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Caraballo, J., Arzamendia, V., Guerrero, R., González, C. (2025): Metazoan endoparasites of *Erythrolamprus poecilogyrus caesius* (Cope, 1862) (Serpentes: Dipsadidae) in South American Chaco: Structural attributes at different organization levels. Acta Herpetol. 21. doi: https://doi.org/10.36253/a_h-17983

Metazoan endoparasites of *Erythrolamprus poecilogyrus caesius* (Cope, 1862) (Serpentes: Dipsadidae) in South American Chaco: Structural attributes at different organization levels.

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Submitted on: 2025, 9th June ; revised on: 2025, 4th November; accepted on: 2025, 5th November.

Editor: Andrea Costa

Abstract. In this study, the structure of metazoan endoparasites infracommunities and component community in *Erythrolamprus poecilogyrus caesius* (Cope, 1862) (Serpentes: Dipsadidae) is presented. From 21 specimens (15 females; 6 males) collected between February 2017 and March 2022 at Ingeniero Juárez, Formosa, Argentina, 90.5% of individuals surveyed (n= 19) were infected with at least one species of metazoan endoparasite. Nine hundred sixty specimens were collected (117 adults; 843 larvae), from 11 taxa. *Kalicephalus appendiculatus* (Nematoda), *Raillietiella furcocerca* (Pentastomida), *Ophiotaenia joanae, Catadiscus uruguayensis, Opisthogonimus lecithonotus* (Platyhelminthes) were found as adults. Larvae identified were *Oligacanthorhynchus* sp. (Acanthocephala), *Physaloptera* sp. (Nematoda), *Strigea* spp. and *Alaria* sp. (Digenea). Digenea was the richest group (S= 6). Adults were collected in intestines, trachea and esophagus, while larvae were found in mesenteries and body cavity. *Ophiotaenia joanae* was the most prevalent species (38.1%) and *K. appendiculatus* had the highest mean abundance (3.7). Considering larvae, *Strigea* spp. were dominant and *Oligacanthorhynchus* sp. was subdominant. Between pairs of metazoans, positive and negative covariations were obtained. In general, intensity of metazoan taxa had positive correlation to host weight and body condition but had negative relationships with snout-vent length. Mean infracommunity richness (including larvae and adults) was 4.35 ± 1.27 taxa/host. Richness and diversity were higher in larval infracommunities than those composed by adults. This is the first ecological study of endoparasites in snakes from Argentina. New reports to parasite biodiversity in Dry Chaco were added, also, information about habitat use, diet, and position in trophic webs of host was generated.

Keywords. Community, endoparasitism, *Erythrolamprus poecilogyrus caesius*, metazoan.

INTRODUCTION

Parasitism is one of the most diverse life forms on Earth (Poulin and Morand, 2000). Among parasitic organisms, wildlife metazoan endoparasites, and helminths in particular, are often considered a 'hidden' and 'cryptic' biodiversity by several authors. 'Hidden', considering their life histories and the difficulty of note their presence related to their endoparasite living form, despite their important ecological, frequently undetected (Wood and Johnson, 2015). 'Cryptic' refers to the challenges in distinguishing them morphologically from other similar taxa within the same taxonomical group, or the necessity of using molecular biology techniques to identified them due to their high mutational rates and genetic diversity (Pérez-Ponce de León and Poulin, 2016; 2018).

Helminths parasites, as one of the most numerous and frequent components of this cryptic biodiversity, are far from being fully understood in certain vertebrate classes, including reptiles (Carlson et al*.,* 2020a). The decline of their populations, caused by anthropogenic interventions and their environmental consequences, could be one of the major obstacles preventing us from achieving this goal (Carlson et al*.,* 2020b).

In South America, 'Gran Chaco' region represents the second most extensive forest area following the Amazon rainforest (Eva et al., 2004). Sixty-two percent of this region is located in Argentina, representing 23% of the total extension of the country (TNC, 2005). Dry Chaco ecoregion comprise 489,000 km^2 of pastures and semi-deciduous forests that includes Chaco and Formosa provinces, two of the provinces with highest snake species richness (De Marzo et al., 2022; Williams and Vera, 2023). Nevertheless, only 9,1% of this surface is under a protected area regime (Nori et al, 2016).

Seasonal precipitation, vegetation, and soil structure of Dry Chaco landscapes allow the formation of temporal, semi-permanent and permanent ponds - environments and microhabitats where several vertebrates species, especially herpetofauna, coexists (Lescano et al., 2015).

Nevertheless, these landscapes and their endemic fauna are constantly threatened by intentional fires, deforestation, extensive pasture for cattle, and land uses changes. As a result of these activities, the loss of vegetation cover in the Dry Chaco has reached 200,000 hectares per year, highlighting the urgent need to establish conservation zones for snakes, which are highly threatened by these environmental changes and by climate change. A future biotic homogenization is predicted for this region (Andrade-Diaz et al., 2019; Cabral et al., 2024).

Erythrolamprus poecilogyrus (Wied-Neuwied, 1825) (Serpentes: Dipsadidae) is a species distributed in Argentina, Brazil, Bolivia, Paraguay, Peru, Uruguay, and Venezuela (Williams et al., 2021; Williams and Vera, 2023). *Erythrolamprus poecilogyrus caesius* (Cope, 1862) is one of the three subspecies present in Argentina with a wide distribution in the Argentine Chaco including provinces of Chaco, Corrientes, Formosa, Salta, Santa Fe, Santiago del Estero, and Tucumán (Williams et al., 2021; Williams and Vera, 2023). Quantitative studies on the diet of *E. poecilogyrus* in Argentina and Paraguay indicate that it is a specialist species with a predominantly batrachophagous diet, although it also consumes reptiles in a smaller proportion (Prieto et al., 2012; Bellini et al., 2015). In Brazil, some dietary analyses have identified additional prey items, including fish and mammals (Corrêa et al., 2016).

Erythrolamprus poecilogyrus caesius inhabits near to cricks, temporal ponds or humid pastures, where it could be seeing aggregated in groups until 10 individuals in different developmental stages together in a same pond, giving it reproductive advantages and protection against predators (Williams et al., 2021; Cabral et al., 2022; Williams and Vera, 2023).

At specific level, *E. poecilogyrus* is considered as of 'least concern' by Nogueira et al. (2020); at subspecific level, *E. p. caesius* is considered as 'not threatened' by Giraudo et al. (2012).

To date, three reports of digeneans and one of pentastomid were made for this species in three Argentinean provinces: *Opisthogonimus artigasi* Ruiz et Leão 1942 in Misiones (Caubisens Poumarau, 1968), *Travtrema stenocotyle* (Cohn, 1902) Goodman, 1951 and *Catadiscus* *uruguayensis* Freitas et Lent, 1939 both in Buenos Aires (Ostrowski de Núñez, 1979; Lunaschi and Drago, 2002), and *Kiricephalus* cf. *coarctatus* in Formosa (Montes et al., 2025).

