Seasonal occurrence of Cosmocerca podicipinus *(Nematoda: Cosmocercidae) in* Pseudopaludicola boliviana *(Anura: Leiuperidae) from natural environments in Corrientes Province, Argentina and aspects of its population structure*

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ORIGINAL PAPER

Seasonal occurrence of *Cosmocerca podicipinus* (Nematoda: Cosmocercidae) in *Pseudopaludicola boliviana* (Anura: Leiuperidae) from natural environments in Corrientes Province, Argentina and aspects of its population structure

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Abstract This study examines the seasonal changes in a population of cosmocercid nematode parasites in a natural environment in an amphibian host of the Neotropical realm. A total of 232 individuals (83 females, 105 males, and 44 larvae) of *Cosmocerca podicipinus* were collected from 105 *Pseudopaludicola boliviana* from Corrientes, Argentina, between December 2002 and December 2003. The prevalence of infection was high during all the seasons (>80.0 %); the mean intensity decreased from summer to winter and then increased in spring. The sex ratios of *C. podicipinus* were significantly different ($P<0.05$) from the expected 1.00:1.00 ratio in winter and in the entire study period. There were no significant differences in the mean length of female and male nematodes between seasons ($P>0.05$). All adult nematodes collected (both males and females) were mature. The pattern of distribution of nematodes was aggregated in the entire study and in summer, autumn, and spring. The body size of the host was not related to the intensity of infection ($P>0.05$). The seasonal occurrence of *C. podicipinus* in *P. boliviana* did not show a marked seasonality.

Introduction

Studies about seasonal fluctuations of helminths in anurans have been carried out in the northern hemisphere with trichostrongylid, rhabdisid, and cosmocercid nematodes in ranid and bufonid hosts (Lees 1962; Baker 1978a, b, 1979; Vanderburgh and Anderson 1987; Bolek and Coggins 2000, 2001) and in the Australian region with rhabdisid nematodes in bufonid hosts (Barton 1998). In the Neotropical realm, Hamann (2004, 2006) and Hamann et al. (2010) reported seasonal occurrence of trematoda and acanthocephalan in hylid hosts and Hamann et al. (2009a) in leptodactylid hosts. These investigations also report the relationship between the infection and the body size and sex of the host and their habitat and feeding preferences.

The only study of seasonal variation of nematodes in amphibians of the Neotropical realm was carried out in the cosmocercid *Cosmocerca podicipinus* Baker and Vaucher 1984 in *Pseudopaludicola falcipes* (Hensel, 1867) in an agricultural area located in the northwest of the province of Corrientes, Argentina (González and Hamann 2009). Working in a rice field, these authors found that the infection was related to the different periods of rice cultivation and planting: the highest prevalence of infection was related to the sowing phase and that the lowest prevalence of infection was related to the field preparation phase. In addition, these authors found that the body size and sex of the host do not influence the rate of infection with this nematode. So far, the seasonal occurrence of cosmocercids in natural environments in the Neotropical realm has not been reported. In the present study, research was undertaken to test the following hypotheses: (1) the seasonal population dynamics of a parasite varies according to abiotic factors (e.g., season, rainfall), (2) the population dynamics of a parasite is influenced by the reproductive cycle of the host, (3) the characteristics of the population of a nematode parasite are influenced by the habitat use of the host, and (4) large amphibians commonly have more nematode individuals than small amphibians. These hypotheses were tested by analyzing the samples of *C.*

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podicipinus from *Pseudopaludicola boliviana* Parker, 1927 from the four seasons.

C. podicipinus, originally described from *Leptodactylus podicipinus* (Cope, 1862) of Capitan Bado, Amambay Province, Paraguay (Baker and Vaucher 1984), is a very common nematode parasite in amphibians (see González and Hamann 2012). The leptodactylid *P. boliviana* belongs to the *Pseudopaludicola pusilla* group whose distribution is widespread. This frog is distributed in disjunct regions of eastern Colombia, northern Brazil, and southern Venezuela through Guyana to Surinam and French Guiana, eastern Bolivia, Paraguay, southwestern Brazil, and northern Argentina in the provinces of Formosa, Chaco, northern Santa Fé, and Corrientes (Frost 2011). It has a generalist diet and is an actively foraging predator found in permanent, semipermanent, and temporary ponds (Duré et al. 2004). It is common in natural environments, but it can also be found in agricultural areas (Duré et al. 2008).

