.5/8.5	2.5	2	—	0.43	*13.81
Rhabdias sp.† Lung	1.5	2	1	Absent	Absent	Absent	—	—
Acanthocephala								
Centrorhynchus sp.‖ Mesentery	3.0	15	3.8/3.7	7.5	5	1.7/0.5	1.27	*5.05

* $P < 0.05$; ** $P < 0.001$.
† Site of infection: Ant-Int, anterior portion of the small intestine; Bod-Cav, body cavity; Lar-Int, large intestine; Mid-Int, midportion of the small intestine; Pha-Zon, pharyngeal zone; Uri-Blad, urinary bladder.
‡ Prevalence (%), intensity (#), mean intensity (MI) ± 1 SD, statistical difference between 2 areas in prevalence (z) and intensity (χ^2) are shown.
§ Adult.
‖ Larva.

periods of abundant water or dry conditions. The nonagricultural habitat of 250 ha is forested, with areas that include grasslands, numerous cacti, and terrestrial bromeliads. Temporary, semipermanent, and permanent ponds characterize this site.

Analytical procedure

Samples of *L. chaquensis* were collected from November 2002 to November 2003, from an agricultural habitat (n = 132; males, 58; females, 74) and a nonagricultural habitat (n = 40; males, 17; females, 23). Frogs were hand-captured, preferentially at night, using the sampling technique defined as ''visual encounters survey'' (Crump and Scott, 1994). Frogs were transported live to the laboratory, killed in a chloroform ($CHCl_3$) solution, and their snout-vent length and body weight were recorded. At necropsy, hosts were sexed and the esophagus, stomach, gut, lungs, liver, urinary bladder, kidneys, body cavity, musculature, skin, and brain were examined for parasites. Helminths were observed in vivo, counted, and killed in hot distilled water and pre-

TABLE II. Results of conditional effects of the infection in different sites showing the significance of these variables from *Leptodactylus chaquensis* of agricultural and nonagricultural areas.

Site of infection‡	Agricultural area†				Nonagricultural area†			
	No.	Lambda A	*P*	*F*	No.	Lambda A	*P*	*F*
Uri-Bla	7	0.140	*0.002	6.590	3	0.180	*0.004	3.960
Lung	6	0.190	*0.002	6.890	2	0.170	*0.002	4.190
Bod-Cav	4	0.160	*0.002	6.350	10	0.110	*0.024	2.650
Liver	9	0.290	*0.002	9.080	11	0.110	*0.012	2.800
Mesentery	5	0.090	0.026	4.220	8	0.090	*0.040	2.510
Lar-Int	3	0.040	0.090	1.810	1	0.070	*0.038	2.230
Mid-Int	2	0.150	*0.010	6.030	5	0.080	*0.042	2.320
Pha-Zon	—	—	—	—	9	0.050	0.138	1.500
Ant-Int	1	0.20	*0.002	6.840	4	0.040	0.234	1.240
Muscle	—	—	—	—	7	0.020	0.748	0.580
Kidney	8	0.360	*0.002	10.550	6	0.020	0.822	0.450

* $P < 0.05$.
† P = probability, F = Fisher's ratio.
‡ Site of infection: Ant-Int, anterior portion of the small intestine; Bod-Cav, body cavity; Lar-Int, large intestine; Mid-Int, midportion of the small intestine; Pha-Zon, pharyngeal zone; Uri-Blad, urinary bladder.

served in 70% ethyl alcohol. Digeneans, cestodes, and acanthocephalans were stained with hydrochloric carmine, cleared in creosote, and mounted in Canada balsam. Nematodes were cleared in glycerine or lactophenol, and examined as temporary mounts. Helminths were identified using criteria provided by Yamaguti (1961, 1963, 1971, 1975), Anderson et al. (1974), Baker (1987), Anderson (2000), Gibson et al. (2002), and Jones et al. (2005). Specimens of the various parasite species were deposited in the Helminthological Collection of Centro de Ecología Aplicada del Litoral (CECOAL-CONICET, Corrientes City, Corrientes, Argentina). Site of infection categories recorded for individual parasites included the lung, pharyngeal zone (Pha-Zon), anterior portion of the small intestine (Ant-Int), midportion of the small intestine (Mid-Int), large intestine (Lar-Int), body cavity (Bod-Cav), mesenteries, urinary bladder (Uri-Bla), kidney, liver, and muscle.