On the other hand, comprehensive ecological studies in parasite fauna associated to reptiles, and specifically snakes, are non-existent in Argentina (Caraballo et al., 2024).

The aim of this study was to determine, for the first time, the metazoan endoparasites (from now referred as ME) community structure in *E. p. caesius* across its entire distribution range, based on specimens collected in Formosa province, located in the Argentine Dry Chaco. Additionally, the study explores possible relationships between the ME taxa reported and host biological characteristics.

MATERIAL AND METHODS

Site of study, host collection, and taxonomical ME identification.

Ingeniero Juárez (23°54′S, 61°51′W) is a locality in Matacos Department of Formosa province, Argentina. It is located in the Dry Chaco ecoregion. 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., *Aspidosperma quebracho-blanco*, *Prosopis ruscifolia* and *Schinopsis lorentzii*) is sparse, and the herbaceous species are predominantly grasses (*Gouinia* sp., *Setaria argentina* and *Trichloris* sp.). The landscape is flat and the climate is featured 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 (Maldonado et al., 2006). Twenty – one *E. p. caesius* specimens (15 females; 6 males) (Fig. 1) were collected by direct observation in microhabitats (temporal ponds at both sides of rural ways, surrounded by pastures and native forest patches) between February 2017 and March 2022. Hosts were euthanized using an intracoelomic injection of commercial anesthesia according to size of host (carticaine clorhydrate, 4%; L-adrenaline 1:100.000 units). Bioethical considerations and guidelines for host catching and euthanasia follow Beaupre et al. (2004). Each snake was sexed by direct observation of gonads or eggs in uterus. Specimens were weighted (in g), using an electronic scale, and the snout-vent length (SVL) was measured (in mm). Differences in mean weight and SVL between sexes were evaluated using a Mann-Whitney U test, and normality was assessed with an Anderson-Darling test. Snakes systematics, synonyms and distribution follow Williams et al. (2023). A snout-cloaca vent incision and body organs were isolated and surveyed (trachea, heart, lungs, esophagus, stomach, small and large intestines, kidneys, mesenteries, and coelomic cavity). All ME were fixed in hot formaldehyde 10% v/v and studied with standard techniques for helminths and pentastomids described in Amato and Amato (2010) and Barton and Riley (2004), respectively. Taxonomic identification followed Amin (1987, 2013) for acanthocephalans, Christoffersen and De Assis (2013) for pentastomids, Anderson et al. (2009) for nematodes, Khalil et al. (1994) for cestodes, Jones et al. (2005), Bray et al. (2008), and Fernandes and Kohn (2014) for digeneans. For larval stages of Platyhelminthes, identification followed Hamann et al. (2019; 2022 a). Voucher material from sampled hosts (12 specimens, 10 females, 2 males) were deposited in Colección Herpetológica of Instituto Nacional de Limnología (INALI) (accession numbers: INALI 7391, 7397, 7398, 7402, 7404, 7405, 7406, 7407, 7408, 7413, 7539, 7540). ME were deposited in the Helminthological Collection of Reference of Centro de Ecología Aplicada del Litoral (CECOAL-CONICET); accession numbers are provided in Supplementary Materials, table S1.

Description of component community

ME taxa were classified in function of their life cycle in geohelminths or biohelminths by consulting specialized literature for each genus (Table S1, Supplementary Materials). Prevalence (P), mean abundance (MA), and mean intensity (MI) were calculated following Bush et al. (1997). Dispersion index was calculated for each taxon through the variance/mean ratio in order to assign every taxon to their correspondent distribution ($\sigma^2/X << 1$ when a ME taxon followed a normal distribution; $\sigma^2/X = 1$ when a ME taxon followed a Poisson's distribution; $\sigma^2/X >> 1$ when a ME taxon followed a negative binomial distribution). We avoid to presenting standard deviations for ME taxa with negative binomial distribution; following Reiczigel et al. (2024) considerations (presenting standard deviations for mean values is not congruent with non-symmetrical distributions as negative binomial distribution). On the other hand, Bush and Holmes (1986) criterium (B&H), based on prevalence for the dominance of ME (>40% for core species, 10-20% for secondary species, and <10% for satellite species), were compared with the ecological roles assigned to each metazoan taxon. These roles were obtained by three different indices, which are defined and described as follows: (a) *Infection index* (ii= MA x P/100) with three ecological roles (dominants, subdominants, and accessories) based on logarithmic differences among values obtained by the index for each taxon [Janion (1967) *apud* Pence and Eason (1980) modified by Guerrero (1996)]; (b) *Specific importance index* [(SII= P + (MA x 100)] where no categories of importance are established, but, arithmetic differences between scores obtained by each taxon could be compared. We assign the following categories: high, medium and lesser importance (Bursey et al., 2001); (c) *Thul's index* (TI) with four categories (dominants, when $TI \geq 1.0$; codominants, when $0.01 \leq TI < 1.0$; subordinates, when $0 < I < 0.01$, and unsuccessful pioneer, when: $TI = 0$) (Thul et al., 1985). Ecological roles were represented graphically using Olmstead-Tukey diagrams. These representations are generated using means of P and ln (MA) + 1 of all taxa of ME of the component community. Representation of these in a cartesian plane allows the obtention of four quadrants, with a previous assignation of roles: I for dominant species; II for subdominants or constant species; III for accessory or rare species, and IV for indicator species.

Interspecific relations by site of infection, influence of host biological characteristics and structural attributes.

Interspecific relations between pairs of ME taxa or the influence of host biological characteristics on the intensity of each taxon was analyzed in two levels: infrapopulations and component populations. An infrapopulation is a group of ME of the same taxon in an individual host. On the other hand, component populations include all stages of ME from the same species in a host population (Bush et al., 1997). Frequency (F) of each ME taxon component population by site of infection was calculated following Morales and Pino (1987) and plotted by bars graphs. In each pair of taxa collected in the same organ, a Spearman's rank correlation coefficient was obtained in order to analyze the covariation of their infrapopulation intensities and identify possible interactions among them. The influence of weight and SVL on the intensity of each ME infrapopulations was assessed using Spearman's rank correlation coefficient (p) between these variables. Hosts body condition was measured through Quetelet's index of body mass (defined as weight/SVL^2 and expressed in kg/m^2). Quetelet's index has been proven on other snakes' species successfully (Falk et al., 2017). The approach to structural attributes was performed in two levels, infracommunities and component community. An infracommunity includes all the infrapopulations of ME in an individual host. Consequently, component community includes all the component populations of ME in the host population (Bush et al., 1997). Infracommunity mean richness was estimated counting the number of ME taxa in each host (±1 standard deviation). Shannon-Weaver's diversity index (H'), and Simpson's dominance index (λ) were obtained at infracommunity and component community levels and compared with the ranges proposed by Margalef (1972) and Magurran (1988): (a) high dominance/low diversity ($0 < H' < 1.35 / 0.01 < \lambda < 0.33$); (b) medium dominance/medium diversity ($1.36 < H' < 3.5 / 0.34 < \lambda < 0.66$) or (c) low dominance/high diversity ($H' \geq 3.6 / \lambda \geq 0.67$). For measuring the effect of the sample size in the estimation of component community richness and its precision, an accumulation species curve based in Chao-2 index was constructed using the "Mao's tau" method described in Colwell et al. (2004). All statistical analysis was performed at 95% confidence level using Paleontological Statistics (Past) in its version 4.16c (Hammer et al., 2001).

