


Predictors of parasite and pathogen infections in urban rodents of central Argentina

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Research Paper

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Abstract

Urban rodents are associated with parasites and pathogens, which present health risks for humans, but information on factors related to parasite and pathogen infection in rodents in cities of Latin America is scarce. This study analyzes the hosts, host community structure and environmental characteristics of parasite and pathogen fauna present in the three species of urban rodents in an urban area of South America. Rodents were captured seasonally in seven different neighborhoods. Digestive tracts were dissected under stereoscopic microscopy and feces were processed using a sedimentation technique. Protozoa and bacteria were detected through polymerase chain reaction and indirect immunofluorescence techniques. In *Rattus norvegicus*, *Rattus rattus* and *Mus musculus*, ten helminths, three protozoa and two bacteria were found. Six were zoonotic: *Toxoplasma gondii*; *Hymenolepis diminuta*; *Rodentolepis nana*; *Strobilocercus fasciolaris*; *Leptospira borgpetersenii*; and *Leptospira interrogans*. The parasite and pathogen infections were influenced by the host species, the host community structure, the season, and the presence of streams in the neighborhood. Urban rodents may be the infection source of many zoonotic diseases and it is important to generate public policies for this problem. This study is one example of the situation of many cities of Latin America, where peripheral neighborhoods are growing dramatically.

Introduction

Human activities throughout the ages have led to dramatic alterations of the environment, but never as marked as in the 20th and 21st centuries (Behnke *et al.*, 2004). In many developing countries, unplanned growth in urban centers leads to the emergence of precarious dwellings in areas that are unsuitable for civil construction; this does not foster the practice of good hygiene habits and contributes to the deterioration of environmental conditions. Urbanization processes and problems related to the disposal of solid waste, drainage of rain-water, and sewage collection and treatment have become serious and almost uncontrollable issues (de Masi *et al.*, 2009).

The disturbances created by city growth destroy the habitats of native species and create habitats for the relatively few species that can adapt to urban and suburban conditions, favored by the stable availability of food and shelter (Chace & Walsh, 2006; Bradley & Altizer, 2007; Cavia *et al.*, 2009). Clear examples of such invasive synanthropic species are the urban rodents: the Norway rat (*Rattus norvegicus* Berkenhput, 1769) and the black rat (*Rattus rattus* Linnaeus, 1758), originally from Southeast Asia and North Africa/West Asia, respectively, and the house mouse (*Mus musculus* Linnaeus, 1758), originally from Southeast Asia (Lobos *et al.*, 2005; Nagorsen, 2005; Bonnefoy *et al.*, 2008; Puckett *et al.*, 2016). Many aspects of their biology, such as an enormous reproductive potential, their feeding behavior and adaptation to urban environments, contribute to the success of their worldwide invasion (Cavia *et al.*, 2009; Himsworth *et al.*, 2013; Vadell *et al.*, 2014; Kosoy *et al.*, 2015).

Studies involving urban rodents are scarce compared to their importance to public health and there is a lack of interest in studies carried out on widely distributed species when the contributions are regional. However, this information is valuable for understanding the behavior of diseases transmitted by rodents to humans and animals. A large number of pathogens and parasite species utilize rodents to fulfill part of their life cycle (Battersby *et al.*, 2002; Milazzo *et al.*, 2003; Easterbrook *et al.*, 2007; Meerburg *et al.*, 2009; Hancke & Suárez, 2017; Panti-May *et al.*, 2018). Among the most common helminth species recorded are *Capillaria hepatica* (Bancroft, 1893), *Heterakis spumosa* Schneider, 1866, *Nippostrongylus brasiliensis* Travassos, 1914, *Hymenolepis diminuta* Rudolphi, 1819, *Rodentolepis nana* (Von Siebold, 1852) and *Hidatiguera taeniaeformis* (Batsch, 1786), some of which present health

risks (Landaeta-Aqueveque *et al.*, 2007; Kataranovski *et al.*, 2011; Zain *et al.*, 2012; Fitte *et al.*, 2017). Protozoa parasites with health implications, such as *Giardia muris* Blanchard, 1888, *Neospora caninum* Dubey *et al.*, 1988, and *Toxoplasma gondii* Nicolle & Manceaux, 1908 (Franjola *et al.*, 1995; Muradian *et al.*, 2012; Seifollahi *et al.*, 2016) have also been recorded, as well as many bacteria that affect health, such as *Leptospira* spp. Noguchi 1917 and *Yersinia pestis* Lehmann & Neumann, 1896 (Meerburg *et al.*, 2009; Himsworth *et al.*, 2013).

Identifying and understanding the biology of rodent-associated parasites and pathogens, and their relationship with internal and/or external factors which favor their presence, is fundamental for the prevention of severe disease in humans and domestic animals (Bordes *et al.*, 2015). Some helminths and protozoa species (e.g., *T. gondii*, *Hymenolepis* spp.) are worrying because they are not subject to mandatory reporting (Lykins *et al.*, 2016; Dellarupe *et al.*, 2019). Also, the symptoms caused by some pathogens (e.g., *Leptospira* spp., *Hantavirus* spp.) are often confused with other common pathologies, leading to serious cases and even death when they are diagnosed late (Ministerio de Salud de la Nación, 2014).

The richness and composition of parasite assemblages depends on a series of factors related to the host species, their geographic range, body size, population density, social behavior and diet (Morand & Poulin, 1998; Arneberg, 2002; Poulin, 2004; Poulin & George-Nascimento, 2007), as well as variations in environmental conditions that operate as specific sources of selection pressures (Behnke *et al.*, 2004; Deter *et al.*, 2007). In urban areas, structural and environmental conditions play a fundamental role in relation to the presence of rodents and the associated parasite fauna (Traweger & Slotta-Bachmayr, 2005; Traweger *et al.*, 2006; Cavia *et al.*, 2009; Hancke *et al.*, 2011), and these become a threat to human health due to the proximity in which people, domestic animals and rodents coexist (Himsworth *et al.*, 2013; Rothenburger *et al.*, 2017). Moreover, community interactions in pathogen transmission are being increasingly studied to understand the multi-host ecology of zoonotic pathogens, since most infectious agents circulate in communities of hosts infected with multiple parasites (Johnson *et al.*, 2015; Hassell *et al.*, 2017). Changes in the community structure, including pathogens and hosts, have epidemiological consequences (Telfer *et al.*, 2010; Johnson *et al.*, 2015).

The aim of this study was to record the parasite and pathogen fauna present in the three species of urban rodents in seven neighborhoods of the city of Gran La Plata, province of Buenos Aires, Argentina, analyzing the relation of parasite and pathogen infection with host characteristics, host community structure and environmental characteristics.

Material and methods

Study area

The study was conducted in the La Plata and Berisso departments in the area of Gran La Plata, in the north-east of the province of Buenos Aires, Argentina. Sampling was carried out in seven neighborhoods; five peripheral to La Plata (fig. 1): Malvinas Argentinas (34.5643°S, 58.0036°W), La Isla (34.5328°S, 57.5925°W), El Retiro (34.5751°S, 58.0017°W), La Latita (34.5831°S, 57.5830°W) and Abasto (34.5805°S, 58.0147°W); one peripheral to Berisso: El Carmen (34.5533°S, 57.5309°W); and one belonging to the inner city of La Plata: Casco Urbano (34.5516°S, 57.5716°W).

These neighborhoods present different levels of urbanization. El Carmen, El Retiro, La Latita and Malvinas Argentinas are characterized by poor environmental and structural features such as inadequate garbage removal, lack of a sanitation network and potable water, with areas susceptible to flooding and with domestic animals without sufficient care. El Retiro, El Carmen and La Isla neighborhoods are crossed by highly contaminated streams. Abasto is situated in a rural area, with important agricultural activity. Casco Urbano, being part of La Plata city center, presents all services.

Sample collection

Rodent trapping surveys were performed from September 2014 to September 2015. Each neighborhood was sampled for four consecutive seasons. Rodents were captured using cage live traps (15 × 16 × 31 cm), Sherman traps (8 × 9 × 23 cm) and snap traps (17.5 × 8.5 cm). The bait consisted of a mixture of oats, banana and animal fat, carrot, and meat pieces. During seasonal samplings, between 30 and 50 traps were set daily for three consecutive nights inside or in the backyard of houses of each neighborhood, resulting in a trapping effort of 90–150 trap-nights in each neighborhood for each season.

