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# A Diverse Flea (Siphonaptera) Assemblage from the Small Mammals of Central New Mexico

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**Abstract**
The geographical ranges of many mammals and their associated parasites are dynamic. Comprehensive documentation of these communities over time provides a foundation for interpreting how changing environmental conditions, driven by accelerating climate change, other anthropogenic disturbances, and natural events, may influence host-parasite interactions. Fleas (Order Siphonaptera) are obligate, hematophagous parasites of birds and mammals with medical interest because of their role in transmitting pathogens. From 2016 to 2019, we sampled the small mammal and associated flea communities in El Malpais National Conservation Area (El Malpais) in Cibola County, New Mexico. Among 898 mammalian specimens, 925 fleas representing 29 species were collected from 18 host species. *Pleochaetis exilis* was the most abundant flea species, composing 27% of the total fleas collected, whereas *Aetheca wagneri* was the most prevalent flea species, parasitizing 8% of the community sampled. Across a total of 284 hosts recorded with fleas, *A. wagneri*, *Malaraeus eremicus*, and *Peromyscopsylla hesperomys adelpha* parasitized the most host species (n = 6 each). *Onychomys leucogaster* (Wied-Neuwied, 1841), the northern grasshopper mouse, a rodent highly implicated in plague dynamics, was host for the highest number of flea species (n = 15), followed by *Peromyscus truei* (Shufeldt, 1885) (n = 10). Our aims are to (a) describe the flea-mammal assemblage of a central New Mexico site, creating a baseline for diversity against which changing patterns of association can be assessed over time; (b) identify previously unrecognized host associations; and (c) examine infestation parameters, including the relationships of flea prevalence and mean abundance to host sex, host abundance, and seasonality. As such, our study exemplifies the Documentation and Assessment phases of the DAMA protocol (Document, Assess, Monitor, Act), a central component of exploring distribution and diversity of complex pathogen-host communities across space and time that are essential to a proactive understanding of emerging disease.

**Keywords:** ectoparasite, fleas, host-parasite community, Southwest United States

## Introduction

Fleas (Order Siphonaptera) are tiny, holometabolous obligate ectoparasites of birds and mammals (approximately 4% and 96% respectively) representing more than 2,500 nominal species in 18 families (Medvedev, 1996; Whiting et al., 2008; Zhu et al., 2015). Rodents are the predominant mammalian hosts, likely because of their high taxonomic diversity and diverse ecological roles (Medvedev, 2017). Fleas influence host biology in various ways, including their ability to serve as vectors for an assemblage of microparasites and potential zoonotic pathogens and to act as intermediate hosts for other mammalian parasites, including helminths (Hubbard, 1947; Smit, 1953). For example, fleas are implicated in the maintenance and transmission cycle of sylvatic plague by vectoring the plague bacterium (*Yersinia pestis*) among susceptible mammalian hosts (Gage and Kosoy, 2005; Bitam et al., 2010). Several flea species in the Southwest (e.g., *A. wagneri*, *P. exilis*, and *Oropsylla hirsuta*) are considered important vectors of pathogens (Eisen et al., 2009; Eisen and Gage, 2012). In New Mexico, fleas host *Y. pestis*, *Rickettsia* spp., *Bartonella* spp., and *Borrelia* spp. (Stevenson et al., 2003; Stevenson et al., 2005; Morway et al., 2008; Kosoy et al., 2017; Goodrich et al., 2020).

Characterizing flea species and their host associations provides a framework for assessing the impacts of changes (i.e., anthropogenic disturbances) to these communities (Eisen et al., 2009; Friggens and Beier, 2010). Although fleas are recognized as important vectors of pathogens circulating among humans, companion animals, and livestock, research on flea and host diversity conducted in southwestern North America has mainly targeted potential and recognized foci of plague transmission. Field studies generally have not been designed to develop comprehensive, annotated, specimen-based collections of mammals, their fleas, and other associated hosts and pathogens (Dunnum et al., 2017; Galbreath et al., 2019). Such vouchered baselines, linked to expanding informatics resources of natural history collections, provide opportunities to assess environmental conditions and changing ecological interfaces within mammalian communities that may relate to disease dynamics over space and time (Brooks et al., 2014; Brooks et al., 2019; Colella et al., 2021). In New Mexico, comprehensive surveys of flea and small mammal communities have been conducted in only a few counties, including Santa Fe (Holdenried and Morlan, 1956), Chavez (Rail et al., 1969; Graves et al., 1974), Rio Arriba (Link, 1949), and Sandoval (Haas et al., 1973). Typically, flea and small mammal surveys have focused on prairie dog communities or solely prairie dogs (Clark et al., 1982; Cully et al., 1997; Friggens et al., 2010; Eads et al., 2015; Hoogland et al., 2018), while other surveys have targeted specific mammals, including woodrats (Kosoy et al., 2017), hares and rabbits (Graves et al., 1978; Pfaffenberger and Valencia, 1988), foxes (Patrick and Harrison, 1995), and squirrels (Patrick and Wilson, 1995). Archival deposition of voucher specimens from some of these surveys has been incomplete, hindering consistent development of a comprehensive environmental baseline for hosts, fleas, and pathogens that spans geography and time.

Parameters that define infestation, such as prevalence, mean abundance, and mean intensity, provide context for the distribution and aggregation of parasite species, from the individual host to the entire host community. These baseline quantitative measurements are key components of careful documentation of a community (Bush et al., 1997) and allow us to begin to understand how these assemblages are structured. Both biotic (e.g., vegetation, host identity, sex, age, host body size) and abiotic (e.g., seasonality, temperature, precipitation, and humidity) components can influence the structure of these communities, but fundamental processes often remain poorly understood (Krasnov, Morand, Hawlena, et al., 2005; Krasnov, Morand, Khokhlova, et al., 2005; Young et al., 2015; Reiczigel et al., 2019). Highlighted is the original insight proposed by Darwin (1872) for the interaction of the nature of the organism and the nature of the conditions that define capacity and ecological opportunity in structuring biotic assemblages in changing conditions (Brooks et al., 2019; Agosta and Brooks, 2020).

We aim to first characterize the host and flea assemblage of El Malpais by assessing aspects of flea diversity, prevalence, abundance, and seasonal variation. We then aim to test whether host sex or seasonality influence flea abundance. Studies of flea and small mammal communities have shown a sex-bias with higher flea infestation on male versus female hosts (Krasnov, Morand, Hawlena, et al., 2005; Kowalski et al., 2015). Male sex-bias hypothetically is caused by lower immunocompetence and differences in spatial occupancy between the sexes (Khokhlova et al., 2011; Krasnov et al., 2011). In the community characterized at El Malpais, we hypothesize that abundance is dependent on host sex, with higher flea abundance in males than females. Seasonality has also been shown to affect flea abundance because of biotic factors including physiological changes in the host (e.g., breeding cycles) during different seasons (Krasnov, Morand, Hawlena, et al., 2005) or by abiotic factors such as seasonal changes in precipitation (Moore et al., 2015). For our community, we also hypothesize that abundance is dependent on seasonality. This study provides a permanent specimen-based foundation, or baseline, that will enable future comparative assessments

of ecology and evolution of dynamic host-parasite communities across time and space.

### *Key Findings*

- Previously unrecognized flea and host associations were identified.
- Most flea species parasitized multiple hosts.
- *Onychomys leucogaster* was parasitized by the highest number of flea species (15).
- Flea species richness varied among host species.
- Flea prevalence is positively correlated with flea mean abundance.
- Host sex and season influenced flea abundance.

## Methods and Materials

### *Study Site*

Field surveys were conducted between October 2016 and October 2019 at the El Malpais National Conservation Area in Cibola County (34°51′32″N, 108°01′16″W) approximately 130 km west of Albuquerque, New Mexico (Fig. 1). The El Malpais National Conservation Area (El Malpais) is a protected wilderness managed by the Bureau of Land Management (BLM) and shares boundaries with the El Malpais National Monument Area. The study area is adjacent to the Grants Lava Flows, with geological features including ancient lava tubes, caves, and sandstone formations. This area is in the Upper Sonoran Life Zone, and elevation ranged from 2,062 to 2,335 m (6,765–7,660 ft). This area is a mosaic of ecological communities that lie at the southern end of the Colorado Plateau, including habitats varying across ecotones ranging from short-grass prairies and pygmy piñon-shrub juniper shrublands at lower elevations to piñon-juniper woodlands and mixed-conifer montane forests at higher elevations (Mutz and Cannon, 2005). Soils consist mainly of alluvium and basalt (Maxwell, 1986). Temperatures range from –11°C to 29°C (12°F–85°F), and annual precipitation is approximately 27 cm (National Park Service, 2017). Anthropogenic impacts in this rural area include cattle grazing, camping, and seasonal hunting activities. The National Scenic and Historic Continental Divide Trail intersects the study site.

Diverse mammalian communities inhabit El Malpais, including carnivores, wild and domestic ungulates, lagomorphs, chiropterans, shrews, and rodents. Between 2009 and 2013, 2,273 Gunnison's prairie dogs (*Cynomys gunnisoni* (Baird, 1855)) were relocated from Santa Fe on multiple occasions into areas of El Malpais National Conservation Area (NCA) and areas south of the El Malpais National Monument in an attempt to develop a sustainable prey base for the future reintroduction of the endangered black-footed ferret (*Mustela nigripes* (Audubon and Bachman, 1851)). Prior to translocation, these prairie dogs were dusted with insecticide to kill ectoparasites. Areas surveyed in our study included prairie dog colonies in lower elevation shrub/grasslands, but sample sites ranged up to higher elevation coniferous habitats.

### *Field and Data Collection*

Specimens were collected following guidelines of the American Society of Mammalogists (Sikes and Animal Care, 2016) and under an Institutional Animal Care and Use protocol (IACUC protocol #19-200908-MC) at the University of New Mexico. Small mammals were collected with Sherman® live traps, Victor® rat traps, and museum special traps, all baited with a mixture of oats and peanut butter. In colder months, cotton nestlets were placed in live traps to reduce mortality from exposure. A typical trapline consisted of 80 traps set in 40 trap stations about 8 m apart. Macabee® gopher traps were used in areas where gopher mounds were identified, and pitfall traps were placed at Cebolla Springs. Some mammals (e.g., prairie dogs) were collected with small-bore firearms. Roadkill mammals were also collected. Exact locality coordinates were recorded for each capture, and entire traplines were recorded using Garmin® geographical positioning system (GPS) instruments. All specimens were processed at a central field laboratory site (Galbreath et al. 2019). Mammals and ectoparasites were euthanized in plastic sandwich bags with a small dose (1–2 mL) of chloroform, and each mammalian voucher specimen was combed onto a white plate, or the ectoparasites (fleas, lice, ticks, mites) were directly removed from the host using forceps (Galbreath et al., 2019). Ectoparasites collected were separated by taxon and placed into cryotubes containing 95% ethanol (EtOH). In addition to ectoparasites, endoparasites (e.g., primarily cestodes and nematodes) were collected. Blood was collected on Nobuto blood filter strips; embryos, heart, liver, kidney, spleen, and feces were frozen in liquid nitrogen; and traditional museum skin and skeleton or fluid preparations were preserved (Galbreath et al., 2019). All specimens were accessioned into the Museum of Southwestern Biology, University of New Mexico, Albuquerque, and are available via the Arctos collection management system (Arctosdb.org). Mammals were identified to species based on morphology. In select cases for which cryptic mammalian species were anticipated, a molecular barcode (mitochondrial cytochrome *b* gene sequence) was used to confirm host identity. Mammal taxonomy for New Mexico follows Malaney et al. (2022). Fleas were identified at the Centers for Disease Control and Prevention, Vector-Borne Diseases Division (Fort

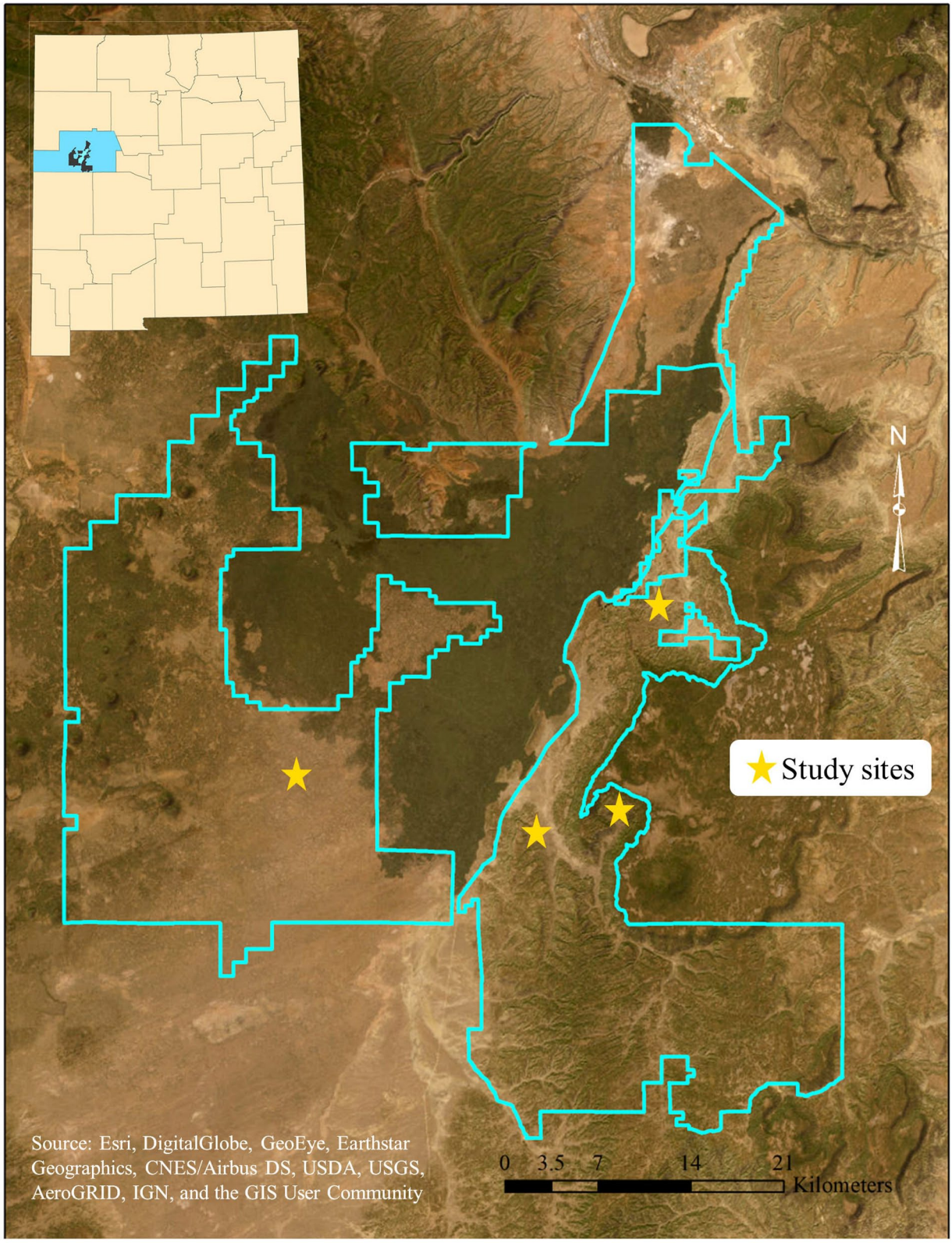


**Figure 1.** Map of El Malpais National Conservation Area and approximate sampling areas.

Collins, Colorado) and at the University of New Mexico using published taxonomic keys (Hubbard, 1947; Furman and Catts, 1982; Lewis et al., 1988) and the classification system of Medvedev et al. (2000).

