



ANIMAL SCIENCE

Helminth-fauna of Patagonian armadillos: comparative analysis of parasites geographical variation

JORGE ALBERTO GALLO, MARÍA CECILIA EZQUIAGA, LAURA FASOLA & AGUSTÍN M. ABBA

Abstract: The similarity between parasites communities' decay with distance and its analysis may explain important ecological process such host dispersion. Patagonia is inhabited by two armadillo species, *Chaetophractus villosus* and *Zaedyus pichiy*. In this study we describe and analyze the variation on helminth fauna of these armadillos in Patagonia compared with northern localities described in previous studies. A total of 49 armadillos were collected in Patagonia. Quantitative descriptors of parasite ecology were calculated and community structure of helminths was analyzed following the central-satellite species hypothesis. The parasite richness in Patagonia decreases almost 50% in both armadillos. *Zaedyus pichiy* present the same central species in Patagonia as in northern localities. For *C. villosus* central-satellite species analysis could not be applied. The loss of some helminths in *Z. pichiy* could be the result of lower temperatures or the absence of intermediate arthropods hosts. But in *C. villosus* the absence of some helminths with Patagonian distribution could be explained by its recent dispersion in Patagonia. *Trichoelax tuberculata* still being the only helminth in *C. villosus* introduced population of Tierra del Fuego.

Key words: endoparasites, Xenarthra, Patagonia, geographical variation, *Zaedyus pichiy*, *Chaetophractus villosus*.

INTRODUCTION

Parasite diversity in vertebrates depends mainly on host exposure to parasites, which is strongly related to morphological traits, habits and environmental factors (Krasnov et al. 2004, Ezenwa et al. 2006, Luque & Poulin 2008). However, parasite richness is also the result of parasite life-history, host ecology and host defenses (Bush et al. 1997). In this context, numerous studies considered that latitude is one of the main factors correlated to parasite diversity and richness (Poulin 1995, Krasnov et al. 2004, Nunn et al. 2005, Lindenfors et al. 2007, Poulin & Leung 2011). Parasite diversity is expected to decrease in high latitude areas

as result of lack of intermediate hosts or high mortality rates due to harsh conditions in winter (Bordes et al. 2010). Geographical patterns of host are also extremely associated to parasite community. The similarity between parasites communities' decay with distance (Poulin & Krasnov 2010). The difference or similarity in parasite species composition between localities may explain important ecological process such host dispersion (Poulin & Krasnov 2010). Thus, natural dispersion or introduction of hosts into new areas results in loss, transference or acquisition of their parasites (Lafferty et al. 2010). In this context, Lymbery et al. (2014) proposed using the terminology of *co-introduced* for

those parasites which have been introduced and established in a new area outside of their native range with an alien host, and *co-invader* for those parasites which have been co-introduced and then switched from alien to native hosts.

Chaetophractus villosus and *Zaedyus pichiy* are the only two armadillo species present in Patagonia (Abba et al. 2014). These armadillos are among to the 9 genera and 14 species of armadillos present in Argentina (Teta et al. 2018). The large hairy armadillo, *C. villosus*, is present in the Gran Chaco of Bolivia, Paraguay, and Argentina as far south as Tierra del Fuego - Argentina and Chile (Gardner 2005, Gallo et al. 2020). This armadillo inhabits a wide variety of habitats including grasslands, forest, steppe, and areas degraded by agricultural use (Abba et al. 2015, 2016, Gallo J.A. et al., unpublished data). The pichi, *Z. pichiy*, is endemic from Argentina and Chile and frequent in the Patagonian steppe (Superina & Abba 2018), and the main distribution area occurs in Argentina from La Rioja to Santa Cruz provinces (Superina et al. 2019). The diet of both armadillos is similar and includes invertebrates, plant material and small vertebrates (Gallo et al. 2019, Superina et al. 2019).

The colonization process of southern Patagonia is different for each species. Abba et al. (2014) suggest that *Z. pichiy* is a frequent species in northern and central Patagonia since the Holocene. But the presence of *C. villosus* in central and southern Patagonia is recent. This armadillo dispersed from the Pampas region, considered as the original area of the species (Poljak et al. 2010), through the south of Chubut river in the last century, with an estimated expansion rate of 13 km/year (Abba et al. 2014). The expansion in the continental area of Patagonia seemed facilitated by human structures and activities such as roads, bridges and the increase of agricultural production (Abba

et al. 2014). In the Isla Grande of Tierra del Fuego (TDF), the large hairy armadillo was introduced in 1980 decade (Poljak et al. 2007). Since then, this armadillo has increased its distribution at an expansion rate of 10.9 km/year and now is frequently seen in the northern part of the island (Gallo et al. 2020). In this context, the presence of *C. villosus* in continental and insular Patagonia (Isla Grande of Tierra del Fuego) is relatively recent.

The parasite fauna of these armadillos in the center-northern of Argentina is well documented (Navone 1988, 1990, Ribicich et al. 2010, Ezquiaga et al. 2012, Ezquiaga 2013, Ezquiaga & Navone 2014, Ríos T.A., unpublished data), but only a few studies describe the helminths fauna of *C. villosus* and *Z. pichiy* in Patagonia (Ezquiaga et al. 2009, 2016, 2017). Ezquiaga (2013) described 11 helminths species in *C. villosus* for localities northern at the Chubut province. The last and only study for large hairy armadillo in southern Patagonia was conducted by Ezquiaga et al. (2016) in the Isla Grande of Tierra del Fuego analyzing samples collected between 2005 and 2006 (after 23 years since introduction, see Poljak et al. 2007). The authors described a dramatically decline of parasite richness in Tierra del Fuego population compared with those of Pampas region (1 versus 11). The only helminth species was *Trichostrongylus tuberculata* (Parona & Stossich 1902) (Trichostrongylina: Molineidae).