The individuals captured were identified for species, sexed, and measured (full body and tail length). Specimens were sacrificed following procedures and protocols approved by national laws (Animal Protection National Law 14.346 and references in the provincial permits) and the Laboratory, Farm and Wildlife Animals Research Ethics Committee of the National Council of Scientific and Technical Research (CONICET).

Parasitological analysis

The digestive tract, kidneys, and fecal samples were fixed in 10% formalin or stored at −20°C, according to the technique applied to analyze the tissue. Rodent samples were studied in the Centro de Estudios Parasitológicos y de Vectores (CEPAVE) of La Plata and in the Laboratorio de Inmunoparasitología (LAINPA) of the Facultad de Ciencias Veterinarias (FCV) of the Universidad Nacional de La Plata (UNLP).

Digestive tracts were dissected under stereoscopic microscopy (Olympus SZ61-TR). Parasites were removed and preserved in 70% alcohol. Nematodes were diaphanized with lactophenol and mounted. Cestoda were overstained with acid carmine, dehydrated through an alcohol series, diaphanized in eugenol and mounted in Canada balsam for their identification. Specimens were observed under Olympus BX 51 (40–1000 X) optic microscopy. Helminths were identified following the keys from Travassos (1914), Anderson *et al.* (2009) and Gibbons (2010) for Nematoda, and Khalil *et al.* (1994) for Cestoda, and specific literature, i.e., Wardle & McLeod (1952); Robles *et al.* (2008); Guerreiro Martins *et al.* (2014); Fitte *et al.* (2017); Lavikainen *et al.* (2016); and Swain *et al.* (2016). Fecal samples were processed using a sedimentation technique modified for this study, which included homogenization, filtration and microcentrifugation in 1.5-ml Eppendorf tubes for 2 min. at 3000 rpm, to concentrate the largest number of eggs in the minimum possible volume for identifying protozoa and eggs or larvae of helminths. The identification was based on Thienpont *et al.* (1979). For the detection of *Eimeria* spp. Schneider, 1875, fecal samples were processed using the sedimentation technique modified for this study (detailed above) and observed under Olympus BX 51 (40–1000

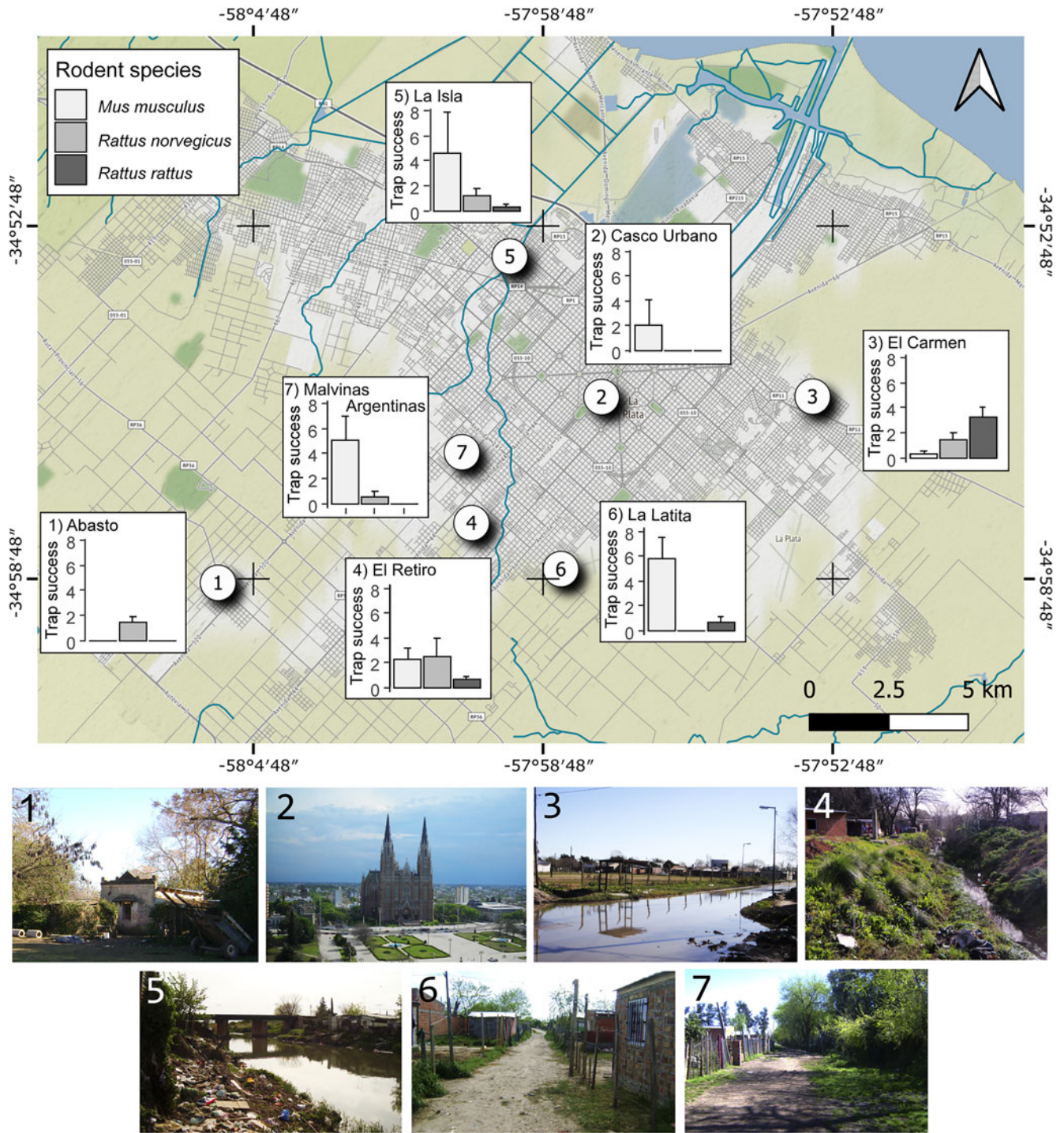


Fig. 1. Map of Gran La Plata, Buenos Aires province, Argentina; the annual mean trap success of each host species registered in each neighborhood and images of neighborhoods involved in the present study: (1) Abasto; (2) Casco Urbano; (3) El Carmen; (4) El Retiro; (5) La Isla; (6) La Latita; and (7) Malvinas Argentinas.

X) optic microscopy. Two complementary analyses were conducted for detection of *T. gondii* and *N. caninum*. First, a simple polymerase chain reaction (PCR) technique was applied from rodent brain samples; for *T. gondii* Tox5-Tox8 primers, and for *N. caninum* Np6+/Np21+ primers were used (Moré *et al.*, 2010). The PCR conditions used are detailed in Dellarupe *et al.* (2019). Secondly, an indirect immunofluorescence (IFI) analysis was applied following Dubey & Frenkel (1998), and Dellarupe

et al. (2019). For *Leptospira* spp. detection, a conventional PCR was applied targeting the lipL32 gene in a kidney sample (Agudelo-Flórez *et al.*, 2009). The PCR was performed using the primers lipL32/270 F and lipL32/692R (Agudelo-Flórez *et al.*, 2009). The PCR conditions are detailed in Agudelo-Flórez *et al.* (2009). Samples positive for *Leptospira* spp. were identified as two species by sequencing and comparing with other closely related species (Fitte & Kosoy, 2021).

Statistical analysis

For each parasite and pathogen taxon, the prevalence (P) for each host and neighborhood was calculated, and for helminths, parasite mean abundance (MA) and mean intensity (MI) indexes were also estimated following Bush *et al.* (1997).

