

Norway rat (*Rattus norvegicus*) ectoparasites in livestock production systems from central Argentina: Influencing factors on parasitism



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ABSTRACT

Haematophagous ectoparasites are worldwide vectors of many zoonotic bacterial diseases, both emerging and re-emerging, whose incidences are rising. Livestock development alters different environmental characteristics such as the microclimate of a site, changing the availability, density and susceptibility of the hosts to pathogens and vectors, indirectly influencing the spread and persistence of a disease within an ecosystem. The Norway rat (*Rattus norvegicus*), the most abundant vertebrate pest species found on livestock farms from Argentina, is a reservoir for several important zoonotic bacteria and may harbor ectoparasite species, which act as their vectors. Even though the Norway rat is widely known for its role as an ectoparasite host, the ecological characteristics of their ectoparasite communities and the related factors with parasitism on livestock farms have never been described. In the present study, we describe the ectoparasite community in Norway rats from central Argentina livestock farms, while also depicting the influencing factors on both ectoparasite occurrence and abundance. Ectoparasites were collected from rats captured in 20 sites from Buenos Aires province, between the winter of 2016 and the summer of 2018. A total of 1441 ectoparasite individuals were collected from 159 Norway rat individuals [Total ectoparasite prevalence = 69.2%; Mean ectoparasite specimen abundance (\pm CI) = 9.06 ± 2.32 ectoparasite individuals per rat; Mean ectoparasite specimen intensity (\pm CI) = 13.10 ± 3.08 ectoparasite individuals per infested rat found]. Ectoparasite assemblage consisted of four cosmopolitan species, recognized for their sanitary relevance: mites (Laelapidae: *Laelaps nuttalli* and *Laelaps echidninus*), lice (Polyplacidae: *Polyplox spinulosa*) and fleas (Pulicidae: *Xenopsylla cheopis*). We observed higher Norway rat abundance in sites related to higher ectoparasite occurrence and abundance frequencies on the rats. Additionally, ectoparasites were more abundant on rats in warm seasons and on male individuals, over female rats. Moreover, the geographical location of the studied sites influenced the ectoparasite assemblage structure observed on the rats. This study broadens the knowledge on the role of Norway rats as zoonotic ectoparasites hosts and analyzes the drivers influencing ectoparasite occurrence and abundance on the most populated region of Argentina, which is also the region with the most intensive livestock farming. Therefore, this survey may assist in evaluating potential risks for humans and generate effective sanitary control strategies for ectoparasite-borne infectious diseases.

1. Introduction

The most diverse ectoparasite fauna, including fleas, mites, ticks, and lice, is associated with rodents on all continents and biomes (Krasnov et al., 2006; Whiting et al., 2008). These parasite taxa differ substantially in their biology: fleas and lice are obligate haematophagous, while feeding modes are vastly variable among mites, ranging from obligatory haematophagy to predation on small arthropods found

in host burrows (Marshall, 1981; Radovsky, 1985). In general, ectoparasite community structure (species richness, abundance, and prevalence) varies according to the geographical distribution of the rodents. These variations are generated by interactions among intrinsic parasite factors (e.g. host specificity, biology), host factors (e.g. body size, immunology, physiology, geographic range) and environmental characteristics (e.g. temperature, humidity, vegetation), which limit or favor the parasite development (Krasnov, 2008; Linardi and

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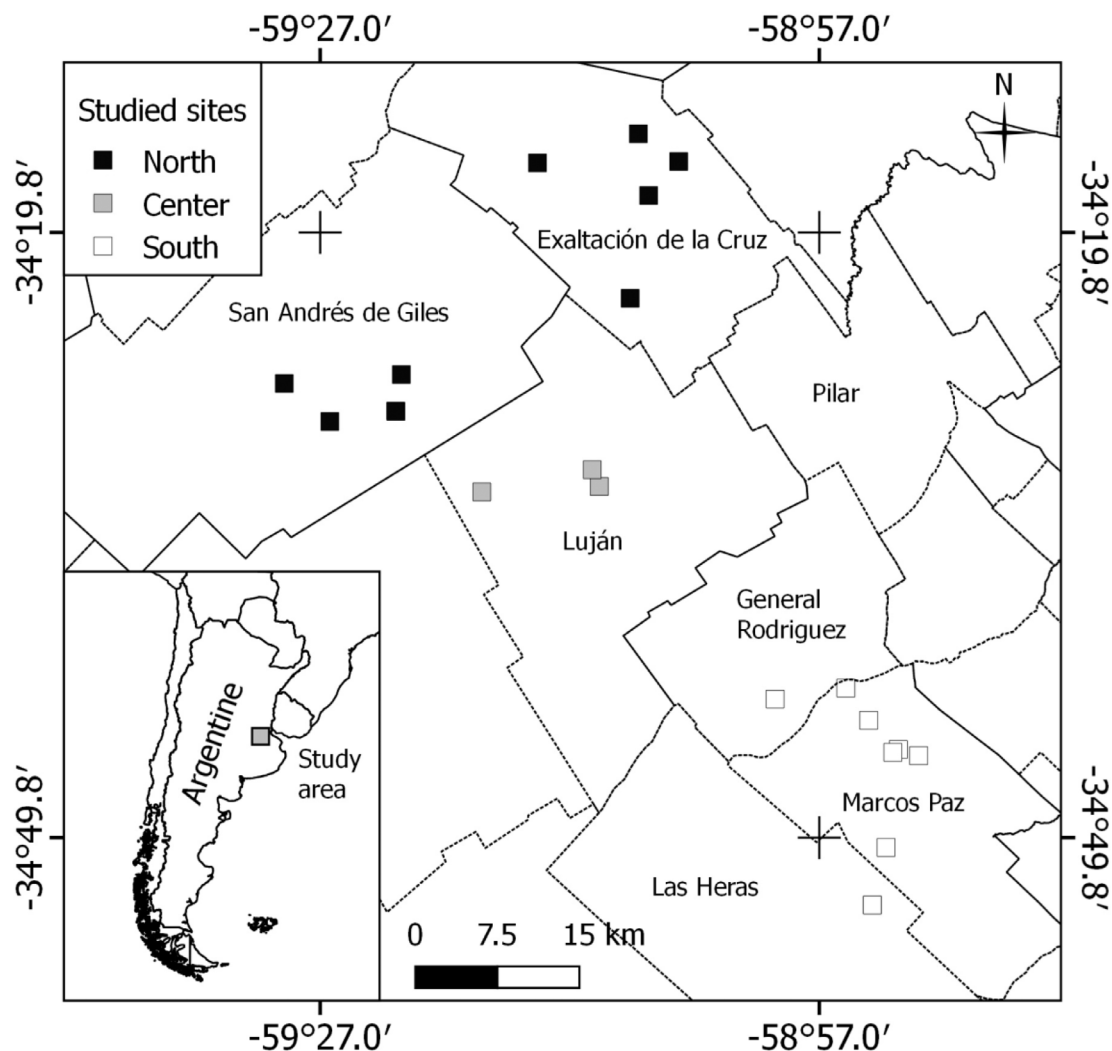