RESULTS

Description of component community

Eleven ME taxa from three phyla were identified: Excluding *Kalicephalus appendiculatus*, all taxa identified were biohelminths. *Eryhtrolamprus poecilogyrus caesius* ME were generalist, parasitizing in larval stages other amphibians and reptiles or for their predators in the adult stage, excepting *Kalicephalus* and *Opisthogonimus* genera, which have strict parasitic specificity for snakes as definitive hosts. Detailed information about taxonomical classification of each ME and their intermediate, paratenic or definitive hosts, and is provided in Supplementary Material (Table S1).

Nine hundred sixty ME specimens were collected; 843 of them were found in larval stages and 117 were in adult stage. Of all host examined, 90.5% (n= 19) were infected at least by one ME. The most prevalent ME species in adult stage was *O. joanae*, meanwhile *K. appendiculatus* showed the highest mean abundance (table 1). In larval stages, *Strigea* sp. 1 metacercariae and *Alaria* sp. mesocercariae showed the highest prevalence and mean abundance. With the exception of *O. joanae*, all ME component populations showed an aggregation pattern and overdispersion in the host population, proper of the negative binomial distribution (table 1).

Considering only adult ME taxa, *K. appendiculatus* and *O. joanae* were not classified in the same ecologic role by the four indices applied. These species presented dominant and subdominant ecologic roles for ii, respectively, but were considered as secondary species by Bush and Holmes (1986) criterium, of medium and lesser importance by the SII and, codominant and subordinate species by TI. *Opisthogonimus lecithonotus*, *C. uruguayensis*, and *R. furcocerca* were considered as less importance ME by all indices compared (table 2).

According to the TI index, all the larvae were classified as unsuccessful pioneers; no taxa were identified as dominant. All indices excepting TI consider *Alaria* sp. and *Strigea* sp. 1 as core/dominant/high importance taxa. Plotting all identified taxa without considering their developmental stage in an Olmstead-Tukey diagram, 3 taxa (1 adult, 2 larval) were dominant, one taxon (*O. joanae*) was subdominant, 6 taxa (3 adults, 3 larval) were accessory, and *Oligacanthorhynchus* sp. was an indicator taxon (Fig. 2).

Interspecific relations by site of infection, influence of host biological characteristics and structural attributes

Erythrolamprus poecilogyrus caesius ME were site-specific. Most of the adult ME (4 taxa) were found at higher frequencies in the small intestine, while larval stages (6 taxa) were predominantly found in the mesenteries or free in the body cavity, most frequently associated with the trachea, as *Alaria* sp. (Fig. 3).

Covariation between abundances of ME parasitizing the same organ did not show a clear pattern, and the correlation coefficients were generally weak and not statistically significant (Fig. 4). Two pairs of larval mesenterial ME (*Oligacanthorhynchus* sp. – *Alaria* sp., *Strigea* sp. 1 – *Strigea* sp. 3), and two pairs of ME from the digestive system (*O. joanae – Physaloptera* sp., *K. appendiculatus – Physaloptera* sp.) had negative correlation coefficients. Contrastingly, in three pairs of larval mesenterial ME (*Oligacanthorhynchus* sp. – *Strigea* sp. 3, *Strigea* sp. 2 – *Strigea* sp. 3, *Alaria* sp. – *Strigea* sp. 1), and one pair of ME from the digestive system (*K. appendiculatus – O. joanae*), the correlation coefficients were positive.

The estimated number of taxa for our sample size was 11 taxa, with an expected richness of 11.95 taxa based on the Chao-2 index (Fig. 5). This estimate reached 92.1% of the potential taxa that could be detected with a large sample size.

The infracommunity mean richness of snakes parasitized by both adults and larvae ME simultaneously was of 4.35 ± 1.27 taxa per host; in contrast, mean richness was higher in snakes infected solely by larval taxa compared to those infected only by adult taxa (table 3). Shannon-Weaver's diversity and Simpson's dominance indices showed that, their associated ME at infracommunity and component community levels are generally dominated by few species (*K. appendiculatus*, *Alaria* sp., and *Strigea* spp.), resulting in low diversity at this level. Diversity increased slightly and lower dominance were observed at infracommunities and component communities composed by adults and larvae at same time (table 3).

Snakes showed slight variations in their weight (26.6±11.2) and SVL (43.8±6.9); SVL did not show statistically significant differences among sexes (U= 26.5; P = 0.16). On the other hand, weights show statistically significant differences among sexes (U= 6; P = 0.027). However, given the unbalanced sample—with more females (15) than males (6)—sex was not considered in subsequent analyses. All variables followed a normal distribution ($A_{Weights} = 0.55$; $A_{SVL} = 0.23$; $P_{Weights} = 0.14$; $P_{SVL} = 0.77$).

In general, host weight and the intensity of each ME infrapopulation showed weak positive correlations, with the exception of *Oligacanthorhynchus* sp., when SVL and intensity of infrapopulations were considered, only *O. joanae,* and *Physaloptera* sp. showed negative and weak correlation coefficients. Regarding of Quetelet's index of body mass vs. intensity, *O. joanae* and *Oligacanthorhynchus* sp. showed negative correlations and *Oligacanthorhynchus* sp. showed statistical significance, while the correlations coefficients for the other taxa were weak (table 4).

DISCUSSION

Studies on the ecology of helminths in snakes are extremely scarce in South American portion of Neotropics (Ávila et al., 2013; Mati et al., 2015; Carvalho et al., 2018; Matias et al., 2018, Oliveira et al., 2024). This study represents the first contribution to the knowledge of the ME ecology in snakes in Argentina, focusing on the genus *Erythrolamprus*.

Despite the lack of ecological studies in Argentina, several taxonomic studies, species distribution reports, new host records, and species listings have been conducted (see Caraballo et al., 2024). A compilation of parasitological studies from Argentina, Brazil, and Uruguay in *Erythrolamprus* species and subspecies reveal high parasite richness. Notably, acanthocephalans are the only helminth group with reported larval stages (Table S2, Supplementary Materials). With the exception of *C. uruguayensis*, all ME reported herein are being documented for first time in *E. p. caesius* as host in Argentina.

