

Helminth community structure of the oven frog *Leptodactylus latinasus* (Anura, Leptodactylidae) from Corrientes, Argentina

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Abstract

A total of 36 adult individuals of *Leptodactylus latinasus* were collected near the city of Corrientes, Province of Corrientes in Argentina. The main goals of this study were: (1) to determine the helminth parasite fauna of *L. latinasus*; (2) to determine the richness and diversity of parasites at the component and infracommunity levels; (3) to analyze the relationships between helminth, frog body size and sex; and (4) to identify and examine species affinity of helminth communities. The helminth component community of this frog's population consisted of 17 species. The predominant groups of parasites were the trematodes (adults: *Glypthelmins repandum*, *Catadiscus inopinatus* and *Haematoloechus longiplexus*; larvae: *Travtrema* aff. *stenocotyle*, *Bursotrema* aff. *tetracotyloides*, *Styphlodora* sp., unknown opisthogonimid species, *Petasiger* sp. and unknown strigeid species), followed by the nematodes (*Cosmocerca podicipinus*, *C. parva*, *C. rara*, *C. cruzi*, *Schrankiana schranki* and *Aplectana hylambatis*); other groups of parasites were represented by only one species (unknown larval cestode species and *Centrorhynchus* sp.). All parasite helminth species showed an aggregated pattern of distribution. The most infected organs were kidneys, small intestine, large intestine and pharyngeal zone. The host body size was important in determining the parasites abundance of *G. repandum*. At the level of component community *G. repandum* was the species with highest prevalence of infection and *Bursotrema* aff. *tetracotyloides* was the dominant species. Helminth species showed four significant pairs of covariation and two significant pairs of association in the infracommunities of *Leptodactylus latinasus*.

Key words

Parasite ecology, helminth parasites, Anura, *Leptodactylus latinasus*, Argentina

Introduction

Studies on the helminth communities of amphibians in the northern hemisphere have increased in recent years. These studies demonstrated that the parasite community structure depended on many different factors, including both host and parasite life histories (i.e., coevolution) (Janovy *et al.* 1992, Brooks *et al.* 2006), the host's characteristic habitat, and host feeding preferences (McAlpine and Burt 1998, Muzzall 1991, Muzzall *et al.* 2001, Bolek and Coggins 2003, Zelmer *et al.* 2004). In addition, host species, body size and sex (Tucker and Joy 1996; McAlpine 1997; Joy and Pennington 1998; Bolek and Coggins 2001; Goldberg and Bursey 2002; Goldberg *et al.* 2002a, b) are important factors in the intricate inter-relationships between parasites and their host in addition to the colonization probabilities of parasites. In Argentina, despite the great diversity of amphibian's fauna (Frost 2004), this area of research is only beginning (Kehr *et al.* 2000, Kehr and

Hamann 2003, Hamann *et al.* 2006). Nevertheless, the helminth parasites of amphibians have been analyzed primarily at the infrapopulation level. These studies have reported that the seasonal maturation of parasites in the host is likely dictated by environmental conditions, such as rainfall and dry periods, since temperature is not a limiting factor in determining seasonal maturation on parasites in the Corrientes Province (Hamann 2004, 2006). On the other hand, biotic (e.g., host body size) characteristic are one of the factors that is likely associated with parasitic infections (Hamann and Kehr 1998, 1999a, b).

The present study analyzes the infracommunity of helminth parasites in the frog *Leptodactylus latinasus* Jiménez de la Espada, 1875. This frog belongs to the *fuscus* group within the genus *Leptodactylus* (Fitzinger, 1826). Adult *L. latinasus* can survive in both dry and moist substrata, i.e. near to the shore of temporary, semipermanent and permanent ponds, and also in the flooded grass. It may be considered as a generalist feeder with a foraging strategy intermediate between sit-and-

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wait and an actively foraging predator (Duré and Kehr 2004). *L. latinasus* is distributed in Argentina in the provinces of: Buenos Aires, Córdoba, Santa Fé, Chaco, Formosa, Entre Ríos, Corrientes and Misiones, and also occurs in Uruguay and Brazil (Frost 2004).

The main goals of this study were: (1) to report the helminth parasite fauna of *L. latinasus*; (2) to determine the richness and diversity of parasites at the component and infracommunity levels; (3) to analyze the relationships between helminth, frog body size and sex; and (4) to identify and examine species affinity of helminth communities.

Materials and methods

Study area

Study area is located in the northwest of the Province of Corrientes in Argentina ($27^{\circ}27'S$, $58^{\circ}47'W$). The predominant vegetation of the study area is forest, with herbaceous strata composed of grasslands, numerous cacti and terrestrial bromeliads. Also, temporary, semipermanent and permanent ponds characterize the habitat.

