



Helminth fauna of the screaming hairy armadillo *Chaetophractus vellerosus* from Argentina: the consequence of host isolation on parasite diversity



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ABSTRACT

Chaetophractus vellerosus in Argentina has a north-west and central distribution. An isolated population is located in the east of the Buenos Aires province, separated from the population of central Argentina by about 500 km. We compared the component community of *C. vellerosus* between the main population in central Argentina and the isolated population, evaluating the impact of the host isolation on parasite diversity. Sixteen species of helminths were found, namely *Ancylostoma caninum*, *Aspidodera fasciata*, *Aspidodera scoleciformis*, *Mazzia bialata*, *Pterygodermatites chaetophracti*, *Pterygodermatites argentinensis*, *Strongyloides* sp., *Trichoelax tuberculata*, *Cruzia tentaculata*, *Cyclobulura superinae*, *Delicata ransomi*, *Macielia jorgei*, *Moennigia celinae*, *Orihelia anticlava* (Nematoda), *Mathevotaenia* sp. (Cestoda) and *Travassosia* sp. (Acanthocephala). Only the first 8 species, however, were present in both populations. Prevalences and intensities of the shared species were similar. The parasite community of the isolated population, however, was less rich and diverse than that of the main population. The poor parasite community in the isolated population could have several causes: the founding population was composed of few specimens that were only infected with the most prevalent parasite species and intermediate hosts for parasites with indirect cycles were absent. In addition, coexistence with another Chlamyphoridae would have contributed to maintaining a group of species that are usual in armadillos along their distribution.

1. Introduction

Parasite diversity is strongly shaped by host exposure to parasites, which is mainly due to host-related factors such as morphological or life-history traits, and to biotic and abiotic environmental factors (Bordes et al., 2010). Factors such as temperature and humidity, soil type and composition, moisture content, vegetation and altitude can affect host and parasite distributions in terrestrial environments (Bush et al., 2001). Consequently, differences in habitat characteristics could explain differences in parasite species richness among host populations. Additionally, related host species have similar parasite faunas, because the host species have similar physiological, immunological, ecological and distributional characteristics (Krasnov et al., 2006; Poulin, 2007). Therefore, the ability to exploit different host species depends on the phylogenetic relationships they have with each other (Krasnov et al., 2006).

The screaming hairy armadillo, *Chaetophractus vellerosus* (Mammalia: Xenarthra: Chlamyphoridae) is a carnivorous-omnivorous mammal with a high consumption of coleopterans (both larvae and adults) and plant material and, to a lesser extent, of ants, small mammals and orthopterans

(Abba et al., 2011). The mean body mass of this armadillo is 800 g (Abba et al., 2011). It is found in south and central Bolivia, southern Peru, northern Chile, north-west Paraguay and central Argentina in sandy soils of arid and semiarid regions and in high-altitude environments (Abba et al., 2015a). In Argentina, the main population inhabits the north-west and center of the country and its distribution does not exceed 62° 50' W to the east, and 39° 20' S to the south (IUCN SSC Anteater, Sloth and Armadillo Specialist Group, 2017). Poljak et al. (2018), based on studies of phylogeography of this species, have recently indicated that the older lineages are in the north-central area of the species distribution range in Argentina (i.e. ancestral area of distribution).

There is another population in the east of the Buenos Aires province that is separated from the main population by about 500 km and that has an approximate extension of 35° S to 36° S (Carlini and Vizcaino, 1987; Abba et al., 2011). That population is found in xerophytic forests similar to the forests of central Argentina and characterized by having loose and permeable soils associated with cords of calcareous deposits of shells parallel to the Atlantic coast (Cavallotto, 2009). The vegetation is characterized by presenting *Celtis ehrenbergiana* and *Scutia buxifolia* (Oyarzabal et al., 2018). The area inhabited by this population is a narrow strip

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of 160 km long and 3 km wide, occupying approximately 500 km² (A.M. Abba, unpublished data). In the same region, there is another Chlamyphoridae, *Chaetophractus villosus*, which coexists with the screaming hairy armadillo (Abba et al., 2015b). Two hypotheses were formulated to explain this isolated population. Carlini and Vizcaíno (1987) proposed that this population was a relic of a wider distribution resulting from different climatic conditions during the Late Pleistocene and part of the Holocene. On the other hand, Poljak et al. (2018) suggested long-distance colonization, possibly caused by translocation of individuals by human activity.

