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**A DIVERSE FLEA (SIPHONAPTERA) ASSEMBLAGE FROM  
THE SMALL MAMMALS OF CENTRAL NEW MEXICO**

**by**

**DIANNE ESTHER PETERSON**

**B.A., CHEMISTRY,  
UNIVERSITY OF NEW MEXICO, 2000**

**THESIS**

Submitted in Partial Fulfillment of the  
Requirements for the Degree of

**Master of Science**

**Biology**

The University of New Mexico  
Albuquerque, New Mexico

**May, 2022**

## DEDICATION

“No great and enduring volume can ever be written on the flea, though many there be that have tried it.” – Herman Melville, *Moby-Dick; or The Whale*

I dedicate this thesis to Dr. Ralph Eckerlin who forever changed the trajectory of my life toward studying biology through the eyes of the flea (for those species that have them).

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**A diverse flea (Siphonaptera) assemblage from the small mammals of  
central New Mexico**

**by**

**Dianne Esther Peterson**

B.A., Chemistry, University of New Mexico, 2000

M.S., Biology, University of New Mexico, 2022

**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 due to 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 comprising 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, *Aetheca wagneri*, *Malaraeus eremicus*, and *Peromyscopsylla hesperomys adelpha* parasitized the most host species (n = 6 each). The northern grasshopper mouse (*Onychomys leucogaster*), a rodent highly implicated in plague dynamics, was host for the highest number of flea species (n =

15), followed by *Peromyscus truei* ( $n = 10$ ). 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 new host associations; and c) examine infestation parameters including the relationships of flea prevalence and mean abundance to host sex, host abundance, and seasonality.



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## Chapter 1

### **A diverse flea (Siphonaptera) assemblage from the small mammals of central New Mexico**

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#### **Introduction**

Fleas (Order Siphonaptera) are tiny, holometabolous obligate parasites of birds and mammals (approximately 4% and 96% respectively) representing over 2,500 nominal species in 18 families (Medvedev, 1996; Whiting *et al.*, 2008; Zhu *et al.*, 2015). Rodents are the predominate mammalian hosts, likely due to 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 & Kosoy, 2005; Bitam *et al.*, 2010). Several flea species in the Southwest (e.g., *Aetheca wagneri*, *Pleochaetis exilis*, and *Oropsylla hirsuta*) are considered important vectors of *Y. pestis* and other pathogens (Eisen *et al.*, 2009; Eisen & Gage, 2012). Throughout the Southwest and specifically in New Mexico, fleas are carriers of pathogens including *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 & 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 (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 & 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 & Valencia, 1988), foxes (Patrick & Harrison, 1995), and squirrels (Patrick & Wilson, 1995). Archival deposition of voucher specimens from some of these surveys has been incomplete, hindering consistent development of an environmental baseline for hosts, fleas and pathogens across geography and time.

Qualitative parameters defining infestation, such as prevalence, mean abundance, and mean intensity, provide context on 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 *et al.*, 2005a; Krasnov *et al.*, 2005b; Young *et al.*, 2015; Reiczigel *et al.*, 2019).

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 *et al.*, 2005a; Kowalski *et al.*, 2015). A male sex-bias is hypothesized due to lower immunocompetence and difference in spatial behavior in males than females (Khokhlova *et*

*al.*, 2011; Krasnov *et al.*, 2011). In the community characterized at El Malpais, we hypothesize abundance is dependent on host sex, with a higher association in abundance in males than females. Seasonality has also been shown to affect flea abundance due to biotic factors including physiological changes in the host (e.g., breeding cycles) during different seasons (Krasnov *et al.*, 2005a) or by abiotic factors such as seasonal changes in precipitation (Moore *et al.*, 2015). For our community, we hypothesize abundance is dependent on seasonality. This study provides a permanent specimen-based foundation that will enable future comparative assessments of ecology and evolution of dynamic host-parasite communities across time and space.

**Key words:** ectoparasite, host-parasite community, Southwest, fleas

#### Key Findings

- New flea and host associations have been identified.
- The majority of flea species parasitized multiple hosts.
- *Onychomys leucogaster* was parasitized by the highest number of flea species (15).
- Species richness varied among host species.
- Flea prevalence is positively correlated with flea mean abundance.
- Host sex and season influence flea abundance.

#### Materials and methods

##### *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 2,062-2335m (6,765-7,660ft). 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 & Cannon, 2005). Soils consist mainly of alluvium and basalt (Maxwell, 1986). Temperatures range from -11 to 29C (12-85F), and annual precipitation is approximately 27cm (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, soricomorphs, and rodents. Between 2009 and 2013, 2,273 Gunnison's prairie dogs (*Cynomys gunnisoni*), 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*). Prior to translocation, these prairie dogs were dusted with insecticide to kill ectoparasites. Prairie dogs, as well as black-footed ferrets, are highly susceptible to plague which is hypothesized to be transmitted in the Southwest by several rodents and their fleas (Gage & Kosoy, 2005); therefore, it was crucial to develop a comprehensive understanding of the associated mammalian and flea community. Areas surveyed included lower elevation shrub/grasslands,



prairie dog colonies of the NCA, higher elevation coniferous habitats, and an ecotone between desert habitat and intermittent springs.

### *Field and Data Collection*

Specimens were collected following guidelines of the American Society of Mammalogists (Sikes *et al.* 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 using a mix of Sherman<sup>®</sup> live traps, Victor<sup>®</sup> rat traps, and museum special traps 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 8m apart. Macabee<sup>®</sup> 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<sup>®</sup> 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 (1-2mL) of chloroform and each mammalian voucher specimen was combed onto a white plate or by directly removing the ectoparasites (fleas, lice, ticks, mites) 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 (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 when cryptic 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 Collins, CO) and at the University of New Mexico using published taxonomic keys (Hubbard, 1947; Furman & 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 (Oksanen J *et al.*, 2020). Fleas that could not be identified to species in the genera *Catallagia*, *Megarhthroglossus*, *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 / 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 / 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 / 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 / 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), autumn (September-November). Mammal species with sample sizes < 10 individuals were not included in statistical analyses on 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- 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  $33 \pm 3.9$  species for the flea community (Fig. 4) and  $19 \pm 1.3$  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 only collected during a single season. *Callistopsyllus terinus*, *M. jamesoni*, *O. neotomae*, and *P. paradisea* were only collected in the spring. *Catallagia decipiens*, *M. bisetis*, *M. telchinus* and *P. allos* were only collected 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%).

### *Host-parasite composition*

Out of 898 mammals examined, 284 were infested with fleas (overall prevalence = 32%).

Mammals with the highest community composition were *P. maniculatus* (30%), *R. megalotis* (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). *Onychomys leucogaster* was the host with the highest species richness, parasitized by 15 flea species, followed by *P. truei* (10 species), and *R. megalotis* and *N. stephensi* (8 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).

### *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 New Mexico karyotype (NK) numbers.

### **Family Ceratophyllidae**

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

1 male, 2 females ex *Neotoma stephensi* NK 299840, NK303485; 3 males, 2 females ex *Onychomys leucogaster* NK 261749, NK 290288, NK 299843; 17 males, 49 females ex *Peromyscus maniculatus* NK 261763, NK 290272, NK 290391, NK 290464, NK 290466, NK 290500, NK 292894, NK 292906, NK 292913, NK 293388, NK 299506, NK 299762, NK 299773, NK 299778, NK 299783, NK 299792, NK 299793, NK 299797, NK 299802, NK 299803, NK 299804, NK 299808, NK 299810, NK 299811, NK 299813, NK 299821, NK 299825, NK 299827, NK 299833, NK 299836, NK 299837, NK 299879, NK 299880, NK 299884, NK 303431, NK 303434, NK 303448; 3 males, 3 females ex *Peromyscus nasutus* NK 231889, NK 290393, NK 290454, NK 290457, NK 303468; 13 males, 17 females ex *Peromyscus truei* NK 231878, NK 231885, NK 231887, NK 231890, NK 272450, NK 290499, NK 299765, NK 299816, NK 299817, NK 299818, NK 299828, NK 299830, NK 299877, NK 303441, NK 303447, NK 303453, NK 303466, NK 303470; 4 females ex *Reithrodontomys megalotis* NK 286622, NK 286624, NK 286631, NK 299807.

*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 & Morlan, 1955; Holdenried & 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.

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

1 male, 1 female ex *O. leucogaster* NK 261331, NK 290279; 1 male, 4 females ex *P. maniculatus* NK 231994, NK 292799, NK 293388.

This flea has an amphiberian distribution and has been collected from *P. maniculatus*, *P. truei*, and *Myodes gapperi* in New Mexico. We report *O. leucogaster* as a new host for this flea (Morlan, 1955; Holdenried & Morlan, 1956; Thomas, 1988; Ford *et al.*, 2004). Lewis *et al.* (1988) regarded *A. 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.

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

1 male, 3 females ex *Tamias dorsalis* NK 272439, NK 303454.

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

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

5 males, 6 females ex *O. leucogaster* NK 231978, NK 261782, NK 261785, NK 293395, NK 293403, NK 299508, NK 299511; 26 males, 20 females ex *Thomomys bottae* NK 292920, NK 292925, NK 299755, NK 299798, NK 303410, NK 303423, NK 303424, NK 303425, NK 303426, NK 303427.

The distribution of *Foxella ignota* in western North America ranges from southern Canada to central Mexico. This species is most commonly associated with pocket gophers (*Thomomys* spp.) in the Southwest, but it also has been collected from *U. cinereoargenteus*, *Vulpes macrotis* Merriam, and *O. leucogaster* (Patrick & Harrison, 1995; Harrison *et al.*, 2003; Pigage *et al.*, 2005; Lewis & Wilson, 2006). While many subspecies of *F. ignota* were recognized by Traub *et al.* (1983), we recognize only a single species. In our study, *F. ignota* was prevalent in 1.9% of the community, parasitizing *O. leucogaster* and *T. bottae*, and was collected in all seasons except winter. All *T. bottae* specimens (n = 10) were parasitized by this species.

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

1 female ex *O. leucogaster* NK 303415; 5 males, 4 females ex *Peromyscus boylii* NK 261398, NK 261420, NK 290267, NK 290493; 2 males ex *P. maniculatus* NK 261783, NK 290461; 3 males, 5 females ex *P. nasutus* NK 261419 NK 290393, NK 290397, NK 290454, NK 290457; 7 males, 8 females ex *P. truei* NK 231885, NK 231888, NK 261339, NK 261407, NK 261414, NK 261756, NK 290458, NK 299759, NK 299767, NK 299828, NK 303455; 2 females ex *R. megalotis* NK 261748, NK 303405.

