ECOLOGICAL FACTORS INFLUENCING COMMUNITY STRUCTURE OF PARASITES AND THEIR HOSTS

by

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ABSTRACT

Understanding patterns and processes underlying the structure and assembly of ecological communities is a major goal of ecology. Community assembly involves a balance between dispersal events and interactions with biotic and abiotic elements that make up the local environment. Determining which processes dominate and under what circumstances remains unclear for parasite communities.

Parasite communities of deer mice are examined to determine whether host traits, parasite interactions, and/or parasite dispersal is important in structuring within host parasite community structure. The results suggest that within host parasite communities accumulate in heavier, older hosts. Parasite dispersal plays a role in structuring parasite communities in deer mice. Helminths and ticks accumulated in older hosts, while fleas and lice did not. Helminths and lice were predicted to accumulate in older hosts because they are associated with their hosts for longer periods of time than ticks and fleas.

In studies of parasite communities, it is important to document most, if not all, parasites of interest on or in a host. Using histopathology, I show that deer mice are not infected by parasites in other tissues that are not typically examined during standard parasitological surveys. I also survey rodents in the Great Basin for diseases that are caused by both infectious and non-infectious sources. Two pathogens were found in deer mice: the fungus *Emmonsia crescens* and the nematode *Capillaria hepatica.* The most common disease was extramedullary hematopoiesis (11%).

I also investigated how habitat change influences species turnover. A major change in the environments of the Intermountain West is the expansion of pinyon-juniper woodlands (P-J). Rodent communities in the Great Basin are assessed to document species turnover following P-J conversion. I found that there was a diversity deficit (immigration credit) following P-J conversion because immigration of new species into P-J converted areas is slower than local species extinction. Diversity may increase if the immigrating species become more abundant.

Parasites are also subject to environmental change, but little empirical data exist about how parasites will respond. Resampling historical sites following environmental change suggests that helminth diversity increased throughout the Great Basin region. This change was driven by a decrease in the prevalence and abundance of the pinworm *Syphacia peromysci*, making the relative abundances of helminth species more even. Complex life cycle parasites appear to be more stable to environmental change than those with direct life cycles because, in this system, complex life cycle parasites have lower host specificity.

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CHAPTER 1

INTRODUCTION

Background

Understanding patterns and processes underlying the structure of ecological communities is a major goal of ecology (Ricklefs and Schluter 1994). Ecological communities consist of all the populations in a given area that are interacting or have the potential to interact. Community assembly concerns the processes that give rise to the structure of local ecological communities. The structure of a community, such as species composition, species richness, and relative species abundance, results from processes operating at several scales. The species that make up local communities are generally a subset of the species found at larger, regional scales (Zobel 1997). It is these regional species pools from which individuals disperse to colonize a given area and possibly become a member of the local community (Kraft and Ackerly 2014). Following dispersal, deterministic and stochastic processes act to structure local communities.

Community assembly involves a balance between dispersal events and interactions with biotic and abiotic elements that make up the local environment (Fukami et al. 2005). However, the abiotic and biotic portions of the environment are not static; environments change and species respond. This dissertation will examine the assembly and structure of rodents and their parasite communities. First, parasite communities of rodents will be studied within the context of within host (intrahost) community assembly.

Rodent and parasite communities will then be investigated in terms of environmental change and species turnover.

Two general models have received attention for their role in assembling and structuring communities: deterministic assembly models (ecological selection) and neutral, dispersal-based assembly models (ecological drift). Deterministic assembly is the result of community structure being influenced by available niches and is defined by resource use and competition (MacArthur 1972; Diamond 1975). Deterministic processes are the result of biotic and abiotic characteristics of the environment that act as filters to determine which species from the regional pool are able to establish viable populations in the local community. Biotic factors such as interspecific competition and predation influence whether a species is able to compete and successfully establish (Kraft and Ackerly 2014). Environmental factors, such as habitat structure (e.g. habitat heterogeneity), and abiotic factors (e.g. temperature and precipitation) further restrict the species able to colonize a given location. If biotic and abiotic filters significantly influence the structure of a community, the community is structured based on deterministic processes that are predictable and repeatable (Shipley et al. 2012).

Alternatively, dispersal-based models suggest that assembly is generated by haphazard dispersal and establishment of species from the regional species pool (Bell 2000; Hubbell 2001). Dispersal of individuals away from the natal area is an important life history characteristic that plays a significant role in the population dynamics of a species (Bowler and Benton 2005). Dispersal maintains gene flow in a population and decreases the negative consequences of inbreeding, competition, and density-dependent predation (Janzen 1970; Connell 1971). Dispersal to new areas also allows species ranges

to expand or contract following environmental change (Travis et al. 2013). During the assembly of a local community, individuals from the species pool must first disperse to the given area. Once individuals disperse, those individuals are subject to abiotic and biotic filters that may determine whether the species will establish to become a member of the local community (Kraft and Ackerly 2014). If random dispersal and colonization of individuals determine the structure of a community, then there will not be patterns related to environmental factors and biotic interactions (i.e. no ecological selection) (Cottenie 2005). Both dispersal and deterministic processes can be important in structuring the same ecological community. A major goal of ecology is finding which processes dominate assembly and under what circumstances.

Parasites represent a large portion of the world's biodiversity (Price 1980), yet little is currently known about which processes dominate the structure of parasite communities (Johnson et al. 2015). Dispersal and deterministic processes may both influence the assembly of parasite communities (Rynkiewicz et al. 2015; Budischak et al. 2016). Which processes dominate parasite community assembly and under what circumstances remains unclear (Johnson et al. 2015). Understanding the assembly of parasite communities in the context of parasite dispersal, host environment (host traits), and parasite interactions (i.e. within host parasite competition) is receiving attention recently (Johnson et al. 2015; Rynkiewicz et al. 2015; Budischak et al. 2016). However, few empirical studies have investigated parasite community assembly under this framework (but see Budischak et al. 2016).

This dissertation examines the ecological factors influencing community structure in parasites and their hosts. I address this concept using a rodent-parasite system in the

Great Basin. I test whether parasite dispersal, host traits, and/or parasite interactions are most important in shaping the community structure of deer mouse parasites (Chapter 2). I then investigate whether parasites, pathogens, or non-infectious diseases are found in tissues not typically examined by parasitologists or ecologists in wild rodents using histology (Chapter 3). Environments are not static, and environmental change can impact species composition and diversity of both parasites and their hosts. First, I explore how environmental change impacts species turnover of rodents in the Great Basin. Specifically, I test for a biodiversity deficit or surplus following pinyon-juniper (P-J) conversion (Chapter 4). I then examine how P-J conversion may impact species diversity, community structure, and species turnover of deer mouse parasites (Chapter 5).

Chapter summaries

Chapter 2: The importance of host traits and parasite dispersal on the structure of parasite communities of deer mice

Chapter 2 investigates whether parasite communities in individual hosts are structured through host traits, parasite dispersal, and/or parasites interactions. Hosts, including humans, are often infected with more than parasite species, some with widely different life history characteristics and transmission dynamics. Parasites within a single host individual represent an ecological community in which several parasite species may interact. In this chapter, deer mice were sampled from the Great Basin in Utah and Nevada to test the null hypothesis that parasite community structure is independent of host traits and parasite interactions. I found that body condition, sex, and within host parasite interactions were not significant in predicting parasite community structure. Data show that host body mass was a significant predictor of parasite group richness and total

parasite abundance, indicating that heavier, older mice have more parasites. When taxonomic groups were analyzed separately, helminths (nematodes and cestodes) and ticks accumulated in older hosts. Helminths are often associated with their hosts for longer periods of time than fleas and ticks, so fleas and ticks were not predicted to be correlated with host mass. Lice are permanent parasites and were predicted to accumulate on hosts similar to helminths. Lice are associated with their hosts for long periods of time and can maintain infections indefinitely. However, infection with lice was not correlated with mass. The results suggest that dispersal differences among taxonomic groups should be taken into account rather than grouping parasites by whether they are found on the outside or the inside of a host.

Chapter 3: Histological survey of diseases and parasites of wild rodents in the Great Basin

Wild animals often have disease, whether caused by infectious pathogens or non-infectious sources. Standard collection techniques for parasites may miss parasites or diseases associated with infectious pathogens. Background levels of disease in animals, whether caused by infectious or non-infectious agents, may be important to consider in wildlife disease studies and disease ecology. We used histology to survey diseases in wild rodent populations. We examined liver, lung, heart, and kidney tissue in ten species of rodents from five locations (143 rodents total). We found diseases caused by both infectious pathogens and non-infectious sources. One parasite was found in liver tissue from one deer mouse. One other pathogen, a fungus, was found in four rodents. The most common pathologies found in rodents were either non-infectious in origin or unknown. This information can be used to create baseline data for disease in wild populations to

assess population health. Baseline data can aid in identifying emerging diseases, finding causes of disease, and assessing the success of control efforts. Pathology from non-infectious sources, such as environmental contaminants, genetics, or general health conditions is important to consider in the context of disease ecology.

Chapter 4: Species turnover of rodents following habitat change

Chapter 4 examines how environmental change influences species turnover of rodents in the Great Basin. Estimating changes in biodiversity and species composition following environmental change is essential for predicting species responses to future change. Species respond to environmental change by expanding or contracting their ranges, resulting in the establishment or disappearance of species from a given area. These changes in biodiversity are referred to as species turnover. Following environmental change, there may be delays in species immigrating to the new habitat or becoming locally extinct, which can lead to diversity surpluses or deficits. One type of environmental change occurring around the world is the conversion of savannahs and shrublands to dense woodlands. In the Great Basin, pinyon-juniper woodlands are expanding and replacing sagebrush steppe habitat. In this chapter, I test whether there is a diversity surplus or deficit in rodent communities following pinyon-juniper conversion and whether the species composition changes. P-J conversion resulted in turnover of rodent species. Results suggest that species immigration is slower and more variable after P-J conversions than local extinction. Estimates of rodent diversity soon after woody plant conversions may underestimate the ultimate diversity that will be supported because of the slow rate of immigration.

Chapter 5: Impact of environmental change on parasite communities

Chapter 5 explores the impacts of environmental change on parasite communities. Several contradictory hypotheses have been proposed in the literature regarding parasite responses to environmental change. In this chapter, I test whether parasite community structure is affected by environmental change using both historical and recent host-parasite data in the Great Basin. I also test the hypothesis that parasites with complex life cycles will be less affected by environmental change than those with direct life cycles. Diversity increased in two sites that converted from low P-J cover to high P-J cover. There was a big decrease in prevalence and abundance of the direct life cycle parasite *Syphacia peromysci,* which caused the relative abundances of helminth communities to be more even. I found that P-J conversion was not the main cause of the decrease in *S. peromysci* prevalence and abundance based on recent sampling in low P-J and high P-J sites. This chapter suggests that parasites with direct life cycles may be more affected by environmental change than those with complex life cycles. In this system, direct life cycle parasites are generally more host specific than complex life cycle parasites, which may make them more vulnerable to environmental change.

References

Bell, G. 2000. The distribution of abundance in neutral communities. The American Naturalist 155:606-617.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Budischak, S. A., E. P. Hoberg, A. Abrams, A. E. Jolles, and V. O. Ezenwa. 2016. Experimental insight into the process of parasite community assembly. Journal of Animal Ecology 85:1222-1233.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7:241-253.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175-1182.

Diamond, J. M. 1975. Assembly of species communities. Pp. 342-444 in Ecology and Evolution of Communities (M. L. Cody, and J. M. Diamond, eds). Harvard University Press. Boston, Massachusetts.

Fukami, T., T. Martijn Bezemer, S. R. Mortimer, and W. H. Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8:1283-1290.

Hubbell S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press. Princeton, New Jersey.

Johnson, P. T., J. C. De Roode, and A. Fenton. 2015. Why infectious disease research needs community ecology. Science 349:1259504.

Kraft, N. J., and D. D. Ackerly. 2014. Assembly of plant communities. Pp. 67-88 in Ecology and the Environment (R. K. Monson, ed.). Springer. New York City, New York.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York City, New York.

Ricklefs, R. E., and D. Schluter. (eds.). 1993. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press. Chicago, Illinois.

Rynkiewicz, E. C., A. B. Pedersen, and A. Fenton. 2015. An ecosystem approach to understanding and managing within-host parasite community dynamics. Trends in Parasitology 31:212-221.

Travis, J. M., M. Delgado, G. Bocedi, M. Baguette, K. Bartoń, D. Bonte, I. Boulangeat, J.A. Hodgson, A. Kubisch, V. Penteriani, and M. Saastamoinen. 2013. Dispersal and species' responses to climate change. Oikos 122:1532-1540.

Zobel, M. 1997. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends in Ecology and Evolution 12:266-269.

CHAPTER 2

IMPORTANCE OF HOST TRAITS AND PARASITE DISPERSAL ON THE STRUCTURE OF PARASITE COMMUNITIES IN DEER MICE

Abstract

Hosts are often infected by more than one species of parasite. Parasites on or within hosts represent an ecological community in which parasite species have the potential to interact, but how or why hosts are infected with many parasites remains unclear. Deterministic processes related to host traits and parasite interactions, and parasite dispersal, may influence how parasite communities are structured. I test the null hypothesis that parasite community structure is independent of host traits and parasite interactions. To test this hypothesis, ectoparasitic arthropods and endoparasitic helminths were collected from deer mice (*Peromyscus maniculatus*) over three years in the Great Basin. I found that habitat, host body condition, and parasite interactions were not significant in predicting parasite community structure. Data show that parasite richness and total parasite load is best explained by body mass, which, in deer mice, is highly correlated with age. When parasite taxonomic groups were analyzed separately, host body mass was a significant predictor of tick prevalence, opposite of predictions. Ticks were predicted to follow the same pattern as fleas because they both are associated with their hosts for short periods of time (i.e. up to a few days). Like helminths, lice are associated with their hosts longer than ticks and fleas, and were predicted to accumulate

on their hosts. Nematodes and cestodes accumulated in heavier, older hosts, while lice did not. These results suggest that host age is an important trait in structuring parasite communities in deer mice. Dispersal differences among taxonomic groups should be taken into account rather than grouping parasites by whether they are found on the outside or inside of a host.

Introduction

Hosts often have more than one parasite species infecting them. Parasites within hosts represent ecological communities in which many parasite species may interact (Cox 2001; Poulin 2007; Griffiths et al. 2014). Interactions among parasites and with their hosts affect parasite transmission, disease severity, disease recovery, and susceptibility to other parasites and pathogens (Hartgers and Yazdanbakhsh 2006; Telfer et al. 2010; Blackwell et al. 2013). For example, *Anaplasma phagocytophilum* increases the susceptibility of field voles (*Microtus agrestis*) to cowpox virus by a factor of five, while also decreasing the susceptibility to *Bartonella* spp. (Telfer et al. 2010). Given the frequency and importance of coinfections, how or why individuals acquire many parasites remains unclear.

Finding which factors lead to individuals becoming infected with many parasites is a critical step in understanding how parasite communities are structured. Dispersal, deterministic processes, and stochastic forces all act to structure free-living communities (MacArthur 1972; Diamond 1975; Bell 2000). These processes also apply to parasite communities (Pedersen and Fenton 2007; Johnson et al. 2015). Most studies on coinfection focus on hosts infected with two or three parasite species (e.g. trematodes) or taxonomic groups (e.g. nematodes and *Mycobacterium* spp.) within a host population

(Graham 2008; Telfer et al. 2010; Ezenwa and Jolles 2011; Johnson and Hoverman 2012; Lass et al. 2012). However, the distribution of all parasites on a given host species can shape community-level processes (Balestrieri et al. 2006; Holmstad et al 2008; Ferrari et al. 2009; Krichbaum et al. 2009; Kamath et al 2014). Applying a community ecology framework to parasite communities allows several hypotheses to be tested in the same host-parasite system.

Parasites must disperse (transmit) to new hosts, and different parasites have different modes of transmission to encounter hosts. Parasites are encountered throughout the entire life of a host and from different sources. Hosts encounter most intestinal helminths by consuming infective stages, often from arthropod intermediate hosts, while ticks and fleas are encountered when foraging or searching for mates. Whether an individual is infected with a certain parasite at a given time point (i.e. time sampled for parasites) may be determined by parasite life history traits and transmission dynamics (Johnson et al. 2015; Rynkiewicz et al. 2015). These characteristics may be used to determine whether certain guilds (ectoparasites vs. endoparasites) or taxonomic groups are more likely to infect a subset of the population. These data will help predict whether parasites with similar properties will infect hosts following similar patterns.

Following dispersal, parasites are subject to filtering by the environment and stochastic processes. Deterministic processes (ecological selection) result from interactions with the environment, host traits, and from interactions among parasite species forming predictable and repeatable infection patterns (Johnson et al. 2015; Rynkiewicz et al. 2015). If stochastic processes dominate infection, parasite structure will be unpredictable through differential exposure and susceptibility related to temporal,

spatial, or demographic heterogeneity (Johnson et al. 2015; Rynkiewicz et al. 2015; Budischak et al. 2016). This is called ecological drift. For example, certain areas may be "hotspots" for parasites in some years or seasons (Ezenwa 2003; Wolinska and King 2009; Paull et al. 2012). Stochasticity will produce no visible patterns of infection.

Deterministic processes result in infection patterns that are repeatable such that a subset of the host population is most likely to be infected by many parasites. For host-parasite interactions, this involves host traits such as host species, dispersal ability, body size, and dietary breadth (Dallas and Presley 2014). Within a species, examples of host traits influencing infection include males often having more parasites than females due to hormone differences (Zuk and McKean 1996). Hosts in poor body condition may also be more susceptible to infection because of low immunocompetence (Tella et al. 2001; Beldomenico and Begon 2010; Johnson et al. 2015; Warburton et al. 2016). Host defense can also structure communities by influencing colonization-extinction events. Hosts have behaviors to decrease exposure to parasites, such as avoiding areas rich in parasites or infected mates (Folstad et al. 1991; Houde and Torio 1992; Gilbert 1997; Penn and Potts 1998; Karvonen et al. 2004). Hosts also preen or groom themselves to remove ectoparasites once infested (Murray 1987; Clayton 1991; Mooring et al 1996). After infection, hosts may become tolerant to infections or resistant to future infections through the immune system (Schmid-Hempel 2011; Barbour 2017). For example, juvenile birds and mammals often have a higher intensity of parasites than adults (Gregory et al 1992; Allander and Bennett 1994; Dawson and Bortolotti 1999; Sol et al. 2003), presumably because of adaptive immunity in adults (Sol et al. 2003). Both dispersal and deterministic processes can be important in structuring the same community. A major goal of ecology

is finding which processes dominate and under what circumstances.

Positive or negative interactions between species or groups can act to structure parasite communities by influencing susceptibility to other parasite species (Lello et al. 2004; Cattadori et al. 2008; Graham 2008; Telfer et al. 2010). Parasites can interact with each other directly through competition or indirectly through changes in host immunity (Cox 2001). If infection is determined by competition among parasites, or through facilitation (i.e. positive interactions, such as through suppression of host defense), then the abundance of one parasite species will negatively or positively influence the abundance of another parasite species.

Here, I test the null hypothesis that parasite community structure is independent of host traits and parasite interactions. This hypothesis is tested using deer mice (*Peromyscus maniculatus*) and their ecto- and endoparasites. I also examine whether there are patterns of infection based on life history similarities among different taxonomic groups of parasites.

Taxonomic groups can be organized according to life history traits and transmission dynamics (Table 2.1). Fleas and ticks differ from lice because they have greater dispersal ability and feed for a short amount of time. Ticks feed up to five days (Piesman et al. 1987; Jones et al. 2015), and fleas feed intermittently up to several days if they are not groomed off (Krasnov et al. 2003; Krasnov 2008). Lice, on the other hand, are permanent parasites. Once lice infect a host, they can complete their entire life cycle on that host. Helminths are often transmitted through ingestion and are associated with their hosts for longer periods of time that ticks and fleas. Lice and helminths are similar in the time they are associated with their host. However, unlike lice, most helminths

cannot maintain an infection indefinitely. I predict that flea and tick infestations will be based on random colonization-extinction events because being infected at a given time will be independent of host age/mass. In contrast, I predict lice and helminths will accumulate in older, heavier hosts because they are found on or in their hosts longer than ticks and fleas.

Methods

Study system

The focal species for this study is the North American deer mouse (*Peromyscus maniculatus*), which occupies nearly every habitat in North America. Deer mice are nocturnal and active year-round. Deer mouse home ranges vary from 0.032 to 1.2 hectares (Stickel 1968) with an average home range of between 590m^2 and 1 hectare (Blair 1942; Wolff 1985). Males and females disperse from the natal area but often do not travel more than 1 km to establish their own home ranges and territories (Howard 1960). Several taxonomic groups of parasites parasitize deer mice. Ectoparasites include ticks, lice, and fleas. Endoparasitic helminths include nematodes (roundworms), cestodes (tapeworms), trematodes (flukes), and acanthocephalans (thorny-headed worms).

This study was conducted in the Great Basin of Utah and Nevada from 2014 to 2016. Within the Great Basin, there are north to south spanning mountain ranges, resulting in a topography characterized as basin and range. Sagebrush (*Artemesia* spp.) and associated grasses dominate sagebrush steppe habitat in the valley floors and occur as elevation increases until pinyon-juniper (P-J) woodlands are reached. In each mountain range, Utah juniper (*Juniperus osteosperma*) and singleleaf pinyon pine (*Pinus monophylla*) are the predominate species present in P-J woodlands (Banner 1992).

Between sagebrush and P-J woodlands are transition zones (ecotones), which have both sagebrush and grasses as well as juniper trees and pinyon pine (Appendix A). These different mountain ranges are used as replicates; sagebrush, P-J woodlands, and ecotones are sampled.

Animal trapping and processing

Deer mice were trapped in seven mountain ranges (locations) in the Great Basin (Fig. 2.1). Four were in Utah and three were in Nevada. Throughout these seven locations, deer mice were trapped at 19 individual sites. Seven sites were located in the Stansbury Mountains, six were in the Oquirrh Mountains, and two were in the Cedar Mountains. The other locations were each sampled once. Each site was either sagebrush, P-J woodland, or the transition zone between the two habitat types (ecotone). The site in the San Francisco Mountains was a mix of P-J woodland and mountain mahogany (*Cercocarpus* spp.). Two of the sites in the Stansbury Mountains were sampled in 2015 and then resampled in 2016.

Sherman live traps (H.B. Sherman Traps, Inc.) were used to catch deer mice. Traps were placed in transects five to ten meters apart. Traps were baited with whole oats and birdseed. When 25 deer mice were trapped and euthanized at a given site, trapping stopped. Because deer mice populations were low in abundance, two sites had less than 25 animals trapped (San Francisco Mountains, n = 16 and Cedar Mountains ecotone, n = 12). Captured mice and contents of the trap were emptied into Ziploc bags. Emptying the contents of the bag ensured that ectoparasites that came off the animal could be recovered. Each deer mouse was euthanized with the anesthetic isoflurane and placed on ice until it was taken to the lab for further processing. In the lab, mass, body length, tail

length, ear length, and leg length were measured for each mouse. Age classes were determined based on coat color for a subset of mice (mice were not aged in 2014). Juveniles were gray in color, subadults were gray-brown, and adults were brown. Masses of the subset of mice that were aged by coat color were used to divide all mice into the three age classes. Similar age classes have been used in deer mice (Douglass et al. 2001; Calisher et al. 2007).

Parasite collection

After measurements were taken, the digestive tracts, including the stomach, small intestine, caecum, and large intestine of each mouse, were removed and either dissected immediately or frozen at -80°C for later dissection. Mice were then placed in a freezer (-20°C) until they could be combed for ectoparasites. All animal handling and processing was approved by the Institutional Animal Care and Use Committee of the University of Utah. Each mouse was thawed and then combed for ectoparasites (fleas, ticks, lice) using a LiceMeister comb over a white surface to help see any parasites removed by combing. After combing, forceps were used to examine the mouth, nose, and ears to find ticks. The fur was also examined for any parasites not dislodged during the combing process. Once fully processed, mouse carcasses were deposited at the Natural History Museum of Utah. All ectoparasites were stored in 95% ethanol. Ectoparasites were identified to the following taxonomic groups: lice, fleas, and ticks. These ectoparasites are the most common ectoparasites of deer mice. Mites were extremely rare (< 1% of mice), and we were not certain of how many microscopic mites were missed since these were not the focus.

Digestive tracts were thawed and dissected for helminths. The small intestine,

stomach, caecum, and large intestine were dissected separately. Each part of the digestive tract was cut open using ball tipped scissors. The inside wall of each part of the digestive tract was scraped with a glass slide to remove any parasites attached with their mouthparts (i.e. cestodes and acanthocephalans). Intestinal contents were examined under a stereoscope to help find all helminths. Helminths were placed in 70% ethanol and stored in a freezer until they were needed for further identification. Helminths were identified to the following taxonomic groups: nematodes, cestodes, trematodes, and acanthocephalans.

Statistical analyses

All statistical analyses were completed in the software program R (R Core Team 2016). Body condition was calculated using a scaled body mass index (Peig and Green 2009). Total body length, not including the tail, was used as the scaling factor. This index has been shown to be an accurate predictor of deer mouse condition (Peig and Green 2009).

In order to account for total parasite load in an individual, a rank sum method was used, which allows hosts to be compared relative to each other (Holmstad et al. 2005, 2008). This relative measure of parasite load allows for comparisons of total parasite abundance per host when many types of parasites are being considered (Holmstad et al. 2005). For each parasite group, individual mice were ranked 1 to n according to how many parasites of that group that individual was infected with. Individuals not infected with a given parasite group received a zero for that group. Individuals with the same number of a given parasite group (ties) all received the same ranking. Parasite ranks were summed up for each individual to get a total rank sum.

Generalized linear models (GLM) and generalized linear mixed models (GLMM) were used to find what best predicts group richness and total abundance of parasites. Site-specific differences (i.e. habitat type and mountain range of sampling locations) in parasite richness or total rank sum of parasites were determined to inform the models involving host traits. To test for infection differences in the three habitat types, the initial GLM included habitat as a predictor variable. The number of parasite groups per individual (Poisson distribution) was the measure of parasite group richness and total parasite rank sum (Poisson distribution) was the measure of parasite abundance. Mountain range was also run in a separate GLM to determine if there were differences in group structure infecting mice across all seven mountain ranges.

To test for effects of host mass, body condition, and sex, GLMMs were used. Group richness and total parasite rank were the response variables for each model. In the mixed effects models, mountain range was treated as a random effect to control for differences among sampling locations (see supplemental Table 2.S.1). Body mass and body condition (scaled mass index) were treated as fixed effects to determine the best predictor of group richness within individual hosts. Separate models were run for body condition and body mass because body mass was used in the calculation of body condition. Pregnant females (n=19) were not included in analyses related to body mass and body condition.

Parasites were split to determine whether there were similar patterns of infection among groups with similar traits. Ectoparasites consisted of three groups: fleas, ticks, and lice. Endoparasites consisted of four groups: nematodes, cestodes, acanthocephalans, and trematodes. Nematodes consisted of species that have intermediate hosts (complex life

cycles) and species that are directly transmitted between hosts (e.g. pinworms). To test for whether life history traits of each parasite group are better predictors of infection, parasite taxonomic groups were analyzed separately using generalized linear models with binomial distributions. Because we are interested in infection throughout a host's life, body mass is used as a proxy for host age (Douglass et al. 2001). Status of infection (binomial distribution) was the response variable and body mass (proxy for age) was the predictor variable in each model. Whether an individual was infected or not was used because I was interested in probability of infection with respect to age. Intensity of each taxonomic group was not used because it was not possible to determine whether each parasite in or on a host was the result of one or multiple infection events.

