Annals of Parasitology 2020, 66(1), 39–47
doi: 10.17420/ap6601.236

Original papers

Structure of the helminth community in *Dermatonotus muelleri* (Anura: Microhylidae) from the driest area of the American Chaco

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ABSTRACT. The present study describes the helminth community collected from juveniles of *Dermatonotus muelleri* (Anura: Microhylidae) from the Chaco Seco Ecoregion. Helminths were found in 80.0% of specimens examined (n = 16). The helminth community of this microhylid presented very low species richness; a total of 1,339 specimens belonging four helminth species were found; three adult nematodes, *Aplectana hylambatis*, *Cosmocerca podicipinus* and *Parapharyngodon* sp., and an adult cestode, *Ophiotaenia* sp. Parasites were found in the large and small intestines. Maximum helminth richness was 2 species per infected frog. The nematode *A. hylambatis* presented the highest prevalence and was the most abundant ($d = 0.97$) indicating that it is the dominant species in the community ($I = 63.0$). Host snout-vent length did not influence the intensity of infection or the richness of helminth species at the community component level. Two species showed significant co-variation (*A. hylambatis* and *Parapharyngodon* sp.). The high prevalence of infection and number of parasites found for *A. hylambatis* could be related to the characteristics of their life cycles; the possession of the infective stage (L3) protected inside the egg membrane would have benefits against extreme drought in the area in which the study was conducted. The studies of helminths in the Chaco Seco Ecoregion, an area seriously threatened in terms of its biodiversity, are incipient. This is the second study that has been carried out to determine the structure of the parasite community in amphibians of this ecoregion.

Keywords: Amphibia, parasites, dry Chaco ecoregion, Formosa province, Argentina

Introduction

One of the most threatened subtropical woodland savannahs in the world is the Gran Chaco ecoregion; this is an area that lost an impressively amount of forest cover in the last few years as a consequence of high deforestation rates [1]. The main studies of the loss of diversity in this ecoregion refer to forests and different groups of vertebrates such as mammals, birds and amphibians [2–4].

The Muller's termite frog *Dermatonotus muelleri* (Boettger, 1885) is a member of the family Microhylidae Günther, 1858 (1843), which is found in South America in Brazil, Paraguay, Bolivia, and Argentina [5]. Its distribution in Argentina includes the provinces of Chaco, Corrientes, Formosa, Jujuy, Salta, Santa Fe, and Santiago del Estero [6].

These amphibians are highly specialised for burrowing; they build a subterranean chamber that is utilised for estivation during the dry season, and emerge only during the wet season for reproduction and feeding [7]. They are explosive breeders, and several reproductive events may occur in the wet season; during these times, females mate only once, while males are polygynous [8]. This species is specialized in eating termites; they employ flexible prey search tactics that depend on temporal fluctuations in prey density as well as the patch distribution of the food resources [9]. Adults can be predated by birds, marsupials, and snakes [8]. *Dermatonotus muelleri* is categorized as a Least Concern (LC) by the IUCN [10], and as Not Threatened by the last categorization of the state of conservation of amphibians and reptiles from Argentina [6].

Lunaschi and Drago [11] and González and Hamann [12] summarised the digenean and nematode parasites in Argentinean amphibians, respectively. In these works, the authors agree on the need to increase knowledge of the parasitofauna of this host group. Although research into helminths in amphibians has increased after these publications, *D. muelleri* has been a poorly studied host in its distribution area in Argentina. However, in its distribution area in the Neotropical region, outside of Argentina, some studies on helminths have been carried out in this microhylid. The parasitic helminth community was studied by Alcantara et al. [13], from adult hosts collected in different localities from the Ceará State, Brazil. Also, systematic studies of helminths were carried out in this microhylid, which were summarised by Campião et al. [14], and other later researches such as those of Aguiar et al. [15], Araújo-Filho et al. [16], and González et al. [17]. However, in juvenile hosts, and in the Chaco Seco ecoregion, studies referring to the parasite helminth community have not been carried out to date.

Therefore, the objectives of this study were: (1) to determine the richness and diversity of helminth parasites at the component community level; (2) to analyse the helminth cycles of transmission; (3) to examine the species affinities (co-variation and association) of helminth species; and (4) to evaluate the influence of body size on the abundance and mean species richness in juveniles of the frog *D. muelleri*.