Statistical analysis

Prevalence, intensity, and abundance were calculated according to criteria provided by Bush et al. (1997). The measures of community richness and diversity employed included the total number of helminth species (= richness), mean richness, Shannon index (H') (Shannon and Weaver, 1949), evenness (J') as H'/H' maximum (Pielou, 1966; Zar, 1996). The diversity index was used with decimal logarithms ($\log_{10}$). A *t*-test was used to test for significant difference in H' (Hutcheson, 1970). A Mann-Whitney *U*-test was used to test for differences in helminth richness among the sexes and to compare differences in species richness between agricultural and nonagricultural environments. A Spearman Rank test (r_s) was calculated for the correlation between host size and helminth species richness. The statistic z was used to compare 2 proportions (prevalence) of helminth infection. A chi-square test with Yates correction for continuity was used for comparing the intensity of helminth infection between the 2 habitats, and for comparing the sex ratio of the frogs. A 2×2 contingency table was used for comparing the infection between the sexes.

Species covariation was analyzed with the Spearman test correlation. The species associations were analyzed with a Jaccard test. Relationships between site of infection and parasite species and infection strategy were tested through a canonical correspondence analysis (CCA; Ter Braak, 1986, 1987). The CCA is a multivariate direct gradient analysis method derived from correspondence analysis, but it has been modified to incorporate environmental data into the analysis. The result is that the axes of the final ordination, rather than simply reflecting the dimensions of the greatest variability in the species data, are restricted to linear combinations of the environmental variables and the species data. The CCA interpretation is very important in considering the species localization, the abundance variability at the time, and the vector length. The vector length is directly proportional to importance on the total variance of the system (i.e., the community). When the species are nearest to the arrowhead, there is more correlation between them. When the species are near the central point in the diagram (0 values), lower abundance variability is indicated. For CCA, the only species considered were those that had at least 5% occurrences in each of the amphibian's populations (agricultural area = 14 species; nonagricultural area = 10 species). The software we used was Canoco 4.5 (Ter Braak and Smilauer, 2004).

We used the Mantel test to compare matrices with the covariation and association values among the parasites of each environment (Mantel, 1967). Significance was calculated using 10,000 randomized permutations through the Monte Carlo test. The software we used was Xlstat 7.5 (Addinsoft, 2004). Because the samples sizes were different in the 2 habitats, we used rarefaction methods for comparing the mean diversity and the mean richness. Rarefaction uses probability theory to derive expressions for the expectation and variance of species diversity and richness for a sample of a given size. This method ''rarefies'' its samples down to a common abundance level and then compares species diversity and richness. The process was repeated 1,000 times to generate a mean and a variance of species diversity and richness. For this calculation, we used EcoSim 7 software (Gotelli and Entsminger, 2004).

RESULTS

General characteristics

Twenty-four helminth species were found in the 172 individuals of *L. chaquensis* from the 2 habitats. The predominant groups of parasites were the trematodes (16 species), followed by the nematodes (5 species); other groups of parasites were represented by only 1 or 2 species (Table I). Parasites were found in all the major organs, with highest prevalence and intensity in the small intestine (Ant-Int; Mid-Int), large intestine, lung, liver, and kidney. Among adult helminths encountered, 7 have indirect life cycles (*Haematoloechus longiplexus*, *Gorgoderina parvicava*, *Gorgoderina rocholimai*, *Glypthelmins palmipedis*, *Glypthelmins repandum*, *Catadiscus inopinatus*, and *Catadiscus propinquus*) and 4 have direct life cycles (*Cosmocerca podicipinus*, *Cosmocerca parva*, *Aplectana hylambatis*, and *Rhabdias* sp.).

Community structure analysis

The helminth component community in the agricultural habitat consisted of 19 species: 11 trematodes, 2 cestodes, 5 nem-

TABLE III. Summary of main results of the canonical correspondence analysis relating helminth species to the site of infection variables in an agricultural area.