Analytical procedure

Samples of *L. latinasus* were collected in September 2002 ($n = 5$ specimens), and from January to November 2003 (January = 3 specimens, February = 2, March = 4, May = 4, September = 14, October = 2 and November = 2). Frogs were hand-captured, mainly 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 solution; and their snout-vent length (SVL) and body weight were recorded. At necropsy, hosts were sexed and the oesophagus, stomach, gut, lungs, liver, urinary bladder, kidneys, body cavity, musculature, integument and brain examined for parasites. Helminths were observed *in vivo*, counted, killed in hot distilled water and preserved 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. The systematic determination of the helminths was carried out following the approaches given by Yamaguti (1961, 1963, 1971, 1975), Anderson *et al.* (1974), Gibson *et al.* (2002) and Jones *et al.* (2005). Specimens of parasite species were deposited in the Helminthological Collection of Centro de Ecología Aplicada del Litoral (CECOAL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Corrientes, Argentina [accession numbers CECOAL: 03092406, *Glypthelmins repandum* (Rudolphi, 1819); 03092404, *Catadiscus inopinatus* Freitas, 1841; 03042402, *Haematoloechus longiplexus* Stafford, 1902; 05022430, *Styphlodora* sp.; 03092401, *Bursotrema* aff. *tetracotyloides* Szidat, 1960; 03092404, *Travtrema* aff. *stenocotyle* Cohn, 1902; 03022001, unknown opisthogonimid species; 03091002, *Petasiger* sp;

02113237, unknown cestode species; 03052907, *Cosmocerca podicipinus* Baker et Vaucher, 1984; 03051609, *Cosmocerca parva* Travassos, 1925; 03092404, *Cosmocerca rara* Freitas et Vicente, 1966; 03092405, *Cosmocerca cruzi* Rodriguez et Fabio, 1970; 0301333, *Aplectana hylambatis* (Baylis, 1927); 03023524, *Schrankiana schranki* (Travassos, 1925); 03052908, *Centrorhynchus* sp.].

Statistical analysis

The infection prevalence, intensity and abundance were calculated for helminths according to Bush *et al.* (1997). The measures of community richness and diversity employed included: The total number of helminth species (= richness), Shannon's index (H') (Shannon and Weaver 1949), and evenness (J') as H'/H' maximum (Pielou 1966, Zar 1996). Mean helminth species richness is the sum of helminth species per individual frog, including uninfected individuals, divided by the total sample size. The diversity index was used with decimal logarithms (\log_{10}). Berger-Parker's index of dominance (d) was used to determine the most abundant species (Magurran 2004). All values are expressed as a mean \pm standard deviation. Helminth communities have been classified at the infracommunity (all helminth infrapopulations within a single oven frog) and component community (all helminth infracommunities within a population of the oven frog) levels. Mann-Whitney's U-test was used to test for differences in helminth richness among the sex. Chi-square test (χ^2), with Yates correction for continuity, was used for comparing the sex ratio of the frogs. Fisher's exact test (P) was used for comparing the infection between the sexes. Pearson's coefficient correlation (r) was used to indicate the relationship between host body size and infracommunity descriptors. Spearman's rank test (r_s) was used to calculate possible correlations between host body size and parasitic abundance. Species covariation was analyzed with the Spearman's test correlation. The species associations was analyzed with a chi-square test, with Yates correction for continuity. The software used was XLstat 7.5 (Addinsoft 2004). For covariation and associations, the only species considered were those that had at least 10% occurrences in each of the amphibian's populations (six species).

Results

Community structure analysis

The helminth component community of this frog's population consisted of 17 helminth species (Table I). The predominant groups of parasites were trematodes (53%) followed by nematodes (35%); the other groups of parasites were represented by only 1 species (unknown larval cestode species and *Centrorhynchus* sp.). Helminth diversity ($H' = 0.90$) and evenness ($J' = 0.73$) were high. The metacercariae *Bursotrema* aff. *tetracotyloides* was the dominant species ($d = 0.30$). All helminth parasites of *L. latinasus* showed the typical aggregated pattern

of distribution observed in many helminths (Table I). Parasites were found in kidneys, small intestine, large intestine and pharyngeal zone with high level of prevalence and intensity. Of all helminths examined, 3 are assumed to have indirect life cycles (*G. repandum*, *C. inopinatus* and *H. longiplexus*, and 6 are assumed to have direct life cycles (*C. podicipinus*, *C. parva*, *C. rara*, *C. cruzi*, *A. hylambatis* and *S. schranki*).