To test for interactions among parasite groups, generalized linear models with quasi-poisson error distributions were used in order to account for the overdispersed distributions of parasites. Parasite abundance of each parasite group was used for these models because interactions among parasite groups may be dependent on the number of parasites within a host, rather than being infected or not. Five models were created. The five most abundant parasite groups were the response variables (one for each model), with the predictor variables being the other four groups. Because of the low prevalence of both trematode and acanthocephalan infections, they were not included in these analyses. Mixed models were run using the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016) packages in R (R Core Team 2016).

Results

Deer mice (n = 519) were trapped at 19 sites throughout the Great Basin in Utah and Nevada from 2014-2016. Over half (51%) of captured deer mice were co-infected

with at least one individual from two or more parasite groups (Table 2.2). Thirty-three percent of mice were coinfected with two or more ectoparasite groups, while 4% of mice were coinfected with two or more endoparasite groups (Table 2.2).

There was a significant difference in parasite group richness and total parasite rank in individual mice across the seven sampling locations (Table 2.S1). Therefore, in the analyses of parasite group richness in individual hosts, mountain range was used as a random effect in the generalized linear mixed models. The number of parasite groups per individual did not significantly differ across habitat types (Fig. 2.2A, Table 2.3). The total parasite rank of host individuals was significantly higher in pinyon-juniper habitat types than in sagebrush (GLM: $z = 1.798$, $p < 0.001$, Fig. 2.2B, Table 2.3) and ecotone habitat types (GLM: $z = -7.686$, $p < 0.001$, Fig. 2.2B, Table 2.3). To investigate this pattern further, I found that masses were significantly different in the three habitat types (ANOVA, $F = 11.08$, $p < 0.001$; Fig. 2.S1). Masses were significantly higher in mice from pinyon-juniper than in both sagebrush (Tukey post-hoc, $p < 0.001$) and ecotone (Tukey post-hoc, $p < 0.001$) habitat types when all mice were pooled according to habitat type (Fig. 2.S1).

Based on the pelage color of mice, three age classes were used: juvenile, subadult, and adult. The masses of individuals in the three age classes differed significantly (ANOVA, $F = 189.8$, $p < 0.001$; Fig. 2.3A). Therefore, mass was used as a proxy for age. In addition, 19 pregnant mice were excluded from analyses with body mass and body condition. Six other mice were excluded because their masses were not recorded. Therefore, 494 deer mice were used in the analyses for body mass and body condition.

Number of parasite groups infesting individuals increased with body mass

(GLMM: $z = 2.963$, $p = 0.003$; Fig. 2.3B; Table 2.4). Body condition was not correlated with number of parasite groups found in individual mice (GLMM: $z = 0.917$, $p = 0.36$; Fig. 2.3C; Table 2.4). Rank sum of total parasites increased with increasing mass (GLM: $z = 7.932$, $p < 0.001$, Fig. 2.3D, Table 2.5), meaning heavier (and older) individuals had higher parasite loads (total rank sum). In contrast, body condition was not significant in explaining the total rank sum of parasites per individual mouse (GLMM: $z = 0.467$, $p = 0.64$, Table 2.5). Males did not differ from females in group richness (GLMM: $z = 1.623$, $p = 0.11$) or in total rank sum of parasites (GLMM: $z = 1.586$, $p = 0.11$).

Each parasite group was analyzed separately to determine if similar life history traits among parasite groups predict whether heavier, older individuals have a higher probability of being infected with certain groups. Mass was not a significant predictor of either flea (GLM: $z = 0.999$, $p = 0.32$; Fig. 2.4A; Table 2.S2) or louse infection (GLM: $z = -1.633$, $p = 0.10$; Fig. 2.4C; Table 2.S2). However, mass was a significant predictor of tick infection (GLM: $z = 1.956$, $p = 0.051$; Fig. 2.4B; Table 2.S2). In contrast to fleas and lice, infection by the two endoparasite groups was predicted by mass. Mass was a significant predictor of nematode (GLM: $z = 3.939$, $p < 0.001$; Fig. 2.4D; Table 2.S2) and cestode infection (GLM: $z = 2.764$, $p = 0.006$; Fig. 2.4E; Table 2.S2).

There were no significantly positive or negative associations between any two parasite groups (GLM: all p-values > 0.05; Table 2.S3), suggesting that there are no positive or negative interactions among parasite groups based on parasite groups abundances.

Discussion

I tested the hypothesis that infection is independent of host traits and parasite interactions. A community framework allows for testing multiple predictions related to community structure across several scales using the same host-parasite system. Host body mass was positively correlated with parasite group richness and total parasite rank sum in individual deer mice. In both measures of community structure, males did not differ from females. In deer mice, mass is a strong predictor of age (Douglass et al. 2001; Calisher et al. 2007). These results are in contrast to previous studies showing juveniles have higher parasite loads than adults in birds (Allander and Bennett 1994; Dawson and Bortolotti 1999; Sol et al. 2003) and mammals (Michel 1952; Gregory et al. 1992). Results suggest that parasite communities are structured independently of host traits since parasites accumulate in hosts throughout their life. Assembly in which parasites accumulate in larger, older hosts is seen in other systems, including helminths of fish (Poulin and Valtonen 2001). These results also indicate an additive assembly process, which implies unsaturated parasite assemblages (Poulin 2007; Johnson and Hoverman 2012).

Not all parasite groups accumulated in heavier, older hosts. In this system, dispersal is an important process in structuring parasite communities. The four endoparasitic helminth groups include species that are trophically transmitted (Goater et al. 2013). All cestode, acanthocephalan, and trematode species require arthropod intermediate hosts that need to be consumed by definitive hosts to be transmitted (Goater et al. 2013). In this study, deer mice are the definitive hosts (i.e. host in which parasite sexual reproduction occurs). A few nematode species in this system also require arthropod intermediate hosts, although there are some species can be transmitted directly

from host to host, the most prevalent of which are pinworms (*Syphacia peromysci*) (Frandsen 1960; Derrick 1971). Development times of these endoparasitic helminths vary, but can often be greater than two weeks; some species shed eggs for up to a year in rodent hosts depending on conditions and host physiology (Anya 1966; Munger et al. 1989; Lass et al. 2012). As a result, endoparasites are typically associated with their hosts for longer periods of time than ticks and fleas. Because infective stages of helminths need to be ingested, older hosts have had more time to consume arthropods and contaminated material in the environment. However, some helminths can die and not be able to re-infect the same host without the host consuming more infective stages within the environment. Pinworms, on the other hand, are different from other helminths because they can re-establish infections through coprophagy or grooming around the anus. Therefore, lice are most similar to pinworms than to other helminths that can only infect a host through consuming arthropod intermediate hosts or infective stages that are in the environment. In this study, pinworms (*S. peromysci*) had a 7% prevalence, while total nematode prevalence was 28%. Even though the majority of helminths in this system are trophically transmitted, the pattern of helminths accumulating in older hosts was still observed.

Mass may be more important than strictly the age of the host. For example, two mice that are the same age may differ in mass. One host may have eaten more and consumed more infective stages. Disentangling the effects of mass and age would require very precise measurements of host age, such as measuring protein in eye lenses (Dapson and Irland 1972). Regardless of whether these results are caused by mass or age, it suggests that the probability of being infected with helminths increases from juveniles to

subadults to adults (see Fig. 2.4B).

Deer mice often live less than one year in the wild (O'Farrell 1978; Baker 1983), and hosts have a higher probability of having more helminth parasites later in life. Deer mice may not invest heavily in immune responses to helminth infections. If the immune system was important in regulating helminth infection, then adult mice would have fewer helminths than younger hosts, a pattern observed in other systems (Gregory et al. 1992; Allander and Bennett 1994; Dawson and Bortolotti 1999; Sol et al. 2003). Raush and Tiner (1949) suggest that low numbers of helminth parasites do not cause significant harm to their rodent hosts. Investing more in reproduction, foraging, and thermoregulation may outweigh the benefits of reducing parasite infections for this short-lived species (Pedersen and Greives 2008).

The pattern of accumulating parasites as hosts get older was not observed for two ectoparasite groups. It was predicted that lice would show similar patterns to nematodes and cestodes and show a positive correlation with host body mass. Lice are permanent parasites and once they infest a mouse, they can complete their entire life cycle on one host individual. Therefore, lice can maintain infestations indefinitely. Our data were not consistent with this prediction. It appears that lice infect hosts independently of host age, which may be mediated by parasite defense. Mice are known to significantly reduce ectoparasite numbers, including lice, through grooming (Murray 1961; Glicken and Schwab 1980; Murray 1987; Hart 1994) and the immune system (Wikel 1982; Volf 1994).

Even though ticks, like fleas, feed for relatively short amounts of time and can be groomed off hosts (Shaw et al. 2003; Hawlena et al. 2007), heavier, older individuals had

a significantly higher probability of tick infection. In contrast, there was no relationship between flea infection and mass. Both ticks and fleas are similar in their life history characteristics. One explanation for the observed difference is that, while both fleas and ticks can be encountered in the environment while foraging or searching for mates, fleas can also be encountered in nests (Bitam et al. 2010) and may infect mice at younger ages than ticks.

Habitat type was not an important factor influencing parasite group richness, suggesting that, in terms of the habitat types examined, there were no hotspots resulting in higher parasite group richness per individual. Total parasite rank was higher in P-J habitats than in sagebrush and ecotone habitats. This was further investigated, and in P-J habitat types, deer mice weighed significantly more than those in the other two habitat types (see Fig. 2.S1). It is unclear if mice in P-J habitats are eating more and have a higher probability of consuming more infective stages of parasites, or if they live longer than in the other two habitat types (see Appendix C).

Parasite interactions were also not important in structuring parasite communities within individual deer mice. These data suggest parasite infection is independent of parasite interactions (i.e. no competition or facilitation), which is consistent with other systems, such as ectoparasite assembly in fish (Gotelli and Rohde 2002). It also confirms an additive assembly pattern. Whether a deer mouse becomes infested with a particular parasite is more dependent on the age of the mouse rather than being outcompeted or facilitated by the presence or absence of other parasites. The lack of significant within host associations in deer mice makes sense considering the low prevalence of every parasite group (< 30%), except fleas (63%), and the high level of aggregation, which is a

general and consistent observation of parasite populations (Poulin 2007; Goater et al. 2013). Infection by the seven groups may be independent of each other because of the low prevalence of coinfections between most groups. In order to observe significant non-random associations between parasites, a greater sample size may be needed. However, even with 494 deer mice, significant associations were not found.

In conclusion, sex, body condition, and habitat type were not correlated with group richness and total parasite abundance, suggesting that these factors do not influence parasite infection in this system. Older deer mice have higher parasite group richness and higher total parasite abundance than younger mice. This appears to be driven by differences in dispersal among different parasite groups. Infection by parasite taxonomic groups was not consistent with predictions, specifically with ectoparasite groups. Tick infection was significantly correlated with body mass, while lice were not correlated with mass, contrary to predictions. Flea infection was not correlated with age, which was consistent with predictions. Finally, the abundances of parasite taxonomic groups are independent of each other, further suggesting that parasite infection within hosts is cumulative. These results suggest that host age and dispersal differences among taxonomic groups are important in determining parasite community structure in deer mice.

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References

Anya, A. O. 1966. Studies on the biology of some oxyurid nematodes. II. The hatching of eggs and development of *Aspiculuris tetraptera* Schulz, within the host. Journal of Helminthology 40:261-268.

Baker, R. H. 1991. Michigan Mammals. Michigan State University Press. East Lansing, Michigan.

Balestrieri, A., L. Remonti, N. Ferrari, A. Ferrari, T. L. Valvo, S. Robetto, and R. Orusa. 2006. Sarcoptic mange in wild carnivores and its co-occurrence with parasitic helminths in the Western Italian Alps. European Journal of Wildlife Research 52:196-201.

Bates, D., M. Maechler, B. Bolker, S. Walker. 2015. Fitting linear mixed effects models using lme4. Journal of Statistical Software 67:1-48. doi:10.18637/jss.v067.i01.

Bell, G., 2000. The distribution of abundance in neutral communities. The American Naturalist 155:606-617.

Bitam, I., K. Dittmar, P. Parola, M. F. Whiting, and D. Raoult, 2010. Fleas and flea-borne diseases. International Journal of Infectious Diseases 14:667-676.

Blackwell, A. D., M. Martin, H. Kaplan, and M. Gurven. 2013. Antagonism between two intestinal parasites in humans: the importance of co-infection for infection risk and recovery dynamics. Proceedings of the Royal Society of London B: Biological Sciences 280:20131671. doi: 10.1098/rspb.2013.1671

Calisher, C. H., K. D. Wagoner, B. R. Amman, J. J. Root, R. J. Douglass, A. J. Kuenzi, K. D. Abbott, C. Parmenter, T. L. Yates, T. G. Ksiazek, and B. J. Beaty. 2007. Demographic factors associated with prevalence of antibody to Sin Nombre virus in deer mice in the western United States. Journal of Wildlife Diseases 43:1-11.

Cattadori, I. M., B. Boag, and P. J. Hudson. 2008. Parasite co-infection and interaction as drivers of host heterogeneity. International Journal for Parasitology 38:371-380.

Clayton, D. H. 1991. Coevolution of avian grooming and ectoparasite avoidance. Pp.

258-289 in Bird-Parasite Interactions. Oxford University Press; Ornithology Series, 2. Oxford, United Kingdom.

Cox, F. E. G. 2001. Concomitant infections, parasites and immune responses. Parasitology 122:S23-S38.

Dallas, T., and S. J. Presley. 2014. Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. Oikos 123:866-874.

Dawson, R. D., and G. R. Bortolotti. 1999. Prevalence and intensity of hematozoan infections in a population of American kestrels. Canadian Journal of Zoology 77:162-170.

Derrick, P. I. 1971. The concept of "landscape epidemiology" as it applies to endoparasitism of small mammals in selected habitats of South Willow Canyon, Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Diamond, J. M. 1975. Assembly of species communities. Pp. 342-444 in Ecology and Evolution of Communities (M. L. Cody, and J. M. Diamond, eds). Harvard University Press. Boston, Massachusetts.

Douglass, R. J., T. Wilson, W. J. Semmens, S. N. Zanto, C. W. Bond, R. C. Van Horn, and J. N. Mills. 2001. Longitudinal studies of Sin Nombre virus in deer mouse-dominated ecosystems of Montana. The American Journal of Tropical Medicine and Hygiene 65:33-41.

Ezenwa, V. O. 2003. Habitat overlap and gastrointestinal parasitism in sympatric African bovids. Parasitology 126:379-388.

Ezenwa, V. O., and A. E. Jolles. 2011. From host immunity to pathogen invasion: the effects of helminth coinfection on the dynamics of microparasites. Integrative and Comparative Biology 51:540–551.

Ferrari, N., I. M. Cattadori, A. Rizzoli, and P. J. Hudson. 2009. Heligmosomoides polygyrus reduces infestation of Ixodes ricinus in free-living yellow-necked mice, *Apodemus flavicollis.* Parasitology 136:305-316.

Folstad, I., A. C. Nilssen, O. Halvorsen, and J. Andersen. 1991. Parasite avoidance: the cause of post-calving migrations in Rangifer? Canadian Journal of Zoology 69:2423-2429.

Frandsen, J. C. 1960. Endoparasitism in isolated populations of rodents of the Lake Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Gilbert, K. A. 1997. Red howling monkey use of specific defecation sites as a parasite avoidance strategy. Animal Behaviour 54:451-455.

Glicken, A., and R. G. Schwab. 1980. Modes of ectoparasite reinfestations of deer mice (Peromyscus maniculatus). Journal of Wildlife Diseases 16:577-586.

Goater, T. M., C. P. Goater, and G. W. Esch. 2013. Parasitism: The Diversity and Ecology of Animal Parasites. 2nd ed. Cambridge University Press. Cambridge, United Kingdom.

Gotelli, N. J., and K. Rohde. 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. Ecology Letters 5:86-94.

Graham, A. L. 2008. Ecological rules governing helminth–microparasite coinfection. Proceedings of the National Academy of Sciences 105:566-570.

Griffiths, E. C., A. B. Pedersen, A. Fenton, and O. L. Petchey. 2014. Analysis of a summary network of co-infection in humans reveals that parasites interact most via shared resources. Proceedings of the Royal Society of London B: Biological Sciences 281:20132286.

Hart, B. 1994. Behavioural defense against parasites: interaction with parasite invasiveness. Parasitology 109:S139-S151. doi:10.1017/S0031182000085140.

Hartgers, F. C., and M. Yazdanbakhsh. 2006. Co-infection of helminths and malaria: modulation of the immune responses to malaria. Parasite Immunology 28:497-506.

Hawlena, H., D. Bashary, Z. Abramsky, and B. R. Krasnov. 2007. Benefits, costs and constraints of anti-parasitic grooming in adult and juvenile rodents. Ethology 113:394-402.

Holmstad, P. R., P. J. Hudson, and A. Skorping. 2005. The influence of a parasite community on the dynamics of a host population: a longitudinal study on willow ptarmigan and their parasites. Oikos 111:377-391.

Holmstad, P. R., K. H. Jensen, and A. Skorping. 2008. Ectoparasite intensities are correlated with endoparasite infection loads in willow ptarmigan. Oikos 117:515-520.

Houde, A. E., and A. J. Torio. 1992. Effect of parasitic infection on male color pattern and female choice in guppies. Behavioral Ecology 3:346-351.

Johnson, P. T., J. C. De Roode, and A. Fenton. 2015. Why infectious disease research needs community ecology. Science 349:1259504.

Johnson, P. T., and J. T. Hoverman. 2012. Parasite diversity and coinfection determine pathogen infection success and host fitness. Proceedings of the National Academy of Sciences 109:9006-9011.

Kamath, P. L., W. C. Turner, M. Küsters, and W. M. Getz. 2014. Parasite-mediated selection drives an immunogenetic trade-off in plains zebras (*Equus quagga*). Proceedings of the Royal Society of London B: Biological Sciences 281:20140077.

Karvonen, A., O. Seppälä, and E. T. Valtonen, 2004. Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. Parasitology 129:159-164.

Krasnov, B. R. 2008. Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology. Cambridge University Press. Cambridge, United Kingdom.

Krasnov, B. R., M. Sarfati, M. S. Arakelyan, I. S. Khokhlova, N. V. Burdelova, and A. A. Degen. 2003. Host specificity and foraging efficiency in blood-sucking parasite: feeding patterns of the flea *Parapulex chephrenis* on two species of desert rodents. Parasitology Research 90:393-399.

Krichbaum, K., S. Perkins, and M. R. Gannon. 2009. Host-parasite interactions of tropical bats in Puerto Rico. Acta Chiropterologica 11:157-162.

Kuznetsova, A., P. B. Brockhoff, R. H. B. Christensen. 2016. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33. https://CRAN.R-project.org/package=lmerTest.

Lass, S., P. J. Hudson, J. Thakar, J. Saric, E. Harvill, R. Albert, and S. E. Perkins. 2012. Generating super-shedders: coinfection increases bacterial load and egg production of a gastrointestinal helminth. Journal of the Royal Society Interface 10:20120588; PMID: 23256186.

Lello, J., B. Boag, A. Fenton, I. R. Stevenson, and P. J. Hudson. 2004. Competition and mutualism among the gut helminths of a mammalian host. Nature, 428, 840-844. doi:10.1038/nature02490.

MacArthur, R.H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York City, New York.

Michel, J. F. 1952. Self-cure in infections of Trichostrongylus retortaeformis and its causation. Nature, 169.

Munger, J. C., W. H. Karasov, and D. Chang. 1989. Host genetics as a cause of overdispersion of parasites among hosts: how general a phenomenon? The Journal of Parasitology 75:707-710.

Murray M. D. 1961. The ecology of the louse *Polyplax serrataq* (Burn.) on the Mouse Mus musculus L. Australian Journal of Zoology 9:1-13.

Murray, M. D. 1987. Effects of host grooming on louse populations. Parasitology Today 3:276-278.

Paull, S. H., S. Song, K. M. McClure, L. C. Sackett, A. M. Kilpatrick, and P. T Johnson. 2012. From superspreaders to disease hotspots: linking transmission across hosts and space. Frontiers in Ecology and the Environment 10:75-82.

Pedersen, A. B., and A. Fenton. 2007. Emphasizing the ecology in parasite community ecology. Trends in Ecology and Evolution 22:133-139.

Pedersen, A. B., and T. J. Greives. 2008. The interaction of parasites and resources cause crashes in a wild mouse population. Journal of Animal Ecology 77:370–377.

Penn, D., and W. K. Potts. 1998. Chemical signals and parasite-mediated sexual selection. Trends in Ecology and Evolution 13:391-396.

Piesman, J., T. N. Mather, R. J. Sinsky, and A. Spielman. 1987. Duration of tick attachment and *Borrelia burgdorferi* transmission. Journal of Clinical Microbiology 25:557-558.

Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883-1891.

Poulin, R., and E. T. Valtonen. 2001. Nested assemblages resulting from host size variation: the case of endoparasite communities in fish hosts. International Journal for Parasitology 31:1194-1204.

Poulin, R. 2007. Evolutionary Ecology of Parasites. 2nd ed. Princeton University Press. Princeton, New Jersey.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rynkiewicz, E. C., A. B. Pedersen, and A. Fenton. 2015. An ecosystem approach to understanding and managing within-host parasite community dynamics. Trends in Parasitology 31:212-221.

Schmid-Hempel, P. 2011. Evolutionary Parasitology: The Integrated Study of Infections, Immunology. Ecology and Genetics. Oxford University Press. Oxford, United Kingdom.

Shaw, M. T., F. Keesing, R. McGrail, and R. S. Ostfeld. 2003. Factors influencing the distribution of larval blacklegged ticks on rodent hosts. The American Journal of Tropical Medicine and Hygiene 68:447-452.

Tella, J. L., M. G. Forero, M. Bertellotti, J. A. Donázar, G. Blanco, and O. Ceballos. 2001. Offspring body condition and immunocompetence are negatively affected by high breeding densities in a colonial seabird: a multiscale approach. Proceedings of the Royal Society of London B: Biological Sciences 268:1455-1461.

Telfer, S., X. Lambin, R. Birtles, P. Beldomenico, S. Burthe, S. Paterson, and M. Begon. 2010. Species interactions in a parasite community drive infection risk in a wildlife population. Science 330:243-246.

Volf, P. 1994. Localization of the major immunogen and other glycoproteins of the louse *Polyplax spinulosa.* International Journal for Parasitology 24:1005-1010.

Warburton, E., C. Pearl, and M. Vonhof. 2016. Relationships between host body condition and immunocompetence, not host sex, best predict parasite burden in a bat-helminth system. Parasitology Research 115:2155–2164.

Wikel, S. K. 1982. Immune responses to arthropods and their products. Annual Review of Entomology 27:21-48.

Wolinska, J., and K. C. King. 2009. Environment can alter selection in host–parasite interactions. Trends in Parasitology 25:236-244.

Zuk, M., and K. A. McKean. 1996. Sex differences in parasite infections: patterns and processes. International Journal for Parasitology 26:1009-1024.

Table 2.1. Life history traits of the seven taxonomic groups of parasites. In the column of time spent with host, short (S) refers to parasites that are associated with their hosts for up to several days or feed intermittently. Long (L) refers to parasites being associated with their hosts for long period of time (several weeks to months).

Group	Free-living stage off the host	Transmitted through ingestion	Time spent with host	Permanent parasite
Fleas	X		S	
Ticks	X		S	
Lice			L	X
Nematodes		X	L	
Cestodes		X	L	
Acanthocephalans		X	L	
Trematodes		X	L	

Table 2.2. The prevalence and mean intensity (± se) of ectoparasites and endoparasites found in 525 deer mice. The prevalence of coinfections is also shown.

	Prevalence	Mean intensity ± se
Ectoparasites		
Fleas	0.63	2.99 ± 0.15
Ticks	0.29	4.94 ± 0.20
Lice	0.28	6.08 ± 0.99
Ectoparasite group coinfections	0.33	NA
Endoparasites		
Nematodes	0.28	16.39 ± 3.45
Cestodes	0.09	2.16 ± 0.49
Trematodes	0.008	2.75 ± 1.18
Acanthocephalans	0.025	4.15 + 1.72
Endoparasite group coinfections	0.04	NA
*All coinfections**	0.51	NA

* Animals coinfected with individuals from at least two different parasite groups

Table 2.3. Summary of GLMs for parasite group richness with a Poisson distribution (A) and total parasite rank sum (B) for the different habitat types.

(A) Generalized linear model with a Poisson distribution for parasite group richness and the different habitat types. Intercept is set at ecotone.				
	estimate	*standard error*	*z-value*	*p-value*
Intercept	-0.102	0.171	-0.598	0.55
Sagebrush	0.021	0.265	0.078	0.94
Pinyon-juniper	0.311	0.215	1.447	0.15
(B) Generalized linear model with a Poisson distribution for total parasite rank sum and the different habitat types. Intercept is set at ecotone.				
	estimate	*standard error*	*z-value*	*p-value*
Intercept	1.72	0.036	47.974	< 0.001*
Sagebrush	0.097	0.054	1.798	< 0.001*
Pinyon-juniper	0.32	0.043	7.686	0.07

* p-value significant at 0.05

Table 2.4. Summary of GLMMs for parasite group richness with poisson distribution for 494 mice over seven sampling locations. Separate models were run for body mass (A) and body condition (B).

(A) Generalized linear mixed model for parasite group richness and body mass with intercept is set at mean mouse mass.				
Random effect	*variance*	*standard deviation*		
Mountain range	0.014	0.118		
Fixed effect	*estimate*	*standard error*	*z-value*	*p-value*
Intercept	0.432	0.067	6.482	<0.001*
Mass (g)	0.030	0.010	3.113	0.001*
(B) Generalized linear mixed model for parasite group richness and body condition with intercept is set at mean mouse body condition.				
Random effect	*variance*	*standard deviation*		
Mountain range	0.018	0.133		
Fixed effect	*estimate*	*standard error*	*z-value*	*p-value*
Intercept	0.455	0.070	6.500	< 0.001*
Body condition	0.016	0.015	1.087	0.28

* p-value significant at 0.05

Table 2.5. Summary for GLMMs for total parasite rank sum with Poisson distribution for 494 mice over seven sampling locations for body mass (A), body condition (B)

(A) Generalized linear mixed model for total parasite rank sum with poisson distribution and intercept set at mean body mass.				
Random effect	*variance*	*standard deviation*		
Mountain range	0.221	0.470		
Fixed effect	*estimate*	*standard error*	*z-value*	*p-value*
Intercept	2.031	0.179	11.32	< 0.001*
Mass (g)	0.017	0.005	3.46	< 0.001*

(B) Generalized linear mixed model for total parasite rank sum with poisson distribution and intercept set at mean body condition.				
Random effect	*variance*	*standard deviation*		
Mountain range	0.231	0.480		
Fixed effect	*estimate*	*standard error*	*z-value*	*p-value*
Intercept	2.039	0.183	11.132	< 0.001*
Body condition	-0.001	0.007	-0.078	0.94

* p-value significant at 0.05

Table 2.S1. Summary of GLMs for parasite group richness with a Poisson distribution (A) and total parasite rank sum with a Poisson distribution (B) for the seven sampling locations.

(A) Generalized linear model with a Poisson distribution for parasite group richness and the seven sampling locations. Intercept is set at the Cedar Mountains.				
	estimate	*standard error*	*z-value*	*p-value*
Intercept	-0.916	0.374	-2.449	0.014*
Stansbury Mountains	1.318	0.398	3.308	<0.001*
Oquirrh Mountains	0.660	0.409	1.613	0.11
San Francisco Mountains	2.303	0.746	3.086	0.002*
Dolly Varden Mountains	1.253	0.558	2.245	0.025*
Toano Range	0.654	0.563	1.162	0.25
Pilot Range	1.179	0.563	2.094	0.036*
(B) Generalized linear model with a Poisson distribution for total parasite rank sum and the seven sampling locations. Intercept is set at the Cedar Mountains.				
	estimate	*standard error*	*z-value*	*p-value*
Intercept	0.082	0.162	0.507	0.612
Stansbury Mountains	0.496	0.170	2.924	0.003*
Oquirrh Mountains	0.251	0.176	1.425	0.15
San Francisco Mountains	0.675	0.240	2.815	0.005*
Dolly Varden Mountains	0.477	0.224	2.132	0.033*
Toano Range	0.337	0.234	1.441	0.15
Pilot Range	0.366	0.233	1.573	0.12

* p-value significant at 0.05

Table 2.S2. Summary for generalized linear models for fleas (A), ticks (B), lice (C), nematodes (D), and cestodes (E) separately with binomial distributions for 494 mice over seven sampling locations.

