Drivers of flea (Siphonaptera) community structure in sympatric wild carnivores in northwestern Mexico

Andrés M. López-Pérez[1,4], Kenneth Gage[2], Andre V. Rubio[3], John Montenieri[2], Libertad Orozco[4], and Gerardo Suzan[1]✉

[1]*Departamento de Etología, Fauna Silvestre y Animales de Laboratorio, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Ciudad Universitaria, México D.F., México, gerardosuz@gmail.com*
[2]*Division of Vector-Borne Diseases, Centers for Disease Control and Prevention, Fort Collins, CO, U.S.A.*
[3]*Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile*
[4]*Fundación para el Manejo y la Conservación de la Vida Silvestre FMCOVIS A.C. Ciudad de México, México*

Received 3 June 2017; Accepted 13 October 2017

ABSTRACT: Host identity, habitat type, season, and interspecific interactions were investigated as determinants of the community structure of fleas on wild carnivores in northwestern Mexico. A total of 540 fleas belonging to seven species was collected from 64 wild carnivores belonging to eight species. We found that the abundances of some flea species are explained by season and host identity. *Pulex irritans* and *Echidnophaga gallinacea* abundances were significantly higher in spring than in fall season. Flea communities on carnivore hosts revealed three clusters with a high degree of similarity within each group that was explained by the flea dominance of *E. gallinacea*, *P. simulans,* and *P. irritans* across host identity. Flea abundances did not differ statistically among habitat types. Finally, we found a negative correlation between the abundances of three flea species within wild carnivore hosts. Individual hosts with high loads of *P. simulans* males usually had significantly lower loads of *P. irritans* males or tend to have lower loads of *E. gallinacea* fleas and vice-versa. Additionally, the logistic regression model showed that the presence of *P. simulans* males is more likely to occur in wild carnivore hosts in which *P. irritans* males are absent and vice-versa. These results suggest that there is an apparent competitive exclusion among fleas on wild carnivores. The study of flea community structure on wild carnivores is important to identify the potential flea vectors for infectious diseases and provide information needed to design programs for human health and wildlife conservation. ***Journal of Vector Ecology* 43 (1): 15-25. 2018.**

Keyword Index: Carnivores, ectoparasite, flea community, interspecific competition, Mexico, season.

INTRODUCTION

Fleas are highly specialized blood-sucking ectoparasites with a wide range of hosts, including birds and mammals. In addition to their role as ectoparasites, fleas have medical relevance as vectors of pathogens that infect humans and animals (Dobler and Pfeffer 2011). Carnivores are the second most important mammalian hosts of fleas (Krasnov 2008), and several studies have suggested that wild carnivores may be potential reservoirs or have a role in the transmission cycles of flea-borne infections, such as plague, bartonelloses, and rickettsioses. For instance, skunks and wild canids are suspected to be reservoirs of *Bartonella rochalimae* (López-Pérez et al. 2017), which have been associated with bacteremia in humans (Eremeeva et al. 2007). Also, wild canids have been identified as potential carriers of *Yersinia pestis* (the causal agent of plague) among prairie dog colonies (McGee et al. 2006), while fleas collected from beach martens (*Martes foina*) have been reported to be infected with *Rickettsia felis*, the causative agent of an emergent rickettsiosis (Lledó et al. 2010). Furthermore, many flea species that are important as vectors of flea-borne diseases (*Pulex* spp., *Oropsylla* spp., and *Ctenocephalides* spp.) have been recorded from various mammalian carnivores, such as wild felids, canids, mephitids, and mustelids (McGee et al. 2006, Márquez et al. 2009, López-Pérez et al. 2017).

The drivers of patterns of the flea community structure have important implications for human and animal health (Friggens and Beier 2010). The community structure of ectoparasites is determined mainly by host factors and the off-host environmental conditions. Host factors act at different ecological levels of organization (individual, species, and community), such as host sex and age, body condition, host species, body size, host abundances, and species diversity and composition (Krasnov 2008, Linardi and Krasnov 2013, Young et al. 2015). However, the associations of many flea species, particularly those found on carnivores, are often accidental instead of host-specific and can be explained by ecological rather than phyletic factors. For example, fleas could switch between host species due to the exploration or exchange of burrows or such host exchanges could reflect predator-prey relationships (Beaucournu et al. 2005, Hastriter and Whiting 2005, Krasnov 2008).

On the other hand, it is known that a strong relationship exists between fleas and environmental factors. This is explained by the fact that fleas, including the larval stages which rarely are parasites, spend most of their life-cycle off-host (Marshal 1981). Pertinent environmental factors include habitat and climate and, consequently, the season of the year. Several studies have reported a relationship between either development rates of flea larvae or abundances of fleas and temperature and rainfall (Krasnov et al. 2001a, Krasnov et al. 2001b, Gálvez et al. 2016, Kreppel et al. 2016). Finally, fleas are influenced not only by environmental and host factors, but also by the interspecific interactions, such as competitive exclusion between sympatric flea species (Barnes

1965, Day and Benton 1980, Krasnov et al. 2005).

The drivers of patterns of abundances and assemblage structure of fleas have been studied mainly in rodents (Krasnov et al. 2006b, Chotelersak et al. 2015, Young et al. 2015) and domestic carnivores (Gracia et al. 2013, Gálvez et al. 2016). In contrast, these patterns are poorly understood in wild carnivores. To our knowledge, there is only one study on habitat as a driver of flea assemblages in skunks (Brinkerhoff 2008).

For these reasons, the aims of this study were to: (1) investigate the flea community structure in different wild carnivore species, (2) identify changes in flea abundances among seasons, habitats, and between host species, and (3) identify if competitive exclusion may be occurring among flea species.

MATERIALS AND METHODS

Study area

Sampling was carried out in the Janos Biosphere Reserve (JBR) in Chihuahua, Mexico (30º 51´50´´N, 108º 30´09´´W) (Figure 1). JBR is in a transition zone between the Sierra Madre Occidental and the Chihuahuan Desert, which comprises a mosaic of grasslands, mesquite shrubland, oak forest, and riparian vegetation. The climate is arid-temperate. Mean annual temperatures vary with altitude from a mean annual of 15.7º C in plains at 1,200 m above sea level to a mean annual of 11.8º C at 2,700 m above sea level. A rainfall gradient occurs from a mean annual precipitation of 381 mm to 581 mm, with 77% of that precipitation falling from April through August (García 1981).

Host sampling, flea collection, and identification

Wild carnivores were live-trapped and fleas collected in five locations (El Cuervo, La Bascula, Monte Verde, Ojitos, and Rancho San Pedro) over two seasons (fall: October-November, 2013 and spring: May-June, 2014). Each of the five sampling locations was surveyed one per season with sixteen trapping sets placed at 0.5-0.8 km intervals along a 10 km transect. Each trapping set consisted of one box trap (Tomahawk Live Trap Inc. WI) and one leg-hold trap (Victor Coil Soft Catch™). The traps were baited with canned sardine, chicken, and commercial lures. Traps were set for nine consecutive days per site and checked at least once a day. Each individual was chemically restrained with an IM injection of ketamine hydrochloride and xylazine hydrochloride, according to the recommended doses for wild carnivores (Kreeger and Arnemo 2012). Animals were identified, weighed, and sexed. Each carnivore was visually examined and inspected systematically for fleas by combing for 10-15 min. Removed fleas were placed in a cryovial containing 70% ethanol and stored in liquid nitrogen. In order to see the structures required for identification, we placed the fleas in 2% saline with Tween 80 detergent (2 drops/liter). Fleas were placed individually in single petri dishes for examination using a stereo microscope and identified morphologically using published taxonomic keys (Hubbard 1968, Furman and Catts 1982). In some instances, such as *Pulex* males, when the structures are not visible, we made an incision in the abdomen to open it up and make the structures visible. We could not classify *Pulex simulans* and *Pulex irritans* females because they are morphologically indistinguishable. However, we assumed that if we only found the males of one species in the collection from an individual animal that all other *Pulex* fleas were of the same species. All procedures for handling