Twelve helminths species were described for northern distribution of *Z. pichiy*. In the Patagonian steppe of Mendoza province, Ezquiaga et al. (2009) described 5 helminths using coproparasitological technics. Then, Ezquiaga et al. (2013) analyzed the digestive tracts of hosts and found 11 helminths species, including those described for Mendoza province (see Ezquiaga et al. 2009), except for *Trichuris* sp.

In this context some questions have arisen: (1) is the helminth diversity of armadillos of

southern Patagonia comparable to that analyzed in the northern localities (Ezquiaga 2013)? (2) If variation exists, are parasites indicators of the recent colonization of *C. villosus* in central-southern Patagonia? (3) Helminth fauna of the *C. villosus* introduced population of Tierra del Fuego have changed in the last 5 years? The objective of this study is to answer these questions by describing and analyzing the variation on helminth fauna of both armadillo species of central and southern Patagonia.

MATERIALS AND METHODS

During summer season of 2017-2019 principal and secondary roads of Chubut, Santa Cruz and Tierra

del Fuego were tracked. A total of 49 armadillos were collected, 23 road-killed *C. villosus* and 14 road-killed *Z. pichiy* from Chubut and Santa Cruz (Fig. 1). In Tierra del Fuego, 12 *C. villosus* of the introduced invasive population were euthanized in accordance with the guidelines of the American Society of Mammologists for the use of wild mammals in research (Sikes et al. 2016) and the Resolución S.A.D.SyC.C.064/2014 of Tierra del Fuego, Antártida e Islas del Atlántico Sur province). Digestive systems were extracted and fixed in formaldehyde 10% solution until their dissection in the laboratory. Nematodes were stored in alcohol 70%, cleared with Amman’s lactophenol and mounted on a temporary slide under a coverslip. Cestodes were stored in

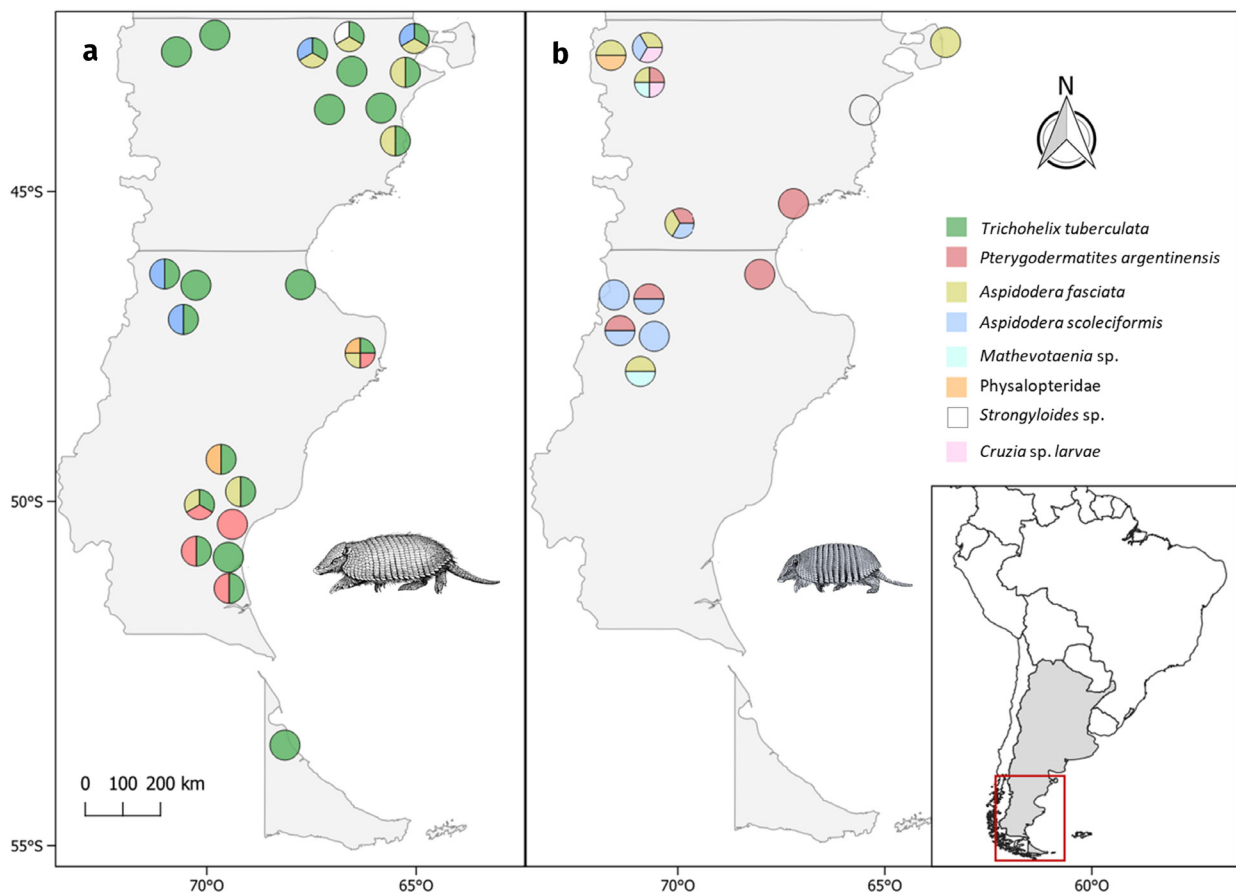


Figure 1. Sites of sample collection in Patagonia and helminthes species found in *Chaetophractus villosus* (a) and *Zaedys pichiy* (b). Illustrations modified from Díaz & Barquez (2002), and Parera & Erize (2002).