The effects of species, sex, and body length or age among host characteristics, as well as host (rodent) community structure, the presence of a stream in the neighborhood and the season as environmental characteristics, were analyzed in relation to parasite and pathogen infection and parasite abundance. The presence of streams in the neighborhoods was considered because of the role that these play in urban rodent settlement (Traweger & Slotta-Bachmayr, 2005; Cavia *et al.*, 2019a) as well as in the transmission of some pathogens (Soares *et al.*, 2010). Age in months was estimated for *R. norvegicus*, based on body length following Gómez Villafaña *et al.* (2012), while body length was used as an age reference for *R. rattus* and *M. musculus*.

To characterize the rodent community structure in the neighborhood where each individual host was caught, we first estimated the abundance of each rodent species in each season and neighborhood by trap success: the number of individuals captured/number of trap-nights (Mills *et al.*, 1991). Then, to synthesize the host community structure, a principal components analysis (PCA) was performed from the covariance matrix with the mean annual trap success for each species captured in each neighborhood (Legendre & Legendre, 2012). The scores from the first principal component from each study site were used to describe the host community structure of each neighborhood (from now on the host community score).

Due to the low number of individuals caught in some seasons, they were grouped by season: autumn–winter (April–September, with monthly temperatures below 16°C and monthly precipitation below 100 mm); and spring–summer (October–March, with mean monthly temperatures equal to or above 16°C and monthly precipitation averaging 100 mm). To analyze whether the parasite/pathogen assemblage present in each individual host depends on the host species, sex, body length or age, or the host community score, or if it was caught in the cold or warm season, or in a neighborhood with the presence of a stream, canonical correspondence analyses (CCA) were performed, using each helminth species abundance and the infestation status (infected or not infected) for protozoa and bacteria as the response variables, and host species, sex, body length or age, host community score, season, and presence of a stream as explanatory variables. A forward selection procedure was used based on Akaike information criterion (AIC) to include variables that explain pathogen/parasite assemblage structure in the individuals. This analysis was performed using the *vegan* package (Oksanen *et al.*, 2013) of the R software, version 3.0.1 (R Core Team, 2013).

For each host species separately and for each parasite or pathogen taxon, we analyzed the effects on individual infection of host sex and body length/age, the season and the presence of a stream. We also analyzed, for each parasite or pathogen taxon, whether the infection depends on the host species. For this, multiple regression analysis was applied with generalized linear mixed models, with binomial distribution of errors and logistic link function for individual infection, and Poisson distribution for helminth abundance (Zuur *et al.*, 2009). When overdispersion was observed in helminth abundance analyses, models with negative binomial distribution of errors and logit link function were used (Zuur *et al.*, 2009). Neighborhood was included in the

model as a random effect because these were sampled repeatedly in each season. When the random effect did not improve the model, the neighborhood factor was removed and generalized linear models were used (Zuur *et al.*, 2009). A forward stepwise procedure was used for factor selection on these multiple regression analyses, based on the greater change in deviance for factors or interactions. When more than one candidate model was found, we employed the AIC for model selection, reporting only models with $\Delta\text{AIC} < 3$ in relation to the best-fit model with the lowest AIC (Burnham & Anderson, 2002). For the accuracy measures, Kappa index (K) and proportion of correct classifications (PCC) are reported (Titus *et al.*, 1984).

Results

A total of 136 rodents, of the urban species *M. musculus*, *R. norvegicus*, and *R. rattus*, were captured with a trapping effort of 972 Sherman trap-nights, 972 cage live trap-nights and 1044 snap trap-nights. The three host species were captured in El Carmen, La Isla and El Retiro, two species in La Latita and Malvinas Argentinas, and only one species was caught in Abasto and Casco Urbano (fig. 1). According to the PCA, abundance of the three rodent species was not independent in the neighborhoods. The first principal component (PC1) explained 76.6% of the association between the mean trap success of the captured host species in the neighborhoods. This component distinguishes neighborhoods with comparatively higher abundances of *M. musculus* (Pearson $r = 0.95$) and lower abundances of *R. rattus* (Pearson $r = -0.20$) and *R. norvegicus* (Pearson $r = -0.24$) from neighborhoods with comparatively higher abundances of *R. rattus* and *R. norvegicus* and lower abundances of *M. musculus*.

A total of 62.5% of the rodents were infected with at least one parasite or pathogen taxon. *Rattus norvegicus* was the dominant host species in Abasto and El Retiro with a total of 89.29% individuals parasitized; *R. rattus* was the dominant species in El Carmen with 90.48% of individuals parasitized; while *M. musculus* was the dominant host species in La Isla, La Latita, Malvinas Argentinas and Casco Urbano with 41.12% of individuals parasitized (fig. 1).

A total of 15 parasite and pathogen taxa were found: ten corresponded to helminths; three to protozoa; and two to bacteria. The occurrence of parasite and pathogen taxa varied between neighborhoods. *Strobilocercus fasciolaris* was the only species found in all the neighborhoods, followed by *T. gondii*, found in all the neighborhoods except Casco Urbano (table 1). The highest numbers of parasites and pathogens were recorded in neighborhoods with streams (table 1). Among the taxa with health risk, *H. diminuta*, *Rodentolepis nana* and *S. fasciolaris* (Helminths), *T. gondii* (Protozoa), and *Leptospira borgpetersenii* and *Leptospira interrogans* (Bacteria) were found (table 1).

According to the CCA, the host species ($F_{2,83} = 9.56$, $P < 0.001$) and the PC1 (host community structure, $F_{1,83} = 4.87$, $P < 0.001$) were the only features that explained the variation of the composition and abundance of parasite and pathogen assemblages, explaining 23.92% of their variation (fig. 2; CCA, $F_{3,83} = 8.70$, $P < 0.001$). Ten parasite and pathogen taxa were found in *R. norvegicus*, and nine in *R. rattus* and *M. musculus*. *Nippostrongylus brasiliensis*, *H. spumosa*, *S. fasciolaris*, *Eimeria* spp. and *T. gondii* were recorded in the three host species. The rest of the parasite and pathogen taxa were found in two or one host species (table 2). The CCA indicated that both *Rattus* species showed a similar composition and abundance of parasites and

Table 1. Prevalence % (P), mean abundance (MA), mean intensity (MI), parasite/pathogen richness (S) and number of individuals analyzed (n) for each neighborhood, and proportion of neighborhoods in which each parasite/pathogen were registered on rodents captured over the seven neighborhoods studied (Prop) in Gran La Plata, from 2014 to 2015.

Neighborhood	Abasto			Casco Urbano			El Carmen			El Retiro		
	(n = 5, S = 6)			(n = 9, S = 1)			(n = 21, S = 11)			(n = 24, S = 8)		
Parasite/pathogen	P	MA	MI	P	MA	MI	P	MA	MI	P	MA	MI
<i>Leptospira borgpetersenii</i>	0	-	-	0	-	-	4.76	-	-	0	-	-
<i>Leptospira interrogans</i>	0	-	-	0	-	-	0	-	-	8.33	-	-
<i>Eimeria</i> spp.	1/5	-	-	0	-	-	9.52	-	-	4.17	-	-
<i>Toxoplasma gondii</i>	2/5	-	-	0	-	-	33.33	-	-	37.50	-	-
<i>Neospora caninum</i>	0	-	-	0	-	-	0	-	-	0	-	-
<i>Strobilocercus fasciolaris</i>	1/5	1/5	1/1	1/9	1/9	1/1	9.52	0.10	1	33.33	0.67	2
<i>Rodentolepis nana</i>	0	0	0	0	0	0	4.76	0.05	1	8.33	0.29	3.5
<i>Hymenolepis diminuta</i>	2/5	5/5	5/2	0	0	0	14.29	0.48	3.33	0	0	0
<i>Heterakis spumosa</i>	2/5	16/5	16/2	0	0	0	42.86	4.71	11	0	0	0
<i>Nippostrongylus brasiliensis</i>	3/5	141/5	141/3	0	0	0	61.90	46.10	74.46	45.83	9.46	20.36
<i>Strongylides ratti</i>	0	0	0	0	0	0	4.76	1.86	39	16.67	0.88	5.25
<i>Syphacia obvelata</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acantocephala</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trichuris muris</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calodium hepaticum</i>	0	0	0	0	0	0	4.76	0	0	0	0	0
Neighborhood	La Isla			La Latita			Malvina Argentinas			Prop.		
	(n = 26, S = 13)			(n = 28, S = 6)			(n = 23, S = 4)					
parasite/pathogen	P	MA	MI	P	MA	MI	P	MA	MI	Prop.		
<i>L. borgpetersenii</i>	23.08	-	-	14.29	-	-	0	-	-	3/7		
<i>L. interrogans</i>	0	-	-	0	-	-	0	-	-	1/4		
<i>Eimeria</i> spp.	3.85	-	-	0	-	-	0	-	-	4/7		
<i>T. gondii</i>	42.31	-	-	21.43	-	-	21.74	-	-	6/7		
<i>N. caninum</i>	3.85	-	-	0	-	-	0	-	-	1/7		
<i>S. fasciolaris</i>	30.77	0.69	2.25	14.29	0.18	1.25	13.04	0.17	1.33	7/7		
<i>R. nana</i>	3.85	0.12	3	0	0	0	0	0	0	3/7		
<i>H. diminuta</i>	3.85	0.12	3	0	0	0	0	0	0	3/7		
<i>H. spumosa</i>	30.77	4.38	14.25	3.57	0.39	11	0	0	0	4/7		
<i>N. brasiliensis</i>	30.77	22.23	72.25	0	0	0	0	0	0	4/7		