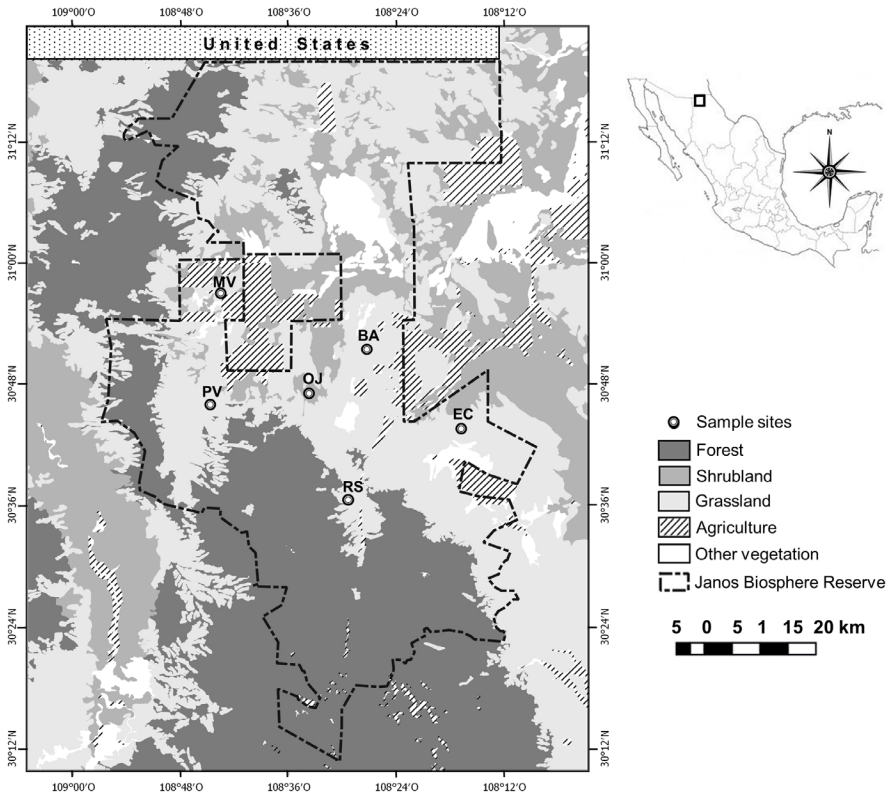

Figure 1. Location of sites and habitat types where carnivores and their fleas were sampled in the Janos Biosphere Reserve, northwestern Mexico (INEGI 2013).

carnivores were carried out in accordance with the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by the Ministry of Environment and Natural Resources of Mexico (Permit FAUT-0250).

Habitat classification

Using satellite images available in Google Earth (GoogleEarth_7.1.8 2016), we calculated the proportion of the different land-cover types within a 100 m radius of each trapping set location. We used the tool Polygon to measure the area of each identified land cover type and then classified the habitat based on the most predominant one. To validate the classification, we verified on-site the predominant habitat using the central point quadrants method reported by Gallina and López-González (2011). A total of four habitat types were recognized in all five locations: 1) grassland, 2) shrubland, 3) grassland-forest ecotone, and 4) oak forest. The grasslands are dominated by the annual grasses, *Aristida adscensionis*, *Bouteloua aristidoides*, and *B. barbata*, while perennial grasses include *A. divaricate Muhlenbergia arenacea*, *Scleropogon brevifolius*, *Panicum obtusum*, *Pleuraphis mutica*, *B. gracilis*, *B. eriopoda*, and *B. trifida*. Some of the grasslands are associated with *Ephedra trifurca*. The shrublands are mainly composed of *Prosopis glandulosa* (mesquite) and *Opuntia imbricata*. The grassland-forest ecotones are dominated by *Bouteloua gracilis*, *B. curtipendula*, and *Muhlenbergia* sp., *Quercus* spp., and *Juniperus* sp. Finally, the oak forests are composed by *Quercus* spp., *Juniperus* sp., and *Pinus* sp.

Grassland was recognized in El Cuervo, La Bascula, and Monte Verde; shrubland was recognized in La Bascula, Monte Verde, and Ojitos; grassland-forest ecotone and oak forest were distinguished particularly in Rancho San Pedro.

Data analysis

Incidence-based rarefaction and extrapolation were used to evaluate sample efficiency of flea assemblages across wild carnivore species (Chao et al. 2014). This procedure was based on species richness (q=0) and estimated by sample coverage using iNEXT package (Chao et al. 2016).

Cumulative relative abundance was plotted to visualize changes in host species rank of the flea assemblage. Relative abundances (RA) were estimated by calculating the abundance of a given species divided by the total abundances of flea assemblages for each wild carnivore host. The Morisita-Horn index based on relative abundance was used to compare the similarity coefficient between flea assemblages of each carnivore host species. Similarity coefficient was performed in R software (R Development Core Team 2014) (Supplementary file S1) and a dendrogram was created using UPGMA clustering of Morisita-Horn similarity values in Past software (Paleontological Statistics Software Package for Education and Data Analysis, 2001).

To determine if host and environmental factors had an effect on flea abundances we used generalized linear models (GLM) with quasi-Poisson distribution and log-link function to account for overdispersion in response variables. The response variables were the abundance of flea species at a given individual host. The explanatory variables were host identity (carnivore species), season, and habitat. We performed the analysis on three flea species (*Pulex simulans*, *Pulex irritans,* and *Echidnophaga gallinacea*) that were dominant species on host species.

In order to identify interspecific relationships between flea species in wild carnivores, we conducted two statistical tests. First, Spearman's rank correlations were performed to assess the intensity and direction of the linear relationships between the abundances of *Pulex simulans*, *P. irritans,* and *E. gallinacea*. The non-parametric correlation coefficient was used because none of the analyzed datasets are normally distributed. Second, logistic regression model with binomial distribution was used to evaluate the associations of the presence/absence of a given flea species with the presence/absence of the other flea species. The logistic regression was reported as the adjusted odds ratio (OR) with the 95%

Table 1. Abundances of wild carnivore species captured in four habitat types at five locations in the Janos Biosphere Reserve, northwestern Mexico.

Carnivore Host	Habitats n (Locations[a])				
	Grassland	Shrubland	Grassland-forest ecotone	Oak forest	Total
Canis latrans	6 (EC, LB, MV)	4 (LB, OJ)	6 (RS)	1 (RS)	17
Lynx rufus	1 (EC)	3 (OJ)	0	1 (RS)	5
Mephitis macroura	0	3 (OJ)	0	0	3
Mephitis mephitis	1 (LB)	1 (OJ)	6 (RS)	0	8
Procyon lotor	0	2 (OJ)	2 (RS)	0	4
Taxidea taxus	3 (EC)	3 (LB, MV, OJ)	0	0	6
Urocyon cinereoargenteus	0	0	3 (RS)	4 (RS)	7
Vulpes macrotis	13 (EC, LB, MV)	1(MV)	0	0	14
Total	24	17	17	6	64

[a]EC: El Cuervo; LB: La Bascula; MV: Monte Verde; OJ: Ojitos; RS: Rancho San Pedro.

Table 2. Flea infestation patterns of eight wild carnivore species captured in the Janos Biosphere Reserve, in northwestern Mexico.

