

## Seasonal and among-site variation in the occurrence and abundance of fleas on California ground squirrels (*Otospermophilus beecheyi*)

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**ABSTRACT:** An improved understanding of the ecology of fleas on California ground squirrels, *Otospermophilus beecheyi*, is warranted given the role of fleas in the transmission, and perhaps persistence, of the plague-causing bacterium *Yersinia pestis*. We sampled *O. beecheyi* on a seasonal basis from three study sites, each representing a different land use type (preserve, pasture, and agriculture) in the San Joaquin Valley, CA. Overall, the abundance of fleas on squirrels was greatest in spring at the preserve site, in summer at the agriculture and pasture sites, and in winter at the pasture site. *Hoplopyllus anomalus*, the species most frequently found on squirrels, was most abundant in spring at the preserve site and in summer at the agriculture and pasture sites. *Oropsylla montana* was most abundant in winter at the pasture site and on adult squirrels. *Echidnophaga gallinacea* was most abundant in fall on juvenile squirrels at the preserve site. All three flea species we encountered are known to be potential vectors of *Y. pestis*. Future efforts to predict flea species occurrence and abundance (and plague risk) at sites of concern should consider seasonal microclimatic conditions and the potential influence of human land use practices. *Journal of Vector Ecology* 36 (1): 117-123. 2011.

**Keyword Index:** California ground squirrel, *Echidnophaga gallinacea*, fleas, *Hoplopyllus anomalus*, *Oropsylla montana*.

### INTRODUCTION

A parasite's habitat is considered to be a place in or on the host organism that provides for living, foraging, and reproduction. However, for ectoparasites, off-host environments are also often inhabited (Wobeser 2006). Periods of contact with hosts or the off-host environment vary widely among ectoparasites (Wall and Shearer 1997). For instance, lice (Order: Phthiraptera) spend the majority of time on hosts, whereas ticks (Ixodida) and fleas (Siphonaptera) are only on hosts intermittently. Thus for many ectoparasite species, host characteristics and environmental conditions are both likely to influence patterns in ectoparasite infestations.

Fleas are hematophagous, holometabolous insects for which the duration of each life stage is dependent on the flea species as well as host characteristics and environmental conditions (Kennedy and Bush 1994, Krasnov 2008). Egg laying typically is adapted to the behavior of the host (Kim 1985). Eggs are either laid on the host, after which they drop to the ground, or in the nest of the host, where they adhere to the nest material and surrounding soil. The larvae are free living organisms that feed primarily on organic materials and adult excreta (Krasnov 2008). Flea pupae enclose themselves in a cocoon made from secretions of their labial glands and surrounding soil and undergo metamorphosis into adult body form. Environmental stimuli prompt adults to leave their cocoons and find a host (Krasnov 2008). Thus, fleas are subjected to environments on and off the host at

different life stages. Variations in these conditions can influence survival and reproduction at different life stages and thus affect flea occurrence, abundance, and species composition (Krasnov et al. 1997, 2006, Bossard 2006).

An understanding of factors that influence flea occurrence, abundance, and species composition on California ground squirrels (*Otospermophilus beecheyi*) is particularly important given the role of *O. beecheyi* and its fleas in the dynamics of plague (Eskey and Hass 1940), the disease caused by the primarily flea-borne bacterium *Yersinia pestis*. This semi-fossorial squirrel is a known host of *Oropsylla montana*, a flea species linked with many cases of plague in humans in the western United States (Adjemian et al. 2006). In the state of California, *O. beecheyi* and its associated fleas have been linked with the greatest number of reported cases of plague in humans relative to other host-flea systems (Lang 2004). *Otospermophilus beecheyi* are prolific in the San Joaquin Valley of California, not only inhabiting agricultural lands of valleys and foothills but also roadsides, rural parks, and higher elevation sites along forest breaks or meadow edges (Hubbart 2002a). These squirrels and associated flea species are commonly found in heavily urbanized areas and areas converted by humans for various other land use practices. Contacts between humans and fleas or squirrels infected by *Y. pestis* have increased with the intermingling of human and *O. beecheyi* habitats (Clark 1994).

Given that current efforts to combat plague focus on flea control (Seery et al. 2003, Borchert et al. 2009), information

about flea ecology is urgently needed to support those efforts (Wilder et al. 2008, Eisen et al. 2009). For instance, an improved understanding of the phenology of *O. beecheyi* fleas could provide insight into means of optimizing the timing of flea control. Also, because the abundance and composition of fleas on a host species can vary among sites and seasons (Brinkerhoff 2008, Krasnov 2008), greater understanding of the seasonal ecology of fleas in different habitats of *O. beecheyi* is needed to optimize spatial and temporal patterns of flea control.