Description of component community

The taxonomic composition of ME component community in *E. p. caesius* could be indicative of semi-aquatic habitat uses of this subspecies, as well as, the amplitude of its diet. *Erythrolamprus poecilogyrus caesius* has been described as a dietary generalist, preying on a broad range of taxa such as arthropods, fishes, anurans, amphisbaenas, lizards, birds, and rodents (Amaral, 1978; Corrêa et al., 2016; Di Pietro et al., 2020). Nevertheless, studies from Argentina and Paraguay suggest a degree of specialization, with a diet composed mainly by tadpoles, frogs, and toads (Prieto et al., 2012; Bellini et al., 2015; Cabral et al., 2017). In general, published data on trophic ecology studies in *E. poecilogyrus* did not present identification of snakes surveyed at subspecific level. In this sense, plausible differences in diet among subspecies in its distribution have to be considered, as well as its influence in catalogue them as generalist or specialist.

Despite the developmental stage of the ME reported herein, ecological conditions affect the spatial and temporal overlap of the host and parasite, while species-specific behaviors characteristics can modify these interactions. Adaptations that increase encounter with potential hosts will likely lead to higher infection probabilities (Combes, 2005; Bolek et al., 2024).

Several potential routes for host infection were identified, including or not intermediate or paratenic hosts.

In regard of adult ME, *Kalicephalus* spp. could be considered as a geohelminth. Infections may occur when the host explores soil, introducing infective stages with tongue movement (Schad, 1956; Anderson, 2000). Values of parasitological descriptors of *K. appendiculatus* could represent parasitological evidence of the terrestrial habitat use in this snake. Nevertheless, the other four taxa were biohelminths with freshwater-associated intermediate hosts, together supporting the semi-aquatic habits of this subspecies.

The life cycle in *Ophiotaenia* species is not completely elucidated and studies about this topic are scarce (Scholz and De Chambrier, 2003). Two transmission pathways had been suggested: a three-host cycle including copepods as first intermediate hosts, fishes or amphibians as secondary intermediate hosts, and reptiles as definitive hosts, or a two-host cycle with a tissue phase of development in the final host, followed by migration to the intestine, without intermediate or paratenic vertebrate host (Biserkov and Kostadinova, 1997; De Chambrier et al., 2021). The first transmission route is considered more likely for *O. joanae*, given the semi-aquatic habits of *E. p. caesius* and its most common prey items (tadpoles and adult anurans).

For *Catadiscus* and *Opisthogonimus*, Planorbidae snails are obligatory intermediate hosts in their life cycle. *Catadiscus* cercariae encyst in vegetation, where it can be ingested by herbivorous tadpoles or during predation activity (Yamaguti, 1975; Hamann and Kehr, 2003). Metacercariae of *Opisthogonimus* have been found parasitizing the body cavity, muscle, pharyngeal region, and tegument of tadpoles (Hamann and González, 2009), and adult anurans (Hamann et al., 2009). Both amphibians life stages are plausible prey for *E. p. caesius*. Seasonal conditions in the Dry Chaco may limit water availability and shorter pond duration, limiting resources for anurans and explaining the low prevalence and mean abundances of these digeneans in adult stage.

Raillietiella furcocerca commonly infects lizards, where both nymphs and adults occur, using insect prey as intermediate hosts (Fain, 1966; Melhorn, 2004 *apud* Fredes and Raffo, 2006). Lizards are occasional prey for *E. p. caesius* (Andrade et al., 2020) and the low prevalence of this ME suggests they are minor component of its diet.

Parasite ecology studies in snakes from Nearctic and Neotropical do not report frequently the presence of larval helminths (see Detterline et al., 1984; Fontenot and Font, 1994; Jiménez-Ruiz et al., 2002; Ávila et al., 2013; Mati et al., 2015; Carvalho et al., 2018; Matias et al., 2018; Oliveira et al., 2024; Silva-Trejo et al., 2025). Interestingly, 81.87% of ME collected in our study were larval stages of biohelminths.

Oligacanthorhynchus sp. and *Physaloptera* sp. are biohelminths of broad host range that include arthropods (myriapods and several insect orders) as intermediate hosts. Their ocurrence in *E. p. caesius* suggests a paratenic role and potential predator-prey interactions with birds or mammals, as possible definitive hosts (Cawthorn and Anderson, 1976; Anderson, 2000; Kennedy, 2006; Richardson, 2006).

Pioneer studies in Argentine snakes reported high number of larval digeneans (mesocercariae and metacercariae) in mesenteries and epiploic folds (Caubisens Poumarau, 1968); in this particular case, from 960 digeneans collected, 797 were larval, indicating high abundance.

Alaria and *Strigea* include one obligatory intermediate host (Planorbidae), with snakes as secondary intermediate hosts, and reach adult stages in carnivorous mammals or birds of Accipritidae, Strigidae, and Falconidae families (Niewiadomska and Pojmańska, 2011). At Ingeniero Juárez and other localities from Dry Chaco, metacercariae of *Strigea* species and mesocercariae of Alariinae were found parasitizing anuran in previous research. These were reported as dominant and more abundant taxa in community of *Lepidobatrachus llanensis* Reig et Cei, 1963 (Hamann et al., 2019, 2022a,b). We confirm the presence of larval stage of Digenea with this identity in the material collected from this snake species.

Considering the dynamics of microhabitats in Dry Chaco, where host as resource for ME are neither permanent nor abundant, and environmental conditions fluctuate drastically, ME as *Strigea* and *Alaria* may maximize their prevalence by enlarging their host range in secondary intermediate or paratenic roles in function of their temporal availability. The accumulation of stages in other suitable hosts, such an anurans or snakes, allows that predation could facilitate potential transmission to definitive hosts (birds for *Strigea* spp. or mammals for *Alaria* spp.). Several *Strigea* species had been recorded in Formosa province, Argentina, parasitizing *Rupornis magnirostris* (Gmelin, 1788) (=*Buteo magnirostris*), *Buteogallus meridionalis* (Latham, 1790) (Accipritidae), and *Caracara plancus* (Miller, 1777) (Falconidae) (Lunaschi et al., 2007; Drago and Lunaschi, 2015). In Argentina and Brazil, predation on *Erythrolamprus* species and other dipsadids by birds of these and other families (de Souza et al., 2021; Fernández-Reinoso et al., 2022) and carnivores as *Procyon cancrivorus* (Cuvier, 1978) and *Cerdocyon thous* (Linnaeus, 1766) are reported (Quintela et al., 2014; Castellari-González et al., 2016). Another transmission route is the consumption of rodents that had been reported as prey as well as a paratenic host for *Strigea* and *Alaria* species in Holartic (Möhl et al., 2009; Batista et al., 2019). These could support acquisition routes of infective larval stages of these taxa by this snake and reaching maturity in predators in this site of study.