Materials and Methods

Study area. Frog populations host were captured in an area (181 m.a.s.l., 24°10’45.48”S and 61°56’28.51”W) located approximately 32 km north Ingeniero Juárez city, Matacos Department, Formosa Province, Argentina. The study area is located within the Chaco Seco ecoregion, specifically in the Semiarid Chaco environment. In this area the forest is adapted to dry conditions (xerophytic deciduous forest), with predominance of small leaved deciduous and thorny species adapted to fluctuations in water availability, as well as to seasonal thermal variations. Woody vegetation (e.g., *Bulnesia sarmientoi*, *Prosopis ruscifoli*, *Stetsonia coryne*, and *Trithinax biflabellata*) is sparse, and the herbaceous species are predominantly grasses (*Trichloris* sp., *Gouinia* sp. and *Setaria argentina*). The landscape is flat, gently sloping toward the east. The climate is characterized by low rainfall (mean annual about <700 mm), and high temperatures, at times exceeding 47°C since this area comprises part of the South American Heat Pole [18].

Collection and examination of frogs and parasites. Twenty juveniles of *D. muelleri* were collected between February 2017 and April 2018. Specimens were hand-capture between 18:00 and 21:00 hours. Specimens were anesthetized topically using a lidocaine 2% cream and necropsied. Their snout-vent length (SVL) and body weight (g) were recorded. All the internal organs were examined digestive tract, lungs, liver, kidneys, urinary bladder, coelomic cavity and musculature. Helminths were observed *in vivo*, counted, then fixed in 10% hot formalin solution and preserved in 70% alcohol. The nematodes were clarified in Amman’s lactophenol, mounted on temporary slides and examined under a light microscope. Cestodes were stained with hydrochloric carmine, cleared in creosote, and mounted in Canada balsam. Helminths were deposited in the Helminthological Collection of Centro de Ecología Aplicada del Litoral (CECOAL) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Corrientes city, Corrientes, Argentina [accession numbers CECOAL 17022112 *Aplectana hylambatis* (Baylis 1927) Travassos, 1931 (10 females, 10 males); CECOAL 17022134 *Cosmocerca podicipinus* Baker and Vaucher, 1984 (2 females); CECOAL 17022131 *Parapharyngodon* sp. (5 females, 5 males); CECOAL 18042449 *Ophiotaenia* sp. (one whole mounted slide)].

Statistical analysis. The infection prevalence, intensity, and abundance were calculated for helminths according to Bush et al. [19]. The measures of community richness and diversity employed included the following: the total number of helminth species (= richness), Shannon index (H') [20], and evenness (J') as H'/H' maximum [21]. The diversity index was used with decimal logarithms (logn). Species richness is the number of helminth species, and mean helminth species richness is the sum of helminth species, per

Table 1. Helminth parasites record of juvenile *Dermatonotus muelleri* from Chaco Seco Ecoregion, Argentina

	n	%	MI ± SD	MA ± SD	Site of infection	$S^2/\bar{x}$	I
A. hylambatis	1302	75 (15/20)	86.8 ± 135.9	65.1 ± 122.8	LI	231.97	63.0*
C. podicipinus	2	5 (1/20)	2	0.1 ± 0.44	LI	2.0	0.00†
Parapharyngodon sp.	31	25 (5/20)	6.2 ± 9.4	1.55 ± 5.12	LI	16.94	0.5‡
Ophiotaenia sp.	4	10 (2/20)	2 ± 0	0.2 ± 0.6	SI	1.85	0.02‡

n: number of helminths; %: prevalence; MI ± SD: mean intensity ± standard deviation; MA ± SD: mean abundance ± standard deviation; $S^2/\bar{x}$: dispersion
Site of infection: LI: large intestine; SI: small intestine
Classification of helminths: * I ≥ 1.0, dominant species; † I = 0, unsuccessful pioneer species; ‡ 0.01≤ I <1.0, codominant species; *Cosmocerca podicipinus*: new host record

individual frogs, divided by the total sample size. Berger-Parker index of dominance (*d*) was used to determine the most abundant species [22]. Helminth communities have been classified at the infra-community (all helminth infra-populations within a single *D. muelleri*) and component community (all helminth infra-communities within a population of the *D. muelleri*) levels [19]. Spearman's rank test (r_S) was used to test possible relationship between host body size (length and weight), parasitic abundance, parasitic intensity, and mean species richness. Also, Spearman's rank test (r_S) was used to calculate possible species covariation. The species associations were analysed by a chi-square test (χ^2), with Yates correlation. The degree of aggregation of different species of parasites was calculated by the variance (S^2) and mean ($\bar{x}$) relation.