Canonical axes	I	II	III	IV
Eigenvalues	0.43	0.39	0.27	0.25
Cumulative percentage of variance of species data	13.40	25.50	34.00	41.90
Cumulative percentage variance of species-site relation	26.30	50.20	67.00	82.40
Species-infection site correlation	0.87	0.82	0.83	0.79
Correlation of the infection sites variable with the axes				
Ant-Int*	0.15	0.37	−0.41	0.40
Mid-Int*	0.27	0.48	−0.03	0.18
Lar-Int*	−0.41	0.08	−0.08	−0.10
Bod-cav*	0.12	−0.08	0.47	0.48
Mesentery	0.04	0.05	0.48	0.26
Lung	−0.52	−0.48	−0.20	−0.22
Uri-Bla*	0.54	−0.60	−0.19	−0.09
Kidney	0.69	−0.60	−0.15	−0.12
Liver	−0.40	−0.23	−0.45	0.71
Total of unconstrained eigenvalues 3.19.				
Total of canonical eigenvalues 1.62 (51% of explained variance).				

* Site of infection: Ant-Int, anterior portion of the small intestine; Bod-Cav, body cavity; Lar-Int, large intestine; Mid-Int, midportion of the small intestine; Pha-Zon, pharyngeal zone; Uri-Blad, urinary bladder.

atodes, and 1 acanthocephalan (Table I). Helminth diversity (H' = 0.73) and evenness (J' = 0.57) were high. At the infracommunity level, the mean helminth richness was 2.1 ± 1.2 (maximum = 6) species per frog infected. Multiple infections were common, with 0, 1, 2, 3, 4, 5, and 6 species occurring in 40, 39, 27, 14, 7, 4, and 1 frog, respectively.

In the nonagricultural habitat, the helminth component community consisted of 18 species: 13 trematodes, 4 nematodes, and 1 acanthocephalan (Table I). Helminth diversity (H' = 0.35) and evenness (J' = 0.28) were low. At the infracommunity level, the mean helminth richness was 4.7 ± 1.8 (maximum = 8) species per infected frog. Multiple infections were common, with 1, 2, 3, 4, 5, 6, 7, and 8 species occurring in 2, 3, 4, 10, 9, 5, 5, and 2 frogs, respectively.

Correlation between helminth and site of infection

Among the 9 sites of infection in hosts from agricultural localities, those with heaviest infections were selected for modeling (Table I). The model is based on the following formula: y = (Ant-Int + Mid-Int + Lar-Int + Bod-Cav + mesenteries + lung + Uri-Bla + kidney + liver)/(season + weight). In this case, ''season'' and host ''weight'' were considered as covariables. The site of infection variables selected explained 51% of the total variation in helminth specie frequency of occurrence. Moreover, the first 4 canonical axes account for 82% of the variance explained by these variables (Table III). The species-site relationship was highly significant according to the Monte Carlo permutation test (F = 11.43; P = 0.002; 499 permutations), as well as the first canonical axis (F = 8.48; P = 0.002; 499 permutations).

A biplot of site of infection and CCA variable scores on the first 2 ordination axes of helminths from the agricultural area showed that the kidney and urinary bladder exhibited the greatest variability in the abundance of the helminth parasites, and included 2 parasite groups on the axis I (Fig. 1). There was a positive correlation formed by *Bursotrema* aff. *tetracotyloides* with the kidney and *G. parvicava* with urinary bladder. The second parasite group exhibited a negative correlation with the first group and was characterized by associations between *H. longiplexus* and the lung, *C. podicipinus* with large intestine, and an unknown strigeid species No. 2 with liver.

Among the 11 sites of infection in hosts from nonagricultural localities, those with heaviest infections were selected for modeling (Table II). The model is based on the following formula: y = (Lar-Int + lung + Uri-Bla + Mid-Int + mesenteries + Bod-Cav + liver)/(season + weight). Similar to the other habitat, ''season'' and host ''weight'' were considered as covariables in the model. The site of infection variables selected explained 45% of the total variation in helminth taxa frequency of occurrence. Moreover, the first 4 canonical axes account for 78% of the variance explained by these variables (Table IV). The species-site relationship was highly significant according to the Monte Carlo permutation test (F = 3.47; P = 0.018; 499 permutations), as well as the first canonical axis (F = 3.93; P = 0.002; 499 permutations).

A biplot of site of infection and CCA variable scores on the first 2 ordination axes showed that the urinary bladder, lung, and large intestine exhibited the greatest variability in the abundance of parasites species, with 2 parasite groups on axis I (Fig. 2). There was a high positive correlation formed by *H. longiplexus* with the lung and *C. inopinatus* with the large intestine. The second parasite group exhibited a negative correlation to the first group and was characterized by low species-infection site correlations. Other important associations that contributed significantly to the variance explained for the ordination on the axis II was formed by the positive correlation between *G. parvicava* and urinary bladder (Fig. 2).