Fig. 1. Study area, northeast of Buenos Aires province, central Argentina (34°S, 58.5° W).

Krasnov, 2013; Marshall, 1981; Sánchez and Lareschi, 2018).

Generally, ectoparasites impact negatively on host populations and communities through reduction of host survival, fecundity and growth (Krasnov et al., 2006; Marshall, 1981). Moreover, as vectors of several causative agents of infectious diseases in humans and other animals (Bitam et al., 2010; Ereemeeva et al., 2007; Linardi and Guimarães, 2000; Loftis et al., 2006), haematophagous ectoparasites are of tremendous medical and economic importance. Thus, besides their ecological relevance, the characterization of the rodent-ectoparasite relationship has substantial epidemiological implications.

In the last years, ectoparasite-borne infectious diseases have been emerging or re-emerging throughout the world and their incidence is on the rise, given that their distribution, as that of their vectors, is shifting and expanding (Bitam et al., 2010). In Argentina, an increase in the occurrence of human cases of rickettsial diseases in urban areas has been observed, where new human pathogens, such as *Rickettsia massiliae* and *Rickettsia felis*, have emerged. What is more, other rickettsial diseases typical of natural environments, such as *Rickettsia rickettsii* and *Rickettsia parkeri*, began to occur in urban areas and are associated with the dispersion of different vectors and reservoirs, generally due to human activity (Cicuttin et al., 2015).

Anthropogenic disturbances have the potential to change the availability, density and susceptibility of the hosts to pathogens and vectors and thus, indirectly influence the spread and persistence of a disease within an ecosystem (Harvell et al., 2002; Keesing et al., 2006).

In this context, livestock development alters different environmental characteristics, such as the microclimate of a site (relative humidity, temperature of soil), representing an important factor and a common path for the emergence and re-emergence of infectious diseases (Jones et al., 2013).

Within Argentina, the Pampas region accounts for approximately 70% of the national swine production farms (SENASA 2014). These farms are plagued with murine rodents, such as *Rattus* (Linnaeus, 1758), *R. norvegicus* (Berkenhout, 1976) and *Musculus* (Linnaeus, 1758), due to the availability of food sources, shelter and water (Lovera et al., 2015; Montes de Oca et al., 2017). As reservoirs and mechanical vectors of several diseases, these rodents represent a serious livestock and human health risk worldwide (Glass et al., 1997; Kosoy et al., 2015; Lovera et al., 2017; Webster et al., 1995).

Particularly, the Norway rat (*R. norvegicus*) is one of the most abundant vertebrate pest species found in animal husbandry systems (Lambert et al., 2008; Lovera et al., 2015, 2019). Its presence in these environments is a risk factor of pathogen occurrence in production animals (Lovera et al., 2017). Moreover, Norway rats harbor a suite of ectoparasite species including fleas and sucking lice, as well as gamasid mites that act as important vectors for zoonoses and vector-borne diseases (Eisen and Gage, 2012). Several of these ectoparasites are registered in Argentina (Castro et al., 1987; Lareschi et al., 2016); however, the factors influencing their occurrence, abundance and prevalence in murine rodents from animal production systems are unknown.

Consequently, although some researches on ecological aspects of rodent-associated ectoparasite communities were carried out in Argentina, all of them are restricted to sigmodontine rodents captured in natural areas (Lareschi and Krasnov, 2010; Lareschi et al., 2007, 2003; Nava and Lareschi, 2012; Nava et al., 2003; Sánchez and Lareschi, 2018). In this sense, the aim of this research was to describe Norway rat ectoparasite communities and assess factors related to livestock parasitism in central Argentina. Knowledge about these drivers may usher effective sanitary and control measures for ectoparasite-borne diseases.

2. Materials and methods

2.1. Study area

This study was conducted on sixteen pig farms, two poultry farms, one dairy farm and one refuge of dogs near a landfill, all located in six counties in the northeast of Buenos Aires province, Argentina (34°S, 58.5° W, Fig. 1): San Andrés de Giles (34°26'00"S 59°26'00"W), Exaltación de la Cruz (34°17'39"S 59°05'57"W); Luján (34°33'59"S 59°06'53"W), General Rodríguez (34°37'00"S 58°57'00"W); Marcos Paz (34°46'00"S 58°50'00"W) and General Las Heras (34°56'00"S 58°57'00"W). The area is located in the Rolling Pampa a subunit of the Pampas ecoregion (Morello et al., 2012; Soriano et al., 1991). The landscape is dominated by crop fields and rangelands, with scattered towns and cities, as well as farms, mainly poultry, pig, dairy and feedlots (Fraschina et al., 2014). The climate is temperate, with an annual precipitation mean of 1005.2 mm (Pérez et al., 2015), and an annual temperature mean of 16.4 °C (Portela et al., 2009).