Until now, several studies on systematics and distribution of

helminths parasitizing *C. vellerosus* were conducted in central Argentina (i.e. west of Buenos Aires, Chaco, Córdoba, Formosa, Jujuy, La Rioja, San Juan, San Luis and Santiago del Estero provinces) (Mazza et al. 1932; Khalil and Vogelsang, 1932; Vogelsang, 1932; Lombardero and Moriena, 1977; Martinez, 1984; Navone, 1986, 1987, 1988; Notarnicola and Navone, 2003; Navone et al., 2010; Ezquiaga and Navone, 2013, 2014). However, only one coproparasitological study about the influence of host and environment-related factors on the parasite fauna of an isolated population of this host species was carried out (Ezquiaga et al., 2014).

On the other hand, previous studies in *C. villosus* analyzed the parasite fauna of this host and described characteristics of its component

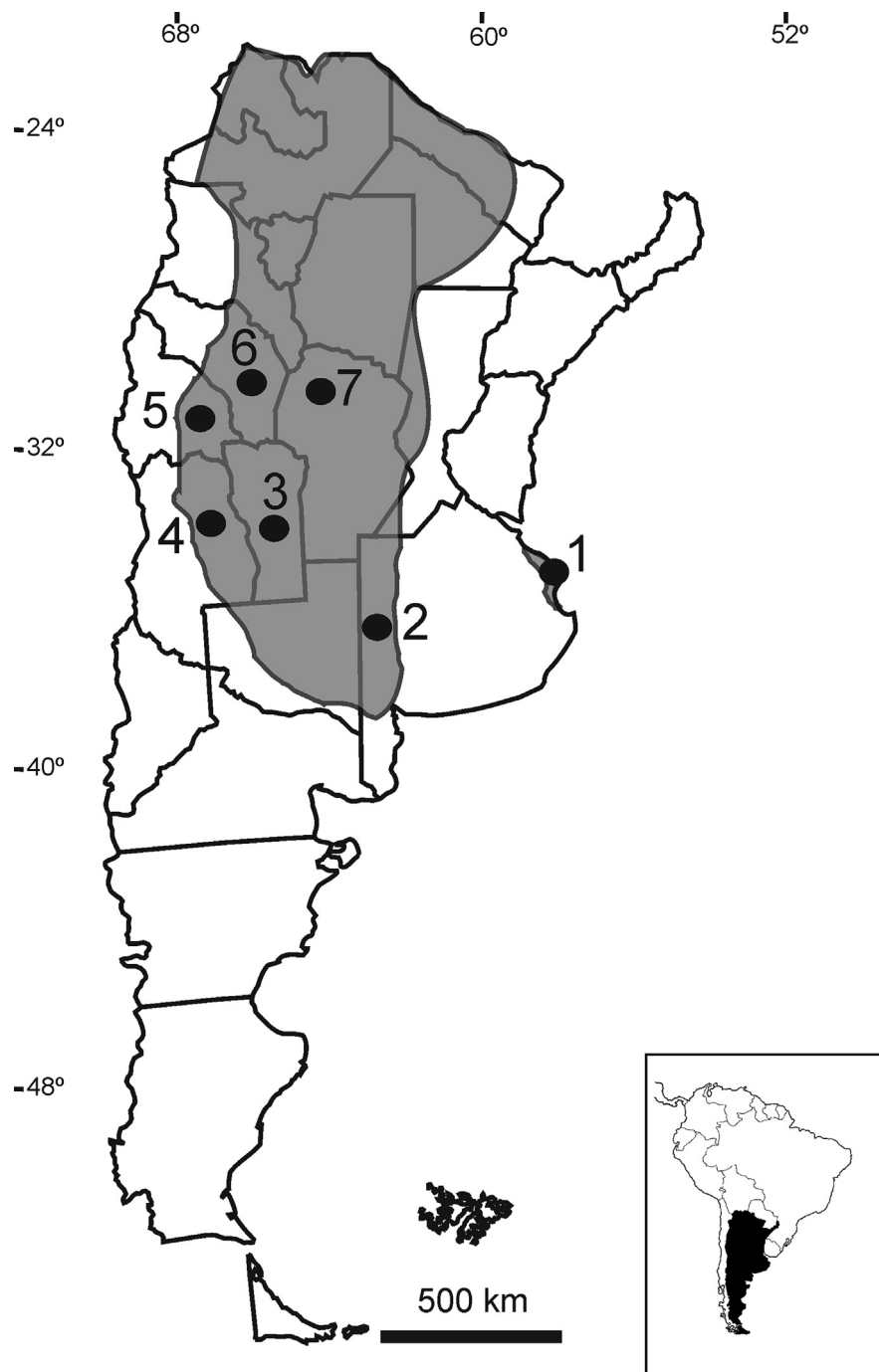


Fig. 1. Map showing the distribution of *Chaetophractus vellerosus* in Argentina and sampling sites (black circles). 1. East of Buenos Aires. 2. West of Buenos Aires. 3. San Luis. 4. Mendoza. 5. San Juan. 6. La Rioja. 7. Córdoba.