Species serving as intermediate hosts tend to lie in different trophic levels in food web to that for definitive host species. In these positions, they tend to have many different predators, mediating many food chains, acting as focal points of predation interactions involving species across various trophic levels, from higher to lower. Those mechanisms could promote frequent and stable predator-prey interactions, which are essential for the successful completion of parasite life cycles (Chen et al., 2008).

In regard of parasitological descriptors, in the limited studies on ME ecology in semi-aquatic to aquatic snakes in Neotropics and Holartic, it is observed that a single taxon or a few from one phylum often show high prevalence and mean abundances, while other taxa are less abundant or prevalent. In this sense, ME component populations prevalence in studies from Neotropical snakes, prevalence did not exceed 63% (see Jiménez-Ruiz et al., 2002; Avila et al., 2013; Mati et al., 2015; Carvalho et al., 2018; Matias et al., 2018; Oliveira et al., 2024; Silva-Trejo et al., 2025), while in Holarctic snakes can reach 100% (see Fontenot and Font, 1994; Santoro et al., 2013). In both realms, mean abundances were between 0.02 and 262 parasites/host. Our results are similar to those obtained in other realms in terms of prevalence and mean abundance. Regarding ME proportion of phyla in taxonomic structure, in Neotropical studies, Nematoda taxa show higher richness, prevalence, and mean abundance, while other as Acanthocephala, Pentastomida, and Platyhelminthes (Digenea and Cestoda) appears occasionally with lower richness, prevalence, and mean abundance (Ávila et al., 2013; Mati et al., 2015; Carvalho et al., 2018; Matias et al., 2018; Oliveira et al., 2024). In contrast, North American studies on *Akgistrodon* Palisot de Beauvois, 1799, *Nerodia* Baird et Girard, 1853 and *Thamnophis* Fitzinger, 1843 showed high variability in the number of taxa and parasitological descriptors (Fontenot and Font, 1994; Jiménez-Ruiz et al., 2002; Silva-Trejo et al., 2025). Our results resemble with studies on colubrid snakes from Nearctic and Palearctic realms (Fontenot and Font, 1996; Santoro et al., 2013), where digeneans and larval helminths dominate the communities. However, contrast with finding in Neotropical Dipsadidae were geohelminths and Nematoda are often the most diverse (Table S3). These differences may reflect spatial and host-related variation in ME prevalence and mean abundances.

Despite their relevance, importance and dispersion indices are rarely included in Nearctic and Neotropical studies on snake parasite ecology (Fontenot and Font, 1994; Jiménez-Ruiz et al., 2002; Ávila et al., 2013; Mati et al., 2015; Carvalho et al., 2018; Matias et al., 2018). Their use can yield key insights into community structure, parasite transmission dynamics, and the selection of appropriate biomarkers for characterizing parasite assemblages (Poulin, 1993; 1999; McVinish and Lester, 2020; Lester and Blomberg, 2021).

Generally, parasite populations follow a negative–binomial distribution which reflects the common pattern of parasite dynamics in natural hosts' populations (many hosts with few parasites and few hosts with many parasites) (Reiczigel et al., 2024). According to metapopulations theory, this distribution support transmission dynamics by ensuring uninfected hosts serve as available 'patches' for parasites recruitment. In our results, only *O. joanae* showed a regular distribution, likely due to its constant abundance at infrapopulation level, making the mean and variance ratio close to 1.

In our study, the high abundance of larval forms, compared to adult, makes traditional importance indices less effective in assessing the true ecological role of these species. These indices tended to assign similar roles to species that are equally abundant and prevalent, or, in some cases, classify them into categories that exclude them from being considered 'important'. Therefore, it is crucial to analyze the helminth community considering both mature and immature stages, both simultaneously and separately. Additionally, it is necessary to employ other qualitative and quantitative techniques to prevent the exclusion of species categorized as 'unsuccessful pioneers', a label based solely on their maturation stage. This approach is essential, as it considers for the role of paratenic hosts in maintaining the life history of parasites and recognizes the potential of parasites as indicators of possible predators.

Interspecific relations by site of infection, influence of host biological characteristics and structural attributes.

ME in adult stage exhibited high specificity for the site of infection. However, a high number of larval taxa, which lower specificity and wide host range, may influence interspecific interactions, aiding their survival until they reach full development in suitable hosts.

Some ME pairs of taxa showed positive correlation. Aho (1990) suggested that helminth communities in amphibians and reptiles tend to be isolationist and non-interactive. Nevertheless, recent studies on fish and mammal parasite communities supports that facilitation among parasite species is more common than negative interactions. Positive interactions contribute more significantly to increasing communities' richness (Dallas et al., 2019; Rodgers and Bolnick, 2024). The mechanisms are unclear, but may involve a pioneer species weakening the host's immune system, allowing secondary species to colonize. However, considering the indirect approach in testing these associations (Poulin, 2001), we suggest that a larger sample size could be needed to provide more statistically robust results.

Parasite community studies in aquatic snake in Nearctic and Palearctic region reported 11 to 13 taxa (Fontenot and Font, 1994; Santoro et al., 2013), similar to our finding, though, only Santoro et al. (2013) included larval stages. In contrast, the richness reported for Neotropical snake appears lower, which may be related to the absence or lack of reporting of larval stages.

Excluding larval stages underestimates infracommunity richness. Infracommunities that include larval stages, either exclusively or combined with adult, show greater richness than those composed only of adult. Larval and larval-adult communities show slightly higher diversity and dominance than adult-only communities. A similar pattern was observed by Santoro et al. (2013) in the habitat generalist snake *Hierophis viridiflavus carbonarius* (Bonaparte, 1833) (Colubridae) in southern Italy. The low diversity and dominance indices observed in our results are consistent with research on snakes with different habitat uses (Fontenot and Font, 1994; Jiménez-Ruiz et al., 2002; Santoro et al., 2013).

Weight and SVL are variables linked to host characteristics as body condition and age (Poulin, 1997). The most accepted hypothesis suggests that larger hosts may harbor more parasites due to their greater size which provides more resources and space. Additionally, age may influence parasite richness or abundance due to longer exposure to infections or changes in feeding preferences (Poulin, 1997). Studies on host size or mass as predictors of parasite richness or abundance in snakes are scarce (Lettoof et al., 2019; Oliveira et al., 2024), and no general pattern has been established. For example, while SVL predicts higher richness in Neotropical amphibians (Campião et al., 2015), no such relationship was found in lizards (Leung and Koprivnikar, 2019).

In snakes, a particularly relevant issue is the possibility that food availability early in life can have a disproportionate impact on later growth patterns and, ultimately, on maximum adult body size. Such an effect could generate substantial size variation among cohorts, even in the absence of genetic differences (Madsen and Shine, 2000; Brown et al., 2017).

Minor SVL and weight variation among specimens suggest they belong to the same cohort, consistent with Cabral et al. (2022), who observed newborn groups for this subspecies. These individuals were likely born in the pond and stayed nearby, using its water, shelter, and amphibian prey as a food source. Juveniles exhibit opportunistic feeding behavior, which—although not yet specifically reported for this subspecies—could be associated with site fidelity, efficient use of resources, and the absence of alternative water bodies in the area (Cabral et al., 2017, 2022).