Previous studies identified ectoparasites and vector-borne diseases of *O. beecheyi*, including fleas and plague (Holdenried et al. 1951). However, few studies compared the seasonal abundance of fleas among habitats of this host species (Smith et al. 2010). In this study we examined the prevalence (i.e., occurrence), abundance, and intensity of fleas parasitizing *O. beecheyi* in three sites representing different land use types in the San Joaquin Valley of California. We aimed to identify patterns of flea infestation on this host species among sites (i.e., preserve, pasture, or agriculture), among seasons, and among hosts of differing attributes (i.e., age, sex, and mass).

## MATERIALS AND METHODS

### Study sites

Research was conducted in Fresno and Madera counties in the south-central region of the San Joaquin Valley, CA (Figure 1). Specimens were collected strictly from the valley floor so that elevation, a factor known to influence flea species composition and abundance (Krasnov 2008), was similar among sites. All study sites were within approximately 40 km from each other and climate attributes

were similar. Annual precipitation ranged from 20 to 25 cm, average annual temperature was 17° C, and average annual frost-free season ranged from 225 to 250 days (Hubbart 2002a). Prior to human development, study sites were savannah and oak grassland landscapes. The sites were converted to agriculture in the mid 1900s and then to the land use types present during this work in the early 1980s (described below).

The preserve study site was approximately 32 ha in size (elevation 65 m) and located in Madera County, in Kerman, CA (36°41'37"N, 120°03'17"W). The site was classified as a "preserve" because it had not been treated with pesticides or grazed by livestock for more than 10 years prior to this study (Hubbart 2002a). The vegetation community was classified as "California annual grassland series" and included species of *Bromus*, *Hordeum*, *Vulpia*, and *Erodium* (Sawyer and Keeler-Wolf 1995, Hubbart 2002a). Soils were Hesperia sandy loam and were well to moderately well drained, with available water holding capacity ranging from 10 to 25 cm (Huntington 1971).

The pasture site was approximately 112 ha in size (elevation 112 m) and located in Madera, CA (36°57'56"N, 119°49'52"W). The site was classified as "pasture" because of persistent cattle grazing and no pesticide applications for more than ten years prior to this study (Hubbart 2002a). Like the preserve site, vegetation was classified as "California annual grassland series" (Sawyer and Keeler-Wolf 1995, Hubbart 2002a). Soil types consisted of Atwater loamy sand, Bear Creek loam, and Cometa sandy loam, which were moderate to well drained (Ulrich and Stromberg 1962).

The agriculture site was approximately 16 ha in size (elevation 114 m) and located in Sanger, CA (36°46'02"N, 119°35'36"W). The site was classified as "agriculture" because it was intensively managed for almond grove production and was regularly treated with pesticides, insecticides, and/or herbicides during the ten years prior to this study (Hubbart 2002a). Sawyer and Keeler-Wolf (1995) classified the habitat type as ruderal (i.e., plant species that are first to colonize disturbed lands). Due to frequent use of herbicides, this site had a relatively low abundance of vegetation. Dominant vegetation included *Tribulus terrestris*, *Echinochloa* spp., *Salsola tragus*, *Conyza bonariensis*, and *Amaranthus* spp. (Hubbart 2002a). The site consisted of well-drained Atwater sandy loam soils (Ulrich and Stromberg 1962).

### Sampling and identification of fleas

In each of the study sites, *O. beecheyi* were collected during each of four annual seasons between April, 2001 and January, 2002. To avoid accidental trapping of sensitive or endangered species, which is prohibited under California State law, specimens were shot (Hubbart 2002b) at distances ranging from 50 to 150 m. Collection was conducted in early morning hours (approximately 05:30 to 09:00 PDT) with the goal of collecting 15 individuals per site in each season. We sampled the first 15 individuals encountered, which required one to two days per site each season.

Each specimen of *O. beecheyi* was placed in an individual

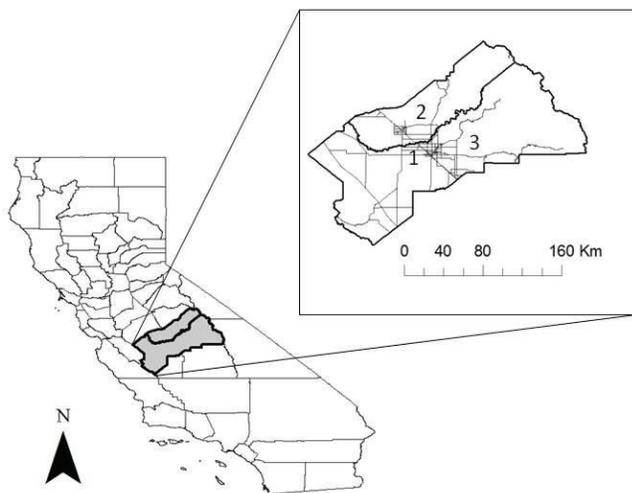


Figure 1. Location of the study area in Fresno and Madera counties in the south central region of the San Joaquin Valley, CA. Flea species were collected (April, 2001-January, 2002) and identified from California ground squirrels, *Otospermophilus beecheyi*, sampled from three study sites (inset map) highlighted 1 (Preserve), 2 (Pasture), and 3 (Agriculture).

sterile sealable bag <2 min post-shooting, transported to a laboratory, and placed in a freezer at  $-6.0^{\circ}$  C. Specimens remained in the freezer until necropsied. During necropsies, ectoparasites were sampled by examining the entire body of each *O. beecheyi* carcass for 3 min. A dissecting microscope and the taxonomic key developed by Lewis et al. (1988) were used to identify fleas to species.