community in the east of Buenos Aires (Ezquiaga, 2013), showing that a group of parasite species accompanies armadillos in their distribution. In addition, Ezquiaga et al. (2016) studied the parasite community of *C. villosus* in its main distribution and in an introduced population in Tierra del Fuego Island. The authors observed a significant loss of diversity in the isolated population, with only one parasite species present. They suggested that severe climatic conditions and long winters in the island prevented encounters between potential hosts and infective forms of parasites.

Poulin and Krasnov (2010) indicated that a decrease in the proportion of species shared by two communities corresponds with the geographical distance between them. Thus, nearby communities tend to have many species in common, whereas distant communities share very few (Poulin and Krasnov 2010). Moreover, isolated habitats can limit the exposure of hosts to new parasites and prevent the acquisition of novel parasite species from other host species if these are too far away (Poulin and Morand, 2004).

Considering the distance decay of similarity and that there is a population of *C. vellerosus* separated from the main population by about 500 km, the aim of this work was to compare the component community of *C. vellerosus* between the main population in central Argentina and the isolated population, evaluating the impact of the host isolation on parasite diversity.

2. Material and methods

A total of 41 specimens of *C. vellerosus* were analyzed: 26 belonged to the main population (west of Buenos Aires, Córdoba, La Rioja, Mendoza, San Juan and San Luis provinces) and 15 to the isolated population (35–36°S, 57°W, east of the Buenos Aires province) (Fig. 1). Part of the specimens were taken from mammal collections (Museo de La Plata -MLP- and Instituto Argentino de Investigaciones de las Zonas Áridas -CMI-), others were collected (permission issued by Ministerio de Asuntos Agrarios, Buenos Aires province, Argentina; Exp. N°2578-1404/05 and Exp. N°22300-24/2008) and some others were donated by T. Rogel and A. Agüero (Universidad Nacional de La Rioja, Sede Chamental, Transit guide N° 000057–000058). Collection numbers of the deposited material are CMI7595, MLP 7.V.10.3, MLP 7.V.10.4, MLP 7.V.10.5, MLP 2220–2224, MLP 2226, MLP 2229–2232, MLP 2234–2246, MLP 2251, MLP 2252. Twelve individuals were obtained from local people that use this species for food and could not be admitted to any collection. Specimens were collected in different seasons between 2005 and 2011.

Table 1

Richness (S), Prevalence (P), mean intensity (MI) and mean abundance (MA) ($\pm$ Standard Deviation) in the main population and in the isolated population of *Chaetophractus vellerosus* in Argentina. When prevalences and mean intensities of the species present in both host populations were compared, no significant differences were observed (Table 2).