Fleas/Hosts	*C. latrans* (17)	*L. rufus* (5)	*M. macroura* (3)	*M. mephitis* (8)	*P. lotor* (4)	*T. taxus* (6)	*U. cinereoargenteus* (7)	*V. macrotis* (14)	Total
Pulex simulans									
% infested hosts	64.7	80	100	75	50	40	71.4	21.4	
Number of fleas	62	7	16	50	5	14	45	8	207
Pulex irritans									
% infested hosts	5.9	-	-	-	-	-	-	92.9	
Number of fleas	2	0	0	0	0	0	0	161	163
Pulex spp.									
% infested hosts	27.8	-	33.3	12.5	25	60	28.6	14.3	
Number of fleas	13	0	6	2	1	4	12	17	55
Echidnophaga gallinacea									
% infested hosts	5.9	80	33.3	50	100	100	14.3	50	
Number of fleas	3	35	3	8	13	21	1	26	110
Euhoplopsyllus glacialis									
% infested hosts	-	-	-	-	-	-	14.3	-	
Number of fleas	0	0	0	0	0	0	1	0	1
Thrassis aridis									
% infested hosts	-	20	33.3	-	-	-	-	-	
Number of fleas	0	1	1	0	0	0	0	0	2
Orchopeas sexdentatus									
% infested hosts	5.9	-	-	-	-	-	-	-	
Number of fleas	1	0	0	0	0	0	0	0	1
Oropsylla montana									
% infested hosts	-	-	-	12.5	-	-	-	-	
Number of fleas	0	0	0	1	0	0	0	0	1
Total	81	43	26	61	19	39	59	212	540

confidence interval (CI). Goodness of fit of the logistic regression model was assessed using Tjur's pseudo-R^2. This coefficient of discrimination (D) can be interpreted similarly as the traditional R2 values, with a scale of 0 to 1 (Tjur 2009). We considered that the presence of *P. simulans* males was substantially explained by the presence/absence of the other flea species when the value of Tjur's pseudo-R2 was >0.15 (Bouchard and Boudreault 2016). Given that females cannot be morphologically differentiated between *P. simulans* and *P. irritans*, only males of these two species were included in the GLM, correlation, and logistic regression models. A p-value < 0.05 was considered statistically significant. GLMs and correlation coefficients were performed using R software (R Foundation for Statistical Computing, Vienna, Austria 2014).

RESULTS

Carnivore and flea community structure

Sixty-four wild carnivores belonging to eight species of seven genera within five families (Canidae, Felidae, Mephitidae, Mustelidae, and Procyonidae) were sampled for fleas in four habitat types (Table 1). In total, 540 fleas were collected, representing two families (Ceratophyllidae and Pulicidae), six genera, and seven species (Table 2). The incidence-based and coverage-based rarefaction procedures suggest that the flea species richness was well represented for the eight carnivore species with a sample coverage of over 90% in all cases. The flea community was dominated by three flea species. *Echidnophaga gallinacea* was the predominant species in bobcats (*Lynx rufus*), raccoons (*Procyon*

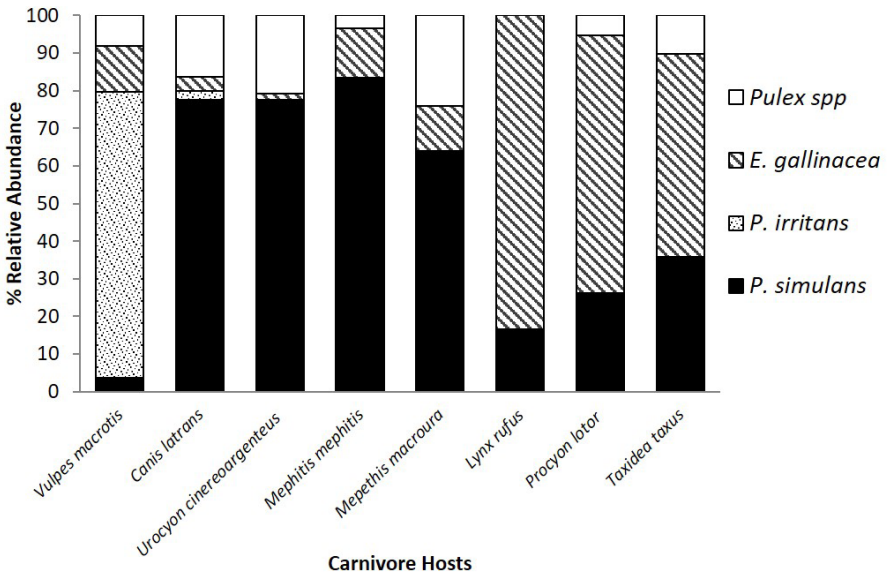

Figure 2. Flea-host association of the three most abundant flea species collected from eight wild carnivore species in the Janos Biosphere Reserve, northwestern Mexico.

lotor), and badgers (*Taxidea taxus*) with a relative abundance (RA) range between 53.9 and 81.4%. *Pulex simulans* was the most abundant flea on coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), and skunks (*Mephitis* spp.) with a RA range between 61.5 and 82.0%. Both *P. simulans* and *E. gallinacea* were represented in all wild carnivore species. Finally, *P. irritans* was the predominant species and almost strictly associated with kit fox (*Vulpes macrotis*).

The other four flea species that we found were less represented in wild carnivores. One *Orchopeas sexdentatus* flea was collected from a coyote (*C. latrans*), one *Oropsylla montana* collected from a striped skunk (*Mephitis mephitis*), one *Euhoplopsyllus glacialis* collected from a gray fox (*U. cinereoargenteus*), and two *Thrassis aridis* fleas collected from a hooded skunk (*Mephitis macroura*) and a bobcat (*Lynx rufus*) (Figure 2, Table 2).

Flea species composition

The Morisita-Horn abundance index of the flea assemblages across carnivore hosts revealed three clusters with a high degree of similarity within each group (range between 88.8-99.7 %) and a low degree of similarity between groups (range between 7.7-57.7%) (Figure 3). These three clusters were associated with the pattern of flea dominance found by host identity, including *P. simulans*, *P. irritans,* and *E. gallinacean,* the species that explain this clustering pattern (Figure 2).

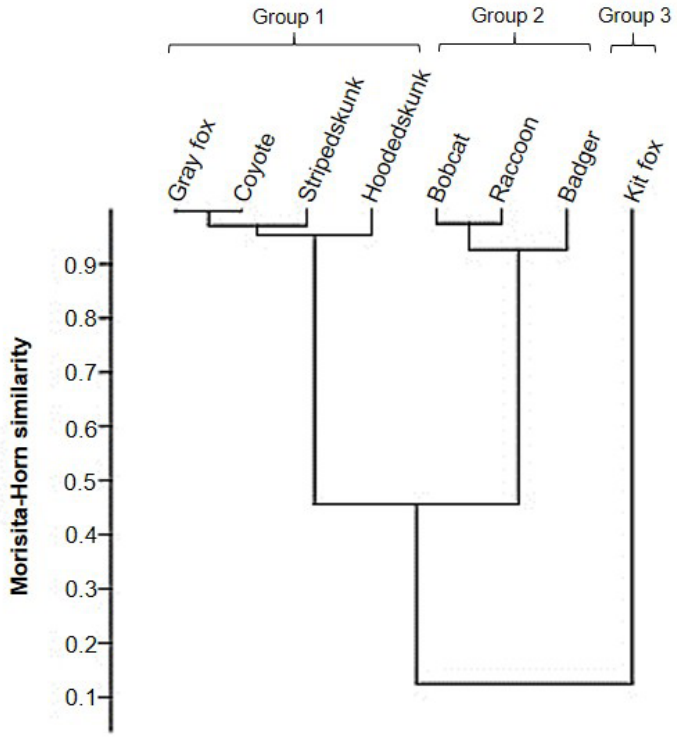

Figure 3. Degree of similarity among flea species assemblages in wild carnivores from the Janos Biosphere Reserve. The similarity within each group ranges between 88.8-99.7 % and between groups ranges between 7.7-57.7%. Tree was created using UPGMA clustering based on species abundances of Morisita Horn similarity values.