### Data analysis

We measured the prevalence (proportion of hosts infested by one or more fleas), abundance (number of fleas observed on an individual host), and intensity (number of fleas observed on an infested host) of fleas collected on *O. beecheyi*. These indices summarize general patterns of parasitism (Bush et al. 1997).

We also modeled relationships between the prevalence or abundance of fleas on hosts and environment (site and season) and host characteristics (sex, age, and mass). The investigations of flea prevalence and abundance included general flea models (all species combined) and species-specific models. We classified sampling temporally into spring (March-May), summer (June-August), fall (September-November), and winter seasons (December-February). We treated mass as a continuous variable and used it to determine age class, where *O. beecheyi* weighing  $\leq 350$  g were classified as juveniles and those weighing  $> 350$  g as adults (per Tomich 1962, Hubbard 2002a). Male and female sex classes were determined during post-mortem inspections.

We used logistic regression in Program R version 2.8.1 (Ihaka and Gentleman 1996) to model flea prevalence for each flea species based on host and environmental conditions. This involved investigation of main effects and all possible two-way interactions, with backward elimination via likelihood ratio tests ( $\alpha = 0.05$ ). If an interaction was retained, we retained the main effects from the interaction. We found that all logistic regression models retained interactions that included the season variable; therefore, we separated each model containing an interaction by season to investigate seasonal variations.

We used generalized linear models in Program R version 2.8.1 to relate flea abundance to host characteristics and environmental conditions. Abundance estimates of all flea species combined and of individual flea species were over-dispersed; that is, few hosts carried many fleas, and many hosts carried few fleas (Krasnov 2008). Thus, we accounted for over-dispersion using negative binomial regression with the log of the summed response variable (all fleas or species-specific) as an offset variable (McCullagh

and Nelder 1989). We used the step-wise model selection approach described above but with backward elimination via *F*-tests (Crawley 2007). For these generalized linear models, all but one interaction contained the season variable and, in such instances, season-specific models were investigated. A host-age  $\times$  site interaction (abundance of *E. gallinacea*) suggested separate analyses by site.

## RESULTS

From 182 *O. beecheyi*, we collected 805 fleas of three species (*Hoplopsyllus anomalus*, *Oropsylla montana*, and *Echidnophaga gallinacea*) (Table 1). *Hoplopsyllus anomalus* was most prevalent and abundant and occurred at the highest intensity, followed by *O. montana* and *E. gallinacea*. The sexes of two individual squirrels were not discernable; thus, the analyses of flea prevalence and abundance included fleas collected from 180 squirrels.

### All fleas

The prevalence of fleas on *O. beecheyi* was best explained by a site  $\times$  season interaction (LR  $X^2_6 = 12.58$ ,  $P = 0.050$ ). In winter, at the pasture and preserve sites, all squirrels (100%) were parasitized by fleas; prevalence of fleas was lowest at the agriculture site (69.23%, LR  $X^2_2 = 10.57$ ,  $P = 0.005$ ). Differences in flea prevalence among sites were not discernible for other seasons.

Variation in total flea abundance was best explained by host-age  $\times$  season ( $F_{2,152} = 3.34$ ,  $P = 0.038$ ) and site  $\times$  season interactions ( $F_{6,146} = 9.77$ ,  $P < 0.001$ ). In spring, fleas were more abundant on adult (mean = 6.48, CI = 4.01-8.94) than juvenile squirrels (mean = 3.17, CI = 1.65-4.70). No effect of host-age was discernible for other seasons. Regarding the site  $\times$  season interaction, in spring, fleas were more abundant at the preserve site (mean = 9.20, CI = 6.32-12.08) than pasture (mean = 2.81, CI = 0.83-4.80) and agriculture sites (mean = 2.60, CI = 1.21-3.99). The opposite pattern was found for summer, when fleas were more abundant at the agriculture (mean = 6.71, CI = 4.47-8.96) and pasture sites (mean = 5.73, CI = 3.46-8.01) than the preserve site (mean = 2.29, CI = 1.46-3.13). We did not detect differences in flea abundance among sites in fall. In winter, fleas were more abundant at the pasture (mean = 9.47, CI = 5.01-13.93) than preserve (mean = 3.27, CI = 1.96-4.57) and agriculture sites (mean = 1.85, CI = 0.99-2.70).