### *Data analyses*

Alpha diversity (species richness) for the flea and host community was determined by constructing species accumulation curves using the vegan package version 2.5-7 in R (Oksanen et al., 2020). Fleas that could not be identified to species in the genera *Catallagia*, *Megarthroglossus*, *Meringis*, *Peromyscopsylla*, and *Stenistomera* were excluded from estimates of richness, except for *Monopsyllus* sp., which was represented by a single individual. Parameters for infestation followed the definitions according to Bush et al. (1997). Prevalence is defined as the total number of parasitized hosts / the total number of hosts examined (per host species) and represents the proportion of hosts parasitized by fleas. Abundance is the number of fleas on a single host including individual hosts with no fleas. Mean abundance is defined as the total number of fleas divided by the total number of hosts (per host species) and describes how fleas are dispersed among the community. Mean intensity is defined as the total number of fleas divided by the total number of infested hosts and measures the degree of parasitism in the infested community. Relative abundance is defined as the total number of individuals of a particular flea species divided by the total number of fleas on a particular host species. Calculations describing flea infestation within and among mammalian specimens and hosts were performed using Quantitative Parasitology (QPWeb, Version 1.0.15) and follow the statistical tests as described by Reiczigel et al. (2019). The 95% confidence interval (CI) for prevalence was calculated using Blaker's method, while the bias-corrected and accelerated (Bca) bootstrap with 2000 bootstrap replications were used for mean abundance and mean intensity. Standard error (SE) and relative abundance were calculated using Excel. Standard error was calculated as the standard deviation of the data range divided by the square root of the count of the data range. Spearman's (nonparametric) correlation analysis was performed for prevalence and mean abundance analysis, and Pearson's chi-squared analyses for sex and season using R version 4.1.2 (R Core Team, 2021). Sex (i.e., male or female) was reported for each host species. Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Mammal species with sample sizes < 10 individuals were not included in statistical analyses of the relationship between prevalence and mean abundance, sex, and seasonality.

### *Historical Distributional Records*

Historical data documenting distributional records for fleas and their mammalian hosts were accumulated through a comprehensive search of the published literature. Searches were conducted from March 2019 through December 2021 using the Google Scholar and PubMed databases and the key words "fleas," "New Mexico," "mammal," and "host." Publication dates searched were "Any time" in Google Scholar, and no date range was set for PubMed.

## Results

### *Flea community composition*

Fleas totaling 925 specimens representing four families and 29 species (including *Monopsyllus* sp.) were collected (Fig. 2). At the familial level, Hystrichopsyllidae and Ceratophyllidae were equally represented at 12 (41%) species each, whereas Pulicidae and Leptopsyllidae were the least represented at four (14%) and one (4%) species (Fig. 3). Based on the species accumulation curves, species estimates were 33 ± 3.9 species for the flea community (Fig. 4) and 19 ± 1.3 for the host community (Fig. 5) Considering flea species richness, associations within and across this mammalian assemblage varied based on the temporal limits of our collections (Fig. 6) Across flea species, 19 of 29 species were found on multiple hosts (two to six host species), and 10 flea species were associated with a single host species (Fig. 7). The broadest host range among fleas was found in *A. wagneri*, *M. eremicus*, and *P. hesperomys adelpha*, with each infesting six rodent species. Flea species community composition was highest during autumn and spring (25 and 24 species, respectively), while winter and summer had the lowest flea species richness (16 and 7 species respectively). Some flea species were collected only during a single season. *Callistopsyllus terinus*, *M. jamesoni*, *O. neotomae*, and *P. paradisea* were collected only in the spring. *Catallagia decipiens*, *M. bisetis*, *M. telchinus*, and *P. allos* were collected only in autumn. For seasonal abundance, *P. exilis* was the most abundant flea species and had the highest numbers of any flea species in the autumn and winter, while *A. wagneri* had the highest numbers for the spring and *O. leucopus* for summer (Fig. 8).

### *Mammal community composition*

A total of 898 mammals representing two orders, five families, nine genera, and 18 species is included in our dataset. The Order Rodentia represented 99% of our host community, while Lagomorpha represented 1%. Distribution at the familial level was Cricetidae (94%), Sciuridae (2%), Heteromyidae (2%), Geomyidae (1%), and Leporidae (1%).

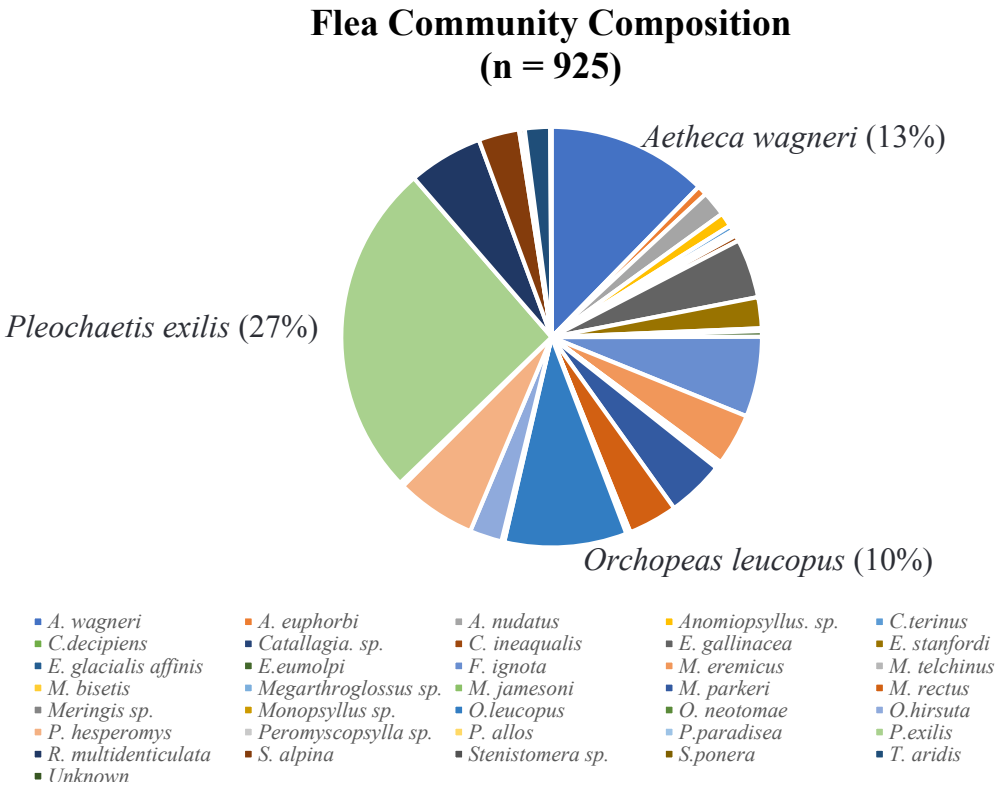


**Figure 2.** Flea species composition. The majority (82%) of the flea species in this community are either ceratophyllids or hystrichopsyllids.

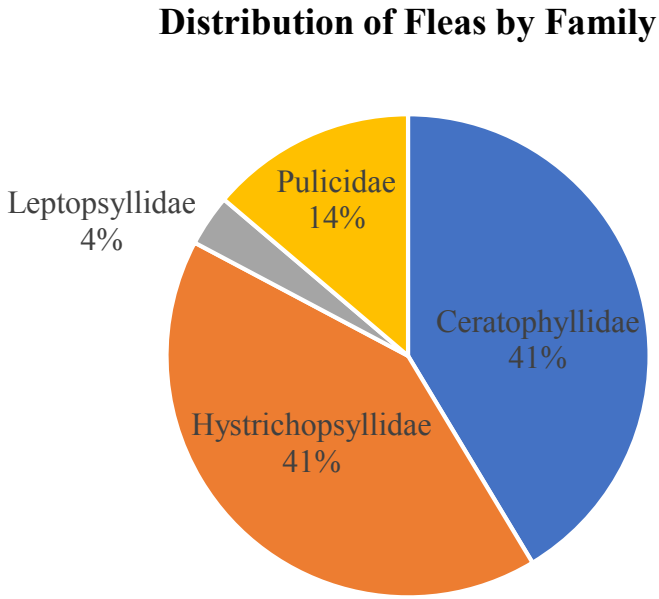


**Figure 3.** The flea community was mostly composed of species of the Ceratophyllidae and Hystrichopsyllidae.

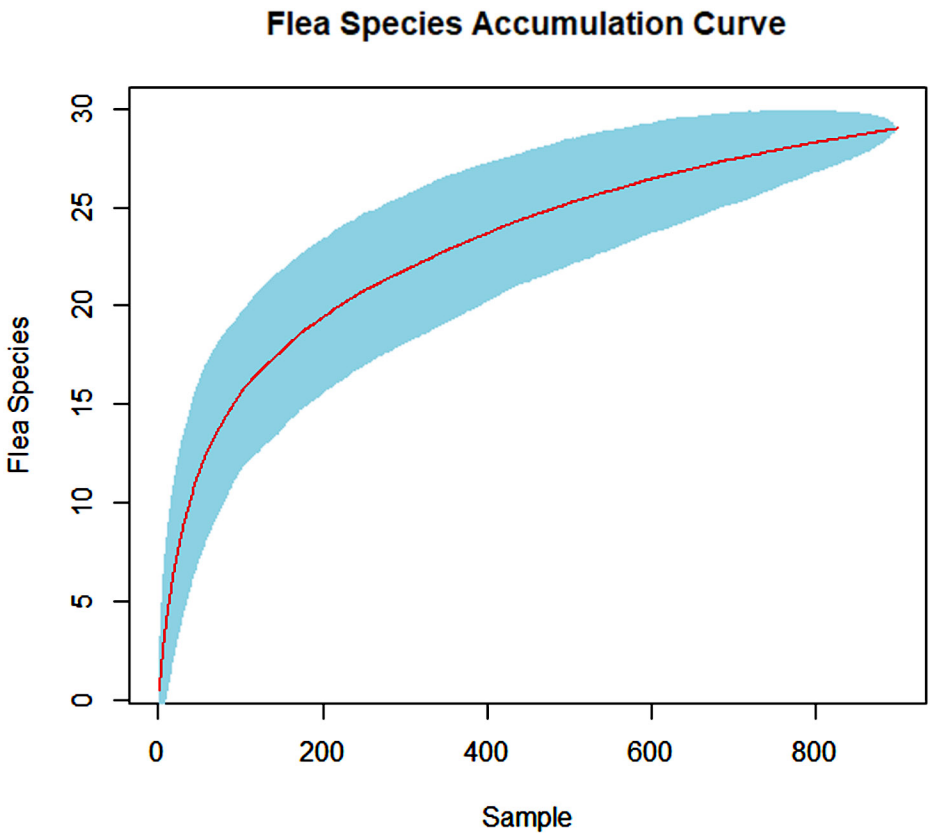


**Figure 4.** Flea species accumulation curve. Chao estimates 33 (SE ±3.9) flea species.

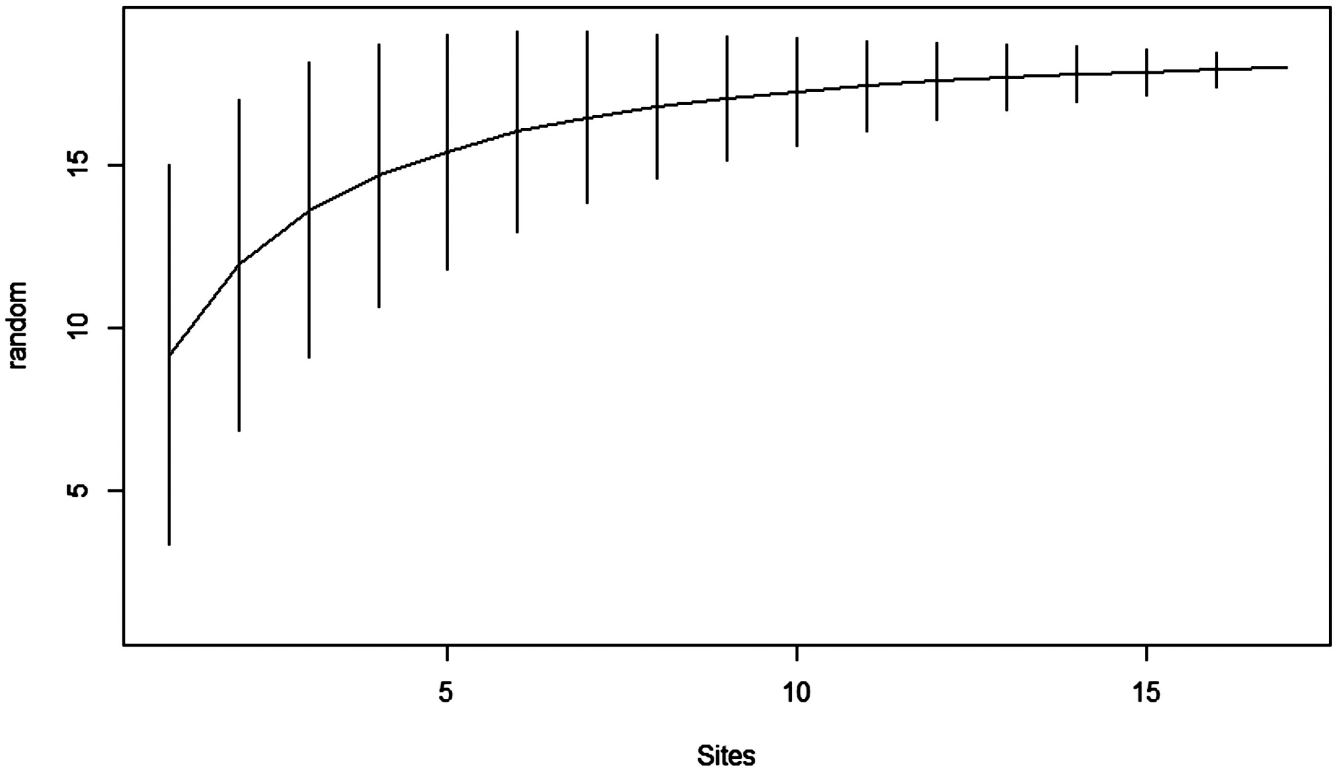


**Figure 5.** Host species accumulation curve. Chao estimator predicts 19 (SE ± 1.26) species found at approximately 13 visits.

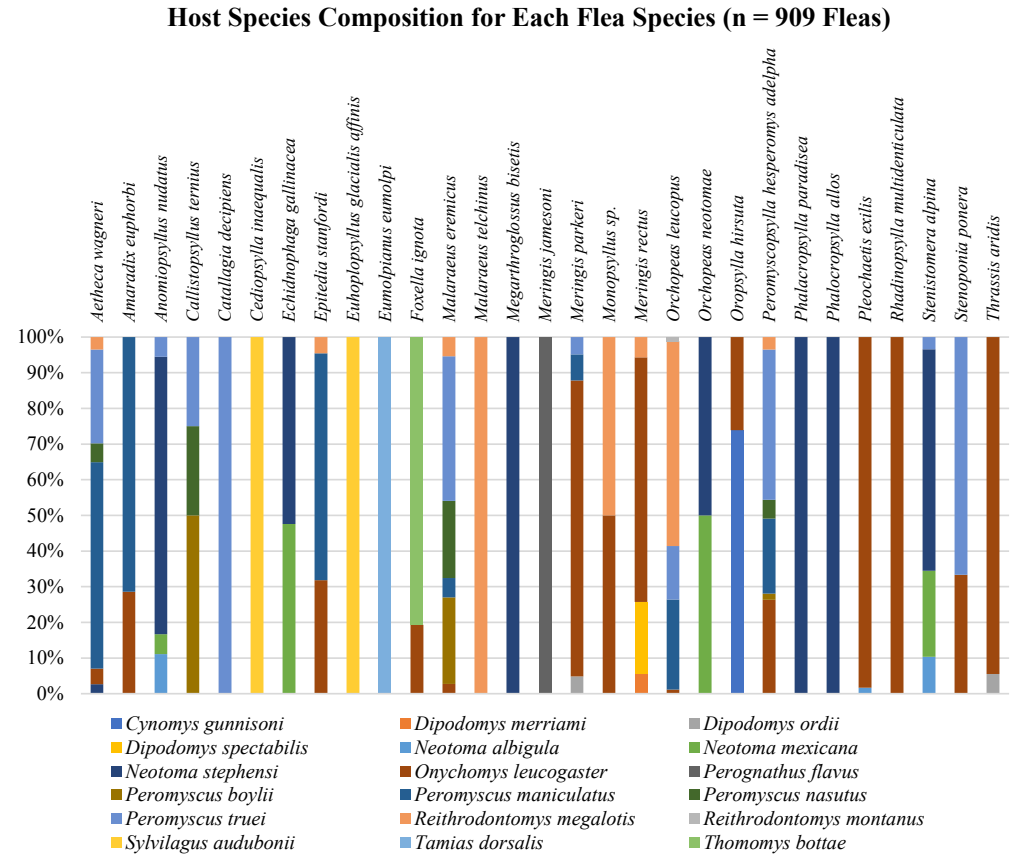


**Figure 6.** Interspecific variation in host species diversity. Fleas in genera not identified to species (except *Monopsyllus* sp.) are excluded

