CrossMark

ORIGINAL PAPER

Prevalence and intensity of fleas parasitizing an isolated population of screaming hairy armadillo in Buenos Aires province, Argentina: host-related factors and temporal dynamics

M. Cecilia Ezquiaga[1] · Agustín M. Abba[1] · Guillermo H. Cassini[2] · Marcela Lareschi[1]

Abstract Fleas (Siphonaptera) of an isolated population of *Chaetophractus vellerosus* (Mammalia: Xenarthra) from Magdalena (Buenos Aires province) were studied, and their presence was associated with host-related factors (age, sex, weight, size, and physical condition) and temporal dynamics (seasonality and year). Three species of fleas were identified: *Polygenis* (*Polygenis*) *platensis* (Rhopalopsyllidae), *Tunga penetrans* (Tungidae), and *Pulex irritans* (Pulicidae). Prevalences were significant for year, season, and physical condition. Intensities were significantly different for year, physical condition, and weight. The intensities of fleas were higher in 2009 than in other years, probably because of lower rainfall than the annual average leading to extremely dry climatic conditions in 2008. Intensities decreased in individuals with major body weight and increased in individuals with poor physical condition. In this study, the dynamics of the flea community associated with an armadillo population is analyzed for the first time taking into account host-related factors and temporal dynamics, and also how these factors influence the community.

✉ M. Cecilia Ezquiaga
  cecilia@cepave.edu.ar

1 Centro de Estudios Parasitológicos y de Vectores (CEPAVE), CONICET, UNLP, Calle 120 s/n entre 60 y 64, La Plata, Argentina

2 División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET. Departamento de Ciencias Básicas, Universidad Nacional de Luján, Rutas 5 y 7, 6700 Luján, Argentina

Introduction

Fleas represent a relatively small order of highly specialized holometabolous insects. All adult fleas are obligatory haematophagous parasites of mammals and birds. Fleas are cosmopolitan and have the ability to inhabit different environments. To date, 127 species and subspecies belonging to 11 different families have been recorded from Argentina (Lareschi et al. 2016), of which only a few are known from armadillos (Del Ponte and Riesel 1939; Mauri and Navone 1993; Ezquiaga et al. 2008, 2015; Lareschi et al. 2010).

The screaming hairy armadillo, *Chaetophractus vellerosus*, is found in southern Bolivia, northwestern Paraguay, and central Argentina, in sandy soils of arid and semi-arid regions (Abba et al. 2011). Populations living in high-altitude environments of southern Peru, central Bolivia, northern Chile, and northern Argentina were previously considered to be a single, separate species, the Andean hairy armadillo (*Chaetophractus nationi*), but were recently synonymized with *C. vellerosus* (Abba et al. 2015). In Argentina, the main population of the screaming hairy armadillo is located to the north and center of the country, and its distribution does not exceed 62° 50′ W to the east and 39° 20′ S to the south. Another population is located in the northeast of the Pampa region, separated from the main population by about 500 km, and has an approximate extension of 34° 56′ S to 36° S. The latter population is associated with the shelly beach ridges on the coast of the Río de la Plata estuary (Carlini and Vizcaíno 1987; Abba et al. 2011). Until now, several species of fleas were found associated with this armadillo: *Malacopsylla grossiventris*, *Phthiropsylla agenoris* (Malacopsyllidae),

Springer

Tunga perforans, *T. penetrans*, *T. terasma*, and *Polygenis* (*Polygenis*) *platensis* (Ezquiaga et al. 2008, 2015; Lareschi et al. 2010). Previous studies only discussed the geographical and host distributions of the fleas of armadillos in Argentina. The aim of the present work is to survey the fleas of an isolated population of *C. vellerosus* from Magdalena (Buenos Aires province) and associate their presence with host-related factors (age, sex, weight, size, and physical condition) and temporal dynamics (seasonality and year).

Material and methods

Sampling was conducted during the winter and summer seasons of 2006–2007 and 2009–2012 in a 100 ha cattle farm located in Magdalena, province of Buenos Aires, Argentina (35°10′ S, 57°20′ W). Armadillos were captured by hand or using nets and handled minimally, to reduce stress to the animal. Armadillos were sexed, measured, weighed, marked, and released. Forceps were used to collect fleas. The field study was carried out under permission issued by Ministerio de Asuntos Agrarios, provincia de Buenos Aires, Argentina (Exp. N°2578-1404/05 and Exp. N°22300-24/2008).