### *Hoplopsyllus anomalus*

The prevalence of *H. anomalus* was best explained by host-sex (LR  $X^2_1 = 4.07$ ,  $P = 0.044$ ) and a site  $\times$  season

Table 1. Summary of flea species sampled from California ground squirrels, *Otospermophilus beecheyi*, in the San Joaquin Valley, CA, April, 2001-January, 2002.

	<i>O. montana</i>	<i>H. anomalus</i>	<i>E. gallinacea</i>	All fleas
Total fleas (% of total fleas)	248 (30.8)	425 (52.8)	132 (16.4)	805
Prevalence (% of hosts infested)	41.4 (68)	60.3 (99)	31.2 (52)	87.8 (144)
Mean flea abundance (95% CI)	1.5 (1.0, 2.1)	2.6 (2.1, 3.1)	0.8 (0.6, 1.0)	4.9 (4.2, 5.7)
Intensity of fleas (95% CI)	3.7 (2.5, 4.9)	4.3 (3.6, 5.1)	2.6 (2.1, 3.1)	5.6 (4.8, 6.4)

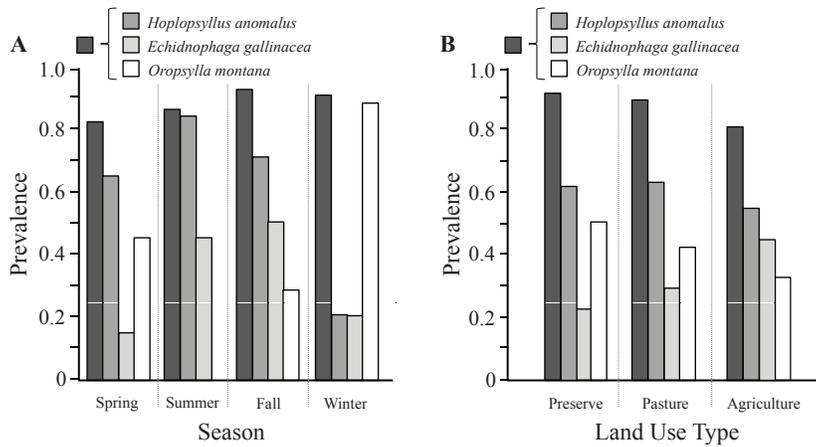


Figure 2. Prevalence of fleas on California ground squirrels, *Otospermophilus beecheyi*, in the San Joaquin Valley, CA (April, 2001-January, 2002), (A) in spring (n=46), summer (n=56), fall (n=28), and winter (n=43), and (B) at the preserve (n=51), pasture (n=59), and agriculture (n=53) sites.

interaction (LR  $X^2_6 = 17.38$ ,  $P = 0.008$ ). *Hoplopyllus anomalus* was more prevalent on juvenile (81.08%) than adult squirrels (53.97%). Also, *H. anomalus* was most prevalent in spring at the preserve site (86.67%, LR  $X^2_2 = 9.79$ ,  $P = 0.008$ ). For other seasons, inter-site differences in *H. anomalus* prevalence were not discernible.

Variation in the abundance of *H. anomalus* was best explained by a site  $\times$  season interaction ( $F_{6,149} = 9.92$ ,  $P < 0.001$ ). In spring, *H. anomalus* was most abundant at the preserve site (mean = 7.44, CI = 4.81-10.07), relative to the agriculture (mean = 1.60, CI = 0.61-2.59) and pasture sites (mean = 1.38, CI = 0.12-2.63). The opposite pattern was found for summer, when *H. anomalus* was most abundant at the agriculture (mean = 5.08, CI = 3.23-6.93) and pasture sites (mean = 4.33, CI = 2.43-6.23), relative to the preserve site (mean = 1.88, CI = 1.23-2.53). For fall, inter-site differences in the abundance of *H. anomalus* were not detected. The few *H. anomalus* found in winter (n = 12) were primarily from the pasture site (60%).

**Oropsylla montana**

The prevalence of *O. montana* was best explained by host-age (LR  $X^2_1 = 5.31$ ,  $P = 0.021$ ) and season (Figure 2, LR  $X^2_3 = 87.26$ ,  $P < 0.0001$ ). *Oropsylla montana* was more prevalent on adult (47.62%) than juvenile squirrels (18.92%). Also, *O. montana* was more prevalent in winter

than spring, summer, or fall (Figure 2).

The abundance of *O. montana* was best explained by host-age ( $F_{1,156} = 7.44$ ,  $P = 0.007$ ), season ( $F_{3,157} = 51.47$ ,  $P < 0.001$ ), and site ( $F_{2,154} = 16.25$ ,  $P < 0.001$ ). *Oropsylla montana* was more abundant on adult (mean = 1.88, CI = 1.17-2.61) than juvenile squirrels (mean = 0.27, CI = 0.07-0.47) and in winter (Figure 2). We found no *O. montana* in summer, and few in spring and fall (Figure 3). Regarding inter-site differences, *O. montana* was most abundant at the pasture site (Figure 3).