At the level of infracommunity, the mean helminth richness was 2.40 ± 1.50 (maximum = 8) species per frog infected. Multiple infections were common, with 0, 1, 2, 3, 4, 5, and 8 species occurring in 1, 9, 12, 7, 4, 2, and 1 frog, respectively. The mean helminth value of diversity ($H' = 0.25 \pm 0.19$)

and evenness ($J' = 0.57 \pm 0.36$) were low. The Berger-Parker's index of dominance for the infracommunities was 0.75 ± 0.20 .

Infection in relation to host's sex and body size

Of 36 frogs examined, the infection prevalence was 44% for females, and 53% for males; there was no significant difference in the number of infected females (16) vs. the males (19) ($P = 0.47$). The sex ratio of the frogs was not significantly different ($\chi^2 = 0.14$; $df = 1$; $P > 0.05$; females = 17, males = 19). Parasite richness was not correlated with host sex (Mann-Whitney's U-test = 182; $P > 0.05$; $n_1 = 19$; $n_2 = 17$). Total length of the frogs ranged from 16 to 31 (24.51 ± 4.16) mm,

Table I. Prevalence (%), total number of parasite (min.–max. intensity), abundance, dispersion index (DI) and site of infection of helminths in *Leptodactylus latinasus* from Corrientes, Argentina

Helminths Site of infection	%	No. (min.– max.)	Mean intensity \pm SD	Mean abundance \pm SD	DI
Trematoda					
<i>Glypthelmins repandum</i> ^{†‡£}	52.8	40 (1–5)	2.1 \pm 1.3	1.1 \pm 1.4	1.8
Small intestine		12 (1–10)	4.0 \pm 4.2	0.3 \pm 1.7	8.2
<i>Haematoloechus longiplexus</i> ^{†‡£}	8.3	28 (1–7)	4.0 \pm 1.9	0.8 \pm 1.8	4.1
Lungs		4 (1–2)	1.3 \pm 0.5	0.1 \pm 0.4	1.5
<i>Catadiscus inopinatus</i> ^{†‡£}	19.4	158 (6–58)	22.6 \pm 18.5	4.5 \pm 12.2	32.3
Kidneys		129 (2–49)	16.1 \pm 13.7	3.7 \pm 9.4	24.0
<i>Travtrema aff. stenocotyle</i> ^{‡£}	22.2	26 (6–13)	8.7 \pm 3.1	0.7 \pm 2.6	9.1
Mus/Pha-Zon/Mes/Bod-Cav*		7 (2–5)	3.5 \pm 1.5	0.2 \pm 0.9	3.1
Unknown opisthogonimid sp. ^{‡£}	8.3	1 —	—	0.03 \pm 0.2	1.0
Pharyngeal zone		—	—	—	—
<i>Petasiger</i> sp. ^{‡£}	5.6	—	—	—	—
Pharyngeal zone		—	—	—	—
Unknown strigeid species ^{‡£}	2.8	—	—	—	—
Mesentery		—	—	—	—
Cestoda					
Unknown cestode species ^{‡£}	2.8	1 —	—	0.03 \pm 0.2	1.0
Liver		—	—	—	—
Nematoda					
<i>Cosmocerca podicipinus</i> ^{†‡£}	38.9	46 (1–7)	3.3 \pm 2.1	1.3 \pm 2.1	3.3
Large intestine		49 (1–13)	3.8 \pm 3.1	1.4 \pm 2.6	4.9
<i>Cosmocerca parva</i> ^{†‡£}	36.1	4 —	—	0.1 \pm 0.7	4.0
Large intestine		4 —	—	0.1 \pm 0.7	4.0
<i>Cosmocerca rara</i> ^{†‡£}	2.8	4 —	—	0.2 \pm 1.0	5.9
Large intestine		—	—	—	—
<i>Cosmocerca cruzi</i> ^{†‡£}	2.8	4 —	—	0.3 \pm 1.7	8.5
Large intestine		—	—	—	—
<i>Schrankiana schranki</i> ^{†‡£}	2.8	6 —	—	—	—
Large intestine		—	—	—	—
<i>Aplectana hylambatis</i> ^{†‡£}	5.6	12 (2–10)	6.0 \pm 4.0	0.06 \pm 0.2	1.0
Large intestine		—	—	—	—
Acanthocephala					
<i>Centrorhynchus</i> sp. ^{‡£}	5.6	2 (1–1)	1 —	0.06 \pm 0.2	1.0
Mesentery		—	—	—	—