Parasite	Main population (N = 26) (S = 16)			Isolated population (N = 15) (S = 8)		
	P (%)	MI ($\pm$ SD)	MA ($\pm$ SD)	P (%)	MI ($\pm$ SD)	MA ($\pm$ SD)
Nematoda						
<i>Ancylostoma caninum</i>	11	9.6 ($\pm$ 10.1)	1.1 ($\pm$ 4.2)	20	5.3 ($\pm$ 6.6)	1.1 ($\pm$ 3.3)
<i>Aspidodera fasciata</i>	81	254 ($\pm$ 356.1)	205.4 ($\pm$ 334.5)	93	372 ($\pm$ 323.4)	346.9 ($\pm$ 326.1)
<i>Aspidodera scoleciformis</i>	88	219 ($\pm$ 293.6)	193.5 ($\pm$ 284.5)	93	143 ($\pm$ 116.8)	133.6 ($\pm$ 118.5)
<i>Cruzia tentaculata</i>	4	2	0.1 ($\pm$ 0.4)	—	—	—
<i>Cyclobulura superinae</i>	19	19.6 ($\pm$ 17.6)	3.8 ($\pm$ 10.5)	—	—	—
<i>Delicata ransomi</i>	11	2 ($\pm$ 1)	0.23 ($\pm$ 0.7)	—	—	—
<i>Macielia jorgei</i>	8	13 ($\pm$ 15.5)	1 ($\pm$ 4.7)	—	—	—
<i>Mazzia bialata</i>	8	2.5 ($\pm$ 2.1)	0.2 ($\pm$ 0.8)	13	1.5 ($\pm$ 0.7)	0.2 ($\pm$ 0.6)
<i>Moennigia celinae</i>	4	38	1.5 ($\pm$ 7.4)	—	—	—
<i>Orihelia anticlava</i>	15	1.7 ($\pm$ 0.9)	0.3 ($\pm$ 0.7)	—	—	—
<i>Pterygodermatites chaetophracti</i>	42	6.5 ($\pm$ 7.1)	2.7 ($\pm$ 5.6)	46	11.6 ($\pm$ 8.5)	5.4 ($\pm$ 8.2)
<i>P. argentinensis</i>	31	5.5 ($\pm$ 5.1)	1.7 ($\pm$ 3.7)	60	53 ($\pm$ 126.8)	31.6 ($\pm$ 99.5)
<i>Strongyloides</i> sp.	27	4.8 ($\pm$ 6.4)	1.3 ($\pm$ 3.8)	46	17 ($\pm$ 10.1)	7.8 ($\pm$ 10.8)
<i>Trichoelax tuberculata</i>	69	62.8 ($\pm$ 85.3)	43.5 ($\pm$ 76.4)	86	20 ($\pm$ 18.2)	17.4 ($\pm$ 18.1)
Cestoda						
<i>Mathevotaenia</i> sp.	11	5.3 ($\pm$ 3.5)	0.6 ($\pm$ 1.9)	—	—	—
Acantocephala						
<i>Travassosia</i> sp.	15	5.5 ($\pm$ 7.7)	0.8 ($\pm$ 3.3)	—	—	—

Material from collections was fixed in 10% formaldehyde solution and conserved in 70% ethanol.

The collected specimens were fixed in 10% formaldehyde solution and stored for no longer than a year until dissection. Abdominal and thoracic cavities and digestive tracts were dissected in the laboratory. Nematodes and acanthocephalans were stored in 70% ethanol, cleared with Amman's lactophenol and mounted on a slide under a coverslip. Cestodes were stained with hydrochloric carmine, dehydrated in a series of ethanol solutions of increasing concentration, cleared with eugenol and mounted with Canada balsam on a slide under a coverslip. Helminths were examined using an Olympus BX51 compound microscope (Olympus Corporation, Tokyo, Japan) and identified taking into account the keys, descriptions and records of Navone (1986), Navone (1987), Navone (1988), Notarnicola and Navone (2003), Anderson et al. (2009), Hoppe et al. (2009), Navone et al. (2010), Ezquiaga and Navone (2013).

Prevalence (P), mean intensity (MI), mean abundance (MA), richness (S) and Shannon's Diversity Index (H) were calculated for each host population (Bush et al., 1997). Population parameters of the main and isolated populations were compared for each helminth species present in both populations; prevalences were analyzed using the Chi-square test

Table 2

p values of prevalence and mean intensity of the 8 species present in both populations (main population and the isolated population) of *Chaetophractus vellerosus* in Argentina.

Parasite	Prevalence ($\alpha = 0.05$)		Mean intensity ($\alpha = 0.05$)	
	Chi square p-value (2-sided)	Fisher's exact test Exact p-value (2-sided)	Wilcoxon-Mann-Whitney p-value (2-tailed)	Bootstrap p-value (2-tailed)
<i>Ancylostoma caninum</i>	0.460	0.651	0.5066	0.3890
<i>Aspidodera fasciata</i>	0.5237	0.3878	0.0859	0.0990
<i>A. scoleciformis</i>	0.9681	1.0000	0.7780	0.7560
<i>Mazzia bialata</i>	0.558	0.615	1.0000	0.4940
<i>Pterygodermatites chaetophracti</i>	0.786	1.000	0.2541	0.2400
<i>P. argentinensis</i>	0.067	0.102	0.1906	0.1680
<i>Strongyloides</i> sp.	0.199	0.3061	0.0521	0.0570
<i>Trichoelax tuberculata</i>	0.210	0.277	0.6163	0.6490

and/or Fisher's exact test ($\alpha = 0.05$) and mean intensities were studied conducting non-parametric Wilcoxon-Mann-Whitney and Bootstrap tests. The analyses were performed using the program Quantitative Parasitology 3.0 (Reiczigel et al., 2005; Rózsa et al., 2000).