**Echidnophaga gallinacea**

The prevalence of *E. gallinacea* was best explained by season (LR  $X^2_3 = 16.94$ ,  $P < 0.0001$ ) and site (Figure 2, LR  $X^2_2 = 6.72$ ,  $P < 0.035$ ). *Echidnophaga gallinacea* was most prevalent in fall and summer and at the agriculture and pasture sites (Figure 2).

Variation in the abundance of *E. gallinacea* was best explained by season ( $F_{3,157} = 13.67$ ,  $P < 0.001$ ) and a host-age  $\times$  site interaction ( $F_{2,152} = 3.59$ ,  $P = 0.030$ ). The season main-effect demonstrated *E. gallinacea* was most abundant in fall; we found few *E. gallinacea* in winter and spring (Figure 3). At the preserve site, *E. gallinacea* was more abundant on juvenile (mean = 1.00, CI = 0.12-1.88) than adult squirrels (mean = 0.23, CI = 0.06-0.40); we detected no inter-age differences in the abundance of *E. gallinacea* at

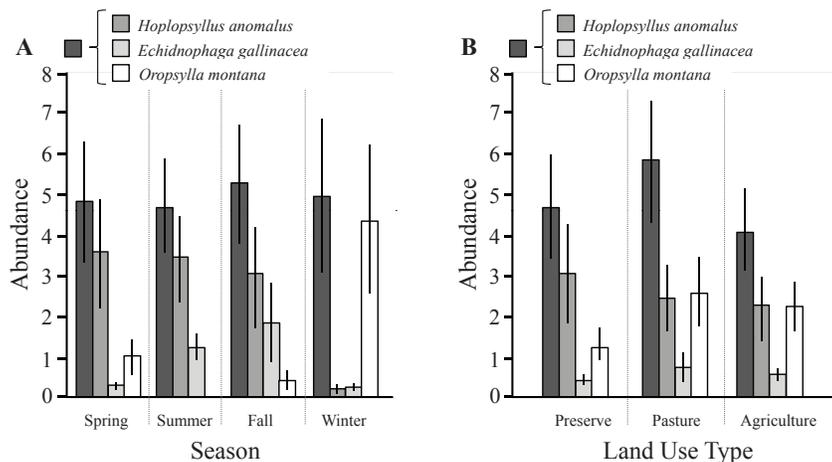


Figure 3. Mean abundance of fleas (with 95% confidence intervals) found on California ground squirrels, *Otospermophilus beecheyi*, in the San Joaquin Valley, CA (April, 2001-January, 2002), in spring (n=46), summer (n=56), fall (n=28), and winter (n=43), and (B) at the preserve (n=51), pasture (n=59), and agriculture (n=53) sites.

the agriculture and pasture sites.

## DISCUSSION

The diversity of fleas found on *O. beecheyi* in this study (*H. anomalous*, *O. montana*, and *E. gallinacea*) corresponds with previous studies in California that recorded similar species composition. According to previous work, and our data, *H. anomalous* and *O. montana* are the two most commonly encountered flea species on *O. beecheyi* (Holdenried et al. 1951, Ryckman et al. 1954, Ryckman 1971, Davis et al. 2002, Bursten et al. 1997, Lang 2004). *Echidnophaga gallinacea* was encountered less frequently. Unlike *H. anomalous* and *O. montana* that primarily parasitize rodents (Lewis 1972), *E. gallinacea* parasitizes birds and several mammals (Durden et al. 2005). Thus, although *E. gallinacea* will parasitize *O. beecheyi*, this rodent is not considered its primary host, which may partly explain why *E. gallinacea* was found at low occurrence and abundance on *O. beecheyi* in this study.

Our findings confirm general seasonal patterns of abundance for the three flea species on *O. beecheyi*. *Hoplopyllus anomalous* and *E. gallinacea* normally are found in greater numbers on *O. beecheyi* during dry, warmer months, while *O. montana* normally is found on *O. beecheyi* during moist, cooler months (Stewart and Evans 1941, Holdenried et al. 1951, Longanecker and Burroughs 1952, Ryckman et al. 1954, Ryckman 1971, Lang 1996, Davis et al. 2002). This seasonality has been attributed to differing rates of mortality of each flea species under differing abiotic conditions (Metzger and Rust 1999). At high temperatures when soils are dry, *H. anomalous* and *E. gallinacea* are less susceptible to mortality and are thus more abundant than *O. montana* (Metzger and Rust 1999). In contrast, when air temperatures are low and soils are moist, *O. montana* is less susceptible to mortality and is more abundant than *H. anomalous* and *E. gallinacea* (Metzger and Rust 1999). Indeed, we did not encounter *O. montana* during summer and rarely encountered *H. anomalous* and *E. gallinacea* in winter.