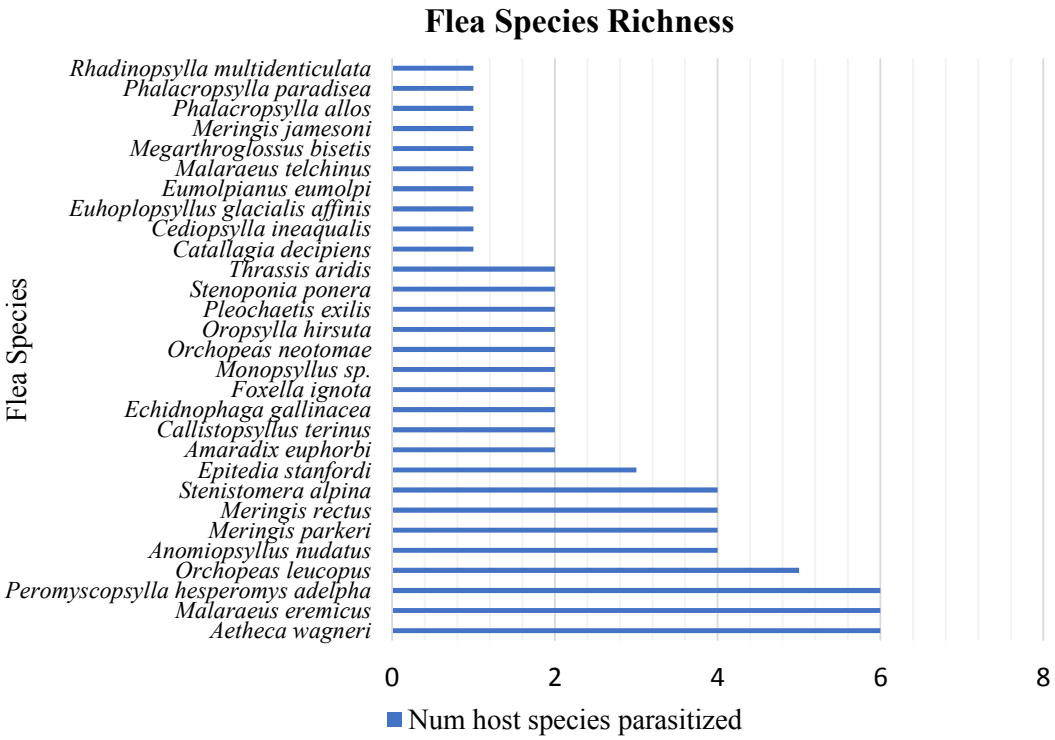


**Figure 7.** Number of host species parasitized by flea species. This chart shows that the majority of flea species parasitized either one or two host species.

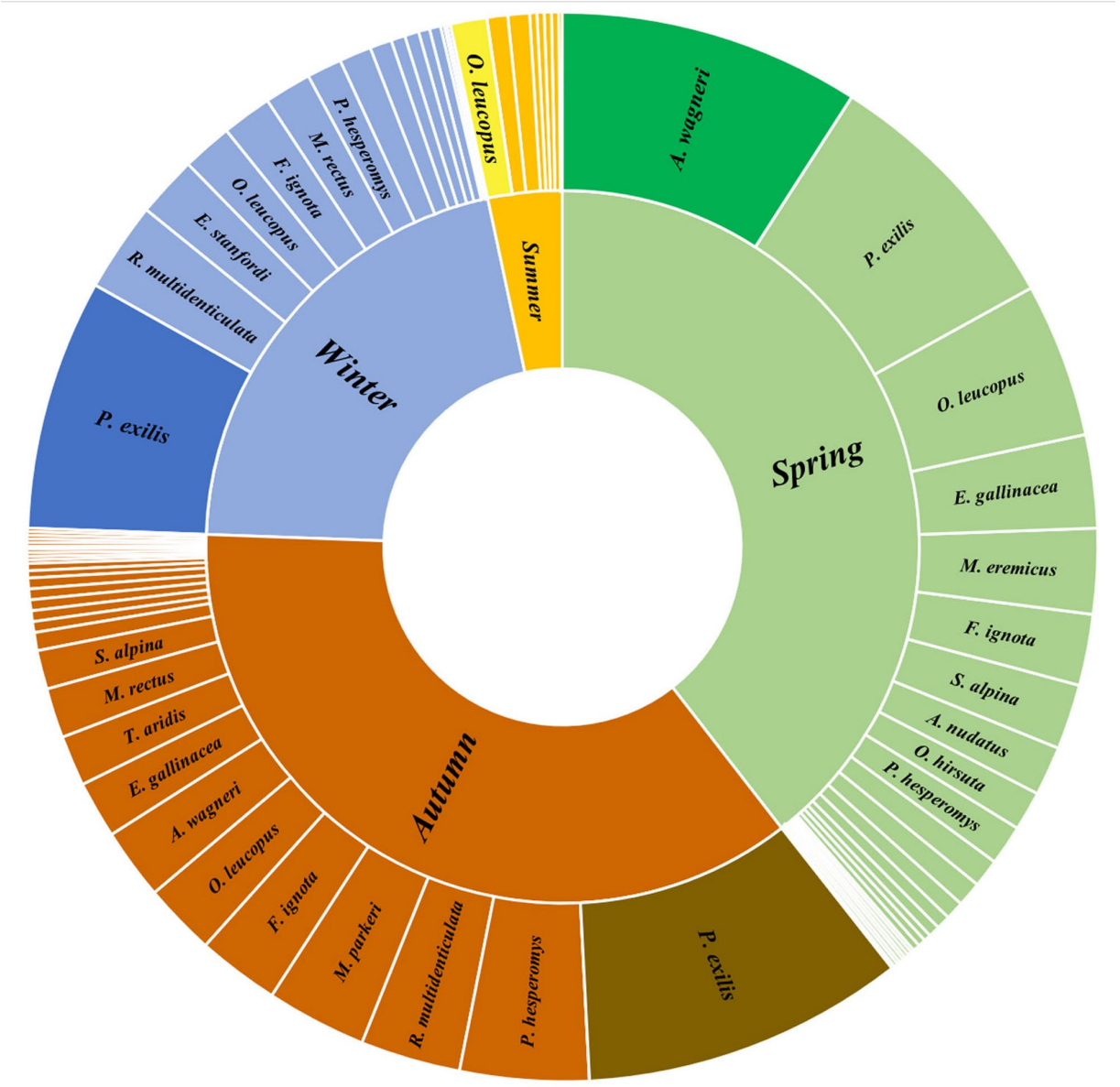


**Figure 8.** Seasonal flea community composition. *Aetheca wagneri*, *M. eremicus*, *M. parkeri*, *O. hirsuta*, *O. leucopus*, and *P. exilis* were present during all seasons.

***Host-parasite composition***

Out of 898 individual mammals examined, 284 were shown to be infested with fleas (overall prevalence = 32%). Mammals with the highest community composition were *Peromyscus maniculatus* (Wagner, 1845) (30%), (Baird, 1857) (16%), *P. truei* (15%), and *O. leucogaster* (13%) (Fig. 9). Two or more flea species parasitized the majority of hosts (61%), while only one flea species parasitized the remainder (39%) (Fig. 10). Cricetid rodents had the highest flea diversity (25 species) of all families of mammals (Fig. 11). *O. leucogaster* hosted the highest species richness, parasitized by 15 flea species, followed by *P. truei* (10 species) and *Reithrodontomys megalotis* (Baird, 1857) and *Neotoma stephensi* (Goldman, 1905) (eight species each). Within individual hosts, *O. leucogaster* was co-infested by the highest number of flea species, with two individual hosts each parasitized by six different flea species. Similar to flea community composition, host community composition was the highest during autumn and spring (17 and 16 host species, respectively) and lowest during summer and winter (13 and 10 host species, respectively) (Fig. 12). For seasonal relative abundance, *P. maniculatus* was the most abundant host in all seasons (winter = 52%, spring = 35%, summer = 22%, autumn = 23%) (Fig. 12).

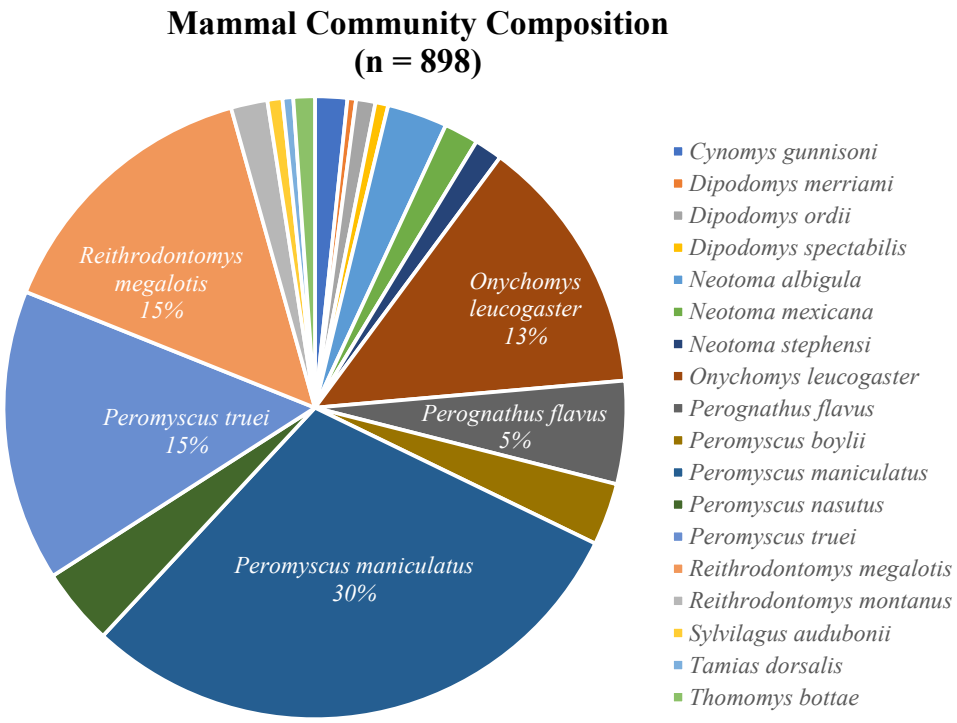


**Figure 9.** Mammal community composition. Cricetid rodents were the majority (94%) of host species, with approximately half of all hosts belonging to the genus *Peromyscus*.

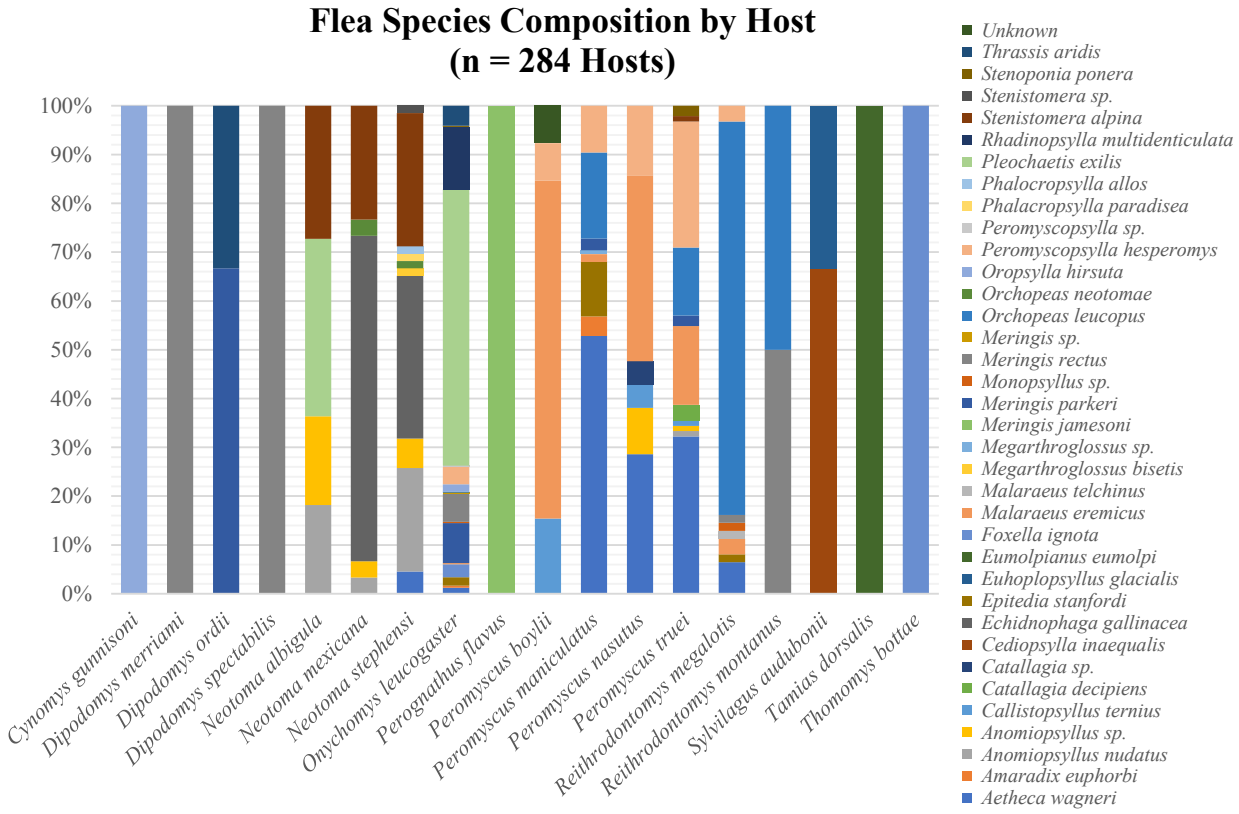


**Figure 10.** Flea species composition for each host species. Most hosts (61%) hosted multiple flea species, while 39% hosted only a single flea species.

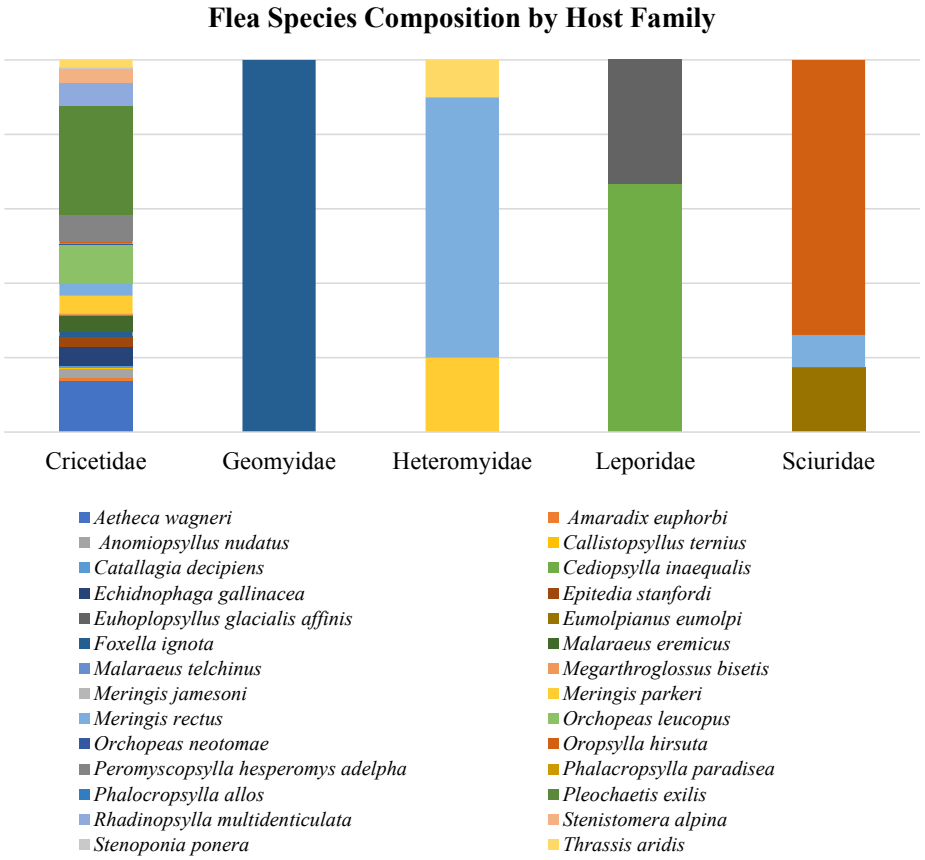


**Figure 11.** Flea species composition by host family. Cricetid rodents had the highest diversity of fleas (25 species) among all taxa.