(A) Generalized linear model for tick infection with binomial distribution and intercept set at mean mouse mass.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	-0.879	0.100	-8.823	< 0.001*
Mass (g)	0.053	0.027	1.956	0.051*
(B) Generalized linear model for flea infection with binomial distribution and intercept set at mean mouse mass.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	0.535	0.094	5.703	< 0.001*
Mass (g)	0.025	0.025	0.999	0.32
(C) Generalized linear model for louse infection with binomial distribution and intercept set at mean mouse mass.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	-0.922	0.101	-9.161	< 0.001*
Mass (g)	-0.044	0.0268	-1.633	0.10
(D) Generalized linear model for nematode infection with binomial distribution and intercept set at mean mouse mass.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	-0.916	0.102	-8.978	< 0.001*
Mass (g)	0.111	0.0281	3.939	<0.001*
(E) Generalized linear model for cestode infection with binomial distribution and intercept set at mean mouse mass.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	-2.621	0.186	-14.099	< 0.001*
Mass (g)	0.133	0.048	2.764	0.006*

* p-value significant at 0.05

Table 2.S3. Summary for generalized linear models for parasite associations with quasi-Poisson distribution for 494 observations over seven sampling locations.

Generalized linear model for flea abundance with quasi-Poisson distribution.

	estimate	*standard error*	*t-value*	*p-value*
Intercept	0.651	0.070	9.342	< 0.001*
Tick	0.004	0.0142	0.285	0.78
Lice	-0.006	0.011	-0.589	0.56
Nematodes	-0.004	0.004	-1.109	0.27
Cestodes	0.044	0.101	0.438	0.66

Generalized linear model for tick abundance with quasi-Poisson distribution.

	estimate	*standard error*	*t-value*	*p-value*
Intercept	0.333	0.166	2.001	0.046*
Fleas	0.013	0.147	0.273	0.76
Lice	0.005	0.015	0.343	0.73
Nematodes	0.002	0.004	0.476	0.63
Cestodes	0.124	0.175	0.705	0.48

Generalized linear model for louse abundance with quasi-Poisson distribution.

	estimate	*standard error*	*t-value*	*p-value*
Intercept	0.661	0.228	2.899	0.0039*
Fleas	-0.048	0.078	-0.622	0.53
Ticks	0.016	0.037	0.436	0.66
Nematodes	0.004	0.005	0.811	0.42
Cestodes	-1.106	1.082	-1.022	0.31

Table 2.S3 continued.

Generalized linear model for nematode abundance with quasi-Poisson distribution.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	1.767	0.272	6.505	< 0.001*
Fleas	-0.142	0.117	-1.219	0.22
Ticks	0.024	0.040	0.598	0.55
Lice	0.014	0.017	0.821	0.41
Cestodes	-0.845	1.072	-0.788	0.43
Generalized linear model for cestode abundance with quasi-Poisson distribution.				
	estimate	*standard error*	*t-value*	*p-value*
Intercept	-2.031	0.276	-7.365	< 0.001*
Fleas	0.035	0.069	0.510	0.61
Ticks	0.033	0.037	0.878	0.38
Lice	-0.269	0.200	-1.342	0.18
Nematodes	-0.031	0.042	-0.721	0.47

* p-value significant at 0.05

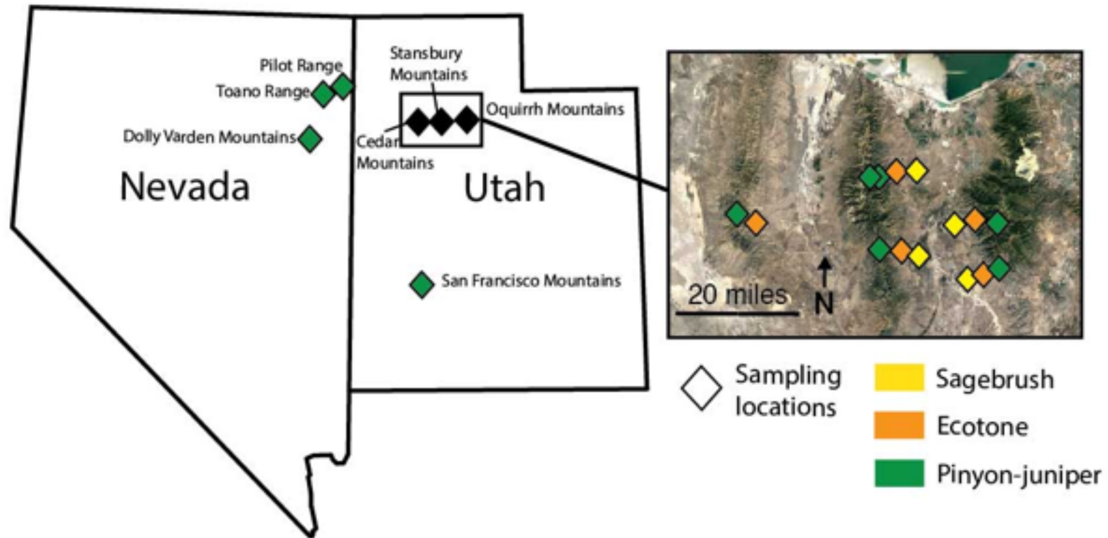

Figure 2.1. Map of sampling sites in Utah and Nevada. Diamonds represent mountain ranges (locations) that were sampled. Inset: The Cedar Mountains were sampled at two sites (ecotone and P-J habitat types). The Stansbury Mountains and Oquirrh Mountains each consisted of two locations, and each location was sampled at three habitat types (sagebrush, ecotone, and P-J).

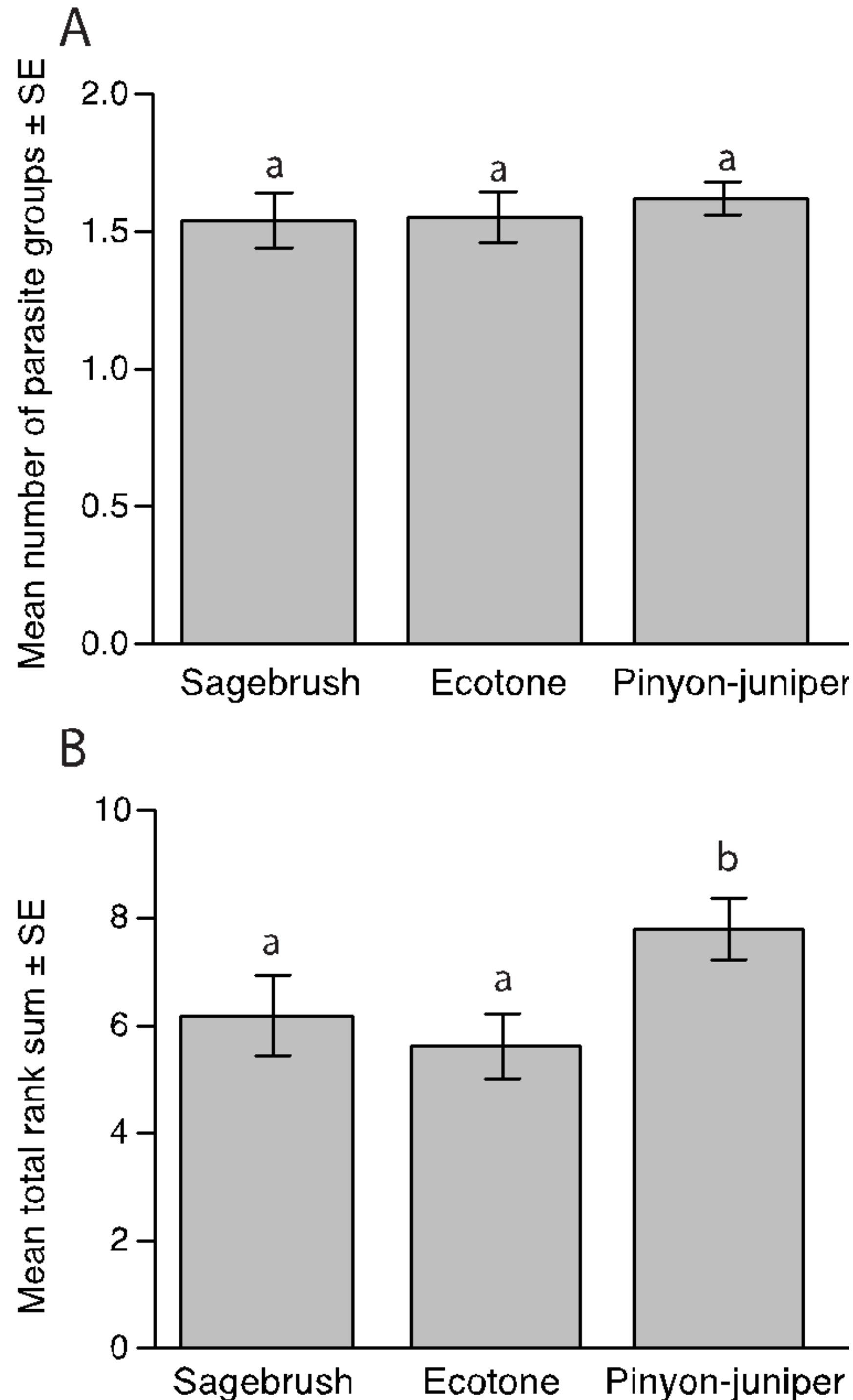

Figure 2.2. Number of parasite groups and parasite rank sum for the different habitat types. A) Mean number of parasite groups per mouse in the three habitat types. The three habitats did not significantly differ. B) Mean total parasite rank sum per mouse for each habitat type. Different letters indicate significant differences between habitat types. Mice in pinyon-juniper had significantly more parasites than mice from sagebrush and ecotone habitats.

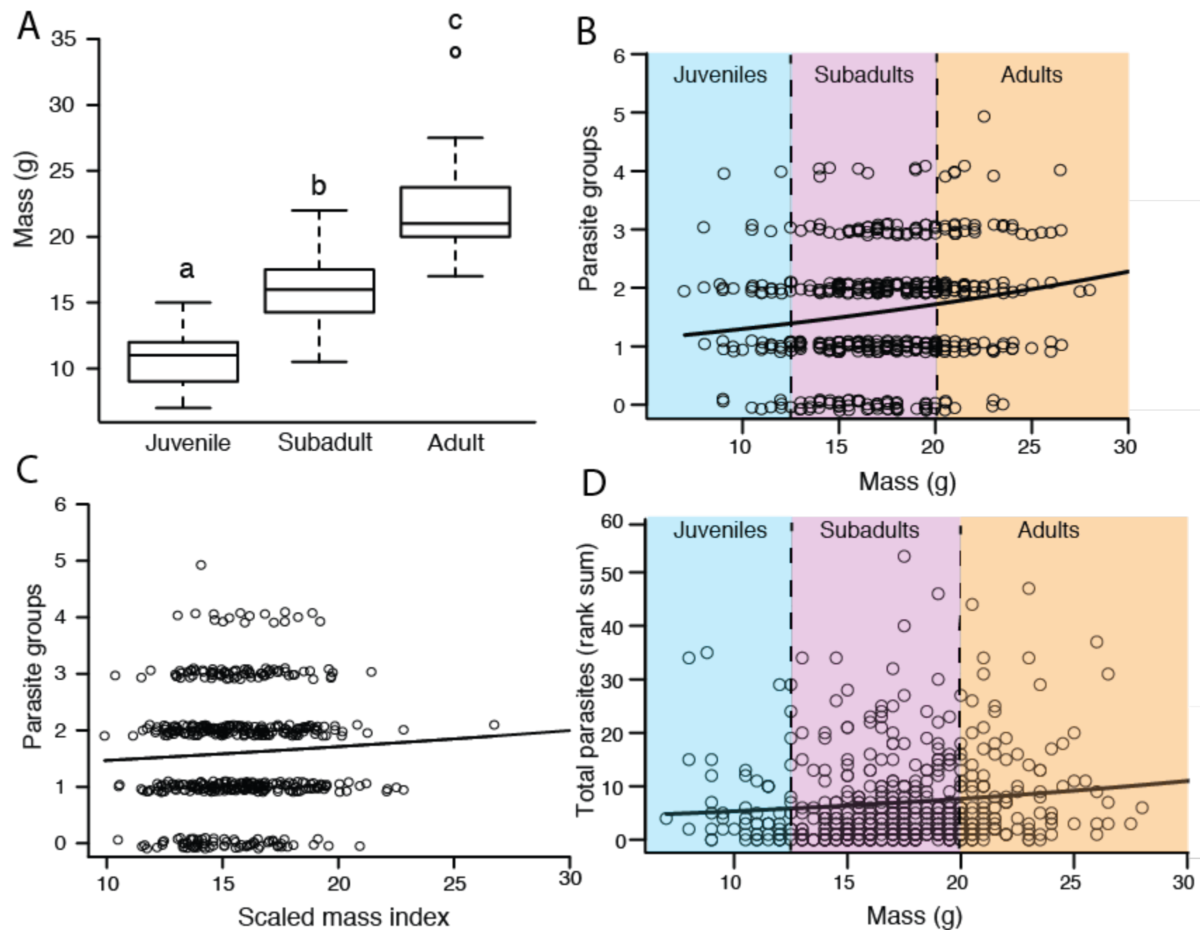

Figure 2.3. Mass and body condition of deer mice and their relationship to the number of parasite groups and total parasite rank sum. A) Three age classes (juvenile, subadult, and adult) of deer mice (*Peromyscus maniculatus*) and the associated masses of individuals within those classes. N=40 for each class. Age classes of mice were based on pelage color after capture in the field. Different letters indicate significant differences. B) The number of parasite groups within each individual mouse and the associated mass of that mouse. Age class delineations were based on masses in A. There was a significant positive correlation between number of parasite groups and mouse mass (GLMM: $z = 3.113$, $p = 0.001$). C) Number of parasite groups and associated body condition of each mouse. There was no significant correlation between number of groups and body condition (GLMM: $z = 1.087$, $p = 0.28$). D) Total parasite rank sum index (abundance) and the relationship to body mass. Total parasite abundance was significantly correlated with body mass (GLM: $z = 7.932$, $p < 0.001$). The data are jittered in B and C along the y-axis to see more of the data.

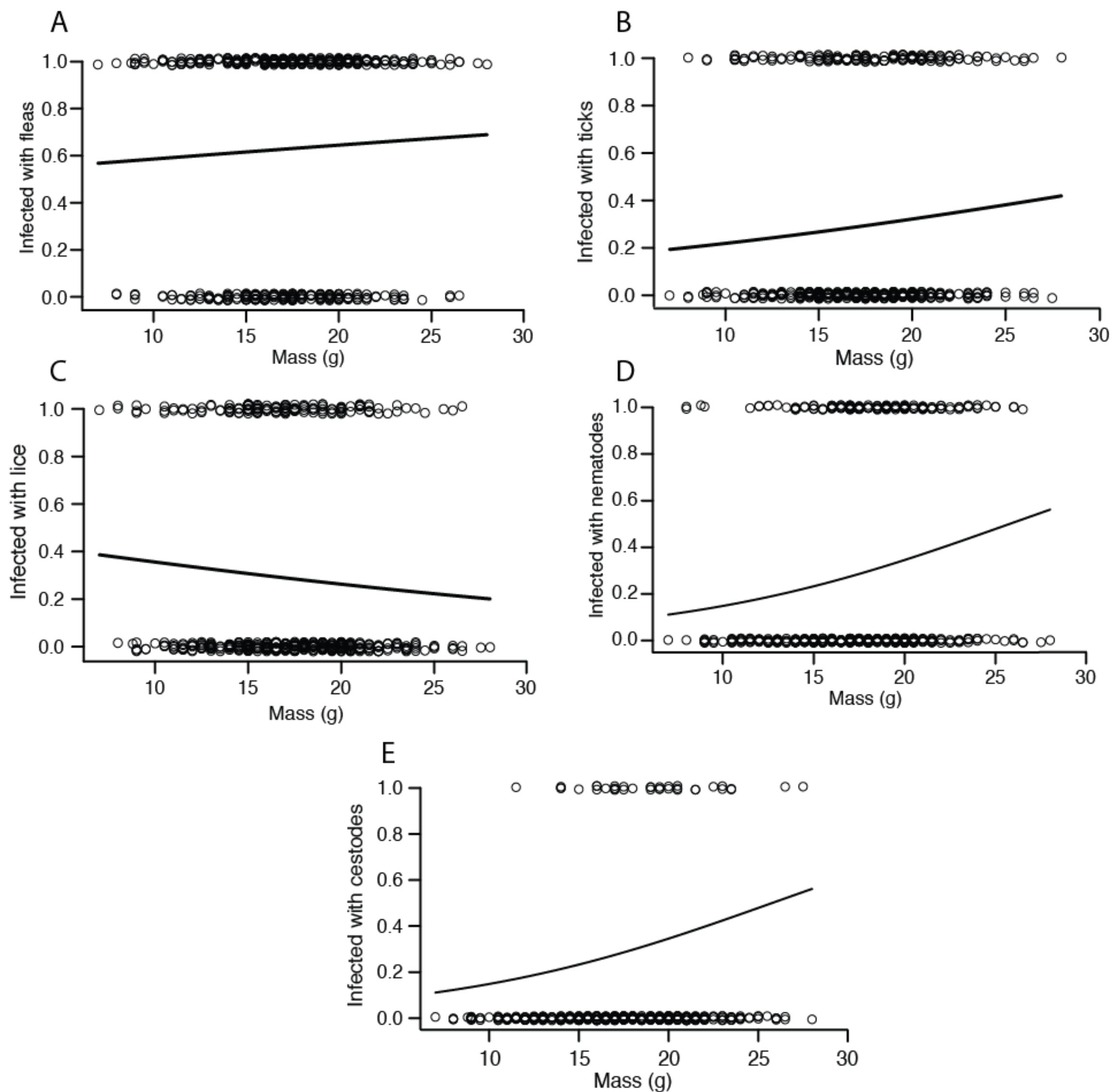

Figure 2.4. The relationships between mouse mass and the infection status (infected/not infected) for fleas (A), ticks (B), lice (C), nematodes (D), and cestodes (E). Tick, nematode, and cestode infection were significantly correlated with mouse mass. The data are jittered along the y-axis to see more of the data.

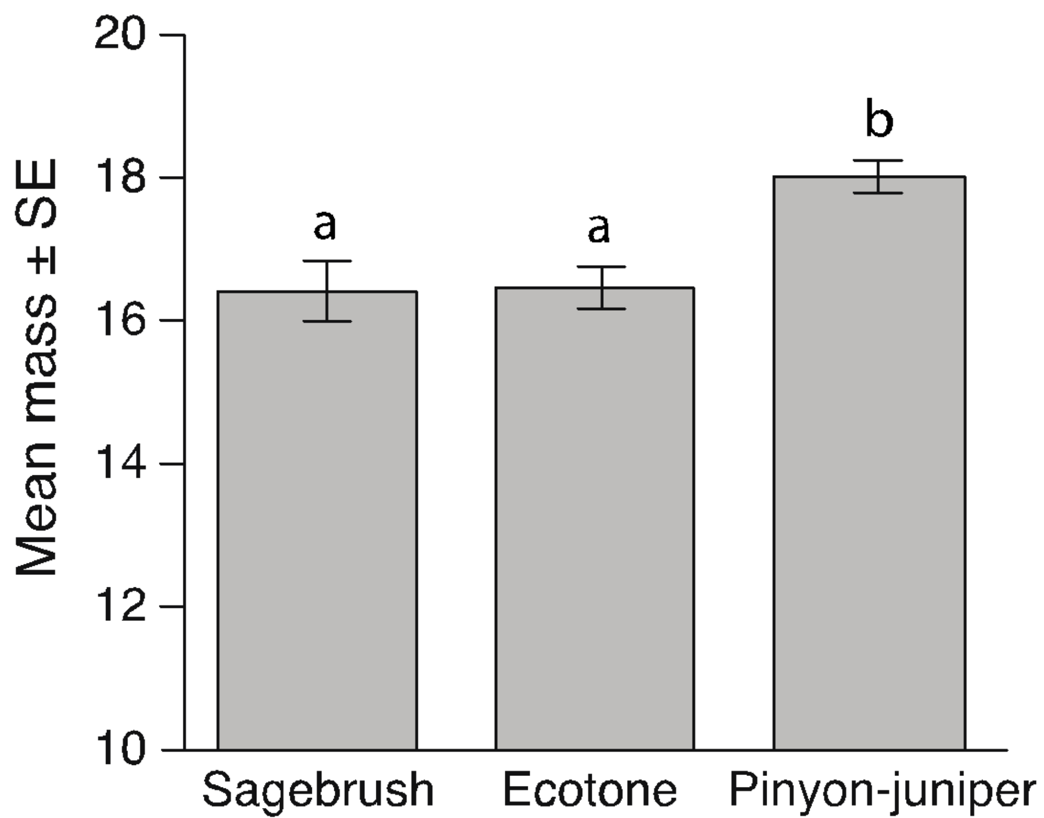

Figure 2.S1. Mean mass of mice in the three habitat types. Different letters indicate significant differences. Mice in pinyon-juniper had significantly higher masses than in sagebrush and ecotone habitat types.

CHAPTER 3

HISTOLOGICAL SURVEY OF DISEASES AND PARASITES OF WILD RODENTS IN THE GREAT BASIN

Abstract

Wild animals have diseases caused by both infectious and non-infectious agents. In wild populations, non-infectious diseases are typically less understood than transmission dynamics of parasites and pathogens (e.g. helminthes, bacteria, viruses). However, non-infectious diseases can reduce host fitness and can also affect a host's ability to deal with infectious disease. Consequences of multiple infections within a host are beginning to receive attention because of the combined effects on host recovery, susceptibility, and fitness. Here, histology is used to survey tissues of rodents in the Great Basin to document baseline levels of pathology caused by both infectious and non-infectious agents. This method was also used to determine if parasites are being overlooked during routine parasitological surveys of rodents. Ten species of rodents were trapped and euthanized at five sites in Utah and Nevada. Liver, lung, heart, and kidney tissues were examined using histology. Results show that only two pathogenic diseases were found: hepatic capillariasis caused by the nematode *Capillaria hepatica* and adiaspiromycosis caused by the fungus *Emmonsia crescens*. These diseases were rare. Thirty-one percent of rodents were found to have diseases that were either non-infectious in origin or had unknown causes (e.g. inflammation). The most common disease was

extramedullary hematopoiesis (11%).

Introduction

Wild animals often have disease, whether caused by infectious agents (e.g. parasites and pathogens), non-infectious agents (e.g. environmental contaminants and toxins), or factors related to animal physiology (e.g. genetic defects and nutrition) (Daszak et al. 2000; Wobeser 2006). The most widely studied diseases in wild populations, infectious diseases, reduce the fitness of their hosts (Moller et al. 1990; Hudson et al. 2002; Knowles et al. 2013) and are involved in structuring ecological communities (Dobson and Hudson 1986; Hudson et al. 2002). Diseases have implications for conservation as well as for humans, such as the increased emergence of zoonotic diseases (McNamara 2015) and diseases threatening livestock (Bennett 2003).

Recent work has focused on the importance of studying entire parasite and pathogen communities, instead of focusing on one or two species in isolation (Pedersen and Fenton 2006; Ferrari et al. 2009; Telfer et al. 2011). Interactions among parasites and pathogens affect transmission, disease severity, disease recovery, and susceptibility to other parasites and pathogens (Ferrari et al. 2009; Telfer et al. 2011). However, non-infectious diseases can influence the ability of an animal to deal with infectious disease and can alone act to reduce host fitness (Dmowski et al. 1998; Wobeser 2006; Acevedo-Whitehouse and Duffus 2009; Tete et al. 2014). Non-infectious diseases are important to consider under the framework of parasite community ecology.

Several factors are known to cause non-infectious disease in animals, including poor nutrition, environmental change, and environmental contaminants (Wobeser 2006; Acevedo-Whitehouse and Duffus 2009). For example, contaminants from zinc smelters

cause significant disease in wild bank voles and wood mice that live near them (Dmowski et al. 1998; Tete et al. 2014). Moreover, mercury (Dietz et al. 1996; Renzoni et al. 1998; Wadaan 2006) and lead (Fair and Myers 2002; Beier et al. 2013; Tete et al. 2014) are known to cause various states of disease in marine and terrestrial animals. Various states of disease can occur from tissue pathology to declines in general body condition (Van Saun 2005; Beldomenico and Begon 2009). For example, lead poisoning in birds causes anemia, paralysis, and histopathological lesions, including tissue necrosis, kidney degeneration, and encephalopathy (Golden et al. 2016). Mercury is known to cause severe liver and kidney damage in mammals, birds, and fish (Mela et al. 2007; Dardouri et al. 2016; López-Islas et al. 2017).

To understand these interactions, and to understand how they may change over time, a baseline knowledge of infectious and non-infectious disease is needed in a study system that allows for large sample sizes from a variety of habitat types. Baseline data on disease can be used to assess changes to environmental conditions (Dietz et al. 1996; Plowright et al. 2008). Without sufficient baseline data for comparison, finding causes of disease and assessing the success of control efforts may not be achievable (Plowright et al. 2008; Artois et al. 2009). In addition, emerging diseases in wild populations cannot be properly identified without information on whether certain diseases have, in fact, increased in prevalence (Artois et al. 2009). In this study, rodents are sampled in the Great Basin.

Histology is the technique of examining tissues microscopically to identify disease at the cellular and tissue level. Thin slices of tissues are stained to visualize cellular components and then examined under a microscope. Histology is often used to

document diseases of both infectious and non-infectious origin in humans or domestic animals (e.g. inflammation, tissue damage, chronic disease, cancer) (Kierszenbaum and Tres 2012). This technique can also detect parasites and pathogens in tissues that are not easily dissected, such as lung, liver, and kidney tissue. Histology has long been used to find parasite stages too small to see during dissection like helminth eggs and larvae, especially in veterinary medicine (Gardiner and Poynton 1999). Helminths can be identified to species based on morphology of the parasite within tissues (Gardiner and Poynton 1999). Histology is a useful tool, both to diagnose pathology and to find parasites in animal tissues.

The goal of the present study is to survey wild rodents for diseases caused by both infectious and non-infectious agents in the Great Basin using histology. Another goal of this study is to determine if there are parasites and pathogens that are being missed by standard parasitological dissections of rodents in the Great Basin. Here, the terms disease and pathology are used interchangeably to refer to a disease state in an animal whether or not that disease is caused by a parasite, pathogen, or by non-infectious sources. The focus of this study is to examine and survey heart, liver, lung, and kidney tissues.

Materials and methods

Rodents trapping

Rodents were trapped in the Great Basin of Utah and Nevada from May 2014 through September 2014. Rodents were captured at five sites (Fig. 3.1). Three sites were located in Nevada and two were located in Utah. Each site was dominated by pinyon-juniper woodland. The San Francisco Mountain site in southern Utah was half pinyon-juniper, half mountain mahogany (*Cercocarpus* spp.). Rodents were live-trapped using

Sherman traps (H.B. Sherman Traps, Inc.). Traps were placed in straight line transects five to ten meters apart. Twenty-five traps were placed in each transect. Some sites required two or three transects to capture the target number of deer mice. Traps were baited with whole oats and bird seed. Traps were placed under logs, by sagebrush plants, and under juniper trees. Traps were set in the evening and checked the following morning. Traps were also checked one to two times during the day for diurnal species (*Tamias* spp. and *Microtus* spp.). Once captured, each animal was euthanized using isoflurane and identified to species. Rodent identifications were confirmed by E.A. Rickart (Natural History Museum of Utah). All individuals regardless of age class were kept. Trapping stopped once 25 deer mice (*Peromyscus maniculatus*) were captured and euthanized. Rodent species other than *P. maniculatus* were also kept and processed. All animal handling and processing was approved by the Institutional Animal Care and Use Committee of the University of Utah.