Site of infection: mesentery (Mes), body cavity (Bod-Cav), pharyngeal zone (Pha-Zon), muscle (Mus); [†]adult, [‡]larvae, [£]new host, *number of parasites per organs 11/54/27/37 and percentage of infection per organs 9/18/36/36.

and weights ranged from 0.47 to 2.64 (1.51 ± 0.66) g. Infracommunity descriptors were not significantly correlated with host body size (richness vs. length: $r = 0.04$, $n = 35$, $P > 0.05$, and weight: $r = 0.06$, $n = 35$, $P > 0.05$; diversity vs. length: $r = 0.01$, $n = 35$, $P > 0.05$, and weight: $r = 0.05$, $n = 35$, $P > 0.05$; evenness vs. length: $r = -0.06$, $n = 35$, $P > 0.05$, and weight: $r = -0.04$, $n = 35$, $P > 0.05$); there were also no significant correlations between abundance of helminth species and host's body size (*C. inopinatus* vs. length: $r_s = 0.21$, $P > 0.05$, and weight: $r_s = 0.23$, $P > 0.05$; *Bursotrema aff. tetracotyloides* vs. length: $r_s = 0.24$, $P > 0.05$, and weight: $r_s = 0.30$, $P > 0.05$; *Travtrema aff. stenocotyle* vs. length: $r_s = -0.17$, $P > 0.05$, and weight: $r_s = -0.23$, $P > 0.05$; *C. podicipinus* vs. length: $r_s = -0.24$, $P > 0.05$, and weight: $r_s = -0.28$, $P > 0.05$; *C. parva* vs. length: $r_s = 0.20$, $P > 0.05$, and weight: $r_s = 0.23$, $P > 0.05$). Nevertheless, only for *G. repandum* was observed a significant correlation between abundance of infection and host's body size (length: $r_s = -0.37$, $P < 0.05$; weight: $r_s = -0.36$, $P < 0.05$).

high diversity, with more equitable distribution and increased species richness. Additionally, we observed an increased adult and larval stage infection by trematodes, with the dominant species in the larvae by *Bursotrema aff. tetracotyloides*. Providing the metacercariae of the *Bursotrema aff. tetracotyloides* and *Travtrema aff. stenocotyle* can mature in their respective definitive hosts and considering their high prevalence in *L. latinus*, this would suggest *L. latinus* could be important prey items for the definitive host and could serve as a main second intermediate host in their life cycle. The definitive hosts for the *Bursotrema aff. tetracotyloides*'s and *Travtrema aff. stenocotyle*'s larval stages are mammals and snakes, respectively (M.I. Hamann, per. obs.).

Adult trematodes were represented by two different ecological groups: One group corresponded to *C. inopinatus* and *G. repandum*, with indirect life cycles completely in the aquatic environment possibly resembling *Diplodiscus subclavatus* (Pallas, 1760) and *Glypthelmins quieta* (Stafford, 1900), respectively (Leigh 1946, Grabda-Kazubska 1976, Smyth and

Table II. Covariation based on Spearman's coefficient correlations (r_s) among six common species in *Leptodactylus latinus* from Corrientes, Argentina

	<i>Bursotrema aff. tetracotyloides</i>	<i>Travtrema aff. stenocotyle</i>	<i>Glypthelmins repandum</i>	<i>Catadiscus inopinatus</i>	<i>Cosmocerca podicipinus</i>	<i>Cosmocerca parva</i>
<i>Bursotrema aff. tetracotyloides</i>	1,000					
<i>Travtrema aff. stenocotyle</i>	0,086	1,000				
<i>Glypthelmins repandum</i>	-0,166	-0,011	1,000			
<i>Catadiscus inopinatus</i>	0,344*	0,383*	-0,401*	1,000		
<i>Cosmocerca podicipinus</i>	0,109	0,050	-0,126	0,195	1,000	
<i>Cosmocerca parva</i>	0,070	0,098	0,049	-0,142	-0,583*	1,000

* $P < 0.05$.

Species affinity in the infracommunity

Two correlations between species were positive and significant: *C. inopinatus/Bursotrema aff. tetracotyloides* and *C. inopinatus/Travtrema aff. stenocotyle* and two were negative and significant: *C. podicipinus/G. repandum* and *C. parva/C. podicipinus* (Table II). Only two associations were found among the six species considered: *C. inopinatus/Bursotrema aff. tetracotyloides* ($\chi^2 = 5.3$, $df = 1$, $P < 0.05$) and *C. inopinatus/Travtrema aff. stenocotyle* ($\chi^2 = 10.5$, $df = 1$, $P < 0.05$).