**Figure 12.** Host abundance and community composition by season. Host species richness was greatest during autumn and spring seasons. *P. maniculatus* was the most abundant host in all four seasons.

## Flea Species Accounts

The following flea species account is organized by family (Ceratophyllidae, Leptopsyllidae, Hystrichopsyllidae, and Pulicidae) with species arranged alphabetically. Flea counts and sex precede the host from which they were collected. Hosts are identified by their catalog number.

### *Family Ceratophyllidae*

***Aetheca wagneri*** (Baker, 1904)

*Aetheca wagneri* is one of the most common fleas reported in the Southwest. Peromyscine rodents are reported to be the principal hosts for this flea, although many other mammals host this species (Johnson, 1961; Haas et al., 2004). In our community, *A. wagneri* was recorded from the highest number of host species, parasitizing six species of mammals. It was the most prevalent flea (7.7%), parasitizing 69 hosts, and *P. maniculatus* (n = 37) was the most common host. *Aetheca wagneri* and *P. maniculatus* are implicated in the sylvatic plague maintenance cycle (Holdenried and Morlan, 1955; Holdenried and Morlan, 1956); however, the apparently low transmission efficiency of this flea indicates that a *P. maniculatus–A. wagneri* transmission cycle is seldom a direct contributor in sylvatic outbreaks (Fagerlund et al., 2001; Eisen et al., 2008). This flea was collected during all seasons but was most common during spring.

**Specimens Deposited:** 1 male, 2 females ex *N. stephensi* MSB:Mamm:322260, MSB:Mamm:329258; 3 males, 2 females ex *O. leucogaster* MSB:Mamm:299066, MSB:Mamm:306260, MSB:Mamm:322262; 17 males, 49 females ex *P. maniculatus* MSB:Mamm:299051, MSB:Mamm:299080, MSB:Mamm:299095, MSB:Mamm:299097, MSB:Mamm:299145, MSB:Mamm:306120, MSB:Mamm:306254, MSB:Mamm:322114, MSB:Mamm:322136, MSB:Mamm:322148, MSB:Mamm:322155, MSB:Mamm:322183, MSB:Mamm:322188, MSB:Mamm:322194, MSB:Mamm:322202, MSB:Mamm:322212, MSB:Mamm:322213, MSB:Mamm:322217, MSB:Mamm:322222, MSB:Mamm:322223, MSB:Mamm:322224, MSB:Mamm:322228, MSB:Mamm:322230, MSB:Mamm:322231, MSB:Mamm:322233, MSB:Mamm:322241, MSB:Mamm:322245, MSB:Mamm:322247, MSB:Mamm:322253, MSB:Mamm:322256, MSB:Mamm:322257, MSB:Mamm:322298, MSB:Mamm:322299, MSB:Mamm:322303, MSB:Mamm:329204, MSB:Mamm:329250, MSB:Mamm:329266; 3 males, 3 females ex *Peromyscus nasutus* (J.A. Allen, 1891) MSB:Mamm:299082, MSB:Mamm:299087, MSB:Mamm:299088, MSB:Mamm:304290, MSB:Mamm:329286; 13 males, 17 females ex *P. truei* MSB:Mamm:299128, MSB:Mamm:299182, MSB:Mamm:304279, MSB:Mamm:304286, MSB:Mamm:304288, MSB:Mamm:304291, MSB:Mamm:322197, MSB:Mamm:322236, MSB:Mamm:322237, MSB:Mamm:322238, MSB:Mamm:322248, MSB:Mamm:322249, MSB:Mamm:322296, MSB:Mamm:329211, MSB:Mamm:329265, MSB:Mamm:329271, MSB:Mamm:329284, MSB:Mamm:329288; 4 females ex *Reithrodontomys megalotis* MSB:Mamm:299112, MSB:Mamm:299114, MSB:Mamm:299121, MSB:Mamm:322227.

***Amaradix euphorbi*** (Rothschild, 1905)

This flea has an amphiberingian distribution and has been collected from *P. maniculatus*, *P. truei*, and *Myodes gapperi* (Vigors, 1830) from New Mexico. We report *O. leucogaster* as a previously unrecognized host for this flea (Morlan, 1955; Holdenried and Morlan, 1956; Thomas, 1988; Ford et al., 2004). Lewis et al. (1988) regarded *Amaradix euphorbi* as a montane species associated with *Neotoma* spp. and *Peromyscus* spp. but not common to either. This flea species was collected in all seasons except for summer and was prevalent in 0.6% of our sample population.

**Specimens Deposited:** 1 male, 1 female ex *O. leucogaster* MSB:Mamm:299057, MSB:Mamm:322053; 1 male, 4 females ex *P. maniculatus* MSB:Mamm:301682, MSB:Mamm:306112, MSB:Mamm:322114.

***Eumolpianus eumolpi*** (Rothschild, 1905)

A widespread Holarctic flea, *Eumolpianus eumolpi* commonly parasitizes western chipmunks and squirrels (Patrick and Wilson, 1995). According to Lewis and Jameson (2002), this genus requires systematic revision because of insufficient representation of taxa other than *Eumolpianus* (Lewis, 1975; Lewis and Jameson Jr., 2002; Pigage et al., 2017). In our dataset, *E. eumolpi* had 0.2% prevalence, parasitized only one species of host (*Tamias dorsalis* Baird, 1855), and was collected during summer and autumn.

**Specimens Deposited:** 1 male, 3 females ex *T. dorsalis* MSB:Mamm:299199, MSB:Mamm:329272.

***Foxella ignota*** (Baker, 1895)

The distribution of *Foxella ignota* across western North America ranges from southern Canada to central Mexico. In the southwestern United States, this species is most commonly associated with pocket gophers (*Thomomys* spp.), but it also has been collected from *Urocyon*

*cinereoargenteus* (Schreber, 1755), *Vulpes macrotis* Merriam, 1888, and *O. leucogaster* (see Patrick and Harrison, 1995; Harrison et al., 2003; Pigage et al., 2005; Lewis and Wilson, 2006). In our study, *F. ignota* was prevalent in 1.9% of the community, parasitizing *O. leucogaster* and *Thomomys bottae* (Eydoux and Gervais, 1836), and was collected in all seasons except winter. All *T. bottae* specimens (n = 10) were parasitized by this species.

**Specimens Deposited:** 5 males, 6 females ex *O. leucogaster* MSB:Mamm:306097, MSB:Mamm:306122, MSB:Mamm:306125, MSB:Mamm:322094, MSB:Mamm:322097, MSB:Mamm:322121, MSB:Mamm:322129; 26 males, 20 females ex *T. bottae* MSB:Mamm:322162, MSB:Mamm:322167, MSB:Mamm:322174, MSB:Mamm:322218, MSB:Mamm:329229, MSB:Mamm:329242, MSB:Mamm:329243, MSB:Mamm:329244, MSB:Mamm:329245, MSB:Mamm:329246.

***Malaraeus eremicus*** (Baker, 1904)

The nomen *Malaraeus sinomus* is commonly applied to this species; however, Lewis (2008) regarded *M. sinomus* as a junior synonym of *M. eremicus*, as we do here. *Malaraeus eremicus* is distributed across the semidesert and desert regions of the United States and northern Mexico, mainly at higher elevations (Lewis, 2008). In New Mexico, this species is regarded as a generalist, commonly found parasitizing several species of cricetid rodents (Morlan, 1955; Holdenried and Morlan, 1956; Thomas, 1988; Morway et al., 2008). Like *A. wagneri* and *Peromyscopsylla hesperomys adelpha*, *M. eremicus* occurred on six different species of hosts. This flea species had a prevalence of 2.8% in our mammal community and was most abundant on *P. truei*, being present in all seasons but collected most commonly in the spring.

**Specimens Deposited:** 1 female ex *O. leucogaster* MSB:Mamm:329234; 5 males, 4 females ex *Peromyscus boylii* (Baird, 1855) MSB:Mamm:299046, MSB:Mamm:299126, MSB:Mamm:299131, MSB:Mamm:299172; 2 males ex *P. maniculatus* MSB:Mamm:299092, MSB:Mamm:322095; 3 males, 5 females ex *P. nasutus* MSB:Mamm:299082, MSB:Mamm:299086, MSB:Mamm:299087, MSB:Mamm:299088, MSB:Mamm:299171; 7 males, 8 females ex *P. truei* MSB:Mamm:299135, MSB:Mamm:299140, MSB:Mamm:304286, MSB:Mamm:304289, MSB:Mamm:306247, MSB:Mamm:322061, MSB:Mamm:322191, MSB:Mamm:322199, MSB:Mamm:322248, MSB:Mamm:329273; 2 females ex *R. megalotis* MSB:Mamm:306241, MSB:Mamm:329224.

***Malaraeus telchinus*** (Rothschild, 1905)

The most widely distributed species in this genus, *Malaraeus telchinus* occurs mainly at lower elevations (< 2300 m) in New Mexico, the southernmost geographical region for *M. telchinus*. It is sympatric with *M. eremicus* in the Upper Sonoran Zone (Haas, 1973; Lewis, 2008). Haas (1973) remarked that while males of *M. eremicus* and *M. telchinus* are easily distinguishable, females are nearly impossible to resolve because of high intraspecific variation in the outline of sternum VII. This species is not well represented in our dataset and was prevalent in only 0.1% of the community.

**Specimen Deposited:** 1 male ex *R. megalotis* MSB:Mamm:329222.

***Monopsyllus* sp.**

One female was collected on *R. megalotis* and had 0.1% prevalence. Because of damage, identification to species could not be determined.

**Specimens Deposited:** 1 female ex *O. leucogaster* MSB:Mamm:329295; 1 female ex *R. megalotis* MSB:Mamm:299115.

***Orchopeas leucopus*** (Baker, 1904)

This widely distributed Nearctic genus, *Orchopeas*, is mainly differentiated by characteristic chaetotaxic arrangement of the male clasper—specifically, the shape of the process and finger, the arrangement of spiniforms on the finger, and shape and size of sternum nine (Lewis, 2000). *Orchopeas leucopus* is the flea of this genus that is most broadly distributed, extending across most of the contiguous United States and north to Canada and Alaska. This species mainly parasitizes peromyscine rodents (Lewis, 2000), and in New Mexico, *O. leucopus* is strongly associated with cricetid rodents, including *O. leucogaster* and *R. megalotis*. This species had the third highest prevalence (5.5%) in our community, was most abundant on *R. megalotis*, and was collected in all seasons but mostly in the summer.

***Orchopeas neotomae*** (Auguston, 1943)

This species, restricted to the southwestern United States and Mexico, commonly parasitizes species of *Neotoma* (Lewis, 2000). *Orchopeas neotomae* was prevalent in 0.2% of our community and collected only in the spring.

**Specimens Deposited:** 1 female ex *Neotoma mexicana* (Baird, 1855) MSB:Mamm:299161; 1 male ex *N. stephensi* MSB:Mamm:322259; 1 male ex *O. leucogaster* MSB:Mamm:299187; 10 males, 12 females ex *P. maniculatus* MSB:Mamm:299037, MSB:Mamm:299092, MSB:Mamm:299095, MSB:Mamm:299143,

MSB:Mamm:299151, MSB:Mamm:299197, MSB:Mamm:322087, MSB:Mamm:322127, MSB:Mamm:322135, MSB:Mamm:322136, MSB:Mamm:322139, MSB:Mamm:322143, MSB:Mamm:322145, MSB:Mamm:322228, MSB:Mamm:322243, MSB:Mamm:322257, MSB:Mamm:329248, MSB:Mamm:329251; 6 males, 7 females ex *P. truei* MSB:Mamm:299183, MSB:Mamm:306246, MSB:Mamm:306250, MSB:Mamm:322197, MSB:Mamm:322198, MSB:Mamm:322200, MSB:Mamm:322251, MSB:Mamm:322301; 27 males, 23 females ex *R. megalotis* MSB:Mamm:299076, MSB:Mamm:299077, MSB:Mamm:299078, MSB:Mamm:299079, MSB:Mamm:299094, MSB:Mamm:299117, MSB:Mamm:299188, MSB:Mamm:299189, MSB:Mamm:299190, MSB:Mamm:299191, MSB:Mamm:299194, MSB:Mamm:301710, MSB:Mamm:301713, MSB:Mamm:301718, MSB:Mamm:322056, MSB:Mamm:322103, MSB:Mamm:322219, MSB:Mamm:322225, MSB:Mamm:322227, MSB:Mamm:329227, MSB:Mamm:329296; 1 male ex *Reithrodontomys montanus* (Baird, 1855) MSB:Mamm:329236.

***Oropsylla hirsuta*** (Baker, 1895)

Members of the genus *Oropsylla* parasitize sciurid rodents, especially spermophilids (Lewis, 2002). In New Mexico, *O. hirsuta* mainly parasitizes *Cynomys* spp., but it is also known on *Callospermophilus lateralis* (Say, 1823) and *Ictidomys tridecemlineatus* (Mitchill, 1821) (Link, 1949; Cully et al., 1997; Friggens et al., 2010). This finding is the first association with *O. leucogaster* for New Mexico (Eskey and Haas, 1939; Pfaffenberger and Valencia, 1988; Cully et al., 1997; Ford et al., 2004; Eads et al., 2015; Eads et al., 2016), but the association has been documented elsewhere (e.g., northern Colorado) (Stapp and Salkeld, 2009). In the southwestern United States, *O. hirsuta* is implicated in the maintenance of sylvatic plague because of high vectorial and transmission efficiency and strong associations with highly susceptible prairie dogs (*Cynomys* spp.) and with other sympatric hosts including *O. leucogaster* (Gage et al., 1995; Wilder, Eisen, Bearden, Montenieri, Gage, et al., 2008; Wilder, Eisen, Bearden, Montenieri, Tripp, et al., 2008; Kraft and Stapp, 2013). *Oropsylla hirsuta* was prevalent in 1.0% of the community, was collected in all seasons, and parasitized *C. gunnisoni* and *O. leucogaster*.

**Specimens Deposited:** 12 males, 5 females ex *C. gunnisoni* MSB:Mamm:299167, MSB:Mamm:299185, MSB:Mamm:322209, MSB:Mamm:322295; 3 males, 3 females ex *O. leucogaster* MSB:Mamm:306125, MSB:Mamm:306129, MSB:Mamm:306243, MSB:Mamm:322105, MSB:Mamm:322152.

***Pleochaetis exilis*** (Jordan, 1937)

*Pleochaetis exilis* was the most abundant flea in our community, the second most prevalent species (7.2%), and the parasite of a total of 65 individual hosts. This species was collected in all seasons and was the most collected flea in the winter and autumn. *O. leucogaster* was considered an almost exclusive host for *P. exilis*, but this flea has been collected on several species of *Neotoma* and *Peromyscus* (Hubbard, 1947; Johnson, 1961), and we found it on three *Neotoma albigula* Hartley, 1894. This species is a competent vector for *Y. pestis* and has been identified as important in plague outbreaks in prairie dog communities, caused by the flea-sharing dynamics between *O. leucogaster* and prairie dogs (Kartman and Prince, 1956; Stapp et al., 2009).