The differences we observed in flea species prevalence and abundance among seasons could result from seasonal variations in microclimate conditions for fleas among sites. Our study sites (<40 km apart) were similar in temperature, precipitation, and elevation. However, microclimate conditions, which might better relate to flea ecology, likely varied among sites. For instance, on sites where vegetative ground cover is reduced, water evaporation is likely higher in summer (Lovich and Bainbridge 1999), thereby supporting flea species such as *H. anomalous* that fare better in hot, arid microclimatic conditions (Metzger and Rust 1999). Our findings support this hypothesis because we observed *H. anomalous* being most abundant in the summer at the agriculture and pasture sites where vegetation was reduced by herbicides and cattle grazing. In addition, soil moisture and temperatures vary outside and inside *O. beecheyi* burrows (Longanecker and Burroughs 1952). These subsurface microclimatic conditions likely varied among sites due to differing soil types and chemistry, and

differing burrow depths.

Variations in flea species abundance among sites could also reflect variations in host (resource) abundance, perhaps partly due to land use practices. Across our study sites, *O. beecheyi* pups are born, and thus squirrel abundance is at its peak, in late February to early March (Evans and Holdenried 1943, Holdenried et al. 1951, Fitch 1948). Among land use types, *O. beecheyi* likely varied in abundance due to differences in forage availability, which could also have influenced the abundance of certain flea species. For example, herbicides were not used and cattle did not graze at the preserve site, suggesting greater forage abundance than at the other two sites. Where forage is abundant, rodents (Ernest et al. 2000), including *O. beecheyi* (Fitch 1948), often produce more offspring. Therefore, it is likely that squirrels were more abundant at the preserve site in spring and summer, when *H. anomalous* breeds (Ryckman 1971), potentially explaining why *H. anomalous* was most abundant at the preserve site in spring and most prevalent on juvenile squirrels.

Our results suggest that land use practices influence flea ecology. However, additional investigation with greater replication within land use types (i.e., >one site per land use category) is needed to determine if land use practices do indeed influence flea ecology. For instance, future research could investigate how land use practices influence surface and subsurface microclimatic conditions for fleas, and then relate flea community composition and abundance to land use practices. Also, future research is needed to investigate how land use practices influence *O. beecheyi* abundance and how influences of land use practices on hosts relate to influences on fleas.

Our findings have potentially important implications to the spatial dynamics of plague activity. Previous work predicting plague risk typically focused on plague dynamics at a landscape scale (Stenseth et al. 2006, Augustine et al. 2008). However, these predictions did not incorporate differences in flea species abundance and species composition among sites, such as those found here. This is particularly important for areas occupied by *O. beecheyi*, since all three flea species we encountered are known vectors of *Y. pestis* (Eisen et al. 2009). Research linking flea species with transmission risk (review in Eisen et al. 2009) could be incorporated with studies of flea ecology among sites to predict plague risk at fine spatial scales (e.g., among sites).

Our findings also have important implications for the temporal dynamics of plague activity and efforts to mitigate plague risk. Flea control insecticides are currently the most widely used tool for mitigating plague risk in *O. beecheyi* (Davis 1999, Barnes 1982, Mian et al. 2004, Borchert et al. 2009) and other ground-dwelling rodent species (Seery et al. 2003, Hoogland et al. 2004). However, all previous efforts to evaluate the utility of flea control products have failed to examine how variations in the timing of applications could improve vector control and mitigate plague risk despite the need for such approaches, considering the phenology and transmission efficiency of certain flea species (Wilder et al. 2008, Eisen et al. 2009). For our study area and host

species, *O. montana* is likely the most efficient flea species at acquiring and acting as a vector of *Y. pestis* (Eisen et al. 2009). Since *O. montana* is most abundant and produces offspring in winter (Ryckman 1971), flea control insecticides could be applied during late fall or winter. Future studies should examine the efficacy of using insecticides prior to or during levels of high flea abundance to reduce numbers of fleas found on *O. beecheyi* and other mammalian species impacted by flea-borne *Y. pestis*.