alcohol 70%, stained with hydrochloric carmine, dehydrated in a series of ethanol solutions of increasing concentration, cleared with eugenol and mounted in Canada balsam on a slide under a coverslip. Helminths were examined using an Olympus BX51 compound microscope (Olympus Corporation, Tokyo, Japan). CellSens v1.11 (Olympus Corporation) image analyzer software was used to take corresponding morphometric measurements (X40–X600). Parasites were identified using specific keys (Anderson 2000, Anderson et al. 2009) and descriptions of Navone (1987) and Ezquiaga et al. (2017). For the relevant comparisons on helminths diversity, different areas of host populations were defined. For *Z. pichiy*: a Northern population (Ezquiaga et al. 2009, Ezquiaga 2013) and a Southern population (this study). For *C. villosus* three populations were distinguished: a Core population (Pampas region, Ezquiaga 2013); a Southern Patagonian population (Chubut and Santa Cruz provinces, this study) and the exotic population of Isla Grande of Tierra del Fuego TDF, which includes samples of *C. villosus* of two periods of time that allowed a temporal comparison: 2005-2006 analyzed by Ezquiaga et al. (2016) and 2017-2018 (this study).

We calculated prevalence (P), mean abundance (MA), mean intensity (MI), richness (S) and Shannon's Diversity Index (H) for each host population (Bush et al. 1997). We analyzed the structure of the helminth community of the Patagonian populations following central-satellite species hypothesis (Hanski 1982, Bush & Holmes 1987, Holmes 1987). Two statistical assumptions must be considered to classify helminths community in central-satellite species: 1) significant correlation between prevalence and mean intensity and 2) bimodal or trimodal distribution of prevalence frequencies. The results were contrasted with those found by Ezquiaga (2013) following the next comparisons

between host populations: *Z. pichiy* Northern population vs. *Z. pichiy* Southern population; *C. villosus* core population vs. *C. villosus* Southern Patagonia population and *C. villosus* TDF population 2005-2006 vs. *C. villosus* TDF population 2017-2018.

Differences in prevalence values of helminths shared by both hosts were tested with a Chi square test ($\alpha = 0.05$). Helminths eggs described by Ezquiaga et al. (2009) were excluded.

RESULTS

In this study the total prevalence of helminths was 100% for *C. villosus* (n = 35) and 92.8% for *Z. pichiy* (n = 14; 95 % C. I. = 86% – 97%). Eight helminths taxa were found, 7 were nematodes and 1 cestode. The richness was the same for both hosts (S=6). The Shannon diversity index (H') was 0.954 for *C. villosus* and 0.755 for *Z. pichiy*. *Aspidodera fasciata* (Schneider, 1866) (Ascaridida: Aspidoderidae), *A. scoleciformis* (Diesing 1851) (Ascaridida: Aspidoderidae), *Pterygodermatites argentinensis* (Ezquiaga, Rios, Abba and Navone 2017) (Spirurida: Rictulariidae) and Physalopteridae (Larvae) (Railliet, 1893) (Spirurida: Physalopteridae), were present in both hosts with low-moderate prevalence (<50%; Table I). The cestode *Mathevotaenia* sp. and the nematode *Cruzia* sp. (larvae) were found only in *Z. pichiy* while the nematodes *Strongyloides* sp. and *Trichoelax tuberculata* were present only in *C. villosus*. The highest values of mean intensity and mean abundance were for the helminth *T. tuberculata*, *A. fasciata* and *A. scoleciformis* in *C. villosus* and both *Aspidodera* species in *Z. pichiy*. There was significant difference in prevalence of *A. scoleciformis* ($X^2 = 18.2$; $p = <0.001$; $d.f. = 1$) and *P. argentinensis* ($X^2 = 16.1$; $p = <0.005$; $d.f. = 1$) for both hosts.

Table I. Prevalence (P), mean intensity (MI) and mean abundance (MA) estimated for the helminths found in armadillos from Patagonia. (Larvae stages are indicated with L.).

Parasite	<i>Chaetophractus villosus</i>						<i>Zaedyus pichiy</i>		
	Southern Patagonia			TDF			Southern Patagonia		
	P(%)	IM	AM	P(%)	IM	AM	P(%)	IM	AM
<i>Aspidodera fasciata</i>	39.1	138.7	54.3	-	-	-	50.0	163.1	96.6
<i>Aspidodera scoleciformis</i>	17.4	117.8	20.5	-	-	-	42.9	80.8	34.6
<i>Cruzia</i> sp. (L)	-	-	-	-	-	-	14.3	11.0	1.6
<i>Mathevotaenia</i> sp.	-	-	-	-	-	-	14.3	6.5	0.9
Physalopteridae (L)	8.7	23.5	2.0	-	-	-	7.1	1.0	0.1
<i>P. argentinensis</i>	26.1	8.0	1.4	-	-	-	50.0	5.0	2.5
<i>Strongyloides</i> sp.	4.3	83.0	3.6	-	-	-	-	-	-
<i>Trichohelix tuberculata</i>	95.7	102.7	102.7	100	116.08	116.08	-	-	-

Analysis of community structure of *Chaetophractus villosus* and *Zaedyus pichiy* in Patagonia

The correlation between the prevalence and mean intensity was not significant ($r = 0.52$; $p > 0.05$) for the large hairy armadillo and therefore the central-satellite species analysis could not be applied to describe the helminth community structure of this species.