The main goals of this study were (1) to analyze the seasonal fluctuation of a *C. podicipinus* population in a natural environment, (2) to report the prevalence and mean intensity of infection of *C. podicipinus* by host size and gender, and (3) to determine the site of infection of male and female nematodes.

Materials and methods

Study area

The study area is located in the northwest of the province of Corrientes in Argentina (27°27′S , 58°47′ W). This habitat of 250 ha is forested, with areas that include grasslands, numerous cacti, and terrestrial bromeliads. Temporary, semipermanent, and permanent ponds characterize this site. The mean annual temperature is 23 °C, and the mean annual precipitation is 1,500 mm, without a pronounced dry season; however, periods of rain short ages occur every 4 to 6 years (Carnevali 1994).

Analytical procedure

One hundred and five *P. boliviana* (51 males and 54 females) were collected during 2002–2003: summer (n=17), autumn (n=28), winter (n=30), and spring (n=30). Frogs were hand captured by two people between 1800 and 2100 hours, 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 ($CHCL_3$), and dissected following standard protocols (Goater and Goater 2001).Their snout-vent length (SVL, in millimeter) and body weight (WW, in gram) were recorded. At necropsy, hosts were sexed (by examination of gonads and external sexual features), and the alimentary tract and lungs were examined for parasites. Nematodes were observed and counted in vivo, then killed in hot distilled water before being fixed in 70 % ethyl alcohol. Specimens were cleared in glycerine or lactophenol for microscopic examination. Measurements of nematodes are reported in millimeters. Specimens of *C. podicipinus* were deposited in 70 % ethyl alcohol in the Helminthological Collection of the Centro de Ecología Aplicada del Litoral (male: CECOAL 02073003, female: CECOAL 02072727), Corrientes, Argentina. The frog specimens were deposited in the Herpetological Collection of the Centro de Ecología Aplicada del Litoral (CECOAL 4587-91)

Statistical analyses

The intensity, prevalence, and mean intensity of infection were calculated according to Bush et al. (1997). Student's t test was used in comparing the weight and length of frogs, but before that, body length and weight data were logarithmically normalized. Differences in intensities of infection between males and females frogs were analyzed using a nonparametric Mann–Whitney U test. Comparison of two proportions (Z test) was used to test for differences in prevalence of nematode parasites infection between sexes. Comparison of k proportion (X^2) was used to test for differences in prevalence between seasons. Chi-square test (X^2) with Yates correction for continuity was used for comparing the sex ratio of nematodes by each period of study and for comparing the location of sex nematodes by organs of host. A Spearman rank (r_s) correlation was used to calculate possible relationships between host body size and intensity of infection. A Kruskal–Wallis test was used to compare the differences in mean intensity between seasons; the same test was used to compare the length of nematodes between seasons. P values <0.05 were considered significant for all tests. Degree of aggregation of nematodes among frogs was determined by calculation of a variance-to-mean ratio. The software used was Xlstat 7.5 (Addinsoft 2004).

Results

Temporal changes affecting *C. podicipinus*

The prevalence of infection was greater than 80.0 % in all seasons, and the highest prevalence (96.6 %) was observed in spring (Fig. 1). There was no significant difference in prevalence between seasons (X^2=3.00, df=3, P>0.05). The mean intensity of infection decreased from summer to winter and then increased in spring; the difference between seasons was significant (Kruskal–Wallis H=19.93, df=3, P=0.0001) (Fig. 1). The lowest numbers of specimens were found in the summer (37) and the highest in the spring (100).