The nomen *Malaraeus sinomus* is commonly applied to this species; however, Lewis (2008) regards *M. sinomus* as a junior synonym of *M. eremicus*, as we do here. *Malaraeus eremicus*



is distributed in 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 & Morlan, 1956; Thomas, 1988; Morway *et al.*, 2008). Like *A. wagneri* and *Peromyscopsylla hesperomys adelpha*, *M. eremicus* parasitized six different hosts. This flea species had a prevalence of 2.8% in our mammal community, was most abundant on *P. truei*, and was present in all seasons, but collected mostly in the spring.

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

1 male ex *R. megalotis* NK 303403

The most widely distributed species in this genus, New Mexico is the southernmost geographical region for *M. telchinus* which occurs mainly at lower elevations (< 2300m) and 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 due to 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.

***Monopsyllus* sp.**

1 female ex *O. leucogaster* NK 303409; 1 female ex *R. megalotis* NK 286625.

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

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

1 male ex *O. leucogaster* NK 272432; 10 males, 12 females ex *P. maniculatus* NK 216807, NK 261408, NK 261775, NK 290257, NK 290461, NK 290464, NK 290496, NK 292893,

NK 292894, NK 292897, NK 292901, NK 292903, NK 293401, NK 299808, NK 299823, NK 299837, NK 303432, NK 303429; 6 males, 7 females ex *P. truei* NK 261424, NK 261755, NK 261759, NK 299765, NK 299766, NK 299768, NK 299831, NK 299882; 27 males, 23 females ex *R. megalotis* NK 216804, NK 261334, NK 261436, NK 261791, NK 272433, NK 272434, NK 272435, NK 286627, NK 290189, NK 290192, NK 290197, NK 290387, NK 290388, NK 290389, NK 290390, NK 290463, NK 299799, NK 299805, NK 299807, NK 303408, NK 303478; 1 male ex *Reithrodontomys montanus* NK 303417

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 most broadly distributed flea of this genus extending across the majority of the contiguous United States and then 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)

1 female ex *N. mexicana* NK 290385; 1 male ex *N. stephensi* NK 299839.

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 only collected in the spring.

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

12 males, 5 females ex *Cynomys gunnisoni* NK 261416, NK 272441, NK 299789, NK 299876; 3 males, 3 females ex *O. leucogaster* NK 261751, NK 261793, NK 292910, NK 299511, NK 299515.

The genus *Oropsylla* parasitizes sciurid rodents, especially spermophilids (Lewis, 2002). In New Mexico, *O. hirsuta* mainly parasitizes *Cynomys* spp., but it also known from *Callospermophilus lateralis* and *Ictidomys tridecemlineatus* (Link, 1949; Cully *et al.*, 1997; Friggens *et al.*, 2010). This is the first association with *O. leucogaster* for New Mexico (Eskey & Haas, 1939; Pfaffenberger & Valencia, 1988; Cully *et al.*, 1997; Ford *et al.*, 2004; Eads *et al.*, 2015; Eads *et al.*, 2016), but not elsewhere in the Southwest (e.g., northern Colorado) (Stapp & Salkeld, 2009). In the southwestern United States, *O. hirsuta* is implicated in the maintenance of sylvatic plague due to 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 *et al.*, 2008a; Wilder *et al.*, 2008b; Kraft & Stapp, 2013). *Oropsylla hirsuta* was prevalent in 1.0% of the community, was collected in all seasons, and parasitized *C. gunnisoni* and *O. leucogaster*.

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

2 males, 5 females ex *N. albigula* NK 299752, NK 299753, NK 299754; 96 males, 136 females ex *O. leucogaster* NK 216802, NK 216803, NK 231967, NK 231969, NK 231971, NK 231972, NK 231973, NK 231974, NK 231975, NK 231978, NK 261328, NK 261330, NK 261331, NK 261418, NK 261749, NK 261752, NK 261753, NK 261794, NK 271738, NK 271741, NK 271742, NK 272432, NK 290178, NK 290180, NK 290181, NK 290182, NK 290183, NK 290278, NK 290279, NK 290288, NK 292806, NK 292890, NK 292891,

NK 292892, NK 292898, NK 292904, NK 292905, NK 292907, NK 292908, NK 292910, NK 292912, NK 292919, NK 292922, NK 293395, NK 299505, NK 299508, NK 299509, NK 299510, NK 299511, NK 299512, NK 299514, NK 299515, NK 299757, NK 299843, NK 299847, NK 299896, NK 299897, NK 303409, NK 303411, NK 303415, NK 303476, NK 303479.

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

***Thrassis aridis* Prince, 1944**

1 male ex *D. ordii* NK 303421; 1 female ex *N. albigula* NK 299752; 7 males, 9 females ex *O. leucogaster* NK 231796, NK 261329, NK 261330, NK 261753, NK 299508, NK 299511, NK 299513, NK 299515, NK 303415, NK 303477.

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.

## Family Leptopsyllidae

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

8 males, 7 females ex *O. leucogaster* NK 271743, NK 290183, NK 292898, NK 292907, NK 292919, NK 299508, NK 303415, NK 373476, NK 303477, NK 303491; 1 female ex *P. boylii* NK 290498; 5 males, 7 females ex *P. maniculatus* NK 231999, NK 261767, NK 261773, NK 290459, NK 299795, NK 303431, NK 303440; 2 males, 2 females ex *P. nasutus* NK 231878, NK 290454, NK 290457, NK 303467; 5 males, 18 females ex *P. truei* NK 231881, NK 231883, NK 231885, NK 231888, NK 261337, NK 261413, NK 261414, NK 299816, NK 299818, NK 299828, NK 303451, NK 303470; 2 females ex *R. megalotis* NK 303402, NK 303403.

The *adelpha* subspecies belongs to the “*sylvatica*” group due to 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 & Traub, 1954; Salceda-Sánchez & 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.

### *Peromyscopsylla* sp.

1 female ex *O. leucogaster* NK 303477.

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

## Family Hystricopsyllidae

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

1 male 1 female ex *Neotoma albigula* NK 299753; 1 male ex *Neotoma mexicana* NK 303399; 9 males, 5 females ex *N. stephensi* NK 299841, NK 299848, NK 299885, NK 303485; 1 male ex *Peromyscus truei* NK 261339.

*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 is 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.

### *Anomiopsyllus* sp.

2 females ex *N. albigula* NK 261417, NK 272448; 1 female ex *Neotoma mexicana* NK 290385; 4 females ex *N. stephensi* NK 299839, NK 303486; 2 females *P. nasutus* NK 290454; 1 female ex *P. truei* NK 299838.

These 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 when compared to 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 & Fernández, 2009). The presence of these nidicolous fleas on *Peromyscus* spp. is consistent

with use of woodrat middens by deer mice. *Anomopsyllus* sp. was prevalent in 0.8% of our community, but only females were collected therefore we could not morphologically identify these fleas to species.

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

2 males ex *P. boylii* NK 290493; 1 female ex *P. nasutus* NK 290454; 1 male ex *P. truei* NK 299764.

This species 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 only collected in the spring.

***Catallagia decipiens*** Rothschild, 1915

1 male, 2 females ex *P. truei* NK 231885.

This flea species has a wide distribution from western Canada, the Pacific Northwest, and into southern New Mexico (Lewis *et al.*, 1988). In New Mexico, *C. 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.

***Catallagia* sp.** Rothschild

1 female ex *P. nasutus* NK 290454.

*Catallagia* is a Holarctic genus that is primarily associated with *P. maniculatus* in North America and widely distributed from the Midwest and Southwest United States northward into Canada (Lewis & Haas, 2001). In New Mexico, this genus also has been collected from

*N. cinerea*, *M. longicaudus*, *Ictidomys 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.

***Epitedia stanfordi*** Traub, 1944

2 males, 5 females ex *O. leucogaster* NK 261750, NK 261753, NK 292910, NK 299511; 3 males, 11 females ex *P. maniculatus* NK 261772, NK 261778, NK 261783, NK 290495, NK 290500, NK 292893, NK 292897, NK 292906, NK 292918, NK 292921, NK 293388, NK 303415; 1 female ex *R. megalotis* NK 261334.

This genus is restricted to North America and parasitizes several species of rodents, especially deer mice and other 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.

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

1 male ex *N. stephensi* NK 303485.

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 new host record for *Megarthroglossus bisetis* in New Mexico (Méndez & Haas, 1972; Méndez & 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.



***Megarthroglossus* sp.**

1 female ex *P. maniculatus* NK 303442.

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

***Meringis jamesoni* Hubbard, 1943**

2 males ex *Perognathus flavus* Baird NK 299809.

This “uncommon species” is restricted to the Southwest and mainly parasitizes *Perognathus flavus* but has been collected from other heteromyid, cricetid, and spermophiline rodents in New Mexico (Hubbard, 1943b; Eads *et al.*, 1987; Ford *et al.*, 2004). This flea species was prevalent in 0.1% in our community.

***Meringis parkeri* Jordan, 1937**

2 females ex *Dipodomys ordii* Woodhouse NK 299900, NK 303413; 12 males, 22 females ex *O. leucogaster* NK 231968, NK 231969, NK 231974, NK 231976, NK 261418, NK 261753, NK 271738, NK 271743, NK 290178, NK 290180, NK 290182, NK 290184, NK 290185, NK 290278, NK 292806, NK 292912, NK 299505, NK 299508, NK 299511, NK 299514, NK 303411, NK 303491; 1 male, 2 females ex *P. maniculatus* NK 261762, NK 290464; NK 292916; 2 females ex *P. truei* NK 231988.

This common species is distributed throughout the Mid 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.

***Meringis rectus* Morlan, 1953**

2 females ex *Dipodomys merriami* NK 292911, NK 292917; 4 males, 3 females ex *Dipodomys spectabilis* NK 299888; 14 males, 10 females ex *O. leucogaster* NK 261328, NK 261330, NK 261331, NK 261753, NK 261792, NK 290184, NK 292891, NK 292919, NK 299505, NK 299509, NK 299510, NK 299511, NK 299514, NK 299515; 2 males ex *R. megalotis* NK 286625, NK 299516.

This flea species is only known from New Mexico, Texas, and Utah (Morlan, 1953; Oliver & Wright, 2011). While *Dipodomys spectabilis* 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 & Conley, 1983), as has ectoparasitic interactions

between these two hosts in eastern New Mexico (Pfaffenberger & de Bruin, 1986).

***Meringis* sp.**

1 female ex *O. leucogaster* NK 303477.

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.

***Phalacropsylla allos* Wagner, 1936**

1 female ex *N. stephensi* NK 303398.

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

***Phalacropsylla paradisea* Rothschild, 1915**

1 male ex *N. stephensi* NK 299751.

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 & Maser, 1978; Eads & 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 species directly from the host. This species was prevalent in 0.1% our community.