2.2. Trapping surveys

Ectoparasites were collected from rats captured on 19 livestock farms and one refuge of dogs. Live-trapping of rats was conducted from winter 2016 to summer 2018. Each site was sampled in one, two or three seasons. Norway rats were captured with cage traps (15 × 16 × 31 cm), baited with meat and carrot. For all trapping sessions, a total of 20 to 30 traps were set for three consecutive nights in each site and checked for captures every morning. For all captured animals, the location, date of capture, sex, weight (gr) and body length (mm) were recorded. Prior to ectoparasite collection, captured rats were anesthetized with 1:10 ketamine hydrochloride: xylazine sulphate injected intramuscularly. Then, ectoparasites were recovered by examining the furs with combs and brushes, and fixed in 96% ethanol in individual tube per host. Each tube contained the parasites collected from a single host. In the laboratory, ectoparasites were prepared for morphological study and identification: fleas and lice were cleared in aqueous solution of potassium hydroxide (KOH), dehydrated in an increasing ethanol series (from 70% to 100%), diaphanized in eugenol, and mounted in Canada balsam (Palma, 1978; Sanchez, 2013), and mites were cleared in lactophenol and mounted individually in Hoyer's medium (Krantz, 1978). Mites, fleas and lice were identified following Krantz and Walter (2009), Johnson (1957) and Johnson (1972), respectively.

2.3. Data analysis

The studied sites were grouped into three geographical zones: the North, comprised of 9 sites located in San Andrés de Giles and Exaltación de la Cruz; the Center, with three sites located in Luján and the South, constituted by eight sites located in General Rodríguez, Marcos Paz and General Las Heras (Fig. 1).

Parasitological parameters (MA: mean abundance, MI: mean intensity, and P: prevalence) were estimated according to Bush et al. (1997). Norway rats abundance was estimated for each site and season using the trap success index defined as the number of

captured animals in 100 active trap nights (Mills et al., 1991).

At site level, we registered the total number of ectoparasite species occurring in each location studied. We considered an ectoparasite to occur on a site if at least one individual was infested with an ectoparasite species. On the ectoparasite community level, we analyzed the ectoparasite assemblage observed in each individual rat and evaluated the effects of season, geographical zone, abundance, body size and sex of the host studied, on the ectoparasite assemblage structure for each individual host. For this, a Canonical Correspondence Analyses (CCA) was performed, using the abundance of each ectoparasite species registered in each individual host, as the response variables; while the season, the geographical zone, the rats abundance, the host sex and body size (head-body length in mm and weight in grs), as the explanatory ones. A backward selection procedure was used to exclude explanatory variables that did not explain the ectoparasite assemblage structure in the individuals. This analysis was performed using the *vegan* package from the R software, version 3.0.1 (R Core Team, 2013).

Also, we examined the effects of season, geographical zone and abundance, body size and sex of hosts in each site on the infestation status (infested or not infested) and the infestation level (number of specimens of an ectoparasite species registered) on the host individuals, both for the most abundant ectoparasite species and for all ectoparasite species together. We considered an individual host infested with an ectoparasite species if at least one specimen was observed. For the infestation status, Generalized Linear Mixed Models (GLMMs) regression analysis with binomial error structure, a logit-link function and the Laplace approximation method, were used (Bolker et al., 2009; Crawley, 2012; Zuur et al., 2009). For ectoparasite abundance GLMMs regression analysis with negative binomial error structure, a log-link function and the Laplace approximation method were performed, since over dispersion was observed with Poisson error structure. For all regression analyses, sites were included in the model as a random effect, because some of them were sampled in more than one occasion (in different seasons). When the random effect did not improve the model (based on the change of deviance between the model with and without the random factor), it was removed and Generalized Linear Models (GLM) regression analysis were used instead (Zuur et al., 2013). For all GLMs and GLMMs, a forward stepwise multiple regression analysis procedure (Donazar et al., 1993) was performed to select the factors that explain the infestation status and ectoparasite abundance; the simplest significant models are reported. For the stepwise forward selection criteria, we used the significant and greater change of deviance for a variable or interaction and the simplest significant models were reported. We assessed association between all predicted variables using the Variance Inflation Factors (VIFs); if any VIF value was larger than 5, the variable was removed and the process was repeated until all the VIFs were smaller than 5 (Zuur et al., 2010). When more than one candidate model was found, the Akaike Information Criterion (AIC) was used to select the best models and only the ones with $\Delta AIC < 5$, compared to the best model, are reported (Burnham and Anderson, 2002). For the infestation models, we calculated the accuracy measure Kappa index (K), sensitivity, specificity and proportion of correct classifications (PCC). This analysis was conducted using the *vegan* (Oksanen et al., 2013), *ade4* (Dray and Dufour, 2007) and *lme4* (Bates et al., 2015) packages for R Software (R Core Team, 2013).