This may explain the observed pattern: snakes with greater body mass showed higher ME intensities, whereas those with longer SVL had lower ones. In this sense, we suggest that relationships between body weight or SVL in with snakes' age , as well as, associations of these host features with the intensity of some ME cannot be analyzed isolated, or as response of a univariate phenomenon.

In addition, reptiles have a strong innate immune response, a moderate adaptative component with a slower activation, no lymphatic nodes, and seasonal variations in T and B cell activity influenced by temperature (Rios and Zimmerman, 2015). We propose that unconsidered effects on the innate and adaptive immune system during host development may differentially affect the recruitment of ME taxa and the increase of its intensity over time.

Our results suggest that some in hosts with reduced body conditions (and possibly depressed immune system) could facilitate the colonization of some ME species could be facilitated over time. This pattern could not be necessarily only related to host age but could also occur before mating and reproduction seasons, hydric stress, prey availability and host characteristics do not hinder successful ME recruitment.

A non-significant positive correlation between larval ME intensity and host condition suggests that certain snake sizes may be more vulnerable to predation Predators could take advance of the temporal aggregation behavior reported in this species as prey, and consequently, this could increase the likelihood of ME reaching their definitive hosts.

Oligacanthorhynchus sp., was the only larval species showing a significant negative correlation, both with host condition and with other helminths sharing the mesenterial–body cavity site. In this sense, both experimental and meta-analytical approaches show that cystacanth infection has no effect on intermediate host size (Benesh and Tellervo Valtonen, 2007; Fayard et al., 2020). Even, a positive relationship is observed between helminth larvae (cystacanths and metacercariae) and intermediate host size in natural marine environments (Poulin et al., 2003). These patterns contrast with our results; cystacanths and other larval helminths sharing intermediate hosts had positive correlations among them, along with negative correlations with serotonin concentrations. This have been suggested as evidence of host manipulation and the removal of heavily infected hosts by predation (Poulin et al., 2003). However, this also contrasts with our results.

This could suggest that in this study area, larval stages could not present refined mechanisms of host exploitation, possibly due to a recent relation between hosts and parasites, in evolutionary terms. Warburton (2020) consider drylands as ‘natural laboratories’, where hypothesis on virulence evolution, host spectra, and life cycle strategies could be tested, because extreme conditions and low population density represent examples within extremes in understand parasite communities diversity, structure and the transmission dynamic.

Studies in amphibians and reptiles as intermediate or paratenic hosts in these environments are scarce. In this sense, our comparison with previous research has to be as conservative as possible. At the same time, we suggest the design of more field experimental studies in this area in order to tap the potential of these environments, unraveling the challenges and knowledge gaps in the subjacent mechanisms of these parasite-host relationships.

This study provides new insights into the parasitic fauna of snakes, contributing valuable data on the ecology of ME infracommunities and component community of *E. p. caesius*, as well as their relationship with the host's biological characteristics. Its helps fill the research gap in area, specifically within the Dipsadidae family in Neotropics. However, most Neotropical research remains largely descriptive, unlike the more quantitative Holarctic studies.

The sampling effort and sample size, combining scarce field material with museum specimens from different origins and times periods, have provide a valuable approach to parasite communities in areas where knowledge is still limited, as Neotropical zones (Carlson et al., 2020). Nevertheless, these methods have limitations that need to be addressed. The underestimation of certain factors may exclude measurable aspects that must be considered. It is important to account for the heterogeneity of each study area, including environmental conditions and intraspecific host differences.

Evidence has shown that ME in communities associated to amphibians and reptiles belong to generalist species with a broad host range and low specificity. Considering this, studies on the parasitic fauna of amphibian and reptiles species provide valuable insights into the parasitic communities of related species with similar habitat use and trophic ecology. This could be especially relevant for species that are more vulnerable or have restricted distributions due to population declines, often caused by environmental degradation, such as the one the American Chaco has been enduring for decades (Nori et al, 2016).

Acknowledgements. We want to thank deeply to Andres Ulibarrie for provide us photographs of the snake host for illustrate this work and, to Dr. Franco Rosso (Dirección de Recursos Naturales y Gestión – Ministerio de la Producción y Ambiente, Provincia de Formosa, Argentina), for authorizing the capture of the snakes sampled in this study (Dispositions 108/21 and 091/22). We acknowledge an anonymous reviewer whose comments contributed to improving the manuscript significantly.

Financial support. Financial support was received from Universidad Nacional del Nordeste (Grant number PI 21Q001 to C.E.G.), from CONICET (PIP 11220200101582CO to C.E.G.), from Universidad Nacional del Litoral (CAID- UNL 2020), and from Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (PICT-2020-SERIEA-01341).

SUPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <http://www.unipv.it/webshi/appendix> Manuscript number 17983.

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Table 1. Parasitological descriptors of the adult and larval taxa of ME collected in *E. p. caesius* from a locality of Dry Chaco, Argentina. **SINT:** Small intestine. **LINT:** Large intestine. **ESO:** Esophagus. **TRA:** Trachea. **BCAV:** Body cavity. **STO:** Stomach. **MES:** Mesenterium. **G:** Geohelminth. **B:** Biohelminth. **N**: Number of metazoans collected; **P**: prevalence (%), **MA**: mean abundance, **MI**: mean intensity, **min-max**: minimum and maximum value of abundance, **σ^2/X**: Dispersion index. **BN**: Binomial negative distribution. **N**: Normal distribution.

ME taxa	Site of infection	Life cycle/ Transmission of helminth	N	P	MA	MI	min-max	σ^2/X	Distribution
Adult stage									
Nematoda									
Kalicephalus appendiculatus	SINT	G	78	33.3	3.71	4.11	1–37	19.8	BN
Platyhelminthes									
Ophiotaenia joanae	SINT	B	9	38.1	0.43	0.47	1 – 2	0.83	N
Catadiscus uruguayensis	LINT	B	11	4.8	0.52	0.58	1 –11	11	BN
Opisthogonimus lecithonotus	ESO	B	9	19.1	0.43	0.47	1 – 4	3.8	BN

Pentastomida									
Raillietiella furcocerca	TRA	B	10	4.8	0.48	0.53	1 –10	10	BN
Larval stage									
Acanthocephala									
Oligacanthorhynchus sp.	BCAV	B	21	23.8	1.19	1.32	2 – 9	4.5	BN
Nematoda									
Physaloptera sp.	STO	B	25	19.1	1.00	1.11	1 – 15	13.6	BN
Platyhelminthes									
Alaria sp.	BCAV, TRA	B	241	42.9	11.48	12.68	1 – 116	64.2	BN
Strigea sp. 1	MES	B	508	42.9	24.19	26.74	1 – 216	164.7	BN
Strigea sp. 2	MES	B	15	14.3	0.71	0.79	1 – 9	6.7	BN
Strigea sp. 3	MES	B	33	23.8	1.57	1.74	1 – 16	12.8	BN

Table 2. Ecologic role for ME taxa in the community obtained by comparison of four different indices. **D:** Dominant. **SD:** Subdominant. **A:** Accessory. **M:** Medium. **L:** Lesser. **H:** High. **C:** Codominant. **S:** Subordinate. **UP:** Unsuccessful pioneer.