Interspecific relationships in the infracommunity

Four correlations between species in the agricultural habitat were positive and significant: *G. palmipedis*/*G. repandum*, *C. parva*/*A. hylambatis*, *C. parva*/*C. podicipinus*, and an unknown

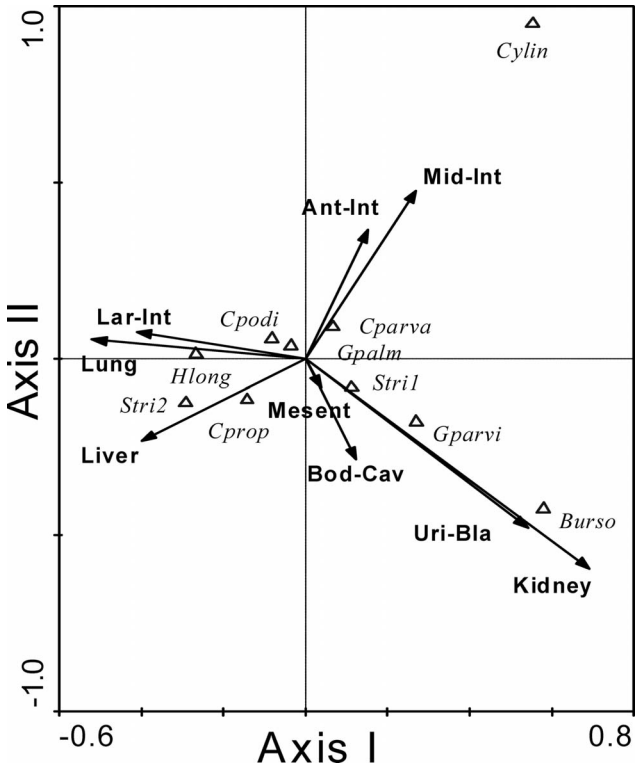

FIGURE 1. Biplot of canonical correspondence analysis (CCA) results for helminth species. Triangles are helminth species of *Leptodactylus chaquensis* in an agricultural area (rice field) near Corrientes City, Argentina. Names of helminth species: *Glypthelmins palmipedis* (*Gpalm*), *Cosmocerca podicipinus* (*Cpodi*), *Gorgoderina parvicava* (*Gparvi*), *Bursotrema* aff. *tetracotyloides* (*Burso*), unknown strigeid species No. 1 (*Stri1*), unknown strigeid species No. 2 (*Stri2*), *Haematoloechus longiplexus* (*Hlong*), *Cosmocerca parva* (*Cparva*), and *Catadiscus propinquus* (*Cprop*). Arrows represent site of infection scores (arrowhead position) and directions of site of infection gradients. Site of infection: urinary bladder (Uri-Bla), large intestine (Lar-Int), small anterior intestine (Ant-Int), small midintestine (Mid-Int), mesentery (Mesent), and body cavity (Bod-Cav).