3. Results

A total of 1441 ectoparasite individuals were collected from 159 Norway rat individuals captured in 20 sites, with a total trapping effort of 1690 cage live trap-nights. Sixty nine point two percent of the Norway rats were found to be infested with at least one ectoparasite. The mean abundance (\pm CI) was 9.06 ± 2.32 ectoparasite individuals per rat and the mean intensity (\pm CI) was 13.10 ± 3.08 ectoparasite individuals per infested rat found (Table 1). Ectoparasite assemblage consisted of three major groups: mites (Laelapidae: *Laelaps nuttalli*

Table 1 Number of ectoparasites, Prevalence (% ± 95% confidence interval, 95% CI), Mean abundance (± 95% CI) and Mean intensity (± 95% CI) of four cosmopolitan ectoparasite species collected in Norway rats captured on livestock farms in central Argentina (2016–2018) by season, sex and geographic area. n: Number of hosts analyzed.

Ectoparasite species	Season			Host sex			Male (n = 77)	Area North (n = 47)	Center (n = 28)	South (n = 84)	TOTAL (n = 159)
	Summer (n = 117)	Fall (n = 21)	Winter (n = 8)	Spring (n = 13)	Female (n = 82)						
<i>L. nuttalli</i>	P	44.90 ± 9.01	33.00 ± 20.11	0	7.70 ± 14.49	28.05 ± 9.72	49.30 ± 11.17	14.90 ± 10.18	28.60 ± 16.73	54.70 ± 10.64	38.40 ± 7.56
	MA	5.57 ± 2.42	3.09 ± 2.93	0	0.15 ± 0.33	2.87 ± 1.69	6.27 ± 3.34	1.23 ± 1.41	4.25 ± 3.46	6.45 ± 3.17	4.52 ± 1.83
<i>L. echidninus</i>	MI	12.30 ± 4.81	9.28 ± 7.78	-	-	10.26 ± 5.06	12.71 ± 6.24	8.28 ± 9.46	14.87 ± 9.37	11.78 ± 5.38	11.79 ± 4.24
	MA	54.00 ± 9.03	19.00 ± 16.79	25.00 ± 30.01	84.60 ± 19.62	41.60 ± 10.67	60.70 ± 10.91	46.00 ± 14.25	55.00 ± 18.43	74.50 ± 9.32	50.90 ± 7.77
<i>P. spinulosa</i>	MI	4.43 ± 1.79	2.04 ± 2.59	0.37 ± 0.62	8.92 ± 7.96	3.33 ± 1.49	5.28 ± 2.65	6.58 ± 3.93	3.60 ± 1.77	3.06 ± 1.69	4.28 ± 1.49
	MI	8.09 ± 3.00	10.75 ± 15.17	1.5 ± 6.35	10.54 ± 9.34	7.18 ± 2.80	9.46 ± 4.42	11.10 ± 5.95	5.94 ± 2.32	7.34 ± 3.70	8.39 ± 2.65
<i>X. cheopis</i>	P	9.30 ± 5.26	0	0	38.00 ± 26.38	12.19 ± 7.08	7.80 ± 5.99	10.60 ± 8.80	0	13.10 ± 7.21	10.00 ± 4.66
	MA	0.15 ± 0.13	0	0	0.92 ± 0.76	0.19 ± 0.13	0.18 ± 0.20	0.25 ± 0.23	0	0.21 ± 0.18	0.19 ± 0.11
All species	MI	1.64 ± 1.21	-	-	2.40 ± 0.68	1.60 ± 0.50	2.33 ± 2.54	2.4 ± 0.68	-	1.63 ± 1.21	1.87 ± 0.82
	P	6.80 ± 4.56	0	0	15.40 ± 19.62	3.66 ± 4.06	9.10 ± 6.42	6.40 ± 6.99	3.30 ± 6.61	7.10 ± 5.49	6.30 ± 3.78
All species	MA	0.08 ± 0.07	0	0	0.15 ± 0.23	0.06 ± 0.08	0.09 ± 0.07	0.06 ± 0.08	0.04 ± 0.07	0.09 ± 0.08	0.07 ± 0.06
	MI	1.25 ± 0.59	-	-	1.00	1.66 ± 2.87	1.00	1.00	1.00	1.33 ± 1.86	1.20 ± 0.59
All species	P	74.50 ± 7.90	42.80 ± 21.16	25.00 ± 30.00	84.60 ± 19.62	64.63 ± 10.35	74.00 ± 9.80	63.80 ± 13.74	71.40 ± 16.74	71.30 ± 9.67	69.20 ± 7.18
	MA	10.23 ± 2.95	5.14 ± 4.35	0.37 ± 0.62	10.15 ± 7.88	6.46 ± 2.28	11.83 ± 4.12	8.40 ± 4.02	7.89 ± 3.86	9.82 ± 3.65	9.06 ± 2.32
	MI	13.61 ± 3.65	12.00 ± 7.96	1.50 ± 6.30	12.00 ± 9.00	10.00 ± 3.15	15.98 ± 5.17	13.17 ± 5.69	11.05 ± 4.76	13.75 ± 4.77	13.10 ± 3.08

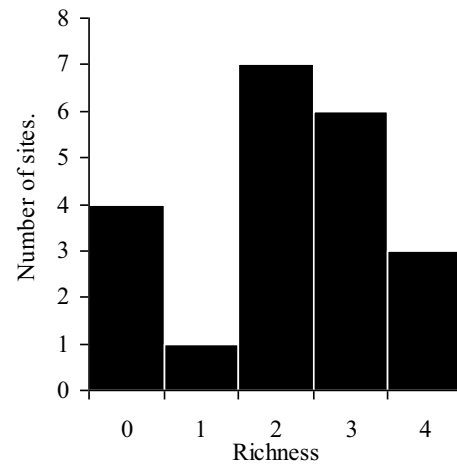


Fig. 2. Ectoparasite species richness in the 20 sampled sites in central Argentina (2016–2018).