In the case of *Z. pichiy*, the assumptions required by the central-satellite species hypothesis were met. The helminths community of the southern population of this armadillo showed a bimodal distribution of frequencies of prevalence and a positive significant correlation between prevalence vs. mean intensity ($r = 0.73$; $p < 0.05$). Then, three central species were identified: *A. fasciata*, *A. scoleciformis* and *P. argentinensis* (Fig. 2).

Comparison of *Zaedyus pichiy* helminth fauna

Northern population vs. Southern population:
The species richness reported in the northern population (Ezquiaga et al. 2009, Ezquiaga 2013) and found in the Southern Patagonia population

(this study) was $S = 11$ and $S = 6$ respectively. Only three species of helminths are shared by both populations: two nematodes, *A. fasciata* and *A. scoleciformis*, and one cestode, *Mathevotaenia* sp. (Table II). Significant differences in prevalence of both populations were found for both species of *Aspidodera* genus, *A. fasciata* ($X^2 = 16.1$; $p < 0.001$; $d.f. = 1$) and *A. scoleciformis* ($X^2 = 7.8$; $p < 0.005$; $d.f. = 1$).

Comparison of *Chaetophractus villosus* helminth fauna

Core population vs. Southern Patagonia population

The species richness reported for the core population (Ezquiaga 2013) and found in the Southern Patagonia population (this study) was $S=11$ and $S=6$ respectively. Only four helminths species are shared in both populations (Table III). Significant differences in prevalence were found for *A. fasciata* ($X^2 = 40.6$; $p < 0.001$; $d.f. = 1$); *A. scoleciformis* ($X^2 = 66.6$; $p < 0.001$; $d.f. = 1$) and *Strongyloides* sp. ($X^2 = 14.8$; $p < 0.001$; $d.f. = 1$).

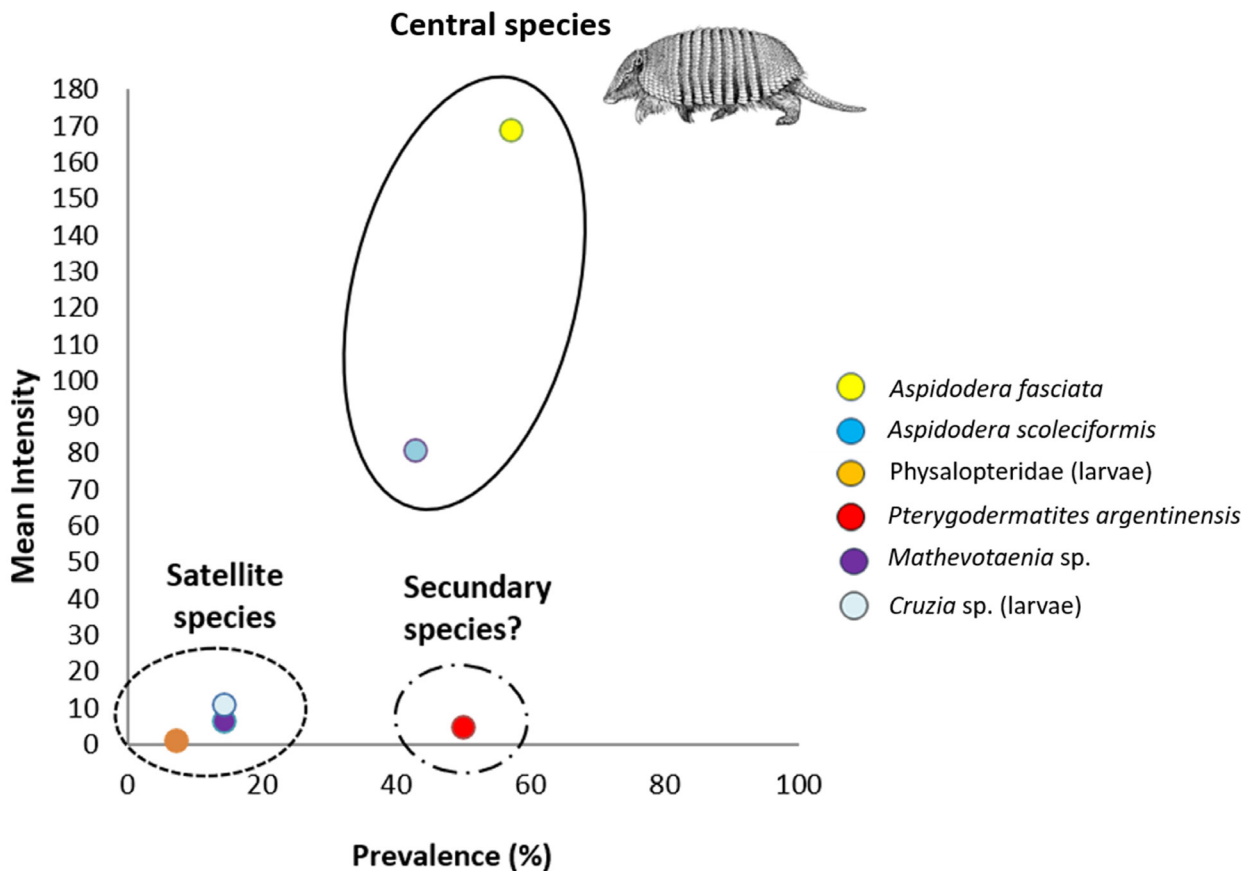


Figure 2. Community structure of helminthes of *Zaedyus pichiy* in Patagonia. Illustration modified from Díaz & Barquez (2002).