ME taxa	**ii** **Janion (1967) *apud* Pence and Eason (1980)**	**B&H** **Bush and Holmes (1986)**	**SII** **Bursey et al. (2001)**	**TI** **Thul et al. (1985)**
Adult stage				
Nematoda				
K. appendiculatus	1.24 (D)	Secondary	404.73 (M)	0.07 (C)
Platyhelminthes				
O. joanae	0.16 (SD)	Secondary	80.96 (L)	0.009 (S)
C. uruguayensis	0.03 (A)	Satellite	52.42 (L)	0.001 (S)
Op. Lecithonotus	0.07 (A)	Secondary	42.11 (L)	0.004 (S)
Pentastomida				
R. furcocerca	0.02 (A)	Satellite	52.42 (L)	0.001 (S)
Larval stage				
Acanthocephala				

Oligacanthorhynchus sp.	0.28 (SD)	Secondary	142.85 (M)	0 (UP)
Nematoda				
Physaloptera sp.	0.19 (SD)	Secondary	119.10 (M)	0 (UP)
Platyhelminthes				
Alaria sp.	4.92 (D)	Core	1190.52 (H)	0 (UP)
Strigea sp. 1	10.38 (D)	Core	2461.95 (H)	0 (UP)
Strigea sp. 2	0.17 (SD)	Secondary	95.23 (L)	0 (UP)
Strigea sp. 3	0.22 (SD)	Secondary	171.44 (M)	0 (UP)

Table 3. Ecological indices at infracommunity and community level for ME taxa parasitizing *E. p. caesius* from a locality of Dry Chaco, Argentina. **MS:** mean number of taxa, **H'**: Shannon-Weaver's index of diversity, **λ**: Simpson's index of dominance, **S**: Number of taxa. **SD**: 1 standard deviation.

Stage	Infracommunity level			Community level		
	MS ± SD	H' ± SD	λ ± SD	S	H'	λ
Only adults	1.47 ± 0.83	0.15 ± 0.31	0.88 ± 0.21	5	1.10	0.45
Only larvae	2.92 ± 1.26	0.43 ± 0.31	0.75 ± 0.19	6	1.06	0.47
Adults + larvae	4.35 ± 1.27	0.61 ± 0.41	0.66 ± 0.24	11	1.43	0.35

Table 4. Spearman's rank correlation coefficients for intensity of each ME infrapopulation *vs.* host weight, snout-vent length (SVL) and Quetelet's index of body mass. Bold correlation coefficients indicate statistical significance for α = 0.05.

ME taxa	**Weight *vs* ME intensity (ρ)**	**SVL *vs* ME intensity (ρ)**	**Quetelet's index of body mass vs ME intensity (ρ)**
Adult stage			
Nematoda			
K. appendiculatus	0.48	-0.18	0.41
Platyhelminthes			
O. joanae	-0.32	-0.24	-0.25
Larval stage			
Acanthocephala			
Oligacanthorhynchus sp.	-0.51	-0.45	**-0.78**
Nematoda			
Physaloptera sp.	-0.71	-0.37	0.00
Platyhelminthes			
Alaria sp.	0.45	0.048	0.62
Strigea sp. 1	0.25	-0.098	0.12
Strigea sp. 2	0.50	1.00	0.50

Strigea sp. 3	0.45	-0.22	0.45

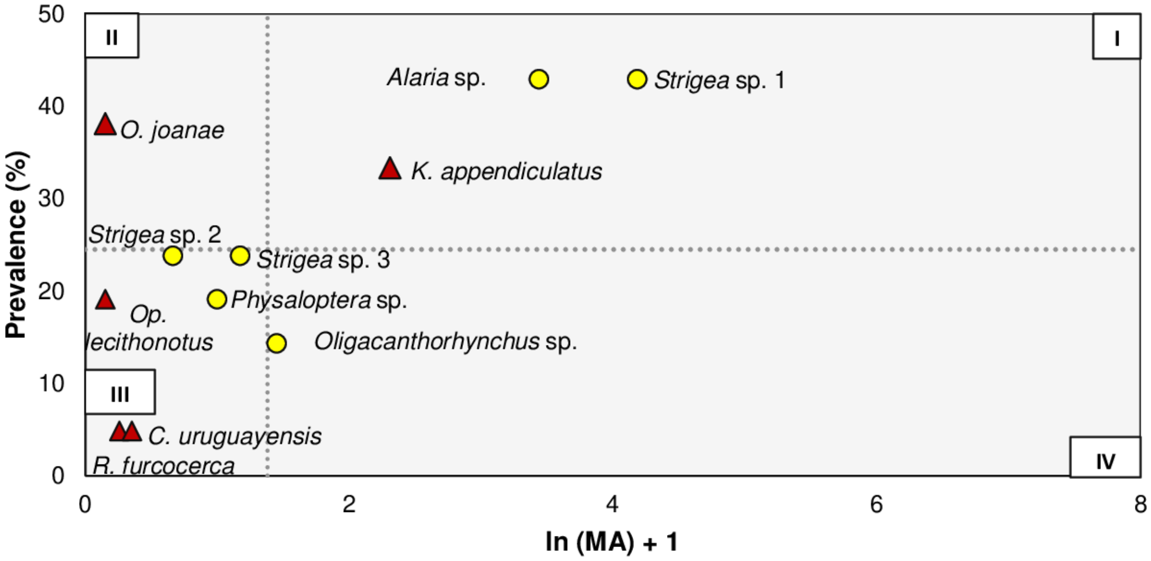
Fig. 1 Lateral view of anterior region of *Erythrolamprus poecilogyrus caesius* (Cope, 1862) (Serpentes: Dipsadidae) from a locality of Dry Chaco, Argentina.