Hirst, 1915 and *Laelaps echidninus* Berlese, 1887), lice (Polyplacidae: *Polyplox spinulosa* Burmeister, 1839) and fleas (Pulicidae: *Xenopsylla cheopis* Rothschild, 1903). The most common was to find two or three ectoparasite species in each studied site (Fig. 2); *Laelaps nuttalli* and *L. echidninus* were the most common and abundant species (Table 1). *Laelaps echidninus* showed the maximum prevalence and *L. nuttalli* the maximum mean, while *X. cheopis* showed the lowest prevalence of the four ectoparasite species (Table 1).

According to the CCA, the geographical zone explained 18.13% of the variation in ectoparasites assemblage structure observed on the individuals (CCA_{2,107} = 11.849, *p* < 0.002). Only the first axis was significant (CCA1 = 17.74%, F_{1,107} = 23.184, *p* < 0.001). This analysis depicted that most Norway rats captured in the North and Center presented higher abundances of *L. echidninus*, compared to those captured in the South; meanwhile, individuals captured in the South presented higher abundances of *L. nuttalli* than those from the North and Center (Fig. 3, Table 1). Ectoparasites *P. spinulosa* and *X. cheopis* showed similar abundances among the three zones, represented by few individuals (Table 1).

According to the regression analysis, two different models explained infestation of total ectoparasites; one indicated that the occurrence of infestation in rats was higher on warm seasons. The second model, which had a lower statistical sustain (ΔAIC_{A,B} = 4.82), showed that the occurrence of ectoparasites was more frequent in females when higher abundances were registered, while for males, the occurrence was constant and higher than in females (Table 2, Fig. 4). The first model showed substantial index values of classification and almost perfect sensitivity index value, while the second showed substantial index values of classification and substantial value of specificity index (Landis and Koch, 1977; Table 2). For *L. nuttalli*, the infestation was more frequent in male rats than in females (Table 3). In turn, *L. echidninus* infestation depended on the season, as higher frequencies were observed in spring, over the other seasons (Table 3).

On the other hand, according to the regression analysis conducted for abundance of all ectoparasite species together; we observed that it was explained by the season and host's sex. Ectoparasites were more abundant in non-winter seasons, or in males compared to females (Table 4). The abundance of *L. echidninus* was also explained by season and host sex. This species presented higher abundances in male Norway rats during the warm seasons, than in females during cold seasons (Table 4, Fig. 5). In turn, the difference in *L. nuttalli* abundance in its hosts was explained only by the season, showing the greatest abundances during spring (Table 4).

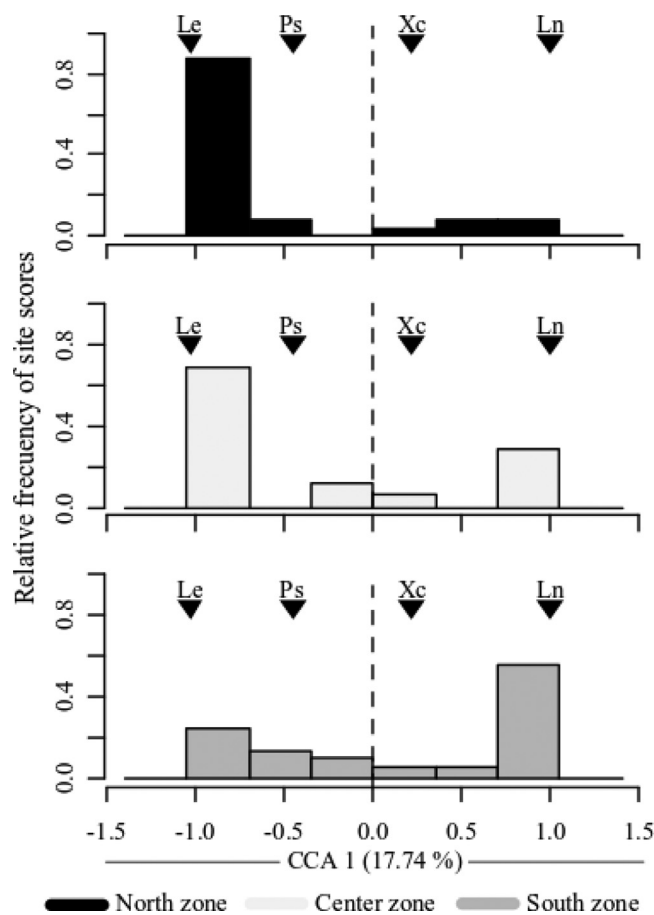


Fig. 3. Relative frequency of each parasitized host according to the abundance of ectoparasites registered in the first Canonical Correspondence Analysis axis (CCA 1) restricted by the geographical zones in central Argentina (2016–2018). Arrows indicate the scores of each ectoparasite species on the axis. Le: *L. echidninus*, Ps: *P. spinulosa*, Xc: *X. cheopis*, Ln: *L. nuttalli*.

Table 2

Summary of the two best Generalized Linear Model for the occurrence of ectoparasites on Norway rats inhabiting livestock farms and a dogs’ refuge of central Argentina (2016–2018). The season (warm or cold), the zone (Center, North and South), Norway rat abundance and sex were evaluated. Rn: *Rattus norvegicus*. df: residual degrees of freedom; Kappa: Kappa index. PCC: proportion of correct classifications; Sens: sensitivity; Spec: specificity; SD: standard deviation.