TDF population 2005-2006 vs. TDF population 2017-2018

In the last study on *C. villosus* exotic population, Ezquiaga et al. (2016) found one helminth species, the nematode *T. tuberculata*, with prevalence of 89%. In this study we recorded the same species with a prevalence of 100%. Prevalence of *T. tuberculata* did not change significantly between periods ($X^2 = 0.640$; $p = 0.423$; $d.f. = 1$).

DISCUSSION

The community of Patagonian helminths of *C. villosus* and *Z. pichiy* was analyzed, and with this work, we contribute to the general description of helminths of both Patagonian armadillos.

The similarity between two parasites communities of different localities decreases with distance (Soininen et al. 2007, Poulin & Krasnov 2010), and latitude is determinant of parasite richness (Nunn et al. 2005, Preisser 2019). The richness found for both hosts in this study decrease considerably compared to northern populations (Ezquiaga 2013). Some parasites such *Mathevotaenia* sp. and *T. tuberculata* were exclusive of *Z. pichiy* and *C. villosus* respectively.

The presence of two larvae of nematodes of Physalopteridae family and the genus *Cruzia* recovered in both armadillo’s hosts was accidental infection due to consumption of arthropods intermediate hosts. These helminths are parasites of carnivorous mammals, marsupials, birds and, amphibians, reptiles and

Table II. Helminths prevalence in *Zaedyus pichiy* northern and southern Patagonian population. H' = Shannon's Diversity Index.

Parasite	Northern population (Ezquiaga, 2013) H' = 1.08	Southern population (This study) H' = 0.75
<i>Ancylostoma caninum</i>	18	-
<i>Aspidodera fasciata</i>	100	50
<i>Aspidodera scoleciformis</i>	73	42.9
<i>Cyclobulura superinae</i>	27	-
<i>Cruzia</i> sp. (L)	-	14.3
<i>Delicata ransomi</i>	23	-
<i>Mathevotaenia</i> sp.	23	14.3
<i>Orihelia anticlava</i>	4	-
<i>Pterygodermatites chaetophracti</i>	23	-
<i>Pterygodermatites argentinensis</i>	-	50
Physalopteridae (L)	-	7.1
<i>Strongyloides</i> sp.	9	-
<i>Travassosia</i> sp.	5	-
<i>Trichohelix tuberculata</i>	23	-

fish (Anderson 2000, Adnet et al. 2009, Vieira et al. 2020). The nematode *Pterygodermatites argentinensis* has been already described in Patagonia by Ezquiaga et al. (2017) in *Z. pichiy* but not in *C. villosus*, which means a new host-parasite association found in this study.

Variation in helminths of northern and southern populations of *Zaedyus pichiy*

In the southern population the specific richness and the parasite diversity was a 50% of the ones reported for the northern population (Ezquiaga 2013). Decrease in parasite richness and significant difference in prevalence of both *Z. pichiy* populations could be result of lower temperatures of Patagonia, which surely affect normal development of infective stages of some parasites, such *Cyclobulura superinae*

and *Travassosia* sp. acanthocephalans. But also these results could be a consequence of the low diversity or the absence of intermediate arthropods hosts in Patagonia (Nunn et al. 2005, Poulin & Leung 2011, Preisser 2019) such *Orihelia anticlava*, which use mites as vectors. According to Ezquiaga et al. 2021, armadillos ectoparasites show a north-south reduction on prevalence.

Variations in helminths of Patagonian populations of *Chaetophractus villosus*

The richness of helminths decreases almost to a 54.5% in *C. villosus* Patagonian populations in relation to central Argentina populations (Ezquiaga 2013). The most prevalent parasite was *T. tuberculata* (95.7%), which is also the only helminth found in Tierra del Fuego by Ezquiaga et al. (2016) and in the present work.

Table III. Helminthes prevalence (%) in *Chaetophractus villosus* core population and southern Patagonia population. H'= Shannon's Diversity Index.

Parasite	Core population (Ezquiaga, 2013) H'= 1.10	Southern Patagonia Population (this study) H'=0.95
<i>Ancylostoma caninum</i>	56	-
<i>Aspidodera fasciata</i>	96	39.1
<i>Aspidodera scoleciformis</i>	96	17.4
<i>Delicata ransomi</i>	26	-
<i>Mazzia bialata</i>	22	-
<i>Moeningia</i> sp.	9	-
<i>Mathevotaenia</i> sp.	26	-
<i>Orihelia anticlava</i>	17	-
<i>Pterygodermatites chaetophracti</i>	9	-
<i>Pterygodermatites argentinensis</i>	-	26.1
Physalopteridae (L)	-	8.7
<i>Strongyloides</i> sp.	22	4.3
<i>Trichohelix tuberculata</i>	96	95.7

The presence of *C. villosus* in Patagonia is relatively recent. As result of anthropogenic causes, this armadillo spread from the core region (Pampas region) to Patagonia, approx. 100 years ago (Abba et al. 2014). The parasites species least prevalent in the core region (prevalence lower than 50%, Ezquiaga 2013) are those absent in individuals from Patagonia. The individuals of *C. villosus* that dispersed in Patagonia derived from a small subset of core population and it is possible that only few hosts were parasitized. Also, the loss of these helminths species could be the result of the absence of intermediate arthropod host and the harsh climatic conditions of Patagonia could affect the life cycles of many parasites. Many authors suggest that these causes of helminths loss are frequent at highest latitudes (Nunn et al. 2005, Poulin & Leung 2011,

Preisser 2019). *Mathevotaenia* sp. is one of the lost helminths in Patagonian population of *C. villosus*. This cestode is frequent in armadillos using Lepidoptera and Coleoptera larvae as intermediate hosts (Bienek & Klikoff 1974). Those arthropods are frequent in diet of both Patagonian armadillos (Gallo et al. 2019) and *Mathevotaenia* sp. is also present in *Z. pichiy*. In this case, the absence of this parasite in *C. villosus* could be the result of the recent spread of this armadillo through Patagonia, while the loss of other helminths with heteroxenous life cycles (*Cyclobulura superinae*, *Orihelia anticlava*, *Travassosia* sp.-Acanthocephala-) could be the result of the absence of intermediate hosts in Patagonia.