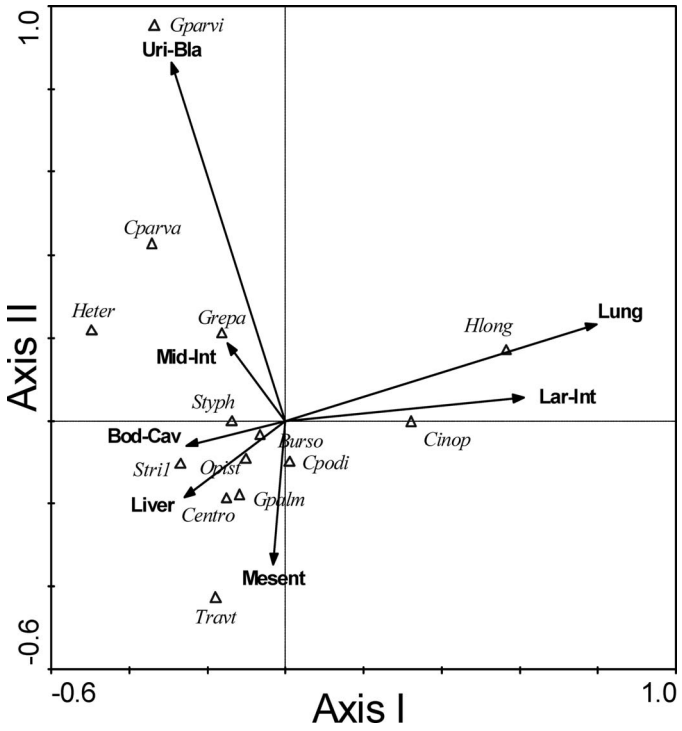

FIGURE 2. Biplot of canonical correspondence analysis (CCA) results for helminth species. Triangles are helminth species of *Leptodactylus chaquensis* in a nonagricultural area near Corrientes City, Argentina. Names of helminth species: *Glypthelmins repandum* (*Grepa*), *Glypthelmins palmipedis* (*Gpalm*), *Cosmocerca podicipinus* (*Cpodi*), *Gorgoderina parvicava* (*Gparvi*), *Bursotrema* aff. *tetracotyloides* (*Burso*), unknown strigeid species No. 1 (*Stri1*), *Travtrema* aff. *stenocotyle* (*Travt*), *Centrorhynchus* sp. (*Centro*), *Haematoloechus longiplexus* (*Hlong*), *Cosmocerca parva* (*Cparva*), *Heterodiplostomum* sp. (*Heter*), *Styphlodora* sp. (*Styph*) and unknown opisthogonimid species (*Opist*). Arrows represent site of infection scores (arrowhead position) and directions of site of infection gradients. Site of infection codes as in Figure 1.

TABLE IV. Summary of main results of the canonical correspondence analysis relating helminth species to the site of infection variables in a nonagricultural area.

Canonical axes	I	II	III	IV
Eigenvalues	0.21	0.19	0.12	0.11
Cumulative percentage of variance of species data	11.60	22.20	29.00	34.90
Cumulative percentage variance of species-site relation	25.90	49.60	64.80	77.90
Species-infection site correlation	0.89	0.92	0.83	0.79
Correlation of the infection site variable with the axes				
Lar-Int*	0.61	0.06	−0.33	0.16
Lung	0.80	0.23	0.38	0.22
Uri-Bla*	−0.29	0.86	−0.08	0.07
Mid-Int*	−0.15	0.19	0.09	−0.15
Mesent	−0.03	−0.35	0.05	0.32
Bod-Cav*	−0.25	−0.06	−0.11	0.77
Liver	−0.26	−0.18	0.73	0.04
Total of unconstrained eigenvalues 1.81.				
Total of canonical eigenvalues 0.81 (45% of explained variance).				

* Site of infection: Bod-Cav, body cavity; Lar-Int, large intestine; Mid-Int, midportion of the small intestine; Uri-Blad, urinary bladder.

TABLE V. Interspecific interaction among 13 species common in both areas.†

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13
S1		*0.98	−0.15	−0.22	−0.15	−0.15	0.22	−0.34	−0.22	−0.15	−0.15	−0.15	−0.15
		1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S2	*0.74		−0.15	−0.22	−0.15	−0.15	−0.22	−0.34	−0.22	−0.15	−0.15	−0.15	−0.15
	0.5		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S3	0.28	−0.15		*0.74	−0.10	−0.10	−0.15	−0.23	−0.15	−0.10	−0.10	*1.00	−0.10
	0.3	0.0		0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
S4	−0.22	−0.15	0.50		−0.15	−0.15	−0.22	−0.34	−0.22	0.59	−0.15	*0.74	−0.15
	0.0	0.0	0.3		0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.5	0.0
S5	−0.15	−0.10	−0.15	−0.15		−0.10	−0.15	−0.23	−0.15	−0.10	−0.10	−0.10	−0.10
	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S6	−0.15	−0.10	−0.15	−0.15	−0.10		−0.15	−0.23	−0.15	−0.10	−0.10	−0.10	−0.10
	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0
S7	−0.22	−0.15	−0.22	−0.22	−0.15	−0.15		0.44	−0.22	−0.15	−0.15	−0.15	−0.15
	0.0	0.0	0.0	0.0	0.0	0.0		0.5	0.0	0.0	0.0	0.0	0.0
S8	−0.15	−0.10	−0.15	−0.15	−0.10	−0.10	−0.15		0.12	−0.23	−0.23	−0.23	0.46
	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.2	0.0	0.0	0.0	0.2
S9	−0.15	−0.10	−0.15	−0.15	−0.10	−0.10	0.59	−0.10		−0.15	*0.74	−0.15	0.59
	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0		0.0	0.5	0.0	1.0
S10	−0.15	−0.10	−0.15	0.59	−0.10	−0.10	−0.15	−0.10	−0.10		−0.10	−0.10	−0.10
	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0
S11	−0.15	−0.10	−0.15	−0.15	−0.10	−0.10	−0.15	−0.10	−0.10	−0.10		−0.10	−0.10
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0	0.5
S12	−0.15	−0.10	*0.74	*0.74	−0.10	−0.10	−0.15	−0.10	−0.10	−0.10	−0.10		−0.10
	0.0	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0
S13	−0.22	−0.15	−0.22	−0.22	−0.15	−0.15	0.28	−0.15	0.59	−0.15	*0.74	−0.15	
	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.5	0.0	0.5	0.0	