Upon collection, fleas were stored in 96% ethanol. In the laboratory, they were cleared in KOH 10%, dehydrated in an increasing series of ethanol dilutions (80–100%), diaphanized in eugenol, and mounted in Canada balsam for later identification with an optic microscope.

A total of 385 armadillos were captured, and 146 were recaptured. Most (88) recaptures were second recaptures. In summer 194 individuals, and in winter 191 were captured as follows: 90 in 2006; 91 in 2007; 57 in 2009; 73 in 2010; 54 in 2011; and 20 in 2012. The animals comprised of 200 females and 185 males in which age was estimated with body length and weight, yielding division into infants ($n = 17$), juveniles ($n = 71$), and adults ($n = 297$). In addition, physical condition was assessed by an iterative outlier test on an ordinary-least-squares (OLS) regression of log10-transformed weight and body length (Ezquiaga et al. 2014). Outliers in each iteration were discarded to fit the OLS regression in the next step. Outliers with positive externally studentized residuals were assigned to a good condition, whereas those with negative externally studentized residuals were assigned to a poor condition. The procedures were concluded when outliers were no longer detected. The remaining observations were assigned then to a normal condition. Prevalence, mean abundance (MA) and mean intensity (MI) follow Bush et al. (1997).

Prevalences were analyzed by means of contingency tables using the log-likelihood ratio chi-square statistic (Zar 2009) and applying the loglm function of MASS 7.3-45 R package (Venables and Ripley 2002). The first step was to evaluate multidimensional contingency tables for mutual independence (i.e., no interactions) among the year, season, age, sex, and physical condition variables. Partial independence was tested whenever mutual independence was significant. According to the results of the multidimensional analyses performed, all variables have been tested by means of two-dimensional contingency tables.

Generalized linear mixed models (GLMM) were used to evaluate differences in the intensities of the total number of fleas related to host factors and temporal dynamics taking into account the repeated measures by recaptures. The number of fleas in the individual host (count data) as the response variable, and year, age (categorical ordinal sequential), season, sex (categorical nominal), body length, and weight (continuous) as explanatory variables. A logarithmic link function was used since all predicted values had to be positive. We obtained the 63 possible combinations of six explanatory variables from six to one. The models which fit better than the null model by means of the Akaike information criterion (AIC) were selected using the log-likelihood ratio test (Zuur et al. 2009). To this end, we calculated the weighted AIC (wAIC) (Akaike 1978; Burnham and Anderson 2002), which can be considered the conditional probability of each model to be the best (Wagenmakers and Farrell 2004). In addition, when the selected model has a wAIC lower than 0.5 or two or more competing models have similar wAIC values, an averaged model was computed using the MuMIn R package (Barton 2016). Additionally, we computed simple GLMMs with the number of fleas in the host (count data) as the response variable and each of the six explanatory variables, plus the physical condition. To evaluate error distribution (Poisson or negative binomial), as well as overdispersion on the count or zero data, we visualized flea counts in Cleveland dot plots and histograms. If graphical analyses were not conclusive, we obtained models using different error distribution (Poisson and negative binomial GLMM) and accounting for zero-inflated data (zero-inflated GLMM), and later compared them using the likelihood ratio test (LRT) (Zuur et al. 2009). The measurement of "false zeros" (absence of fleas recorded when fleas are present) might be random or related to sampling protocols, but there are no biological reasons to believe that the explanatory variables have an effect. Therefore, in all zero-inflated GLMM, a constant was used to model false-zero probability on the count data. All GLMM and statistics analyses were performed with the lmtest 0.9-33 R package (Zeileis and Hothorn 2002), multcomp 1.4-6 R package (Hothorn et al. 2008), and pscl 1.04.4 R package (Zeileis et al. 2008) and lme4 1.1-12 (Bates et al. 2015) on R 3.4.1 statistical software (R Development Core Team 2017).