(Continued)

Table 1. (Continued.)

Neighborhood	Abasto		Casco Urbano		El Carmen		El Retiro		
	(n = 5, S = 6)	(n = 9, S = 1)	(n = 21, S = 11)	(n = 24, S = 8)					
<i>S. ratti</i>	19.23	8.73	45.4	3.57	1.75	49	0	0	4/7
<i>S. obvelata</i>	11.54	5.62	48.67	10.71	1.5	14	21.74	3.83	17.6
<i>Acontoccephala</i> spp.	3.85	19.23	5	0	0	0	0	0	1/7
<i>T. muris</i>	0	0	0	0	0	0	4.35	0.04	1
<i>C. hepaticum</i>	0	0	0	0	0	0	0	0	1/7

Values of neighborhoods with rodent individuals <10 are indicated in fractions. The neighborhoods El Retiro, El Carmen and La Isla are crossed by streams.

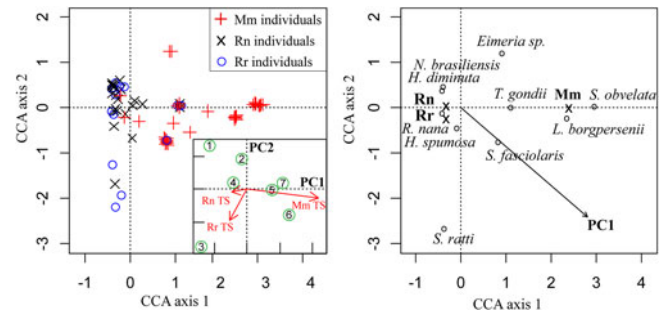


Fig. 2. Spatial ordering of components 1 and 2 (canonical correspondence analyses (CCA) axis 1 and CCA axis 2, respectively) of the (left) host individuals based on helminth abundance, and protozoa and bacterial infection restricted by (right) host species and host community structure (first principal component (PC1)) according to the CCA. [inset: Spatial ordering of components 1 and 2 (PC1 and second principal component (PC2), respectively) according to principal components analysis of mean annual trap success in each neighborhood for each host species used to synthesize the host community structure on the CCA]. Different symbols indicate individuals of different host species. Rn: *Rattus norvegicus*, Rr: *Rattus rattus*, Mm: *Mus musculus*, TS: trap success, PC1: first principal component used to characterize the host community structure in the neighborhoods. Increasing values of PC1 indicate comparatively higher abundance of *M. musculus* and lower abundance of *R. rattus* and *R. norvegicus*, while decreasing values of PC1 indicate the opposite. Numbers in the inset plot correspond to neighborhoods as in fig. 1.

pathogens, which at the same time differed from those of *M. musculus* individuals. A stronger association was observed between *Rattus* species and *H. diminuta*, *R. nana* and *Strongylides ratti* Sandground, 1925, and between *M. musculus* and *L. borgpersenii* and *Syphacia obvelata* Rudolphi, 1802 (tables 1 and 2, fig. 2). Moreover, parasite abundance or pathogen infestation depended on whether the host community was dominated by *M. musculus* or by the *Rattus* species. The abundance of *S. fasciolaris* and *S. ratti* and the frequency of infestation of *S. obvelata* and *L. borgpersenii* were comparatively higher on individuals caught in neighborhoods where *M. musculus* was more abundant, while the abundance of *N. brasiliensis* and *H. diminuta* was higher on individuals in neighborhoods with higher abundance of *R. norvegicus* or *R. rattus* (fig. 2). The frequency of *T. gondii* infection (prevalence) was higher in individuals of *R. norvegicus* than in *M. musculus*, while *R. rattus* showed intermediate values (tables 2 and 3A). The prevalence values of *T. gondii* were similar for both sexes, for the different body lengths/ages, for both seasons and for neighborhoods with or without streams in the three host species ($P > 0.05$ for all cases).

The prevalence of *H. spumosa* was higher in *Rattus* species than in *M. musculus* (table 3B). None of the factors analyzed explained the prevalence differences in *R. norvegicus* and *R. rattus* ($P > 0.05$ for all cases). For *H. spumosa* comparisons, *M. musculus* was eliminated because only three individuals were parasitized. The abundance of this helminth was similar for both *Rattus* species (likelihood-ratio test (LRT) = 0.031; $gl = 1$; $P = 0.859$; table 1). None of the variables analyzed explained the variations in the abundance of this parasite ($P > 0.05$ for all cases).

The prevalence of *N. brasiliensis* was higher in *Rattus* species than in *M. musculus* (table 3C). Its prevalence in *R. norvegicus* was higher during the cold season than in the warm season (89.47% and 55.56%, respectively; table 3 D). In *R. rattus*, all the infected individuals corresponded to neighborhoods with streams (table 1). Abundance was not analyzed in *M. musculus*, since only three individuals were parasitized. The abundance was similar for both *Rattus* species (LRT = 1.748; $gl = 1$; $P =$

Table 2. Prevalence % (P), mean abundance (MA), mean intensity (MI), parasite/pathogen richness (S) and number of individuals analyzed (*n*) for each host species, and proportion of host species in which each parasite/pathogen occurred over the three rodent species (Prop) captured in the seven neighborhoods studied in Gran La Plata, from 2014 to 2015.

Host species	<i>Rattus norvegicus</i> (n = 28, S = 11)			<i>Rattus rattus</i> (n = 21, S = 10)			<i>Mus musculus</i> (n = 87, S = 9)			Prop.
	P	MA	MI	P	MA	MI	P	MA	MI	
<i>Leptospira borgpetersenii</i>	0	-	-	0	-	-	13.75	-	-	1/3
<i>Leptospira interrogans</i>	8	-	-	0	-	-	0	-	-	1/3
<i>Eimeria</i> spp.	3.57	-	-	9.52	-	-	2.3	-	-	3/3
<i>Toxoplasma gondii</i>	45.4	-	-	27.78	-	-	13.95	-	-	3/3
<i>Neospora caninum</i>	0	-	-	0	-	-	2.33	-	-	1/3
<i>Strobilocercus fasciolaris</i>	35.7	0.68	1.9	19.05	0.52	2.75	13.79	0.18	1.33	3/3
<i>Rodentolepis nana</i>	10.7	0.36	3.33	4.76	0.05	1	0	0	0	2/3
<i>Hymenolepis diminuta</i>	10.7	0.18	1.67	14.29	0.48	3.33	0	0	0	2/3
<i>Heterakis spumosa</i>	35.7	4.93	13.8	33.33	3.76	11.29	3.45	0.25	7.33	3/3
<i>Nippostrongylus brasiliensis</i>	78.5	45.32	57.68	47.62	22.86	48	4.6	0.21	4.5	3/3
<i>Strongylides ratti</i>	25	6.32	25.29	19.05	6.67	35	0	0	0	2/3
<i>Syphacia obvelata</i>	0	0	0	0	0	0	16.09	3.6	22.36	1/3
<i>Acanthocephala</i> spp.	3.57	0.18	5	0	0	0	0	0	0	1/3
<i>Trichuris muris</i>	0	0	0	0	0	0	1.15	0.01	1	1/3
<i>Calodium hepaticum</i>	0	0	0	4.76	0	0	0	0	0	1/3

0.186; table 2). For *R. norvegicus*, abundance tended to be higher in males than in females (table 4A). For *R. rattus*, one outlier was observed with 228 parasites and it was therefore dropped from the analyses. After this, none of the variables analyzed explained the variations in abundance of this parasite ($P > 0.05$ for all cases).