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#### REFERENCES CITED

- Adjemian, J.C., E.H. Girvetz, L. Beckett, and J.E. Foley. 2006. Analysis of genetic algorithm for rule-set production (GARP) modeling approach for predicting distributions of fleas implicated as vectors of plague, *Yersinia pestis*, in California. *J. Med. Entomol.* 43: 93-103.
- Augustine, D.J., M.R. Matchett, T.P. Toombs, J.F. Cully, T.L. Johnson, and J.G. Sidle. 2008. Spatiotemporal dynamics of black-tailed prairie dog colonies affected by plague. *Land. Ecol.* 23: 255-267.
- Barnes, A.M. 1982. Surveillance and control of bubonic plague in the United States. *Symp. Zool. Soc. Lond.* 50: 237-250.
- Borchert, J.N., R.M. Davis, and R.M. Poché. 2009. Field efficacy of rodent bait containing the systemic insecticide imidacloprid against the fleas of California ground squirrels. *J. Vector Ecol.* 34: 92-98.
- Bossard, R.L. 2006. Mammal and flea relationships in the Great Basin desert: From H.J. Egoscue's collections. *J. Parasitol.* 92: 260-266.
- Brinkerhoff, R.J. 2008. Habitat-associated differences in flea assemblages of striped skunks (*Mephitis mephitis*). *Comp. Parasitol.* 57: 127-131.
- Bursten, S.N., R.B. Kimsey, and D.H. Owings. 1997. Ranging of male *Oropsylla montana* fleas via male California ground squirrel (*Spermophilus beecheyi*) juveniles. *J. Parasitology* 83: 804-809.
- Bush, A.O., K.D. Lafferty, J.M. Lotz, and A.W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitology* 83: 575-583.
- Clark, J.P. 1994. *Vertebrate Pest Control Handbook*. 4<sup>th</sup> Ed. Calif. Depart. of Food and Agric, Sacramento, CA, 350 pp.
- Crawley, M.J. 2007. *The R Book*. John Wiley and Sons Ltd., West Sussex, England. 942 pp.
- Davis, R. M. 1999. Use of orally administered chitin inhibitor (Lufenuron) to control flea vectors of plague on ground squirrels in California. *J. Med. Entomol.* 36: 562-567.
- Davis, R.M., R.T. Smith, M.B. Madon, and E. Sitko-Cleugh. 2002. Flea, rodent, and plague ecology at Chuchupate Campground, Ventura County, California. *J. Vect. Ecol.* 27: 107- 127.
- Durden, L.A., T.N. Judy, J.E. Martin, and L.S. Spedding. 2005. Fleas parasitizing domestic dogs in Georgia, USA: species composition and seasonal abundance. *Vet. Parasitol.* 130: 157- 162.
- Eisen, R.J., L. Eisen, and K.L. Gage. 2009. Studies of vector competency and efficiency of North American flea for *Yersinia pestis*: State of the field and future research needs. *J. Med. Entomol.* 46: 737-744.
- Ernest, S.K.M., J.H. Brown, and R.R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88: 470-482.
- Eskey C.R. and V.H. Haas. 1940. Plague in the western part of the United States. *Publ. Hlth. Bull.* 254: 1-82.
- Evans, F.C. and R. Holdenried. 1943. A population study of the beechey ground squirrel in central California. *J. Mammal.* 24: 231-260.
- Fitch, H.S. 1948. Ecology of the California ground squirrel on grazing lands. *Am. Midl. Nat.* 39: 513-596.
- Holdenried, R., F.C. Evans, and D.S. Longanecker. 1951. Host-parasite-disease relationships in mammalian community in the central coast range of California. *Ecol. Monogr.* 21: 1-18.
- Hoogland, J.L., S. Davis, S. Benson-Amram, D. Labruna, B. Goossens, and M.A. Hoogland. 2004. Pyreperm kills fleas and halts plague among Utah prairie dogs. *Southwest. Nat.* 49: 376-383.
- Hubbart, J.A. 2002a. *Chemical Composition of the Hair of the California Ground Squirrel (Spermophilus beecheyi) as an Indicator of Heavy Metals and Environmental Stress*. Thesis, California State University Fresno, Fresno, CA, U.S.A.
- Hubbart, J.A. 2002b. Economical tripod rifle mount. *Calif. Fish Game J.* 88: 142-144.
- Huntington, G.L. 1971. *Soil Survey of Eastern Fresno Area California*. United States Department of Agriculture Soil Conservation Service in Cooperation with California Agricultural Experiment Station, Washington, D.C., U.S.A.
- Ihaka, R. and R. Gentleman. 1996. R: a language for data analysis and graphics. *J. Comp. Graph. Stat.* 5: 299-314.
- Kennedy, C.R. and A.O. Bush. 1994. The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* 109: 187-196.
- Kim, K.C. 1985. *Coevolution of Parasitic Arthropods and Mammals*. John Wiley and Sons, New York, NY. 800 pp.
- Krasnov, B.R. 2008. *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology*. Cambridge University Press, Cambridge, UK.
- Krasnov, B.R., G.I. Shenbrot, S.G. Medvedev, V.S. Vatschenok