* $P < 0.05$.

† Superior triangle shows the covariation (superior cell) and association (inferior cell) interspecific in frog of nonagricultural area. Inferior triangle shows the covariation and association interspecific in frog of agricultural area. S1, *Glypthelmins repandum*; S2, *Glypthelmins palmipedis*; S3, *Aplectana hylambatis*; S4, *Cosmocerca podicipinus*; S5, *Gorgoderina parvicava*; S6, *Bursotrema* aff. *tetracotyloides*; S7, unknown strigeid species No. 1; S8, *Travtrema* aff. *stenocotyle*; S9, *Centrorhynchus* sp.; S10, *Haematoloechus longiplexus*; S11, unknown strigeid species No. 2; S12, *Cosmocerca parva*; S13, *Porrocaecum* sp.

strigeid species No.2/*Porrocaecum* sp. (Table V). Seven associations $P \geq 0.5$ were observed among the 13 species analyzed (Table V).

In the nonagricultural habitat, 5 correlations between species were positive and significant: *G. palmipedis*/*G. repandum*, *C. podicipinus*/*A. hylambatis*, *C. parva*/*A. hylambatis*, *C. parva*/*C. podicipinus*, and an unknown strigeid species No. 2/*Centrorhynchus* sp. (Table V). Eight associations $P \geq 0.5$ were registered among the 13 species considered (Table V).

Comparison of infection between the 2 habitats

In both areas, the infracommunity of helminth parasites was similar in a set of 13 species (70%). Diversity of the helminth infracommunity between the 2 localities showed a significant difference ($t = -25.28$; V = 5783.57; $P < 0.001$); the agricultural habitat ($H' = 0.73$) was thus more diverse than the nonagricultural area ($H' = 0.35$). There was also significant variation in helminths between the 2 habitats with respect to prevalence and intensity of infection. The intensity of trematodes was highest in the nonagricultural area, whereas the intensity of the nematodes was highest in the agricultural area (Table I).

Using a rarefaction method, the number of individuals was combined and the values of mean richness and mean diversity for each of the localities were obtained (Table VI). Mean species richness of the helminth infracommunity between the 2 environments were different (i.e., greater in the agricultural area; Mann-Whitney U-test = 109; $P = 0.001$; $n_1 = 23$; $n_2 = 23$). Mean species diversity of the helminth infracommunity between the 2 habitats was also different (i.e., greater in the agricultural area; Mann-Whitney U-test = 529; $P = 0.0001$; $n_1 = 23$; $n_2 = 23$).

In both environments, the interspecific relationships exhibited a very similar pattern (Table V). The 2 covariation matrices (1 for each area) showed a significant correlation (Mantel Test: $r_s = 0.78$; $P_{(0.05;2)} = 0.0001$), suggesting the same relationships in the abundance of the 13 species of parasites analyzed. The same response was observed in the associations of the 13 species using Jaccard's matrix (Mantel test: $r = 0.75$; $P_{(0.05;2)} = 0.001$), which showed the same tendency for the 2 association matrices.