The helminth community structure was examined according to the methodology outlined by Thul et al. [23], in which helminth species are classified into four groups (dominant, codominant, subordinate, and unsuccessful) by taking into account their prevalence, intensity, and maturity factor (equal to 1.0 if at least one mature specimen of species is found and equal to 0 if otherwise), which is related to the degree of host specificity. For abundance and intensity vs. host body size, and covariation and associations of parasites, the species considered were those that had at least 10% occurrences in the amphibian population (three species). The software used were Xlstat 7.5 [24] and PAST [25].

Results

Helminth community characteristics

Sixteen specimens of *D. muelleri* were infected with at least one helminth parasite species (overall prevalence 80.0%). A total of 1,339 helminths were collected with a mean abundance of 66.95 ± 127.40, and a mean intensity of infection of 83.68 ± 138.08.

The helminth component community for this frog population consisted of four species of helminths (Table 1). The predominant groups of parasites were nematodes (3 species; 75%), and only one species of cestodes was found. Helminth diversity (*H*') and evenness (*J*') were 0.14 and 0.10, respectively. *Aplectana hylambatis* was the most abundant species (*d* = 0.97). Nematode species, *C. podicipinus*, *A. hylambatis*, *Parapharyngodon* sp., and the only species of cestode, *Ophiotaenia* sp., identified were found in the adult stage; *D. muelleri* is a definitive host for all of them. Parasite transmission occurs to the frog host by skin penetration in one species of nematodes, and by oral ingestion (of the infective stage in two nematodes species and of the intermediate host in the cestode species).

Parasites were found in different sites of infection in the host. The most parasitized organ was the large intestine, with all species of nematodes. At the infra-community level, the mean helminth richness was 1.43 ± 0.51 (maximum = 2) species per infected frog. Simple infections were observed in 9 hosts: *A. hylambatis* was found in 8 of them, and *Ophiotaenia* sp. in one host. Multiple infections with 2 species were observed in 7 frogs, 5 with *A. hylambatis* and *Parapharyngodon* sp., one with *A. hylambatis* and *C. podicipinus*, and one with *A. hylambatis* and *Ophiotaenia* sp. Most helminth parasites showed aggregated patterns of distribution (Table 1).

Interspecific relationships in the infra-community

Only one correlation between helminth species occurrence was positively significant: that of *A. hylambatis*/*Parapharyngodon* sp. (r_S = 0.58; P < 0.05); the rest of the correlations were not significant (*A. hylambatis*/*Ophiotaenia* sp.: r_S = -

0.07; $P > 0.05$; *Parapharyngodon* sp./*Ophiotaenia* sp.: $r_S = -0.19$; $P > 0.05$). No associations were found between the 3 species considered: *A. hylambatis*/*Parapharyngodon* sp. ($\chi^2 = 2.52$, df = 1, $P > 0.05$), *A. hylambatis*/*Ophiotaenia* sp. ($\chi^2 = 0.72$, df = 1, $P > 0.05$), and *Ophiotaenia* sp./*Parapharyngodon* sp. ($\chi^2 = 0.04$, df = 1, $P > 0.05$).

Parasitic infection related to size of host

The total length of the frogs ranged from 37.5 ± 8.74 mm (21.0–51.76), and their body weight ranged from 5.38 ± 4.09g (0.62–13.9). The total intensity was not significantly correlated with the snout-vent length of host (total intensity vs. length: $r_S = 0.16$; $P = 0.53$; total intensity vs. weight: $r_S = 0.21$; $P = 0.42$), while the total abundance was significantly correlated only with the snout-vent length of hosts (total abundance vs. length: $r_S = 0.43$; $P = 0.04$; total abundance vs. weight: $r_S = 0.45$; $P = 0.06$). The mean species richness was not significantly correlated with the host size (mean species richness vs. length: $r_S = 0.04$; $P = 0.88$; mean species richness vs. weight: $r_S = 0.17$; $P = 0.51$).