A) Total ectoparasite occurrence ~ Season			
Explanatory variables	Coefficients	SD	P -value
Intercept (Cold seasons)	-0.492	0.383	0.198
Warm seasons	1.653	0.434	<0.001*
LRT = 15.093 df = 1 p < 0.001 Residual deviance = 181.31 Residual df = 157			
AIC = 185.31 Null AIC = 196.41			
Accuracy index:			
Kappa = 0.30 PCC = 0.74 Sens = 0.90 Spec = 0.37			
B) Total ectoparasite occurrence ~ Rn abundance*Sex			
Explanatory variables	Coefficients	SD	P -value
Intercept (Rn abundance*Female)	-0.719	0.473	0.198
Male	1.562	0.694	0.024*
Rn abundance	0.092	0.032	0.004*
Rn abundance: Male	-0.081	0.040	0.044*
LRT = 15.093 df = 1 p = 0.035 Residual deviance = 182.13 Residual df = 155			
AIC = 190.13 Null AIC = 196.41			
Accuracy index:			
Kappa = 0.25 PCC = 0.72 Sens = 0.54 Spec = 0.71			

4. Discussion

In the present study, the diversity of ectoparasites on Norway rats from livestock farms in the Buenos Aires province was comprised of one species of flea, *X. cheopis*, one species of louse, *P. spinulosa* and two mite species, *L. echidninus* and *L. nuttalli*. All of them are cosmopolitan species recognized for their sanitary relevance. *Xenopsylla cheopis* is known as a vector of the bacteria that cause the plague (*Yersinia pestis*), tularemia and murine typhus (Bitam et al., 2010; Eisen and Gage, 2012). *Polyplox spinulosa* is vector of the etiologic agents of epidemic typhus, epidemic relapsing fever, and trench fever and has been implicated in maintaining *Rickettsia typhi* and *Y. pestis* within rodent communities (Reeves et al., 2006; Traub et al., 1978). Gamasid mite *L. echidninus* is capable of transmitting the Junin virus, etiological agent of Argentinian haemorrhagic fever, to rats (McLay et al., 2014). Argentinian haemorrhagic fever is a lethal disease, endemic to central Argentina, principally infecting agricultural workers (Kolokoltsova et al., 2014). *Laelaps nuttalli* may play a sanitary role causing dermatitis (Engel et al., 1998). In addition, *L. echidninus* and *L. nuttalli* were the most prevalent and abundant ectoparasites, respectively, collected in this study. Both of these mite species are usually found parasitizing the Norway rat worldwide and are commonly, the most abundant and prevalent species in the ectoparasite communities of this rodent (Frye et al., 2015; Soliman et al., 2001; Ugbomoiko and Obiamiwe, 1991). Although these four identified ectoparasites were previously registered in Argentina (Castro et al., 1987; Lareschi et al., 2016), this is the first study that describes the factors that influence their abundance and prevalence.

Our results showed a high prevalence of infested Norway rats, with high ectoparasite abundance (≈ 70% and 9 individuals per host, respectively). This could be caused by the large number of rats occupying similar locations in the studied habitats, facilitating transmission and multiple parasite infestation through interactions. We observed that higher abundance of Norway rats in a site was related to higher ectoparasite occurrence in the host individuals from those populations. Host density is one of the most important factors in ectoparasite prevalence and abundance (Brunner and Ostfeld, 2008), as density increases the probability of contact among individuals (territorial fights and social interaction; Wolff, 1985), which promotes ectoparasite exchange and thus, the infestation increase (e.g., see Young et al., 2015 for fleas). Larger host populations have less probability of local extinction, thereby promoting the persistence of present ectoparasites. Furthermore, recent studies on movement patterns and habitat selection of Norway rats in the studied area, found that many individuals shared the same runways for moving, as well as the same tunnels (Montes de Oca et al., 2017). These behaviors are typically found in social animals that share nests (Timm, 1994; Macdonald et al., 1999). The social behavior of Norway rats in the studied area, could also explain its high ectoparasite abundance and prevalence. High abundance of Norway rats is also a risk factor for pathogenic organism occurrence on farms, indicating that their abundances should be controlled in livestock production systems (Lovera et al., 2019).

As mentioned earlier, infestation by ectoparasites can be influenced by host associated factors (e.g., population density or sex) or environmental conditions (e.g., humidity, temperature), where higher parasite abundance may indicate a beneficial environment for parasite proliferation (Carrillo et al., 2007; Krasnov et al., 2002). We observed that geographical location influenced ectoparasite assemblage structure on livestock farms from the Buenos Aires province. Additionally, our results suggest that ectoparasite prevalence and abundance were higher in male than in female Norway rats, while also depending on the seasons, being spring or summer the moments of the year with higher infestations values.

With respect to the influence of sex, as reported in other studies, the abundance of parasites in a mammalian host population, generally differs between the sex of the individuals (Fernandes et al., 2012; Krasnov et al., 2005; Zuk, 2009), and the most common causes are the