Infection related to host body size and gender

Of the 132 frogs examined from the agricultural area, infection prevalence was 70%; there was no significant difference in the number of infected females (53) versus the males (39) ($\chi^2 = 0.12$; df = l; $P > 0.05$). The sex ratio of the frogs was not significantly different ($\chi^2 = 1.94$; df = 1; $P > 0.05$; females = 74, males = 58). Parasite richness did not have a relationship with host sex ($U = 2323$; $P = 0.40$; $n_1 = 74$; $n_2 = 58$); however, a significant positive correlation was found between frog size and helminth species richness (weight: $r_s = 0.48$; $P = 0.0001$; body length: $r_s = 0.49$; $P = 0.0001$).

TABLE VI. Summary of main results of the rarefaction method in which the number of individuals was unified and from which the values of mean richness and mean diversity ± 1 SD were obtained for agricultural and nonagricultural areas.

	Agricultural area		Nonagricultural area	
Abundance	Richness $\bar{\chi}$ ± SD	Diversity $\bar{\chi}$ ± SD	Richness $\bar{\chi}$ ± SD	Diversity $\bar{\chi}$ ± SD
100	11.19 ± 3.35	0.69 ± 0.54	8.90 ± 2.98	0.32 ± 0.37
200	13.80 ± 3.71	0.71 ± 0.55	11.43 ± 3.38	0.33 ± 0.38
300	14.97 ± 3.87	0.72 ± 0.56	12.75 ± 3.57	0.34 ± 0.38
400	15.65 ± 3.96	0.72 ± 0.56	13.52 ± 3.68	0.34 ± 0.38
500	16.14 ± 4.02	0.72 ± 0.56	14.16 ± 3.76	0.34 ± 0.38
600	16.49 ± 4.06	0.73 ± 0.56	14.65 ± 3.83	0.35 ± 0.38
700	16.79 ± 4.10	0.73 ± 0.56	15.02 ± 3.88	0.35 ± 0.38
800	17.05 ± 4.13	0.73 ± 0.56	15.32 ± 3.91	0.35 ± 0.39
900	17.29 ± 4.16	0.73 ± 0.56	15.61 ± 3.95	0.35 ± 0.39
1,000	17.50 ± 4.18	0.73 ± 0.56	15.87 ± 3.98	0.35 ± 0.39
1,100	17.67 ± 4.20	0.73 ± 0.56	16.06 ± 4.01	0.35 ± 0.39
1,200	17.86 ± 4.23	0.73 ± 0.56	16.23 ± 4.03	0.35 ± 0.39
1,300	18.02 ± 4.24	0.73 ± 0.56	16.38 ± 4.05	0.35 ± 0.39
1,400	18.18 ± 4.26	0.73 ± 0.56	16.53 ± 4.07	0.35 ± 0.39
1,500	18.31 ± 4.28	0.73 ± 0.56	16.67 ± 4.08	0.35 ± 0.39
1,600	18.41 ± 4.29	0.73 ± 0.56	16.82 ± 4.10	0.35 ± 0.39
1,700	18.52 ± 4.30	0.73 ± 0.56	16.93 ± 4.11	0.35 ± 0.39
1,800	18.63 ± 4.32	0.73 ± 0.56	17.01 ± 4.12	0.35 ± 0.39
1,900	18.73 ± 4.33	0.73 ± 0.56	17.10 ± 4.14	0.35 ± 0.39
2,000	18.79 ± 4.33	0.73 ± 0.56	17.17 ± 4.14	0.35 ± 0.39
2,100	18.88 ± 4.35	0.73 ± 0.56	17.25 ± 4.15	0.35 ± 0.39
2,200	18.94 ± 4.35	0.73 ± 0.56	17.31 ± 4.16	0.35 ± 0.39
2,300	18.98 ± 4.36	0.73 ± 0.56	17.38 ± 4.17	0.35 ± 0.39

Of the 40 frogs examined from the nonagricultural area, the infection prevalence was 100% in both sexes. The sex ratio of the frogs was not significantly different ($\chi^2 = 0.92$; df = 1; $P > 0.05$; females = 23, males = 17). Parasite richness did not show a significant relationship with host sex ($U = 277$; $P = 0.38$; $n_1 = 23$; $n_2 = 17$), whereas a significant positive correlation was found between frog size and helminth richness (weight: $r_s = 0.45$; $P = 0.004$; body length: $r_s = 0.40$; $P = 0.01$).

