

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

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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, bartonellosis, and rickettsiosis. 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 (Marshall 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, Chotellersak 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 (30° 51' 50" N, 108° 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 15.7° C in plains at 1,200 m above sea level to a mean annual of 11.8° 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

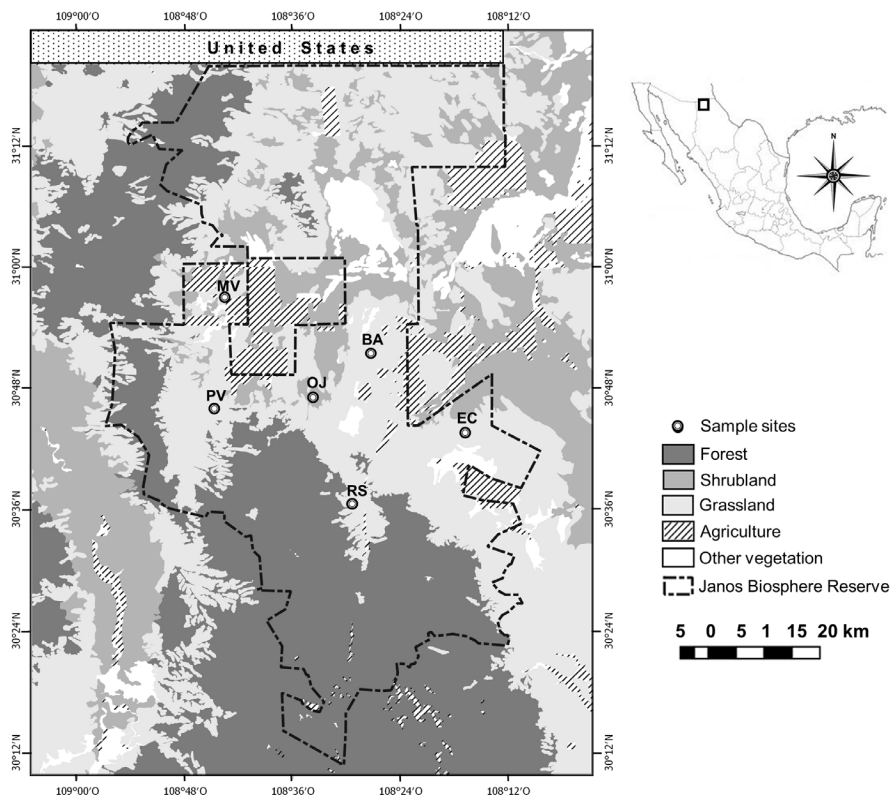


Figure 1. Location of sites and habitat types where carnivores and their fleas were sampled in the Janos Biosphere Reserve, northwestern Mexico (INEGI 2013).

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
<i>Canis latrans</i>	6 (EC, LB, MV)	4 (LB, OJ)	6 (RS)	1 (RS)	17
<i>Lynx rufus</i>	1 (EC)	3 (OJ)	0	1 (RS)	5
<i>Mephitis macroura</i>	0	3 (OJ)	0	0	3
<i>Mephitis mephitis</i>	1 (LB)	1 (OJ)	6 (RS)	0	8
<i>Procyon lotor</i>	0	2 (OJ)	2 (RS)	0	4
<i>Taxidea taxus</i>	3 (EC)	3 (LB, MV, OJ)	0	0	6
<i>Urocyon cinereoargenteus</i>	0	0	3 (RS)	4 (RS)	7
<i>Vulpes macrotis</i>	13 (EC, LB, MV)	1 (MV)	0	0	14
Total	24	17	17	6	64