3. Results

The total prevalence of helminths was 96% in the main population and 100% in the isolated population. Sixteen species of helminths were found, namely *Ancylostoma caninum*, *Aspidodera fasciata*, *A. scoleciformis*, *Cruzia tentaculata*, *Cyclobulura superinae*, *Delicata ransomi*, *Macielia jorgei*, *Mazzia bialata*, *Moennigia celinae*, *Orihelia anticlava*, *Pterygodermatites chaetophracti*, *P. argentinensis*, *Strongyloides* sp., *Trichoelax tuberculata* (Nematoda), *Mathevotaenia* sp. (Cestoda) and *Travassosia* sp. (Acanthocephala). Of them only 8 species were present in both populations (Table 1). There were no differences in the parasite species composition between the museum material and the collected specimens for the present study.

Three species were recorded in *C. vellerosus* for the first time, *M. bialata*, *Strongyloides* sp. and *D. ransomi*, the latter species was only found in the main population.

Aspidodera fasciata and *A. scoleciformis* were the most prevalent and abundant in both populations, followed by *T. tuberculata* and *Pterygodermatites* spp. The least prevalent species were *C. tentaculata*, *M. bialata*, *Mo. celinae* and *Ma. jorgei* (Table 1).

In the main population the diversity was higher than in the isolated population (H: 1.134 vs. 1.029). Individuals captured at the edge of the core distribution (Fig. 1 point 2) were parasitized by 9 species (*T. tuberculata*, *D. ransomi*, *Mo. celinae*, *Mathevotaenia* sp., *An. caninum*, *A. scoleciformis*, *A. fasciata*, *Strongyloides* sp., *O. anticlava*).

4. Discussion

The greatest parasite diversity is observed in specimens of *C. vellerosus* from central Argentina, which was suggested as the ancestral area of distribution (Poljak et al., 2018). In this regard, Poulin and Krasnov (2010) stated that abundance and prevalence often peak close to the center of a parasite species' geographical range and decrease toward its edges. In fact, the host specimens from west of Buenos Aires (the nearest region of the isolated population) had a higher richness than that observed in the isolated population. Moreover, only half of the parasite species appeared in the isolated population, in accordance with Torchin et al. (2003) who observed that introduced animal populations were, on average, infected with less than half the number of parasite species in populations within their native range. Less frequent species of the main population ($P < 20\%$), except for *M. bialata* and *A. caninum*, were absent in the isolated population. In this sense, Torchin et al. (2003) indicated that parasite species left behind tended to be those that were less prevalent in native populations compared with those that did transfer.

Several explanations can be proposed for the presence of only half of parasite species in the isolated population: the parasite fauna went extinct because of environmental factors, the founding individuals brought low parasite diversity, or intermediate hosts for parasites with indirect life-cycles were absent. Environmental conditions seem not to be the cause of the decrease in species richness since the distribution area of the isolated population (i.e. east of Buenos Aires) is similar to the distribution area of the main population (i.e. central Argentina) in terms of soil type and flora. However, the fact that the founding population was composed of few specimens that would only be infected with the most prevalent parasites and also that there were no intermediate hosts for parasites with indirect cycles (e.g. cestodes, acanthocephalans) could be considered factors that may have contributed to a poor parasite community in the isolated population.

At least three related species of Chlamyphoridae coexist with *C. vellerosus* in central Argentina, *C. villosus*, *Tolypeutes matacus* and *Zaedyus pichiy*, and all of them share helminth species in this area

reaching high parasite diversity (Ezquiaga, 2013; Ezquiaga et al., 2016; Rios et al., 2016). On the other hand, in the east of Buenos Aires, *C. vellerosus* only coexists with *C. villosus*, which is parasitized by *An. caninum*, *A. fasciata*, *A. scoleciformis*, *M. bialata*, *T. tuberculata* and *Mathevotaenia* sp. (Ezquiaga, 2013).

Parasites with prevalence higher than 40% and mainly monoxenous (e.g. *Aspidodera* spp., *T. tuberculata*) would accompany their host when the environmental conditions are similar, and species heteroxenous would be present when intermediary hosts are terrestrial insects (e.g. *Pterygodermatites* spp.). Species like *M. bialata* and *Strongyloides* sp. could come from *C. villosus*. In this way, the screaming hairy armadillo would have acquired several parasites from *C. villosus* in the east of Buenos Aires. The presence of *An. caninum* could be explained by the occurrence of dogs parasitized with this species that coexist with armadillos in the East of Buenos Aires as well as in the distribution of the main population (Ezquiaga, 2013).