Trichohelix tuberculata is the only parasite species present in the exotic population of *C.*

villosus in the Isla Grande of Tierra del Fuego as it was recorded by Ezquiaga et al. (2016). Torchin et al. (2003) suggested that parasites with highest prevalence are those presents in invader host population. The prevalence of *T. tuberculata* increased since the last study made on Tierra del Fuego exotic population by Ezquiaga et al. (2016). This nematode is frequent in the Tribe Euphractini of armadillos and the infective free-living larvae stage (L2) retain the moult of the previous stage (L2) as protection cover against harsh climatic conditions (Anderson 2000), which allow them to survive to the extreme climate of Tierra del Fuego as proposed by Ezquiaga et al. (2016).

Helminths community structure of *Zaedyus pichiy* and *Chaetophractus villosus*

The southern and northern populations of *Z. pichiy* present the same central species of helminths, *A. scoleciformis* and *A. fasciata* and the prevalence of both parasites species is lower in the southern population. This difference could be related to the limited encounters between potential hosts and infective forms of parasites.

In *C. villosus* core population, Ezquiaga (2013) found three central species (*T. tuberculata*, *A. fasciata* and *A. scoleciformis*). In Patagonia the structure of helminths community of *C. villosus* did not show a significant correlation between prevalence and mean intensity. Holmes (1987) suggested that this may be the way that the parasites respond to host quality. Considering that both *Aspidodera* species and *T. tuberculata* are frequent in armadillos and occurs along their distribution (Navone 1990, Ezquiaga et al. 2019), this result could respond to the recent dispersion of a small subset of *C. villosus* in Patagonia, carrying a small subset of helminths that were co-introduced with the host. Also, the prevalence of both *Aspidodera* species decreases in Patagonia and some helminths

with Patagonian distribution as *Mathevotaenia* sp. are absent in *C. villosus* southern Patagonian population.

Contributions to knowledge of the Patagonian helminths range

In view of the results of this study, the geographical range of some helminth parasite species was extended. Both *Aspidodera* species occur from southern U.S.A to central Argentina (Jiménez Ruiz & Gardner 2003). *Pterygodermatites argentinensis*, described by Ezquiaga et al. (2017) occurs as far as Chubut province in Argentina. The southern limit of *Strongyloides* sp. and *Mathevotaenia* sp. were Buenos Aires and Rio Negro province respectively (Ezquiaga, 2013). With the results of this study, the species named above increased their geographical range through Patagonia a far as Santa Cruz province (Argentina).

Future prospective

In this context, Patagonian populations of *C. villosus* (Southern Patagonia and TDF) present extreme variations in helminths community as results of the recently presence of this armadillo losing almost 50% of parasites compared to core population. In the next years is possible that exotic population of Tierra del Fuego does not show any changes or develop an event of host-parasite co-invasion, and *T. tuberculata* could infect other hosts in Tierra del Fuego.

Acknowledgments

We would like to thank to M. L. Carranza and E. Curto from Dirección General de Áreas Protegidas y Biodiversidad of Tierra del Fuego; M. L. Marcías; To Dirección de Flora y Fauna de la provincial del Chubut; E. Villanova and J. Barría from Estancia Sara; M. R. Couto from Estancia El Rincón; V. M. Durán Bodelón; N.A. Cossa and M. Malerba for assistance during fieldwork. To G. Martin and D. Udrizar-Sauthier for provide part of samples and help during fieldwork. J. S. Verón and B. J. S. for supporting

us. To the Centro Austral de Investigaciones Científicas (CADIC-CONICET), to Laboratorio de Parasitología (CRUB-UNComa) and to CENAC (PNNH) for providing the infrastructure to analyze the samples. This work was supported by Neotropical Grassland Conservancy-NGC and Programa Patagonia/Aves Argentinas (AOP).