DISCUSSION

Helminth infracommunities of *L. chaquensis* in the 2 areas share a set of 13 species (70%). Despite this similarity, the mean species richness and mean diversity were significantly different ($P < 0.05$). The infections by trematodes were higher in the nonagricultural habitat than in the agricultural area; frogs of the agricultural locality were infected primarily by nematodes. Specifically, *L. chaquensis* in the agricultural area harbored a maximum of 6 species and a high diversity with a more equitable distribution. In contrast, frogs in the nonagricultural habitat were infected by a maximum of 8 species, but exhibited a lower diversity with a less equitable distribution. In both localities, trematodes exhibited the highest species richness. Host characteristics, primarily habitat, diet, and vagility, most likely influenced the probability of infection with the flukes.

Adult amphibians occupied a variety of sites in the nonagricultural area, including patches of dry ground, flooded grassland, and along the shores of ephemeral and permanent ponds, especially those in which there was a higher exposure to cercariae, or potential intermediate hosts. The high intensity of infection of trematodes in this area may be related to both stability and heterogeneity of the habitat, encouraging greater numbers and a higher diversity of intermediate invertebrate hosts. This suggests that nonagricultural habitats provide a significant opportunity to complete the parasite life cycle (Esch et al., 2002) through the acquisition of an array of infective larvae (Vickery and Poulin, 2002).

Adult amphibians in the agricultural area occupied a habitat where the water level was regulated within the rice plantations. The instability (e.g., periodic desiccation and perhaps pollution such as toxic pesticides) in this habitat would not favor the permanency of intermediate hosts, leading to the low occurrence of trematode parasites. These circumstances could also affect transmission and population dynamics of these parasites.

The analysis presented here emphasizes the importance of transmission dynamics in determining the composition of helminth infracommunities in specific habitats. Of the 4 dominant (>50%) parasite species (e.g., *G. palmipedis*, *C. inopinatus*, *Bursotrema* aff. *tetracotyloides*, and *C. podicipinus*) recorded in the frog's component community, only *C. podicipinus* was dominant in both habitats, whereas the remaining species were dominant only in the nonagricultural area. This is particularly important because *C. podicipinus* has a direct terrestrial life cycle in which the larvae penetrate the skin of the host before migrating to the large intestine (Anderson, 2000). The other 3 dominant species have indirect life cycles. Frogs become infected directly when cercariae of *Bursotrema* aff. *tetracotyloides* pass through the skin of the host and metacercariae encyst in the kidney. Mammals (e.g., weasels) are the definitive host for this trematode (M. I. Hamann, pers. comm.). For *G. palmipedis* and *C. inopinatus*, *L. chaquensis* is the definitive host. The life cycle of *C. inopinatus* is not known, but it probably resembles that of other amphibian paramphistomes (Smyth and Smyth, 1980). Cercariae would thus emerge from snail hosts (M. I. Hamann, pers. comm.), encyst as a metacercariae stage on the frog skin or on different substrata, and then be ingested when the frog feeds. The life cycle of *G. palmipedis* most likely is patterned similar to that of *G. quieta*, where their metacercariae encysts in tadpoles and frog skin (Leigh, 1946; Grabda-Kazubsska, 1976; Smyth and Smyth, 1980). The frog acquires infective metacercariae when the cercariae penetrate their skin or when infected tadpoles ingest their own skin at the time of metamorphosis to the adult stage.

Frog body size has been recognized as an important correlate of parasite richness (McAlpine, 1997; Hamann and Kehr, 1998; Kehr et al., 2000; Muzzall et al., 2001; Bolek and Coggins, 2003; Hamann, 2004). Our data indicated that richness of helminth infracommunities in *L. chaquensis* in both localities was affected by frog body size (larger hosts had higher richness of parasites than the smaller ones). This result could be explained by the fact that larger amphibians ingest greater amounts of food (Duré, 1999). The larger surface area of the host may also increase opportunities for infection where parasites with direct life cycles are involved. However, no significant difference was noted between host gender and richness, in agreement with the findings of Poulin (2001).

In previous studies, helminth community structure in amphibians were reported as highly variable, depauperate, and

were shown to have traits characteristic of isolationist communities (Yoder and Coggins, 1996; McAlpine, 1997; Bolek and Coggins, 2003). Working with *Lysapsus limellum* in Argentina, Kehr et al. (2000) found no fixed pattern that could be identified as isolationist/depauperate or interactive. In the present study, the 2 communities can be classified as intermediate point between the extremes (i.e., isolationist and interactive).

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