Strobilocercus fasciolaris tended to be more prevalent in *R. norvegicus* than in the other host species (tables 2 and 3 E). The prevalence was higher in *R. norvegicus* and *M. musculus* during the cold season (prevalence in *R. norvegicus*: 47.37% in cold seasons – 11.11% in warm seasons; prevalence in *M. musculus*: 35.71% in cold seasons – 10.96% in warm seasons; table 3F and G). Its abundance was higher in *R. norvegicus* and *R. rattus* than in *M. musculus* (tables 2 and 4B). *Rattus norvegicus* and *M. musculus* presented higher abundance in cold seasons than in warm seasons (table 4C and D), but no variable explained the abundance differences in *R. rattus* ($P > 0.05$ for all cases).

For *S. ratti*, only specimens of *R. norvegicus* and *R. rattus* were found parasitized, with similar prevalence in both species (LRT = 0.247; $gl = 1$; $P = 0.619$; table 1). Abundance of this helminth was also similar in both *Rattus* species (LRT = 0.496; $gl = 1$; $P = 0.481$). Due to the low number of rodent specimens parasitized, the relation to different factors was not analyzed. However, all the infected individuals of *R. norvegicus* were caught in neighborhoods with streams (table 1).

For *S. obvelata* in *M. musculus*, overdispersion could not be controlled in models (overdispersion parameter > 20). However, females in the warm season showed the highest prevalence and abundance (Supplemental material).

For *Leptospira* spp., there were no differences in the prevalence in *R. norvegicus* and *M. musculus* (LRT = 0.266; $gl = 1$; $P = 0.606$). None of the variables analyzed could explain the infection variations of *L. borgpetersenii* in *M. musculus* ($P > 0.05$ for all cases).

Differences in *L. interrogans* infection in *R. norvegicus* were not analyzed due to the low number (two) of infected individuals. For the other pathogen and parasite taxa studied, analyses could not be conducted because few individuals were infected.

Discussion

Although there are studies on the relationship of urban rodents, pathogens and parasites (Jittapalapong *et al.*, 2009; Himsworth *et al.*, 2013; Costa *et al.*, 2014; Panti-May *et al.*, 2015), only a few focus on the composition of parasite fauna and their relationships with hosts, host community structure and environmental characteristics (Panti-May *et al.*, 2015). Moreover, studies that summarize and compare results, including the three urban rodent species in an integrated way, are scarce (e.g., Hancke & Suárez, 2017). In this survey, a community approach (Johnson *et al.*, 2015) was used in a scenario with zoonotic multi-pathogens and parasites and multi-hosts. This is the first study carried out in Gran La Plata, which serves as an example of the situation of cities of Argentina and Latin America. Here, six parasite and/or pathogen taxa with health risk were found, with evidence that the composition and abundance of parasites and pathogens are influenced not only by host and environmental characteristics, but also by the host community structure, as Johnson *et al.* (2015) proposed. Among environmental characteristics, the changes in environmental conditions due to seasonality and the presence of a stream, explained the variations observed in the prevalence and abundance of some parasite and/or pathogen taxa in the host species.

The three urban rodent species are sympatric, but they are exploiting different microenvironments with different degrees of urbanization (Cavia *et al.*, 2009, 2019a, 2019b, 2019c; Coto,

Table 3. Analysis of the individual infection of parasite and pathogen taxa in relation to hosts and environmental variables in Gran La Plata, from 2014 to 2015 (see text). In all cases, variables were introduced in models when they produced a significant deviance ($P < 0.05$).

A) Individual infection <i>Toxoplasma gondii</i> ~ host species			
Explanatory variables	Coefficients	SE	P -value
intercept (<i>Mus musculus</i>)	-1.344	0.265	<0.001
<i>Rattus norvegicus</i>	1.487	0.462	0.001
<i>Rattus rattus</i>	0.651	0.533	0.222
LRT = 10.662; d.f. = 2 $P = 0.005$; residual deviance = 154.120; residual d.f. = 133; PCC = 0.721; Kappa = 0.263			
B) Individual infection <i>Heterakis spumosa</i> ~ host species			
Explanatory variables	Coefficients	SE	P -value
intercept (<i>M. musculus</i>)	-3.332	0.588	<0.001
<i>R. norvegicus</i>	2.744	0.708	<0.001
<i>R. rattus</i>	2.639	0.748	<0.001
LRT = 24.249; d.f. = 2; $P < 0.001$; residual deviance = 89.331; residual d.f. = 133; PCC = 0.743; Kappa = 0.359			
C) Individual infection <i>Nippostrongylus brasiliensis</i> ~ host species			
Explanatory variables	Coefficients	SE	P -value
intercept (<i>M. musculus</i>)	-3.332	0.588	<0.001
<i>R. norvegicus</i>	4.632	0.747	<0.001
<i>R. rattus</i>	3.237	0.732	<0.001
LRT = 70.853; d.f. = 2 $P < 0.001$; residual deviance = 84.260; residual d.f. = 133; PCC = 0.853; Kappa = 0.660			
D) Individual infection <i>N. brasiliensis</i> in <i>R. norvegicus</i> ~ seasons			
Explanatory variables	Coefficients	SE	P -value
intercept (warm period)	0.223	0.671	0.739
cold period	1.917	1.004	0.056
LRT = 3.944; d.f. = 1; $P = 0.047$; residual deviance = 25.152; residual d.f. = 26; PCC = 0.607; Kappa = 0.287			
E) Individual infection <i>Strobilocercus fasciolaris</i> ~ host species*			
Explanatory variables	Coefficients	SE	P -value
intercept (<i>M. musculus</i>)	-1.739	0.301	<0.001
<i>R. norvegicus</i>	1.151	0.496	0.020
<i>R. rattus</i>	0.292	0.632	0.644
LRT = 5.227; d.f. = 2; $P = 0.073$; residual deviance = 130.333; residual d.f. = 133; PCC = 0.743; Kappa = 0.202			
F) Individual infection <i>S. fasciolaris</i> in <i>R. norvegicus</i> ~ seasons			
Explanatory variables	Coefficients	SE	P -value
intercept (warm period)	-2.079	1.061	0.0499
cold period	1.974	1.156	0.0877
LRT = 3.933; d.f. = 1; $P = 0.473$; residual deviance = 32.566; residual d.f. = 26; PCC = 0.607; Kappa = 0.287			
G) Individual infection <i>S. fasciolaris</i> in <i>M. musculus</i> ~ seasons			
Explanatory variables	Coefficients	SE	P -value
intercept (warm period)	-2.095	0.3747	<0.001
cold period	1.507	0.6719	0.025
LRT = 4.663; d.f. = 1; $P = 0.031$; residual deviance = 68.715; residual d.f. = 85; PCC = 0.805; Kappa = 0.255			

For all cases, the random effect of the neighborhood was deleted because it did not improve the model. Therefore, generalized linear models were applied. LRT: likelihood-ratio test, d.f.: degrees of freedom, PCC: proportion of correct classifications, SE: standard error.

*Marginal significant values.

Table 4. Analysis of helminth abundance in relation to hosts and environmental variables in Gran La Plata, from 2014 to 2015 (see text). In all cases, variables were introduced in models when they produced a significant deviance ($P < 0.05$). The error distribution used for each model is reported in parentheses. LRT: likelihood ratio test, d.f.: degrees of freedom.