Discussion

Previous reports found the American *Leptodactylus*'s helminth communities composition were predominantly nematodes and exhibited relatively reduced species richness (maximum = 12; mean = 5.1 ± 3.2) (Bursey *et al.* 2001; Goldberg and Bursey 2002; Goldberg *et al.* 2002a, b). In this study, *L. latinus*'s helminth component community harboured

Smyth 1980). The other group was only represented by *H. longiplexus*, characterized by indirect life cycle (Krull 1932, Snyder and Janovy 1996). *Haematoloechus longiplexus*'s second intermediary host is aquatic insect's larvae (e.g. dragonflies) thereby linking the aquatic and aerial environments.

Our data showed adult trematodes are represented by auto-genetic species with a definitive host, i.e. *L. latinus*, which can live temporarily in an aquatic habitat, and allo-genetic species (e.g. larvae) with a definitive host including snakes, birds, and mammals, which can leave the immediate aquatic habitat (Esch *et al.* 1988, 1997). Alternatively, *G. repandum*'s high colonization is determined by adaptations of its complex life cycle to ensure transmission, without requiring an intermediate host.

Adult nematodes are the second most abundant helminth, consisting of *C. podicipinus* and *C. parva*, which presumably have exclusive terrestrial life cycles (Anderson 2000). Our results are similar to those reported for *Leptodactylus chaquensis* Cei, 1950 captured in the same area (Hamann *et al.* 2006)

and both hosts, *L. chaquensis* and *L. latinasus*, use the same microhabitat. Adult *L. latinasus* can live either in the dry and humid earth, near the pond shore, and also in the flooded grass which favours trematode infection. *L. latinasus* enter the water for a short period to breed or as tadpoles, acting as intermediate and definitive hosts. Furthermore, this amphibian favours a terrestrial microhabitat, where its contact with the soil makes infection possible by nematode larva. The nematode larva can infect through different modes including oral infection (e.g., *Aplectana* spp.) and skin penetration (e.g., *Cosmocerca* spp.). In addition, *L. latinasus* can be the paratenic host of *Centrorhynchus* spp. (cystacanths), using birds as their definitive hosts (e.g., Falconiformes). The possible intermediary hosts (e.g., coleopterans) of this species are part of *L. latinasus*'s diet (Duré and Kehr 2004).

In general, we did not find a correlation between *L. latinasus* body size and infection. However, the exception was the adult *G. repandum*; our data suggested smaller hosts had more parasites than larger ones. This result could be explained by ontogenetic changes in the host diet and by behaviour; both characteristics have important roles in parasite recruitment and may be correlated with the host's body size. Similarly, Joy and Dowell (1994) found a negative correlation between the intensity of *Glypthelmins pennsylvaniensis* Cheng, 1961 and *Pseudacris c. crucifer* (Wied-Neuwied, 1838) weight in Wayne County, West Virginia. In agreement with Poulin (2001), we found no significant differences between host sex and richness, suggesting host sex is not important factor in structuring parasite communities.

Only one helminth species (*G. repandum*) had a high prevalence (> 50%) of infection, this may be explained by the helminth fauna being composed of generalist helminth species. For example, the major helminth species examined in this study are now known to infect other Leptodactylidae species (e.g., *L. chaquensis*) and a different frog family, sympatric with *L. latinasus* at Corrientes (M.I. Hamann, per. obs.). *L. latinasus* shows a wide variation in its helminth fauna, acquiring helminth characteristic of aquatic and terrestrial frogs.

Several amphibian studies of helminth community structures showed they are depauperate and isolationist (Aho 1990; Muzzall 1991; Yoder and Coggins 1996; Bolek and Coggins 2001, 2003). Working with *Lysapsus limellus* Cope, 1862 and *L. chaquensis* in Argentina, Kehr *et al.* (2000) and Hamann *et al.* (2006) found no fixed pattern, i.e. an intermediate point between isolationist and interactive. In this study, helminth infracommunities of *L. latinasus* show low diversity and species richness. An individual frog generally harbours only two helminths, with scarce evidence of species affinity. We noted two positive associations for those larval and adult species whose individuals were located in different frog organs. For example, *Bursotrema aff. tetricotyloides* is located in the kidneys and *C. inopinatus* is found in the large intestine. Likewise, we found a negative correlation between two species at the infection site, with different nutrition (e.g., *C. podicipinus* / *G. repandum*), and in different parts of the same organ (e.g., *C. parva* / *C. podicipinus*). In agreement with Poulin (2005),

interpretation of these interspecific relationships must be considered cautiously, when compared with natural conditions. There was no discernible pattern or structure to *L. latinasus*'s infracommunities; nevertheless these results provide evidence of an interactive and isolationist communities existing in extreme conditions of a continuum.

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