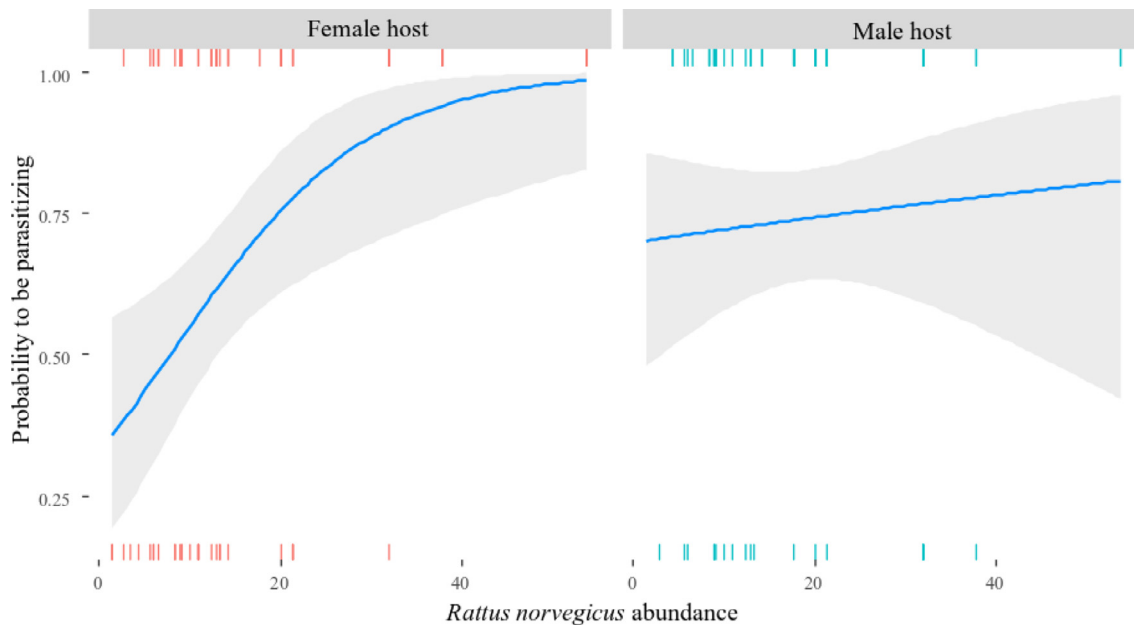


Fig. 4. Observed interaction between Norway rat abundance (Trap success: number of rats caught in 100 trap-nights) and host sex in the occurrence of ectoparasites in the host individuals. Expected ectoparasite occurrence increased more for females than for males when increased the abundance of the host in the sites (Norway rats).

Table 3

Summary of the best Generalized Linear Models or Generalized Linear Mixed Models for the occurrence of A) *L. nuttalli* and B) *L. echidninus* found in Norway rats inhabiting livestock farms and a dogs' refuge of central Argentina (2016–2018). df: residual degrees of freedom; Kappa: Kappa index. PCC: proportion of correct classifications; Sens: sensitivity; Spec: specificity; SD: standard deviation.

A) <i>L. nuttalli</i> occurrence ~ Sex			
Explanatory variables	Coefficients	SD	P-value
Intercept (Female)	-0.942	0.245	<0.001*
Male	0.916	0.335	0.006*
LRT = 15.093 df = 1 p = 0.005 Residual deviance = 204.05 Residual df = 157 AIC = 208.05 Null AIC = 213.73			
Accuracy index:			
Kappa = 0.21 PCC = 0.61 Sens = 0.63 Spec = 0.60			
B) <i>L. echidninus</i> occurrence ~ Season (Spring vs Non-spring seasons) + (1 establishment)			
Explanatory variables	Coefficients	SD	P-value
Intercept (Non spring)	-0.137	0.227	0.545
Spring	1.989	0.875	0.023*
LRT = 15.093 df = 1 p = 0.005 Residual deviance = 204.05 Residual df = 156 AIC = 217.13 Null AIC = 221.83			
Accuracy index:			
Kappa = 0.36 PCC = 0.68 Sens = 0.50 Spec = 0.86			

influence of their physiology and behavior. The first cause is based on a negative relationship between the levels of testosterone and the performance of the immune function, resulting in males more susceptible to infestation than females (Klein, 2004). Specifically in polygynous mating systems, such as *R. norvegicus*, intersexual competition compromises the immune system of males, due to higher levels of testosterone compared to monogamous systems (Barcelar et al., 2011; Carter et al., 1995; Fernandes et al., 2010). This mating system is also associated with aggressive interactions and produce severe physiological stress, increasing the susceptibility of males to parasitic infestation, contributing to the above mentioned sex differences (Klein, 2000; Negro et al., 2010; Ostner et al., 2011). In addition, contact with other infected individuals is facilitated by the active mobility of males, resulting in an important factor for the transmission of parasites within host populations (Bordes et al., 2009; Hillegass et al., 2008; Krasnov et al., 2006, 2011; Soliman et al., 2001). Moreover, males of

Table 4

Summary of the best Generalized Linear Models or Generalized Linear Mixed Models for (A) the total ectoparasite abundance, (B) *L. echidninus* abundance and (C) *L. nuttalli* abundance in Norway rats inhabiting livestock farms and a dogs' refuge of central Argentina (2016–2018). LRT: Likelihood ratio test, df: residual degrees of freedom, dp: overdispersal parameter; SD: standard deviation.

A) Total ectoparasite abundance ~ Season (Winter vs Non-winter seasons) + Sex			
Explanatory variables	Coefficients	SD	P-value
Intercept (Non winter)	1.919	0.176	<0.001*
Winter	-3.207	-3.942	<0.001*
Sex (male)	0.595	0.248	0.016*
LRT = 17.74 df = 2 p = < 0.001* Residual deviance = 174.08 Residual df = 156 AIC = 960.78 Null AIC = 974.52 Theta = 0.44 dp = 1.14%dev = 1.61			
B) <i>L. echidninus</i> abundance ~ Season (Cold season vs warm seasons) *Sex + (1 establishment)			
Explanatory variables	Coefficients	SD	P-value
Intercept (Cold seasons*Female)	0.282	0.589	0.632
Warm seasons	0.905	0.603	0.133
Sex (male)	-2.148	1.116	0.054
Warm season*Sex (Male)	2.498	1.175	0.033*
LRT = 4.32 df = 1 p = 0.030* Residual deviance = 680.7 Residual df = 153 AIC = 692.7 Null AIC = 697.9 Theta = 0.23 dp = 0.98%dev = 9.71			
C) <i>L. nuttalli</i> abundance ~ Season (Cold seasons vs Summer vs Spring) + (1 establishment)			
Explanatory variables	Coefficients	SD	P-value
Intercept (Cold seasons)	0.282	0.589	0.632
Summer	0.885	0.552	0.108
Spring	-2.662	1.104	0.016*
LRT = 10.00 df = 2 p = 0.006* Residual deviance = 622.4 Residual df = 154 AIC = 632.40 Null AIC = 638.41 Theta = 0.17 dp = 0.89%dev = 1.56			

this species may extend their home range during the breeding season, when in search of an oestrus female (Clapperton, 2006). Thus, the greater home range in male than in female Norway rats would increase the probability of encounter between males and ectoparasites, increasing both prevalence and abundance of these parasitic species in the male host population.