Table 3. Generalized linear model analyses of the effects of host identity and season on the abundances of *Pulex simulans*, *P. irritans,* and *Echidnophaga gallinacea* collected from wild carnivores in the Janos Biosphere Reserve, northwestern Mexico. Significant p-values are indicated in bold.

	P. simulans			*P. irritans*			*E. gallinacea*		
Source of variation	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	-0.214	0.430	0.621	-2.450	0.780	**0.002**	-2.210	0.966	**0.026**
C. latrans	0.593	1.095	0.590	-18.558	1.664e + 04	0.999	-14.056	2.052e + 03	0.995
L. rufus	0.613	0.635	0.339	-18.016	7.354e + 03	0.998	3.875	0.974	**0.000**
M. macroura	1.313	0.642	**0.046**	-17.853	9.605e + 03	0.999	2.210	1.340	0.105
M. mephitis	0.968	0.552	0.085	-17.853	5.882e + 03	0.998	2.077	1.142018	0.074
P. lotor	-0.723	1.083	0.507	-18.401	8.228e + 03	0.998	2.593	1.034	**0.015**
T. taxus	-0.459	0.818	0.577	-18.454	6.739e + 03	0.998	2.608	0.998	**0.012**
U. cinereoargenteus	1.079	0.496	**0.034**	18.378	6.213e + 03	0.998	-0.505	1.859	0.787
V. macrotis	-0.824	0.692	0.239	3.444	0.770	**0.000**	2.173	0.982	**0.031**
Season (Spring)	0.314	0.429	0.468	0.705	0.305	**0.025**	0.964	0.398	**0.019**

Abundance analysis

Due to the fact that flea abundances did not differ statistically between habitat types, we removed the habitat variable from the overall model. The GLM shows that the abundances of some flea species are explained by season and host identity (Table 3). *P. irritans* males and *E. gallinacea* abundances were significantly higher in spring than in fall (Figure 4). For host identity, the abundance of flea species varied between carnivore host species. Bobcats, raccoons, badgers, and kit foxes show statistically higher *E. gallinacea* flea abundances in comparison with the other carnivores. The abundance of *P. simulans* males in wild carnivores differed significantly, with gray foxes and striped skunks as hosts that showed the highest abundances of this flea species. In contrast, the abundance of *P. irritans* males was significantly higher on kit foxes than on any other wild carnivore.

We found a tendency and a significant negative correlation among flea abundances within wild carnivore hosts. These results suggest that hosts with high loads of *P. simulans* males had low loads of *P. irritans* males or *E. gallinacea* fleas (Figure 5). Additionally, the logistic regression model showed that the presence of *P. simulans* males is more likely to occur in wild carnivore hosts in which *P. irritans* males is absent and vice-versa. Consistently, the odds of *P. simulans* males presence is lower given the presence of *P. irritans* compared to the absence of this flea species. Since the 95% CI spans from 0.01 to 0.34, the decreased odds (OR: 0.08) of the presence of *P. simulans* with the presence of *P. irritans* does confirm the statistical significance and indicates a higher precision of the OR. Finally, the presence of *P. simulans* fleas was explained by the absence of *P. irritans* (Tjur's pseudo-R^2 0.21).

DISCUSSION

Our results revealed that the patterns of flea assemblages of wild carnivores in JBR were structured by host identity, season, and interspecific interactions. Regarding host identity, we can distinguish some trends of the flea assemblages. Of the seven flea species collected in carnivore hosts, *Pulex simulans*, *P. irritans,* and *Echidnophaga gallinacea* were considered dominant species and *Euhoplopsyllus glacialis*, *Orchopeas sexdentatus*, *Oropsylla montana,* and *Thrassis aridis* were considered rare species. Interestingly, the former group of flea species is classified as generalist and cosmopolitan, whereas the latter are host-specific fleas from rodents and lagomorphs that may be found on wild carnivores as a result of accidental associations.

Several studies agree with our findings that fleas belonging to the genus *Pulex* are the most abundant and prevalent on wild canids and mephitids in the United States as well as Europe. This pattern has been described for kit foxes (*Vulpes macrotis*) (Harrison et al. 2003), swift foxes (*V. velox*) (McGee et al. 2006, Salkeld et al. 2007), Island foxes (*Urocyon littoralis*) (Crooks et al. 2001), gray foxes (*U. cinereoargenteus*) (Gabriel et al. 2009), coyotes (*Canis latrans*) (Hopla 1980), and two species of skunks (*Mephitis mephitis* and *Spilogale gracilis amphiala*) (Crooks et al. 2004; Brinkerhoff 2008) from the U.S. and in red foxes (*V. vulpes*) from Spain (Márquez et al. 2009) and Hungary (Sréter et al. 2003). The *Pulex* genus comprises six species (Whiting et al. 2008), but only two of them, *P. simulans* and *P. irritans*, are reported to infest wild carnivore hosts. In concordance with our findings, *P. irritans* is usually the predominant and the most prevalent flea on the genus *Vulpes*, while *P. simulans* is typically the most common flea on gray foxes and coyotes (Harrison et al. 2003, McGee et al. 2006, Salkeld et al. 2007, Gabriel et al. 2009, Dobler and Pfeffer 2011). As might be expected, we found that *P. simulans* had a broader host distribution than *P. irritans*. While *P. simulans* was found in all carnivore species captured in this study, *P. irritans* was almost always restricted to kit foxes. This finding was consistent with a previous study that concluded that *P. simulans* is more adaptable to a variety of hosts and habitats than *P. irritans* in North America (Hopla 1980). In addition, our results also agree with the hypothesis proposed by the same author that the abundance of *Pulex* species changes by latitude distribution, with *P. simulans* usually being more abundant than *P. irritans* on coyotes in the southern part of their distribution.

On the other hand, the sticktight fleas (*Echidnophaga gallinacea*) are cosmopolitan fleas presumably associated with poultry. However, the wide range of hosts indicate that this flea

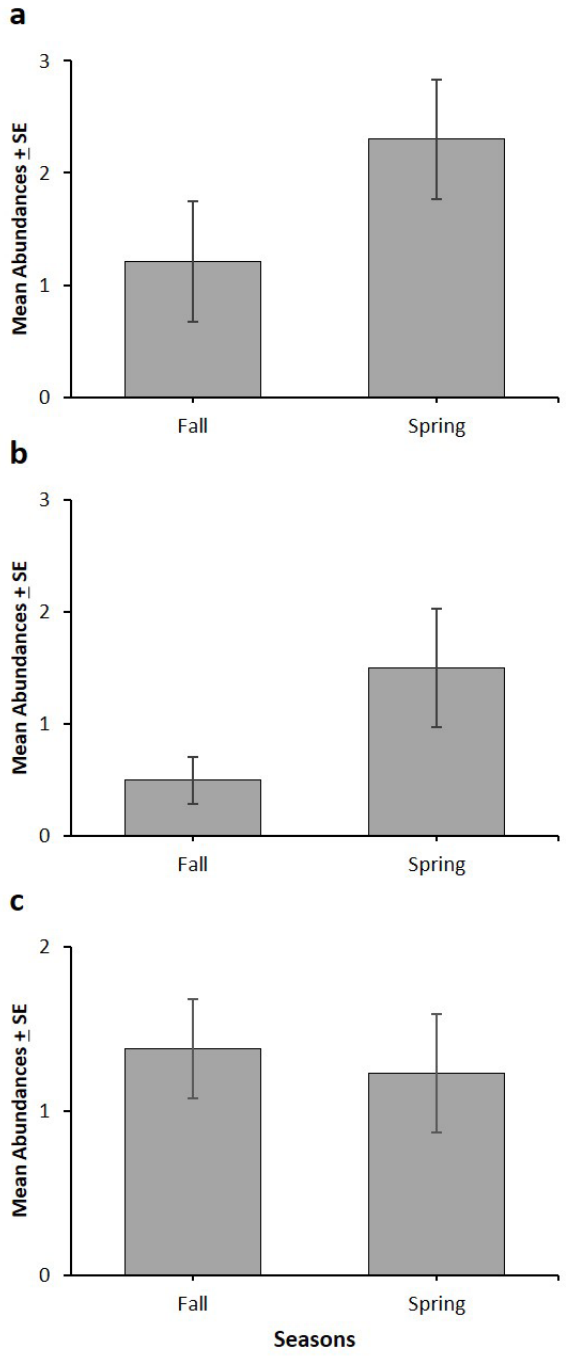

Figure 4. Seasonal variation in mean abundances of (**a**) *E. gallinacea*, (**b**) *P. irritans,* and (**c**) *P. simulans* collected from wild carnivores in the Janos Biosphere Reserve. The values are means ± standard error. Sample sizes for the three-flea species and hosts for each season were: n=41 *E. gallinacea*, n=17 *P. irritans* and n=47 *P. simulans* collected from 34 hosts during autumn, 2013 season and n=68 *E. gallinacea*, n=45 *P. irritans,* and n=37 *P. simulans* collected from 30 hosts during spring, 2014.