**Specimens Deposited:** 1 male, 3 females ex *N. albigula* MSB:Mamm:322173, MSB:Mamm:322189; 97 males, 138 females ex *O. leucogaster* MSB:Mamm:299056, MSB:Mamm:299057, MSB:Mamm:299066, MSB:Mamm:299099, MSB:Mamm:299102, MSB:Mamm:299103, MSB:Mamm:299187, MSB:Mamm:299192, MSB:Mamm:299193, MSB:Mamm:299200, MSB:Mamm:301700, MSB:Mamm:301701, MSB:Mamm:301702, MSB:Mamm:301703, MSB:Mamm:301704, MSB:Mamm:301728, MSB:Mamm:306086, MSB:Mamm:306088, MSB:Mamm:306090, MSB:Mamm:306091, MSB:Mamm:306092, MSB:Mamm:306093, MSB:Mamm:306094, MSB:Mamm:306097, MSB:Mamm:306119, MSB:Mamm:306122, MSB:Mamm:306123, MSB:Mamm:306124, MSB:Mamm:306125, MSB:Mamm:306126, MSB:Mamm:306128, MSB:Mamm:306129, MSB:Mamm:306244, MSB:Mamm:306259, MSB:Mamm:306260, MSB:Mamm:322050, MSB:Mamm:322052, MSB:Mamm:322053, MSB:Mamm:322106, MSB:Mamm:322121, MSB:Mamm:322132, MSB:Mamm:322133, MSB:Mamm:322134, MSB:Mamm:322140, MSB:Mamm:322146, MSB:Mamm:322147, MSB:Mamm:322149, MSB:Mamm:322150, MSB:Mamm:322152, MSB:Mamm:322154, MSB:Mamm:322161, MSB:Mamm:322164, MSB:Mamm:322172, MSB:Mamm:322176, MSB:Mamm:322262, MSB:Mamm:322267, MSB:Mamm:322314, MSB:Mamm:322315, MSB:Mamm:329228, MSB:Mamm:329230, MSB:Mamm:329234, MSB:Mamm:329252, MSB:Mamm:329294.

***Thrassis aridis*** Prince, 1944

This Nearctic species is found in xeric environments where it is highly associated with kangaroo rats (*Dipodomys* spp.), wood rats (*Neotoma* spp.), and grasshopper mice (*O. leucogaster*), as reflected in our sample population (Hubbard, 1947; Traub et al., 1983). This species was prevalent in 1.3% of our community and was collected mostly in autumn.

**Specimens Deposited:** 1 male ex *Dipodomys ordii* Woodhouse, 1853 MSB:Mamm:329240; 7 males, 10 females ex *O. leucogaster* MSB:Mamm:306095, MSB:Mamm:306122, MSB:Mamm:306125, MSB:Mamm:306127, MSB:Mamm:306129, MSB:Mamm:306244, MSB:Mamm:322051, MSB:Mamm:322052, MSB:Mamm:322172, MSB:Mamm:329234, MSB:Mamm:329295.

## *Family Leptopsyllidae*

***Peromyscopsylla hesperomys adelpha*** (Baker, 1904)

The *adelpha* subspecies belongs to the "sylvatica" group because of a morphological distinction of the genal process (Hubbard, 1947). This flea species commonly parasitizes cricetid rodents, especially *Peromyscus* spp., and is widely distributed from northwestern Canada to southern Mexico (Johnson and Traub, 1954; Salceda-Sánchez and Hastriter, 2006). *Peromyscopsylla hesperomys adelpha* was most abundant on *P. truei* and was the fourth most prevalent flea (7.2%). It parasitized the highest number of host species (n = 6) along with *A. wagneri* and *M. eremicus* and was collected mostly in the autumn.

**Specimens Deposited:** 8 males, 7 females ex *O. leucogaster* MSB:Mamm:299104, MSB:Mamm:301704, MSB:Mamm:306122, MSB:Mamm:322140, MSB:Mamm:322149, MSB:Mamm:322161, MSB:Mamm:329234, MSB:Mamm:329294, MSB:Mamm:329295, MSB:Mamm:329300; 1 female ex *P. boylii* MSB:Mamm:299127; 5 males, 7 females ex *P. maniculatus* MSB:Mamm:299090, MSB:Mamm:306117, MSB:Mamm:306258, MSB:Mamm:322085, MSB:Mamm:322215, MSB:Mamm:329210, MSB:Mamm:329250; 1 male, 2 females ex *P. nasutus* MSB:Mamm:299087, MSB:Mamm:299088, MSB:Mamm:329285; 6 males, 18 females ex *P. truei* MSB:Mamm:299139, MSB:Mamm:299140, MSB:Mamm:304279, MSB:Mamm:304282, MSB:Mamm:304284, MSB:Mamm:304286, MSB:Mamm:304289, MSB:Mamm:322059, MSB:Mamm:322236, MSB:Mamm:322238, MSB:Mamm:322248, MSB:Mamm:329269, MSB:Mamm:329288; 2 females ex *R. megalotis* MSB:Mamm:329221, MSB:Mamm:329222.

***Peromyscopsylla* sp.**

Members of the Holarctic genus *Peromyscopsylla* have a distinctive bullet-shaped head with no eyes and a vertical genal comb. *Peromyscopsylla* commonly parasitize wood rats and microtine rodents (Hubbard, 1947; Hopkins and Rothschild, 1971; Lewis et al., 1988). A *Peromyscopsylla* flea was prevalent in 0.1% of our community.

**Specimen Deposited:** 1 female ex *O. leucogaster* MSB:Mamm:329295.

## *Family Hystricopsyllidae*

***Anomiopsyllus nudatus*** (Baker, 1898)

*Anomiopsyllus nudatus* is commonly associated with *Neotoma* spp. and is distributed mainly on the Colorado Plateau in the Sonoran Desert and into Mexico (Barnes et al., 1977). In New Mexico, this species in a known carrier of *Y. pestis* (Fagerlund et al., 2001) and *R. felis* (Stevenson et al., 2005). *Anomiopsyllus nudatus* was prevalent in 0.8% of our community and collected mostly in the spring.

**Specimens Deposited:** 1 male, 1 female ex *N. albigula* MSB:Mamm:322189; 1 male ex *N. mexicana* Baird, 1855 MSB:Mamm:329218; 9 males, 5 females ex *N. stephensi* MSB:Mamm:322261, MSB:Mamm:322268, MSB:Mamm:322304, MSB:Mamm:329258; 1 male ex *P. truei* MSB:Mamm:322061.

***Anomiopsyllus* sp.**

*Anomiopsyllus* fleas are strictly Nearctic, and they are distributed from southern Canada to southern Mexico, west of the Mississippi River. This flea has been described as mainly associated with *Neotoma* spp., but it also parasitizes other sympatric rodent species (Barnes et al., 1977; Lewis et al., 1988). Species of the genus *Anomiopsyllus* have greatly reduced characters compared to species in other flea genera, including the lack of eyes, vestigial exoskeletal structures, and diminished chaetotaxy. Their lack of jumping ability and strong association with woodrats and adaptation to a nidicolous habitat implies a deep evolutionary history (Barnes et al., 1977); however, more research into these relationships is necessary (Acosta and Fernández, 2009). The presence of these nidicolous fleas on *Peromyscus* spp. is consistent with use of woodrat middens by deer mice. *Anomiopsyllus* sp. was prevalent in 0.8% of our community, but only females were collected; therefore, we could not morphologically identify these fleas to species.

**Specimens Deposited:** 2 females ex *N. albigula* MSB:Mamm:299170, MSB:Mamm:299180; 1 female ex *N. mexicana* MSB:Mamm:299161; 4 females ex *N. stephensi* MSB:Mamm:322259, MSB:Mamm:329259; 2

females ex *P. nasutus* MSB:Mamm:299087; 1 female ex *P. truei* MSB:Mamm:322258.

***Callistopsyllus terinus*** (Rothschild, 1905)

The species ***Callistopsyllus terinus*** is distributed from southwestern Canada into southern New Mexico (Tipton et al., 1979). Peromyscine rodents are the main hosts for *Callistopsyllus* (Haas et al., 1973; Tipton et al., 1979), a finding consistent with our study. This species was prevalent in 0.3% of our community and was collected only in the spring.

**Specimens Deposited:** 2 males ex *P. boylii* MSB:Mamm:299126; 1 female ex *P. nasutus* MSB:Mamm:299087; 1 male ex *P. truei* MSB:Mamm:322196.

***Catallagia decipiens*** Rothschild, 1915

This flea species has a wide distribution from western Canada and the Pacific Northwest into southern New Mexico (Lewis et al., 1988). In New Mexico, *Catallagia decipiens* has been found parasitizing cricetid, microtine, and sciurid rodents (Ford et al., 2004) and was collected from a bird's nest (possibly violet-green swallow) in Los Alamos County (Haas et al., 1972). *Catallagia decipiens* was prevalent in 0.1% and not well represented in our community, parasitizing only a single host.

**Specimens Deposited:** 1 male, 2 females ex *P. truei* MSB:Mamm:304286.

***Catallagia* sp.** Rothschild

*Catallagia* is a Holarctic genus that is primarily associated with *P. maniculatus* in North America and widely distributed from the midwestern and southwestern United States northward into Canada (Lewis and Haas, 2001). In New Mexico, this genus has also been collected from *Neotoma cinerea* (Ord, 1815), *Microtus longicaudus* (Merriam, 1888) *I. tridecemlineatus*, and *P. boylii* (Morlan, 1955; Fagerlund et al., 2001). Lack of variability of morphological characteristics in females of this genus makes delineation to species without an accompanying male not possible (Lewis et al., 1988). This flea was prevalent in 0.1% of our sample population.

**Specimen Deposited:** 1 female ex *P. nasutus* MSB:Mamm:299087.

***Epitedia stanfordi*** Traub, 1944

The genus *Epitedia* is restricted to North America and parasitizes several species of rodents, especially species of *Peromyscus* (Hubbard, 1947; Lewis et al., 1988). In New Mexico, cricetid rodents are the main hosts for *E. stanfordi*, as also reflected in our study (Ford et al., 2004). This flea species was prevalent in 1.9% of our sample population and was collected mostly in the winter.

**Specimens Deposited:** 2 males, 5 females ex *O. leucogaster* MSB:Mamm:306125, MSB:Mamm:306242, MSB:Mamm:306244, MSB:Mamm:322152, MSB:Mamm:329234; 3 males, 11 females ex *P. maniculatus* MSB:Mamm:299142, MSB:Mamm:299145, MSB:Mamm:322084, MSB:Mamm:322090, MSB:Mamm:322095, MSB:Mamm:322114, MSB:Mamm:322135, MSB:Mamm:322139, MSB:Mamm:322148, MSB:Mamm:322160, MSB:Mamm:322163; 1 female ex *R. megalotis* MSB:Mamm:322056.

***Megarthroglossus bisetis*** Jordan and Rothschild, 1915

This flea species parasitizes a wide range of mammals in New Mexico, including rodents, lagomorphs, and a carnivore (Ford et al., 2004). We report a single specimen from *N. stephensi* and a previously unrecognized host for *M. bisetis* in New Mexico (Méndez and Haas, 1972; Méndez and Haas, 1973; Ford et al., 2004). Méndez and Haas (1973) observed morphological variation within this species across locations in New Mexico and noted that "the population from the Jemez Mountains is undergoing some racial differentiation." This flea species was prevalent in 0.1% of our community.

**Specimen Deposited:** 1 male ex *N. stephensi* MSB:Mamm:329258.

***Megarthroglossus* sp.**

Fleas in the genus *Megarthroglossus* are widely distributed throughout North America but are rare in collections, likely because they are nidicolous (Morlan, 1954; Méndez and Haas, 1973; Holland, 1985). Because of a lack of definitive characteristics in females of this genus, delineation to species is not possible without male specimens (Eads and Campos, 1977). In New Mexico, species of *Neotoma* are the principal hosts for *Megarthroglossus*, which usually are collected from woodrat middens (Méndez and Haas, 1973). Because peromyscine mice also nest in neotomine middens, these nidicolous fleas also parasitize these hosts (Egoscue, 1976; Cranford, 1982).

**Specimen Deposited:** 1 female ex *P. maniculatus* MSB:Mamm:329212.

***Meringis jamesoni*** Hubbard, 1943

This "uncommon species" is restricted to the Southwest and mainly parasitizes *Perognathus flavus* Baird, 1855 but has been collected from other heteromyid, cricetid, and spermophiline rodents in New Mexico (Hubbard, 1943a; Eads et al., 1987; Ford et al., 2004). This flea species was

prevalent in 0.1% in our community.

**Specimen Deposited:** 2 males ex *P. flavus* Baird, 1855 MSB:Mamm:322229.

***Meringis parkeri*** Jordan, 1937

This common species is distributed throughout the midwestern and southwestern United States and mainly parasitizes *Dipodomys* spp. but has been collected from several other species of sympatric rodents (Eads et al., 1987). In our survey, *M. parkeri* was prevalent in 3.1% of our community, and while it parasitized *D. ordii*, the main host was *O. leucogaster*. This flea species was collected in all seasons (mostly in autumn), which corroborates the observation of Hubbard (1947) on the presence of this species year-round.

**Specimens Deposited:** 2 females ex *D. ordii* MSB:Mamm:322318, MSB:Mamm:329232; 12 males, 22 females ex *O. leucogaster* MSB:Mamm:299056, MSB:Mamm:299099, MSB:Mamm:299104, MSB:Mamm:299200, MSB:Mamm:301700, MSB:Mamm:301701, MSB:Mamm:301703, MSB:Mamm:301705, MSB:Mamm:301706, MSB:Mamm:301728, MSB:Mamm:306087, MSB:Mamm:306088, MSB:Mamm:306093, MSB:Mamm:306095, MSB:Mamm:306119, MSB:Mamm:306122, MSB:Mamm:306125, MSB:Mamm:306128, MSB:Mamm:306244, MSB:Mamm:322154, MSB:Mamm:329230, MSB:Mamm:329300; 1 male, 2 females ex *P. maniculatus* MSB:Mamm:299095, MSB:Mamm:306253, MSB:Mamm:322158; 2 females ex *P. truei* MSB:Mamm:306106.

***Meringis rectus*** Morlan, 1953

This flea species is only known from New Mexico, Texas, and Utah (Morlan, 1953; Oliver and Wright, 2011). While *Dipodomys spectabilis* Merriam, 1890 has been considered the main host for *M. rectus*, this flea has been collected from other species of *Dipodomys* as well as other rodents, lagomorphs, and sciurids (Morlan, 1953; Graves et al., 1974; Eads et al., 1987). *Meringis rectus* was prevalent in 2.1% of our community, and while collected from *Dipodomys* spp., it mainly parasitized *O. leucogaster*. This flea species was collected in all seasons except summer. The occurrence of *M. rectus* on *O. leucogaster* is unsurprising, as three species of *Dipodomys* were syntopic in our study area, and their mounds were common where most *O. leucogaster* were trapped. Interactions between *D. ordii* and *O. leucogaster* have been studied in southern New Mexico (Rebar and Conley, 1983), as have ectoparasitic interactions between these two hosts in eastern New Mexico (Pfaffenberger and de Bruin, 1986).

**Specimens Deposited:** 2 females ex *Dipodomys merriami* Mearns, 1890 MSB:Mamm:322153, MSB:Mamm:322159; 4 males, 3 females ex *D. spectabilis* MSB:Mamm:322307; 14 males, 10 females ex *O. leucogaster* MSB:Mamm:301705, MSB:Mamm:306119, MSB:Mamm:306123, MSB:Mamm:306124, MSB:Mamm:306125, MSB:Mamm:306128, MSB:Mamm:306129, MSB:Mamm:306244, MSB:Mamm:322050, MSB:Mamm:322052, MSB:Mamm:322053, MSB:Mamm:322104, MSB:Mamm:322133, MSB:Mamm:322161; 1 male ex *R. megalotis* MSB:Mamm:299115; 1 male ex *R. montanus* MSB:Mamm:306130.

***Meringis* sp.**

The speciose genus *Meringis* is Nearctic in distribution and is thought to primarily parasitize species of *Dipodomys*, but it has been collected from other heteromyid, cricetid, and spermophiline rodents and lagomorphs (Eads, 1978; Eads et al., 1987; Ford et al., 2004). Eads et al. (1987) note that, apart from *M. altipectin*, females cannot accurately be delineated to species without the accompanying male. Castration or partial castration is common in certain species of *Meringis*, further complicating identification (Eads et al., 1987). This flea was prevalent in 0.1% of our sample population.