^aEC: 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	<i>C. latrans</i> (17)	<i>L. rufus</i> (5)	<i>M. macroura</i> (3)	<i>M. mephitis</i> (8)	<i>P. lotor</i> (4)	<i>T. taxus</i> (6)	<i>U. cinereoargenteus</i> (7)	<i>V. macrotis</i> (14)	Total
<i>Pulex simulans</i>									
% 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
<i>Pulex irritans</i>									
% infested hosts	5.9	-	-	-	-	-	-	92.9	
Number of fleas	2	0	0	0	0	0	0	161	163
<i>Pulex</i> 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
<i>Echidnophaga gallinacea</i>									
% 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
<i>Euhoplosyllus glacialis</i>									
% infested hosts	-	-	-	-	-	-	14.3	-	
Number of fleas	0	0	0	0	0	0	1	0	1
<i>Thrassis aridis</i>									
% infested hosts	-	20	33.3	-	-	-	-	-	
Number of fleas	0	1	1	0	0	0	0	0	2
<i>Orchopeas sexdentatus</i>									
% infested hosts	5.9	-	-	-	-	-	-	-	
Number of fleas	1	0	0	0	0	0	0	0	1
<i>Oropsylla montana</i>									
% 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 R^2 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- R^2 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*

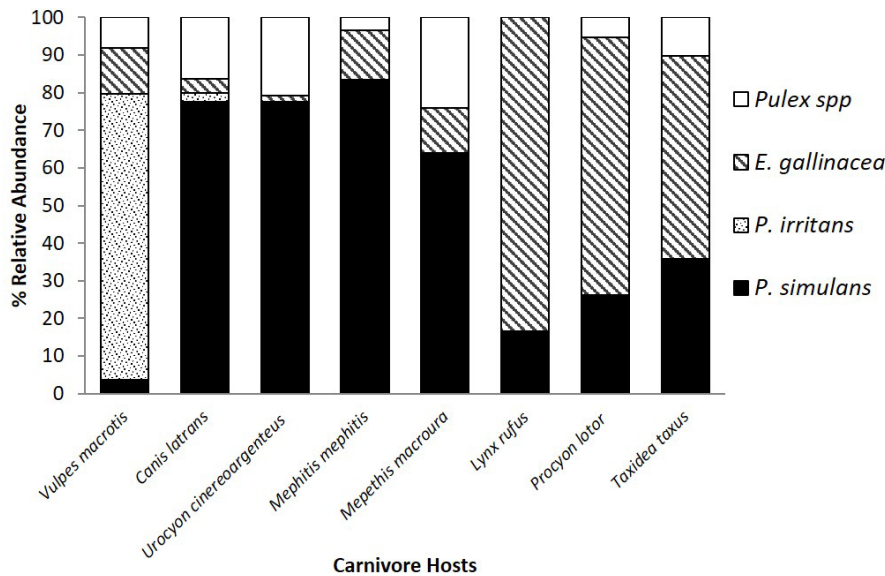


Figure 2. Flea-host association of the three most abundant flea species collected from eight wild carnivore species in the Janos Biosphere Reserve, northwestern Mexico.

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. gallinacea*, the species that explain this clustering pattern (Figure 2).