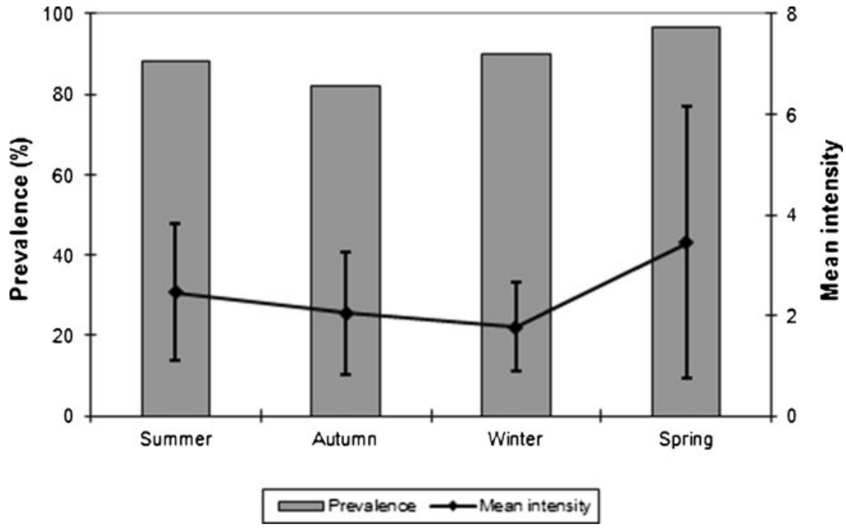

Fig. 1 Seasonal variation in prevalence (in percent) and mean intensity (±1SD) of infection of *C. podicipinus* from *P. boliviana* from Corrientes, Argentina (standard deviations indicated by *vertical lines* limited by *horizontal bars*)

Sex ratios of *C. podicipinus* were not significantly different in summer, autumn, and spring ($P>0.05$). The significantly male-biased sex ratio was found in winter and in the entire study period (Table 1).

There were no significant differences in the length of females between seasons (Kruskal–Wallis $H=3.99$, $df=3$, $P=0.26$) neither in the length of males between seasons (Kruskal–Wallis $H=6.58$, $df=3$, $P=0.08$) (Fig. 2). Significant differences were observed between length of males and females in each one of the seasons (summer: Kruskal–Wallis $H=12.6$, $df=1$, $P=0.0003$; autumn: Kruskal–Wallis $H=27.46$, $df=1$, $P<0.0001$; winter: Kruskal–Wallis $H=29.48$, $df=1$, $P<0.0001$; spring: Kruskal–Wallis $H=12.64$, $df=1$, $P=0.0003$). All adult male and female nematodes collected were mature. Mature males were considered those that had the plectanas of each row completely fused; in the case of females, mature specimen was considered those that had larvate eggs in the uterus.

The pattern of distribution of nematodes was aggregated in summer (1.04), autumn (1.1), and spring (2.24), while in winter, it was uniform or regular (0.62).

Table 1 Numbers of females, males, larvae (L), sex ratios, and X^2 value for sexes of *C. podicipinus* by each period of study

Period	Total number of nematodes	Female	Male	L	Sex ratios, female/male	X^2
Summer	37	15	12	10	1.25:1.00	0.37
Autumn	47	18	22	7	1.00:1.22	0.43
Winter	48	6	36	6	1.00:6.00	21.4*
Spring	100	40	37	23	1.08:1.00	0.13
Combined	232	79	107	46	1.00:1.35	4.22*

* $P<0.05$

Infection by host gender and size

The nematode *C. podicipinus* was found in 94 specimens of *P. boliviana* analyzed (89.5 %). A total of 232 nematodes were found; in male frogs, the number of male nematodes was higher than females and larvae. In female frogs, the number of female nematodes was higher than males and larvae. Statistically significant difference was only observed for the intensity of infection (see Table 2).

Female frogs were larger (13.0±1.29 mm) and heavier (0.26±0.08 g) than males (12.36±0.96 mm, 0.23±0.05 g), and these differences were significant (SVL: $t=2.75$, $df=105$, $P<0.05$; WW: $t=2.32$, $df=105$, $P<0.05$). In female and male *P. boliviana*, the intensity of infection had no relationship with either length or with weight (females: SVL: $r_s=0.003$, $P>0.05$; WW: $r_s=0.025$, $P>0.05$, $n=48$; males: SVL: $r_s=0.04$, $P>0.05$; WW: $r_s=-0.21$, $P>0.05$, $n=46$).