Although there were no significant differences in mean intensities and mean abundances in the 8 species present in both populations, a lower aggregation was observed in the isolated population. This population occupies a small area, individuals have more contact between them (see Pagnutti et al., 2014) and are more exposed to parasitic infections, and therefore probably transmission rates will be higher among individuals. It is believed that acquired immunity develops in response to accumulated experience of infection and acts to decrease parasite establishment, survival and reproduction (Rosà et al., 2006). Thus, in populations where transmission rates are high (i.e. isolated population), the level of parasitic infection will rise rapidly, followed by a rapid increase in the level of acquired immunity, causing a decline in parasite loads. In contrast, in the main population, which inhabits a greater area, parasite transmission rates are low, consequently, parasite loads (and acquired immunity) will increase at a slower rate, and therefore the aggregation will be greater (Rosà et al., 2006; Cattadori et al., 2005).

Concerning the distance between populations, Poulin and Krasnov (2010) indicated that several mechanisms can work to produce a decrease of the similarity in species composition between two communities with an increase of the distance between them. Soinen et al. (2007) grouped these mechanisms into three general classes: first, community similarity may decrease with distance because the similarity of climatic or environmental factors also decreases with distance; second, the topography of the landscape can either facilitate or impede the dispersal of organisms among localities, and third, even in homogeneous and continuous settings, with no environmental gradients or barriers to dispersal, community similarity would also decrease with distance because of the limited dispersal of parasites (Poulin and Krasnov 2010). These processes are not mutually exclusive, and it is not easy to distinguish between them (Poulin and Krasnov 2010), since several of these can act synergistically.

Chaetophractus vellerosus is considered a species with low vagility and that only inhabits sandy soils (Abba et al., 2015a; Poljak et al., 2018). These characteristics contribute to the fact that the main and isolated populations have no contact with each other and prevent encounters between potential host species and infective forms of parasites especially those less prevalent, and Magnanou and Morand (2006) explained that parasite species in depauperate assemblages constitute subset samples of richer assemblages. Thus, the parasite fauna of the isolated population of *C. vellerosus* is characterized by the usual parasite species that accompany armadillos along their distribution (Navone, 1990).

Declarations

Author contribution statement

María Cecilia Ezquiaga: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Agustín Manuel Abba: Performed the experiments; Contributed

reagents, materials, analysis tools or data.

Graciela Teresa Navone: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data.

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Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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References