On the other hand, there were no significant correlations between the abundance of helminth species and the host's snout-vent length (*A. hylambatis* vs. length: $r_S = 0.40$, $P > 0.05$, and weight: $r_S = 0.42$, $P > 0.05$; *Parapharyngodon* sp. vs. length: $r_S = 0.33$, $P > 0.05$, and weight: $r_S = 0.36$, $P > 0.05$; *Ophiotaenia* sp. vs. length: r_S 0.37, $P > 0.05$); only the abundance of *Ophiotaenia* sp. was significantly correlated with the weight of host ($r_S = 0.46$, $P < 0.05$).

Importance of species within the community

Helminth species were classified according to community importance values (Table 1); one species, *A. hylambatis,* was strongly characteristic of the community (dominant), two species, *Parapharyngodon* sp. and *Ophiotaenia* sp. were co-dominant, while *C. podicipinus*, which is able to enter the host but not to attain maturity therein, contributed little to the community and was characteristic of a different host.

Discussion

Nematodes (larvae and adults), cestodes (larvae and adults), and acanthocephalan (larvae) were previously registered from *D. muelleri* in different localities throughout its distribution area (Table 2). Most of the studies (four) were performed in Brazil, with two undertaken in Paraguay, but this is the first study of the helminth community performed in Argentina and in juveniles of *D. muelleri.* With regard to the number of parasite taxa, one of these reports corresponds to acanthocephalan, three to cestodes, and 14 to nematodes. In the case of nematodes, four cosmocercids from three genera were registered (*Aplectana*, *Raillietnema*, *Cosmocerca*), two oxyurids from one genus (*Parapharyngodon*), and a physalopterid from the genus *Physaloptera*.

Two of the four species of helminths found in this study were easily identified at the species level by their morphometric characteristics (*C. podicipinus* and *A. hylambatis*). In the case of *Parapharyngodon*, the specimens belonged to the group with the anterior lip of cloacal smooth and three pairs of caudal papillae; a more specific identification was not possible because the rest of the characters did not coincide with the species of this group (e.g., end of lateral alae, tail shape in the female, cephalic papillae arrangement). For cestode specimens, one proteocephalid from the genus *Ophiotaenia* La Rue, 1911 was identified by the following characters: medullary distribution of gonads as well as the presence of four simple unilocular suckers and two testis fields. Within this genus, it belongs to the group of species with an apical organ formed of *O. bonariensis* Szidat and Soria, 1954, *O. ecuadoriensis* Dyer, 1986, and *O. oumanskyi* de Chambrier and Gil de Pertierra, 2012, but further specimens need to be studied to give a more exact identification.

All parasites found in this study are generalist, being reported for several other anuran species [12,14]; some of them, such as *A. hylambatis*, are very common in other amphibians of the Chaco Seco and Chaco Húmedo ecoregion, e.g. in *Leptodactylus bufonius* and *Rhinella major*, respectively [26,27].

The helminth component community of juveniles of *D. muelleri* from Ingeniero Juárez presented a few species of helminth. This seems to be repeated in other studies; in Paraguay, McAlister et al. [28] reported 3 helminth species, while Alcantara et al. [13] reported five helminth species in Brazil. In addition to the few species found, these studies agree that cosmocercid nematodes have the highest values in the prevalence of infection; 57.1% for *Raillietnema spectans* collected from Brazil, and 100% infection for the same species collected from

Table 2. Previous localities and helminth parasite species found in *Dermatonotus muelleri* in its distribution area, and new reports of this study

Locality	Helminth species	References
Chapada do Araripe, Crato (7°16'47.0''S, 39°26'17.7''W), Pontal de Santa Cruz, Santana do Cariri (7°12'37.8''S, 39°44'00.8''W), Distrito de Cuncas, Barro (7°10'36''S, 38°46'54''W), Estação Ecológica de Aiuaba, Aiuaba (6°49'32''S, 40°44'31''W), Sítio Olho D'água Comprido, Missão Velha (7º15'56.2''S, 39°05'13.8''W), Ceará State, Brazil	*Aplectana membranosa* *Raillietnema spectans* *Parapharyngodon silvoi* *Physaloptera* sp. (larvae) Cystacanths	[13]
Reserva Particular do Patrimônio Natural Foz do Rio Aguapeí, São Paulo State, Brazil	*Aplectana hylambatis*	[15]
Exu, Pernambuco State, Brazil (07º34'S; 39º45'W)	*Parapharyngodon silvoi*	[16]
Las Lomitas, Patiño Department, Formosa Province, Argentina (24°42'26''S, 60°35'40''W)	*Aplectana hylambatis*	[17]
Presidente Hayes Department, Paraguay	*Raillietnema spectans* *Parapharyngodon verrucosus* *Ophiotaenia cohosper*	[28]
Amambay Department, Paraguay	*Aplectana hylambatis*	[29]
São Gonçalo do Amarante, Ceará State, Brazil (3°33'S; 38°49'W)	Spargana infection	[52]
Ingeniero Juárez, Mataco Department, Formosa Province, Argentina (23°54'S, 61°51'W)	*Aplectana hylambatis* *Cosmocerca podicipinus* *Parapharyngodon* sp. *Ophiotaenia* sp.	Present study