Site of infection

In all specimens analyzed of *P. boliviana*, the lungs were infected only by mature males of *C. podicipinus* (43.8 % of prevalence in right lung and 41.0 % in left lung), but males were also found in the small (1.9 %) and large intestines (3.8 %). Mature females and larvae differed in prevalence in the small (females, 33.3 %; larvae, 6.7 %) and large intestines (females, 12.4 %; larvae, 11.4 %). Statistically significant differences were observed between the numbers of male and female nematodes in the small and large intestines; however, the number of male nematodes in the left and right lungs showed no statistically significant differences (Table 3).

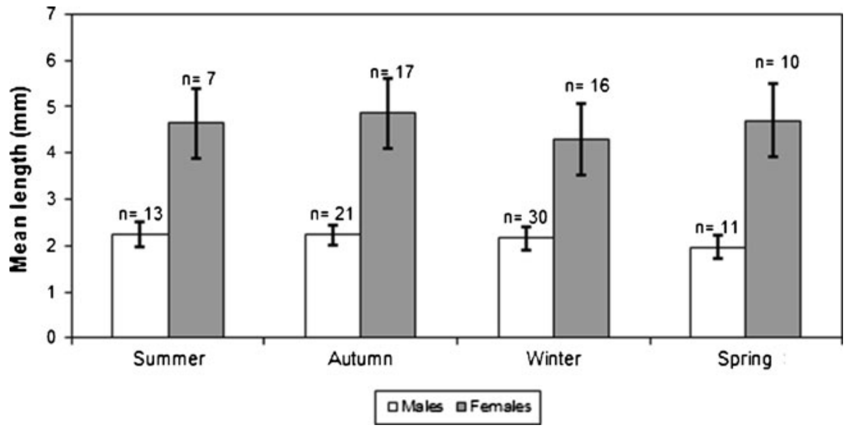

Fig. 2 Seasonal variation in mean length (±1SD) of males and females of *C. podicipinus* from *P. boliviana* from Corrientes, Argentina (standard deviations indicated by *vertical lines* limited by *horizontal bars*)

Discussion

Although the life cycle of *C. podicipinus* has not been studied, we assume that it resembles that of other cosmocercid species. Baker (1978b) studied the transmission of *Cosmocercoides dukae* (Holl, 1928) Travassos, 1931 in amphibian hosts and established that infective larvae penetrate through the skin of the host, migrate to the lungs, develop to the fourth stage there, and then migrate (presumably via the trachea and mouth) to the rectum, where they complete their development to the adult stage. However, we observed the following differences: the males found in the lungs were all mature, and all the larvae were found in the intestine. This is a point that requires further investigation; perhaps, for some reason, the males of this species mature earlier in the lungs of the hosts. No immature *C. podicipinus* was found in the lungs of *P. boliviana*, in contrast to that found by Fotedar and Tikoo (1968) and Baker (1978b). Since *C. podicipinus* is a nematode with direct cycle, the seasonal changes in its populations are not related to changes in the diet (e.g., changes in the availability of their intermediate hosts).

According to the classification of Wells (1977), *P. boliviana* is a prolonged breeder. Specifically in the study area, Schaefer (2007) noted the presence of adults throughout the year, larvae from October to April, and metamorphic larvae from April to July. However, the greatest reproductive activity of this anuran (presence of calling males) was recorded from September to March. Thus, the high prevalence of infection found in all the seasons in this study could be explained by the presence of the host throughout the year. However, it should be emphasized that when the values of prevalence and intensity of infection begin to decrease (late summer and autumn), metamorphic larvae begin to be recorded. A possible reason for the decrease in the mean intensity is that as the population density of the host (frogs of the previous year and metamorphic of the season) increases, the number of parasites that infect each host decreases.

The increase in the number of larvae of *C. podicipinus* in spring does not correspond to a recruitment period of the parasite because all the larvae were found in the small and large intestines and not in the body cavity (Baker 1979). This may represent the transmission period of the parasite, i.e., the infective stages located in the intestine are eliminated with the feces of the host to continue their cycle in the external environment and infect other hosts.