A) <i>Nippostrongylus brasiliensis</i> abundance in <i>Rattus norvegicus</i> ~ sex (negative binomial)*			
Explanatory variables	Coefficients	SE	P -value
intercept (Females)	2.780	0.580	<0.001
males	1.386	0.685	0.043
LRT = 2.648; d.f. = 1; $P = 0.104$; residual deviance = 251.3; residual d.f. = 24			
B) <i>Strobilocercus fasciolaris</i> abundance ~ host species + 1 + neighborhood (Poisson)			
Explanatory variables	Coefficients	SE	P -value
intercept (<i>M. musculus</i>)	-2.143	0.434	<0.001
<i>R. norvegicus</i>	1.320	0.368	<0.001
<i>R. rattus</i>	1.753	0.434	<0.001
LRT = 19.546; d.f. = 2; $P < 0.001$; residual deviance = 174.63; residual d.f. = 132			
C) <i>S. fasciolaris</i> abundance in <i>R. norvegicus</i> ~ seasons + 1 + neighborhood (Poisson)			
Explanatory variables	Coefficients	SE	P -value
intercept (warm period)	-2.143	0.434	<0.001
cold period	1.320	0.368	<0.001
LRT = 7.730; d.f. = 1; $P = 0.005$; residual deviance = 34.919; residual d.f. = 25			
D) <i>S. fasciolaris</i> abundance in <i>Mus musculus</i> ~ seasons + 1 + neighborhood (Poisson)			
Explanatory variables	Coefficients	SE	P -value
intercept (warm period)	-2.340	1.030	0.023
cold period	2.112	1.024	0.039
LRT = 6.050; d.f. = 1; $P = 0.014$; residual deviance = 60.552; residual d.f. = 84			

*Marginal significant values.

2015). If these microenvironments are considered separately, *R. norvegicus* could be expected to share its parasite fauna with *M. musculus* rather than with *R. rattus*, given that those two species live in contact with the ground and water, while the latter lives in higher strata (Coto, 2015; Cavia *et al.*, 2019a, 2019b, 2019c). However, our results show that the parasite fauna of both *Rattus* species are similar, and different from those of *M. musculus* (fig. 2; table 2), in agreement with other studies in which a phylogenetic conservatism is observed, with two closely related host species tending to harbor more similar parasite fauna than two distantly related species (Poulin, 2014).

None of the other host and environmental characteristics explained the structure of the parasite assemblage in each host individual. Future studies with bigger sample sizes, conducted in more neighborhoods, would help to understand the importance of these characteristics in parasite assemblages that have been previously documented at population level (Gómez Villafañe *et al.*, 2008; Lovera *et al.*, 2017).

Notably, pathogen and parasite richness were similar among all the host species, despite the differences in parasite fauna composition between *Rattus* species and *M. musculus* (table 2). Moreover, all host species presented pathogen and parasite taxa with health implications: five in *R. norvegicus* and *R. rattus* and two in *M. musculus*, proving the risk of infection that is found when there is a close coexistence between urban rodents and the human population.

Prevalence values match those of previous studies and confirm urban rodents as important reservoirs and sources of infection of

pathogens and parasites (Milazzo *et al.*, 2003; Panti-May *et al.*, 2015). At the same time, the higher prevalence of parasites and pathogens in *Rattus* species in comparison to *M. musculus* agrees with previous studies (Milazzo *et al.*, 2003; Panti-May *et al.*, 2015) and may be explained from the host abundance and host community structure (Johnson *et al.*, 2015; Lovera *et al.*, 2017).

In terms of the prevalence and abundance of each pathogen and parasite taxon at an individual level, different results were reached. Host characteristics were less important than environmental ones to explain individual infection, which agrees with recent studies (Panti-May *et al.*, 2015). The trends of difference between the abundances of *N. brasiliensis* in *R. norvegicus* and *S. obvelata* in *M. musculus* suggest the need for exhaustive studies to provide more data. In relation to the environmental changes, higher infestation levels were observed in the cold season for *N. brasiliensis* and *S. fasciolaris*. For the case of *N. brasiliensis* in *R. norvegicus*, these results disagree with previous studies showing this parasite as the most prevalent species in countries with warm temperatures (Calero *et al.*, 1950; De León, 1964; Waugh *et al.*, 2006) and with laboratory studies that report that the best temperatures for its development are 22–30°C (Haley, 1962). The association between *S. fasciolaris* in *R. norvegicus* and *M. musculus* suggests that, when their energy requirements increase, individuals may increase their home range, thus presenting a higher risk of infection.

In relation to the presence of streams, although the life cycles of neither *N. brasiliensis* nor *S. ratti* include stages that depend on water bodies, the microenvironments of the banks of streams may

be favorable for the development of the infective stage of both parasite species. This topic needs to be more deeply investigated. Also, future studies need to include other factors, as the variations in infection of some parasites and pathogens were not explained in our study.

This study confirms the role that urban rodents play as reservoirs and infection sources of zoonotic parasites and pathogens. It is one of the few studies that include the pathogen and parasite assemblage in the entire rodent assemblage in various neighborhoods of a city in South America. Our results suggest the need for stronger public health policies, particularly in the field of zoonosis. The results are valuable given that the peripheral neighborhoods of our region have different urban characteristics from other cities of the world and, consequently, different ecological and epidemiological scenarios. During the survey, we observed the closeness with which humans and rodents coexist, even recording rodent attacks (bites) to children while sleeping, reflecting the permanent risk people face.

In many similar cities of Latin America, peripheral neighborhoods are growing dramatically, with characteristics that are a constant health risk to the population (Soares et al., 2010; Chaiblich et al., 2017). Despite limitations related to sampling and consequent analyses, plus logistical issues involved in conducting these kind of studies in such urban areas (Childs et al., 1998; Cavia et al., 2012), our results may serve as a starting point for future studies for each specific zoonotic taxon, and/or for studies with longer sampling periods in larger areas, also using different methods to contribute to greater knowledge about rodent population sizes and variations. Lastly, surveys that include synanthropic animals as reservoirs and/or vectors of pathologies at a regional level should be considered as pieces of the puzzle that help to better understand these issues at a global level (Schapira, 2001).

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0022149X21000523>

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Author contributions. BF was in charge of the rodent sampling, prospection and identification of parasites and pathogens. RC carried out the statistical design and analyses. MRR coordinated the project and participated in rodent sampling as well as in the identification of parasites and pathogens. JMU and AD participated in rodent sampling and carried out molecular analyses for the identification of protozoa. GTN coordinated and managed the project. All authors reviewed the results and approved the final version of the manuscript.