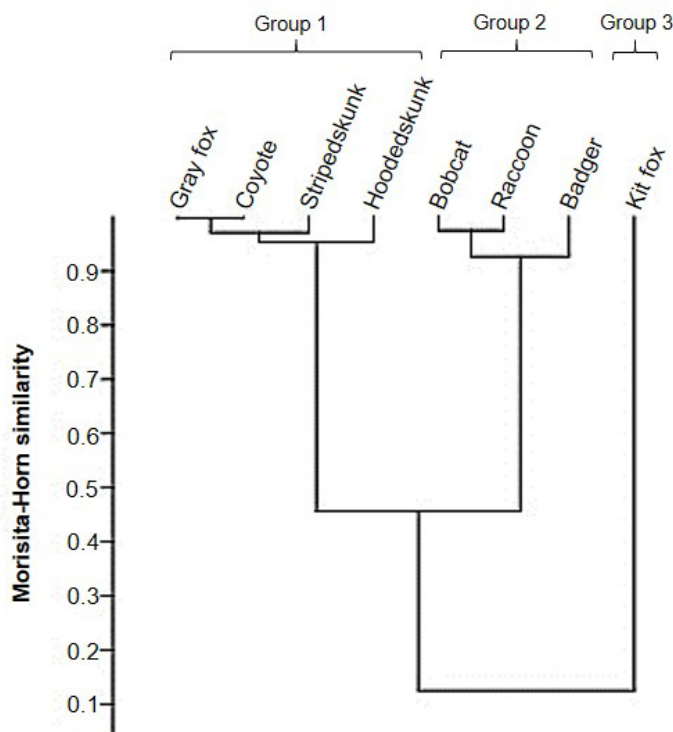


Figure 3. Degree of similarity among flea species assemblages in wild carnivores from the Janos Biosphere Reserve. The similarity within each group ranges between 88.8-99.7 % and between groups ranges between 7.7-57.7%. Tree was created using UPGMA clustering based on species abundances of Morisita Horn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

Source of variation	<i>P. simulans</i>			<i>P. irritans</i>			<i>E. gallinacea</i>		
	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
<i>C. latrans</i>	0.593	1.095	0.590	-18.558	1.664e + 04	0.999	-14.056	2.052e + 03	0.995
<i>L. rufus</i>	0.613	0.635	0.339	-18.016	7.354e + 03	0.998	3.875	0.974	0.000
<i>M. macroura</i>	1.313	0.642	0.046	-17.853	9.605e + 03	0.999	2.210	1.340	0.105
<i>M. mephitis</i>	0.968	0.552	0.085	-17.853	5.882e + 03	0.998	2.077	1.142018	0.074
<i>P. lotor</i>	-0.723	1.083	0.507	-18.401	8.228e + 03	0.998	2.593	1.034	0.015
<i>T. taxus</i>	-0.459	0.818	0.577	-18.454	6.739e + 03	0.998	2.608	0.998	0.012
<i>U. cinereoargenteus</i>	1.079	0.496	0.034	18.378	6.213e + 03	0.998	-0.505	1.859	0.787
<i>V. macrotis</i>	-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