**Specimen Deposited:** 1 female ex *O. leucogaster* MSB:Mamm:329228.

***Phalacropsylla allos*** Wagner, 1936

Fleas from the genus *Phalacropsylla* are not well studied but are thought to exist primarily at higher elevations (Eads and Maupin, 1982). Most species are nidicolous (except for *P. allos*) and are hypothesized to mainly parasitize *Neotoma* spp., other sympatric rodents, and lagomorphs (Eads and Maupin, 1982). The distribution of this genus ranges from southwestern Canada into mideastern Mexico, and the genus comprises six species (Acosta and Morrone, 2013; Acosta and Hastriter, 2017). *Peromyscopsylla allos* is the most widely distributed species, ranging from southwestern Canada to central New Mexico, and has been collected from *N. cinerea* and their middens, and from *N. mexicana*, *R. megalotis*, *O. leucogaster*, and *Peromyscus* spp. (Hubbard, 1947; Eads and Campos, 1982; Ford et al., 2004; Acosta and Hastriter, 2017). No previous records exist for *N. stephensi* as host. This flea species was prevalent in 0.1% of our sample population.

**Specimen Deposited:** 1 female ex *N. stephensi* MSB:Mamm:329217.

***Phalacropsylla paradisea*** Rothschild, 1915

The nomen *Phalacropsylla hamata* was used by Eads and Maupin (1982) and Tipton and Méndez (1968) and is considered a junior synonym of *P. paradisea* by Acosta and Hastriter (2017), as we do here. This flea ranges from the northwestern United States into northern Mexico and mainly parasitizes *Neotoma* spp. and other sympatric rodents, including *Peromyscus* spp. (Lewis and Maser, 1978; Eads and Campos, 1982). An examination of the flea collection of Glenn E. Haas by Acosta and Hastriter (2017) notes a *P. paradisea* flea collected from the nest of *N. stephensi* in the Dragoon Mountains, China Point, Cochise County, Arizona. We report the first collection of this flea directly from this host species. This flea was prevalent in 0.1% our community.

**Specimen Deposited:** 1 male ex *N. stephensi* MSB:Mamm:322171.

***Rhadinopsylla multidenticulata*** Morlan and Prince, 1954

This understudied flea species was first described from Santa Fe County, New Mexico (Morlan and Prince, 1954). It is distributed throughout the western United States and is most prevalent during winter (November through January) (Morlan and Prince, 1954). We collected this flea in both autumn and winter but not spring and summer. It parasitizes mainly *O. leucogaster* but has been collected from *Dipodomys* spp., *Neotoma* spp., and *Peromyscus leucopus* (Morlan and Prince, 1954). *Rhadinopsylla multidenticulata* was prevalent in 2.8% of our community, parasitizing exclusively *O. leucogaster*, and collected only between late October and February.

**Specimens Deposited:** 20 males, 33 females ex *O. leucogaster* MSB:Mamm:301702, MSB:Mamm:306086, MSB:Mamm:306088, MSB:Mamm:306090, MSB:Mamm:306092, MSB:Mamm:306095, MSB:Mamm:306121, MSB:Mamm:306122, MSB:Mamm:306123, MSB:Mamm:306125, MSB:Mamm:306127, MSB:Mamm:306128, MSB:Mamm:306244, MSB:Mamm:306248, MSB:Mamm:306259, MSB:Mamm:306260, MSB:Mamm:322050, MSB:Mamm:322051, MSB:Mamm:322053, MSB:Mamm:322094, MSB:Mamm:322097, MSB:Mamm:322106, MSB:Mamm:322129, MSB:Mamm:322130, MSB:Mamm:322146.

***Stenistomera alpina*** (Baker, 1895)

The distribution of *S. alpina* is in the southwestern United States, but its range extends south into the Oriental Basin of Veracruz, Mexico (Tipton et al., 1979; Acosta and Fernández, 2009). This nidicolous species is mainly associated with *Neotoma* spp. and includes *N. nelsoni*, a previously unrecognized host association identified by Acosta and Fernandez (2009). In New Mexico, this flea species has been collected from a variety of hosts, including cricetid rodents, lagomorphs, sciurids, and carnivores (Ford et al., 2004). In our community, this species parasitized all species of *Neotoma* and a single *P. truei*, and was prevalent in 1.4% of our community.

**Specimens Deposited:** 3 males ex *N. albigula* MSB:Mamm:299098, MSB:Mamm:322189; 3 males, 4 females ex *N. mexicana* MSB:Mamm:299161, MSB:Mamm:322306, MSB:Mamm:329218, MSB:Mamm:329219; 6 males, 12 females ex *N. stephensi* MSB:Mamm:322171, MSB:Mamm:322259, MSB:Mamm:322304, MSB:Mamm:322308, MSB:Mamm:329217, MSB:Mamm:329259; 1 female ex *P. truei* MSB:Mamm:299140.

***Stenistomera* sp.**

Fleas in this genus are exclusively Nearctic in distribution and are distinguishable by their "bullet-shaped" heads. Three species are currently recognized—*Stenistomera alpina*, *S. hubbardi*, and *S. macrodactyla*—with only *S. alpina*, the most prevalent, and *S. macrodactyla* occurring in New Mexico (Tipton et al., 1979; Ford et al., 2004).

**Specimen Deposited:** 1 female ex *N. stephensi* MSB:Mamm:329258.

***Stenoponia ponera*** Traub and Johnson, 1952

Fleas of this genus are mostly distributed in the Palearctic, except for *Stenoponia americana* and *S. ponera*, which are Nearctic (Lewis, 1974); however, little is known about *S. ponera* because of very limited records. This species is distributed from southwestern Colorado, southeastern Arizona, southwestern Texas, and northern Mexico and parasitizes peromyscine mice but was also collected from *T. dorsalis* (Traub and Johnson, 1952; Hastriter et al., 2006). The holotype and allotype were collected in 1950 at 11.3 km north of Pinos Altos, Grant County, New Mexico, and remained the only known record in New Mexico until our survey (Traub and Johnson, 1952; Ford et al., 2004). This species was prevalent in 0.3% of our community, and to our knowledge this is the first host record for *O. leucogaster*.

**Specimens Deposited:** 1 female ex *O. leucogaster* MSB:Mamm:306260; 2 males ex *P. truei* MSB:Mamm:299137, MSB:Mamm:329288.

### *Family Pulicidae*

***Cediopsylla inaequalis*** (Baker, 1895)

Lagomorphs are the main hosts for *Cediopsylla inaequalis*, but this species has been collected in New Mexico from the rodent *Neotoma micropus* Baird, 1855 and predatory carnivores *Urocyon cinereoargenteus* and *Vulpes* spp. (Patrick and Harrison, 1995; Harrison et al., 2003; Morway et al., 2008). *C. inaequalis* was prevalent in 0.2% of our community and parasitized only cottontail rabbits (n = 7). Lewis et al. (1988) delineated *C. inaequalis* to a subspecific trinomial; however, because of sympatry of the subspecies, common co-occurrence of subspecies on the same host, and "considerable intergradation in their diagnostic characters," we do not consider subspecific status here.

**Specimens Deposited:** 4 males ex *Sylvilagus audubonii* Baird 1858 MSB:Mamm:322208, MSB:Mamm:329213.

***Echidnophaga gallinacea*** (Westwood, 1875)

*Echidnophaga gallinacea*, an invasive, cosmopolitan, sticktight "hen flea" mainly associated with avian hosts, is of great veterinary importance because it parasitizes domestic poultry (e.g., chickens), resulting in serious superficial injury and increased disease susceptibility (Eads, 1950; Mullen and Durden, 2019). This flea species has been implicated in plague epizootics, possibly by burrowing owls (*Athene cunicularia* (Molina, 1782)), a species that commonly co-occurs in prairie dog colonies, sharing infected *E. gallinacea* fleas with incidental hosts (i.e., ground squirrels) (Burroughs, 1947). However, a study conducted by Belthoff et al. (2021) on different species of fleas during a plague epizootic of ground squirrels in southwestern Idaho concluded that burrowing owls most likely did not serve as hosts to infected fleas. In New Mexico, this species parasitizes a wide variety of mammals (Holdenried and Morlan, 1955; Holdenried and Morlan, 1956; Rail et al., 1969; Graves et al., 1974; Pfaffenberger and Wilson, 1985; Pfaffenberger and Valencia, 1988; Patrick and Harrison, 1995; Stevenson et al., 2003). This flea species had the highest mean intensity of all flea species in our community and had a prevalence of 0.6%. *E. gallinacea* was collected in the spring and autumn and parasitized only woodrats.

**Specimens Deposited:** 1 male, 19 females ex *N. mexicana* MSB:Mamm:304271, MSB:Mamm:322306; 22 females ex *N. stephensi* MSB:Mamm:322171, MSB:Mamm:322268, MSB:Mamm:322304.

***Euhoplopsyllus glacialis affinis*** (Baker, 1904)

In New Mexico, this species is commonly associated with species of *Sylvilagus* and *Lepus* and their predators (Pfaffenberger and Valencia, 1988; Patrick and Harrison, 1995). *Euhoplopsyllus glacialis affinis* was prevalent in 0.2% in our community. The subspecific delineation of *E. glacialis* is based on geographic location, host, and morphology of the clasper, as described in Hubbard (1947).

**Specimens Deposited:** 2 females ex *S. audubonii* MSB:Mamm:322165, MSB:Mamm:322320.

## Flea Infestation

Of 898 mammalian specimens examined, 284 (32%) were hosts infested with one or more species of fleas (Table 1). Host species (n > 10) with the highest prevalence of infestation included *T. bottae* (100%, CI = 72%–100%), *N. stephensi* (80%, CI = 48%–93%), and *O. leucogaster* (70%, CI = 59%–76%). Host species (n >10) with the highest flea mean abundance were *N. stephensi* 5.1 (SE ± 0.8), *O. leucogaster* 3.4 (SE ± 0.2), and *N. mexicana* 1.9 (SE ± 0.8). Two *O. leucogaster* mice were the most infested hosts; one parasitized with 27 fleas and the other with 26 fleas, followed by an individual *N. mexicana* parasitized by 23 fleas. Hosts with the highest flea mean intensity (n > 10) were *D. spectabilis* 7.0 (SE ± 1.1), *N. stephensi* 6.7 (SE ± 0.8), and *N. mexicana* 6.0 (SE ± 1.0) (Table 2). Both flea prevalence and mean abundance were positively correlated (Spearman $\rho = 0.96$, $P < 0.001$). Flea species with the highest mean abundance were *P. exilis*, which made up 0.27 (SE ± 0.05) of all fleas recorded, while *A. wagneri* was 0.13 (SE ± 0.02) and *O. leucopus* was 0.01 (SE ± 0.02). Flea species with the highest prevalence were *A. wagneri*, found on 7.7% (CI = 6.1%–9.6%) of hosts, *P. exilis* at 7.2% (CI = 5.6%–9.1%), and *O. leucopus* at 5.5% (CI = 4.1%–7.1%) (Table 2). Flea species with the highest mean intensity were *E. gallinacea* 8.4 (SE ± 0.03) fleas per infected host, *P. exilis* 3.7 (SE ± 0.05), and *F. ignota* 3.4 (SE ± 0.02) (Table 2).

### *Host sex and seasonality*

In the El Malpais community, mean flea abundance reflects host sex ($\chi^2 = 109.75$, df = 11, $P < 0.001$), with males having a higher mean abundance than females (Fig. 13). Seasonality also influenced mean flea abundance ($\chi^2 = 328.77$, df = 33, $P < 0.001$), with mean abundance highest in the spring and lowest in the summer (Fig. 14).

## Discussion

The ability of flea species to colonize a broad range of host species is an example of phenotypic flexibility and often occurs among hosts that are phylogenetically related or similar in ecological attributes to hosts previously colonized

**Table 1.** List and number of every flea and host species. **References: Cg:** Cynomys gunnisoni, **Dm:** Dipodomys merriami, **Do:** Dipodomys ordii, **Ds:** Dipodomys spectabilis, **Na:** Neotoma albigula, **Nm:** Neotoma mexicana, **Ns:** Neotoma stephensi, **Ol:** Onychomys leucogaster, **Pf:** Perognathus flavus, **Pb:** Peromyscus boylii, **Pm:** Peromyscus maniculatus, **Pn:** Peromyscus nasutus, **Pt:** Peromyscus truei, **Rm:** Reithrodontomys megalotis, **Rmt:** Reithrodontomys montanus, **Sa:** Sylvilagus audubonii, **Td:** Tamias dorsalis, **Tb:** Thomomys bottae.

| Flea/Host Species (total) | ***Cg*** (15) | ***Dm*** (4) | ***Do*** (9) | ***Ds*** (6) | ***Na*** (28) | ***Nm*** (16) | ***Ns*** (13) | ***Ol*** (121) | ***Pf*** (48) | ***Pb*** (29) | ***Pm*** (267) | ***Pn*** (36) | ***Pt*** (136) | ***Rm*** (147) | ***Rmt*** (1) | ***Sa*** (7) | ***Td*** (5) | ***Tb*** (10) | Total (898) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aetheca wagneri* | | | | | | | 3 | 5 | | | 66 | 6 | 30 | 4 | | | | | 114 |
| *Amaradix euphorbi* | | | | | | | | 2 | | | 5 | | | | | | | | 7 |
| *Anomiopsyllus nudatus* | | | | | 2 | 1 | 14 | | | | | | 1 | | | | | | 18 |
| *Anomiopsyllus sp.* | | | | | 2 | 1 | 4 | | | | | 2 | 1 | | | | | | 10 |
| *Callistopsyllus terinus* | | | | | | | | | | 2 | | 1 | 1 | | | | | | 4 |
| *Catallagia decipiens* | | | | | | | | | | | | | 3 | | | | | | 3 |
| *Catallagia* sp. | | | | | | | | | | | | 1 | | | | | | | 1 |
| *Cediopsylla inaequalis* | | | | | | | | | | | | | | | | 4 | | | 4 |
| *Echidnophaga gallinacea* | | | | | | 20 | 22 | | | | | | | | | | | | 42 |
| *Epitedia stanfordi* | | | | | | | | 7 | | | 14 | | | 1 | | | | | 22 |
| *Euhoplopsyllus glacialis affinis* | | | | | | | | | | | | | | | | 2 | | | 2 |
| *Eumolpianus eumolpi* | | | | | | | | | | | | | | | | | 4 | | 4 |
| *Foxella ignota* | | | | | | | | 11 | | | | | | | | | | 46 | 57 |
| *Malaraeus eremicus* | | | | | | | | 1 | | 9 | 2 | 8 | 15 | 2 | | | | | 37 |
| *Malaraeus telchinus* | | | | | | | | | | | | | | 1 | | | | | 1 |
| *Megarthroglossus bisetis* | | | | | | | 1 | | | | | | | | | | | | 1 |
| *Megarthroglossus sp.* | | | | | | | | | | | 1 | | | | | | | | 1 |
| *Meringis jamesoni* | | | | | | | | | 2 | | | | | | | | | | 2 |
| *Meringis parkeri* | | | 2 | | | | | 34 | | | 3 | | 2 | | | | | | 41 |
| *Meringis rectus* | | 2 | | 7 | | | | 24 | | | | | | 2 | | | | | 35 |
| *Meringis* sp. | | | | | | | | 1 | | | | | | | | | | | 1 |
| *Monopsyllus* sp. | | | | | | | | 1 | | | | | | 1 | | | | | 2 |
| *Orchopeas leucopus* | | | | | | | | 1 | | | 22 | | 13 | 50 | 1 | | | | 87 |
| *Orchopeas neotomae* | | | | | | 1 | 1 | | | | | | | | | | | | 2 |
| *Oropsylla hirsuta* | 17 | | | | | | | 6 | | | | | | | | | | | 23 |
| *P. hesperomys adelpha* | | | | | | | | 15 | | 1 | 12 | 3 | 24 | 2 | | | | | 57 |
| *Peromyscopsylla* sp. | | | | | | | | 1 | | | | | | | | | | | 1 |
| *Phalacropsylla allos* | | | | | | | 1 | | | | | | | | | | | | 1 |
| *Phalacropsylla paradisea* | | | | | | | 1 | | | | | | | | | | | | 1 |
| *Pleochaetis exilis* | | | | | 4 | | | 235 | | | | | | | | | | | 239 |
| *Rhadinopsylla multidenticulata* | | | | | | | | 53 | | | | | | | | | | | 53 |
| *Stenistomera alpina* | | | | | 3 | 7 | 18 | | | | | | 1 | | | | | | 29 |
| *Stenistomera* sp. | | | | | | | 1 | | | | | | | | | | | | 1 |
| *Stenoponia ponera* | | | | | | | | 1 | | | | | 2 | | | | | | 3 |
| *Thrassis aridis* | | | 1 | | | | | 17 | | | | | | | | | | | 18 |
| Unknown | | | | | | | | | | 1 | | | | | | | | | 1 |
| Grand Total | 17 | 2 | 3 | 7 | 11 | 30 | 66 | 415 | 2 | 13 | 125 | 21 | 93 | 63 | 1 | 6 | 4 | 46 | 925 |
| Mean Flea Abundance | 1.1 | 0.5 | 0.3 | 1.2 | 0.4 | 1.9 | 5.1 | 3.4 | 0.0 | 0.4 | 0.5 | 0.6 | 0.7 | 0.4 | 1.0 | 0.9 | 0.8 | 4.6 | 1.3 |
| Prevalence (%) | 27 | 50 | 33 | 16 | 18 | 31 | 77 | 68 | 2 | 17 | 26 | 22 | 32 | 20 | 100 | 57 | 40 | 100 | 32 |