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References

- Agudelo-Flórez P, Londoño AF, Quiroz VH, Ángel JC, Moreno N, Loaiza ET and Rodas JD (2009) Prevalence of *Leptospira* spp. in urban rodents from a groceries trade center of Medellín, Colombia. *American Journal of Tropical Medicine and Hygiene* **81**(5), 906–910.
- Anderson RC, Chabaud AG and Willmott S (2009) *Keys to the nematode parasites of vertebrates: Archival volume*. Wallingford, CAB International.
- Arneberg P (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**(1), 88–94.
- Battersby S, Parsons R and Webster J (2002) Urban rat infestations and the risk to public health. *International Journal of Environmental Health Research* **1**, 57–65.
- Behnke JM, Harris PD, Bajer A, Barnard CJ, Sherif N and Cliffe L (2004) Variation in the helminth community structure in spiny mice (*Acomys dimidiatus*) from four montane wadis in the St Katherine region of the Sinai Peninsula in Egypt. *Parasitology* **129**(3), 379–398.
- Bonnefoy X, Kampen H and Sweeney K (2008) *Public health significance of urban pests*. Copenhagen, World Health Organization.
- Bordes F, Blasdel K and Morand S (2015) Transmission ecology of rodent-borne diseases: new frontiers. *Integrative Zoology* **10**(5), 424–435.
- Bradley CA and Altizer S (2007) Urbanization and the ecology of wildlife diseases. *Trends in Ecology and Evolution* **22**(2), 95–102.
- Burnham KP and Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. vol. 65, no 1, p. 23–35. Fort Collins, Springer Science & Business Media.
- Bush AO, Lafferty KD, Lotz JM and Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* **83**(4), 575–583.
- Calero C, Ortiz O and Souza L (1950) Helminths in rats from Panama city and suburbs. *Journal of Parasitology* **36**(5), 426.
- Cavia R, Cueto G and Suárez O (2009) Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landscape and Urban Planning* **90**(1–2), 11–19.
- Cavia R, Cueto GR and Suárez OV (2012) Techniques to estimate abundance and monitoring rodent pests in urban environments. pp. 147–172 in Marcelo L. Larramendy, Sonia Soloneski (Eds) *Integrated pest management and pest control—current and future tactics*. Rijeka, InTech.
- Cavia R, Gómez Villafaña I, Suárez OV, Gómez MD, Sánchez J and León V (2019a) *Mus musculus* Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina: SAREM. Available at <http://cma.sarem.org.ar> (accessed 30 November 2021).
- Cavia R, Gómez Villafaña I, Suárez OV, Piudo L, Sánchez J and Monteverde M (2019b) *Rattus norvegicus* Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina: SAREM. Available at <http://cma.sarem.org.ar> (accessed 30 November 2021).
- Cavia R, Gómez Villafaña I, Suárez OV, Piudo L, Sánchez J and Monteverde M. (2019c) *Rattus rattus*. Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina: SAREM. Available at <http://cma.sarem.org.ar> (accessed 30 November 2021).
- Chace JF and Walsh JJ (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning* **74**(1), 46–69.
- Chaiblich JV, Lima MLDS, Oliveira RFD, Monken M and Penna MLF (2017) Spatial study of risks to leptospirosis in the municipality of Rio de Janeiro (RJ). *Saúde em Debate* **41**(SPE2), 225–240.
- Childs JE, McLafferty SL, Sadek R, Miller GL, Khan AS, DuPree ER and Glass GE (1998) Epidemiology of rodent bites and prediction of rat infestation in New York city. *American Journal of Epidemiology* **148**(1), 78–87.
- Costa F, Porter FH, Rodrigues G, Farias H and de Faria MT (2014) Infections by *Leptospira interrogans*, Seoul virus, and *Bartonella* spp. among Norway rats (*Rattus norvegicus*) from the urban slum environment in Brazil. *Vector-Borne Zoonotic Diseases* **14**(1), 33–40.
- Coto H (2015) *Protocolos para la vigilancia y control de roedores sinantrópicos*. Washington, D.C., Organización Panamericana de la Salud.
- De León D (1964) Helminth parasites of rats in San Juan, Puerto Rico. *J Parasitol* **50**(3), 478–479.
- Dellarupe A, Fitte B, Pardini L and Campero LM (2019) *Toxoplasma gondii* and *Neospora caninum* infections in synanthropic rodents from Argentina. *Revista Brasileira de Parasitologia Veterinaria* **28**(1), 113–118.

- de Masi E, Vilaça P and Razzolini MTP (2009) Environmental conditions and rodent infestation in Campo Limpo district, Sao Paulo municipality, Brazil. *International Journal of Environmental Health Research* **19**(1), 1–16.
- Deter J, Chaval Y, Galan M, Berthier K, Salvador AR and Garcia JCC (2007) Linking demography and host dispersal to *Trichuris arvicolae* distribution in a cyclic vole species. *International Journal of Parasitology* **37**(7), 813–824.
- Dubey J and Frenkel J (1998) Toxoplasmosis of rats: a review, with considerations of their value as an animal model and their possible role in epidemiology. *Veterinary Parasitology* **77**(1), 1–32.
- Easterbrook JD, Kaplan J, Vanasco N, Reeves W, Purcell R and Kosoy M (2007) A survey of zoonotic pathogens carried by Norway rats in Baltimore, Maryland, USA. *Epidemiological Infection* **135**(7), 1192–1199.
- Fitte B and Kosoy M (2021) Presence of *Leptospira* spp. and absence of *Bartonella* spp. in urban rodents of Buenos Aires province, Argentina. *Pathogens and Global Health*, 1–8.
- Fitte B, Robles M, Dellarupe A, Unzaga JM and Navone GT (2017) *Taenia taeniformis* larvae (*Strobilocercus fasciolaris*) (Cestoda: Cyclophyllidae) from commensal rodents in Argentina: potential sanitary risk. *Mastozoología Neotropical* **24**(1), 227–233.
- Franjola T, Soto G and Montefusco A (1995) Prevalencia de infección por protozoos en roedores sinantrópicos de la ciudad de Valdivia en Chile. *Boletín Chileno de Parasitología* **50**(3/4), 66–72.
- Gibbons LM (2010) *Keys to the nematode parasites of vertebrates: Supplementary volume (Vol. 10)*. Wallingford, CAB International.
- Gómez Villafaña IE, Robles MR and Busch M (2008) Helminth communities and host–parasite relationships in Argentine brown rat (*Rattus norvegicus*). *Helminthologia* **45**(3), 127–130.
- Gómez Villafaña IE, Cavia R, Vadell MV, Suárez OV and Busch M (2012) Differences in population parameters of *Rattus norvegicus* in urban and rural habitats of central Argentina. *Mammalia* **77**(2), 187–193.
- Guerreiro Martins NB, Robles Mdr and Navone GT (2014) Distribución geográfica de cestodes Hymenolepididae de *Oxymycteris rufus* (rodentia - cricetidae) en Argentina. *Revista Argentina de Parasitología* **2**, 16–24.
- Haley AJ (1962) Biology of the rat nematode, *Nippostrongylus brasiliensis* (Travassos, 1914). II. Preparasitic stages and development in the laboratory rat. *Journal of Parasitology* **48**(1), 13–23.
- Hancke D and Suárez OV (2017) Helminth diversity in synanthropic rodents from an urban ecosystem. *EcoHealth* **14**(3), 603–613. doi: 10.1007/s10393-017-1239-8
- Hancke D, Navone GT and Suarez OV (2011) Endoparasite community of *Rattus norvegicus* captured in a shantytown of Buenos Aires city, Argentina. *Helminthologia* **48**(3), 167–173.
- Hassell JM, Begon M, Ward MJ and Fèvre EM (2017) Urbanization and disease emergence: dynamics at the wildlife–livestock–human interface. *Trends in Ecology and Evolution* **32**(1), 55–67.
- Himsworth CG, Parsons KL, Jardine C and Patrick DM (2013) Rats, cities, people, and pathogens: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. *Vector-Borne Zoonotic Diseases* **13**(6), 349–359.
- Jittapalpong S, Herbretau V, Hugot JP, Arresrisom P, Karnchanabanthoeng A, Rerkamnuaychoke W and Morand S (2009) Relationship of parasites and pathogens diversity to rodents in Thailand. *Kasetsart Journal of Natural Science* **43**, 106–117.
- Johnson PT, De Roode JC and Fenton A (2015) Why infectious disease research needs community ecology. *Science* **349**(6252), 1259504.
- Kataranovski M, Mirkov I, Belij S, Popov A, Petrović Z, Gačić Z and Kataranovski D (2011) Intestinal helminths infection of rats (*Rattus norvegicus*) in the Belgrade area (Serbia): the effect of sex, age and habitat. *Parasite* **18**(2), 189–196.
- Khalil LF, Jones A and Bray RA (1994) *Keys to the cestode parasites of vertebrates*. Wallingford, CAB International.
- Kosoy M, Khlyap L, Cosson JF and Morand S (2015) Aboriginal and invasive rats of genus *Rattus* as hosts of infectious agents. *Vector-Borne Zoonotic Diseases* **15**(1), 3–12.
- Kumar S, Stecher G, Li M, Knyaz C and Tamura K (2018) MEGA x: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35**(6), 1547–1549.
- Landaeta-Aqueveque CA, Robles MD and Cattán PE (2007) Helmintofauna del roedor *Abrothrix olivaceus* (Sigmodontinae) en áreas sub-urbanas de Santiago de Chile. *Parasitología Latinoamericana* **62**(3-4), 134–141.
- Lavikainen A, Iwaki T, Haukisalmi V, Konyaev SV, Casiraghi M, Dokuchaev NE and Nakao M (2016) Reappraisal of *Hydatigera taeniaeformis* (Batsch, 1786) (Cestoda: Taeniidae) *sensu lato* with description of *Hydatigera kamiyai* n. sp. *International Journal for Parasitology* **46**(5-6), 361–374.
- Legendre P and Legendre L (2012) *Numerical Ecology*. 990 pages. Amsterdam, Elsevier.
- Lobos G, Ferres M and Palma RE (2005) Presencia de los géneros invasores *Mus* y *Rattus* en áreas naturales de Chile: un riesgo ambiental y epidemiológico. *Revista Chilena de Historia Natural* **78**(1), 113–124.
- Lovera R, Fernández MS, Jacob J, Lucero N, Morici G, Brihuega B and Cavia R (2017) Intrinsic and extrinsic factors related to pathogen infection in wild small mammals in intensive milk cattle and swine production systems. *PLoS Neglected Tropical Diseases* **11**(6), e0005722. <https://doi.org/10.1371/journal.pntd.0005722>.
- Lykins J, Wang K, Wheeler K, Clouser F, Dixon A, El Bissati K and McLeod R (2016) Understanding toxoplasmosis in the United States through “large data” analyses. *Reviews of Infectious Diseases* **63**(4), 468–475.
- Meerburg BG, Singleton GR and Kijlstra A (2009) Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology* **35**(3), 221–270.
- Milazzo C, de Bellocq JG, Cagnin M, Casanova JC, Di Bella C, Feliu C and Santalla F (2003) Helminths and ectoparasites of *Rattus rattus* and *Mus musculus* from Sicily, Italy. *Comparative Parasitology* **70**(2), 199–205.
- Mills JN, Ellis BA, Mckee KT, Maiztegui JI and Childs JE (1991) Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. *Journal of Mammalogy* **72**(3), 470–479.
- Ministerio de Salud de la Nación (MSAL) (2014) Dirección de Epidemiología. Leptospirosis. Guía para el Equipo de Salud. Cdad. Autónoma de Bs. As., Argentina: Dirección de Epidemiología—Ministerio de Salud de la Nación; ISSN 1852-1819 / ISSN 1852-219X (online).
- Morand S and Poulin R (1998) Density, body mass and parasite species richness of terrestrial mammals. *Ecology and Evolution* **12**(6), 717–727.
- Moré G, Pardini L, Basso W, Machuca M, Bacigalupe D, Villanueva M and Venturini L (2010) Toxoplasmosis and genotyping of *Toxoplasma gondii* in *Macropus rufus* and *Macropus giganteus* in Argentina. *Veterinary Parasitology* **169**(1–2), 57–61.
- Muradian V, Ferreira LR, Lopes EG, de Oliveira Esmerini P, de Jesus Pena HF, Soares RM and Gennari SM (2012) A survey of *Neospora caninum* and *Toxoplasma gondii* infection in urban rodents from Brazil. *Journal of Parasitology* **98**(1), 128–134.
- Nagorsen D (2005) *Rodents and lagomorphs of British Columbia* (Vol. 4). British Columbia Royal BC Museum Victoria.
- Oksanen J, Blanchet FG, Kindt R, Oksanen MJ and Suggests M (2013) Package ‘vegan’. Community Ecology Package Version, 2, 0-0.
- Panti-May J, Hernández-Betancourt S, Rodríguez-Vivas R and Robles MR (2015) Infection levels of intestinal helminths in two commensal rodent species from rural households in Yucatan, Mexico. *Journal of Helminthology* **89**(1), 42–48.
- Panti-May J, Digiani MC, Palomo-Arjona EE, Gurubel-González YM, Navone GT, Williams C and Robles M (2018) A checklist of the helminth parasites of sympatric rodents from two Mayan villages in Yucatán, México. *Zootaxa* **4403**(3), 495–512.
- Poulin R (2004) Macroecological patterns of species richness in parasite assemblages. *Basic and Applied Ecology* **5**(5), 423–434.
- Poulin R (2014) Parasite biodiversity revisited: frontiers and constraints. *International Journal of Parasitology* **44**(9), 581–589.
- Poulin R and George-Nascimento M (2007) The scaling of total parasite biomass with host body mass. *International Journal of Parasitology* **37**(3-4), 359–364.
- Puckett EE, Park J, Combs M, Blum MJ, Bryant JE, Caccone A and Himsworth CG (2016) Global population divergence and admixture of the brown rat (*Rattus norvegicus*). *Proceedings of the Royal Society B: Biological Sciences* **283**(1841), 20161762.
- R Core Team (2013) *R: a language and environment for statistical computing*. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0.