Rodent processing

Most animals were processed in the field. Animals were sexed, weighed, and standard museum measurements were taken (body length, tail length, ear length, and leg length). The abdominal cavity of each animal was cut open using scissors. The organs, including the heart, lungs, kidneys, and liver, were removed and placed in either 10% neutral-buffered formalin or 95% ethanol before being processed for histology. Formalin is the standard method for preserving (fixing) organs for histology. Placing organs in 95% ethanol also preserves them for histology. Ethanol has the added advantage of preserving samples so that they can be used for the identification of parasites using molecular methods. This is important if parasites are not able to be identified by

morphology (D. Gardiner, personal communication). Animals not dissected in the field were placed on ice and brought back to the lab. Their organs were processed the same day they were captured. After processing, animals were deposited at the Natural History Museum of Utah in Salt Lake City, UT.

Histology and diagnosis

In the lab, the fixed organs (liver, lungs, heart, and kidneys) were removed from either the formalin or ethanol solution. In some cases, the adrenal glands were still attached to the kidneys and also examined, as described below. Each organ was cut into thin slices (about the width of a nickel) using a scalpel and placed in plastic cassettes. The following procedures were performed at a veterinary pathology clinic (Animal Reference Pathology, Salt Lake City, UT). All the organs for a single individual rodent were in one cassette. Tissues were processed as follows. Tissues were dehydrated to remove most of the water. Tissues were added to a series of ethanol solutions as follows: 70% ethanol for 15 minutes, 90% ethanol for 15 minutes, 100% ethanol for 15 minutes, 100% ethanol for 15 minutes, 100 % ethanol for 30 minutes, and a final 45 minutes in 100% ethanol.

After the water was removed, the ethanol was “cleared” by placing tissues in a series of xylene solutions. They were placed in xylene for 20 minutes, removed, and placed in xylene for another 20 minutes. Tissues were removed and placed in xylene for another 45 minutes. Tissues were then removed from the final xylene solution and infiltrated with paraffin wax to completely replace the xylene. The tissues were placed in wax for 30 minutes, followed by another 30 minutes, followed by 45 minutes, changing the wax in between baths.

Once tissues were infiltrated with wax, the entire cassette was then embedded (blocked out) in paraffin wax by placing the cassette in a mold. The block was left to harden. The embedded organs were then cut with a microtome and placed on glass slides. All the organs for a single individual were in one block of wax and were on one slide.

Slides were stained with hematoxylin and eosin to visualize cellular components during histological evaluation. The standard protocol for this staining method was followed (Fischer et al. 2008). Tissues were examined for evidence of pathology caused either by parasites, pathogens, or non-infectious agents. Each pathology found was identified and described. Parasites and pathogens found were identified to species. Tissue examination and identification of any pathology was performed by a veterinary pathologist (Dr. David Gardiner, Animal Reference Pathology, Salt Lake City, UT).

Results

Rodent sampling

We trapped 143 rodents belonging to ten species in five locations in Utah and Nevada (Table 3.1; Fig. 3.1) from a combined total of 889 trap nights. The most abundant rodent species caught was the deer mouse *Peromyscus maniculatus* (n=116), and was the only species trapped at all five locations. Twenty-five deer mice were captured in four out of the five locations. Only 16 deer mice were captured in the San Francisco Mountains in southern Utah (Fig. 3.1). Other species trapped included *P. truei* (n=10), *Perognathus parvus* (n=2), *Tamias dorsalis* (n=8), *T. minimus* (n=1), *Neotoma lepida* (n=1), *N. cinerea* (n=1), *Lemmiscus curtatus* (n=2), *Microtus montanus* (n=1), and *M. longicaudus* (n=1).

Histology results

Thirty-one percent (44/143) of all the rodents surveyed had at least one disease found using histology. Twenty-eight percent (33/116) of deer mice (*P. maniculatus*) had at least one disease, and only four animals had more than one type of disease. The diseases found using histology varied among rodent species (Table 3.1). Only two diseases were found that were caused directly by parasites and pathogens using histology and these pathogens were identified to species. The eggs of the nematode species *Capillaria hepatica* were found in one deer mouse causing hepatic capillariasis (Table 3.1, Fig. 3.2B). Four individuals were infected with the pathogenic fungus *Emmonsia crescens*, resulting in adiaspiromycosis (Table 3.1, Fig. 3.2A). The fungus was found in two *Peromyscus maniculatus* hosts, one *Microtus montana,* and one *M. longicaudus*. Three of these rodents were from the Stansbury Mountains.

Other diseases found in rodents were all diseases for which either the causative agent was unknown or was a non-infective pathology (Table 3.1). Pathology was found in the lungs, liver, and kidneys. The only organ to show no pathology was the heart. Forty-eight individuals had their adrenal glands examined as well, with only one deer mouse (2%) showing an abnormality. Pathologies ranged from mild mineralization in the liver to mild chronic inflammation in the kidneys. The most prevalent pathology was extramedullary hematopoiesis (EMH) (12%) followed by hyperplastic bronchial associated lymphoid tissue (BALT) (6%, Table 3.1; Fig. 3.3). All the diseases listed in Table 3.1 as unknown could be caused by pathogens or caused by something non-infectious. These pathologies could be caused by bacterial infections or by some other underlying cause, such as injury to the tissue or environmental contaminants.

Discussion

Wild rodents were surveyed for disease in the Great Basin using histology. The survey yielded several pathologies in rodents, some caused by pathogens, while others were non-infectious. The causes of several diseases were not able to be determined based on histology. Only one individual out of 143 rodents captured had a disease known to be caused by a parasite. The eggs of the helminth *Capillaria hepatica* were found in the liver of one deer mouse (*P. maniculatus*). This species of nematode is typically found in the liver of their hosts but is generally not found in deer mice in the Great Basin (Frandsen and Grundmann 1961; Grundmann et al. 1976).

Peromyscus maniculatus is a host of *C. hepatica*, but seems to be much more prevalent in other parts of it range (Freeman and Wright 1960; Solomon and Handley 1971; Meagher 1999). The larvae are ingested and immediately migrate to the liver where they become adults and lay eggs throughout the liver (Wright 1961; Ceruti et al. 2001). Without histology of the liver, *C. hepatica* eggs would have been missed. Whether *C. hepatica* eggs are typically found throughout the entire liver or just a small section should be further investigated. It is unclear if these eggs would have been seen if the right tissue section was not examined. Results suggest that during routine parasitological surveys of rodents in the Great Basin, helminths are not being missed in heart, lung, or kidney tissue at least in deer mice, the most sampled species. Histology of *P. maniculatus* tissue in other parts of its range may yield different results regarding both pathologies present and parasites and pathogens infecting other tissues, such as liver flukes in northern parts of their range (Malek 1977).

Four rodents were infected by the fungus *Emmonsia crescens*. It was found in

three rodent species, *P. maniculatus*, *Microtus longicaudus,* and *M. montana*. This species of fungus, along with two congeneric species, *E. parva* and *E. pasteuriana*, can infect humans causing the disease adiaspiromycosis. This disease is generally not harmful to humans; most infected individuals show no signs or symptoms. However, under certain conditions, such as in immunocompromised patients, it can cause respiratory failure, lung granulomas, and skin disease (Kamalam and Thambiah 1979; Bambirra and Nogueira 1983; Anstead et al. 2012).

These fungal pathogens are known to infect *P. maniculatus* in Canada (Dowding 1947; Bakerspigel 1968), but it is unclear whether *Emmonsia* spp. are prevalent in Great Basin rodents. Grundmann and Tsai (1967) state that these species appear to be widespread in Great Basin rodents, but do not show any data. *Emmonsia crescens* was found in one muskrat (*Ondatra zibethicus osoyoosensis*) captured in the Salt Lake Valley, Utah (Grundmann and Tsai 1967). Dissecting and examining the lungs of infected individuals to find small *Emmonsia* spp. spores may yield false negatives. Histology may more accurately diagnose fungal pathogens. Histological surveys will help determine which rodent species are reservoir hosts for the pathogen and release infectious spores in the environment. It is not clear how much lung tissue should be examined to minimize false negatives. Lungs are small organs, and one section of each lung is a high percentage of total tissue, unlike the liver. The false negative rate is generally low for lung tissue (personal communication, D. Gardiner). This survey may be the first to provide data on *E. crescens* in rodents in the Great Basin.

Pathologies were documented in the lung, liver, and kidney tissue of rodents. We found no parasites or disease in the hearts of any rodent. Most pathologies found in

rodents were liver and kidney tissue diseases. A few diseases may have been caused by either infectious or non-infectious sources. Extramedullary hematopoiesis (EMH), hyperplastic BALT, pyelitis, interstitial nephritis, inflammation, and granulomas may be caused by infectious agents or arise from environmental causes or underlying health issues. In addition to pathogens, inflammatory diseases, such as pyelitis and interstitial nephritis, can be caused by other foreign substances or autoimmune diseases (Wobeser 2006). Extramedullary hematopoiesis can be caused pathogens or be the result of other underlying pathologies such as myelofibrosis, which is a bone disorder that affects the production of red blood cells (Kim 2010)

One pathogen that may cause interstitial nephritis in kidney tissue of rodents is *Leptospira* spp., which causes leptospirosis. These pathogenic bacteria reside in kidneys and are transmitted in the urine (Shearer et al. 2014). Further research should test whether deer mice in the Great Basin are reservoirs of *Leptospira* spp. The most common reservoirs of these bacteria are currently believed to be deer, skunks, and raccoons (Shearer et al. 2014). *Leptospira* spp. can infect humans, resulting in potentially serious disease (Terpstra 2003). Few studies have documented the natural occurrence of *Leptospira* spp. in wild rodents (Yager et al. 1953; Cirone et al. 1978). Microparasites (bacteria, viruses, protozoa) are often found by analyzing blood. Pathogens in other areas of the body such as Leptospira spp. in the kidney may be missed using these methods (Bharti et al. 2003). We suggest targeted sampling and histology of kidney tissue followed by PCR-based screening methods to identify additional reservoir hosts in the Great Basin.

Recording pathologies in wild populations from non-contaminated environments

can be used as a baseline for future studies. Assessing changes in populations as land-use changes or as contaminants are introduced can allow wildlife biologists to determine how wildlife is affected and will be affected in the future. Environmental change is known to cause various diseases in animals, often resulting in a decrease in fitness (Acevedo-Whitehouse and Duffus 2009). A sudden increase in diseases in certain tissues or finding pathologies that were previously absent in certain populations can help assess the general health of these populations and aid in conservation. Disease information can inform management decisions as well as disease control and prevention, including diseases of human importance (McNamara 2015). For example, rodents are often key players for pathogens of human importance (e.g. Lyme disease, Hantavirus, *Bartonella* spp., Leptospirosis). Without knowledge of baseline levels of disease, identifying emerging diseases, whether caused by infectious or non-infectious agents, is challenging. Being able to rapidly and accurately assess populations for an increase in disease prevalence allows affective control measures to be put into place (Dietz et al. 1996; Plowright et al. 2008; Artois et al. 2009). For example, rodents suddenly showing high amounts of kidney disease caused by *Leptospirosis* spp. can be targeted for control, and these areas can be managed to reduce human exposure.

We document several diseases in wild populations of rodents in the Great Basin. Whether the non-infectious diseases found were caused by contaminants, a decrease in animal health due to poor nutrition, or some other factor is unclear. Diseases caused by non-infectious agents can act to reduce host fitness and should be monitored in the future.

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References

Acevedo-Whitehouse, K., and A. L. Duffus. 2009. Effects of environmental change on wildlife health. Philosophical Transactions of the Royal Society B: Biological Sciences 364:3429-3438.

Anstead, G. M., D. A. Sutton, and J. R. Graybill. 2012. Adiaspiromycosis causing respiratory failure and a review of human infections due to Emmonsia and *Chrysosporium* spp. Journal of Clinical Microbiology 50:1346-1354.

Artois, M., Bengis, R., Delahay, R.J., Duchêne, M.J., Duff, J.P., Ferroglio, E., Gortazar, C., Hutchings, M.R., Kock, R.A., Leighton, F.A. and Mörner, T. 2009. Wildlife disease surveillance and monitoring. Pp. 187-213 in Management of Disease in Wild Mammals (R. Delahay, G. C. Smith, and M. R. Hutchings, eds.). Springer. Tokyo, Japan.

Bakerspigel, A. 1966. Additional cases of adiaspiromycosis in Canadian rodents. Sabouraudia: Journal of Medical and Veterinary Mycology 4:176-178.

Bambirra, E. A., and A. M. M. Nogueira. 1983. Human pulmonary granulomas caused by Chrysosporium parvum var. crescens (*Emmonsia crescens*). The American Journal of Tropical Medicine and Hygiene 32:1184-1185.

Beier, E. E., J. R. Maher, T. J. Sheu, D. A. Cory-Slechta, A. J. Berger, M. J. Zuscik, and J E. Puzas. 2013. Heavy metal lead exposure, osteoporotic-like phenotype in an animal model, and depression of Wnt signaling. Environmental Health Perspectives 121:97-104.

Bennett, R. 2003. The ‘direct costs’ of livestock disease: the development of a system of models for the analysis of 30 endemic livestock diseases in Great Britain. Journal of Agricultural Economics 54:55-71.

Bharti, A. R., J. E. Nally, J. N. Ricaldi, M. A. Matthias, M. M. Diaz, M. A. Lovett, P. N.

Levett, R. H. Gilman, M. R. Willig, E. Gotuzzo, and J. M. Vinetz. 2003. Leptospirosis: a zoonotic disease of global importance. The Lancet Infectious Diseases 3:757-771.

Ceruti, R., O. Sonzogni, F. Origgi, F. Vezzoli, S. Cammarata, A. M. Giusti, and E. Scanziani. 2001. *Capillaria hepatica* infection in wild brown rats (*Rattus norvegicus)* from the urban area of Milan, Italy. Zoonoses and Public Health 48:235-240.

Cirone, S. M., H. P. Riemann, R. Ruppanner, D. E. Behymer, and C. E. Franti. 1978. Evaluation of the hemagglutination test for epidemiologic studies of leptospiral antibodies in wild mammals. Journal of Wildlife Diseases 14:193-202.

Dardouri, K., S. Haouem, I. Gharbi, B. Sriha, Z. Haouas, A. El Hani, and M. Hammami. 2016. Combined effects of Cd and Hg on liver and kidney histology and function in wistar rats. Journal of Agricultural Chemistry and Environment 5:159-169.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife–threats to biodiversity and human health. Science 287:443-449.

Dietz, R., F. Riget, and P. Johansen. 1996. Lead, cadmium, mercury and selenium in Greenland marine animals. Science of the Total Environment 186:67-93.

Dmowski, K., A. Kozakiewicz, and M. Kozakiewicz. 1998. Small mammal populations and community under conditions of extremely high thallium contamination in the environment. Ecotoxicology and Environmental Safety 41:2-7.

Dobson, A. P., and P. J. Hudson, P. J. 1986. Parasites, disease and the structure of ecological communities. Trends in Ecology and Evolution 1:11-15.

Dowding, E. S. 1947. The pulmonary fungus, *Haplosporangium parvum*, and its relationship with some human pathogens. Canadian Journal of Research 25:195-206.

Fair, J. M., and O. B. Myers. 2002. The ecological and physiological costs of lead shot and immunological challenge to developing western bluebirds. Ecotoxicology 11:199-208.

Ferrari, N., I. M. Cattadori, A. Rizzoli, and P. J. Hudson. 2009. Heligmosomoides polygyrus reduces infestation of *Ixodes ricinus* in free-living yellow-necked mice, *Apodemus flavicollis*. Parasitology 136:305-316.

Fischer, A. H., K. A. Jacobson, J. Rose, and R. Zeller. 2008. Hematoxylin and eosin staining of tissue and cell sections. Cold Spring Harbor Protocols, pdb-prot4986.

Frandsen, J. C., and A. W. Grundmann. 1961. Endoparasitism in isolated populations of

rodents of the Lake Bonneville Basin, Utah. The Journal of Parasitology 47:391-396.

Freeman, R. S., and K. A. Wright. 1960. Factors concerned with the epizootiology of *Capillaria hepatica* (Bancroft, 1893) (Nematoda) in a population of *Peromyscus maniculatus* in Algonquin Park, Canada. The Journal of Parasitology 46:373-382.

Gardiner, C. H., and S. L. Poynton (ed.). 1999. An atlas of metazoan parasites in animal tissues. Armed Forces Institute of Pathology. American Registry of Pathology. Rockville, Maryland.

Golden, N. H., S. E. Warner, and M. J. Coffey. 2016. A review and assessment of spent lead ammunition and its exposure and effects to scavenging birds in the United States. Reviews of Environmental Contamination and Toxicology 237:123-191.

Grundmann, A. W. and Y. H. Tsai. 1967. Some parasites of the muskrat, *Ondatra zibethicus osoyoosensis* (Lord, 1863) Miller, 1912 from the Salt Lake Valley, Utah. Transactions of the American Microscopical Society 86:139-144.

Grundmann, A. W., R. G. Warnock, and D. L. Wassom. 1976. Some mechanisms of natural regulation of parasitic helminth populations. American Midland Naturalist 95:347-360.

Hudson, P. J., A. P. Dobson, I. M. Cattadori, D. Newborn, D. T. Haydon, D. J. Shaw, T. G. Benton, and B. T. Grenfell. 2002. Trophic interactions and population growth rates: describing patterns and identifying mechanisms. Philosophical Transactions of the Royal Society of London B: Biological Sciences 357:1259-1271.

Kamalam A. and A. S. Thambiah. 1979. Adiaspiromycosis of human skin caused by *Emmonsia crescens.* Sabouraudia 17:377–381.

Kierszenbaum, A. L. and L. Tres. 2012. Histology and Cell Biology: An Introduction to Pathology, 3rd ed. Elsevier Health Sciences. Philadelphia, Pennsylvania.

Kim, C. H. 2010. Homeostatic and pathogenic extramedullary hematopoiesis. Journal of Blood Medicine 1:13-19.

Knowles, S. C. L., A. Fenton, O. L. Petchey, T. R. Jones, R. Barber, and A. B. Pedersen. 2013. Stability of within-host–parasite communities in a wild mammal system. Proceedings of the Royal Society B: Biological Sciences 280:20130598.

López-Islas, M. E., I. Ibarra-Meza, E. Ortiz-Ordóñez, L. Favari, J. Elías Sedeño-Díaz, and E. López-López. 2017. Biological responses of the American Coot (Fulica americana), in wetlands with contrasting environmental conditions (Basin of México). Journal of Toxicology and Environmental Health, Part A 80:349-364.

Malek, E. A. 1977. Geographical distribution, hosts, and biology of *Schistosomatium douthitti* (Cort, 1914) Price, 1931. Canadian Journal of Zoology 55:661-671.

McNamara, T. S. 2016. Wildlife pathology studies and how they can inform public health. ILAR Journal 56:306-311.

Mela, M., M. A. F. Randi, D. F. Ventura, C. E. V. Carvalho, E. Pelletier, and C. O. Ribeiro. 2007. Effects of dietary methylmercury on liver and kidney histology in the neotropical fish Hoplias malabaricus. Ecotoxicology and Environmental Safety 68:426-435.

Møller, A. P., K. Allander, and R. Dufva. 1990. Fitness effects of parasites on passerine birds: a review. Pp. 269-280 in Population Biology of Passerine Birds (J. Blondel, A. Gosler, J. Lebreton, and R. McCleery, eds.). Springer. Berlin, Germany.

Renzoni, A., F. Zino, and E. Franchi. 1998. Mercury levels along the food chain and risk for exposed populations. Environmental Research 77:68-72.

Pedersen, A. B., and A. Fenton. 2007. Emphasizing the ecology in parasite community ecology. Trends in Ecology and Evolution 22:133-139.

Shearer, K. E., M. J. Harte, D. Ojkic, J. DeLay, and D. Campbell. 2014. Detection of *Leptospira* spp. in wildlife reservoir hosts in Ontario through comparison of immunohistochemical and polymerase chain reaction genotyping methods. The Canadian Veterinary Journal 55:240–248.

Solomon, G. B., and C. O. Handley Jr. 1971. Capillaria hepatica in Appalachian mammals. Journal of Parasitology 57:1142-1144.

Telfer, S., X. Lambin, R. Birtles, P. Beldomenico, S. Burthe, S. Paterson, and M. Begon. 2010. Species interactions in a parasite community drive infection risk in a wildlife population. Science 330:243-246.

Terpstra, W. J. 2003. Human leptospirosis: guidance for diagnosis, surveillance and control. World Health Organization.

Tête, N., M. Durfort, D. Rieffel, R. Scheifler, and A. Sánchez-Chardi. 2014. Histology related to cadmium and lead bioaccumulation in chronically exposed wood mice, *Apodemus sylvaticus*, around a former smelter. Science of the Total Environment 481:167-177.

Van Saun, R. J. 2006. Nutritional diseases of South American camelids. Small Ruminant Research 61:153-164.

Wadaan, M. A. 2009. Effects of mercury exposure on blood chemistry and liver histopathology of male rats. Journal of Pharmacology and Toxicology 4:126-131.

Wobeser, G. A. 2006. Essentials of Disease in Wild Animals. John Wiley & Sons, Inc. New York City, New York.

Wright, K. A. 1961. Observations on the life cycle of *Capillaria hepatica* (Bancroft, 1893) with a description of the adult. Canadian Journal of Zoology 39:167-182.

Yager, R. H., W. S. Gochenour Jr, A. D. Alexander, and P. W. Wetmore. 1953. Natural occurrence of *Leptospira ballum* in rural house mice and in an opossum. Proceedings of the Society for Experimental Biology and Medicine 84:589-590.

Table 3.1. Diseases of rodents trapped in the Great Basin that were found using histology. The species affected for each disease is listed along with the prevalence (in parentheses).

Disease/pathology	Causative agent	Organ	Species affected (prevalence)	Location(s) where pathology was found
Hepatic capillariasis	Parasitic nematode (*Capillaria hepatica*)	liver	*Peromyscus maniculatus* (1/116)	Dolly Varden
Adiaspiromycosis	Fungal pathogen (*Emmonsia crescens*)	lungs	*Peromyscus maniculatus* (2/116) *Microtus montanus* (1/1) *Microtus longicaudus* (1/1)	Dolly Varden Stansbury Mountains
Lymphocytic infiltrates	Non-infectious origin	liver	*Peromyscus maniculatus* (1/116)	Dolly Varden
Mineralization	Non-infectious origin	liver, kidneys	*Peromyscus maniculatus* (4/116)	Dolly Varden Toano Range San Francisco Mountains
Abnormal adrenal gland morphology	Non-infectious origin	adrenal gland	*Peromyscus maniculatus* (1/116)	Dolly Varden
Extramedullary hematopoiesis (EMH)	Unknown	liver, kidney, lung	*Peromyscus maniculatus* (14/116) *Tamias dorsalis* (1/8) *Neotoma lepida* (1/1) *Peromyscus truei* (1/10)	Dolly Varden Toano Range San Francisco Mountains Stansbury Mountains
Pneumonia	Unknown	lungs	*Peromyscus maniculatus* (1/116)	Pilot Range
Hyperplastic bronchial associated lymphoid tissue (BALT)	Unknown	lungs	*Peromyscus maniculatus* (6/116) *Peromysycus truei* (1/10) *Tamias dorsalis* (2/8)	Dolly Varden Toano Range San Francisco Mountains Stansbury Mountains

Table 3.1. continued

Interstitial nephritis	Unknown	kidneys	*Peromyscus maniculatus* (4/116)	Pilot Range San Francisco Mountains Stansbury Mountains
Mild chronic pyelitis	Unknown	liver	*Tamias dorsalis* (3/8) *Peromyscus maniculatus* (2/116) *Tamias minimus* (1/1) *Peromyscus truei* (1/10)	Dolly Varden San Francisco Mountains Stansbury Mountains
Granulomas	Unknown	lung	*Peromyscus truei* (1/10)	Stansbury Mountains
Inflammation	Unknown	bile duct, liver	*Peromyscus maniculatus* (1/116) *Tamias dorsalis* (1/8) *Microtus longicaudus* (1/1)	Dolly Varden San Francisco Mountains Stansbury Mountains

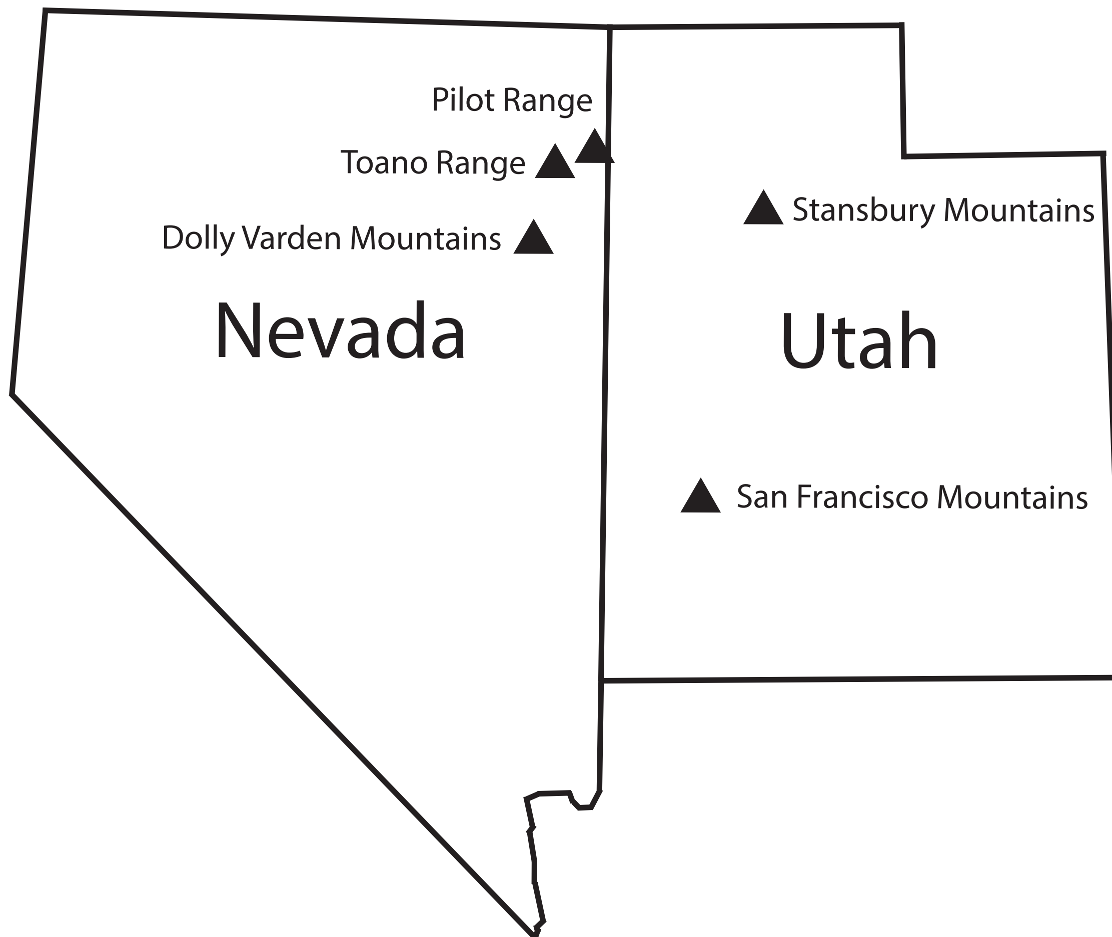

Fig. 3.1. Map of trapping locations in the Great Basin of Utah and Nevada. At each site, all rodents captured were euthanized and histology was performed. Trapping stopped once 25 deer mice (*Peromyscus maniculatus*) were trapped.