Results

Of 385 *C. vellerosus* captured, 69 were parasitized with fleas (prevalence 17.92%) and identified as *Polygenis* (*P.*) *platensis* ($n = 151$; MA = 0.39; MI = 2.43), *T. penetrans* ($n = 28$;
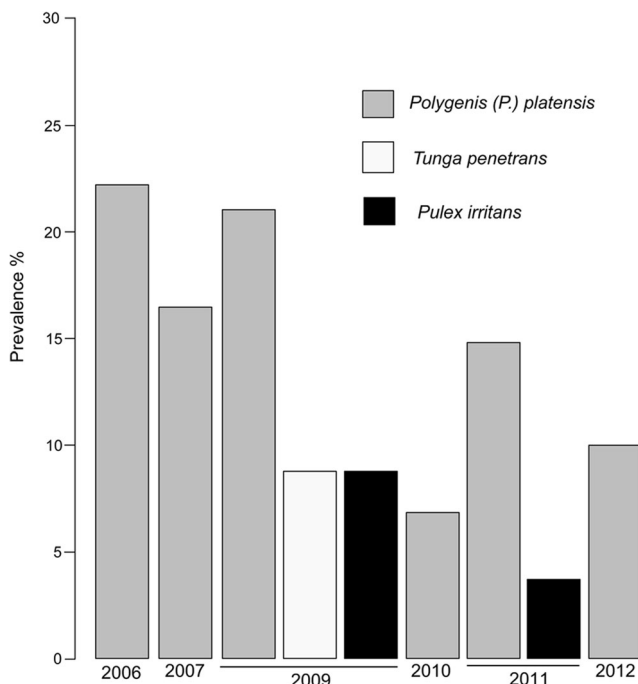
Fig. 1 Prevalence of three flea species partitioned by year, on *Chaetophractus vellerosus* from Magdalena, province of Buenos Aires, Argentina

MA = 0.07; MI = 5.60) and *Pulex irritans* ($n = 10$; MA = 0.02; MI = 1.43). *Polygenis* (*P.*) *platensis* had the highest prevalence (16.10%), whereas *Pu. irritans* and *T. penetrans* showed very low values (1.82 and 1.30%, respectively). With the exception of two cases of *Pu. irritans* registered in the summer of 2011, all findings of *Pu. irritans* and *T. penetrans* were in the summer of 2009 with a prevalence 8.77%, which was lower than the 21.05% of *P.* (*P.*) *platensis* (Fig. 1).

The iterative regression analyses between log-transformed weight and body length showed no bias when regression was fit to the origin. This procedure resulted in a significant regression ($F_{(1, 307)} = 8.775e + 05$; p value < 0.0001) with an elevated coefficient of determination ($R^2 = 0.9997$) and obtained the equation $\log_{10}$ (weight) = 1.256 $\log_{10}$ (body length). This iterative process found 77 outliers: 40 showed positive externally studentized residuals (i.e., good condition) and 37

revealed negative externally studentized residuals (i.e., poor condition). The remaining 308 observations were assigned to a normal condition as no outliers were detected.

The contingency tables showed that multidimensional analyses were significant for all mutual independence tests for the prevalence of all species of fleas grouped plus five variables (Table 1); all five combinations of prevalence plus four variables; and ten possible combinations of prevalence plus three variables (Supplementary material 1). Consequently, the independence of the five variables was tested using two-dimensional contingency tables, which were significant for year, season and physical condition (i.e., dependence of the prevalence on these variables) (Table 1).

The GLMM analyses resulted in three selected models in which the intensities of the total number of fleas are explained by a combination of five and four explanatory variables (year, season, age, and log-transformed body and weight; Table 2). Each of these models explains ~ 3% of total deviance and has a 13% probability of being the best model from the 29 significantly different from the null model (Table 2). So an averaged model was obtained from these three GLMMs (Table 2). Simple GLMM results are summarized in Table 3. From the six simple GLMMs, only year, physical condition, and weight were significantly different from the null model. Intensities of fleas were higher in 2006, 2009, and 2011 than in the other years, with 2010 the year with lowest intensities (Fig. 2). Intensities of fleas decreased in those individuals with greater body weight and increased in those individuals with poor physical condition (Fig. 3).