is more likely a generalist flea that utilizes a variety of hosts (Boughton et al. 2006). There are several records of *E. gallinacea* flea in wild carnivores, including all the species captured in this study (Eads 1948, Turkowski 1974, Wittrock and Wilson 1974, Patrick and Harrison 1995, Adjemian et al. 2010, Falcón-Ordaz et al. 2012). However, in contrast to our findings, the presence and/or dominance of this flea is usually uncommon in flea assemblages of carnivore hosts (Layne 1971, Harrison et al. 2003, Brinkerhoff 2008, Dobler and Pfeffer 2011). There are only a few studies that have reported *E. gallinacea* as the dominant and most prevalent flea species on carnivores, including ones involving at least three wild carnivore species from Africa (Horak et al. 1999, Horak et al. 2004, Matthee et al. 2011) and two mephitid species from the U.S. (Mead 1963).

Although our findings clearly show that host identity is an important driver of flea community structure, the dominance of the different fleas could be additionally explained by interspecific interactions among flea species. Facilitation or competition may result when two or more parasites coexist in a single host (Stone and Roberts 1991, Graham 2008). The negative relationship between the abundances and/or the occurrences among the three most abundant fleas on wild carnivores in JBR suggests competitive exclusion interactions. Specifically, we found that individual hosts with high loads of *P. simulans* males usually had low loads of *P. irritans* males or *E. gallinacea* fleas and vice versa. In addition, the presence of *P. simulans* males explained the absence of *P. irritans* males. These results contrast with reports on two species belonging to the genus *Oropsylla*, which showed a positive relationship between the abundances of two flea species in black-tailed prairie dogs (Brinkerhoff et al. 2006). The previous authors suggested that the findings regarding the facilitation interactions among fleas might be related to host immune suppression ("top-down" regulation). Also, the apparent competitive exclusion among fleas found in this study may be explained by the direct interaction, through physical or chemical communication, or by indirect interaction, through resource exploitation ("Bottom up" regulation). However, these hypotheses have been mainly tested in endoparasite systems (Dobson and Barnes 1995, Graham 2008, Cézilly et al. 2014). Although several studies have described an apparent competitive exclusion among ectoparasites, such as fleas, ticks, and lice (Barnes 1965, Day and Benton 1980, Krasnov et al. 2005, Bush and Malenke 2008, Tello et al. 2008, Hoffmann et al. 2016), to our knowledge only three studies were based on experimental approaches and contribute to understanding the effects and mechanisms mediating the interactions among them. The first one found that the removal of dominant tick species impact directly the abundances of chiggers and lice in sengis (*Rhynchocyon* spp.) (Hoffmann et al. 2016), while the second and third studies found that larvae (Krasnov et al. 2005) and imago (Khokhlova et al. 2016) of different flea species shows competitive interaction which may be driven by resources exploitation. Further experimental studies are needed to test the mechanisms driving the apparent competitive exclusion among fleas of wild carnivores in the JBR.

As far as we know, this is the first evidence of *Orchopeas sexdentatus* collected from coyotes, and *Thrassis aridis* collected from a striped skunk and a bobcat. However, these two-flea species are primarily parasites of woodrats (*Neotoma* spp.) and kangaroo

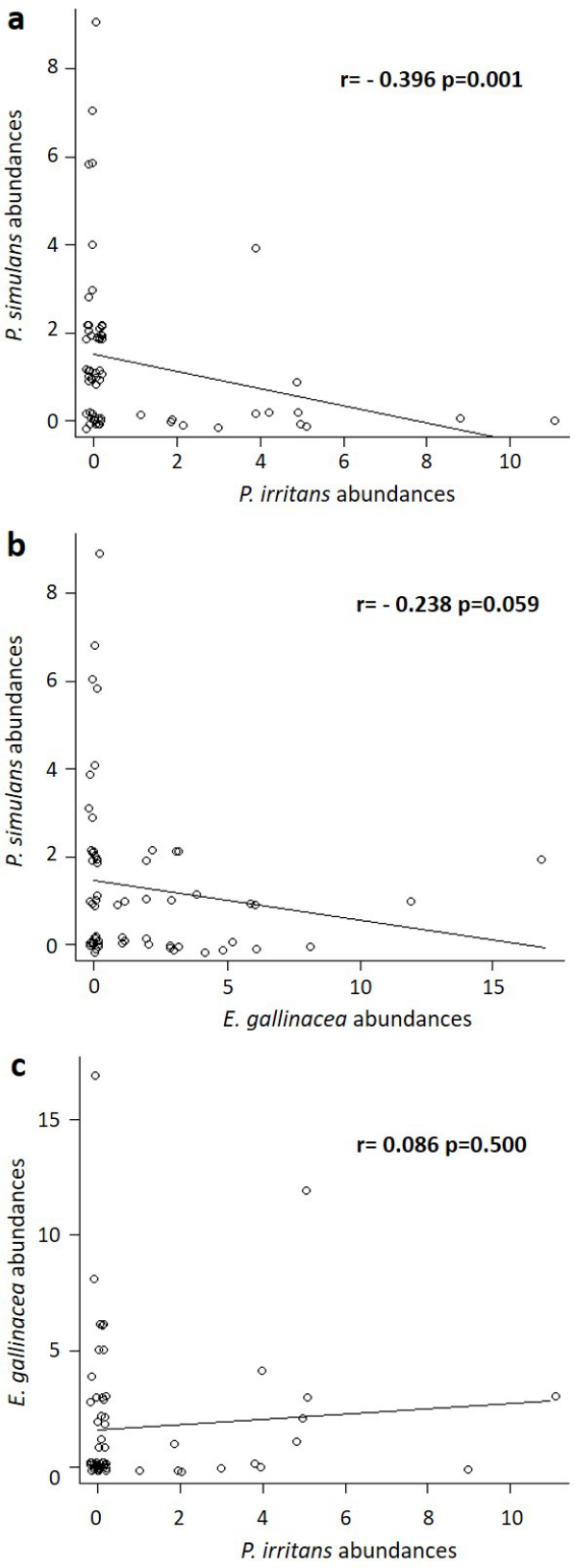

Figure 5. Relationship between *P. simulans* abundances and (a) *P. irritans* and (b) *E. gallinacea* abundances across eight wild carnivore species in the Janos Biosphere Reserve, northwestern Mexico. Plots show the abundances of flea species in each individual host. Lines represent linear correlation of the relationship between flea dominant species.

rats (*Dypodomys* spp.), respectively (Stark 1970, Lewis 2000). In addition, *T. aridis* has been collected from hooded skunks (*Mephitis macroura*) in Mexico (Acosta et al. 2006). *E. glacialis* is a flea that usually infests lagomorphs (Larson et al. 2011) but has also been collected from gray foxes in Mexico (Hernández-Camacho et al. 2016) and in the U.S. (Harrison et al. 2003). *Oropsylla montana*, a flea typically associated with ground squirrel hosts, especially *Spermophilus variegatus* (Lewis 2002), has also been commonly found on skunks from north America (Mead 1963, Hubbard 1968, Brinkerhoff 2008). All these rodent hosts have been previously recorded in Janos Biosphere Reserve (Rubio et al. 2014, Rubio et al. 2015). Hence, the accidental associations of rodent-specific fleas in wild carnivores may be driven by ecological factors, such as the exchange of burrows by burrow-dwelling hosts or predator-prey relationships (Beaucournu et al. 2005, Hastriter and Whiting 2005, Krasnov 2008).