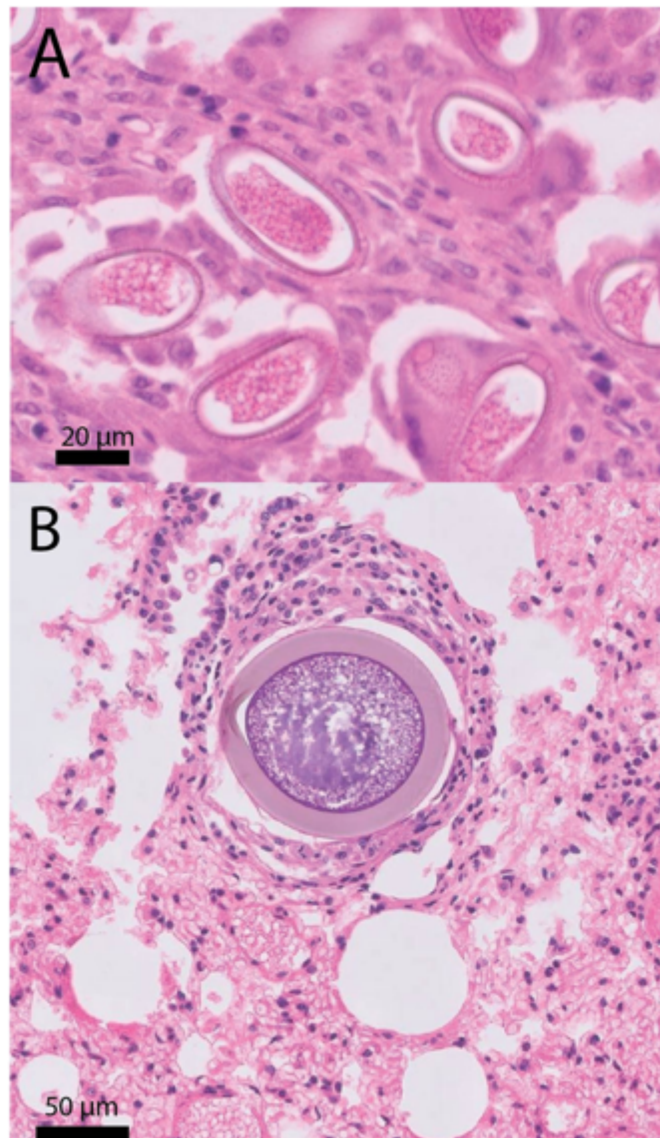

Fig. 3.2. Parasites found during histology in *Peromyscus maniculatus.* A) Eggs of *Capillaria hepatica* in the liver. B) *Emmonsia crescens* spore (fungus) in the lungs.

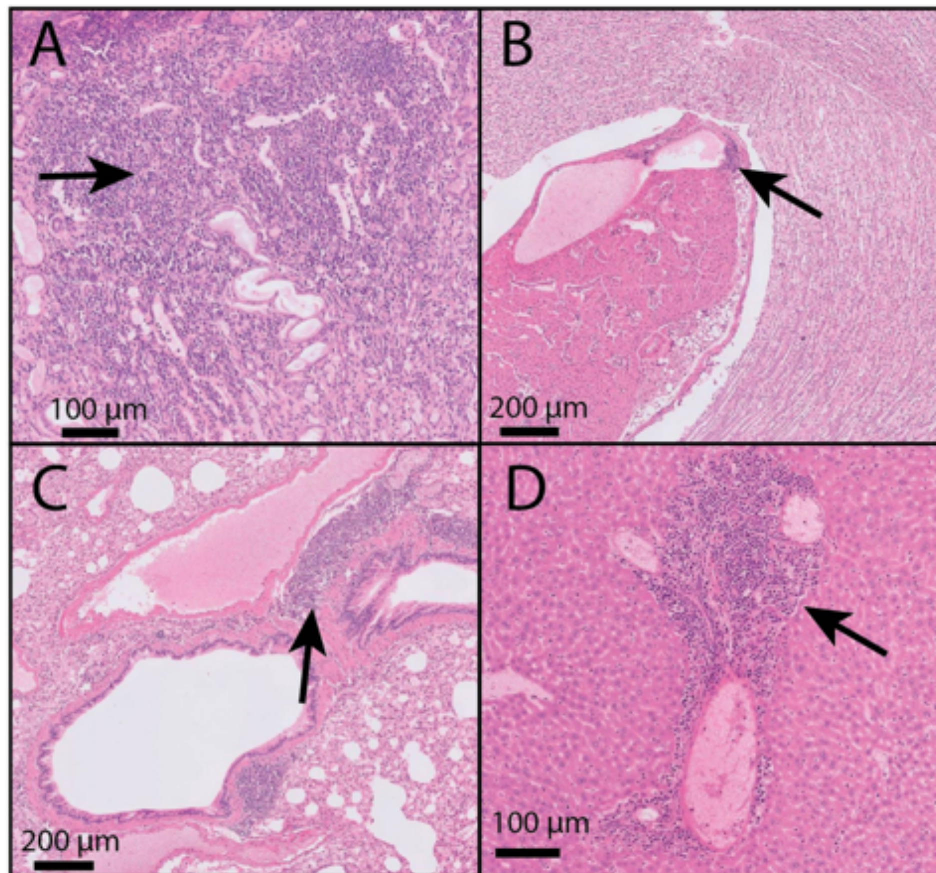

Fig. 3.3. Images of pathologies found in deer mice using histology (H&E stain). A) Severe interstitial nephritis of kidney tissue. B) Mild pyelitis in kidney tissue. C) Hyperplastic BALT in lung tissue. D) Extramedullary hematopoiesis in liver tissue.

CHAPTER 4

SPECIES TURNOVER OF RODENTS FOLLOWING HABITAT CHANGE

Abstract

Estimating biodiversity and community composition is a fundamental goal of community ecology and is becoming an increasing priority as humans modify landscapes. Changes in species composition following environmental change over time and across environmental gradients is called species turnover. A delay in species responding to environmental change means that current diversity may not reflect the diversity that will ultimately be supported by the new environment. Here, changes in rodent community structure following environmental change are investigated. By comparing current diversity to diversity 60 years ago, we determine whether there is a diversity surplus or deficit in habitats that have recently converted to pinyon-juniper woodland (P-J). Rodents were trapped at seven replicate locations in the Great Basin. At each location, sagebrush, P-J woodland, and the ecotone between these two habitats were sampled. Historical data were compared to recent data at three sites that were converted from ecotones to P-J woodlands. Rodent diversity over space and over time showed different patterns. Simpson's diversity decreased from ecotones to P-J habitats, but remained the same or increased following P-J conversion over time. This suggests a diversity surplus; however, the P-J sites sampled spatially were recently converted to P-J woodlands as well, possibly underestimating the diversity that these sites can ultimately support. Moreover, more

species immigrated than underwent apparent extinction, but immigrating species were rare, suggesting an immigration credit, specifically a lag in abundance. Measures of rodent diversity following woodland conversion may underestimate the diversity that will ultimately be supported by the new habitat. We highlight the importance of documenting historical habitat type to make inferences about time lags in diversity.

Introduction

A fundamental goal of community ecology is estimating biodiversity and species composition. Predicting changes in biodiversity after environmental change is increasing in priority due to an increase in land use change by humans (Folley et al. 2005; Sillmann et al. 2013; Ehrlen and Morris 2015). As environments are altered, species respond by expanding or contracting their ranges, which results in species turnover. When distributions of species shift, new assemblages of species are formed (Fagan et al. 1999), which can have drastic effects on ecosystem function (LoGiudice et al 2003; Larsen et al. 2005). Local species extinction and species immigration are two primary forces driving species turnover and shape the composition of the new community (Jackson and Sax 2010). The number of species affected and the time it takes for them to respond can have management and conservation implications (Kuussaari et al. 2009).

In addition to change over time, species turnover also refers to changing community composition as a function of distance between sampling sites or across habitat gradients (Condit et al. 2002; Qian and Ricklefs 2012; LaManna et al. 2015). Species turnover temporally and spatially is mostly driven by habitat preferences, food availability, and interspecific interactions such as competition and predation (Douglas 1989; Peterson et al. 2002; Qian and Ricklefs 2012; LaManna et al. 2015). Here, using

historical data, species diversity and species composition is investigated over time and across a habitat gradient to determine species turnover following environmental change.

Species vary in their responses to environmental change. Some species respond rapidly, while others are delayed, causing transient patterns of diversity. A delay in local species extinction is the “extinction debt”, which refers to the species doomed to become extinct (Jackson and Sax 2010; Halley et al. 2016). Conversely, the species that will eventually immigrate to the area is the “immigration (or colonization) credit” (Jackson and Sax 2010). Immigration credit is different than the similar concept of species credit, which is used to refer to the number of species that will benefit from restoring habitat that was altered (Lira et al. 2012).

Different rates at which species become locally extinct and immigrate can cause either a diversity surplus or a diversity deficit until the “biodiversity ledger” can be balanced (Jackson and Sax 2010; Essl et al. 2015). Understanding these time lags (or relaxation times) can help determine whether biodiversity is being underestimated or overestimated following a change in the environment (Jackson and Sax 2010; Hylander and Weibull 2012; Essl et al. 2015). Most studies examining changes in biodiversity suggest that extinction debt is much more common than immigration credit (Ford et al. 2009; Cousins and Vanhoenacker 2011; Dullinger et al. 2012; Bommarco et al. 2014).

A common type of environmental change is habitat change. Modifications to the size, productivity, structure, and connectivity of habitats cause species to immigrate or disappear (Fritts and Rodda 1998; Kaspari 2000; Fahrig 2003; Jackson and Sax 2010; Haddad et al. 2015; Hanski 2015; Almeida-Gomes et al. 2016). One example of habitat change is the gradual conversion of savannah and shrublands to dense woodlands

(Margolis 2014). Woody plant conversions began approximately 150 years ago and are happening around the world. For example, tree cover increased significantly over nearly 70 years in South Africa (Wigley et al. 2010), and there has been a 42% increase in closed forests in savannas from 1947 to 1997 in northern Australia (Brook and Bowman 2006). These conversions are also documented in Europe (Barbaro et al. 2001) and South America (Cabral et al. 2003). A combination of climate change, overgrazing, changing fire regimes, and increased CO_2 are hypothesized to be drivers of woodland conversions (McPherson et al. 1988; Archer et al. 1995; Van Auken 2000; Weisberg et al. 2007; Clifford et al. 2011; Margolis 2014). Recruitment of woody species in shrublands changes ecosystem processes and occurs across entire landscapes (Allen and Breshears 1998; Beckage et al. 2008).

In the Intermountain West, sagebrush steppe is being converted to dense pinyon-juniper woodlands (P-J), causing drastic changes to western ecosystems (West 1999). P-J woodlands are expanding their distribution and are increasing both upslope and downslope along mountain ranges (Blackburn and Tueller 1970; Weisberg et al. 2007; Bradley and Fleishman 2008). The majority of the expansion is downslope into sagebrush habitats, replacing shrubs and associated grasses (Blackburn and Tueller 1970; Van Auken 2000; Weisberg et al. 2007). Initially, habitat heterogeneity increases when these conversions begin, creating transition zones (ecotones). An increase in heterogeneity increases species diversity because more niches support more species (MacArthur and Wilson 1967; Freemark and Merriam 1986; Germano and Lawhead 1986; Kerr and Packer 1997; Tews et al. 2004).

The gradual expansion of P-J woodlands is well documented in Utah and

surrounding states. One consequence of this expansion is the loss of sagebrush and associated plants and animals that rely on these habitats (Rowe et al. 2010; Santos et al. 2014), such as the greater sage-grouse (*Centrocercus urophasianus*) and the sage thrasher (*Oreoscoptes montanus*) (Crawford et al. 2004; Rottler et al. 2014). Most studies focus on charismatic species that are threatened or have rapidly declining population sizes due to P-J expansion. Studies also monitor wildlife responses after removing P-J associated trees (Bombaci and Pejchar 2016; Gallo et al. 2016). Few studies have addressed species turnover of rodent communities following P-J conversion.

Here, changes in rodent species diversity and species composition following P-J conversion are investigated in the Great Basin. The following questions are addressed: 1) How does species diversity and community composition of rodents change over time and space over a sagebrush to P-J habitat gradient? 2) Is there a diversity surplus or deficit in recently converted P-J habitats?

Two types of data are used. First, rodents are sampled in sagebrush, ecotone, and P-J habitats from 2014 to 2016 at seven replicate locations. Second, sites that underwent P-J conversion from the late 1950s and ‘60s are resampled and compared to historical rodent data. By sampling different habitat types, species composition within each habitat will identify habitat specialists and generalists. These data can be used to make predictions as to which species will become locally extinct or immigrate following P-J conversion. Comparing different habitats at the exact same location controls for site-specific differences that cannot be controlled for when sampling different habitats over space. These two kinds of data can be used to document species turnover and to determine if there are lags in diversity following woody plant expansion.

Materials and methods

Study locations

Both historical and present sampling was conducted in the Great Basin of Utah. The Great Basin is a desert ecosystem with intermittent mountain ranges extending north to south. These montane-desert systems generally have the same vegetation across the region: valley desert, dominated by sagebrush (*Artemesia* spp.) transitioning into P-J woodland at higher elevations. Salt bush (*Atriplex canescen*) and several species of grasses are also present in sagebrush communities. An ecotone occurs between the sagebrush and dense P-J woodland at mid-elevations. At the highest elevations, other conifers including firs, spruces, and pines are dominant tree species. In dense P-J woodlands, Utah juniper (*Juniperus osteosperma*) and singleleaf pinyon pine (*Pinus monophylla*) are the predominate species (Banner 1992). These mountain ranges can be used as replicates for sampling because they have the same habitat gradients moving from low to high elevation: sagebrush, ecotones, and P-J woodlands. P-J woodlands and sagebrush have relatively homogenous vegetation, while the ecotone is made up of vegetation from both habitats and is more heterogeneous. P-J woodlands have very little understory vegetation (Fig. 4.1).

Rodent sampling over the environmental gradient

Rodents were trapped from 2014 to 2016 at eight locations in five mountain ranges in the eastern part of the Great Basin (Fig. 4.2). Trapping occurred from May to the beginning of October. At most sampling locations, three habitat types were sampled: sagebrush, P-J woodland, and the ecotone. All animals were trapped using Sherman live traps (H.B. Sherman Traps, Inc.). Traps were placed in transects with five to ten meters

between traps. One transect was placed in each habitat type at each location. Rodents are generally territorial and have relatively small home ranges. Traps were placed far enough into each habitat type (approx. 1 km) to ensure that the rodents trapped were not individuals from another habitat type that were foraging or searching for mates. Traps were baited with a mixture of whole oats and birdseed. The total number of traps placed each night was recorded to get total trap nights at each site. Trapped animals were processed in the field and in the lab. Once an animal was trapped, the contents of the trap were emptied into a plastic bag. The animal was then euthanized with isoflurane and put on ice until it was taken to the lab for further processing. Animals not euthanized were marked using an ear punch tool to identify recaptures and to avoid counting animals more than once. They were then released where captured. Fully processed animal carcasses were placed in formalin, followed by 95% ethanol, and deposited at the Natural History Museum of Utah. All animal handling and processing was approved by the Institutional Animal Care and Use Committee of the University of Utah.

Historical sampling and site selection

Small mammals were trapped and recorded throughout Utah from 1957 to 1968 by A. Grundmann and his students from the University of Utah (Frandsen 1960; Frandsen and Grundmann 1961; Derrick 1968). On average, each location was trapped for three days (Frandsen 1960; Frandsen and Grundmann 1961). All trapping occurred from May to September. Records were kept for all individuals trapped. A field notebook documenting sampling locations includes directions, site-specific details, and approximate elevations. A subset includes descriptions of habitat type. Six historical locations were found with habitat descriptions that included references to either

sagebrush, P-J woodlands, or a sagebrush-P-J mix.

Aerial photographs were gathered from the USGS (earthexplorer.usgs.gov) from around the same time as sampling occurred to document historical vegetation. Specifically, we were interested in the percent cover of pinyon pine and juniper trees between 1957 and 1970. We used Google Earth to document current vegetation patterns. Both historical and recent images were used to compare P-J cover over time. Three of the six sites showed noticeable habitat differences over time. Two of these sites are located in the Stansbury Mountains (one sampled in 1957 and the other in 1968) and one site is located in the Deep Creek Mountains (sampled in 1960) (Fig. 4.2). Each site had sagebrush and associated vegetation and a low percentage of P-J cover (ecotones) in the late 1950s and 1960s, but converted to P-J woodlands over the last 50 years. The other three sites were used as control sites because they did not change habitat types over time. Two control sites were sampled in 1957 (Deep Creek Mountains and Stansbury Island) and one was sampled in 1964 (House Mountains). Two of the sites were and are still dominated by sagebrush (Deep Creek Mountains and Stansbury Island) and one was and is still a dense P-J woodland (House Mountains).

P-J cover analysis

ImageJ (Rasband 2016) was used to estimate the percentage of P-J cover at all sites sampled (Abramoff et al. 2004; Pérez and Pascau 2013). Each study site was located in Google Earth. Percent cover was estimated per hectare. Hectare square images were imported into ImageJ. Percent tree cover was estimated by measuring the area of all the trees in the image. The color threshold of each image was adjusted so that only trees were selected. We used a threshold cutoff determined by the smallest tree in the image.

Smaller areas selected were excluded because they were not trees and should not be included in the estimation of tree cover. The areas of all the trees were added up and divided by the total area of the one-hectare image to get percent P-J per hectare. Sagebrush sites had zero percent P-J cover (n = 6 sites). Ecotone sites had a mean ± SE of 11.8 ± 2.9% (n = 7 sites) P-J cover, while pinyon-juniper sites had 51.9 ± 4.5% (n = 7 sites) P-J cover.

Historical aerial photographs obtained from USGS were used to calculate percent cover for the six sites with historical mammal data. One image from Derrick (1971) was used that was the exact sampling location of a P-J converted site in the Stansbury Mountains. The same methods were used as above to estimate percent P-J cover.

Species composition and diversity analyses

To determine whether the rodent community at each site was thoroughly sampled, species accumulation curves were produced. The number of species were plotted against the cumulative trap nights throughout the trapping period at each site.

Species community composition and habitat preferences were determined by grouping all sampled sites by habitat type. Each species captured was considered occupying a habitat if it was captured in a habitat type in one of the seven replicate locations. If a species that was captured represented less than 1% of the individuals captured in each habitat type among all study locations, this species was considered “rare”. Species were considered absent if they were not captured in a habitat type among all sampled locations.

Species richness was compared among habitat types. The Chao richness estimator was used to estimate species richness for each site. The means ± SEs of the Chao

estimated richness were calculated for each habitat type (n = 7 for ecotone, n = 7 for P-J sites; n = 6 for sagebrush sites). A linear mixed model (LMM) was used to analyze differences in richness among habitat types. Because each location was sampled three times (sagebrush, ecotone, and P-J), location was included as a random effect in the mixed model, while habitat type was modeled as the fixed effect. The model was based on 20 observations from seven locations.

Species abundance was used to measure the evenness of the species present. At each site, Simpson's D was calculated. We used a linear mixed model to determine if species diversity significantly differed among the three habitat types. Again, location was used as a random effect and habitat was the fixed effect, and this model was based on 20 observations from seven locations. Species diversity (Simpson's D) was also calculated for the three resampled sites separately. Statistical analyses for diversity and species richness were performed using the Vegan package (Oksanen et al. 2016) in R. Mixed models were run using the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016) packages in R (R Core Team 2016).

Historical community composition was compared to the data obtained from resampling. Species absent in both the historical and present sampling data were not included in the comparison between historical and present species composition. Only species that were present in at least one of the sampling time points (historical or present) were used to examine species turnover in response to habitat change over time.

Historical data were used to document the number of sagebrush and P-J specialists in varying amounts of P-J cover. Results of the spatial sampling informed which species were specialists. Sixteen sites (both historical and current) were used to

determine the number of sagebrush and P-J specialists in varying amounts of P-J cover. Data from the six historical sites (three control, three P-J converted) and the data from resampling those sites were included in the analysis. Four more sites from the historical data were added to this analysis. These sites varied in P-J cover, but were not resampled in 2014-2016.

Results

Spatial distribution of rodents over an environmental gradient

We sampled rodent communities at 21 different sites from seven locations. We captured 650 ($n = 163$ for sagebrush, $n = 234$ for ecotone, and $n = 253$ for P-J) individual rodents comprising 17 species over a combined 5,848 trap nights. The sagebrush site in the House Mountains was only trapped for one night (25 trap nights) and no individuals were trapped. This site was not included in any of the analyses. All other sites were sampled for a minimum of 60 trap nights. Most sites (17/20) had at least 150 trap nights. Species accumulation curves indicate that some sites were not thoroughly sampled (Fig. 4.S1). The Chao species richness estimator was used to estimate species richness at each site to control for differences in how thoroughly each site was sampled.

The Chao estimated species richness significantly differed between sites. Specifically, P-J habitats and sagebrush significantly differed (LMM; $t = -3.002$, $p = 0.015$; Fig. 4.3A, Table 4.S1), but there was no significant difference between sagebrush and ecotones (LMM; $t = 0.884$, $p = 0.40$, Fig. 4.3A, Table 4.S1) or between ecotones and P-J (LMM; $t = -2.223$, $p = 0.055$; Fig. 4.3A).

Species diversity (Simpson’s D) differed significantly among habitat types. Species diversity of sagebrush sites did not significantly differ between ecotone (LMM; t

= -1.162, p = 0.27) and P-J sites (LMM; t = -1.162, p = 0.27; Fig. 4.3B; Table 4.S2). However, species diversity of ecotone sites was significantly higher than in P-J sites (LMM; t = -2.413, p = 0.03; Fig. 4.3B, Table 4.S2).

The species present in each habitat type were compiled to determine habitat preferences (Fig. 4.4). *Peromyscus maniculatus* and *Perognathus parvus* were abundant in all three habitat types and are considered habitat generalists. Three species were present in all three habitat types, but were rare in one or more habitat types: these species were *Dipodomys ordii*, *Lemmiscus curtatus,* and *Reithrodontomys megalotis*. There were no species that are strictly found in ecotones, and a few species are sagebrush specialists. Most species are P-J specialists or found in both ecotones and P-J habitats (Fig. 4.4). Sagebrush and ecotone habitats are very similar (see Fig. 4.1); therefore, if a species was found in both sagebrush and ecotones, but not in P-J, they were considered sagebrush specialists. Several species are sagebrush specialists in these study areas, including *Reithrodontomys megalotis*, *Tamias minimus*, *Ammospermophilus leucurus*, *Dipodomys microps*, and *Chaetodipus formosus*. *Peromyscus truei, Tamias dorsalis, Microtus montanus*, *Neotoma cinerea,* and *T. umbrinus*, are P-J specialists.

Temporal biodiversity

Historical P-J cover was estimated and compared to the current P-J cover (Fig. 4.5). Sites that cross from the ecotone habitat to the P-J habitat over time are considered sites that underwent P-J conversion; those in the same habitat zone did not change over time. P-J cover of the three ecotone sites increased dramatically. In the late 1950s, these sites had a mean ± SE P-J cover of 7.6 ± 3.7%. Following P-J conversion, P-J cover increased to 53.9 ± 8.7%. In addition, two sites have zero percent P-J cover. These two

sites were used as control sites along with a P-J site because P-J cover did not change (Fig. 4.5).

We compared historical species diversity (Simpson's D) to diversity in 2014-2016 at six sites, three that underwent P-J conversion and three that did not. In two of the three P-J conversion sites, Simpson's D values were similar (Fig. 4.6). The third site showed an increase in diversity. Species diversity of the two sagebrush control sites remained the same, while species diversity of the P-J control site increased (Fig. 4.6).

We compared historical and recent species composition of rodents in the P-J converted sites. Two species, *Peromyscus maniculatus* and *Perognathus parvus*, are habitat generalists and are still present in P-J converted sites (Table 4.1). P-J specialists immigrated following P-J expansion, including *Neotoma cinerea, Tamias umbrinus*, *Peromyscus crinitus*, and *Lemmiscus curtatus*, but were low in abundance. Some of these species were absent in some recently converted sites. The P-J specialists *Peromyscus truei* and *T. dosalis* both increased in abundance (Table 4.1). Sagebrush specialists, *Reithrodontomys megalotis* and *Tamias minimus*, underwent apparent local extinction, while *Microtus longicaudus* decreased in abundance. In total, two of the eight species present in the 1950s were lost and four species immigrated following P-J conversion for a net increase of two species (Table 4.1).

Most species in the two sagebrush control sites generally the same over time (Table 4.2). The species present historically and currently are all sagebrush specialists based on the spatial data and from published mammalian species accounts. In the P-J control site, P-J specialists *T. dorsalis* and *P. truei* were absent in the past, but are now present (Table 4.2). The sagebrush specialist *A. leucurus* and the generalist *P. parvus*

were present historically, but were absent when the P-J site was resampled.

There is a significant negative correlation between P-J cover and sagebrush specialists (Spearman rank, $r_s = -0.64$, $p = 0.008$; Fig. 4.7A). There is no significant correlation between P-J cover and P-J specialists (Spearman rank, $r_s = 0.35$, $p = 0.19$; Fig. 4.7B).

Discussion

Rodents were trapped in 2014–2016 and compared to historical data to investigate changes in species composition and diversity after P-J conversion. Data gathered from sampling from sagebrush to P-J woodlands can be used to make predictions about which species should immigrate or disappear from the three P-J converted areas. Habitat specialists in sagebrush and in P-J can be identified based on habitat sampling. Species found ecotones and not P-J habitats were *Reithrodontomys megalotis*, *Tamias minimus*, and *Ammospermophilus leucurus*. We would predict that these species would decrease in abundance or go locally extinct following P-J conversion. In addition, *T. dorsalis*, *P. truei*, *Neotoma cinerea*, *T. umbrinus*, *M. montanus*, and *P. crinitus* are predicted to immigrate following P-J conversion since these species are either P-J or higher elevation specialists in our study sites. Two species appeared to go locally extinct in these areas (*R. megalotis* and *T. minimus*). Four species immigrated, most notably *P. truei* and *T. dorsalis*.

Trapping results for one species were not consistent with its documented habitat preferences. Two *R. megalotis* were trapped at one P-J site. This species is generally found in grassy habitats and is very abundant in sagebrush and ecotones (Webster and Jones 1982). This site was a lower elevation site with less P-J cover (40%) than the other

P-J sites (51.9 ± 4.5%).

Several species were trapped over the environmental gradient that were not trapped at the three P-J converted sites during either time point. Even though local species extinction or species immigration were not documented over time for these species, these data can be used to predict changes in their distributions following conversion. We predict that three species will be forced out of areas as juniper encroaches and begins to replace sagebrush and associated plants: *Dipodomys microps*, *Chaetodipus formosus,* and *D. ordii*. These species are often associated with desert grasses and shrubs (Carroll and Genoways 1980; Garrison and Best 1990; Hayssen 1991). We also predict the decline of *Ammospermophilus leucurus* because it is mostly found in shrubby areas and associated grasses (Belk and Smith 1991). This species can be found where juniper is present, but is much less abundant (Belk and Smith 1991). Based on our results, P-J woodlands may not support these four species.

Data over both space and time can be used to determine whether there are any lags in diversity following habitat change in the Great Basin. Following P-J conversion, there were no sagebrush specialists observed being delayed in their apparent extinction. Within the span of 60 years, two species appear to be locally extinct in P-J converted sites, *T. minimus* and *R. megalotis*. In contrast, four species immigrated following P-J conversion and were rare (< 1% of captures in P-J converted areas). These data suggest an immigration credit and abundance lag (Essl et al. 2015) following P-J conversion. An abundance lag suggests that a species may have immigrated but is low in abundance, resulting in lower diversity values until abundance increases (Essl et al. 2015).