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

20 males, 33 females ex *O. leucogaster* NK 231967, NK 231969, NK 231971, NK 231973, NK 231976, NK 261328, NK 261329, NK 261331, NK 261749, NK 261752, NK 261753, NK 261757, NK 261782, NK 261785, NK 261794, NK 290181, NK 292904, NK 293403, NK 293404, NK 299507, NK 299508, NK 299509, NK 299511, NK 299513, NK 299514.

This understudied flea species was first described from Santa Fe County, New Mexico (Morlan & Prince 1954). It is distributed throughout the western United States and is most prevalent during winter (November through January) (Morlan & 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 & Prince, 1954). *Rhadinopsylla multidenticulata* was prevalent in 2.8% of

our community, parasitizing exclusively *O. leucogaster*, and only collected between late October and February.

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

3 males ex *N. albigula* NK 271737, NK 299753; 3 males, 4 females ex *N. mexicana* NK 290385, NK 299887, NK 303399, NK 303400; 6 males, 12 females ex *N. stephensi* NK 299751, NK 299839, NK 299885, NK 299889, NK 303398, NK 303486; 1 female ex *P. truei* NK 261414.

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 & Fernández, 2009). This nidicolous species is mainly associated with *Neotoma* spp. and includes *N. nelsoni*, a new host record 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*, a single *P. truei*, and was prevalent in 1.4% of our community.

***Stenistomera* sp.**

1 female ex *N. stephensi* NK 329258.

Fleas in this genus are exclusively Nearctic in distribution and are distinguishable by their “bullet-shaped” heads. Three species are currently recognized (*S. 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).

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

1 female ex *O. leucogaster* NK 261749; 2 males ex *P. truei* NK 261410, NK 303470.

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*, due to very limited records. This species is distributed from Southwest Colorado, Southeast Arizona, Southwest Texas, and Northern Mexico and parasitizes peromyscine mice but was also collected from *T. dorsalis* (Traub & 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 & 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*.

### **Family Pulicidae**

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

4 males ex *S. audubonii* NK 299788, 303394.

Lagomorphs are the main hosts for *C. inaequalis*, but this species has been collected in New Mexico from the rodent *N. micropus* and predatory carnivores *U. cinereoargenteus* and *Vulpes* spp., (Patrick & Harrison, 1995; Harrison *et al.*, 2003; Morway *et al.*, 2008).

*Cediopsylla inaequalis* was prevalent in 0.2% of our community and only parasitized cottontail rabbits (n=7). Lewis *et al.* (1988) delineated *C. inaequalis* to a subspecific trinomial; however, due to sympatry of the subspecies, common cooccurrence of subspecies on the same host, and “considerable intergradation in their diagnostic characters”, we do not consider subspecific status here.

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

1 male, 19 females ex *N. mexicana* NK 231870, NK 299887; 22 females ex *N. stephensi* NK 299751, NK 299848, NK 299885.

*Echidnophaga gallinacea*, an invasive, cosmopolitan sticktight “hen flea” mainly associated with avian hosts are of great veterinary importance due to parasitizing domestic poultry (e.g., chickens) resulting in serious superficial injury, and increased disease susceptibility (Eads, 1950; Mullen & Durden, 2019). This flea species has been implicated in plague epizootics possibly by burrowing owls (*Athene cunicularia*), 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 & Morlan, 1955; Holdenried & Morlan, 1956; Rail *et al.*, 1969; Graves *et al.*, 1974; Pfaffenberger & Wilson, 1985; Pfaffenberger & Valencia, 1988; Patrick & 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%. *Echidnophaga gallinacea* was collected in the spring and autumn and parasitized only woodrats.

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

2 females ex *Sylvilagus audubonii* NK 292923, NK 299890.

In New Mexico, this species is commonly associated with species of *Sylvilagus* and *Lepus* and their predators (Pfaffenberger & Valencia, 1988; Patrick & 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) .

### *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 $\pm$ 0.8), *O. leucogaster* 3.4 (SE $\pm$ 0.2), and *N. mexicana* 1.9 (SE $\pm$ 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 $\pm$ 1.1), *N. stephensi* 6.7 (SE $\pm$ 0.8), and *N. mexicana* 6.0 (SE $\pm$ 1.0) (Table 2). Both flea prevalence and mean abundance were positively correlated (Spearman  $\rho = 0.95$ ,  $P < 0.001$ ). Flea species with the highest mean abundance were *P. exilis*, which comprised 0.27 (SE $\pm$ 0.05) of all fleas recorded, while *A. wagneri* was 0.13 (SE $\pm$ 0.02), and *O. leucopus* was 0.01 (SE $\pm$ 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 $\pm$ 0.03) fleas per infected host, *P. exilis* 3.7 (SE $\pm$ 0.05), and *F. ignota* 3.4 (SE $\pm$ 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 (Agosta *et al.*, 2010).

Geographic distribution of flea species ranged from cosmopolitan (*E. gallinacea*), to a species restricted to the Southwest and Mexico (*S. ponera*), to species found only in the Southwest (*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 restricted to Texas, New Mexico, Arizona and Mexico until a re-examination of specimens of *Stenoponia americana* and their geographical ranges (Hastriter *et al.*, 2006) that resulted in re-identification to *S. ponera* with a 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 areas after the Pleistocene (Hastriter *et al.*, 2006) that also demonstrated 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).

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 around, 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 behaviour 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. Multi-seasonal and multi-year 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.* (2003) reported a total 99 flea species for New Mexico, and we identified 29 flea species from El Malpais alone, representing 29% of all identified species in 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 *R. montanus* (n=1), *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 *T. bottae* (n=10), *C. gunnisoni* (n=15), 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 due to the grooming behaviors and dust bathing (Hubbard, 1943b), 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 the surrounding Southwest and Pacific states (Hubbard, 1943a; Hubbard, 1947; Egoscue, 1966; Allred, 1968; Kucera & 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 31 species (Eckerlin, 2011), Maine 32 species (Eckerlin & Gardner, 2021), and West Virginia 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 & Britten, 2017). The cricetid rodent, *O. leucogaster*, was common across all of these communities. Although not necessarily the most predominant rodent (except for PNG), *O. leucogaster* 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 due to their predatory behavior, burrowing lifestyle, and omnivorous diet (Thomas, 1988; Kraft & 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 in North America. This is lower when compared to Campos *et al.* (1985) who report 23 flea species from *P. maniculatus* at Weaver Ranch, Larimer County, Colorado but the same as Davis *et al.* (2002) who reported 15 flea species each collected from deer mice (*Peromyscus spp.*) and woodrats (*Neotoma spp.*) at Chuchupate Campground, Ventura County, California. Due to 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 was mostly comprised of species of the Ceratophyllidae and Hystrichopsyllidae families. This is moderately different compared to 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 also similar to reported abundance in prairie dog communities in South Dakota (LB), for *A. wagneri*, and Colorado (PNG), for *P. exilis* (Stapp *et al.*, 2009; Maestas & Britten, 2017). Like 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 LB, PNG, and TBNG locations consist of black-tailed prairie dogs (*Cynomys ludovicianus*), whereas El Malpais consist of Gunnison's prairie dogs. Differences in prairie dog species may influence flea and mammal community composition due to 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 dog's 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 similarities and dissimilarities of flea and host assemblages also are hypothetically due to habitat (Krasnov *et al.*, 2006b), host phylogeny, shelter architecture (Krasnov *et al.*, 2022), dynamic ecological context, and a history of mosaic faunal assembly through ecological fitting, along with host and geographic colonization (Hoberg & 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 *et al.*, 2005b; Krasnov *et al.*, 2005c; Poulin, 2007). Overall abundance for our community was highly aggregated and unevenly distributed (Fig. 15), 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 0.04-5.08 for mean abundance and 2.0-100% for prevalence. Flea mean intensity varied among flea species and ranged from 1.0-8.4. *Peromyscus maniculatus* was the most common host, comprising 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 & 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 be due to 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, in which 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 *et al.*, 2006a).

#### *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 *et al.*, 2005a) and warrants more detailed exploration. For example, Krasnov *et al.* (2005a) hypothesized that lower immunocompetence in male hosts due to 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 *et al.*, 2005a), with host body mass potentially an important predictor of flea abundance due to 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 third largest mean intensity weighs approximately half as much as woodrats. *Cynomys gunnisoni*, the largest host species, had the fourth highest mean abundance and fifth highest mean intensity. While body size may contribute to larger flea abundance due to 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 & 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 only present during the spring, while *C. decipiens*, *M. bisetis*, *M. telchinus*, and *P. allos* were only present 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 due to 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 due to the effect of environmental conditions including temperature and precipitation on flea fecundity (Krasnov *et al.*, 1997; Krasnov *et al.*, 2002). There are several components to seasonality including temperature, precipitation, and amount of daylight which warrant examination to provide a more robust assessment of how seasonal variation impacts infestation

Climate change and anthropogenic activities are rapidly altering habitats and impacting extant communities and have historically structured these assemblages in the Southwest. The movement or dispersal of animals along with their parasites and pathogens due to global climate change can result in establishment of new interfaces, faunal mixing and colonization events across susceptible communities (Brooks & 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 were parasitized by *O. hirsuta*, a species highly associated with ground squirrels. Hypothetically, *O. hirsuta* fleas were either introduced with the prairie dogs due to 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 population at El Malpais would be consistent with the principal of ecological fitting in faunal persistence and assembly (Hoberg & 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, has occurred throughout the Southwest in recent years and provides an opportunity to better understand host-parasite dynamics (Hoberg & Brooks, 2015). *Onychomys 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 Stockholm Paradigm (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 & Brooks, 2008; Hoberg & 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 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 & 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 depauperate communities (LoGiudice *et al.*, 2003; Keesing *et al.*, 2006). Diversity is only one component, and ecological fitting in pathogen circulation among mammalian hosts across interfaces that drive opportunities for exchange and dissemination result from breakdown in ecological isolation and are critical in persistence on landscape scales and 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). A proactive approach to mitigating risk is central to the DAMA (Document, Assess, Monitor, Act) protocol (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 to 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 measure changes overtime. These steps are crucial in

mitigating transmission risk, among mammals and at interfaces with people, through development of pathways (Act) for essential information about hosts, fleas and pathogens that can be communicated to public health, resource agencies, and local communities. Such a refined understanding of diversity is essential in developing reintroduction programs for endangered species including the black-footed ferret.

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## **Author Contribution**

Dianne Peterson oversaw this project as part of her master's thesis from conception to completion, Jonathan Dunnum and Joseph Cook provided help on study conception, design, funding, field work, mammal identifications, specimen curation and digitization, analyses, and manuscript reviews.

Karen Boegler provided flea identifications and instruction on how to identify fleas.