- and I.S. Khokhlova. 1997. Host-habitat relation as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. *Parasitology* 114: 159-173.
- Krasnov, B.R., M. Stanko, D. Miklisova, and S. Morand. 2006. Habitat variation in species composition of flea assemblages on small mammals in central Europe. *Ecol. Res.* 21: 460-469.
- Lang, J.D. 1996. Factors affecting the seasonal abundance of ground squirrel and wood rat fleas (*Siphonaptera*) in San Diego County, California. *J. Med. Entomol.* 33: 790-804.
- Lang, J.D. 2004. Rodent-flea-plague relationships at the higher elevations of San Diego County, California. *J. Vector Ecol.* 29: 236-247.
- Lewis, R.E. 1972. Notes on the geographical distribution and host preferences in the order Siphonaptera. Part 1. Pulicidae. *J. Med. Entomol.* 9: 511-520.
- Lewis, E.L. J.H. Lewis, and C. Maser. 1988. *The Fleas of the Pacific Northwest*. Oregon State University Press, Corvallis, Oregon. 296 pp.
- Longanecker, D.S. and A.L. Burroughs. 1952. Sylvatic plague studies, IX. Studies of the microclimate of the California ground squirrel burrow and its relation to seasonal changes in the flea population. *Ecology* 33:488-499.
- Lovich, J.E. and D. Bainbridge. 1999. Anthropogenic degradation of the Southern California desert ecosystem and prospects for natural recovery and restoration. *Envir. Manag.* 24: 309-326.
- McCullagh, P., and J.A. Nelder. 1989. *Generalized Linear Models*. 2<sup>nd</sup> ed. Chapman & Hall, New York, NY.
- Metzger, M.E. and M.K. Rust. 1999. Abiotic factors affecting the development of fleas (Siphonaptera) of California ground squirrels (Rodentia:Sciuridae) in southern California, USA. pp. 235-239. In: W.H. Robinson and G.W. Rambo, (eds.) *Proceedings of the 3rd International Conference on Urban Pests*.
- Mian, L.S., J.C. Hitchcock, M.B. Madon, and C.M. Myers. 2004. Field efficacy of deltamethrin for rodent flea control in San Bernardino County, California, U.S.A. *J. Vector Ecol.* 29: 212-217.
- Ryckman, R.E., C.C. Lindt, C.T. Ames, and R.D. Lee. 1954. Seasonal incidence of fleas on the California ground squirrel in Orange County, California. *J. Econ. Entomol.* 47: 1070-1074.
- Ryckman, R.E. 1971. Plague vector studies. Part II. The role of climatic factors in determining seasonal fluctuations of fleas species associated with the California ground squirrel. *J. Med. Entomol.* 8: 541-549.
- Sawyer, J.O. and T. Keeler-Wolf. 1995. *A Manual of California Vegetation*. California Native Plant Society, Sacramento, California, U.S.A.
- Seery, D.B., D.E. Biggins, J.A. Monteneri, R.E. Enscoe, D.T. Tanda, and K.L. Gage. 2003. Treatment of black-tailed prairie dog burrows with deltamethrin to control fleas (Insecta: *Siphonaptera*) and plague. *J. Med. Entomol.* 40: 718-722.
- Smith, C.R., J.R. Tucker, B.A. Wilson, and J.R. Clover. 2010. Plague studies in California: a review of long-term disease activity, flea-host relationships and plague ecology in the coniferous forests of the Southern Cascades and northern Sierra Nevada mountains. *J. Vector Ecol.* 35: 1-12.
- Stenseth, N.C., N.I. Samia, H. Viljugrein, K.L. Kausrud, M. Begon, S. Davis, H. Leirs, V.M. Dubyanskiy, V.M. Dubyanskiy, J. Esper, V.S. Ageyev, N.L. Klassovskiy, S.B. Pole, and K. Chan. 2006. Plague dynamics are driven by climate variation. *Proc. Natl. Acad. Sci. U.S.A.* 103: 13110-13115.
- Stewart, M.A. and F.C. Evans. 1941. A comparative study of rodent and burrow flea populations. *Proc. Soc. Exp. Biol. Med.* 47: 140-142.
- Tomich, Q.P. 1962. The annual cycle of the California ground squirrel *Citellus beecheyi*. *Univ. Cal. Pub. Zool.* 65: 213-282.
- Ulrich, R. and L.K. Stromberg. 1962. *Soil Survey of Madera Area California*. United States Department of Agriculture, Soil Conservation Service, in Cooperation with California Agricultural Experimental Station. Series 1951. Number 11, Washington, D.C., U.S.A.
- Wall, R. and D. Shearer. 1997. *Veterinary Entomology: Arthropod Ectoparasites of Veterinary Importance*. Chapman & Hall. London, UK.
- Wilder, A.P., R.J. Eisen, S.W. Bearden, J.A. Monteneri, D.W. Tripp, R.J. Brinkerhoff, K.L. Gage, and M.F. Antolin. 2008. Transmission efficiency of two flea species (*Oropsylla tuberculata cynomuris* and *Oropsylla hirsuta*) involved in plague epizootics among prairie dogs. *EcoHealth* 5: 205-212.
- Wobeser, G.A. 2006. *Essentials of Disease in Wild Animals*. Blackwell Publishing, Ames, IA. 243 pp.