The difference between the seasonal occurrence of *C. podicipinus* and that of *Cosmocerca ornata* (Dujardin, 1845) Diesing, 1861 studied in England by Lees (1962) is

Table 2 Total number, prevalence, mean intensity ± 1SD and range indicated in brackets of *C. podicipinus* by sexes of *P. boliviana* from Corrientes, Argentina

	Number of nematodes[a]	Prevalence of infection[b]	Mean intensity ± SD (range)
Male host	98 (53 males, 29 females, 16L)	90.2 (46 of 51)	2.13±1.85 (1–12)
Female host	134 (52 males, 54 females, 28L)	88.9 (48 of 54)	2.79±1.86 (1–10)
Combined	232 (105 males, 83 females, 44L)	89.5 (94 of 105)	2.46±1.88 (1–12)

L larvae

[a] Intensity of infection: female host vs. male host: Mann–Whitney *U* test=1,414.5, $P<0.05$, $n_{female}=48$, $n_{male}=46$

[b] Prevalence of infection: female host vs. male host: $Z=1.35$, $df=1$, $P>0.05$

Table 3 Number of *C. podicipinus* in *P. boliviana* (males and females) by site of infection from Corrientes, Argentina

	Right lung[a]	Left lung[a]	Small intestine[b]	Large intestine[c]
Males	49	50	2	4
Females	–	–	57	26
Larvae	–	–	21	23
Combined	49	50	80	53

[a] Male nematodes: right lung vs. left lung: X^2 =0.02, df=1, P>0.05

[b] Small intestine: female nematodes vs. male nematodes: X^2 =51.3, df=1, P<0.05

[c] Large intestine: female nematodes vs. male nematodes: X^2 =16.2, df=1, P<0.05

that *C. ornata* presents the highest prevalence and mean intensity in winter, when the host, *Rana temporaria* Linnaeus, 1758, is hibernating and that the lowest prevalence and intensity are observed in summer, possibly linked to the recruitment of transformed frogs into the population. On the other hand, Bolek and Coggins (2000) suggested that the American toad, *Anaxyrus americanus* (Holbrook, 1836) (syn. = *Bufo americanus americanus*), becomes infected with *Cosmocercoides variabilis* (Harwood, 1930) Travassos, 1931 during the breeding season and that there seems to be a decline during summer and early autumn in Wisconsin, USA. Vanderburgh and Anderson (1987) reached similar conclusions with *C. variabilis* in *A. americanus* from Ontario, Canada.

Finally, in contrast with that found by González and Hamann (2009) in an agricultural environment, in this study, the sampling area does not show fluctuations in the water levels as the rice field which would affect the rate of infection with *C. podicipinus.*

P. boliviana is a semiaquatic amphibian linked to terrestrial and aquatic habitats, which can be found in moist soil and mud, in the shore of the temporary ponds, in ditches, or in flooded grasslands (Duré et al. 2004); the use of this kind of habitat would allow a greater infection by nematodes. The prevalence and mean intensity of infection found in this study were higher than those reported by González and Hamann (2009) for *P. falcipes*. This difference could be explained by the fact that González and Hamann (2009) collected the frogs in a rice field where the period of filling with water could affect the free-living stage of the nematode (infective stage). This result contrasts with those found in hylid frogs captured in the same area but with a different habitat (arboreal habitat, e.g., bromeliads), which showed lower values of infection parameters of nematode parasites (Hamann et al. 2009b, 2010).

In nematodes, female-biased sex ratios among adult worms are commonly reported but, specifically in amphibians, previous reports have shown different results. In *C. variabilis*, Joy and Bunten (1997) found a highly significant female bias, whereas González and Hamann (2009) found a slight male bias in *C. podicipinus*. Our study shows contrasting results in the different periods but a significant difference only in winter (P<0.05).

Poulin (1997) expressed that "when female nematodes are abundant relative to males, males tend to be relatively small, but in situations where the operational sex ratio is closer to unity or even male-biased selection appears to have favored relatively larger males' sizes." In this study, this situation was observed only in spring when female nematodes were more numerous than males, and these males presented smaller size. In summer, females were also abundant but the lengths recorded for males did not agree with the expected ones.

Nematodes showed an aggregation distribution in every season, except in winter. In general, parasites use only a fraction of the host individuals available; inside these hosts, nematodes are aggregated, with most of the infected hosts harboring few parasites and a few hosts harboring many parasites and not distributed evenly or randomly (Anderson and May 1978). In addition, if the levels of aggregation among nematodes are analyzed with their body size, one would expect a decrease in the levels of aggregation with increased body size of the helminths (Poulin and Morand 2000). In our study, the larger sizes of female and male nematodes were observed in seasons with aggregation distribution (females in autumn and males in summer).