Ralph Eckerlin assisted in field work, mentoring with flea identification and vouchering, and manuscript review.

Eric Hoberg assisted in field work, and manuscript writing and review.

Schuyler Liphardt provided support in field collections, mammal identifications and molecular barcode identification of problematic mammal taxa.

David Garnand and Katrina Dereig assisted with field work and specimen collection.

Mariel Campbell assisted with field work, specimen collection and digitization, and flea and mammal loan preparation.

Martha O. Perez-Arriaga assisted with data analysis and manuscript reviews.

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### **Conflicts of Interest**

The authors declare there are no conflicts of interest.

### **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, 2016).

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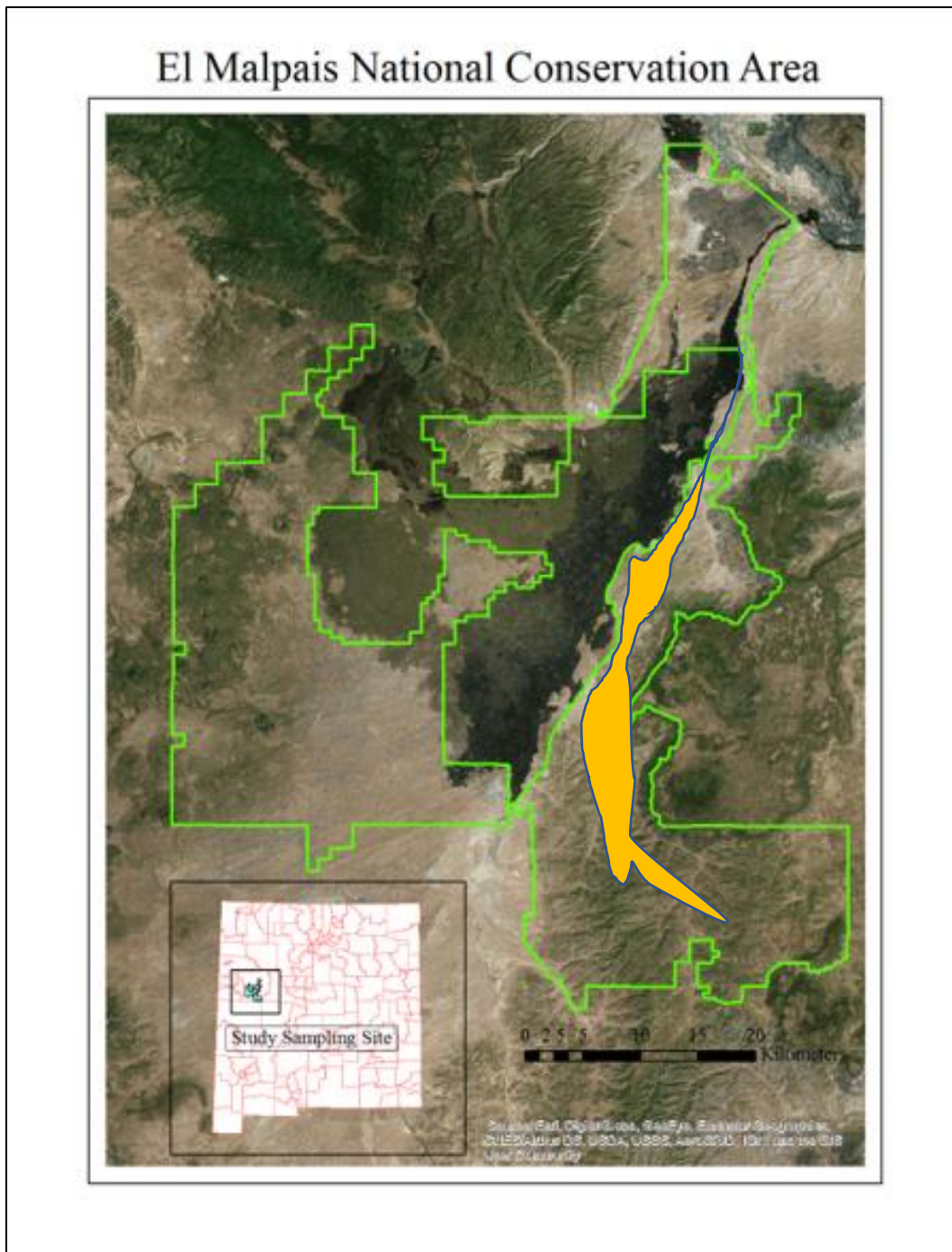
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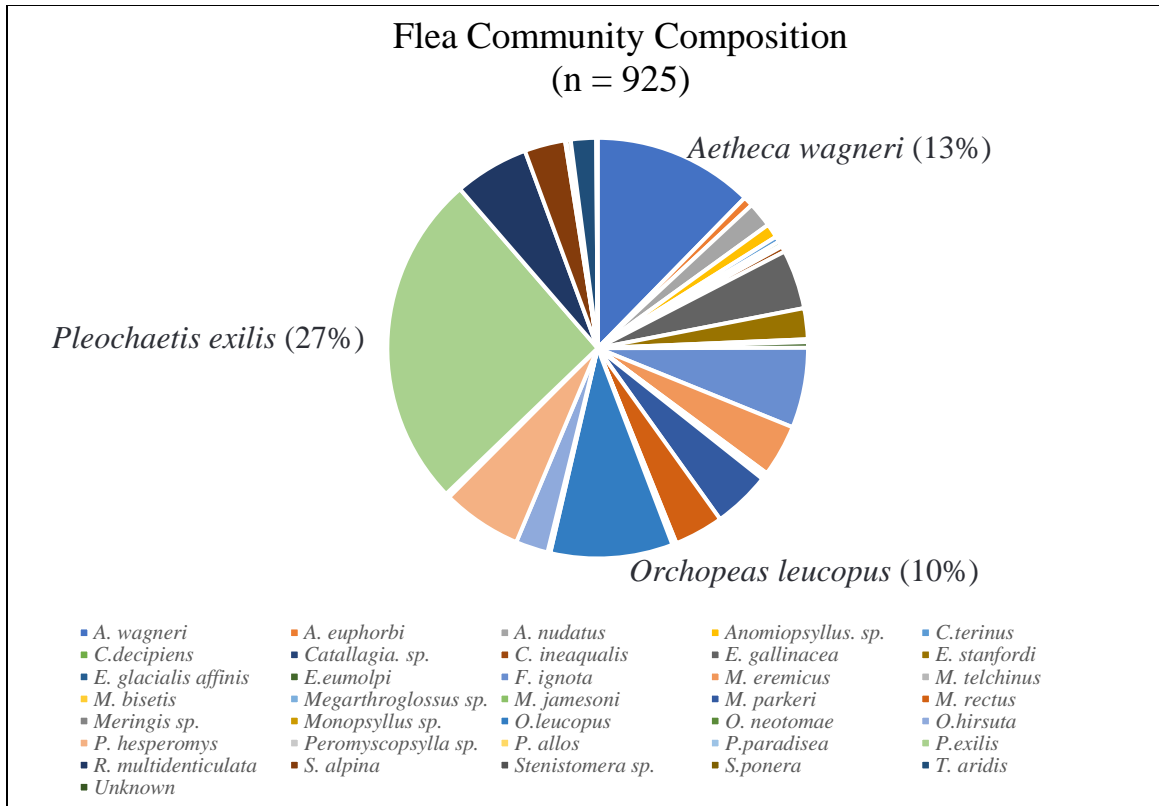
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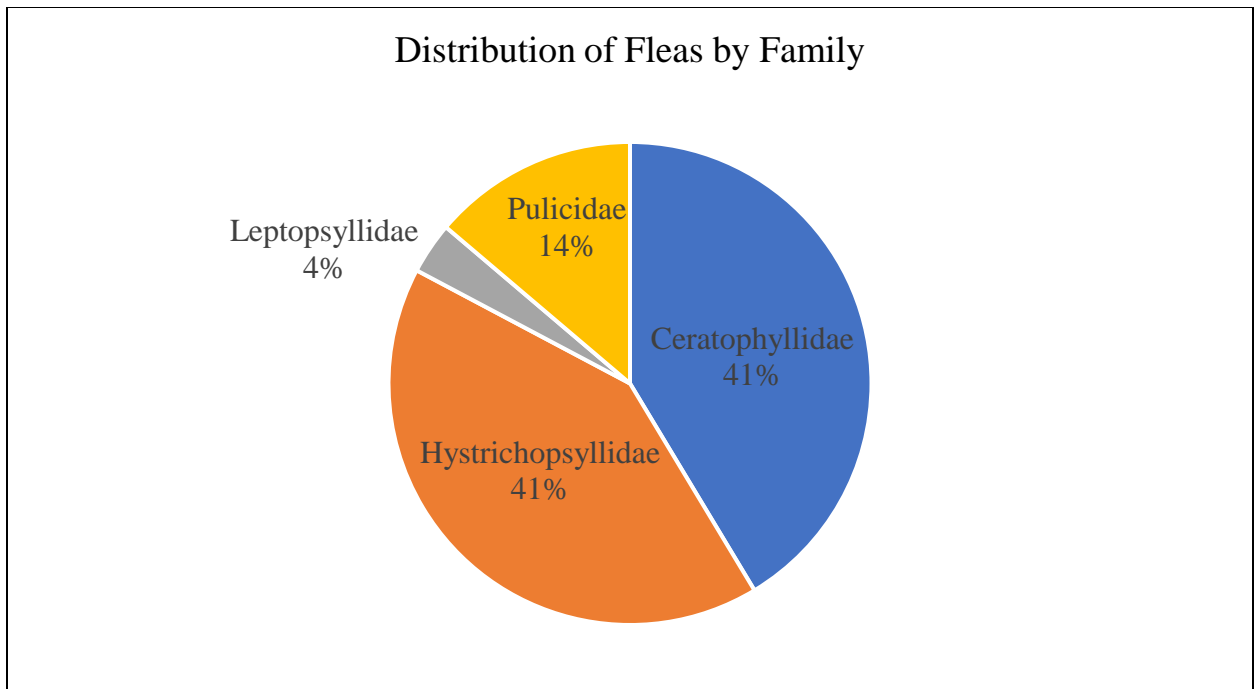
## Figures and Tables