We found non-significant differences of flea abundances among the different habitats. Various studies have found that the habitat is an important driver for explaining the flea assemblage structure on striped skunks (Brinkerhoff 2008) and small mammal hosts (Krasnov et al. 1997, Krasnov et al. 2006c). However, the changes in the patterns of flea assemblages among habitat types within host species are often explained directly by both the habitat selection of the hosts and environmental factors (Krasnov et al. 1997). This is consistent with our findings, because the lack of this relationship between flea abundance and habitat type might be explained by the fact that the three distinct assemblage clusters of fleas in wild carnivores were grouped by host identity instead of habitat. The similarity among all clusters was low and these clusters were composed of different carnivore species found in distinct habitats. Only the cluster characterized by the dominance of *P. irritans* was specifically associated to kit foxes, a carnivore species which is in turn almost always restricted to grassland habitat. Similarly, previous studies have found that the segregation patterns of flea communities in small mammals is better explained by host factors, such as host identity (composition), instead of habitat types (Krasnov et al. 2006b, Cevidanes et al. 2016). In addition, similar to other studies (Krasnov et al. 1997, Cevidanes et al. 2016) we found that the community structure of fleas on wild carnivores in JBR is related to environmental factors explained by seasonal changes. This relationship between fleas and season is often driven by climatic variations, such as temperature and rainfall (Krasnov et al. 2001a, Krasnov et al. 2001b, Gálvez et al. 2016, Kreppel et al. 2016). Our results showed that the higher abundances of fleas in spring season are associated with the rainy season in the study area. Although this relationship may vary according to flea species, consistently in most of the studies the rainfall was positively correlated with flea abundances (Chotelersak et al. 2015, Gálvez et al. 2016).

Almost all the flea species found in this study have been identified as potential vectors of different flea-borne diseases. Among these fleas are *Echidnophaga gallinacea*, *Euhoplopsyllus glacialis*, *Pulex simulans*, *P. irritans*, *Orchopeas sexdentatus*, and *Oropsylla montana*, all of which have been found naturally infected with *Yersinia pestis*, the causative agent of plague (Harrison et al. 2003, Brinkerhoff et al. 2008, Tripp et al. 2009). In addition, *Pulex* spp. and *E. gallinacea* have been reported to be naturally infected with other vector-borne disease agents, such

as bartonellosis (Gabriel et al. 2009, López-Pérez et al. 2017) and rickettsioses (Leulmi et al. 2014, Rakotonanahary et al. 2017). In addition, previous studies have found that the maintenance and transmission of flea-borne diseases is positively related to prevalence and abundance of fleas on hosts (Lorange et al. 2005, Krasnov et al. 2006a). Hence, our findings may be of relevance regarding flea-borne disease risks. Furthermore, the human settlements and farming activities are increasing in Janos and nearby areas (Ceballos et al. 2010), which in turn may affect the dynamics at the wildlife-livestock-human interface. For instance, a previous study showed that domestic dogs occur at high densities in settlements of the JBR and have free roaming activities that may increase encounters with wild carnivores (Almuna 2016, unpublished thesis, Universidad de Chile). Therefore, knowledge of flea composition and flea infestation of wild carnivores in this region is important not only because it identifies the potential flea vectors, but it also provides information needed to design and implement programs to manage flea-borne diseases for purposes of human health or wildlife conservation.

Acknowledgments

This study was supported by CONACyT project no. 179482, Graduate student Support *program (PAEP-UNAM) and CDC Global Diseases Detection program. We would like to thank A*. Vigueras, H. Mendoza, J. Lopez, L. Aguilar, and M. Moguel for helping us during field sampling. We thank J. Diaz, E. Ponce and R. Sierra (Janos Grassland Biological Station, IE-UNAM) and A. Esquer and L. Garcia (Rancho El Uno TNC) for logistical support in the field. We are grateful to L. Lecuona (APHIS-USDA) for logistical support. A.M. López-Pérez is a student in the Ph.D. program, Programa de Doctorado en Ciencias de la Producción y la Salud Animal (FMVZ-UNAM) and was supported by CONACYT Grant Scholarship.

REFERENCES CITED

Acosta, R., J.A. Fernández, and J. Falcón-Ordaz. 2006. New records of mammal fleas (Siphonaptera) in northern and central Mexico. Entomol. News 117: 69–72.

Adjemian, J., S. Parks, K. McElroy, J. Campbell, M.E. Eremeeva, W.L. Nicholson, J. McQuiston, and J. Taylor. 2010. Murine typhus in Austin, Texas, USA, 2008. Emerg. Infect. Dis. 16: 412–417.

Barnes, A.M. 1965. Three new species of the genus *Anomiopsyllus*. Pan Pacific Entomol. 41: 272–280.

Beaucournu, J.C., B. Degeilh, and C. Guiguen. 2005. Bird fleas (Insecta: Siphonaptera): taxonomic diversity, biogeographical distribution. Parasite 12: 111–21.

Bouchard, M. and C. Boudreault. 2016. Is metapopulation size important for the conservation of understory plants and epiphytic lichens? Biol. Conserv. 195: 187–195.

Boughton, R.K., J.W. Atwell, and S.J. Schoech. 2006. An introduced generalist parasite, the sticktight flea (*Echidnophaga gallinacea*), and its pathology in the threatened Florida scrub-jay (*Aphelocoma coerulescens*). J. Parasitol. 92: 941–948.

Brinkerhoff, R., C. Ray, B. Thiagarajan, S.K. Collinge, J.F. Cully, B. Holmes, and K.L. Gage. 2008. Prairie dog presence affects occurrence patterns of disease vectors on small mammals. Ecography 31: 654–662.

Brinkerhoff, R.J. 2008. Habitat-associated differences in flea assemblages of striped skunks (*Mephitis mephitis*). Comp. Parasitol. 75: 127–131.

Brinkerhoff, R.J., A.B. Markeson, J.H. Knouft, K.L. Gage, and J.A. Montenieri. 2006. Abundance patterns of two *Oropsylla* (Ceratophyllidae: Siphonaptera) species on black-tailed prairie dog (*Cynomys ludovicianus*) hosts. J. Vector Ecol. 31: 355–363.

Bush, S.E. and J.R. Malenke. 2008. Host defence mediates interspecific competition in ectoparasites. J. Anim. Ecol. 77: 558–564.

Ceballos, G., A. Davidson, R. List, J. Pacheco, P. Manzano-Fischer, G. Santos-Barrera, and J. Cruzado. 2010. Rapid decline of a grassland system and its ecological and conservation implications. PLoS One 5(1): e8562.

Cevidanes, A., T. Proboste, A.D. Chirife, and J. Millán. 2016. Differences in the ectoparasite fauna between micromammals captured in natural and adjacent residential areas are better explained by sex and season than by type of habitat. Parasitol. Res. 115: 2203–2211.

Cézilly, F., M.J. Perrot-Minnot, and T. Rigaud. 2014. Cooperation and conflict in host manipulation: interactions among macro-parasites and micro-organisms. Front. Microbiol. 5: 1–10.