REFERENCES

- ABBA AM, POLJAK S, GABRIELLI M, TETA M & PARDIÑAS UFJ. 2014. Armored invaders in patagonia: recent southward dispersion of armadillos (Cingulata, Dasypodidae). *Mastozool Neotrop* 21: 311-318.
- ABBA AM, ZUFIAURRE E, CODESIDO M & BILENCA DN. 2016. Habitat use by armadillos in agroecosystems of central Argentina: does plot identity matter? *J Mammal* 20: 1-7.
- ABBA AM, ZUFIAURRE E, CODESIDO M & BILENCA DN. 2015. Burrowing activity by armadillos in agroecosystems of central Argentina: Biogeography, land use, and rainfall effects. *Agric Ecosyst Environ* 200: 54-61.
- ADNET FAO, ANJOS DHS, MENEZES-OLIVEIRA A & LANFREDI RM. 2009. Further description of *Cruzia tentaculata* (Rudolphi, 1819) Travassos, 1917 (Nematoda: Cruzidae) by light and scanning electron microscopy. *Parasitol Res* 104: 1207-1211.
- ANDERSON RC, CHABAUD AG & WILLMOTT S. 2009. Keys to the nematode parasites of vertebrates, Wallingford, UK: CAB International, 463 p.
- ANDERSON RCC. 2000. Nematode parasites of vertebrates: their development and transmission. 2nd ed., New York: CABI publishing, 635 p.
- BIENEK GK & KLIKOFF LG. 1974. Parasitological evidence of arthropods as food for *Dipodomys merriami vulcani*. *Am Midl Nat*: 251-253.
- BORDES F, MORAND S, KRASNOV BR & POULIN R. 2010. Parasite diversity and latitudinal gradients in terrestrial mammals. In: Morand S & Krasnov BR (Eds), *The Biogeography of Host-Parasite Interactions*, New York: Oxford University Press, p. 89-98.
- BUSH A, LAFFERTY K, LOTZ J & SHOSTAK A. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83: 575-583.
- BUSH AO & HOLMES JC. 1986. Intestinal helminths of lesser scaup ducks: patterns of association. *Can J Zool* 64: 132-141.
- DÍAZ MM & BARQUEZ RM. 2002. Los mamíferos de Jujuy, Argentina. Buenos Aires: LOLA (Literature of Latin America), p. 308.
- EZENWA VO ET AL. 2006. Host traits and parasite species richness in even and odd-toed hoofed mammals, *Artiodactyla* and *Perissodactyla*. *Oikos* 115: 526-536.
- EZQUIAGA C, DIGIANI MC & NAVONE GT. 2012. A New Molineid (Nematoda: Trichostrongylina) parasite of *Dasypus hybridus* (Xenarthra: Dasypodidae) from Argentina. *J Parasitol* 98: 1156-1160.
- EZQUIAGA MC. 2013. Estudios parasitológicos en Dasypodidae (Mammalia, Xenarthra) de Argentina: el valor de la diversidad en la interpretación de las asociaciones parásito-hospedador-ambiente. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. <http://sedici.unlp.edu.ar/handle/10915/26116>.
- EZQUIAGA MC, ABBA AM & NAVONE GT. 2016. Loss of helminth species diversity in the large hairy armadillo *Chaetophractus villosus* on the Tierra del Fuego Island, Argentina. *J Helmitol* 90: 145-248.
- EZQUIAGA MC, ABBA AM & NAVONE GT. 2019. Helminth fauna of the screaming hairy armadillo *Chaetophractus vellerosus* from Argentina: the consequence of host isolation on parasite diversity. *Heliyon* 5: e01605.
- EZQUIAGA MC & NAVONE GT. 2014. A New Species of *Moennigia* (Trichostrongylina: Molineidae) a Parasite of *Chaetophractus* Spp. (Xenarthra: Dasypodidae) from Argentina. *J Parasitol* 100: 500-503.
- EZQUIAGA MC, RIOS TA, ABBA AM & NAVONE GT. 2017. A New Rictulariid (Nematoda: Spirurida) in Xenarthrans from Argentina and new morphological data of *Pterygodermatites* (Paucipectines) *chaetophracti*. *J Parasitol* 103: 727-735.
- EZQUIAGA MC, SUPERINA M & NAVONE GT. 2009. Parásitos intestinales de *Zaedyus pichiy* (Xenarthra: Dasypodidae) en Mendoza, Argentina. *Mastozool Neotrop* 16: 309-319.
- EZQUIAGA MC, GALLO JA, D'AGOSTINO RL, SAUTHIER DEU, ABBA AM & SANCHEZ J. 2021. Fleas and ticks in armadillos from Argentinean Patagonia: Diversity, abundance and distribution. *Acta Tropica* 219: 105-911.
- GALLO J, FASOLA L & ABBA A. 2019. Armadillos as pest controllers? Food habits of five armadillos in Argentina. *Mastozool Neotrop* 26: 116-117.
- GALLO JA, FASOLA L & ABBA AM. 2020. Invasion success of the large hairy armadillo (*Chaetophractus villosus*) in a sub-antarctic insular ecosystem (Isla Grande, Tierra del Fuego, Argentina). *Polar Biol* 43: 597-606.