- Abba, A.M., Cassini, G.H., Cassini, M.H., Vizcaíno, S.F., 2011. Historia natural del piche llorón *Chaetophractus vellerosus* (Mammalia: Xenarthra: Dasypodidae). *Rev. Chil. Hist. Nat.* 84, 51–64.
- Abba, A.M., Cassini, G.H., Valverde, G., Tilak, M.K., Vizcaíno, S.F., Superina, M., Delsuc, F., 2015a. Systematics of hairy armadillos and the taxonomic status of the Andean hairy armadillo (*Chaetophractus nationi*). *J. Mammal.* 96, 673–689.
- Abba, A.M., Zufiaurre, E., Codesido, M., Gado, P.A., Bilencia, D., 2015b. Distribución de tres especies de armadillos en la región pampeana comprendida en la provincia de Buenos Aires, Argentina. *Mastozool. Neotrop.* 22, 359–365.
- Anderson, R.C., Chabaud, A.G., Willmott, S., 2009. Keys to the Nematode Parasites of Vertebrates. Archival Volume. CAB International, U.K.
- Bordes, F., Morand, S., Krasnov, B.R., Poulin, R., 2010. Chapter 7. Parasite diversity and latitudinal gradients in terrestrial mammals. In: Morand, S., Krasnov, B.R. (Eds.), *The Biogeography of Host-Parasite Interactions*. Oxford University Press Inc., New York, pp. 89–98.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: margolis et al. revisited. *J. Parasitol.* 83, 575–583.
- Bush, A.O., Fernández, J.C., Esch, G.W., Seed, J.R., 2001. Parasitism. The Diversity and Ecology of Animal Parasites. Cambridge University Press, Cambridge.
- Carlini, A.A., Vizcaíno, S.F., 1987. A new record of the armadillo *Chaetophractus vellerosus* in the Buenos Aires Province of Argentina: possible causes for the disjunct distribution. *Stud. Neotrop. Fauna Environ.* 22, 53–56.
- Cattadori, I.M., Boag, B., Björnstad, O.N., Cornell, S.J., Hudson, P.J., 2005. Peak shift and epidemiology in a seasonal host-nematode system. *Proc. Royal Soc. B* 272, 1163–1169.
- Cavallotto, J.L., 2009. Caracterización e historia evolutiva del sustrato sobre el que se desarrollan los talares del nordeste bonaerense. In: Athor, J. (Ed.), *Parque Costero del Sur. Naturaleza, conservación y patrimonio cultural*. Fundación de Historia Natural Félix de Azara, Buenos Aires, pp. 66–81.
- Ezquiaga, M.C., 2013. Estudios parasitológicos en Dasypodidae (Mammalia, Xenarthra) de Argentina: el valor de la diversidad en la interpretación de las asociaciones parásito-hospedador-ambiente. Doctoral dissertation, Facultad de Ciencias Naturales-Universidad Nacional de La Plata, Argentina.
- Ezquiaga, M.C., Navone, G.T., 2013. Trichostrongylina parasites of dasypodidae (Xenarthra) from Argentina; a new species of *Macielia* (Molineidae: Anoplostrongylinae) in *Chaetophractus vellerosus* and redescription of *Trichohelix tuberculata*. *J. Parasitol.* 99, 821–826.
- Ezquiaga, M.C., Navone, G.T., 2014. A new species of *Moennigia* (Trichostrongylina: Molineidae) a parasite of *Chaetophractus* spp. (Xenarthra: Dasypodidae) from Argentina. *J. Parasitol.* 100, 500–503.
- Ezquiaga, M.C., Abba, A.M., Cassini, G.H., Navone, G.T., 2014. Evidencias de parásitos internos en animales vivos: una población de *Chaetophractus vellerosus* como modelo de estudio coproparasitológico. *Rev. Mex. Biodivers.* 85, 845–853.
- Ezquiaga, M.C., Abba, A.M., Navone, G.T., 2016. Loss of helminth species diversity in the large hairy armadillo *Chaetophractus villosus* on the Tierra del Fuego Island, Argentina. *J. Helminthol.* 90, 245–248.
- Hoppe, E.G.L., Araújo de Lima, R.C., Tebaldi, J.H., Athayde, A.C.R., Nascimento, A.A., 2009. Helminthological records of six-banded armadillos *Euphractus sexcinctus* (Linnaeus, 1758) from the Brazilian semi-arid region, Patos county, Paraíba state, including new morphological data on *Trichohelix tuberculata* (Parona and Stossich, 1901) Ortlepp, 1922 and proposal of *Hadrostrongylus ransomi* nov. comb. *Braz. J. Biol.* 69, 423–428.
- IUCN SSC Anteater, Sloth and Armadillo Specialist Group, 2017. *Chaetophractus vellerosus* (Amended Version of 2016 Assessment). The IUCN Red List of Threatened Species 2017: e.T89604632A119877197. (Accessed 2 July 2018).
- Khalil, M.B., Vogelsang, E.G., 1932. On a new genus of nematodes *Mazzia mazzia* n. g., n. sp. from an Argentine Edentate. *Institut für Schiffs und Tropenkrankheiten, Hamburg*, pp. 1016–1019.
- Krasnov, B.R., Poulin, R., Morand, S., 2006. Chapter 12. Patterns of macroparasite diversity in small mammals. In: Morand, S., Krasnov, B.R., Poulin, R. (Eds.), *Micromammals and Macroparasites. From Evolutionary Ecology to Management*. Springer-Verlag, Tokyo, pp. 197–231.