In a congeneric species, *P. falcipes*, González and Hamann (2009) found no significant differences between the sexes of the host and infections by *C. podicipinus*; similarly, cosmocercid nematodes from other amphibians have shown no preference for one sex of the hosts (Joy and Bunten 1997; Bolek and Coggins 2000; Santos and Amato 2010). In the present study, only the intensity of infection of *C. podicipinus* between female and male hosts was significantly different whereas the prevalence of infection was not significantly different between sexes.

On the other hand, some authors have found a significant correlation between the intensity of cosmocercid nematodes and the size of frogs; these authors have argued that larger toads present higher intensities because they have a greater contact surface for the penetration of infective nematode larvae (Bolek and Coggins 2000, 2001). However, in cosmocercids of the Neotropical realm, some authors have found that the body size of both sexes of the hosts is not related to the intensity of infection (e.g., *C. podicipinus* in *P. falcipes* and *Leptodactylus latinasus* Jiménez de la Espada, 1875 from Argentina (González and Hamann 2009; Hamann et al. 2006) and *Cosmocerca parva* in *Rhinella fernandezae* (Gallardo, 1957) from Brazil (Santos and Amato 2010)). In the present study, similar results were found.

Male specimens of *C. podicipinus* have no preference for either the right or the left lung, similarly to that found by Barton

(1998) in *Rhabdias* cf. *hylae* from *Rhinella marina* (Linnaeus, 1758). Mature females were found in greater numbers in the small intestine, in agreement with that found by González and Hamann (2009). Future research should determine whether the copula occurs in the lungs and then the fertilized females migrate to the intestine or whether the females found in the intestine are fertilized by the few males present there.

In conclusion, the infection with the nematode *C. podicipinus* in the Neotropical realm seems to occur throughout the year in the leiuperid frog in natural environments. This would be demonstrated by the nonsignificant differences in prevalence between seasons, the slight variation in the length of males and females during the seasons, and the mature condition of both sexes throughout the study period. The period of transmission of this nematode might be demonstrated by the high number of larvae in the intestine in spring.

References

Addinsoft (2004) Xlstat for excel, version 7.5. Addinsoft, New York

Anderson RC, May RM (1978) Regulation and stability of host–parasite population interactions. I. Regulatory processes. J Anim Ecol 47:219–247

Baker MR (1978a) Development and transmission of *Oswaldocruzia pipiens* Walton, 1929 (Nematoda: Trichostrongylidae) in amphibians. Can J Zool 56:1026–1031

Baker MR (1978b) Transmission of *Cosmocercoides dukae* (Nematoda: Cosmocercoidea) to amphibians. J Parasitol 64:765–766

Baker MR (1979) Seasonal population changes in *Rhabdias ranae* Walton, 1929 (Nematoda: Rhabdiasidae) in *Rana sylvatica* of Ontario. Can J Zool 57:179–183

Baker MR, Vaucher C (1984) Parasitic helminthes from Paraguay VI: *Cosmocerca* Diesing, 1861 (Nematoda: Cosmocercoidea) from frogs. Rev Suisse Zool 91:925–934

Barton DP (1998) Dynamics of natural infection of *Rhabdias* cf. *hylae* (Nematoda) in *Bufo marinus* (Amphibia) in Australia. Parasitology 117:505–513

Bolek MG, Coggins JR (2000) Seasonal occurrence and community structure of helminth parasites from the eastern American toad, *Bufo americanus americanus* from southeastern Wisconsin, U.S.A. Comp Parasitol 67:202–209

Bolek MG, Coggins JR (2001) Seasonal occurrence and community structure of helminth parasites in green frogs, *Rana clamitans melanota*, from southeastern Wisconsin, U.S.A. Comp Parasitol 68:164–172

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

Carnevali R (1994) Fitogeografía de la Provincia de Corrientes. Ediciones Litocolor. Asunción, Paraguay

Crump ML, Scott NJ Jr (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

Duré MI, Schaefer EF, Hamann MI, Kehr AI (2004) Consideraciones ecológicas sobre la dieta, la reproducción y el parasitismo de *Pseudopaludicola boliviana* (Anura, Leptodactylidae) de Corrientes, Argentina. Phyllomedusa 3:121–131