Discussion

Fleas vary greatly in host specificity, from being highly specific to highly host-opportunistic. Host-opportunistic fleas are usually habitat-dependent rather than host-dependent (Krasnov et al. 1997). They occupy a certain habitat where they exploit a number of ecologically similar host species (Medvedev and Krasnov 2006). *Pulex irritans* in Argentina

Table 1 Contingency table with independence tests for the prevalence of fleas plus five explanatory variables in *Chaetophractus vellerosus* from Magdalena, province of Buenos Aires, Argentina.

Independence Test	Dimensions	Variables	χ^2	d.f.	p value
Mutual	$2 \times 6 \times 2 \times 3 \times 2 \times 3$	Prev + year + season + age + sex + p.cond	494.65	419	0.00632
Two-dimensional	2×6	Prev + year	16.0308	5	0.00676
Two-dimensional	2×2	Prev + season	6.8096	1	0.00907
Two-dimensional	2×3	Prev + age	0.6047	2	0.7391
Two-dimensional	2×2	Prev + sex	0.7066	1	0.4006
Two-dimensional	2×3	Prev + physical condition	6.5825	2	0.0372

Prev prevalence; *P.cond* physical condition

Table 2 General Linear Mixed Models selected by Akaike information criterion (AIC)

Selected models	AIC	w (n)	PsR^2	χ^2	p-Bonf.	d.f.	C.S.	dist. Error
Year + season + age + body	576.571	0.133 (29)	2.705	42.75	< 0.0002	9	0.192	*Negative binomial*
Year + season + body + weight	576.667	0.123 (29)	3.763	40.66	< 0.0002	8	0.192	*Negative binomial*
Year + season + age + body + weight	576.517	0.137 (29)	3.214	44.81	< 0.0002	10	0.198	*Negative binomial*
Averaged model	Intercept	Explicative variables coefficients						
Year + season + weight + body + age	−5.197 (15.36)	−0.677(0.432) Year2007 + 1.777(0.744) Year2009 −1.53(0.661) Year2010 + 0.343(0.518) Year2011 −1.566(0.951) Year2012 + 0.505(0.379) SeasonWinter −8.028(2.918) Weight + 7.253(7.668) Body −1.402(1.31) AgeC −0.435(0.493) AgeJ						

w weighted Akaike; *p-Bonf* probability after Bonferroni correction; *d.f.* degree of freedom; *C.S.* overdispersion parameter. AIC null model = 601.327

parasitizes carnivores, rodents, marsupials, lagomorphs, and cervids (Lareschi et al. 2010, 2016). We found this flea associated with *C. vellerosus* for the first time. Taking into account that *Pu. irritans* is an opportunistic flea, its occurrence can be explained by the presence of humans and domestic animals in the area, especially dogs.

Tunga penetrans in Argentina has been recorded parasitizing humans, domestic animals, and a few species of dasypodids, including *Chaetophractus villosus*, *C. vellerosus*, *Dasypus hybridus*, and *Tolypeutes matacus* (González et al. 2003; Ezquiaga et al. 2008; Ezquiaga 2013). In the region surrounding our study area, this flea was reported on *C. villosus* and *D. hybridus* (Ezquiaga et al. 2008).

Polygenis (*P.*) *platensis* parasitizes a variety of hosts, including birds and humans, but most records are from marsupials and rodents (Lareschi et al. 2016). This flea was also recorded parasitizing *C. vellerosus* in the study area (Ezquiaga et al. 2008). Bossard (2006) found that the richness of flea species on a mammal was not determined by balanced immigration and extinction but by the social interactions of the mammal, such as shared nests and predation. In contrast, the prevalence of a flea species on a host was determined by how closely related the host was to the usual host of the flea. If the host was the usual one, or closely related to the usual host, then the flea species was more prevalent. If the host was not the usual one but interacted with the usual host, then the flea species was often a minor member of the flea community on

the host. If the host was neither the usual host nor the one interacting with the usual host, then the flea species was absent (Bossard 2014). Thus, the presence of *P. (P.) platensis* in *C. vellerosus* suggests a strong interaction with *Ctenomys talarum* (Rodentia, Ctenomyidae), which is present in high densities in the study area, is parasitized by this flea (Ezquiaga et al. 2008), and has similar fossorial habits as *C. vellerosus*.