- Robles MdR, Navone GT and Villafañe IEG** (2008) New morphological details and first records of *Heterakis spumosa* and *Syphacia muris* from Argentina. *Comparative Parasitology* **75**(1), 145–149.
- Rothenburger JL, Himsworth CH, Nemeth NM, Pearl DL and Jardine CM** (2017) Environmental factors and zoonotic pathogen ecology in urban exploiter species. *EcoHealth* **14**(3), 630–641.
- Schapira MFP** (2001) Fragmentación espacial y social: conceptos y realidades. *Revista de la Facultad Latinoamericana de Ciencias Sociales, Sede México* **9** (19), 33–56.
- Seifollahi Z, Sarkari B, Motazedian MH, Asgari Q, Ranjbar MJ and Abdolahi Khabisi S** (2016) Protozoan parasites of rodents and their zoonotic significance in Boyer–Ahmad District, southwestern Iran. *Veterinary Medicine International* **2016**. doi:10.1155/2016/3263868.
- Soares TSM, Latorre MDRDDO, Laporta GZ and Buzzar MR** (2010) Spatial and seasonal analysis on leptospirosis in the municipality of São Paulo, Southeastern Brazil, 1998 to 2006. *Revista de Saúde Pública* **44**(2), 283–291.
- Swain K, Routray A, Panigrahi S, Rath AP, Sahoo S and Ganguly S** (2016) *Nippostrongylus brasiliensis*, an experimental model: a review. *International Journal* **2**(2), 37.
- Telfer S, Lambin X, Birtles R, Beldomenico P, Burthe S, Paterson S and Begon M** (2010) Species interactions in a parasite community drive infection risk in a wildlife population. *Science* **330**(6001), 243–246.
- Thienpont D, Rochette F and Vanparijs O** (1979) *Diagnóstico de las helmintiasis por medio del examen coprológico* (Vol. V617 THId). Beerse, Janssen Research Foundation.
- Titus K, Mosher JA and Williams BK** (1984) Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* **111**(1), 1–7.
- Travassos L** (1914) Contribuições para o conhecimento da fauna helmintológica brasileira: III. *Memórias Do Instituto Oswaldo Cruz* **6**, 150–162.
- Traweger D and Slotta-Bachmayr L** (2005) Introducing GIS-modelling into the management of a brown rat (*Rattus norvegicus* Berk.) (Mamm. Rodentia Muridae) population in an urban habitat. *Journal of Pest Science* **78**(1), 17–24.
- Traweger D, Travnitzky R, Moser C, Walzer C and Bernatzky G** (2006) Habitat preferences and distribution of the brown rat (*Rattus norvegicus* Berk.) in the city of Salzburg (Austria): implications for an urban rat management. *Journal of Pest Science* **79**(3), 113–125.
- Vadell M, Villafañe IG and Cavia R** (2014) Are life-history strategies of Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*) dependent on environmental characteristics? *Wildlife Research* **41**(2), 172–184.
- Wardle MA and Mcleod JA** (1952) *The zoology of tapeworms*. 780 pp. Minneapolis, University of Minnesota Press.
- Waugh CA, Lindo JF, Foronda P, Ángeles-Santana M, Lorenzo-Morales J and Robinson RD** (2006) Population distribution and zoonotic potential of gastrointestinal helminths of wild rats *Rattus rattus* and *R. norvegicus* from Jamaica. *Journal of Parasitology* **92**(5), 1014–1019.
- Zain SNM, Behnke JM and Lewis JW** (2012) Helminth communities from two urban rat populations in Kuala Lumpur, Malaysia. *Parasites Vector* **5**(1), 47.
- Zuur A, Ieno EN, Walker N, Saveliev AA and Smith GM** (2009) *Mixed effects models and extensions in ecology with R*. New York, Springer.