**Fig. 1.** Map of El Malpais National Conservation Area and approximate sampling area (yellow).

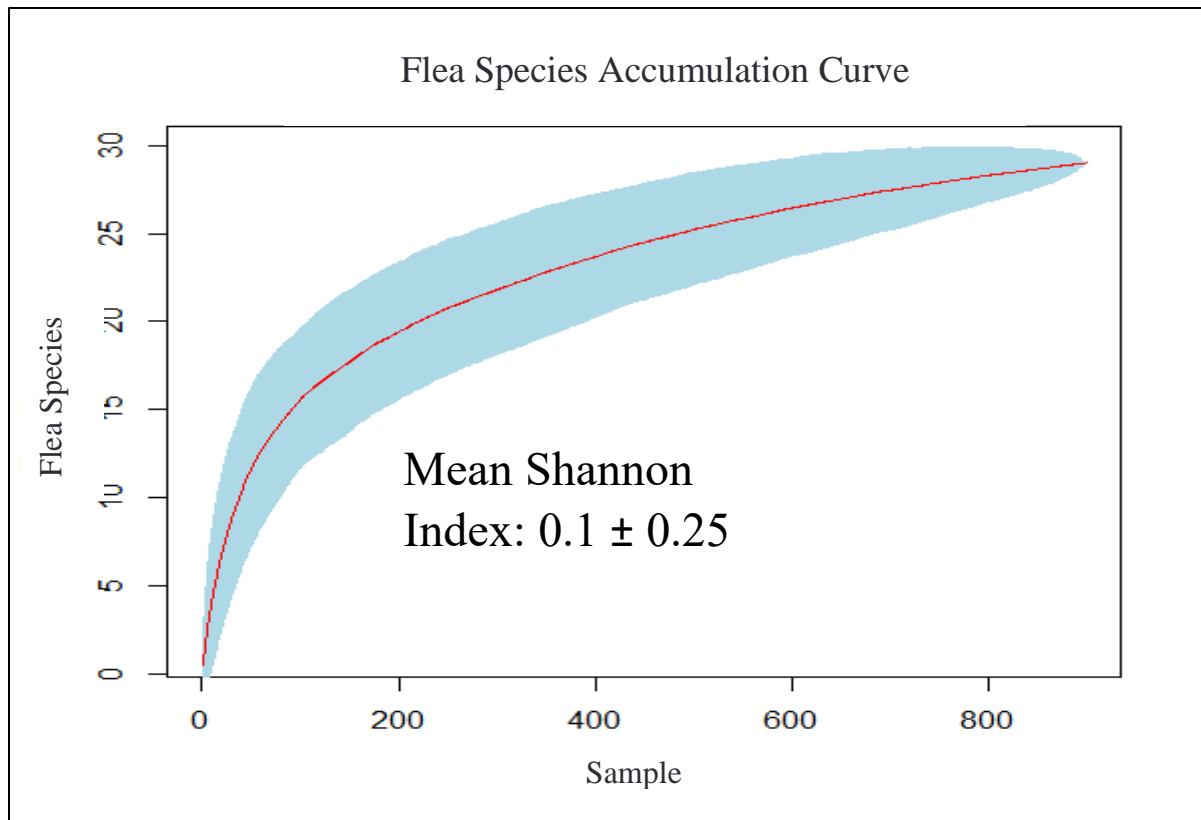


**Fig. 2.** Flea species composition. The majority (82%) of the flea species in this community are either ceratophyllids or hystrihopsyllids.