The two most common fleas in armadillos, *M. grossiventris* (Weywn) and *P. agenoris* (Rothschild) (Malacopsyllidae) (Ezquiaga 2013), were not found in *C. vellerosus*. One of the possible explanations for this absence could be the isolation of the population of this armadillo species. However, other sympatric species, such as *C. villosus* and *D. hybridus*, do not carry these fleas, either. Their absence may therefore be due to environmental conditions, such as high relative humidity, and not to species-related factors. Krasnov (2008) suggests that diversity of flea assemblages is most influenced by local factors. In most host species analyzed by Krasnov (2008), the diversity of flea assemblages correlated with one or more environmental (climatic) variables.

Regardless of sex and age, screaming armadillos had similar flea communities. However, the season and year of collection, and the physical condition of animal influenced its flea communities. Intensity and prevalence were higher in 2009 probably because the previous year was extremely dry with rainfall lower than the annual average (662 vs. 1000 mm

Table 3 Statistical parameters of GLMM of intensities vs host-related factors (age, sex, weight, size, and physical condition) and environment-related variables (season and year) in *Chaetophractus vellerosus*

| Variable	PseudoR2	AIC null	AIC model	χ^2	*p*-value	d.f.	Differences	Error dist.
Year	4.1492	601.327	586.628	24.699	0.0002	5	2009=2006=2011(a); 2007=2012ab; 2010b	NB (θ = 0.157)
Season	0.5711	601.327	599.859	3.468	0.0626	1		NB (θ = 0.124)
Age	0.0404	993.306	996.859	0.447	0.7997	2		P
Sex	0.091	993.306	994.365	0.941	0.332	1		P
Physical condition	2.6523	993.306	974.8434	22.463	> 0.0001	2	poor>normal=good	P
Weight	1.5958	601.327	593.838	9.489	0.0021	1	Decreasing with BW	NB (θ = 0.133)
Body	0.2556	601.327	601.649	1.679	0.1951	1		NB (θ = 0.121)
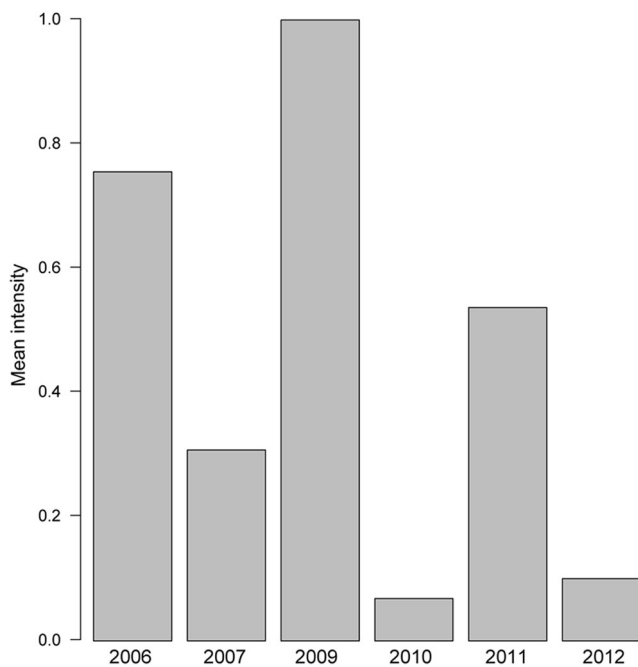
Fig. 2 Mean intensities of all species of fleas grouped by year in *Chaetophractus vellerosus* from Magdalena, province of Buenos Aires, Argentina

in 2008, Servicio Meteorológico Nacional of Argentina, Exp_144540). Environmental factors, especially ambient temperature and relative humidity (RH), affect both the imago and pre-imago stages of any arthropod, including fleas. An increase in precipitation may lead to increased RH in host burrows. Moderately high RH influences the survival and development of fleas positively (Krasnov et al. 2001a, b). However, host burrows in areas characterized by high annual precipitation may become flooded, thus causing most ectoparasite species and individuals to perish (Linardi and Krasnov 2013). In
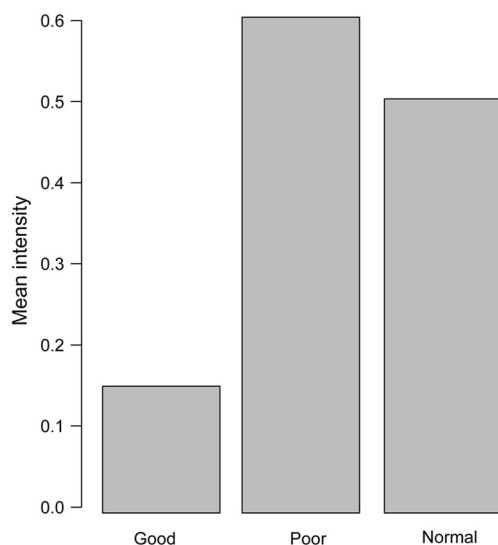