**Table 2.** Infestation levels. *Flea species that have tested positive for *Y. pestis* in New Mexico according to Fagerlund et al. (2001). **References: P** = prevalence, **CI** = confidence intervals, **MA** = mean abundance, **SE** = standard error.

| Flea Species | P | CI | MA | SE (±) | MI | SE (±) |
|---|---|---|---|---|---|---|
| *Aetheca wagneri** | 7.70% | 6.1–9.6% | 0.13 | 0.02 | 1.65 | 0.02 |
| *Amaradix euphorbi* | 0.60% | 0.2–1.3% | 0.01 | 0.00 | 1.4 | 0 |
| *Anomiopsyllus nudatus** | 0.80% | 0.3–1.6% | 0.02 | 0.01 | 2.57 | 0.01 |
| *Anomiopsyllus sp.* | 0.80% | 0.3–1.6% | 0.01 | 0.00 | 1.43 | 0 |
| *Callistopsyllus terinus** | 0.30% | 0.1–1.0% | 0.00 | 0.00 | 1.33 | 0 |
| *Catallagia decipiens** | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 3 | 0 |
| *Catallagia sp.* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Cediopsylla inaequalis** | 0.20% | 0.0–0.8% | 0.00 | 0.00 | 2 | 0 |
| *Echidnophaga gallinacea** | 0.60% | 0.2–1.3% | 0.05 | 0.03 | 8.4 | 0.03 |
| *Epitedia stanfordi** | 1.90% | 1.1–3.0% | 0.02 | 0.01 | 1.29 | 0.01 |
| *Euhoplopsyllus glacialis affinis** | 0.20% | 0.0–0.8% | 0.00 | 0.00 | 1 | 0 |
| *Eumolpianus eumolpi** | 0.20% | 0.0–0.8% | 0.00 | 0.00 | 2 | 0 |
| *Foxella ignota** | 1.90% | 1.1–3.0% | 0.06 | 0.02 | 3.35 | 0.02 |
| *Malaraeus eremicus** | 2.80% | 1.8–4.1% | 0.04 | 0.01 | 1.48 | 0.01 |
| *Malaraeus telchinus* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Megarthroglossus bisetis** | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Megarthroglossus sp.* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Meringis jamesoni* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 2 | 0 |
| *Meringis parkeri* | 3.10% | 2.1–4.5% | 0.05 | 0.01 | 1.46 | 0.01 |
| *Meringis rectus* | 2.10% | 1.3–3.2% | 0.04 | 0.01 | 1.84 | 0.01 |
| *Meringis sp.* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Monopsyllus sp.* | 0.20% | 0.0–0.8% | 0.00 | 0.00 | 1 | 0 |
| *Orchopeas leucopus** | 5.50% | 4.1–7.1% | 0.10 | 0.02 | 1.78 | 0.02 |
| *Orchopeas neotomae** | 0.20% | 0.0–0.8% | 0.00 | 0.00 | 1 | 0 |
| *Oropsylla hirsuta** | 1.00% | 0.5–1.9% | 0.03 | 0.01 | 2.56 | 0.01 |
| *Peromyscopsylla hesperomys adelpha** | 4.00% | 2.8–5.5% | 0.06 | 0.01 | 1.58 | 0.01 |
| *Peromyscopsylla sp.* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Phalacropsylla allos* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Phalacropsylla paradisea** | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Pleochaetis exilis** | 7.20% | 5.6–9.1% | 0.27 | 0.05 | 3.68 | 0.05 |
| *Rhadinopsylla multidenticulata* | 2.80% | 1.8–4.1% | 0.06 | 0.02 | 2.12 | 0.02 |
| *Stenistomera alpina** | 1.40% | 0.8–2.5% | 0.03 | 0.01 | 2.23 | 0.01 |
| *Stenistomera sp.* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |
| *Stenoponia ponera* | 0.30% | 0.1–1.0% | 0.00 | 0.00 | 1 | 0 |
| *Thrassis aridis** | 1.30% | 0.7–2.3% | 0.02 | 0.01 | 1.5 | 0.01 |
| *Unknown* | 0.10% | 0.0–0.6% | 0.00 | 0.00 | 1 | 0 |

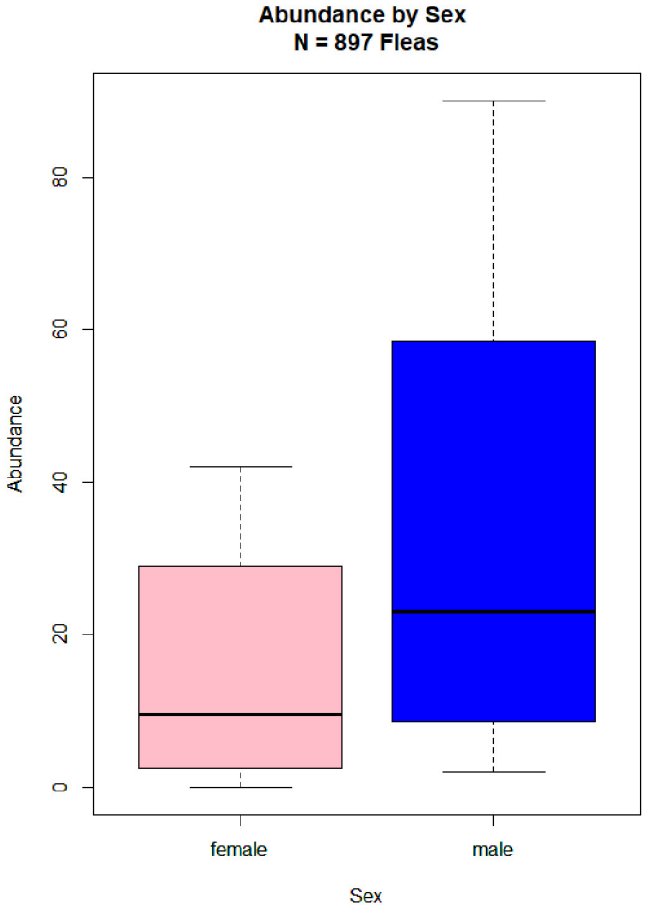


**Figure 13.** Overall abundance by host sex. Host sex is a significant ($p < 0.001$) variable in flea abundance.

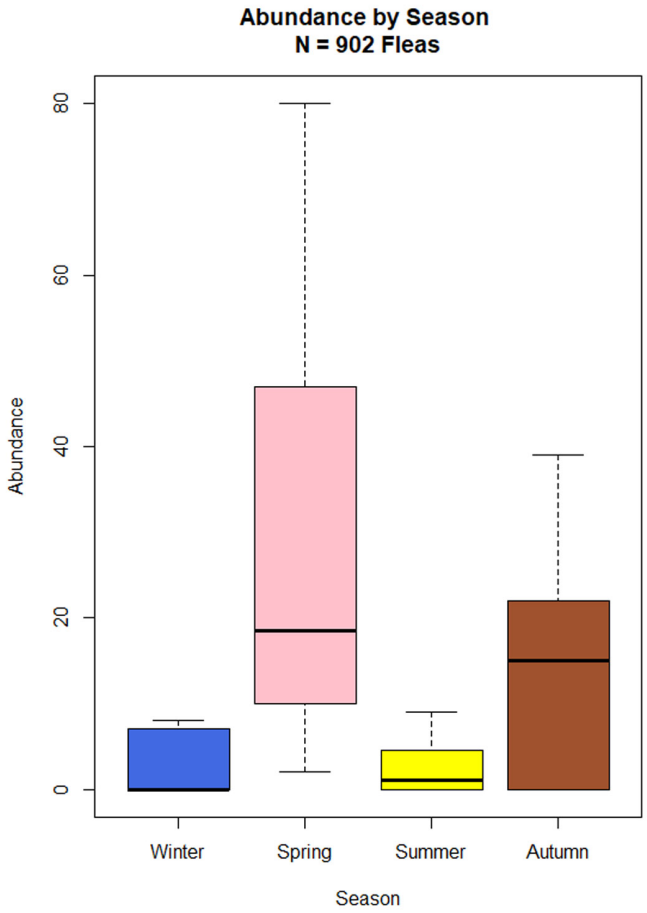


**Figure 14.** Overall flea abundance by season. Seasonality is a significant ($p < 0.001$) variable in abundance.

(Agosta et al., 2010). Flea distributions revealed in our study demonstrate the interaction of fundamental fitness space (the range of all hosts upon which a flea could persist) and realized fitness space (the actual host range at any particular place and time). Reflected is the interaction of capacity by parasites (to use widely and conserved host-based resources) and opportunity (the particular shifting ecological facilitators or limitations on host range) that define "sloppy fitness space" through ecological fitting (Araujo et al., 2015; Hoberg and Brooks, 2015; Brooks et al., 2019). These interactions, under the Stockholm paradigm (SP) are fundamentally important in driving the structure of complex parasite-host associations apparent across local faunas to extended communities (Brooks et al., 2019).

Geographic distribution of flea species ranged from a cosmopolitan species (*E. gallinacea*) to a species restricted to the US Southwest and Mexico (*S. ponera*) to species found only in the southwestern United States (*M. jamesoni*). In some cases, apparent range restriction of certain flea species may simply reflect limited record availability. The range of *S. ponera* was previously considered to be restricted to Texas, New Mexico, Arizona, and Mexico until a reexamination of specimens of *S. americana* and their geographical ranges (Hastriter et al., 2006) resulted in re-identification to *S. ponera* with an apparent range extension into Colorado. It is hypothesized that *S. ponera* and *S. americana* were originally allopatric (geographically isolated), with subsequent colonization of their currently sympatric distributions after the Pleistocene (Hastriter et al., 2006), demonstrating a broader potential host range for these flea species. This potential host range, or "sloppy fitness space" (Agosta et al., 2010), increases the capacity for flea colonization of new hosts and associated expanded geographic range (Audy, 1958). Further, consistent with SP dynamics, Audy (1958) noted that the distribution of a pathogen is always considerably broader than the distribution of disease attributed to that pathogen, which will have particular significance or relevance in understanding the role of fleas as vectors and the mosaic occurrence of pathogens and hosts.

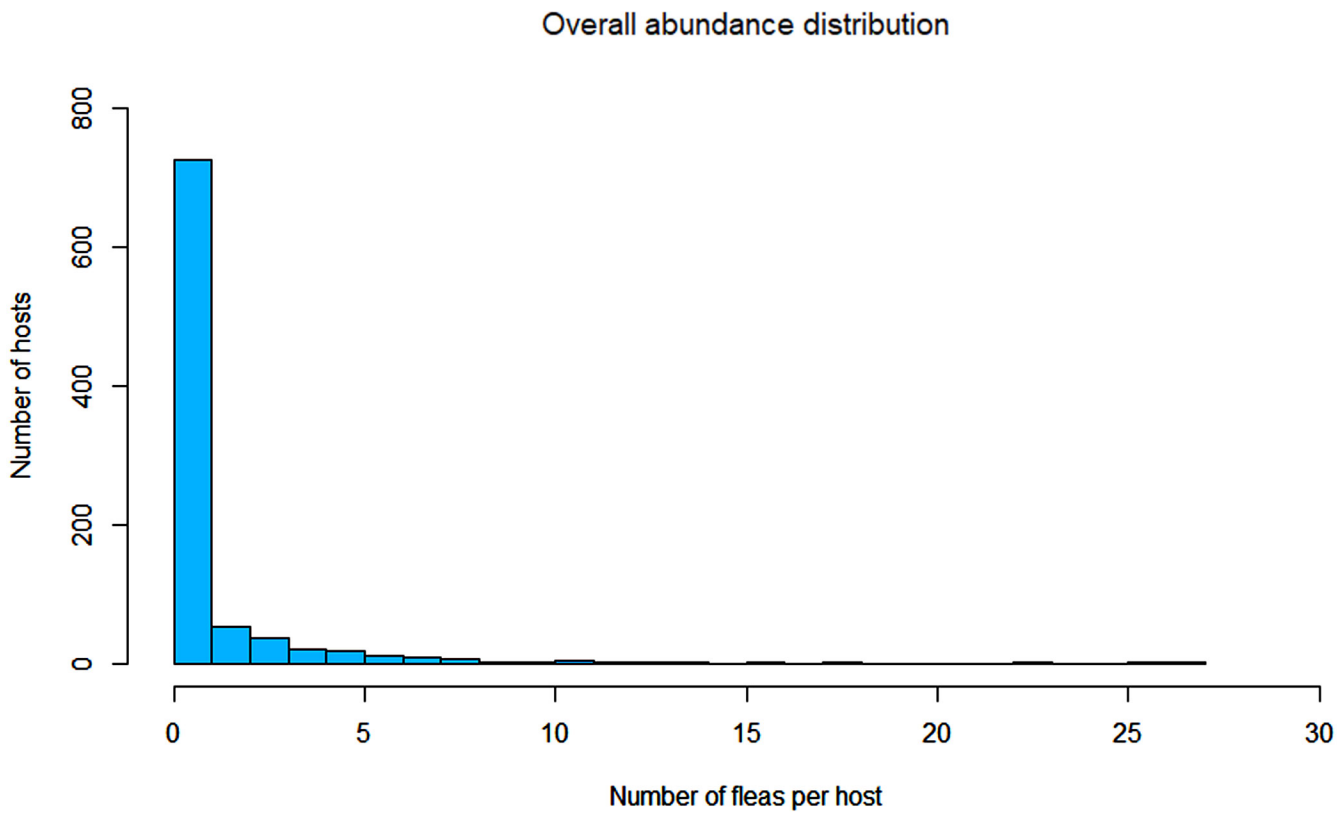


**Figure 15.** Abundance frequency histogram shows an uneven, right-skewed distribution, with most mammals found to have no fleas.

Documentation of the complex small mammal–flea community for El Malpais in central New Mexico provides a baseline foundation for future studies. We identified new host associations for *M. bisetis*, *P. allos*, and *P. paradisea* for the host *N. stephensi*, and *S. ponera* for the host *O. leucogaster*. We also identified one of the highest flea diversities for *O. leucogaster* in a single collection area in North America. We identified six species of fleas (21% of flea species) that persist as adults year-round, whereas eight species of fleas (28% of flea species) were collected in only a single season. Variation in the persistence of adult flea species may reflect abiotic factors, such as climate affecting the flea's lifecycle (egg, larva, and pupae) (Van der Mescht et al., 2016). Seasonal change alters behavior in some host species (e.g., hibernation, mating) which, in turn, may also drive the persistence of adult flea species. Hibernation would decrease the availability of new hosts (no births), whereas host mating increases contact between host species and provides new hosts for fleas from births. Multiseasonal and multiyear sampling of El Malpais revealed comparatively high diversity in both the small mammal and flea community and provides insight into the temporal structure of our flea and host community.