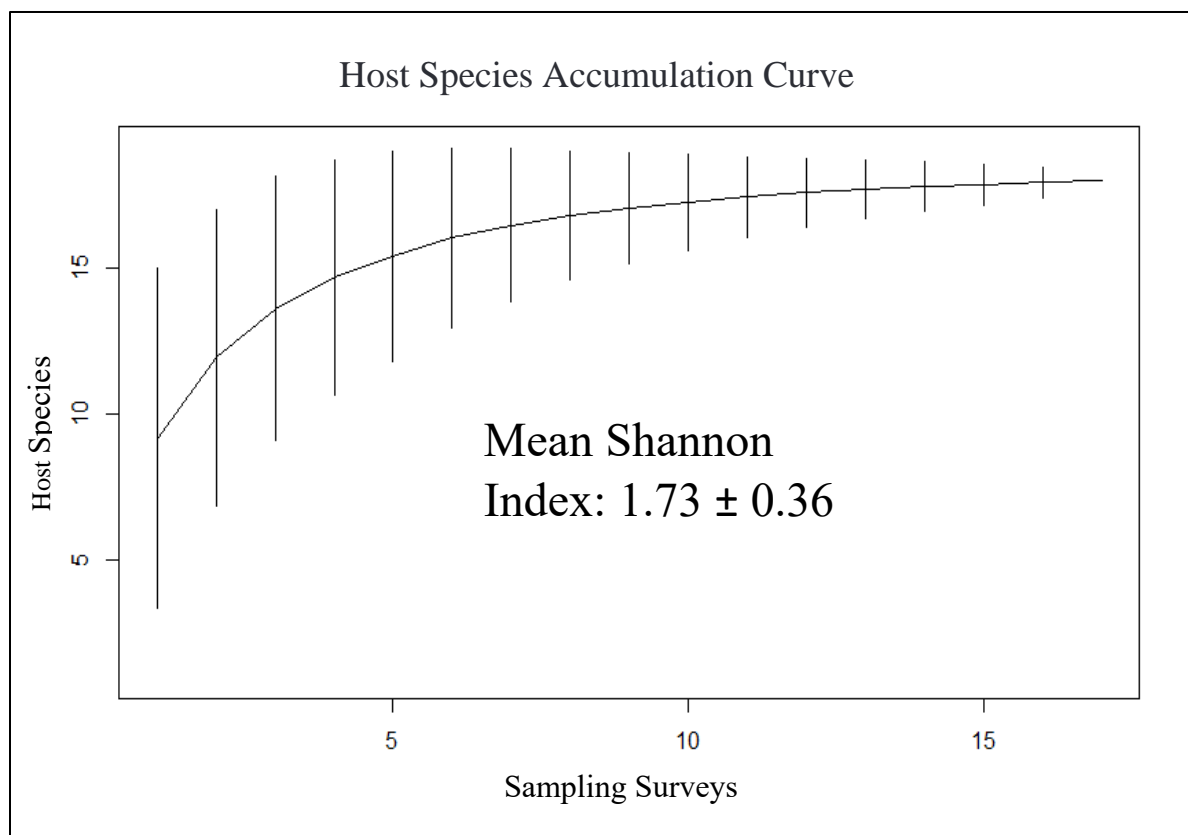


**Fig. 3.** The flea community was comprised mostly of species of the Ceratophyllidae and Hystrichopsyllidae.

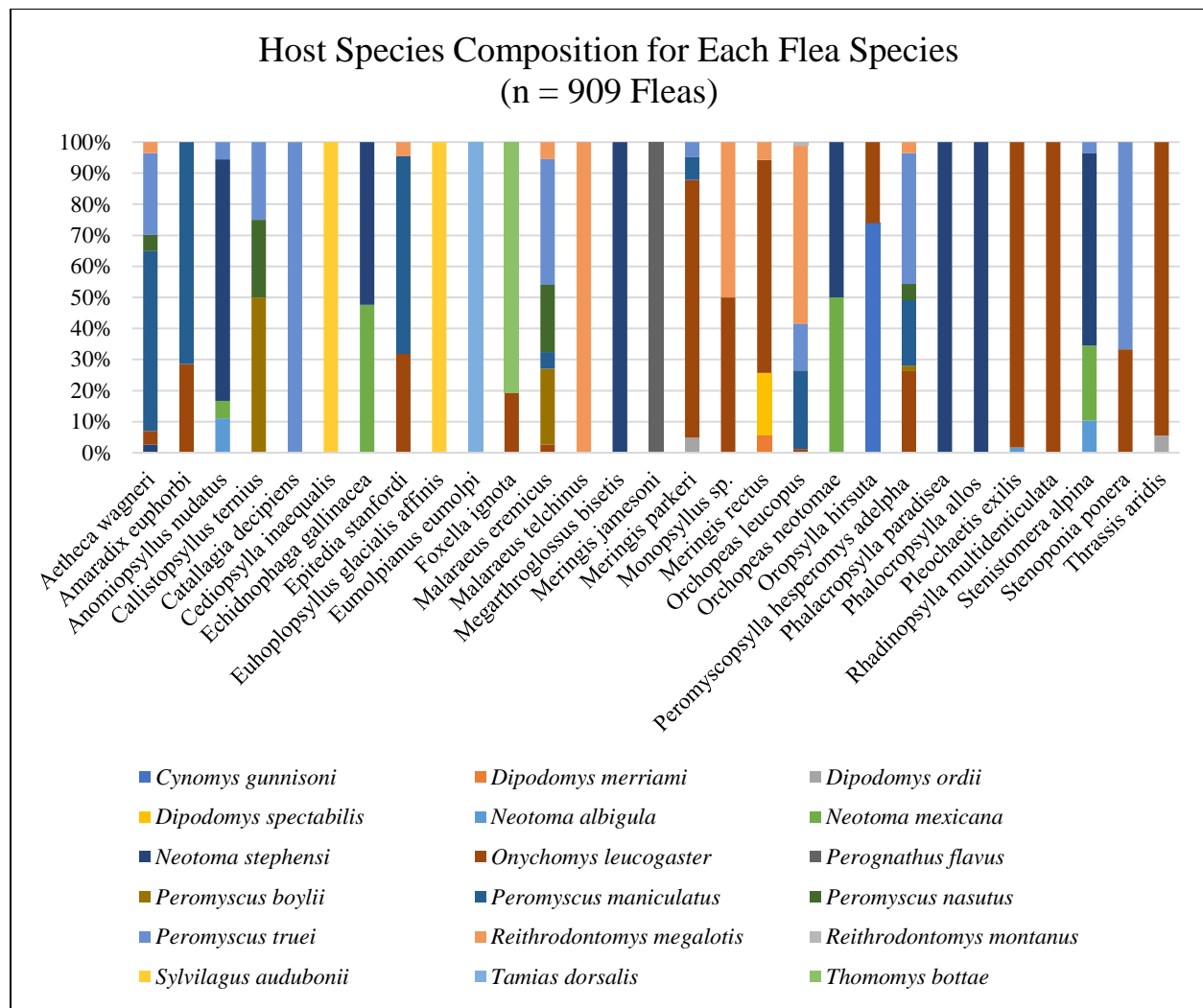




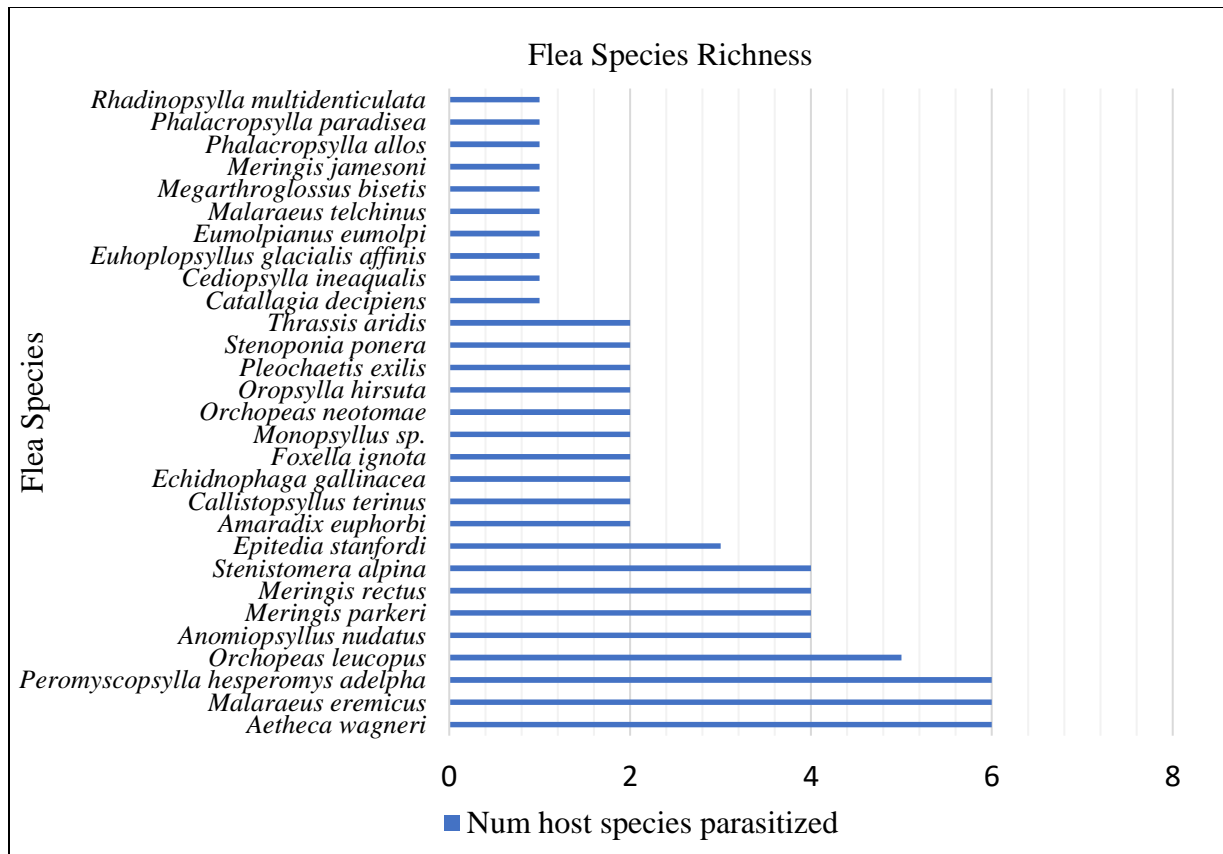
**Fig. 4.** Flea species accumulation curve. Chao estimates 33 (SE  $\pm 3.9$ ) flea species.



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



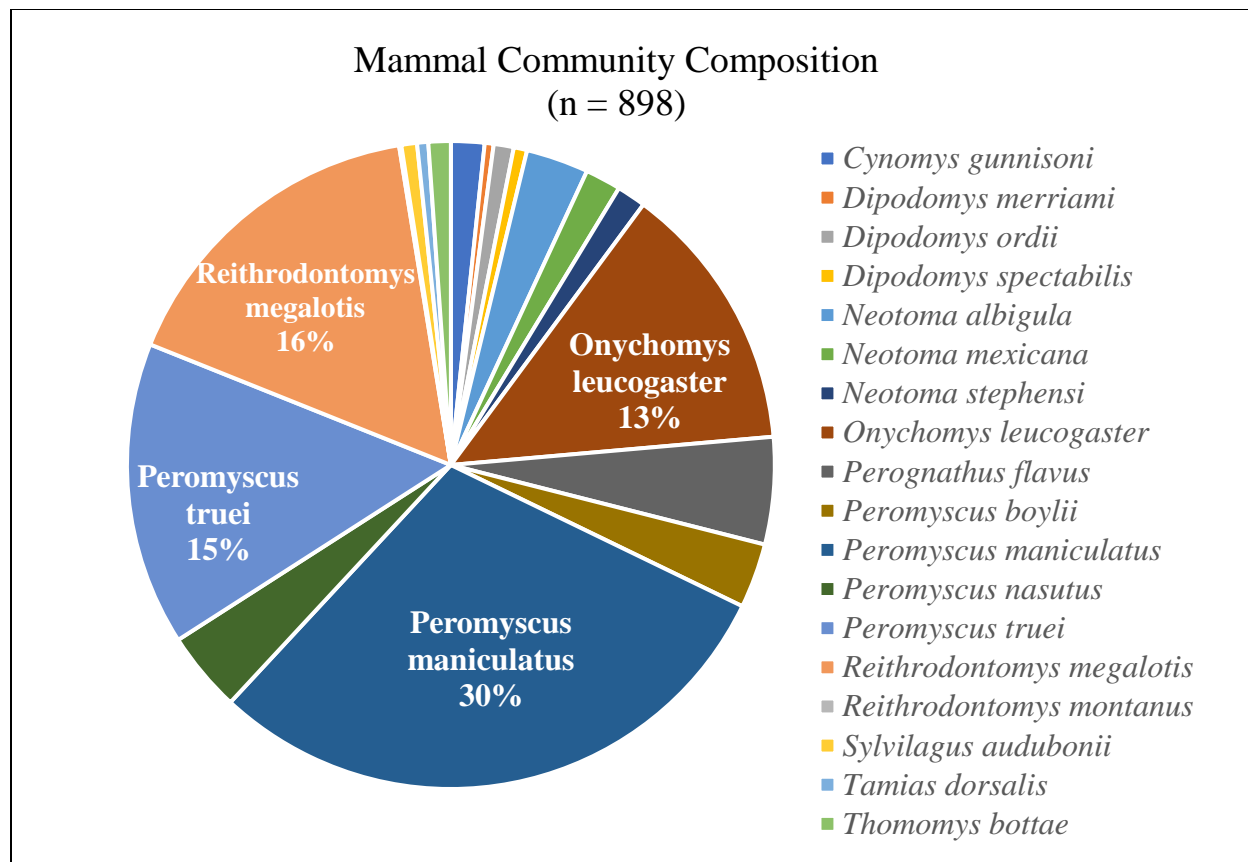
**Fig. 6.** Interspecific variation in host species diversity. Fleas in genera not identified to species (except *Monopsyllus* sp.) are excluded.



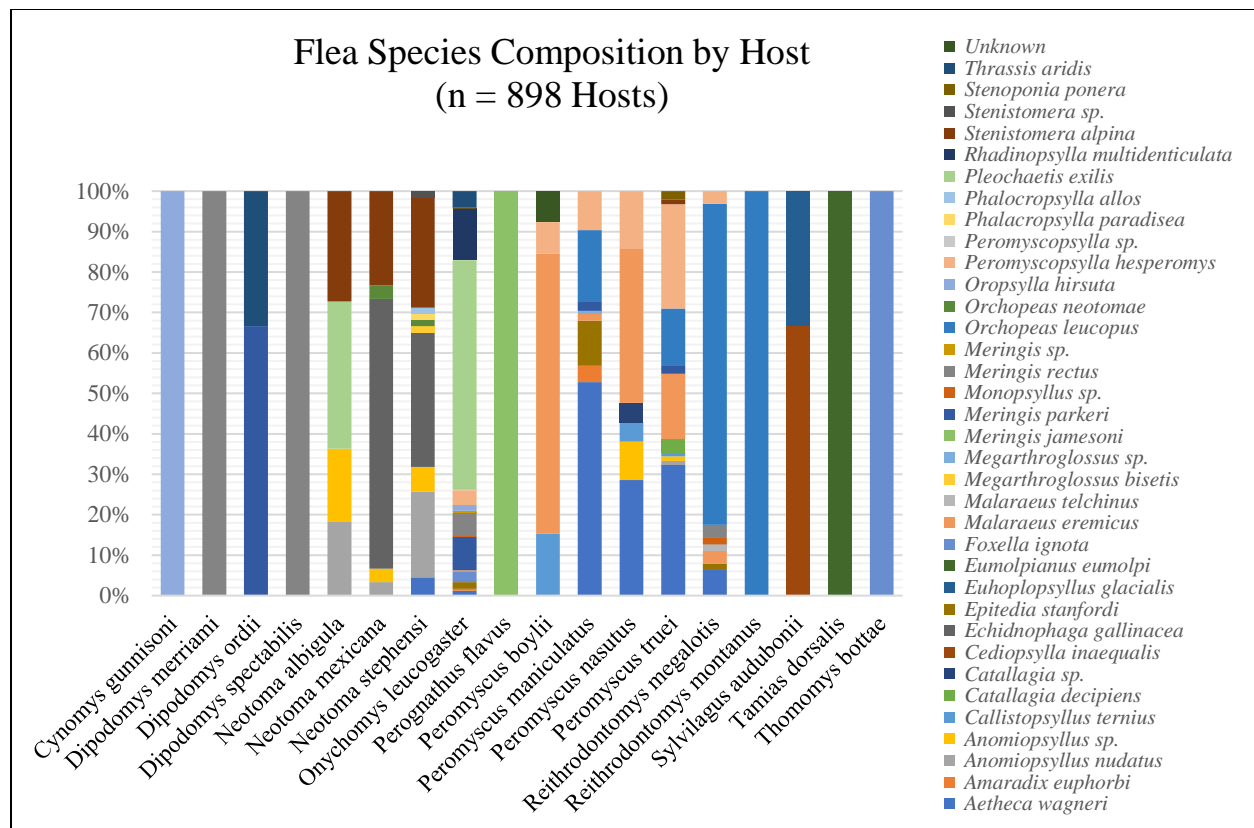
**Fig. 7.** Number of host species parasitized by flea species. This chart shows that the majority of flea species parasitized either one or two host species.