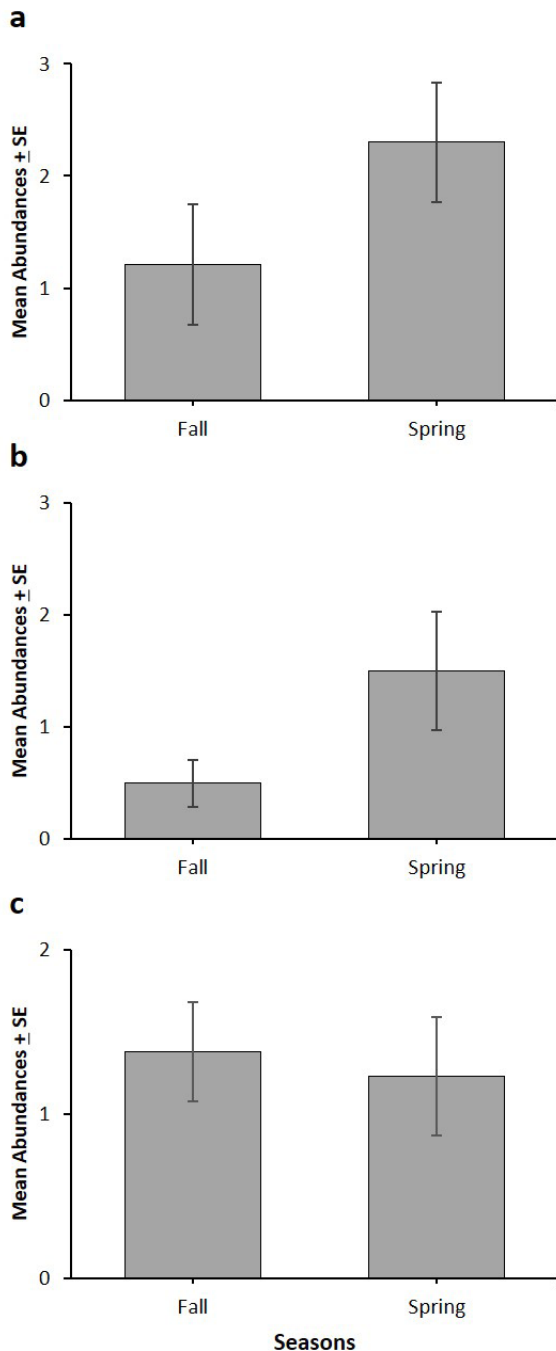


Figure 4. Seasonal variation in mean abundances of (a) *E. gallinacea*, (b) *P. irritans*, and (c) *P. simulans* collected from wild carnivores in the Janos Biosphere Reserve. The values are means \pm standard error. Sample sizes for the three-flea species and hosts for each season were: $n=41$ *E. gallinacea*, $n=17$ *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

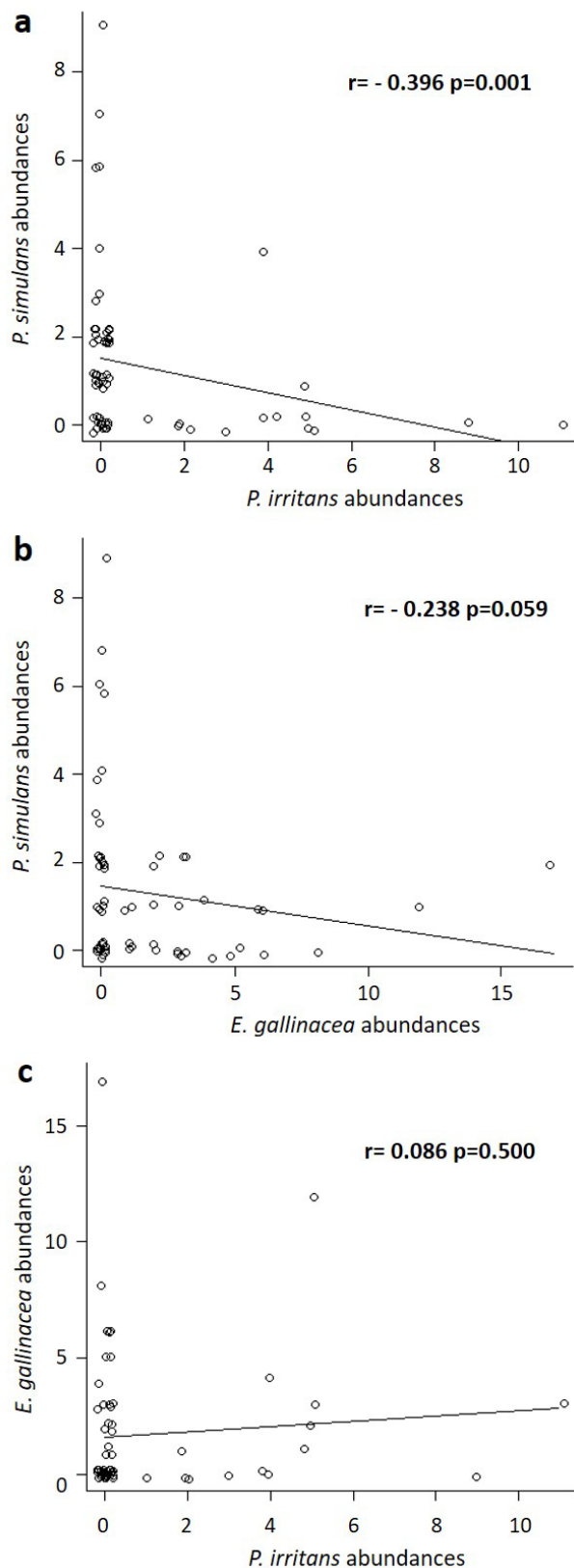


Figure 5. Relationship between *P. simulans* abundances and (a) *P. irritans* and (b) *E. gallinacea* abundances across eight wild carnivore species in the Janos Biosphere Reserve, northwestern Mexico. Plots show the abundances of flea species in each individual host. Lines represent linear correlation 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, Cevitanes et al. 2016). In addition, similar to other studies (Krasnov et al. 1997, Cevitanes 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 (Chotellersak 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.

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