Fig. 3 Mean intensities of all species of fleas grouped in individuals with different physical condition in *Chaetophractus vellerosus* from Magdalena, province of Buenos Aires, Argentina

line with our results, these authors found that the effect of precipitation on species richness and abundance was mainly negative in fleas.

The greater prevalence of fleas in winter than in summer might be related to host sharing. For example, *Polygenis (P.) platensis* infests *C. talarum* in the study area (Ezquiaga et al. 2008), a host which coexists with *C. vellerosus*, including the use of the same burrows. Winter mortality of *C. talarum* (Malizia et al. 1991) could therefore lead *P. (P.) platensis* to migrate to other nearby hosts.

Hosts in poor condition showed more prevalence and higher intensities. Beldomenico and Begon (2009) observed that the intensity of parasitism can be both the cause and effect of its interaction with the host condition. These authors suggested that parasites may be more abundant in hosts in poor condition, and such hosts may acquire more new infestations, leading to further deterioration. This vicious circle could have important implications in the parasite dynamics and a considerable impact on host populations.

In Argentina, most ecological studies on ectoparasites have focused on cricetid rodent hosts. Some of these works concentrated on host-related factors (e.g., Lareschi 2010; Nava and Lareschi 2012), others on environment-related ones (e.g., Lareschi 2007) and others dealt with both host and environmental factors (Lareschi and Krasnov 2010). The present study is the first to analyze the dynamics of a flea community associated with an armadillo population, and is also novel in taking into account host-related factors as well as temporal variation.

Both *T. penetrans* and *Pu. irritans* can cause several disorders to humans and domestic animals, and the geographical, ecological, and host-distributional data provided here may be useful for further epidemiological studies and for understanding local risk factors.

References

Abba AM, Cassini GH, Cassini MH, Vizcaíno SF (2011) Historia natural del piche llorón *Chaetophractus vellerosus* (Mammalia: Xenarthra: Dasypodidae). Rev Chil Hist Nat 84:51–64

Abba AM, Cassini GH, Valverde G, Tilak MK, Vizcaíno SF, Superina M, Delsuc F (2015) Systematics of hairy armadillos and the taxonomic status of the Andean hairy armadillo (*Chaetophractus nationi*). J Mammal 96:673–689

Akaike H (1978) On the likelihood of a time series model. Statistician 27: 217–235

Barton, K (2016) MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Beldomenico PM, Begon M (2009) Disease spread, susceptibility and infection intensity: vicious circles? Trends Ecol Evol 25:21–27

Bossard RL (2006) Mammal and flea relationships in the Great Basin Desert: from H. J Egoscue's collections. J Parasitol 92:260–266

Bossard RL (2014) Flea (Siphonaptera) species richness in the Great Basin Desert and island biogeography theory. J Vector Ecol 39:164–167

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach, 2d edn. Springer-Verlag, New York

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Carlini AA, Vizcaíno SF (1987) A new record of the armadillo Chaetophractus vellerosus in the Buenos Aires Province of Argentine: possible causes for the disjunct distribution. Stud Neotrop Fauna E 22:53–56

Del Ponte E, Riesel MA (1939) Notas sobre Siphonaptera argentinos. Physis 17:543–551

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. PhD Thesis. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata

Ezquiaga MC, Lareschi M, Abba AM, Navone GT (2008) Nuevos registros de pulgas (Siphonaptera) parásitas de dasipódidos (Mammalia: Xenarthra) en el noreste de la provincia de Buenos Aires, Argentina. Mastozool Neotrop 15:193–196