Chao, A., N.J. Gotelli, T.C. Hsieh, E.L. Sander, K.H. Ma, R.K. Colwell, and A.M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84: 45–67.

Chao, A., K.H. Ma, and T.C. Hsieh. 2016. iNEXT (iNterpolation and EXTrapolation) Online: software for interpolation and extrapolation of species diversity. program and user's guide published athttp//chao.stat.nthu.edu.tw/wordpress/software_download/.

Chotelersak, K., C. Apiwathnasorn, S. Sungvornyothin, C. Panasoponkul, Y. Samung, and J. Ruangsittichai. 2015. Correlation of host specificity, environmental factors and oriental rat flea abundance. Southeast Asian J. Trop. Med. Publ. Hlth. 46: 198–206.

Crooks, K.R., D.K. Garcelon, C.A. Scott, J.E. Depue, J.T. Wilcox, R.B. Kimsey, and D.H. Van Vuren. 2004. Ectoparasites of a threatened insular endemic mammalian carnivore: the island spotted skunk. Am. Midl. Nat. 151: 35–41.

Crooks, K.R., C.A. Scott, L. Angeloni, L. Bowen, R.B. Kimsey, and D.H. Van Vuren. 2001. Ectoparasites of the island fox on Santa Cruz island. J. Wildl. Dis. 37: 189–193.

Day, J.F. and A.H. Benton. 1980. Population dynamics and coevolution of adult siphonapteran parasites of the southern flying squirrel (*Glaucomys volans volans*). Am. Midl. Nat. 103: 333–338.

Dobler, G. and M. Pfeffer. 2011. Fleas as parasites of the family Canidae. Parasit. Vectors 4: 1-12.

Dobson, R.J. and E.H. Barnes. 1995. Interaction between *Ostertagia circumcincta* and *Haemonchus contortus* infection in young lambs. Int. J. Parasitol. 25: 495–501.

Durden, L. and N. Hinkle. 2009. Fleas (Siphonaptera). In: G. Mullen and L.A. Durden (eds.), *Medical and Veterinary Entomology*. Academic Press, San Diego CA. pp. 115–136.

Eads, R.B. 1948. Ectoparasites from a series of Texas coyotes. J. Mammal. 29: 268–271.

Eremeeva, M., H. Gerns, S. Lydy, J. Goo, E. Ryan, S. Mathew, M. Ferraro, J. Holden, W. Nicholson, G. Dasch, and J. Koehler. 2007. Bacteremia, fever, and splenomegaly caused by a newly recognized *Bartonella* species. N. Engl. J. Med. 356: 2381–2387.

Falcón-Ordaz, J., R. Acosta, J.A. Fernández, and G. Lira-Guerrero. 2012. Helmintos y sifonáptoreos parásitos de cinco especies de roedores en localidades de la Cuenca Oriental, en el Centro de México. Acta Zool. Mex. 28: 287–304.

Friggens, M.M. and P. Beier. 2010. Anthropogenic disturbance and the risk of flea-borne disease transmission. Oecologia 164: 809–820.

Furman, D.P. and P.E. Catts. 1982. *Manual of Medical Entomology*. Cambridge University Press, NY. 207 pp.

Gabriel, M.W., J. Henn, J.E. Foley, R.N. Brown, R.W. Kasten, P. Foley, and B.B. Chomel. 2009. Zoonotic *Bartonella* species in fleas collected on gray foxes (*Urocyon cinereoargenteus*). Vector Borne Zoonot. Dis. 9: 597–602.

Gallina, S. and López-González. 2011. *Manual de Técnicas para el Estudio de la Fauna*. Volume 1. Universidad Autónoma de Queretaro-Instituto de Ecología, A.C. Queretaro, Mexico. 377 pp.

Gálvez, R., A. Montoya, R. Checa, O. Martin, V. Marino, and G. Miró. 2016. Flea species infesting dogs in Spain: updated spatial and seasonal distribution patterns. Med. Vet. Entomol. 31: 107–113.

García, E. 1981. *Modificaciones al Sistema de Clasificación Climática de Köeppen*. Instituto de Geografía. Universidad Nacional Autónoma de México, D.F., México. 246 pp.

Gracia, M.J., C. Calvete, R. Estrada, J.A. Castillo, M.A. Peribáñez, and J. Lucientes. 2013. Survey of flea infestation in cats in Spain. Med. Vet. Entomol. 27: 175–180.

Graham, A.L. 2008. Ecological rules governing helminth microparasite coinfection. Proc. Natl. Acad. Sci. 105: 566–570.

Harrison, R.L., M.J. Patrick, and C.G. Schmitt. 2003. Foxes, fleas, and plague in New Mexico. Southwest Nat. 48: 720–722.

Hastriter, M.W. and M.F. Whiting. 2005. Records of fleas (Siphonaptera) of carnivores from Idaho. Proc. Entomol. Soc. Wash. 107: 417–427.

Hernández-Camacho, N., R.F. Pineda-López, M.Guerrero-Carrillo, G.J. Cantó-Alarcón, R.W. Jones, M.A. Moreno-Pérez, J.J. Mosqueda-Gualito, S. Zamora-Ledesma, and B. Camacho-Macías. 2016. Gray fox (*Urocyon cinereoargenteus*) parasite diversity in central Mexico. Int. J. Parasitol. Parasites Wildl. 5: 207–210.

Hoffmann, S., I.G. Horak, N.C. Bennett, and H. Lutermann. 2016. Evidence for interspecific interactions in the ectoparasite infracommunity of a wild mammal. Parasit. Vectors 9: 1-11.

Hopla, C. 1980. A study of the host associations and zoogeography of *Pulex*. In: R. Traub and H. Starcke (eds.) *Proceedings of the International Conference on Fleas.* Rotterdam, Aston Wold, Peterbotough, UK. pp. 185–207.

Horak, I.G., J.C. Beaucournu, and L.E. Braack. 2004. Parasites of domestic and wild animals in South Africa. XLIV. Fleas (Insecta: Siphonaptera: Pulicidae) collected from 15 carnivore species. Onderstepoort J. Vet. Res. 71: 9–14.

Horak, I.G., F. Chaparr, J. Beaucournu, and J.P. Louw. 1999. Parasites of domestic and wild animals in South Africa. XXXVI. Arthropod parasites of yellow mongooses, *Cynictis penicillata* (G . Cuvier, 1829). Onderstepoort J. Vet. Res. 66: 33–38.

Hubbard, C.A. 1968. *Fleas of Western North America*. Hafner Publishing, NY.

INEGI. 2013. Espacio mapa Nacozari H12-6. Aguascalientes, Ags. Mexico.

Khokhlova, I.S., E.M. Dlugosz, and B.R. Krasnov. 2016. Experimental evidence of negative interspecific interactions among imago fleas: flea and host identities matter. Parasitol. Res. 115: 937–947.

Krasnov, B. 2008. *Functional and Evolutionary Ecology of Fleas: a Model for Ecological Parasitology*. Cambridge University Press, Cambridge. 593 pp.

Krasnov, B.R., N.V. Burdelova, I.S. Khokhlova, G.I. Shenbrot, and A. Degen 2005. Larval interspecific competition in two flea species parasitic on the same rodent host. Ecol. Entomol. 30: 146–155.

Krasnov, B.R., I.S. Khokhlova, L.J. Fielden, and N.V. Burdelova. 2001a. Development rates of two *Xenopsylla* flea species in relation to air temperature and humidity. Med. Vet. Entomol. 15: 249–258.

Krasnov, B.R., I.S. Khokhlova, L.J. Fielden, and N.V. Burdelova. 2001b. 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, B.R., G.I. Shenbrot, S.G. Medvedev, V.S. Vatschenok, and I.S. Khokhlova. 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, B.R., G.I. Shenbrot, D. Mouillot, I.S. Khokhlova, and R. Poulin. 2006a. Ecological characteristics of flea species relate to their suitability as plague vectors. Oecologia 149: 474–481.