Based on the results of the spatial sampling, P-J expansion was expected to cause

an increase in species richness. This was observed after resampling P-J converted if all three sites are combined (eight species in historical ecotones and ten species in current P-J). When these three sites are split up, two of the sites had the same species richness, while the third increased by two (Table 4.1). The diversity, measured by Simpson's D, showed different patterns over space vs. over time. Spatially, diversity was significantly less in P-J woodlands than in ecotone habitats, whereas over time, diversity either remained the same or increased. These data imply a diversity surplus, but based on the habitat preferences, we do not predict any more species will become locally extinct or decrease in abundance in P-J habitats. We do, however, predict that more species will immigrate and/or increase in abundance (depending on the species). Moreover, the other P-J sites sampled in this study might not have been P-J for very long since conversion is occurring throughout the Great Basin. This would underestimate diversity and make inferences about time lags difficult since the true diversity would be unknown.

To find historical cover for these sites, aerial photographs were obtained of the three P-J sites not compared with historical data (Cedar Mountains and both locations in the Oquirrh Mountains) to estimate P-J cover at approximately the same time as the historical data were collected. In 1954, the Cedar Mountain site had 17% P-J cover. The P-J sites in the Oquirrh Mountains had 11% and 28% P-J cover. These sites underwent P-J conversion recently and may be still being paid the immigration credit. Studies investigating species turnover over space and time should consider the habitat of the same site historically. Sites may still lag behind the diversity values that can ultimately be supported, and make inferences about diversity difficult.

Deficits in diversity have been documented following environmental change

(Walther et al. 2005; Piqueray et al. 2011; Hylander and Weibull 2012), and have mainly been recorded for plants. Lags in plant colonization are often attributed to slow dispersal, resulting in few opportunities to establish a viable population (Verheyen and Hermy 2004; Piqueray et al. 2011). Here, we show that relatively high dispersing animals also undergo lags in immigration and colonization. Our results suggest that reduced fitness and survival following P-J conversion may occur faster than dispersing from suitable habitat and establishing a viable population in the new habitat.

One P-J converted site increased in diversity. This site was located in the Deep Creek Mountains and had the highest percent P-J cover historically out of the three P-J converted sites (14.5%). This site also has the highest P-J cover currently (65%). The conversion of this site started prior to the other two sites. The increase in diversity at this site was caused by a decrease in *P. maniculatus* and the immigration of *P. truei* (Table 4.1). Moreover, if there is an immigration credit, we would predict that the P-J control site would increase in diversity after being P-J woodland for the last 60 years. Our data are consistent with this prediction because diversity did, in fact, increase. *Peromyscus truei* and *T. dorsalis* were recent immigrants to this site. However, this is only one site, and this may be well within the normal fluctuation of this site.

P-J expansion is gradual and species may respond only after a threshold of P-J cover is reached. Our results show that P-J specialists may be less responsive to P-J cover than sagebrush specialists. When P-J cover was 40 % or greater, no sagebrush specialists were found (Fig. 4.7). This was not as clear-cut for P-J specialists. Even at 60% P-J cover, there are one site with zero P-J specialists, despite P-J specialists being documented in this mountain range (Brown 1971; Rickart 2001). For instance, *P. truei*

was not trapped in the Stansbury B site even though P-J cover was high (Table 4.1).

During P-J conversion, ecotones are created when juniper trees begin to colonize a new area, producing an initial increase in habitat heterogeneity (Blackburn and Tueller 1970). An increase in species diversity following an increase in habitat heterogeneity is expected and is documented for several free-living groups (MacArthur and Wilson 1967; Kerr and Packer 1997; Tews et al. 2004). In the present study, sagebrush and ecotone habitats did not significantly differ in terms of rodent species richness or diversity. Based on these results, going from sagebrush to ecotones is not predicted to result in an increase in species richness or diversity. The difference in vegetation between sagebrush and ecotone sites is small compared to the difference between ecotone and P-J sites. As juniper and pinyon pine dominate the landscape, the understory disappears. The loss of understory vegetation may play a major role in determining rodent composition. Shrubs and grasses provide cover and food for many rodent species occupying the Great Basin Desert (West 1983). We found significant differences in species diversity from ecotones to P-J woodlands.

P-J woodlands are expanding (Bradley and Fleishman 2008), and these expansions are likely to continue in the future (Neupane and Powell 2015). Species turnover due to P-J conversion was documented over a time period of 50 years. We show that species immigration may take longer than apparent species extinction, leading to a diversity deficit. Species that immigrated following P-J conversion were rare or absent, suggesting that they are in the initial stages of immigration. The diversity over space vs. over time suggests a diversity surplus; however, the P-J sites sampled spatially were recently converted to P-J woodlands as well. Measures of rodent diversity following

woodland conversion may underestimate the diversity that will ultimately be supported by the new habitat. Rodent diversity is predicted to increase if the rare and/or absent rodent species increase in abundance or immigrate. Understanding species responses to environmental change is important for predicting future distributions and responses to unforeseen change at a time when land use is being altered at an alarming rate.

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References

Abràmoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. Image processing with ImageJ. Biophotonics International 11:36-42.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape to climate variation. Proceedings of the National Academy of Sciences 25:14839-14842.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? Climatic Change 29:91-99.

Barbaro, L., T. Dutoit, andP. Cozic, P. 2001. A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps. Biodiversity and Conservation 10:119-135.

Bates, D., M. Maechler, B. Bolker, S. Walker. 2015. Fitting linear mixed effects models using lme4. Journal of Statistical Software 67:1-48. doi:10.18637/jss.v067.i01.

Beckage, B. B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences 105:4197-4202.

Belk, M. C., and H. D. Smith. 1991. *Ammospermophilus leucurus*. Mammalian Species 368:1-8.

Blackburn, W. H. and P. T. Tueller. 1970. Pinyon-juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51:841-848.

Bombaci, S. and L. Pejchar. 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. Forest Ecology and Management 365:34-50.

Bommarco, R., R. Lindborg, L. Marini, and E. Öckinger. 2014. Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. Diversity and Distributions 20:591-599.

Bradley, B. A., and E. Fleishman. 2008. Relationships between expanding pinyon-juniper cover and topography in the central Great Basin, Nevada. Journal of Biogeography 35:951- 964.

Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences 159:1010-1017.

Brook, B. W., and D. M. Bowman. 2006. Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. Landscape Ecology 21:1253-1266.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist, 105:467-478.

Cabral, A. C., J. M. De Miguel, A. J. Rescia, M. F. Schmitz, and F. D. Pineda. 2003. Shrub encroachment in Argentinean savannas. Journal of Vegetation Science 14:145-152.

Carroll, L. E., and H. H. Genoways. 1980. *Lagurus curtatus*. Mammalian Species 124:1-6.

Clifford, M.J., N.S. Cobb, and M. Buenemann. 2011. Long-term tree cover dynamics in a pinyon-juniper woodland: climate-change-type drought resets successional clock. Ecosystems 14:949-962.

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núnez, P., Aguilar, S., Valencia, R., Villa, G. and Muller-Landau, H.C., 2002. Beta-diversity in tropical forest trees. Science, 295, 666-669.

Cousins, S. A., and D. Vanhoenacker. 2011. Detection of extinction debt depends on scale and specialisation. Biological Conservation 144:782-787.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.

Derrick, P. I. 1971. The concept of "landscape epidemiology" as it applies to endoparasitism of small mammals in selected habitats of South Willow Canyon, Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, N E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, and M. Caccianiga. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2:619-622.

Ehrlén, J., and W. F. Morris. 2015. Predicting changes in the distribution and abundance of species under environmental change. Ecology Letters 18:303-314.

Essl, F., S. Dullinger, W. Rabitsch, P. E. Hulme, P. Pyšek, J. R. Wilson, and D. M. Richardson. 2015. Historical legacies accumulate to shape future biodiversity in an era of rapid global change. Diversity and Distributions 21:534-547.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. The American Naturalist 153:165-182.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Ford, H. A., J. R. Walters, C. B. Cooper, S. J. Debus, and V. A. Doerr. 2009. Extinction debt or habitat change?– Ongoing losses of woodland birds in north-eastern New South Wales, Australia. Biological Conservation 142:3182-3190.

Frandsen, J. C. 1960. Endoparasitism in isolated populations of rodents of the Lake Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Frandsen, J. C., and A. W. Grundmann. 1961. Endoparasitism in isolated populations of rodents of the Lake Bonneville Basin, Utah. The Journal of Parasitology 47:391–396.

Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115-141.

Fritts, T. H., and G. H. Rodda, 1998. The role of introduced species in the degradation of island ecosystems: A case history of guam 1. Annual Review of Ecology and Systematics 29:113-140.

Gallo, T., L. T. Stinson, and L. Pejchar. 2016. Pinyon-juniper removal has long-term effects on mammals. Forest Ecology and Management 377:93-100.

Garrison, T. E,. and T. L. Best. 1990. *Dipodomys ordii*. Mammalian Species 353:1-10.

Germano, D. J., and D. N. Lawhead. 1986. Species diversity and habitat complexity: Does vegetation organize vertebrate communities in the Great Basin? The Great Basin Naturalist 46:711-720.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, and W. M. Cook. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:p.e1500052.

Halley, J. M., N. Monokrousos, A. D. Mazaris, W. D. Newmark, and D. Vokou. 2016. Dynamics of extinction debt across five taxonomic groups. Nature Communications:7 doi:10.1038/ncomms12283

Hanski, I. 2015. Habitat fragmentation and species richness. Journal of Biogeography 42:989-993.

Hayssen, V. 1991. *Dipodomys microps*. Mammalian Species 389:1-9.

Hylander, K., and H. Weibull. 2012. Do time-lagged extinctions and colonizations change the interpretation of buffer strip effectiveness?–a study of riparian bryophytes in the first decade after logging. Journal of Applied Ecology 49:1316-1324.

Jackson, S. T., and D. F. Sax. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology and Evolution 25:153-160.

Kaspari, M., S. O'Donnell, J. R. Kercher. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. The American Naturalist 155:280-293.

Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252-254.

Kuznetsova, A., P. B. Brockhoff, R. H. B. Christensen. 2016. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33. https://CRAN.R-project.org/package=lmerTest.

LaManna, J. A., A. B. Hemenway, V. Boccadori, and T. E. Martin. 2015. Bird species turnover is related to changing predation risk along a vegetation gradient. Ecology 96:1670-1680.

Larsen, T. H., N. M. Williams, C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538-547.

Lira, P. K., R. M. Ewers, C. Banks-Leite, R. Pardini, and J. P. Metzger. 2012. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest. Journal of Applied Ecology 49:1325-1333.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press. Princeton, New Jersey.

Margolis, E. Q. 2014. Fire regime shift linked to increased forest density in a pinon-juniper savanna landscape. International Journal of Wildland Fire 23:234-245.

McPherson, G. R. 1988. Patterns of shrub invasion in semiarid Texas grasslands. American Midland Naturalist 120:391-397.

Neupane, R. C., and J. A. Powell. 2015. Mathematical model of seed dispersal by frugivorous birds and migration potential of pinyon and juniper in Utah. Applied Mathematics 6:1506.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2016. vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan.

Pérez, J. M. M., and J. Pascau. 2013. Image processing with ImageJ. Packt Publishing Ltd.

Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sánchez-Cordero, J. Soberón, R. H. Buddemeier, and D. R. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626-629.

Piqueray, J., S. Cristofoli, E. Bisteau, R. Palm, and G. Mahy. 2011. Testing coexistence of extinction debt and colonization credit in fragmented calcareous grasslands with complex historical dynamics. Landscape Ecology 26:823-836.

Qian, H., and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and

environmental dissimilarity on global patterns of species turnover. Global Ecology and Biogeography 21:341–351.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rasband, W. S. 2016. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Rickart, E. A. 2001. Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. Global Ecology and Biogeography 10:77-100.

Rottler, C. M., C. E. Noseworthy, B. Fowers, and J. L. Beck. 2014. Effects of conversion from sagebrush to non-native grasslands on sagebrush-associated species. Rangelands 37:1-6.

Rowe, R. J., J. A. Finarelli, and E. A. Rickart. 2010. Range dynamics of small mammals along an elevational gradient over an 80-year interval. Global Change Biology 16:2930-2943.

Santos, M. J., J. H. Thorne, and C. Moritz. 2014. Synchronicity in elevation range shifts among small mammal and vegetation over the last century is stronger for omnivores. Ecography:doi: 10.1111/ecog.00931.

Sillmann, J., V. V. Kharin, F. W. Zwiers, X. Zhang, and D. Bronaugh. 2013. Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections. Journal of Geophysical Research: Atmospheres 118:2473-2493.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79-92.

Van Auken, O. W. 2000. Shrub invasion of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197-215.

Verheyen, K., and M. Hermy. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of Vegetation Science 15:125-134.

Walther, G. R., S. Beißner, and C. A. Burga. 2005. Trends in the upward shift of alpine plants. Journal of Vegetation Science 16:541-548.

Webster, W. D. and J. K. Jones. 1982. *Reithrodontomys megalotis*. Mammalian Species 167:1-5.

Weisberg, P. J., E. Lingua, and R. B. Pillai. 2007. Spatial patterns of pinyon-juniper woodland expansion in central Nevada. Rangeland Ecology and Management 60:115-124.

West, N. E. 1983. Great Basin-Colorado plateau sagebrush semi-desert. Pp. 331-369 in Temperate Deserts and Semi-Deserts (N. E. West, ed.). Elsevier. Amsterdam, Netherlands.

West, N. E. 1999. Juniper-Pinon savannas and woodlands of western North America. Pp. 288– 308 in Savannas, Barrens, and Rock Outcrop Plant Communities of North America (R. C. Anderson, J. S. Fralish, and J. M. Gaskin, eds.). Cambridge University Press. Cambridge, United Kingdom.

Wigley, B. J., W. J. Bond, and M. Hoffman. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology 16:964-976.

Table 4.1. Abundance of each species at each site that was resampled after P-J conversion. In total, historical sites had eight species, and recently sampled sites had ten.

Species	Stansbury Mountains A (Historical ecotone)	Stansbury Mountains A (P-J)
Peromyscus maniculatus	103	31
Perognathus parvus	0	0
Microtus montanus	0	1
Reithrodontomys megalotis	7	0
Tamias minimus	8	0
Microtus longicaudus	17	1
Tamias dorsalis	2	2
Peromyscus truei	0	4
Tamias umbrinus	0	0
Neotoma cinerea	0	0
Peromyscus crinitus	0	0
Lemmiscus curtatus	0	0
Species	Stansbury Mountains B (Historical ecotone)	Stansbury Mountains B (P-J)
Peromyscus maniculatus	24	28
Perognathus parvus	3	5
Microtus montanus	0	0
Reithrodontomys megalotis	1	0
Tamias minimus	0	0
Microtus longicaudus	0	0
Tamias dorsalis	0	1
Peromyscus truei	2	0
Tamias umbrinus	0	0
Neotoma cinerea	0	0
Peromyscus crinitus	0	0
Lemmiscus curtatus	0	1
Species	Deep Creek Mountains (Historical ecotone)	Deep Creek Mountains (P-J)
Peromyscus maniculatus	84	40
Perognathus parvus	2	0
Microtus montanus	1	0
Reithrodontomys megalotis	0	0
Tamias minimus	3	0
Microtus longicaudus	0	0
Tamias dorsalis	0	1
Peromyscus truei	0	12
Tamias umbrinus	0	1
Neotoma cinerea	0	1
Peromyscus crinitus	0	1
Lemmiscus curtatus	0	0

Table 4.2. Abundance of each species captured at each site that was resampled for control sites.

Species	Stansbury Island (Historical sagebrush)	Stansbury Island (Sagebrush)
Peromyscus maniculatus	18	8
Perognathus parvus	4	14
Reithrodontomys megalotis	0	0
Dipodomys microps	6	0
Dipodomys ordii	16	6
Ammospermophilus leucurus	0	0
Neotoma leopida	0	0
Chaetidopus formosus	0	0
Species	Deep Creek Mountains (Historical sagebrush)	Deep Creek Mountains (Sagebrush)
Peromyscus maniculatus	11	0
Perognathus parvus	2	0
Reithrodontomys megalotis	0	0
Dipodomys microps	1	0
Dipodomys ordii	0	5
Ammospermophilus leucurus	0	2
Neotoma leopida	4	0
Chaetidopus formosus	4	2
Species	House Mountains (Historical P-J)	House Mountains (P-J)
Peromyscus maniculatus	24	2
Perognathus parvus	1	0
Peromyscus truei	0	14
Tamias dorsalis	0	1
Ammospermophilus leucurus	1	0

Table 4.S1. Summary of mixed model results for estimated species richness for the three habitat types with 20 observations from seven locations.

Linear mixed model for the Chao richness estimator with intercept set at sagebrush				
Random effect	*variance*	*standard deviation*		
Location	0.413	0.643		
Variable	*estimate*	*standard error*	*t-value*	*p-value*
Intercept	6.57	0.688	9.561	<0.001*
Habitat – P-J	2.886	0.961	3.002	0.015*
Habitat – ecotone	0.843	0.953	0.884	0.40

* indicates a p-value < 0.05

Table 4.S2. Summary of linear mixed effects model for species diversity for the three habitat types with 20 observations from seven locations.

Linear mixed model for species diversity with intercept set at ecotone				
Random effect	*variance*	*standard deviation*		
Location	0.001	0.029		
Fixed effect	*estimate*	*standard error*	*t-value*	*p-value*
Intercept	0.543	0.055	9.836	< 0.001*
Habitat – P-J	-0.184	0.076	-2.413	0.03*
Habitat – sagebrush	-0.092	0.079	-1.162	0.27

* indicates a p-value < 0.05

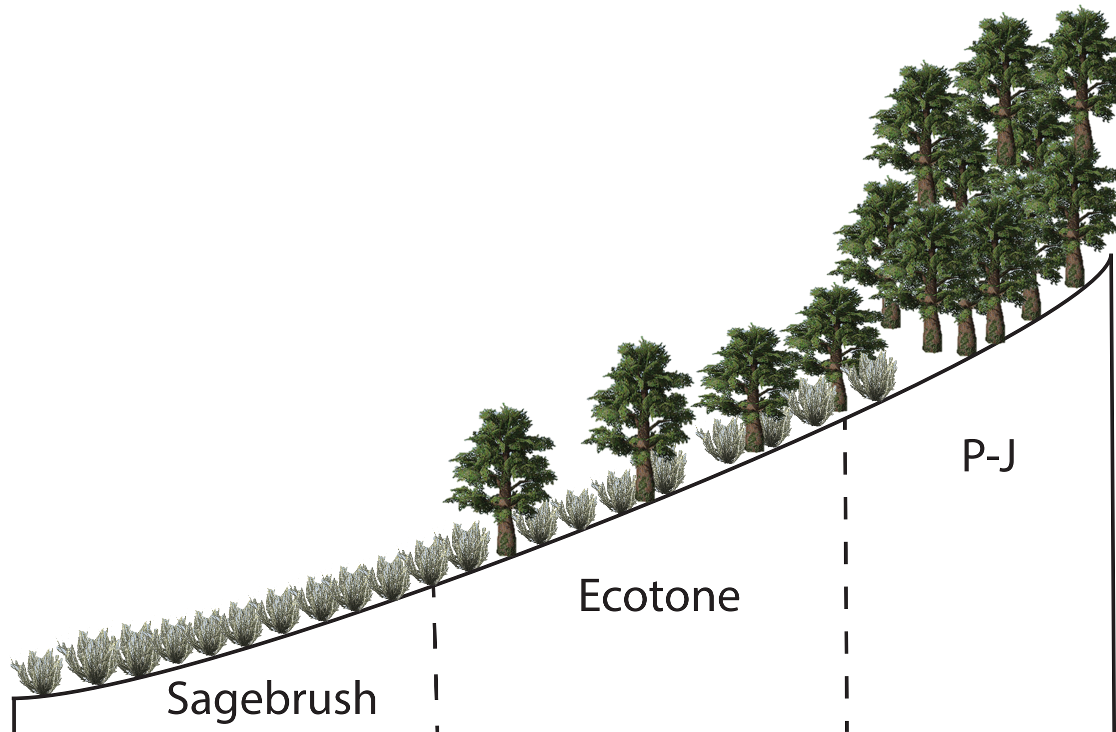

Figure 4.1. Diagram of sagebrush to P-J woodland habitat gradient sampled in the Great Basin with the transition zone (ecotone) between the two primary habitat types. Sagebrush is characterized by having sagebrush and associated grasses and no juniper trees or pinyon-pine. P-J woodlands are dense woodlands of juniper and pinyon-pine with very little understory. Ecotones have both P-J associated trees and an understory of sagebrush and grasses. Most of the trees in ecotones are small compared to those in P-J woodlands.

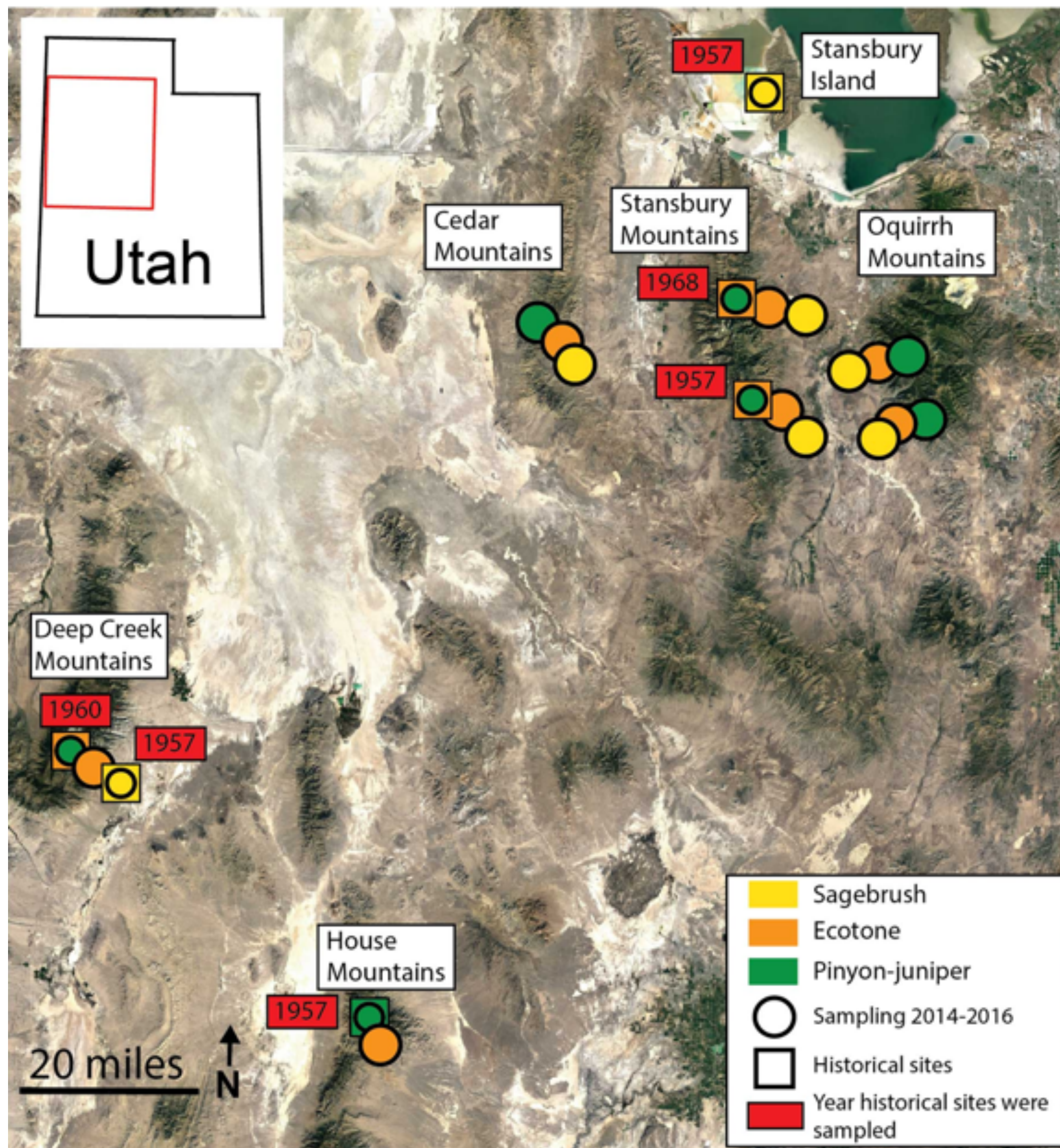

Figure 4.2. Map of recent and historical sampling sites in the Great Basin. Rodents were sampled over sagebrush to PJ woodlands at eight locations. In each location, three habitats were sampled (yellow, brown, and green). Circles represent recent sampling, and squares refer to historical sampling. Squares with circles inside denote sites that were resampled and the colors refer to the habitat types of the sites historically (outer square color) and recently (inner circle color).

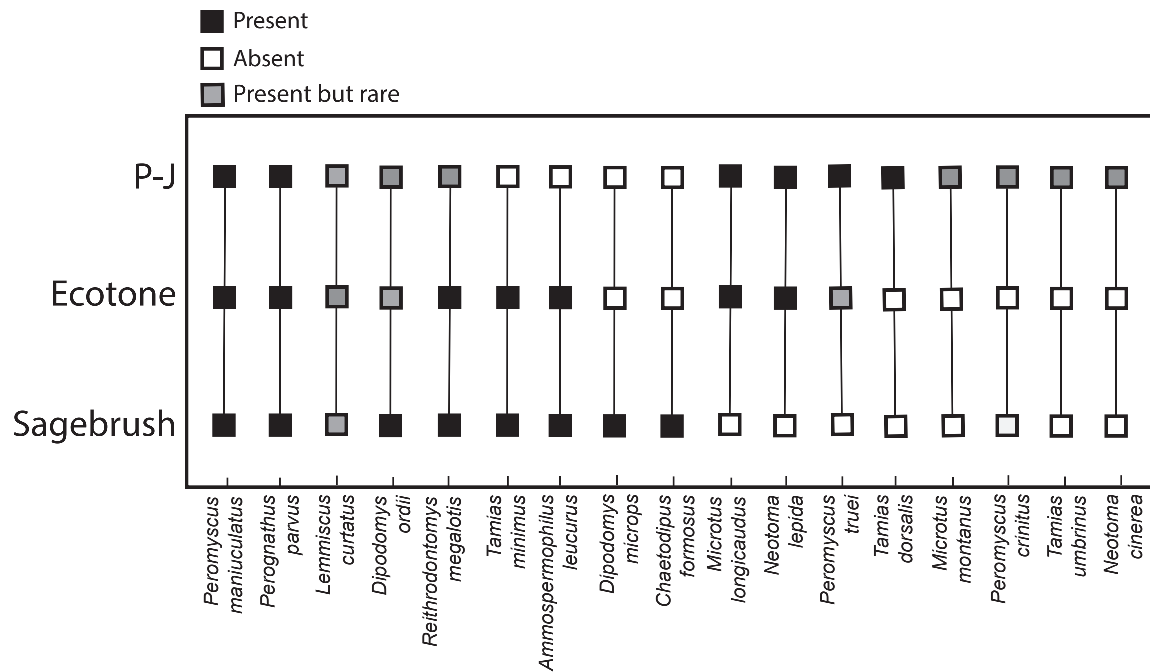

Figure 4.3. The habitat preferences for each species based on where they were captured. All seven sites (six for sagebrush) were pooled together. Species that were less than 1% of total captures for each habitat type were considered present but rare. Rodent species are arranged according to habitat preference. Left to right: generalists, found in sagebrush and ecotones, sagebrush specialists, found in ecotones and P-J, P-J specialists.