- Lombardero, O.J., Moriena, R.A., 1977. *Mazzia mazzia* in Dasipodidae of Argentina (redescription). *Revista de Medicina Veterinaria, Buenos Aires* 58, 141–142.
- Magnanou, E., Morand, S., 2006. Chapter 16. Insularity and micromammal-macroparasite relationships. In: Morand, S., Krasnov, B.R., Poulin, R. (Eds.), *Micromammals and Macroparasites. From Evolutionary Ecology to Management*. Springer-Verlag, Tokyo, pp. 295–315.
- Martínez, F.A., 1984. *Hamanniella carinii* Travassos, 1916 (Acanthocephalo: Gigantorhynchidae) en Dasipodídeos de Argentina. *Bol. Chil. Parasitol.* 39, 37–38.
- Mazza, S., Romaña, C., Fiora, A., 1932. Algunos hemoparásitos de mamíferos del Norte. 7. Reunión Soc. Argent. Patol. Reg. Norte: 990–997.
- Navone, G.T., 1986. Estudios parasitológicos en edentados argentinos. II. Nematodos parásitos de armadillos: *Aspidodera fasciata* (Schneider, 1866); *Aspidodera scoleciformis* (Diesing, 1851) y *Aspidodera vazi* Proença, 1937. (Nematoda-Heterakoidea). *Neotropica* 32, 71–79.
- Navone, G.T., 1987. Descripción del macho de *Pterygodermatites (Pauicipetines) chaetophracti* (Navone y Lombardero, 1980) Sutton, 1984 (Nematoda-Rictulariidae). *Neotropica* 33, 45–49.
- Navone, G.T., 1988. Estudios parasitológicos en edentados argentinos IV. Cestodes pertenecientes a la familia Anoplocephalidae Cholodkovshy, 1902, parásitos de dasipodídeos. *Neotropica* 34, 51–61.
- Navone, G.T., 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, G.T., Ezquiaga, M.C., Notarnicola, J., Jiménez Ruiz, A., 2010. A new species of *Cyclobulura* (Nematoda: Subuluridae) from *Zaedyus pichiy* and *Chaetophractus vellerosus* (Xenarthra: Dasypodidae) in Argentina. *J. Parasitol.* 96, 1191–1196.
- Notarnicola, J., Navone, G.T., 2003. Systematic and distribution of *Orihelia anticlava* (Molin, 1858) (Nematoda, Onchocercidae) from dasypodids of south America. *Acta Parasitol.* 48, 103–110.
- Oyarzabal, M., Clavijo, J., Oakley, L., Biganzoli, F., Tognetti, P., Barberis, I., Maturó, H.M., Aragón, R., Campanello, P.I., Prado, D., Oesterheld, M., León, R.J.C., 2018. Unidades de vegetación de la Argentina. *Ecol. Austral* 28, 40–63.
- Pagnutti, N., Gallo, J., Superina, M., Vizcaíno, S.F., Abba, A.M., 2014. Patrones estacionales de distribución espacial y área de acción del piche llorón, *Chaetophractus vellerosus* (Xenarthra: Dasypodidae), en Magdalena, Buenos Aires, Argentina. *Mastozool. Neotrop.* 21, 59–65.
- Poljak, S., Ferreira, A.M., Chiappero, M.B., Sánchez, J., Gabrielli, M., Lizarralde, M.S., 2018. Phylogeography of screaming hairy armadillo *Chaetophractus vellerosus*: successive disjunctions and extinctions due to cyclical climatic changes in southern South America. *PLoS One* 13 (1), e0190944.
- Poulin, R., 2007. *Evolutionary Ecology of Parasites*, second ed. Princeton University Press, New Jersey, p. 332.
- Poulin, R., Morand, S., 2004. *Parasite Biodiversity*. Smithsonian Books, Washington.
- Poulin, R., Krasnov, B.R., 2010. Chapter 9. Similarity and variability of parasite assemblages across geographical space. In: Morand, S., Krasnov, B.R. (Eds.), *The Biogeography of Host-Parasite Interactions*. Oxford University Press Inc., New York, pp. 115–127.
- Reiczigel, J., Zakariás, I., Rózsa, L., 2005. Bootstrap test of stochastic equality of two populations. *Am. Statistician* 59, 156–161.
- Ríos, T.A., Ezquiaga, M.C., Abba, A.M., Navone, G.T., 2016. Intestinal parasites of *Toxypeutes matacus*, the most frequently consumed armadillo in the Chaco Region. *Int. J. Parasitol. Parasites and Wildlife* 5, 254–257.
- Rosà, R., Rizzoli, A., Ferrari, N., Pugliese, A., 2006. Chapter 17. Models for host-macroparasite interactions in micromammals. In: Morand, S., Krasnov, B.R., Poulin, R. (Eds.), *Micromammals and Macroparasites. From Evolutionary Ecology to Management*. Springer-Verlag, Tokyo, pp. 319–348.
- Rózsa, L., Reiczigel, J., Majoros, G., 2000. Quantifying parasites in samples of hosts. *J. Parasitol.* 86, 228–232.
- Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. *Ecography* 30, 3–12.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., Kuris, A.M., 2003. Introduced species and their missing parasites. *Nature* 421, 628–630.
- Vogelsang, E.G., 1932. Nuevos huéspedes para Ancylostomidae (Looss, 1905) Lane 1917. *Institut für schiffs und Tropenkrankheiten, Hamburg*, pp. 1022–1023.