Duré MI, Kehr AI, Schaefer EF, Marangoni F (2008) Diversity of amphibians in rice fields from Northeastern Argentina. Interciencia 33:523–527

Fotedar DN, Tikoo R (1968) Studies on the life cycle of *Cosmocerca kashmirensis* Fotedar, 1959, a common oxyurid nematode parasite of *Bufo viridis* in Kashmir. Indian Sci Congr Assoc Proc 55:460

Frost DR (2011) Amphibian species of the world: an online reference. Version 3.0. Electronic Database accessible at American Museum of Natural History, New York, USA. http://research.amnh.org/herpetology/amphibia/index.html. Accessed 01 March 2012

Goater T, Goater CP (2001) Ecological monitoring and assessment network (EMAN) protocols for measuring biodiversity: parasites of amphibians and reptiles Canada. http://eqb-dqe.cciw.ca/eman/ecotools/protocols/terrestrial/herp_parasites/intro.html. Accessed 01 March 2012

González CE, Hamann MI (2009) Seasonal occurrence of *Cosmocerca podicipinus* (Nematoda: Cosmocercidae) in *Pseudopaludicola falcipes* (Anura: Leiuperidae) from the agricultural area in Corrientes, Argentina. Rev Ibero-Latinoam Parasitol 68:173–179

González CE, Hamann MI (2012) First report of nematode parasites of *Physalaemus albonotatus* (Steindachner, 1864) (Anura: Leiuperidae) from Corrientes, Argentina. Neotrop Helminthol 6(1):9–24

Hamann MI (2004) Seasonal maturation of *Catadiscus propinquus* (Digenea: Diplodiscidae) in *Lysapsus limellus* (Anura: Pseudidae) from an Argentinean subtropical permanent pond. Physis 9:136–137

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, González CE, Kehr AI (2006) Helminth community structure of the oven frog *Leptodactylus latinasus* (Anura, Leptodactylidae) from Corrientes, Argentina. Acta Parasitol 51:294–299. doi:10.2478/s11686-006-0045-1

Hamann MI, Kehr AI, González CE (2009a) Niche specificity of two *Glypthelmins* (Trematoda) congeners infecting *Leptodactylus chaquensis* (Anura: Leptodactylidae) from Argentina. J Parasitol 95:817–822. doi:10.1645/GE-1860.1

Hamann MI, Kehr AI, González CE, Duré MI, Schaefer EF (2009b) Parasite and reproductive features of *Scinax nasicus* (Anura: Hylidae) from a South American subtropical area. Interciencia 34:214–218

Hamann MI, Kehr AI, González CE (2010) Helminth community structure of *Scinax nasicus* (Anura: Hylidae) from a South American subtropical area. Dis Aquat Org 93:71–82. doi:10.3354/dao02276

Joy JE, Bunten CA (1997) *Cosmocercoides variabilis* (Nematoda: Cosmocercoidea) populations in the eastern American toad, *Bufo a. americanus* (Salienta: Bufonidae), from West Virginia. J Helminthol Soc Wash 64:102–105

Lees E (1962) The incidence of helminth parasite in a particular frog population. Parasitology 52:95–102

Poulin R (1997) Covariation of sexual size dimorphism and adult sex ratio in parasitic nematodes. Biol J Linn Soc 62:567–580

Poulin R, Morand S (2000) Parasite body size and interspecific variation in levels of aggregation among nematodes. J Parasitol 86:642–647. doi:10.1645/0022-3395(2000)086[0642:PBSAIV]2.0.CO;2

Santos VGT, Amato SB (2010) Helminth fauna of *Rhinella fernandezae* (Anura: Bufonidae) from the Rio Grande do Sul Coastland, Brazil: analysis of the parasite community. J Parasitol 96:823–826. doi:10.1645/GE-2388.1

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. Thesis, Universidad Nacional de La Plata. La Plata

Vanderburgh DJ, Anderson RC (1987) Preliminary observations on seasonal changes in prevalence and intensity of *Cosmocercoides variabilis* (Nematoda: Cosmocercoidea) in *Bufo americanus* (Amphibia). Can J Zool 65:1666–1667

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