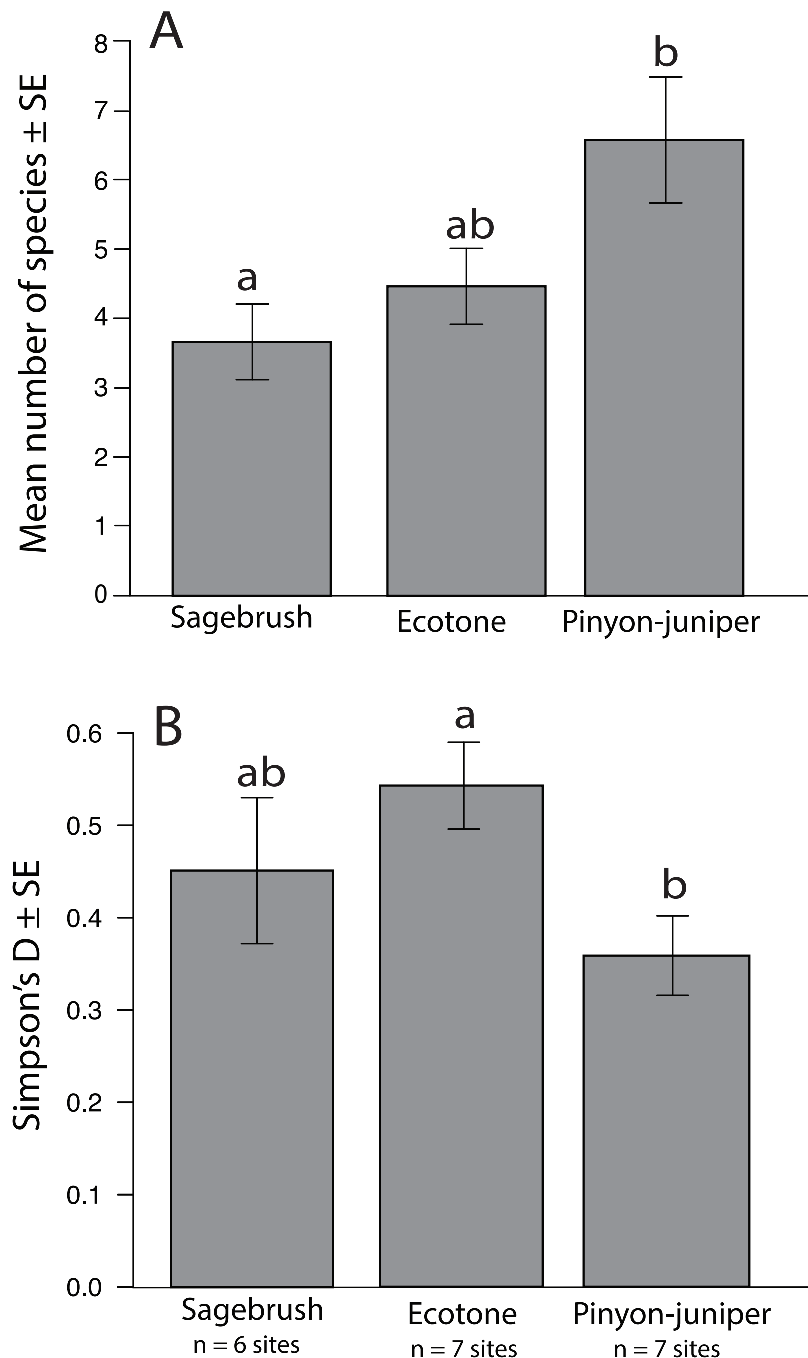

Figure 4.4. Species richness and species diversity for deer mice sampled in 2014 to 2016. A) Estimated species richness using the Chao richness estimator for the three habitat types. Different letters indicate significant differences between habitat types ($P < 0.05$). Sagebrush and P-J sites significantly differed for the Chao estimator. B) Species diversity significantly differs between ecotone and P-J habitat types. Sagebrush did not significantly differ between ecotone or P-J habitats.

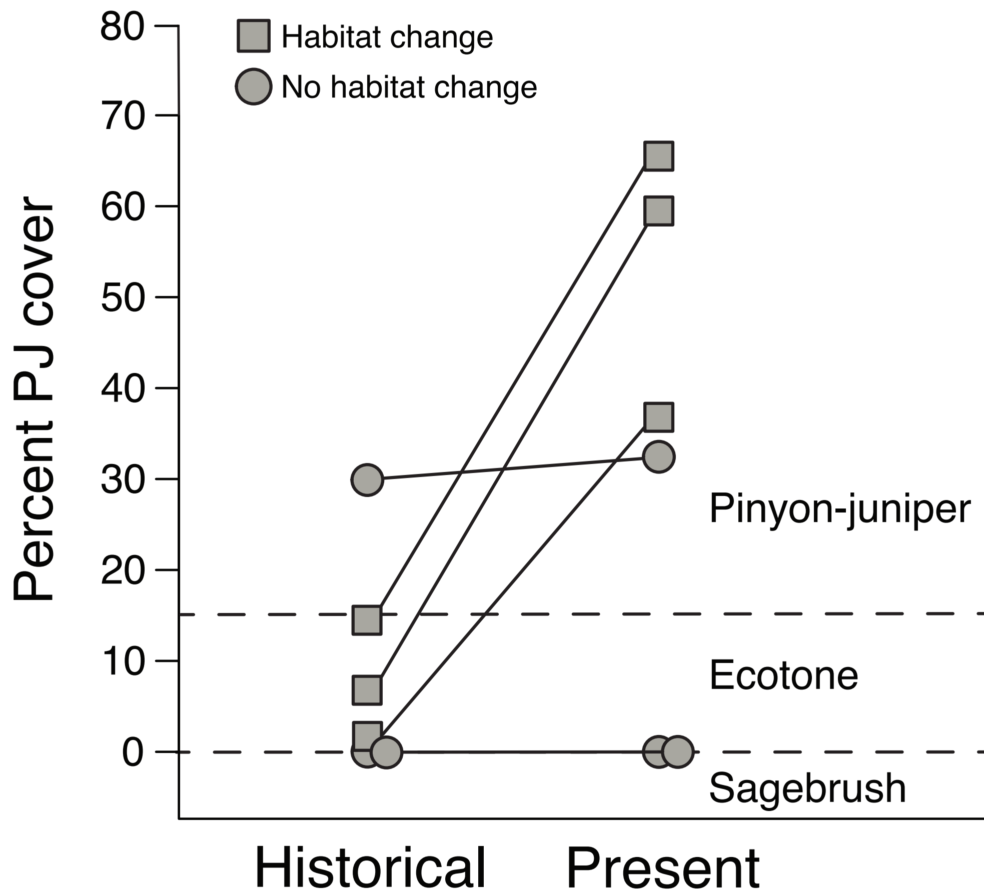

Figure 4.5. Percent pinyon-juniper (P-J) cover in six historically sampled sites when mammals were sampled in the late 1950s, and the percent P-J cover of the same sites sampled in 2014-2016. Sites that cross from one habitat zone to the next are considered sites that changed habitats. Those in the same habitat type did not change over time.

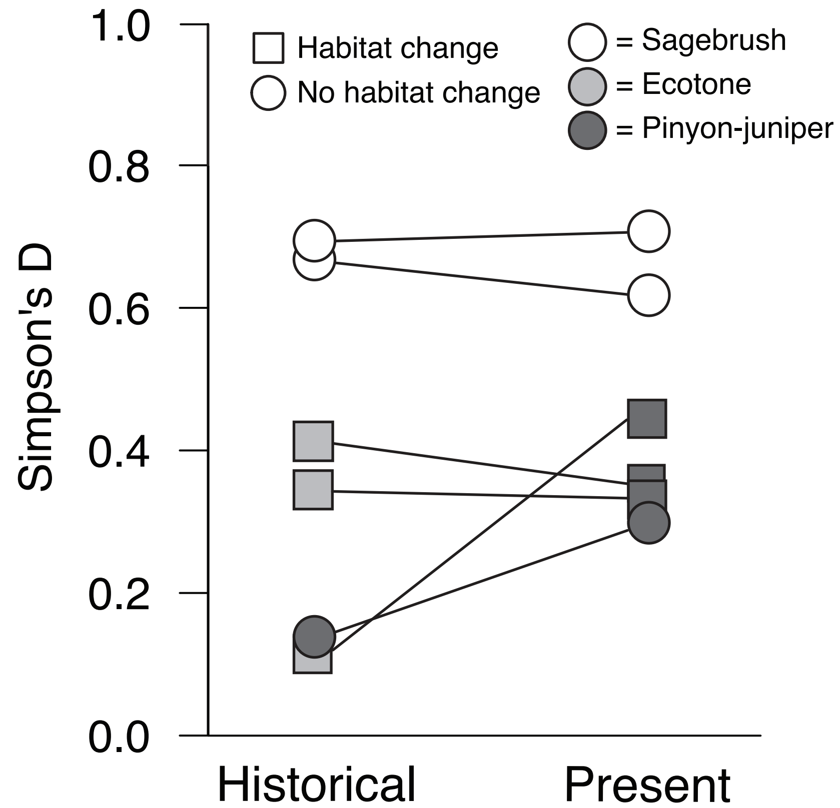

Figure 4.6. Species diversity (Simpson's D) of rodents in historically sampled sites in the 1950s and in 2014-2016. Four of the six sites had no change in diversity. The P-J control site and one P-J conversion site increased in diversity.

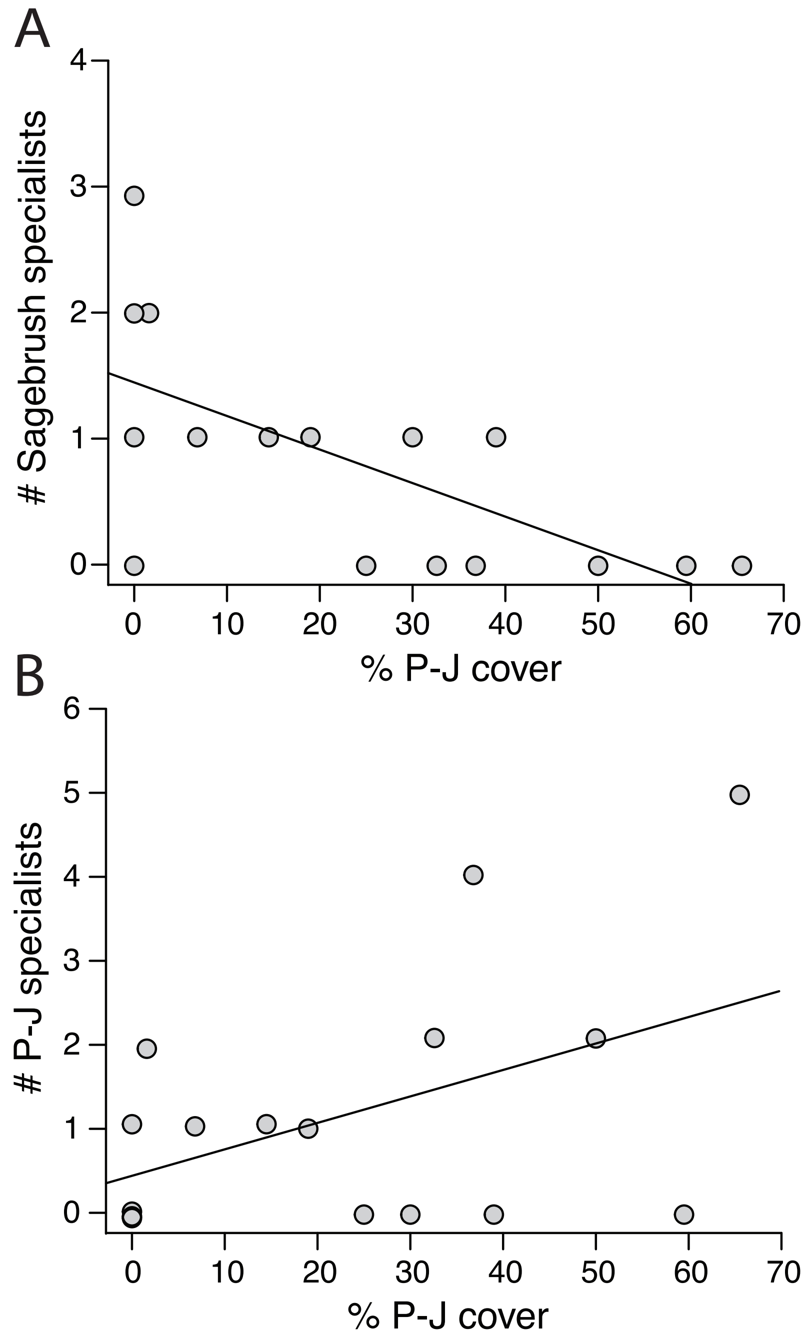

Figure 4.7. The number of sagebrush specialists (A) and P-J specialists (B) plotted against the percent P-J cover for 16 historical sites. There was a significant negative correlation between P-J cover and sagebrush specialists (Spearman rank, $r_s = -0.64$, $p = 0.008$). There is no significant correlation between P-J cover and P-J specialists (Spearman rank, $r_s = 0.35$, $p = 0.19$).

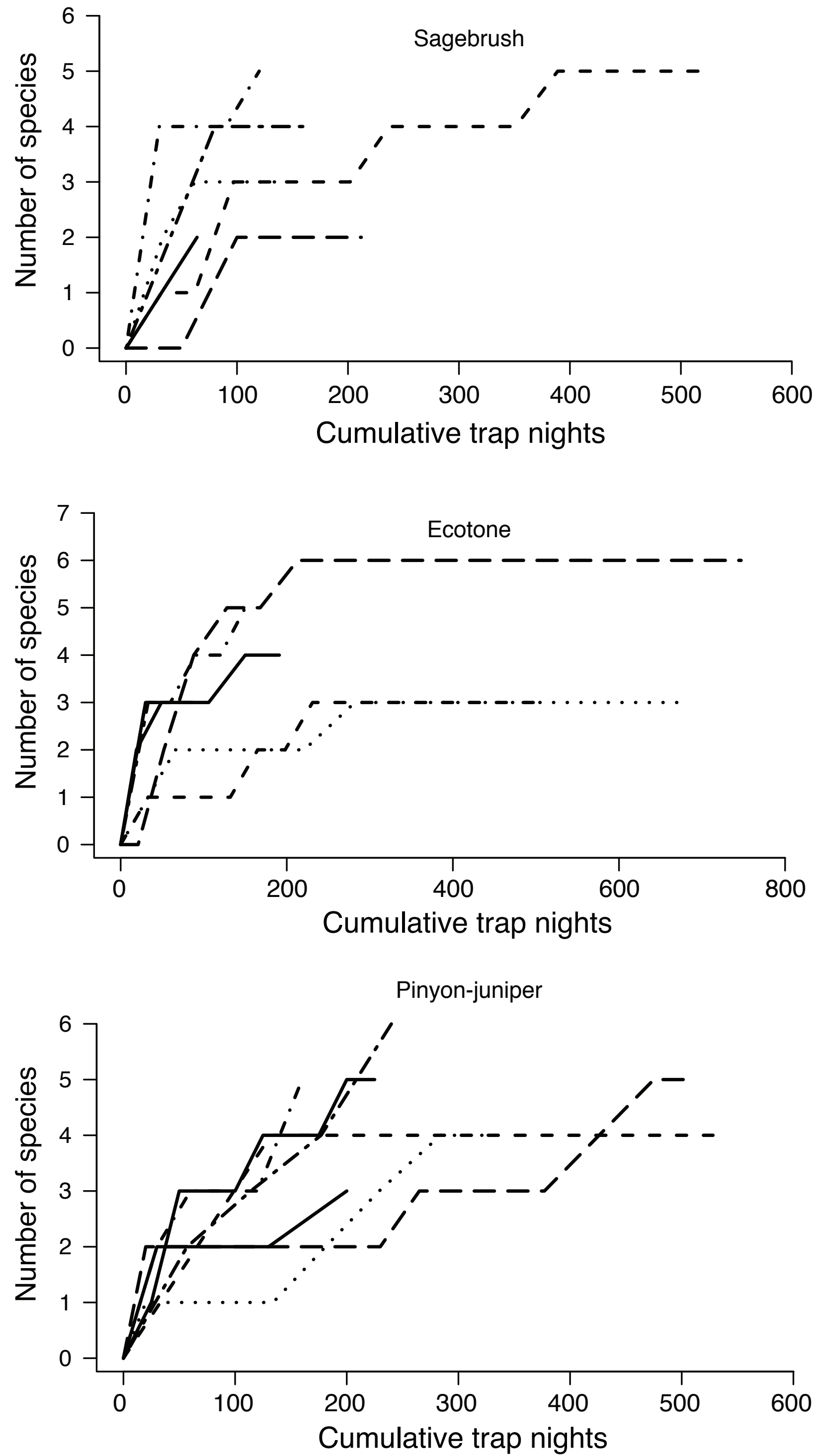

Figure 4.S1. Species accumulation curves for all sites sampled in the Great Basin using cumulative trap nights for each site separated by habitat type.

CHAPTER 5

IMPACT OF ENVIRONMENTAL CHANGE ON PARASITE COMMUNITIES

Abstract

Environmental change is occurring at unprecedented rates and is a threat to biodiversity worldwide. Negative consequences of environmental change are documented for free-living species, but little is known about how parasites will respond to environmental change. Here, we address the question, does parasitic helminth diversity change over time in the Great Basin? Deer mice (*Peromyscus maniculatus*) are sampled for helminth parasites in the Great Basin and compared to historical data from the late 1950s and '60s. Species diversity increased throughout the Great Basin over more than 50 years. This increase in diversity was mainly caused by a decrease in the prevalence and abundance of *Syphacia peromysci*, a direct life cycle nematode, and to a lesser extent, an increase in the number of helminth species. To investigate this pattern, we test whether pinyon-juniper (P-J) expansion or life cycle differences are responsible for these changes to helminth communities. Over the last 50 years, two sites changed from low to high P-J cover over the last 50 years and were resampled in the exact same spots. Both sites showed an increase in parasite diversity and a decrease in *S. peromysci*. However, recent sampling in low and high P-J cover sites did not result in the same patterns, suggesting that habitat change is not the main driver of these differences. Parasite species showing the most changes were ones with direct life cycles. In this system, direct life

cycle parasites are generally more host specific than complex life cycle parasites. Environmental change may impact direct life cycle parasites more than parasites with complex life cycles because of differences in host specificity.

Introduction

Climate change and associated environmental changes are a threat to biodiversity around the world (Travis 2003; Hansen et al. 2010; Sillmann et al. 2013). Climate change has profound effects on wildlife distributions, abiotic components of environments, and species interactions (Parmesan and Yohe 2003; Koh et al. 2004; Tylianakis et al. 2008 Van der Putten et al. 2010). Despite the considerable amount of data on how plants and vertebrates are and will be affected by environmental change (Walther et al 2002; Parmesan and Yohe 2003; Koh et al. 2004; Hamann and Wang 2006; Moritz et al. 2008), there is little empirical data on how parasites are or will be affected. Parasites are traditionally among the last groups to be investigated in ecological systems (Poulin 2007). However, parasites represent a large portion of the world's biodiversity (Price 1980; de Meeûs and Renaud 2002). Understanding how parasite species distributions and interactions will be affected can help predict changes to ecosystem processes and inform conservation decisions in a time of global change (Gomez and Nichols 2013).

It is difficult to predict how parasites will respond to changing environmental conditions due to differences in life history characteristics and transmission dynamics (Rohr et al. 2011; Altizer et al. 2013). Most of the projected responses are the result of predictive models or experiments under laboratory conditions (Patz et al. 2002; Mouritsen et al. 2005; Studer et al. 2010; Altizer et al. 2013; Molnar et al. 2013a, 2013b; Bonnell et al. 2016; Hall et al. 2016). Rising temperatures will cause parasite populations

and distributions to increase because of increased production of infective stages and transmission rates (Harvell et al. 2002; Poulin 2006; Marcogliese 2008). In contrast, Lafferty (2009) suggests that parasites will likely shift their distributions, but there may be little net increase in area (i.e. no expansion or reduction in ranges). Moreover, hosts may undergo range shifts while their parasites lag behind (Phillips et al. 2010; Cizauskas et al. 2017). Developing predictions may depend on characteristics of the parasites themselves, such as life cycle and host specificity (Cizauskas et al. 2017).

Studies examining parasites facing environmental change often focus on endoparasitic helminths, which are typically divided into two categories based on life cycle. Parasites with direct life cycles have one host species required to complete their life cycle. Complex life cycle parasites have two or more required hosts. Several studies suggest that complex life cycle parasites will be affected more than those with direct life cycles because there is a greater chance that one of their obligate host species goes extinct (Rohr et al. 2011; Cizauskas et al. 2017).

An alternative hypothesis predicts that parasites with direct life cycles will be more vulnerable to environmental change, specifically, those which have free-living larvae that must seek new vertebrate hosts (Altizer et al. 2013; Molnar et al. 2013). But not all direct life cycle parasites produce free-living infective larvae. Some species infect new hosts by consumption of the egg stage in the environment (Morand et al. 2007). Eggs of complex life cycle parasites are also consumed in the environment, but they are consumed by intermediate hosts (i.e. snails, arthropods), and infective larvae hatch within these hosts. These larvae are “sheltered” from the environment until the intermediate host is consumed by a vertebrate. Behavioral thermoregulation of intermediate hosts by

seeking more favorable conditions is particularly important for sheltering larvae, especially in higher temperatures (Molnar et al. 2013). If eggs of both direct and complex life cycle parasites are in the environment, one would predict that both would be equally vulnerable to environmental change. However, these life cycles may differ in where most infections take place and how long eggs are subject to environmental conditions.

Different patterns of infection between these two life cycles may help predict which life cycle is most vulnerable to environmental change. Intermediate hosts may aggregate in areas where definitive host spends most of their time (e.g. animal nests, perches) (Smith 2001), especially coprophagous insects. Thus, infective eggs may spend minimal time in the environment before being consumed by an intermediate host through more targeted infection (i.e. consuming infected feces) (Boze et al. 2012). Similarly, direct life cycle parasites may infect new hosts through coprophagy or grooming. However, parasites with direct life cycles may infect new vertebrate hosts more in the environment than through these methods (Stahl 1963; Morand et al. 2007; Spickett et al. 2017). For example, Spickett et al. (2017) found that direct life cycle nematodes transmitted through ingestion of infectious stages in the environment were more prevalent than those that can also be transmitted through coprophagy or grooming. Environmental conditions may have a greater influence on direct life cycle parasites because of where most individuals are infected. We predict that direct life cycle parasites will be more vulnerable to environmental change than those with complex life cycles.

Host specificity is also an important property of parasites and refers to the number of host species that a parasite population can use (Poulin et al. 2007). Parasites with low host specificity should be less affected by environmental change than parasites that can

infect only one host (Bush and Kennedy 1994; Koh et al. 2004; Cizauskas et al. 2017). Parasites that infect many host species can infect other hosts that may still be present following environmental change and extinction of a host species. Low host specificity also allows parasites to spread to new habitats and tolerate environmental change (Poulin et al. 2007). In contrast, parasites with high host specificity may have a higher probability of going extinct with their hosts (co-extinction) (Koh et al. 2004; Lafferty and Kuris 2009).

If differences in life cycle and host specificity matter, habitat change may drive these changes through altering host communities and infection patterns. Throughout the Intermountain West, pinyon-juniper woodlands (P-J) are expanding into and replacing sagebrush steppe habitats (Blackburn and Tueller 1970; Weisberg et al. 2007; Bradley and Fleishman 2008). As P-J replaces sagebrush and canopy cover increases, the understory vegetation becomes less dense (Blackburn and Tueller 1970; Breshears et al. 1998; West 1999). Climate change is a major contributor to these conversions and woody plant expansion worldwide (Idso 1992; Miller and Wigand 1994; Archer et al. 1995; Kelly and Goulden 2008; Clifford et al. 2011). Over the past 50 years, temperatures have increased throughout the Great Basin (Logan et al. 2007) and P-J woodlands have expanded (Bradley and Fleishman 2008). This change in habitat may play a role in altering parasite communities.

Addressing questions related to parasite community structure, life cycles, and host specificity over time are hard to document because there are few historical datasets that document parasites. A historical parasite dataset collected more than 50 years ago is used to address several questions. This dataset includes host-helminth records at sites surveyed

between 1957 and 1968 in the Great Basin in western Utah. From these records, helminth prevalence, abundance, intensity, species composition, and species diversity can be calculated and compared to new data collected more than 50 years later. The most sampled rodent species was deer mice (*Peromyscus maniculatus*). Deer mice are host to a diverse assemblage of helminths, some of which have direct life cycles and some that have complex life cycles.

Here, we address the main question, does parasite diversity change over time in the Great Basin, and if so, which parasite species change? This question will be addressed by comparing current species richness, species diversity, and individual parasite abundance to historical parasite data from the 1950s-1960s in the Great Basin. We then address whether P-J expansion is responsible for any changes in parasite diversity, abundance, or species composition by sampling two sites that have gone from low P-J cover to high P-J cover (P-J conversion). Helminth community structure will be compared to historical data at those sites by sampling in the exact spots where parasites were sampled 50 years ago. Parasites are also sampled in low P-J cover sites and high P-J sites recently to further determine the influence of habitat on parasite community structure. We also determine whether life cycle type contributes to patterns of change over 50 years in the Great Basin by comparing historical nematode prevalence and abundance to recent nematode sampling since some nematodes have direct life cycles and some have complex life cycles. Lastly, we investigate patterns of host specificity between nematodes with direct and complex life cycles.

Methods

Study system

The focal species for this study is the North American deer mouse (*P. maniculatus*), which occupies nearly every habitat in North America. Deer mice are nocturnal and active year-round; they feed primarily on arthropods and seeds. The home range of deer mice varies, but can vary from 0.032 to 1.2 hectares (Stickel 1968). Because deer mice have limited home ranges, we can be confident that the mice are not moving long distances from where they are trapped. Deer mice are host to several groups of endoparasites, including cestodes, nematodes, trematodes, and acanthocephalans. These helminths have either direct life cycles or indirect life cycles (i.e. those with arthropod intermediate hosts).

This study was conducted in the Great Basin from 2014 to 2016. The Great Basin is characterized by a desert ecosystem with north to south running mountain ranges creating a basin and range topography. The valley desert is dominated by sagebrush (*Artemesia* spp.) and associated grasses. In each mountain range, pinyon-juniper woodlands occur at higher elevations. Utah juniper (*Juniperus osteosperma*) and singleleaf pinyon pine (*Pinus monophylla*) are the predominate species (Banner 1992). The mountain ranges are essentially natural replicates because the same habitats occur in each range. Deer mice were trapped in the Stansbury Mountains, Oquirrh Mountains, Cedar Mountains, House Mountains, and Deep Creek Mountains in the Great Basin (Fig. 5.1). Three habitat types were sampled in the Stansbury and Oquirrh Mountains: sagebrush, pinyon-juniper (high P-J cover), and the transition zone between them (ecotone, low P-J cover) (Fig. 5.1).

Historical data

Small mammals were trapped and sampled for parasites throughout Utah and parts of Nevada from 1957 to 1969; each location was trapped for three days on average (Frandsen 1960; Frandsen and Grundmann 1961, Derrick 1971). The animals were dissected to collect all intestinal helminths from the stomach, small intestines, caecum, and large intestines (Frandsen 1960; Derrick 1971). All parasites were identified based on morphology. A record was kept for each individual host trapped and sampled including those that did not have parasites. Field notes from collection trips indicate that all endoparasites from the gastrointestinal tract were collected and counted. Therefore, the prevalence, intensity, abundance, and species diversity of helminth communities can be calculated from these host-parasite records. A field notebook documenting sampling locations includes directions, site-specific details, approximate elevations, and general descriptions of habitat and vegetation. These notes were used to find historically sampled sites, and aerial photographs were obtained from the USDA and USGS to document and verify the historical vegetation. To compare historical and current parasite species composition, only historical sites that were either sagebrush, pinyon-juniper, or a mix of the two habitat types were used (Fig. 5.1). In total, I found 12 sites with those habitat types. From those sites, 400 deer mice were sampled for endoparasitic helminths. Most sites were sampled between 1957 and 1961. One site (Stansbury A) was sampled in 1968.