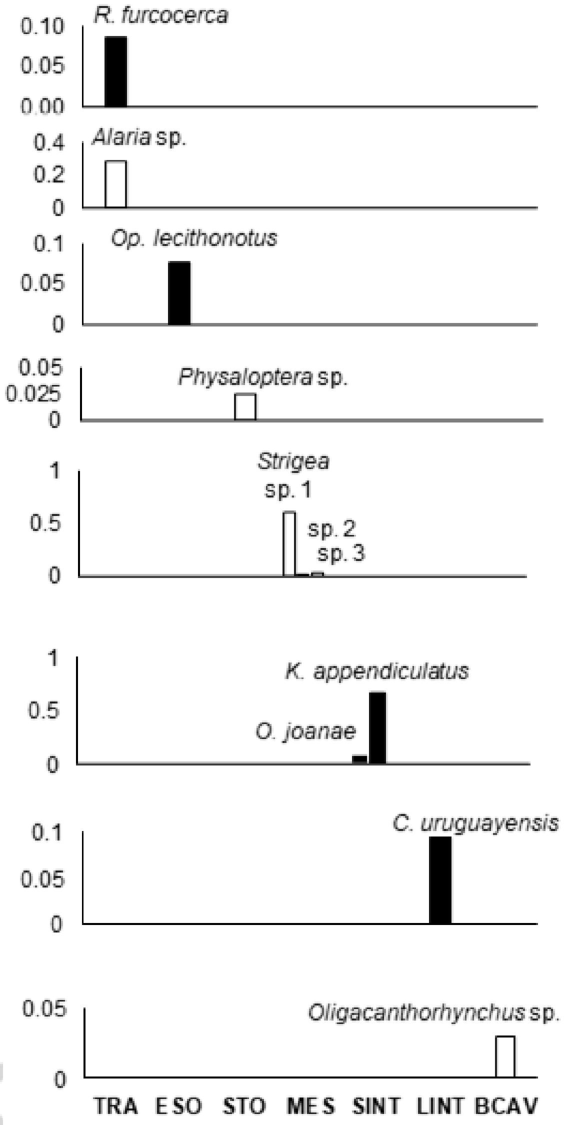
Fig. 2 Olmstead-Tukey diagram of ME in *E. p. caesius* from a locality of Dry Chaco, Argentina. Red triangles are adult species; yellow circles are larval species. Dashed lines represent mean values of ln (MA) + 1 (x axis) and prevalence (y axis). Legend: (I) dominants, (II) subdominants, (III) accessories, and (IV) indicators.

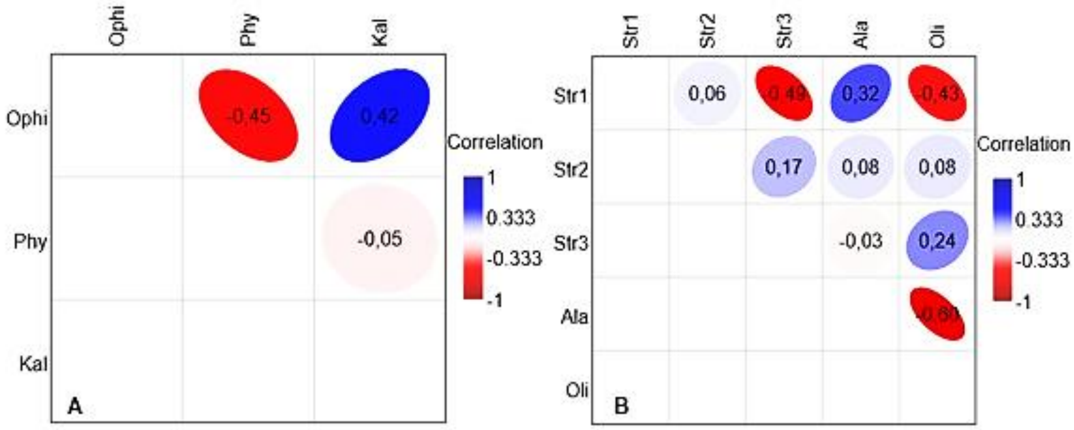
Fig. 3 Relative frequency of ME in adult (black bars) and larval stages (white bars) in different sites of infection. "y" axis for each species is different. **Legend: TRA:** trachea, **ESO:** esophagus, **STO:** stomach, **MES:** mesenteries, **SINT:** small intestine, **LINT:** large intestine, **BCAV:** body cavity.

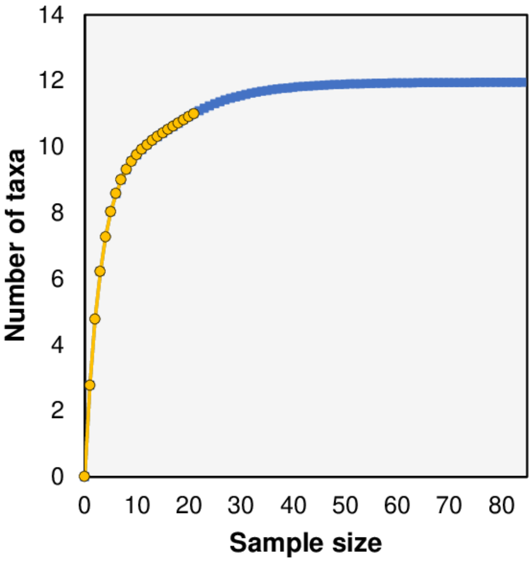
Fig. 4 Spearman's correlation coefficients between pairs of ME taxa parasitizing the same organs. **A:** Stomach, small and large intestines**. B:** Mesenteries and body cavity **Legend: Kal**: *K. appendiculatus*, **Ophi:** *O. joanae*, **Phy:** *Physaloptera* sp., **Ala**: *Alaria* sp., **Str1**: *Strigea* sp. 1, , **Str2:** *Strigea* sp. 2, **Str3:** *Strigea* sp. 3, **Oli:** *Oligacanthorhynchus* sp.

Fig. 5 Species accumulation curve by Mao's tau method. Yellow lines and dots represent observed number of taxa by sample size surveyed; blue lines and squares represent an extrapolation of estimated number of taxa.


II
I
III
IV
Alaria sp.
Strigea sp. 1
O. joanae
K. appendiculatus
Strigea sp. 2
Strigea sp. 3
Physaloptera sp.
Op. lecithonotus
Oligacanthorhynchus sp.
C. uruguayensis
R. furcocerca
Prevalence (%)
ln (MA) + 1
0
10
20
30
40
50
0
2
4
6
8


R. furcocerca
0.10
0.05
0.00
Alaria sp.
0.4
0.2
0
Op. lecithonotus
0.1
0.05
0
Physaloptera sp.
0.05
0.025
0
Strigea
sp. 1
sp. 2
sp. 3
1
0.5
0
K. appendiculatus
O. joanae
1
0.5
0
C. uruguayensis
0.1
0.05
0
Oligacanthorhynchus sp.
0.05
0
TRA
ESO
STO
MES
SINT
LINT
BCAV


Ophi
Phy
Kal
Ophi
Phy
Kal
-0,45
0,42
-0,05
Correlation
1
0.333
-0.333
-1
A
Str1
Str2
Str3
Ala
Oli
Str1
Str2
Str3
Ala
Oli
0,06
-0,49
0,32
-0,43
0,17
0,08
0,08
-0,03
0,24
-0,61
Correlation
1
0.333
-0.333
-1
B


14
12
10
8
6
4
2
0
Number of taxa
0
10
20
30
40
50
60
70
80
Sample size