Paraguay. In our study, *A. hylambatis*, another cosmocercid, presented the highest value for the prevalence of infection (75.0%).

Aplectana hylambatis is a species with a wide host and geographical range [14,17]. Specifically, in *D. muelleri*, it was found with high abundance of infection and, in some cases, with a high prevalence. Baker and Vaucher [29] found 100% (3/3) prevalence of infection and "*each with > 200 worms*" per host, while González et al. [17] reported a prevalence of infection of 100% (1/1) and 136 nematodes in this microhylid host. Aguiar et al. [15] reported a high number of specimens (678 nematodes) but a low prevalence of 15.8% (3/19). Species of *Parapharyngodon* were found with a prevalence of between 14.68% and 67% in previously studies [13,16,28]. As for the cestodes, the prevalence of the Proteocephalidae is usually very low in amphibians, at least in the Neotropical region [30].

The role of *A. hylambatis* in the community is also demonstrated by the importance value; this was a strongly characteristic species of the community. At the other extreme, *C. podicipinus* was an unsuccessful pioneer species; the two specimens found were immature, and it is known to be a characteristic species of another hosts [31,32]. In the middle of these extremes, *Parapharyngodon* sp. and *Ophiotaenia* sp., are co-dominant species in the helminth community; they contributed significantly to the community, although to a lesser extent than *A. hylambatis*.

The helminth species infecting *D. muelleri* presented very unequal abundances and, in terms of distribution, they present a typical aggregated pattern of distribution for parasites. The overdispersed distributions of these helminths are probably due to the different susceptibility of these frogs to infections, at the same time caused by differences related to the age, sex, and immunological state of the hosts [33].

In addition to the poor species richness of helminths in this host, and the small number of species (no more than two) per host, we did not note any associations between helminth species; on the other hand, we only found a positive correlation between two species, *A. hylambatis* and *Parapharyngodon* sp. Therefore, the depauperate infra-communities of *D. muelleri* approach the isolationist extreme of the continuum.

Hamann and González [27] studied the helminth community of *R. major* in two localities of the Chaco Seco ecoregion, one in the same area as our study, Ingeniero Juárez. For this bufonid, the authors found a very low helminth species richness (three species), along with metacercariae of Strigeidae gen. sp., adults of *A. hylambatis* and larvae of *Physaloptera* sp. As in our study, the prevalence of infection of the cosmocercid was high (86.0%), whereas that of the remaining species was very low (7% for Strigeidae, 21% for *Physaloptera* sp.); in addition, in this community, *A. hylambatis* was also the dominant species. These authors suggest that habitat and climate (e.g. amount of rainfall and soil moisture) are important factors affecting the distribution and development of the parasite fauna of *R. major*.

The nematode parasites found in this work present a monoxenous life cycle. In the case of *Aplectana* spp., the infection happens passively through the ingestion of eggs that are in the environment (e.g., contaminated prey with eggs that are ingested by the frogs). In the case of species of the genus *Cosmocerca*, the infection is active, with the penetration of infecting larvae through the skin of the host [34]. Life cycles of pharyngodonids in amphibian hosts were only observed in tadpoles [35]; in metamorphic or adult amphibian, unfortunately, there are still no studies of this type. However, it can be assumed that this species develops as in other oxyurids where the cycle is direct [34]. The genus *Ophiotaenia* principally parasitizing reptiles and amphibians; 26 species of this genus parasitize amphibians, while 10 of them occur in anurans in the Neotropical Region [36]. These cestodes have an indirect life cycle and consist of the following stages: oncosphere, procercoid, cysticercoid (merocercoid according to Chervy [37]), plerocercoid, and adult. The first three stages are presented in copepods (the intermediate host), the fourth stage occurs in the second intermediate host, and the fifth stage in the definitive host, a frog or a reptile [38]. *Dermatonotus muelleri* probably are infected when they spend time in the water during the rainy season and ingests the intermediate host.