Krasnov, B.R., M. Stanko, D. Miklisova, and S. Morand. 2006b. Habitat variation in species composition of flea assemblages on small mammals in central Europe. Ecol. Res. 21: 460–469.

Krasnov, B.R., M. Stanko, D. Miklisova, and S. Morand. 2006c. Host specificity, parasite community size and the relation between abundance and its variance. Evol. Ecol. 20: 75–91.

Kreeger, T.J. and J.M. Arnemo. 2012. *Handbook of Wildlife Chemical Immobilization*. Terry J. Kreeger, Sybille, WY. 448 pp.

Kreppel, K.S., S. Telfer, M. Rajerison, A. Morse, and M. Baylis. 2016. Effect of temperature and relative humidity on the development times and survival of *Synopsyllus fonquerniei* and *Xenopsylla cheopis*, the flea vectors of plague in Madagascar. Parasit. Vectors 9: 1–10.

Larson, O.R., S.G. Platt, Z.F. Horse, T.R. Rainwater, and S.M. Miller. 2011. Distribution records and comments on fleas in Southwestern South Dakota. West North Am. Nat. 71: 240–246.

Layne, J. 1971. Fleas (Siphonaptera) of Florida. Florida Entomol. 54: 35–51.

Leulmi, H., C. Socolovschi, A. Laudisoit, G. Houemenou, B.

Davoust, I. Bitam, D. Raoult, and P. Parola. 2014. Detection of *Rickettsia felis*, *Rickettsia typhi*, *Bartonella* species and *Yersinia pestis* in fleas (Siphonaptera) from Africa. PLoS Negl. Trop. Dis. 8(10): e3152.

Lewis, R.E. 2000. A taxonomic review of the North American genus *Orchopeas* Jordan, 1933 (Siphonaptera: Ceratophyllidae: Ceratophyllinae). J. Vector Ecol. 25: 164–189.

Lewis, R.E. 2002. A review of the North American species of *Oropsylla* Wagner and Ioff, 1926 (Siphonaptera: Ceratophyllidae: Ceratophyllinae). J. Vector Ecol. 27: 184–206.

Linardi, P.M. and B.R. Krasnov. 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.

Lledó, L., C. Giménez-Pardo, G. Domínguez-Peñafiel, R. Sousa, M.I. Gegúndez, N. Casado, and A. Criado. 2010. Molecular detection of hemoprotozoa and Rickettsia species in arthropods collected from wild animals in the Burgos Province, Spain. Vector Borne Zoonotic Dis. 10: 735–738.

López-Pérez, A.M., L. Osikowicz, Y. Bai, J. Montenieri, A. Rubio, K. Moreno, K. Gage, G. Suzán, and M. Kosoy. 2017. Prevalence and phylogenetic analysis of bartonella species of wild carnivores and their fleas in Northwestern Mexico. Ecohealth 14: 116-129.

Lorange, E.A., B.L. Race, F. Sebbane, and B.J. Hinnebusch. 2005. Poor vector competence of fleas and the evolution of hypervirulence in *Yersinia pestis*. J. Infect. Dis. 191: 1907–1912.

Márquez, F.J, J. Millán, J.J. Rodríguez-Liébana, I. García-Egea, and M.A. Muniain. 2009. Detection and identification of *Bartonella* sp. in fleas from carnivorous mammals in Andalusia, Spain. Med. Vet. Entomol. 23: 393–398.

Marshal, A.G. 1981. *The Ecology of Ectoparasite Insects*. Academic Press. London, 446 pp.

Matthee, S., L. van der Mescht, B. Wilson, and N. Lamberski 2011. Flea diversity on small carnivores in the Northern Cape Province, South Africa. African Zool. 46: 27–31.

McGee, B.K., M.J. Butler, D.B. Pence, J.L. Alexander, J.B. Nissen, W.B. Ballard, and K.L. Nicholson. 2006. Possible vector dissemination by swift foxes following a plague epizootic in black-tailed prairie dogs in northwestern Texas. J. Wildl. Dis. 42: 415–20.

Mead, R.A. 1963. Some aspects of parasitism in skunks of the Sacramento Valley of California. Am. Midl. Nat. 70: 164–167.

Patrick, M.J. and R.L. Harrison. 1995. Fleas on gray foxes in New Mexico. J. Med. Entomol. 32: 201–204.

Rakotonanahary, R.J.L., A. Harrison, A.N. Maina, I. Jiang, A.L. Richards, M. Rajerison, and S. Telfer. 2017. Molecular and serological evidence of flea-associated typhus group and spotted fever group rickettsial infections in Madagascar. Parasit. Vectors 10: 1–8.

Rubio, A.V., R. Avila-Flores, L.M. Osikowicz, Y. Bai, G. Suzán, and M.Y. Kosoy. 2014. Prevalence and genetic diversity of bartonella strains in rodents from northwestern Mexico. Vector Borne Zoonotic Dis. 14: 838–845.

Rubio, A.V., A.L. Vigueras-Galván, T. Schountz, K. Moreno-Torres, R. List, R.E. Sarmiento-Silva, R. Ávila-Flores, and G. Suzán 2015. Abundance of hantavirus hosts in a landscape with black-tailed prairie dog colonies in northwestern Mexico. Mamm. Biol. - Zeitschrift für Säugetierkd 80: 491–495.

Salkeld, D.J., R.J. Eisen, P. Stapp, A.P. Wilder, J. Lowell, D.W. Tripp, D. Albertson, and M.F. Antolin. 2007. The potential role of swift foxes (*Vulpes velox*) and their fleas in plague outbreaks in prairie dogs. J. Wildl. Dis. 43: 425–431.

Sikes, R.S. and W.L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92: 235–253.

Sréter, T., Z. Széll, and I. Varga. 2003. Ectoparasite infestations of red foxes (*Vulpes vulpes*) in Hungary. Vet. Parasitol. 115: 349–354.

Stark. H.E. 1970. A revision of the flea genus *Thrassis* Jordan 1933 (Siphonaptera: Ceratophyllidae) with observations on ecology and relationship to plague. Univ. Calif. Publ. Entomol. 53:1-183.

Stone, L. and A. Roberts. 1991. Conditions for a species to gain advantage from the presence of competitors. Ecology 72: 1964–1972.

Tello, J., R.D. Stevens, and C.W. Dick. 2008. Patterns of species co-occurrence and density compensation: A test for interspecific competition in bat ectoparasite infracommunities. Oikos 117: 693–702.

Tripp, D.W., K.L. Gage, J.A. Montenieri, and M.F. Antolin. 2009. Flea abundance on black-tailed prairie dogs (*Cynomys ludovicianus*) increases during plague epizootics. Vector-Borne Zoonotic Dis. 9: 313–321.

Tjur, T. 2009. Coefficients of determination in logistic regression models—a new proposal: the coefficient of discrimination. Am. Stat. 63: 366–372.

Turkowski, F.J. 1974. Fleas of Arizona Gray and Kit foxes. J. Arizona Acad. Sci. 9: 1-55.

Whiting, M.F., A.S. Whiting, M.W. Hastriter, and K. Dittmar. 2008. A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. Cladistics 24: 677–707.

Wittrock, D. and N. Wilson. 1974. Fleas of badger, *Taxidea taxus* (Schreber, 1778), in Northwestern Iowa with a list of species recorded fron North America. Iowa State J. Res. 49: 9–15.

Young, H.S., R. Dirzo, D.J. McCauley, B. Agwanda, L. Cattaneo, K. Dittmar, R.P. Eckerlin, R.C. Fleischer, L.E. Helgen, A. Hintz, J. Montenieri, S. Zhao, and K.M. Helgen. 2015. Drivers of intensity and prevalence of flea parasitism on small mammals in East African savanna ecosystems. J. Parasitol. 101: 327–335.