- GARDNER AL. 2005. Order Cingulata. In: Wilson DE & Reeder DM (Eds), *Mammal species of the world: a taxonomic and geographic reference*, 3rd ed., Baltimore, Maryland: Johns Hopkins University Press, p. 94-99.
- HANSKI I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. *Oikos* 38: 210-221.
- HOLMES JC 1987. The structure of helminth communities. *Int J Parasitol* 17: 203-208.
- JIMÉNEZ RUIZ FA & GARDNER SL. 2003. Aspidoderid nematodes from Bolivian armadillos, with the description of a new species of *Lauroia* (Heterakoidea: Aspidoderidae). *J Parasitol* 89: 978-983.
- KRASNOV BR, SHENBROT GI, KHOKHLOVA IS & DEGEN AA. 2004. Flea species richness and parameters of host body, host geography and host "milieu." *J Anim Ecol* 73: 1121-1128.
- LAFFERTY KD, TORCHIN ME & KURIS AM. 2010. The geography of host and parasite invasions. In: Morand S & Krasnov BR (Eds), *The Biogeography of Host-Parasite Interactions*. New York: Oxford University Press Inc., p. 191-203.
- LINDENFORS P ET AL. 2007. Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Glob Ecol Biogeogr* 16: 496-509.
- LUQUE JL & POULIN R. 2008. Linking ecology with parasite diversity in Neotropical fishes. *J Fish Biol* 72: 189-204.
- LYMBERY AJ ET AL. 2014. Co-invaders: The effects of alien parasites on native hosts. *Int J Parasitol Parasites Wildl* 3: 171-177.
- NAVONE GT. 1990. Estudio de la distribución, porcentaje y microecología de los parásitos de algunas especies de edentados argentinos. *Stud Neotrop Fauna Environ* 25: 199-210.
- NAVONE GT. 1987. Estudios parasitológicos en edentados argentinos. III. Trichostrongílicos, *Macielia elongata* sp. nov.; *Moennigia virilis* sp. nov. y *Trichohelix tuberculata* (Parona y Stossich, 1901) Ortlepp, 1922 (Molineidae-Anoplostrongylinae) parásitos de *ChaetophRACTUS villosus* Desmarest y *Tolypeutes matacus* (Desmarest) (Xenarthra- Dasypodidae). *Neotropica* 33: 105-117.
- NAVONE GT. 1988. Estructura de la infracomunidad parasitaria de *ChaetophRACTUS villosus* Desmarest, de la provincia biogeográfica pampeana (Cabrera y Willink, 1973). In: IV Jornadas Argentinas de Mastozoología, p. 46
- NUNN CL, ALTIZER SM, SECHREST W & CUNNINGHAM AA. 2005. Latitudinal gradients of parasite species richness in primates. *Divers Distrib* 11: 249-256.
- PARERA A & ERIZE F. 2002. Los mamíferos de la Argentina y la región austral de Sudamérica. Editorial El Ateneo, Buenos Aires.
- POLJAK S, CONFALONIERI V, FASANELLA M, GABRIELLI M & LIZARRALDE MS. 2010. Phylogeography of the armadillo *ChaetophRACTUS villosus* (Dasypodidae Xenarthra): Post-glacial range expansion from Pampas to Patagonia (Argentina). *Mol Phylogenet Evol* 55: 38-46.
- POLJAK S, ESCOBAR J, DEFERRARI G & LIZARRALDE M. 2007. A new introduced mammal in Tierra del Fuego: the "large hairy armadillo" *ChaetophRACTUS villosus* (Mammalia, Dasypodidae) in the Isla Grande island. *Rev Chil Hist Nat* 80: 285-294.
- POULIN R. 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol Monogr* 65: 283-302.
- POULIN R & KRASNOV BR. 2010. Similarity and variability of parasite assemblages across geographical space. In: Morand S & Krasnov BR (Eds), *The Biogeography of Host-Parasite Interactions*, New York: Oxford University Press, p. 115-127.
- POULIN R & LEUNG TLF. 2011. Latitudinal gradient in the taxonomic composition of parasite communities. *J Helminthol* 85: 228-233.
- PREISSER W. 2019. Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents. *Ecography (Cop)* 42: 1315-1330.
- RIBICICH M J ET AL. 2010. Trichinella infection in wild animals from endemic regions of Argentina. *Parasitol Res* 107: 377-380.
- SIKES RS & ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal* 97: 663-688.
- SOININEN J, MCDONALD R & HILLEBRAND H. 2007. The distance decay of similarity in ecological communities. *Ecography (Cop)* 30: 3-12.
- SUPERINA M & ABBA AM. 2018. *Zaedyus pichiy* (Cingulata: Dasypodidae). *Mamm Species* 46: 1-10.
- SUPERINA M ET AL. 2019. *Zaedyus pichiy*. In: Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. Website: www.cma.sarem.org.ar.
- TETA P ET AL. 2018. Lista revisada de los mamíferos de Argentina. *Mastozool Neotrop*. 25: 163-198.

TORCHIN ME ET AL. 2003. Introduced species and their missing parasites. *Nature* 421: 628-630.

VIEIRA FM, GONÇALVES PA, LIMA SS, DE SOUSA BM & MUNIZ-PEREIRA LC. 2020. A new species of *Cruzia* (Ascaridida; kathlanidae) parasitizing *Salvator merianae* (squamata, teiidae) from the Atlantic forest in Brazil. *Rev Bras Parasitol Vet.* 29: 1-10.

How to cite

GALLO JA, EZQUIAGA MC, FASOLA L & ABBA AM. 2021. Helminth-fauna of Patagonian armadillos: comparative analysis of parasites geographical variation. *An Acad Bras Cienc* 93: e20210624. DOI 10.1590/0001-3765202120210624.

Manuscript received on April 20, 2021;
accepted for publication on July 27, 2021

JORGE ALBERTO GALLO^{1,2,3}

<https://orcid.org/0000-0003-0985-7492>

MARÍA CECILIA EZQUIAGA⁴

<https://orcid.org/0000-0002-2357-896X>

LAURA FASOLA^{1,2}

<https://orcid.org/0000-0003-4841-0343>

AGUSTÍN M. ABBA⁴

<https://orcid.org/0000-0002-7058-4027>

¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Dirección Regional Patagonia Norte de la Administración de Parques Nacionales (APN), Vicealmirante O'connor 1188, 8400, San Carlos de Bariloche, Rio Negro, Argentina

²Programa Patagonia, Aves Argentinas, Asociación Ornitológica del Plata, Matheu 1246, C1249AB, Ciudad Autónoma de Buenos Aires, Argentina

³Centro de Estudios Aplicados a la Conservación (CENAC-PNNH), Fagnano 244, 8400, San Carlos de Bariloche, Rio Negro, Argentina

⁴Centro de Estudios Parasitológicos y de Vectores (CEPAVE), Universidad Nacional de La Plata, CONICET, 1900 La Plata, Buenos Aires, Argentina

Correspondence to: **Jorge Alberto Gallo**

E-mail: jorgegallo2110@gmail.com

Author contributions

JAG, LF and AMA designed the experiment and collected the samples. JAG analyzed the samples under MCE supervision who also suggested the data analysis. JAG writes the first version of the manuscript. All the authors contributed to the final manuscript.