### *Diversity and species richness*

Ford et al. (2004) reported a total of 99 flea species for New Mexico, and we identified 29 flea species from El Malpais alone, representing 29% of all identified species based on the geopolitically defined dimensions of the state. Based on the predictions for accumulation and sampling in the host community (19 mammal species), we believe that our collection (18 species) sufficiently represented the small mammal community of our survey area. The prediction for accumulation and sampling for the flea community was 33 species, suggesting that there may be greater flea diversity represented relative to our current documentation (29 species). Most hosts (11) were parasitized by two or more flea species, while seven were parasitized by one. Hosts that were parasitized with only one flea species include *C. gunnisoni*, *D. merriami*, *D. spectabilis*, *P. flavus*, *R. montanus*, *T. dorsalis*, and *T. bottae*. Some host species were not well represented by our sampling, including *D. merriami* (n = 4), *D. ordii* (n = 9), *D. spectabilis* (n = 6), and *T. dorsalis* (n = 5), and these species should be further surveyed. Other species with relatively low sampling include *C. gunnisoni* (n = 15), *N. stephensi* (n = 13), *T. bottae* (n = 10), and *S. audubonii* (n = 7). *Perognathus flavus* had only a single individual

parasitized by two *M. jamesoni*, a flea species usually associated with this host (Eads et al., 1987). Low prevalence and abundance on more highly represented species of *Perognathus* may be caused by grooming behaviors and dust bathing (Hubbard, 1943a), possibly creating a more inhospitable environment for adult fleas to remain on their host. While high diversity for our small mammal flea community is similar to that of the surrounding Southwest and Pacific states (Hubbard, 1943b; Hubbard, 1947; Egoscue, 1966; Allred, 1968; Kucera and Haas, 1992; Haas et al., 2004), the number of species identified in our limited survey area is comparable with the total number of mammalian flea species collected across entire eastern states, including Georgia with 26 species (Durden et al., 2012), Maryland with 31 species (Eckerlin, 2011), Maine with 32 species (Eckerlin and Gardner, 2021), and West Virginia with 35 species (Eckerlin, 2016).

With respect to the composition of small mammal communities around prairie dog colonies, diversity for fleas and mammals was greater at El Malpais relative to published studies from other localities such as Lower Brule (LB) in South Dakota, Pawnee National Grassland (PNG) in Colorado, and Thunder Basin National Grassland (TBNG) in Wyoming (Thiagarajan et al., 2008; Stapp et al., 2009; Maestas and Britten, 2017). Prairie dogs, as well as black-footed ferrets, are highly susceptible to plague, which is hypothesized to be transmitted in the American Southwest by several rodents and their fleas (Gage and Kosoy, 2005); therefore, it is crucial to develop a comprehensive understanding of the associated mammalian and flea community. The cricetid rodent *O. leucogaster* was common across all these communities and, although not necessarily the most predominant rodent (except for at PNG), it consistently had the highest flea species richness (15 flea species for El Malpais and 8 species each for LB, PNG, and TBNG). High flea species richness for *O. leucogaster* is hypothetically caused by their predatory behavior, burrowing lifestyle, and omnivorous diet (Thomas, 1988; Kraft and Stapp, 2013). The El Malpais community appears to have the highest recorded species richness (15 species, including *Monopsyllus* sp.) for the northern grasshopper mouse (*O. leucogaster*) (Thomas, 1988), which commonly is sympatric with prairie dogs. To our knowledge, this is one of the higher flea diversities recognized in North America. This diversity is lower when compared to Campos et al. (1985), who reported 23 flea species on *P. maniculatus* at Weaver Ranch, Larimer County, Colorado, but the same as Davis et al. (2002), who reported 15 flea species each collected on deer mice (*Peromyscus* spp.) and woodrats (*Neotoma* spp.) at Chuchupate Campground, Ventura County, California. Because of their ability to harbor both high species richness and abundance, grasshopper mice are highly implicated in plague epizootics (Stapp et al., 2009). The flea community at El Malpais mostly comprised species of the Ceratophyllidae and Hystrichopsyllidae families. This composition is moderately different compared to that of LB, PNG, and TBNG, where fleas from the family Ceratophyllidae were most abundant.

*Pleochaetis exilis* and *A. wagneri* were the two most abundant flea species in our communities, which is similar to reported abundance in prairie dog communities from South Dakota (LB) for *A. wagneri* and from Colorado (PNG) for *P. exilis* (Stapp et al., 2009; Maestas and Britten, 2017). As at El Malpais, the most abundant mammal and flea species for South Dakota and Wyoming (TBNG) were *P. maniculatus* and *A. wagneri*, while *O. leucogaster* and *P. exilis* were most abundant in Colorado. It should be noted, however, that the LB, PNG, and TBNG locations have black-tailed prairie dogs (*Cynomys ludovicianus* (Ord, 1815)), whereas El Malpais has Gunnison's prairie dogs. Differences in prairie dog species may influence flea and mammal community composition through distinctive behaviors. For example, Gunnison's prairie dogs hibernate, whereas black-tailed prairie dogs do not (Rayor et al., 1987; Hoogland, 1995). Interspecific contact between hosts and their fleas may be lower during Gunnison's prairie dogs' hibernation, potentially limiting colonization onto new hosts. The prairie dogs at El Malpais were parasitized by a single flea species, *O. hirsuta*. Flea diversity (i.e., *O. hirsuta*, *Pulex simulans*, *Oropsylla tuberculata cynomuris*, and *Thrassis fotus*) was greater on black-tailed prairie dogs collected during a plague epizootic at PNG (Tripp et al., 2009). Drivers of flea and host assemblages are hypothetically habitat (Krasnov, Stanko, et al., 2006), host phylogeny, shelter architecture (Krasnov et al., 2022), dynamic ecological context, and the history of mosaic faunal assembly through ecological fitting, along with host and geographic colonization (Hoberg and Brooks, 2008; Agosta et al., 2010; Araujo et al., 2015; Brooks et al., 2019).

### *Infestation parameters*

Considering the community at El Malpais, prevalence and mean abundance of fleas were positively correlated. These observations are consistent across most host and parasite communities, especially among desert flea and rodent assemblages (Krasnov, Morand, Khokhlova, et al., 2005; Krasnov, Stanko, et al., 2005; Poulin, 2007). Overall abundance for our community was highly aggregated and unevenly distributed, which supports the law of aggregation in most host and parasite communities (Poulin, 2007). Total flea mean abundance (1.32) and total flea prevalence (31.6%) varied among host species and ranged from 0.04 to 5.08 for mean abundance and 2.0% to 100% for prevalence.

Flea mean intensity varied among flea species and ranged from 1.0 to 8.4. *P. maniculatus* (Wagner, 1845) was the most common host, composing 30% of the community. This mammal, mainly parasitized by *A. wagneri* (relative abundance = 52.8%), also hosted the majority of *A. wagneri* collected (58%), a finding similar to that reported for Chuchupate Campground in central California (Davis et al., 2002). That site is also dominated by cricetid rodents, with 76% of the *A. wagneri* recovered reported from deer mice. A survey conducted at Rocky Mountain National Park (RMNP) in Colorado (Eads and Campos, 1983) also found that *P. maniculatus* and *A. wagneri* were the dominant host and flea association. That site, although higher in elevation, has similar habitat structure (grasses and dwarf shrubs). For *P. maniculatus*, flea mean abundance (1.2), prevalence (48.7%), and mean intensity (2.5) were higher on RMNP, compared to El Malpais (flea mean abundance = 0.47, prevalence = 25.5%, mean intensity = 1.8). Those differences may reflect our survey of all seasons, whereas only summer months were surveyed in RMNP. However, infestation parameters were also lower compared to the small mammal and flea community at Weaver Ranch, where collections took place in all seasons (Campos et al., 1985). Although abundances differed somewhat, the same flea species parasitizing the same host species across different geographical areas is consistent with the hypothesis that abundance is driven by host identity and geographical locality (Krasnov, Shenbrot, et al., 2006).

### *Sex and seasonality*

The significant relationship between host sex and flea abundance, with higher infestation found on males than females, is a finding consistent with the male-biased hypothesis that flea abundance is higher in males than females (Morand et al., 2004). The sex-bias phenomenon is complex (Krasnov, Morand, Hawlena, et al., 2005) and warrants more detailed exploration. For example, Krasnov, Morand, Hawlena, et al. (2005) hypothesized that lower immunocompetence in male hosts caused by higher levels of androgen hormones contributed to higher flea infestation in males than females. For our community, when individuals of host species >10, abundance was higher on male than female host species except for three species, *N. stephensi*, *O. leucogaster*, and *P. boylii*. Those exceptions may be related to factors such as body size dimorphism rather than sex alone (Krasnov, Morand, Hawlena, et al., 2005), with host body mass potentially an important predictor of flea abundance because of increased surface area for fleas to parasitize, rather than sex (Kiffner et al., 2013; Young et al., 2015).

Body size (mass) also has been hypothesized to drive infestation. Two of the larger host species, *N. mexicana* and *N. stephensi*, had the first and third largest mean abundance and the second and first largest mean intensity, implying that body size may be a significant factor. However, *O. leucogaster*, the host with the second highest flea mean abundance and fourth largest mean intensity weighs approximately half as much as woodrats. *Cynomys gunnisoni*, the largest host species, had the fifth highest mean abundance and mean intensity. While body size may contribute to larger flea abundance because of the availability of more surface area in some host species, our results suggest other factors may be contributing to higher abundance. For example, woodrats live in middens, which may provide suitable microhabitats to support all stages of the flea's lifecycle, contributing to higher host abundance. In addition, other rodent species, including deer mice, cohabitate with woodrats, which may contribute to flea sharing and increased abundance; therefore, factors such as the host's natural history should be considered along with body size. We found a significant relationship between seasonality and flea abundance at El Malpais.

Seasonality has been shown to drive abundance in both flea and host communities to various degrees and may partly be explained by differing amounts of precipitation and temperature extremes across seasons (Parmenter et al., 1999; Eads and Hoogland, 2017). Flea species community composition was also affected by seasonality, with the majority of flea species collected during milder seasons (spring and autumn). Seasonal variation may be affecting the natural history and lifecycle of fleas, host physiology, and ecological behavior. Most species of fleas were present during multiple seasons, with the exception of eight species of fleas that were present during a single season. *Callistopsyllus terinus*, *M. jamesoni*, *O. neotomae*, and *P. paradisea* were present only during the spring, while *C. decipiens*, *M. bisetis*, *M. telchinus*, and *P. allos* were present only during autumn. These flea species also were lower in abundance within the community, with only singletons of *P. paradisea*, *M. bisetis*, *M. telchinus*, and *P. allos* collected. The low presence and abundance of these flea species on hosts may be a result of minimal collecting from burrows and middens, as most flea species alternate time on and off the host. However, according to Krasnov et al. (2004), collecting directly from the host is a reliable method for determining infestation parameters. Flea abundance in El Malpais was remarkably lower during the summer months, which did not correspond to host abundance, which was lowest in the winter. This sharp difference in seasonal abundance may be caused by the effect of environmental conditions, including temperature and precipitation on flea fecundity (Krasnov et al., 1997; Krasnov et al., 2002). Several components of seasonality, including temperature, precipitation,

and amount of daylight, warrant examination to provide a more robust assessment of how seasonal variation has an impact on infestation.

Climate change and anthropogenic activities are rapidly altering habitats and having an impact on extant communities in the Southwest and globally. The movement or dispersal of hosts and parasites caused by changing environmental conditions have historically structured these assemblages, and contemporary climate disruption can result in establishment of new interfaces, faunal mixing, and colonization events across susceptible communities (Brooks and Hoberg, 2007; Hoberg et al., 2008; Hoberg et al., 2017; Brooks et al., 2019). The prairie dogs at El Malpais were reintroduced into the community and dusted to eliminate ectoparasites, yet some of their progeny that we sampled were parasitized by *O. hirsuta*, a species highly associated with ground squirrels. Hypothetically, *O. hirsuta* fleas were either introduced with the prairie dogs from incomplete dusting that did not kill these ectoparasites, or these fleas recolonized the introduced prairie dogs from other native hosts (e.g., *O. leucogaster*). Those alternative hypotheses could be tested through a comprehensive phylogeographic study of *O. hirsuta* fleas. Colonization of the reintroduced prairie dog host by the endemic flea populations at El Malpais would be consistent with the principal of ecological fitting in faunal persistence and assembly (Hoberg and Brooks, 2008; Agosta et al., 2010; Araujo et al, 2015; Brooks et al., 2019).

Reintroduction and translocation of prairie dogs, which are considered a keystone species, have occurred throughout the Southwest in recent years and provide an opportunity to better understand host-parasite dynamics (Hoberg and Brooks, 2015). *O. leucogaster* was the only other rodent parasitized by *O. hirsuta*, which may imply that this flea species can successfully exploit a broader range of host species, reflecting a conserved capacity for host-resource use rather than host fidelity, consistent with ecological fitting (Agosta et al., 2010; Araujo et al., 2015). The SP is a synthesis that incorporates the processes of ecological fitting, host and geographic oscillation, recurrent expansion of geographic and host ranges under the taxon pulse, and microevolutionary landscape mosaics to help understand complex faunal assembly and host and parasite dynamics over ecological and evolutionary time (Hoberg and Brooks, 2008; Hoberg and Brooks, 2015; Brooks et al., 2019). We can examine how present-day intraspecific associations are influenced by colonization events of host and new geographic regions, in contrast to models that continue to reflect the relative simplicity of cospeciation processes (Brooks et al., 2015; Brooks et al., 2019). Assembly and structure of the diverse El Malpais fauna is broadly consistent with the complexities of the SP and ecological fitting in shallow and deep time.

In ecological time, colonization events are common and can have devastating consequences, as demonstrated by the introduction of plague into Gunnison's prairie dog communities in New Mexico resulting in > 99% mortality (Cully et al., 1997). The majority of the flea species identified in our community are capable vectors for plague and other pathogens, and 20 species identified in our community are known carriers of *Y. pestis* in New Mexico (Thomas, 1988; Fagerlund et al., 2001; Stevenson et al., 2003; Stevenson et al., 2005). Host species diversity plays a critical role in either driving an increased or decreased risk of pathogen and disease transmission (Ostfeld and Keesing, 2012). The pathogen transmission model for Lyme disease, for example, has demonstrated that intact communities lower transmission of *Borrelia burgdorferi* through dilution effects, whereas transmission increased in altered communities with lower host diversity (LoGiudice et al., 2003; Keesing et al., 2006). A caveat here is the recent expansion of knowledge about diversity of *Borrelia* that may involve more than 21 species and that will dramatically influence our capacity for understanding disease dynamics, etiology, and diagnostics (Stone et al., 2017). Diversity is only one component, however, with ecological fitting in pathogen circulation among mammalian hosts projected to increase across interfaces that drive opportunities for exchange and dissemination. These interfaces result from breakdowns in ecological isolation and are critical as drivers for potential zoonotic risk (Audy, 1958; Brooks et al., 2019; Brooks et al., 2021).

In this respect, the SP provides access to an increasingly nuanced view of the biosphere that links capacity of pathogens to use host resources with opportunities for circulation represented by ecological change and movement (Boeger et al., 2022). An operational extension of the SP is outlined within the DAMA protocol (Document, Assess, Monitor, Act). A proactive approach to mitigating risk is central to DAMA (Brooks et al., 2014; Brooks et al., 2019; Brooks et al., 2021; Colella et al., 2021; Trivellone et al., 2022).

Documenting a host and parasite community through development of archival resources such as those from El Malpais is the crucial first step in understanding diversity and assessing risk (Dunnum et al., 2017). The next steps lead to detailed **assessment** of this complex community (through phylogenetic triage), including additional temporal and spatial sampling for monitoring that will allow us to identify drivers of community structure and to **monitor** changes over time. These steps are crucial in mitigating transmission risk, among mammals and at interfaces with people, through development of **actions** or pathways

for essential information about hosts, fleas, and pathogens that can be communicated to public health offices, resource agencies, and local communities. The SP and DAMA are the core of proactive approaches to anticipation and mitigation of emergent pathogens and disease in a world under accelerating change and movement. Such a refined understanding of diversity is essential in developing reintroduction programs for endangered species including the black-footed ferret.

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**Ethical standards** – Handling procedures were under IACUC protocol number 19-200908-MC and followed Galbreath et al. (2019) and the Guidelines of the American Society of Mammalogists (Sikes and Animal Care, 2016).

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