Ezquiaga MC, Abba AM, Cassini GH, Navone GT (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 MC, Lareschi M, de Avelar DM, Linardi PM (2015) A new species of Tunga perforating the osteoderms of its armadillo host in Argentina and redescription of the male of Tunga terasma. Med Vet Entomol 29:196–204

González A, de Villalobos C, Ranalletta MA (2003) Tungiosis. In: González A, de Villalobos C, Ranalletta MA (eds) Ectoparasitosis Humanas. Ediciones Científicas Americanas, Buenos Aires, pp 284–301

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Krasnov BR (2008) Functional and evolutionary ecology of fleas. A Model for Ecological Parasitology. Cambridge University Press, New York

Krasnov BR, Shenbrot GI, Medvedev SG, Vatschenok VS, Khokhlova IS (1997) Host-habitat relations as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. Parasitology 114:159–173

Krasnov BR, Khokhlova IS, Fielden LJ, Burdelova NV (2001a) The effect of air temperature and humidity on the survival of pre-imaginal stages of two flea species (Siphonaptera: Pulicidae). J Med Entomol 38:629–637

Krasnov BR, Khokhlova IS, Fielden LJ, Burdelova NV (2001b) Development rates of two Xenopsylla flea species in relation to air temperature and humidity. Med Vet Entomol 15:249–258

Lareschi M (2007) Seasonal occurrence of ectoparasites associated with the water rat Scapteromys aquaticus (Muridae, Sigmodontinae) from Punta Lara, Argentina. Acarology XI: Proceedings of the International Congress. Morales-Malacara JB, Behan-Pelletier V, Ueckermann E, Perez TM, Estrada E, Gispert C, Badii M (Eds) Instituto de Biología, UNAM, Sociedad Latinoamericana de Acarología, Mérida, Yucatán, pp 37–44

Lareschi M (2010) Ectoparasite occurrence associated with males and females of wild rodents Oligoryzomys flavescens (Waterhouse) and Akodon azarae (Fischer) (Rodentia: Cricetidae: Sigmodontinae) in Punta Lara's wetlands, Argentina. Neotrop Entomol 39:818–822

Lareschi M, Krasnov BR (2010) Determinants of ectoparasite assemblage structure on rodent hosts from south American marshland: the effects of host species, locality and season. Med Vet Entomol 24:284–292

Lareschi M, Sanchez JP, Ezquiaga MC, Autino AG, Diaz MM, Barquez RM (2010) Fleas associated with mammals from northwestern Argentina, with new distributional reports. Comp Parasitol 77:215–221

Lareschi M, Sanchez JP, Autino A (2016) A review of the fleas (Insecta: Siphonaptera) from Argentina. Zootaxa 4103:239–258

Linardi PM, Krasnov BR (2013) Patterns of diversity and abundance of fleas and mites in the Neotropics: host-related, parasite-related and environment-related factors. Med Vet Entomol 27:49–58

Malizia AI, Vassallo AI, Busch C (1991) Population and habitat characteristics of two sympatric species of Ctenomys (Rodentia: Octodontidae). Acta Theriol 36:87–94

Mauri R, Navone GT (1993) Ectoparásitos (Siphonaptera y Acari) más comunes en Dasypodidae (Mammalia: Xenarthra) de la República Argentina. Rev Soc Entomol Argent 52:121–122

Medvedev SG, Krasnov BR (2006) Fleas: permanent satellites of small mammals. In: Morand S, Krasnov BR, Poulin R (eds) Micromammals and macroparasites: from evolutionary ecology to management. Springer-Verlag, New York, pp 161–177

Nava S, Lareschi M (2012) Ecological characterization of a community of arthropods parasitic of sigmodontine rodents in the Argentinean Chaco. J Med Entomol 49:1276–1282

R Development Core Team (2017) R: a language and environment for statistical computing, software. R Foundation for Statistical Computing, Vienna https://www.R-project.org/

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Wagenmakers EJ, Farrell S (2004) AIC model selection using Akaike weights. Psychon Bull Rev 11:192–196

Zar JH (2009) Biostatistical analysis, 5th edn. Prentice Hall, Inc., New Jersey

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Stat Softw 27:1–25

Zuur AF, Ieno EN, Walker NJ, Savelievand AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York