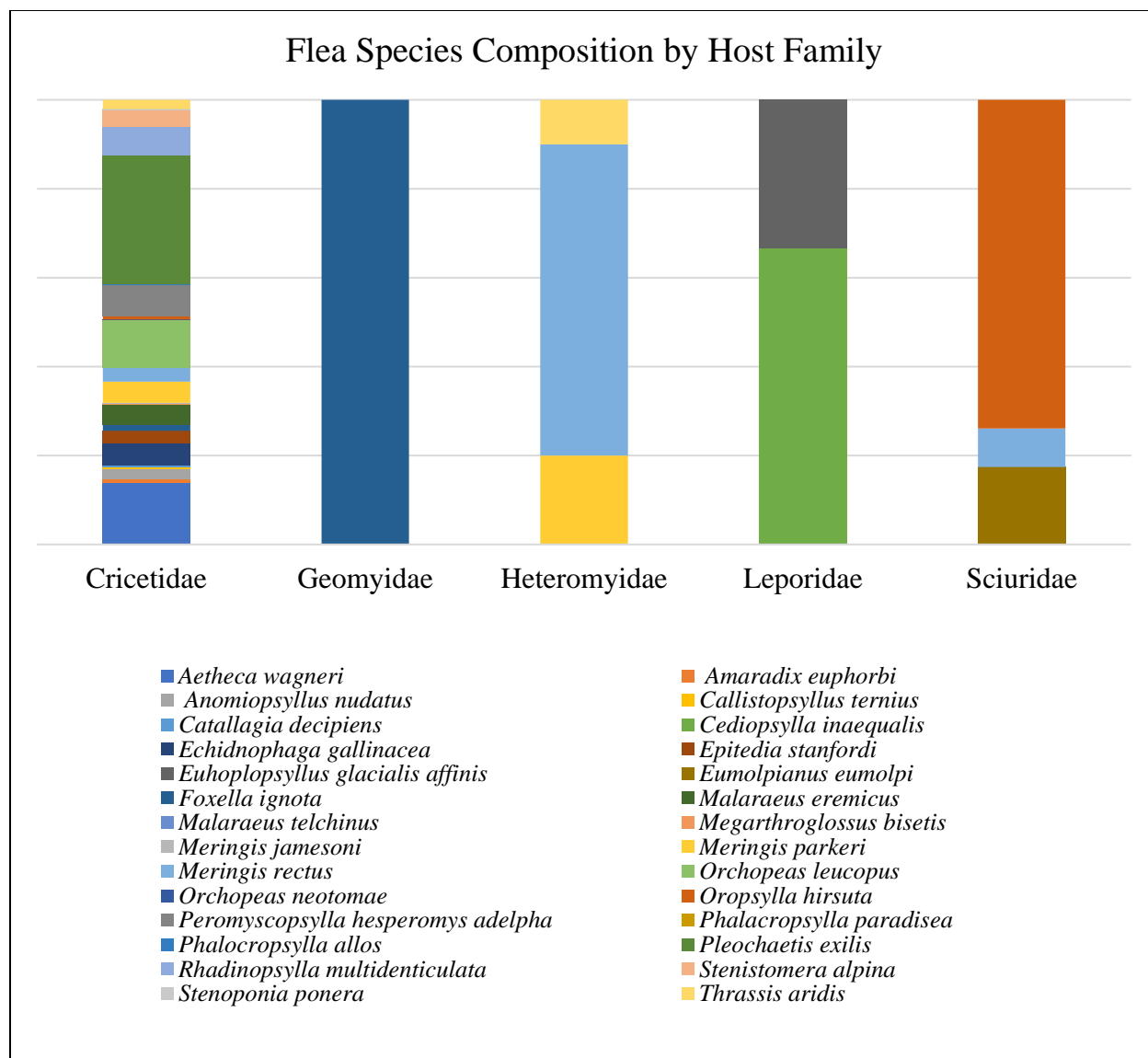
**Fig. 8.** Seasonal flea community composition. *Aetheca wagneri*, *M. eremicus*, *M. parkeri*, *O. hirsuta*, *O. leucopus*, and *P. exilis* were present during all seasons.



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

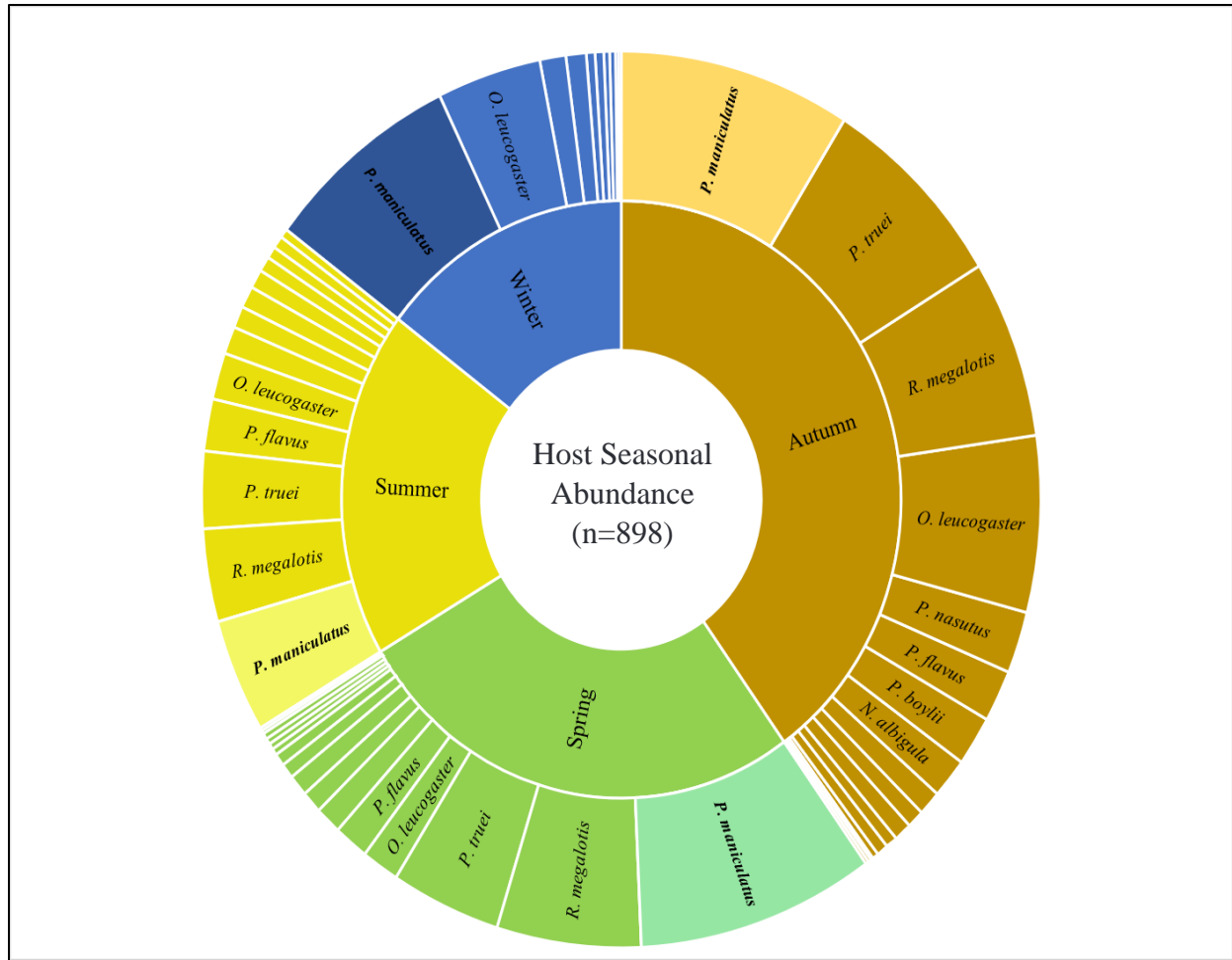


**Fig. 10.** Flea species composition for each host species. Most hosts (61%) hosted multiple flea species, while 39% hosted only a single flea species.

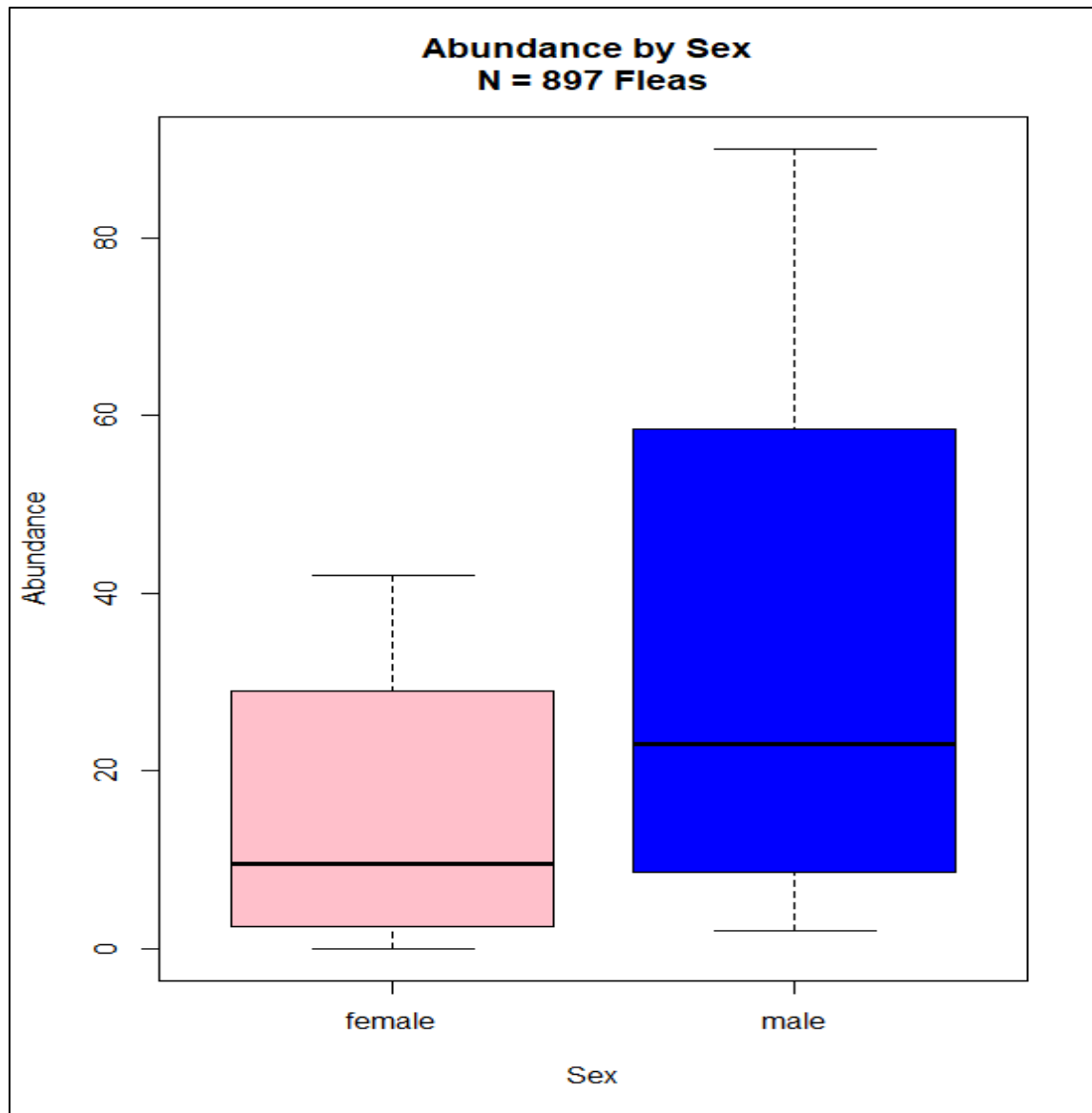


**Fig. 11.** Flea species composition by host family. Cricetid rodents had the highest diversity of fleas (25 species) among all taxa.