In relation to the season of the year, ectoparasite prevalence and intensity are assumed to be higher when environmental conditions are favorable for parasite survival, depending on the particular biological

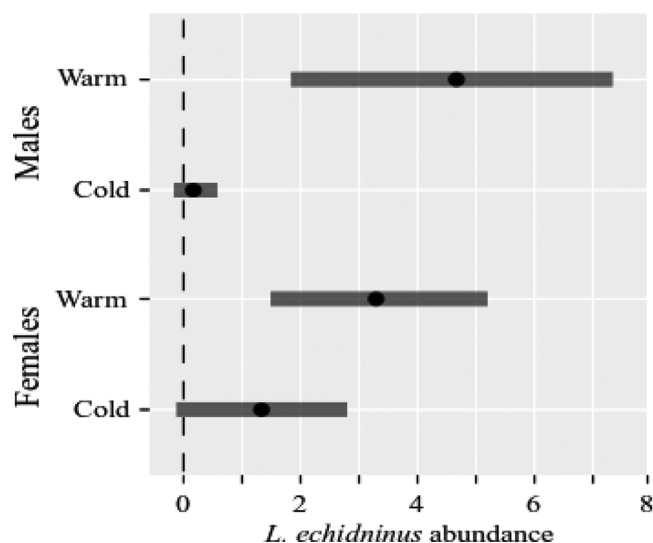


Fig. 5. Mean *L. echidninus* abundance estimates (GLMM), showing the interaction between the host sex and the season. Black dots indicate the mean value and gray bars show the 95% confidence interval for the mean.

requirements of each group (Krasnov, 2008; Linardi and Krasnov, 2013; Sánchez and Lareschi, 2018). Even though ectoparasites are subject to less pronounced microclimatic fluctuations than free-living arthropods, even subtle changes in air temperature and humidity can affect the juvenile stages of fleas and mites, causing a variation of their survival and development time (Khokhlova et al., 2009; Krasnov et al., 2001; Marshall, 1981; Shenbrot et al., 2002). For example, in mites, prevalence and abundance are higher during the warm seasons (Linardi and Krasnov, 2013), because these parasites survive better and develop faster under higher ambient temperature (Krasnov et al., 2001; Nawar, 1992). On the other hand, Linardi and Krasnov (2013) found that the effect of precipitation on abundance of fleas was mainly negative, while it did not demonstrate any consistent trend for mites. However, other mite studies showed higher values of parasitological indexes during the wet season (Altizer et al., 2006).

Analyzing the effect of the studied variables on the occurrence and abundance of the most collected ectoparasites, different responses were observed. *Laelaps nuttalli* occurrence was associated with the sex of the host, being significantly higher in males. On the other hand, the occurrence of *L. echidninus* was associated with seasonality, appearing significantly more during the spring than in the rest of the seasons. With respect to abundance, in *L. nuttalli* it was positively associated with the seasonality and was higher in spring. However, in *L. echidninus* there was a relationship between the season and the sex of the Norway rat individuals. Both variables acted together, with greater abundances observed in male hosts during warm seasons, than in females during cold seasons. The zone analysis showed that most Norway rats captured in the North and Center, presented higher abundances of *L. echidninus*, while individuals captured in the South showed higher abundances of *L. nuttalli*. The differences on the landscape structure within the study area could probably affect ectoparasites on the farms, related to differential environmental preferences among ectoparasite species. Effect of the landscape would affect the host assemblage structure (Cavia et al., 2009), rebounding on parasites assemblage in the individual host (Johnson et al., 2015). Further studies are needed to deeply understand the landscape context effect over ectoparasites in the study area.

Finally, the zoonotic potential of a host species depends, among other things, on its parasitic fauna (Jenkins et al., 2015). This is particularly important when it involves species that frequent environments inhabited by humans and their domestic animals. The Norway rat is the most common vertebrate pest species in animal production systems (Lovera et al., 2019; Montes de Oca et al., 2017) and is commonly

infected with a multitude of zoonotic pathogens on farms (Lovera et al., 2017; Hassell et al., 2017). Our results show that populations of Norway rats from the study area have ectoparasite assemblages composed of species of recognized sanitary importance and these ectoparasite species accompany this rodent throughout its global geographical distribution. However, future studies are necessary to determine the zoonotic bacteria circulation in Norway rats and their ectoparasites, on livestock farms from Buenos Aires province. According to our results, in this region, the warm periods of the year would be expected to have a higher risk of occurrence of ectoparasites vector-borne diseases on cattle and humans, like pest and rickettsial diseases.

This study contributes to a better understanding of the ectoparasite-host-environment complex. Withal, considering the concept of 'One Health', in which human health is considered to be related to animal health and the environment (Hassell et al., 2017; Jenkins et al., 2015), this study allows to know the role of Norway rats as hosts of zoonotic ectoparasites, providing information on the factors that influence both the occurrence and abundance of these ectoparasites. This knowledge is necessary to improve control strategies of the infectious diseases involving Norway rats and transmitted by ectoparasites.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Author statement

RA, RC and JPS conceived and designed the experiments. MR and JPS collected and identified the ectoparasites. RA, RL, DMDO and RC performed the analytic calculations and statistical analysis. All authors provided critical feedback and helped shape the research, analysis and manuscript.

Declaration of Competing Interest

None.

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