No digeneans were found in any of the studies conducted in this host. This could be linked to the burrowing behaviour of *D. muelleri*. The digeneans are flatworms that need to complete their cycle in the presence of a mollusc host, so that the cercariae can emerge in the water [39]. The fact that *D. muelleri* spends much of the time buried, and not linked to any aquatic environment, limits all possible infections with cercariae.

It should also be highlighted that no helminths have been found in the larval stage (such as metacercariae of *Bursotrema* or *Travtrema*, cystacanths of *Centrorynchus*, larvae of cestodes such as *Mesocestoides* or larvae of nematodes such as *Physaloptera*) in the helminth community studied that are common in amphibian communities studied in other areas of the Chaco [27,40]. All of them are helminths that conclude their life cycles in other groups of vertebrates, such as birds, reptiles or mammals; these amphibians act as paratenic or intermediate host. In this aspect, *D. muelleri* would not play a prominent role in the life cycle of heteroxenous helminths in this area of its distribution (in other words, is not significant as prey item for possible definitive hosts) since all of the species found are monoxenic and their adults develop in the same amphibian. This is very different from that found in other amphibian species, where 50% or more of helminth species found have heteroxenous life cycles and amphibians act as paratenic or intermediate hosts [26,27,40,41].

On the other hand, several authors suggest that the body size of amphibian hosts vary positively with species richness and the abundance of helminth parasites [26,27,41,42]. In general, in this study, we did not find a correlation between *D. muelleri* body size and infection at the community parasite level. Likewise, at the population level, the abundance of infection of the helminth species, in general, did not show a correlation with the size of the host. Probably, the fact that the specimens of our study (juveniles) have not yet reached the size and maturity of adults is the reason why these variables are not related. In fact, some changes that occur during ontogeny such as dietary changes, immunocompetence and host behaviour, and time of exposure to different parasitic stages, are considered key in the structure of the helminth community [43,44]. It could be expected that this relationship will be reversed in adults but, Alcantara et al. [13] found that snout-vent length of *D. muelleri* was not correlated with abundance, intensity of infection or parasitic richness. This is possibly the pattern in this microhylid and further studies in adults from other points of geographical distribution are necessary to prove this.

In Argentina, studies about helminth community parasites in amphibians from the Chaco Seco ecoregion [27] are incipient compared with those of Chaco Húmedo [26,40,41,45–50]. These are two very different areas in terms of their geomorphological, floristic, faunal, and climatic characteristics [18,51]. Therefore, it is important to increase the study of helminth communities in an ecoregion with such extreme characteristics as Chaco Seco, in order to determine whether these differences translate into notable differences in the structure of parasitic communities in amphibians.

In conclusion, the features of the community of helminths in *D. muelleri* suggest that the characteristic of the habitat of this amphibian and its specialization to burrowing are the more important factors that influence the community. The helminth community in this microhylid from the Chaco Seco ecoregion is depauperate and is predominated by a nematode species (*A. hylambatis*) which have a direct life cycle including an infection stage (L3) inside the eggs. This characteristic of the life cycle is probably the reason for the high prevalence and abundance of infection. Nematodes with a free infective larval stage, such as *Cosmocerca* spp., are very unlikely to survive in the extreme dry conditions predominant in the area of the study. In the case of *Aplectana* spp., the membrane of the eggs can provide more protection against these conditions. In addition, *D. muelleri* appears to be an intermediate or paratenic host with little importance in the helminth life cycle of other vertebrate groups in this area; it did not present an infection with larval stages of any helminth group, as with other amphibian species.

Acknowledgements

We thank to program of Direccion de Recursos Naturales y Gestión – Ministerio de la Produtión y Ambiente de la Provincia de Formosa, Argentina, to authorize the capture of the amphibians for this research. Financial support was provided by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina, through grant PIP 11220170100 206CO, and by Universidad Nacional del Nordeste (UNNE), through grant PI 18Q001 to M. I. Duré. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Received 16 April 2019
Accepted 16 December 2019