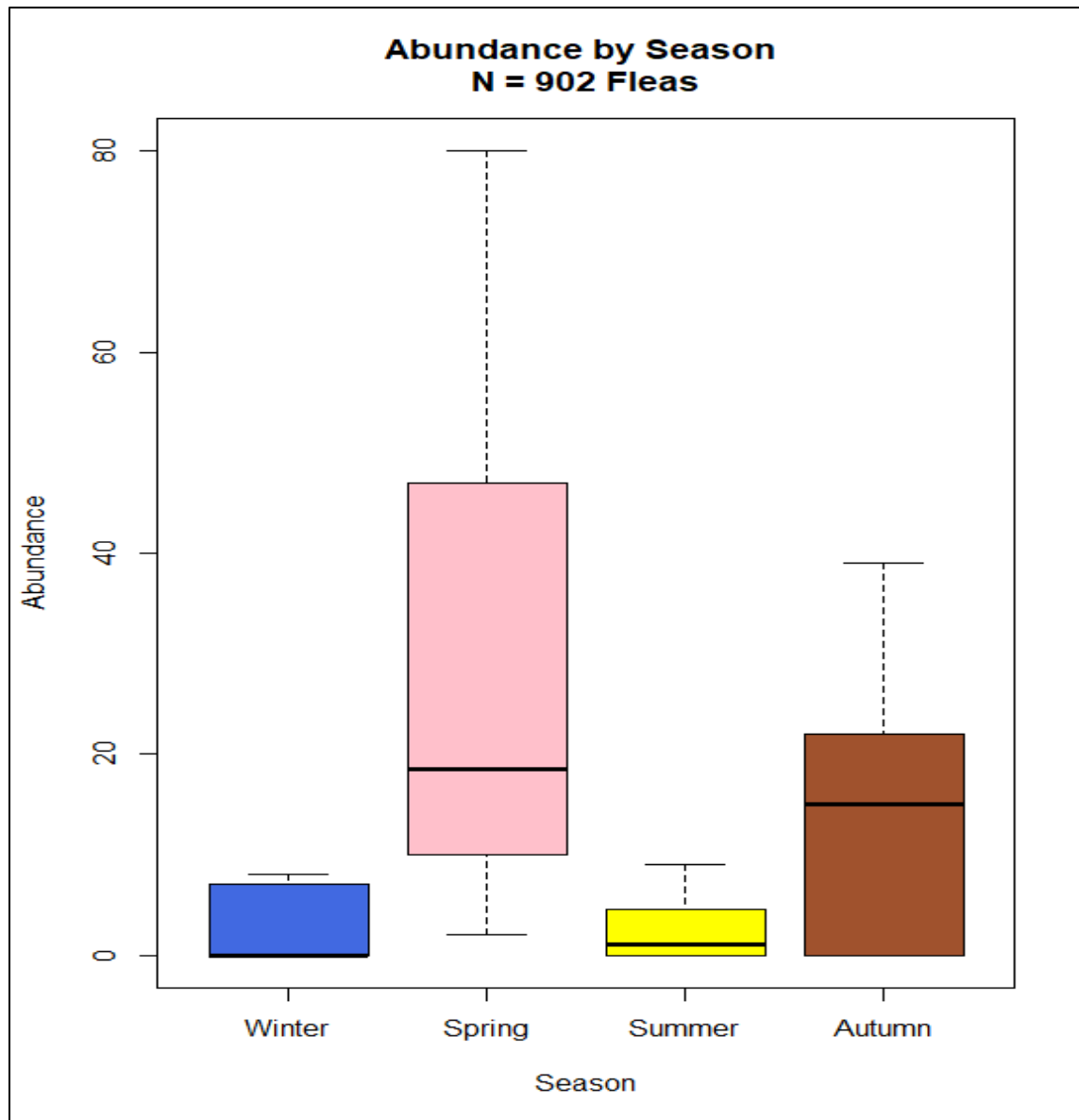




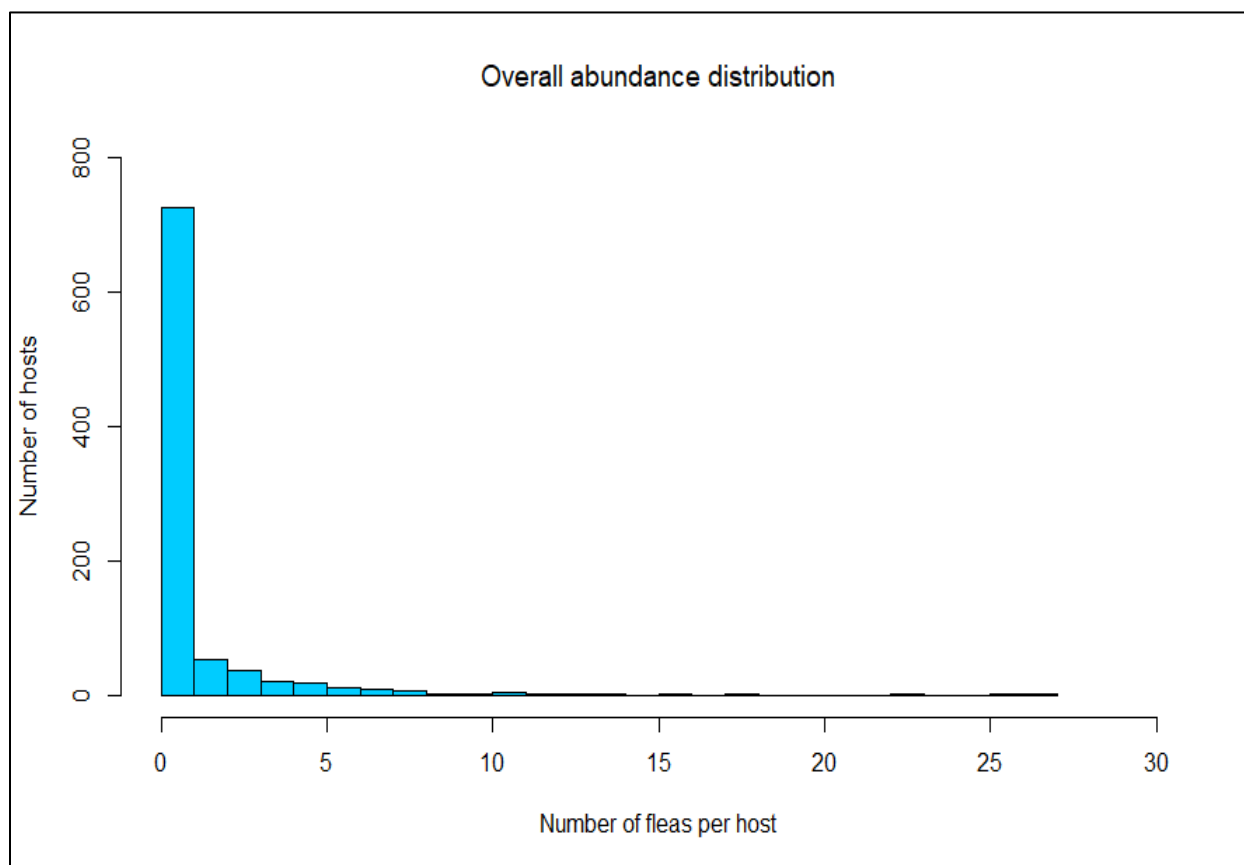
**Fig. 12.** Host abundance and community composition by season. Host species richness was greatest during autumn and spring seasons. *P. maniculatus* was the most abundant host in all four seasons.



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



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



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

**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)	<b>Cg</b> (15)	<b>Dm</b> (4)	<b>Do</b> (9)	<b>Ds</b> (6)	<b>Na</b> (28)	<b>Nm</b> (16)	<b>Ns</b> (13)	<b>Ol</b> (121)	<b>Pf</b> (48)	<b>Pb</b> (29)	<b>Pm</b> (267)	<b>Pn</b> (36)	<b>Pt</b> (136)	<b>Rm</b> (147)	<b>Rmt</b> (1)	<b>Sa</b> (7)	<b>Td</b> (5)	<b>Tb</b> (10)	Total (898)
<i>Aetheca wagneri</i>							3	5			66	6	30	4					114
<i>Amaradix euphorbi</i>								2			5								7
<i>Anomiopsyllus nudatus</i>					2	1	14						1						18
<i>Anomiopsyllus sp.</i>					2	1	4					2	1						10
<i>Callistopsyllus terinus</i>										2		1	1						4
<i>Catallagia decipiens</i>													3						3
<i>Catallagia sp.</i>												1							1
<i>Cediopsylla inaequalis</i>																4			4
<i>Echidnophaga gallinacea</i>						20	22												42
<i>Epitedia stanfordi</i>								7			14			1					22
<i>Euhoplopsyllus glacialis affinis</i>																2			2
<i>Eumolpianus eumolpi</i>																	4		4
<i>Foxella ignota</i>								11										46	57
<i>Malaraeus eremicus</i>								1		9	2	8	15	2					37
<i>Malaraeus telchinus</i>														1					1
<i>Megarhroglossus bisetis</i>							1												1
<i>Megarhroglossus sp.</i>											1								1
<i>Meringis jamesoni</i>									2										2
<i>Meringis parkeri</i>			2					34			3		2						41
<i>Meringis rectus</i>		2		7				24						2					35
<i>Meringis sp.</i>								1											1
<i>Monopsyllus sp.</i>								1						1					2
<i>Orchopeas leucopus</i>								1			22		13	50	1				87
<i>Orchopeas neotomae</i>						1	1												2
<i>Oropsylla hirsuta</i>	17							6											23
<i>P. hesperomys adelpha</i>								15		1	12	3	24	2					57
<i>Peromyscopsylla sp.</i>								1											1

**Table 1. (cont.)**

<i>Phalacroscylla allos</i>							1												1
<i>Phalacroscylla paradisea</i>							1												1
<i>Pleochaetis exilis</i>				4				235											239
<i>Rhadinopsylla multidenticulata</i>								53											53
<i>Stenistomera alpina</i>				3	7	18						1							29
<i>Stenistomera</i> sp.						1													1
<i>Stenoponia ponera</i>								1				2							3
<i>Thrassis aridis</i>			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.

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