Animal trapping and processing

Deer mice were trapped using Sherman traps (H.B. Sherman Traps, Inc.). Traps were placed five to ten meters apart in transects. Whole oats and birdseed were used as bait. All animal handling and processing was approved by the Institutional Animal Care

and Use Committee of the University of Utah. Trapping was terminated at each site when 25 deer mice were trapped and euthanized. Because deer mice populations were low in numbers, four sites had less than 25 animals trapped (The Cedar Mountains, Deep Creek Mountains, and House Mountains; Fig. 5.1), despite 150 trap nights or more. Animals that were captured were placed into a Ziploc bag along with the contents of the trap to recover any ectoparasites that came off the animal while it was in the trap. The animal was euthanized with isoflurane. It was placed on ice and taken to the lab for further processing. In the lab, the mass, body length, tail length, ear length, and leg length of each animal was measured. Animals were then dissected. Their digestive tracts (i.e. stomach, small intestine, caecum, and large intestine) were removed and placed into a vial and frozen at -80 degrees C for later dissection. After processing, animal carcasses were deposited at the Natural History Museum of Utah, in Salt Lake City, UT.

Parasite collection

Digestive tracts were thawed and separated into the small intestine, stomach, caecum, and large intestine and dissected separately. In separate glass petri dishes, each part was cut open and the inside of the intestinal wall was scrapped with a glass slide to remove all attached parasites. The petri dishes were examined under a dissecting microscope to find any helminths. Water was added to the contents of the gastrointestinal tracts in order to make finding worms easier under the dissecting scope by breaking up and diluting food particles and feces. To ensure that worms were not missed, the contents of the gastrointestinal tracts were separated into several smaller petri dishes and examined separately. This ensure that all the liquid could be examined for parasites. This was especially important for finding pinworms in the caecum. All helminths were placed

in 70% ethanol and stored in a freezer until they were used for identification. Helminths were categorized as being either nematodes, cestodes, trematodes, or acanthocephalans based on morphology. Molecular methods were then used to split each taxonomic group into species groups because of potential cryptic species and the number of parasites that were recovered. Gastrointestinal tracts are the areas where most rodent helminths are found (Georgiev et al. 2007; Morand et al. 2007).

Parasite identification

DNA from each helminth specimen (nematode, cestode, trematode, acanthocephalan) was extracted using a Qiagen Blood and Tissue Kit. Fragments of the mitochondrial COI gene was amplified using a different set of primers for each helminth group (Table 5.1). The PCR reaction mixture was a 27μL reaction containing 2 μL of DNA, 0.5 μL of 10 mM dNTP, 0.5 μL of each 10 μM primers, 2.5 μL of NEB 10x buffer, 20.8 μL water, and 0.2 μL Taq DNA polymerase. The reactions ran for an initial denaturing at 95°C for 1 minute, followed by 40 cycles of denaturing at 95°C for 1 minute, annealing at 53°C for 90 s, extension at 72°C for 2 minutes, and a final extension at 72°C for 2 minutes was completed. Successful amplifications were visualized on a 1% agarose gel following electrophoresis by adding 4μL of unpurified PCR product in 2μL of loading dye.

Successful amplifications were sequenced using Sanger sequencing (MCLAB, San Francisco, CA). Sequences were aligned and split into species groups using the software program Geneious (Kearse et al. 2012). Species groups were formed by performing a MAFFT alignment on all sequences for each helminth group (nematodes, cestodes, trematodes, and acanthocephalans) to determine pairwise percent identity. We

used a species group cutoff of 95% pairwise similarity (Derycke et al. 2010; Armenteros et al. 2014). However, each species group we identified had greater than 97% similarity within the group, and differences between species groups was less than 90%. We identified seven species of nematodes in deer mice, four species of cestodes, one species of trematode, and two species of acanthocephalans.

Species names were matched with each species group. For nematodes, DNA was extracted from individual worms that were identified to species based on morphology by Michael Kinsella (HelmWest Laboratory; Gritzen 2012). These identified individuals were then analyzed together with the unknown species groups and matched according to sequence similarity. There were two nematode species groups that we were not able to assign to a particular species. Specimens from these groups were morphology distinct and were identified based on morphology by Michael Kinsella. Cestodes were identified using the same molecular methods. Species names were added to cestode sequences by Vasyl Tkach based on the morphology of the sequenced specimens (University of North Dakota).

Change in P-J cover over time

In addition to the records of parasites throughout the Great Basin, there were two sites that underwent habitat change. These sites were a mix of sagebrush and pinyon-juniper woodlands historically based on habitat descriptions in field notes and aerial photographs. These sites had low P-J cover (ecotones) in the past and are both located in the Stansbury Mountains (Stansbury A and Stansbury B; Fig. 5.1). After 50 years, pinyon-juniper expanded, and these sites are now dense pinyon-juniper woodlands with very little understory plants, such as sagebrush and associated grasses.

ImageJ (Rasband 2016) was used to estimate the percent of P-J cover at two sites both historically and currently using thresholding and particle analysis (Abramoff et al. 2004; Pérez and Pascau 2013). Historical aerial photographs were gathered from the USGS (https://earthexplorer.usgs.gov) and from Derrick (1971). Derrick (1971) describes sampling the rodent community for parasites and includes an aerial photograph of the exact location where traps were placed. Google Earth was used for current P-J cover. Each study site was located in Google Earth or in an aerial photograph. Percent cover was estimated per hectare. Hectare square images produced in Google Earth or from the historical aerial image were imported into ImageJ. Percent tree cover was estimated by measuring the area of all the trees in the image. The color threshold of each image was adjusted so that only trees were selected. A threshold cutoff was used that was determined by the smallest tree in the image. Smaller areas selected were excluded because they were not trees and should not be included in the estimation of tree cover. The areas of all the trees were added up and divided by the total area of the one-hectare image.

Sampling low and high P-J cover sites

To further investigate if habitat is responsible for any changes to parasite community structure, parasites were sampled in low P-J cover sites and high P-J cover sites at four replicate locations (Fig. 5.1). These data were compared to the data over time from historic sampling (low P-J cover) and more recent sampling (high P-J cover). If habitat is responsible for differences in parasite community structure between the two time points, then similar patterns would be observed when sampling from low P-J cover to high P-J cover sites.

Life cycle differences and host specificity

Life cycles were determined for each parasite species. All cestodes, acanthocephalans, and trematodes have complex life cycles. Nematodes have both complex and direct life cycles. The life cycle of each nematode species was determined according to the literature. The host specificity was determined for each nematode species in the southwestern U.S. by searching the literature and dissertations that were written as part of the historical parasite data in the 1950s and 60s.

Analyses

Two types of species accumulation curves were created to determine if each deer mice was thoroughly sampled for parasites. We used number of deer mice sampled (sample-based accumulation) to determine parasite species accumulation (see Fig. 5.S1). The number of parasite individuals (individual-based accumulation) was also used to determine thorough sample coverage by using accumulation and extrapolation using the Chao richness estimator to find whether further parasite sampling would lead to more species. Individual-based accumulation and extrapolation was done using the iNEXT package (Hsieh et al. 2016) in R (R Core Team 2016; see Fig. 5.S2).

Prevalence was calculated by taking the number of hosts infected with a given parasite divided by the total number of hosts sampled throughout the Great Basin or at the site level. Mean intensity (± SE) was calculated by taking the average number of parasite individuals per infected host (Bush et al. 1997). The evenness of the parasite species in the community was determined by using Simpson’s diversity index (Simpson’s D), which takes into account the relative abundance of each species. To compare relative parasite abundances, rank abundance plots were produced for the Great Basin and at the

site level for the two P-J converted sites. Statistical analyses for diversity and species richness were performed using the Vegan package (Oksanen et al. 2016) in R (R Core Team 2016).

Results

Parasite sampling

I trapped 382 deer mice from 16 sites. Out of these 382 mice, 116 (30.4%) were infected with at least one helminth species. Historically, 224 out of 400 mice (56%) were infected with at least one helminth species. Historically and more recently (2014-2016), sample-based species accumulation suggests that helminth parasites were not added after sampling approximately 300 deer mice (Fig. 5.S1A). Using individual parasites (individual-based), rather than hosts as the sampling unit, an asymptote was not reached (Fig. 5.S2A). After using the Chao richness estimator to extrapolate species richness given greater sampling, it is predicted that current sampling will have higher species richness than historical sampling (Fig. 5.S2A).

Comparison throughout the Great Basin

Overall, species richness of parasites in deer mice increased in the Great Basin over 50 years (Table 5.2). There were 13 species historically and 14 species found during current sampling. Parasite species found in deer mice in the Great Basin and the prevalence and mean intensity of each are listed as well as the historical prevalence and mean intensity of the same parasite species (Table 5.2). There is a decrease in the prevalence of *S. peromysci* (Table 5.2). Comparing the current species composition to historical species composition, a few species were either lost or gained following

environmental change. The nematode species *Heligmosomoides vandegrifti*, *Mastophorus muris*, *Syphacia montana*, and a second acanthocephalan species were new species that were not found historically. Additionally, *H. polygyrus, Trichuris stansburyi,* and *Brevistriata skrjabini* were found in the past and were not found in deer mice during current sampling (Table 5.2). Species diversity increased throughout the Great Basin (Fig. 5.2A). Rank abundance plots of parasite species show a dramatic decrease in the abundance of *S. peromysci* (Fig. 5.2B and C).

Comparison following P-J conversion

Pinyon-juniper cover increased in two sites sampled for parasites historically (Fig. 5.3). Both sites were a mix of sagebrush and P-J in the past with a percent P-J cover between two and eight percent. Current estimates of P-J cover show that they are now greater than 30% P-J. The Stansbury B site is approximately 60% P-J.

Sample-based species accumulation curves indicate that enough deer mice were sampled for parasites at the two P-J conversion sites (Fig. 5.S1B and C). Thorough sampling of parasites was also indicated by the asymptotes of individual-based accumulation curves using Chao estimation (Fig. 5.S2B and C).

Parasite prevalence and mean intensity for the two sites resampled after being converted to P-J are also listed (Table 5.3). Species richness increased in P-J converted sites (five historically, eight after current sampling) (Table 5.3). This was mainly driven by one site, Stansbury B. A trematode species, *Brachylaima microti*, and an acanthocephalan species, *Moniliformis clarki,* are now present in this P-J converted site. Only four *Bra. microti* and three *Mo. clarki* were found out of 400 mice sampled historically. *Brachylaima microti* and *Mo. clarki* were found in sagebrush habitats

historically and are now found in P-J woodlands. Additionally, one acanthocephalan species was found historically, while two acanthocephalan species were found following resampling. Species diversity also increased at the two sites that were converted to P-J woodlands (Fig. 5.4A). The reasons for the increase in diversity are slightly different for each site. The Stansbury A site showed a decrease in the abundance of *S. peromysci*, which caused the abundance of each species to be more even (Fig. 5.4B and C). At the Stansbury B site, *S. peromysci* decreased, but the number of species also increased (Fig. 5.4D and Fig. 5.4E).

Comparison of low P-J to high P-J sites

Parasites were also sampled in low P-J cover sites and high P-J cover habitat sites at four replicate locations in the Stansbury and Oquirrh Mountains. To determine if changes to parasite communities were mainly driven by habitat, we compared parasite diversity in these two habitat types. We also compared the abundances of *S. peromysci,* the species that showed the most drastic change in abundance. Three of the sites showed slight increases in diversity, while the fourth one decreased (Fig. 5.5). None of the diversity values for these sites were as low as the diversity values historically (Fig. 5.2A, Fig. 5.4A, and Fig. 5.5). There is no pattern in the prevalence or total abundance of *S. peromysci* between low P-J cover sites and high P-J cover sites (Table 5.4). Prevalence decreased from low to high P-J habitats in two locations and increased slightly at the other two locations. Total abundance increased at three locations from low to high P-J cover, while decreasing at the fourth location (Table 5.4).

Life cycle differences and host specificity

Of the seven direct life cycle nematodes, five (71%) were absent either historically or after resampling. Three nematodes were absent after resampling. *Syphacia peromysci*, a direct life cycle nematode species and the most prevalent and abundant parasite species historically, dramatically decreased in both prevalence (Table 5.2, Table 5.3) and abundance (Fig. 5.2, Fig. 5.4) throughout the Great Basin and at the two P-J converted sites. Of the three complex life cycle nematodes, only one was absent in the past (*Ma. muris*). Taking all complex life cycle parasites into account, no complex life cycle species were absent after resampling. Two species were recorded that were not present in the Great Basin historically (Table 5.2).

The host specificity was determined for each nematode species (Table 5.5). The six nematodes with direct life cycles infect either one or two rodent species in the Great Basin. The three nematodes with complex life cycles have three or more rodent hosts (Table 5.5).

Discussion

We addressed the question, does parasite diversity change over time in the Great Basin, and if so, which parasite species change? There was an increase in parasite diversity in the Great Basin. This was mainly due to the decrease in the direct life cycle nematode *Syphacia peromysci*, which led to greater evenness among the remaining species. The two sites that were converted to P-J also showed a decrease in the abundance *S. peromysci* over time. In the Great Basin, this species mainly parasitizes deer mice. Grundmann and Frandsen (1960) state that this species is almost exclusively found in *Peromyscus* species and was universally distributed throughout the Great Basin. *Syphacia*

peromysci is a pinworm with a direct life cycle. Hosts are infected by *Syphacia* spp. by ingesting infective eggs from the perianal region of other hosts, when licking themselves, or from contaminated materials in the environment (Stahl 1963).

The comparison of low and high P-J habitat types (Table 5.4) suggests that the changes in parasite species diversity and the abundance of *S. peromysci* is not caused solely by habitat change. There was no pattern in *S. peromysci* abundance over the four sampled locations. Further evidence to this is that there was a big decrease in the abundance of *S. peromysci* throughout the entire Great Basin (including sagebrush sites) and not just at sites that were converted to P-J woodlands. Grice and Prociv (1993) found that eggs of a similar species, *Syphacia obvelata*, are not very resistant to desiccation and suggest that this limits the transmission potential of *S. obvelata* compared to other direct life cycle nematodes. Furthermore, Froeschke et al. (2010) found a positive correlation between *S. obvelata* prevalence and rainfall and humidity and a negative correlation between *S. obvelata* prevalence and temperature. Warmer temperatures may cause eggs to desiccate and become less infective, even those eggs on the perianal region of hosts that are subject to outside temperatures. Even though infection and reinfection can occur through coprophagy and grooming behavior (Morand et al 2007), this may not be sufficient to sustain large populations of *S. peromysci* in host populations. Environmental infections may be more important, which would require resistance of infective eggs to environmental conditions. Over the last 50 years, temperatures have increased throughout the Great Basin (see Fig. 5.S3).

Another pinworm found in deer mice is *Aspiculuris americana*. This species has similar prevalence and mean intensity in both time points sampled (Table 5.2). In the two

P-J converted sites, *A. americana* was not present historically when habitats had low P-J cover. Current parasite sampling suggests that this may not be based on habitat. Deer mice collected from both low and high P-J cover sampled recently were infected with *A. americana*. Little is known about the life cycle of *A. americana*, but the life cycle of a similar species, *A. tetraptera*, has been described (Anya 1966). Eggs hatch in the host and are shed in the feces as infective larvae. The larvae, compared to the eggs of *S. peromysci,* may be more tolerant to environmental conditions. The low prevalence in *P. maniculatus* (5/382) and historical sampling suggests *A. americana* mainly infects *Microtus longicaudus* (Frandsen 1960; Derrick 1971). These pinworms may be more dependent on *M. longicaudus* than deer mice. Future work should examine how warmer temperatures or drier conditions may impact the infectiveness of both pinworms, *S. peromysci* and *A. americana.*

Three nematode species were found in 2014-2016 that were not found historically: *Mastophorus muris*, *S. montana*, and *Heligmosomoides vandegrifti*. In a catalogue of parasites from North American rodents, Doran (1955) did not list *Ma. muris* as occurring in *P. maniculatus*. This species was listed as a parasite of *P. leucopus*, which does not occur in the Great Basin. However, this species was found in deer mice in northeastern Quebec (Shad 1956). *Mastophorus muris* is also found in white-footed mice in eastern deciduous forests in Pennsylvania (Vandegrift and Hudson 2009). This species is similar in morphology to *Protospirura numidica* (M. Kinsella, personal communication) but was split from the *Protospirura* genus (Chitwood 1938). This species may have been misidentified in the historical dataset. These species are greater than 5% similar based on COI sequence similarity. This may be the first record *Ma.*

muris in *P. maniculatus* in the Great Basin, especially if this species was misidentified in the past. The other two species not found historically were *S. montana* and *H. vandegrifti*. *Syphacia montana* in *P. maniculatus* may be an accidental infection; only one mouse was infected. This species is not normally a parasite of *P. maniculatus* (Dyer 1969). *Heligmosomoides vandegrifti* is a new species described from white-footed mice (*P. leucopus*) in Pennsylvania (Durette-Desset and Kinsella 2007). There were no undescribed species in the historical data.

There were also three nematode species that were found historically, but were not found during resampling: *Brevistriata skrjabini*, *H. polygyrus* (= *Nematospiroides dubius,* Baylis 1926; Behnke et al. 1991), and *Trichuris stansburyi*. *Brevistriata skrjabini* was found in one deer mouse historically. This parasite is extremely rare and is mainly found in Siberian chipmunks in Asia (*Tamias sibiricus*). Likewise, *T. stansburyi* is also rare and the only documented cases of this species is from a deer mouse in the Great Basin (Frandsen and Grundmann 1961a). *Heligmosomoides polygyrus* in *P. maniculatus* has been suggested to be the result of accidental infections (Forrester 1971), which may explain the low historical prevalence (5/400) and not finding this species during resampling.

In a recent review, Cizauskas et al. (2017) suggest that parasites are as prone to adverse effects as free-living species and suggest that parasites with direct life cycles will be less affected by climate change than parasites with complex life cycles. An alternative hypothesis predicts that complex life cycle parasites are sheltered from environmental conditions because they are almost always in a host (Molnar et al. 2013; Kutz et al. 2014). Our results are consistent with this hypothesis. Of the three nematode species that

were absent following resampling, they all have direct life cycles (Table 5.2). The nematode species showing the biggest change in prevalence and abundance was *S. peromysci*, a direct life cycle parasite.

Host specificity may explain the differences between complex and direct life cycle parasites in this system. Parasites that can infect several host species should be relatively stable to environmental fluctuations. In this system, the complex life cycle parasites, *Protospirura numidica* and *Pterygodermatites peromysci* (= *Rictularia coloradensis,* Lichtenfels 1970), infect insect intermediate hosts. For example, the beetle *Eleodes tuberculata* is the main intermediate host for *P. numidica* (Cook and Grundmann 1964; Anderson 2000), but three other insect intermediate hosts have been found (Healey and Grundmann 1974). These species are also coprophagic on mouse feces and are often found in close proximity to deer mice (Healey and Grundmann 1974). *Protospirura numidica* also infects up to seven other rodent species in the Great Basin besides *P. maniculatus* (Cook and Grundmann 1964). *Ceuthophilus* spp. (camel crickets) are the main intermediate hosts of *Pt. peromysci* (Luong and Hudson 2012). This parasite may also use other arthropod species as intermediate hosts similar to other parasite species in the same genus (Anderson 2000). *Pterygodermatites peromysci* infects up to five other rodent species in the Great Basin (Grundmann and Frandsen 1960; Frandsen and Grundmann 1961b). *Mastophorus muris* parasitizes two more species other than *P. maniculatus*. These records are from eastern New Mexico, and both species are found in the Great Basin (Pfaffenberger et al. 1985). More information is needed for *Ma. muris* regarding host specificity since this may be a new record for this species in the Great Basin. Furthermore, deer mice and the intermediate hosts for these three parasite species

are widely distributed throughout the region. All three parasite species are also found in low and high P-J habitat types. These generalist parasite species would not be as vulnerable to changes in the environment as parasites with hosts that are habitat specialists. Future studies on parasites and environmental change should consider the distributions of all the hosts required for the parasites to complete their life cycle as well as host specificity.

In terms of direct life cycle nematodes, *Syphacia peromysci* is primarily a parasite of *P. maniculatus*, but it also infects one other rodent species in the Great Basin, *Reithrodontomys megalotis* (Grundmann and Frandsen 1960). This rodent is a generally restricted to grassy weedy habitats, such as sagebrush (Webster 1982). The combination of high host specificity and the transmission dynamics within the environment vs. infection due to grooming or coprophagy may account for the dramatic decrease in *S. peromysci* prevalence and abundance. *Brevistriata skrjabini* and *Trichuris stansburyi* may only infect deer mice, but more information is needed on these parasites in the Great Basin in terms of host specificity.

In conclusion, parasite species diversity increased over 50 years in the Great Basin. This was mainly caused by a decrease in the prevalence and abundance of *S. peromysci*. The abundance of *S. peromysci* did not decrease from low to high P-J cover habitat types sampled in 2014-2016, suggesting that this decrease is not caused by strictly habitat change. Increasing temperatures or other changes related to climate change throughout the Great Basin may explain these results; however, further research is necessary. Our results also suggest that parasites with direct life cycles may be affected more by environmental change than those with complex life cycles due to differences in

host specificity.

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References

Abràmoff, M. D., P. J. Magalhães, and S. J. Ram, 2004. Image processing with ImageJ. Biophotonics International 11:36-42.

Anderson, R. C., 2000. Nematode Parasites of Vertebrates: Their Development and Transmission. CABI Publishing, New York City, New York.

Anya, A. O. 1966. Studies on the biology of some oxyurid nematodes. II. The hatching of eggs and development of *Aspiculuris tetraptera* Schulz, within the host. Journal of Helminthology 40:261-268.

Armenteros, M., A. Rojas-Corzo, A. Ruiz-Abierno, S. Derycke, T. Backeljau, and W. Decraemer. 2014. Systematics and DNA barcoding of free-living marine nematodes with emphasis on tropical desmodorids using nuclear SSU rDNA and mitochondrial COI sequences. Nematology 16:979-989.

Bonnell, T.R., Ghai, R.R., Goldberg, T.L., Sengupta, R. and Chapman, C.A. 2016. Spatial patterns of persistence for environmentally transmitted parasites: Effects of regional climate and local landscape. Ecological Modelling 338:78-89.

Boze, B.G., Hernandez, A.D., Huffman, M.A. and Moore, J. 2012. Parasites and dung beetles as ecosystem engineers in a forest ecosystem. Journal of Insect

Behavior 25:352-361.

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. The Journal of Parasitology 83:575-583.

Bush, A. O., and C. R. Kennedy. 1994. Host fragmentation and helminth parasites: hedging your bets against extinction. International Journal for Parasitology, 24, 1333-1343.

Chitwood, B. G. 1938. The status of *Protospirura* vs. *Mastopharus* with a consideration of the species of these genera. Livro jubilar do Professor Lauro Travassos. 115-118.

Cizauskas, C.A., C. J. Carlson, K. R. Burgio, C. F. Clements, E. R. Dougherty, N. C. Harris, and A. J. Phillips. 2017. Parasite vulnerability to climate change: an evidence-based functional trait approach. Royal Society Open Science 4:160535.

Clifford, M. J., N. S. Cobb, and M. Buenemann. 2011. Long-term tree cover dynamics in a pinyon-juniper woodland: climate-change-type drought resets successional clock. Ecosystems 14:949-962.

De Meeûs, T., and F. Renaud. 2002. Parasites within the new phylogeny of eukaryotes. Trends in Parasitology 18:247-251.

Derrick, P. I. 1971. The concept of “landscape epidemiology” as it applies to endoparasitism of small mammals in selected habitats of South Willow Canyon, Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Derycke, S., J. Vanaverbeke, A. Rigaux, T. Backeljau, and T. Moens. 2010. Exploring the use of cytochrome oxidase c subunit 1 (COI) for DNA barcoding of free-living marine nematodes. PLoS One 5:e13716.

Durette-Desset, M. C., and J. Kinsella. 2007. A new species of *Heligmosomoides* (Nematoda, Heligmosomidae) parasitic in *Peromyscus maniculatus* (Rodentia, Cricetidae) from Pennsylvania, USA. Acta Parasitologica 52:342-345.

Dyer, W. G. 1969. A Checklist of the Protozoa and Helminths of the Deer Mouse, *Peromyscus maniculatus*, in North America. American Midland Naturalist 43:258-262.

Forrester, D. J., 1971. *Heligmosomoides polygyrus* (= *Nematospiroides dubius*) from wild rodents of northern California: natural infections, host specificity, and strain characteristics. The Journal of Parasitology 57:498-503.

Frandsen, J. C. 1960. Endoparasitism in isolated populations of rodents of the Lake Bonneville Basin, Utah. Ph.D. Thesis, University of Utah. Salt Lake City, Utah, USA.

Frandsen, J. C., and A. W. Grundmann. 1961a. Trichuris stansburyi and Gongylonema mysciphilia, two new species of nematodes from the deer mouse in Utah. Proceedings of the Helminthological Society of Washington 28:91-94.

Frandsen, J. C., and A. W. Grundmann. 1961b. Endoparasitism in isolated populations of rodents of the Lake Bonneville Basin, Utah. The Journal of Parasitology 47:391-396.

Froeschke, G., R. Harf, S. Sommer, and S. Matthee. 2010. Effects of precipitation on parasite burden along a natural climatic gradient in southern Africa–implications for possible shifts in infestation patterns due to global changes. Oikos 119:1029-1039.

Georgiev, B. B., R. A. Bray, and T. J. Littlewood. 2007. Cestodes of small mammals: Taxonomy and life cycles. Pp. 29-62 in Micromammals and Macroparasites: From Evolutionary Ecology to Management (S. Morand, B. R. Krasnov, and R. Poulin, eds.). Springer. Tokyo, Japan.

Grice, R. L. and P. Prociv. 1993. In vitro embryonation of *Syphacia obvelata* eggs. International Journal for Parasitology 23:257-260.

Gritzen, C. M. D. 2012. Investigating the patterns of coinfections with gastrointestinal helminths and Sin Nombre virus in deer mice. M.S. Thesis, University of Utah. Salt Lake City, Utah, USA.

Grundmann, A. W., and J. C. Frandsen. 1960. Definitive host relationships of the helminth parasites of the deer mouse, *Peromyscus maniculatus*, in the Bonneville Basin of Utah. The Journal of Parasitology 46:673-677.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773-2786.

Hall, R. J, L. M. Brown, and S. Altizer. 2016. Modeling vector-borne disease risk in migratory animals under climate change. Integrative Comparative Biology 56:353-364. doi: 10.1093/icb/icw049.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158-2162.

Healey, M. C., and A. W. Grundmann. 1974. The Influence of intermediate hosts on the infection pattern of *Protospirura numidica criceticola* Quentin, Karimi, and

Rodriguez De Almeida, 1968 (Nematoda: Spiruridae) in the Bonneville Basin, Utah. Proceddings of the Helminthological Society of Washington 41:59-63.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12 URL: http://chao.stat.nthu.edu.tw/blog/software-download/.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Mentjies, and A. Drummond. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647-1649.

Kelly, A. E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences 105:11823-11826.

Koh, L. P., R. R. Dunn, N. S. Sodhi, R. K. Colwell, H. C. Proctor, and V. S. Smith, 2004. Species coextinctions and the biodiversity crisis. Science 305:1632-1634.

Kutz, S. J., E. P. Hoberg, P. K. Molnár, A. Dobson, and G. G. Verocai. 2014. A walk on the tundra: host–parasite interactions in an extreme environment. International Journal for Parasitology: Parasites and Wildlife 3:198-208.

Lafferty, K. D., and A. M. Kuris. 2009. Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364:1659-1663.

Logan, J. A., J. Régnière, D. R. Gray, and A. S. Munson. 2007. Risk assessment in the face of a changing environment: gypsy moth and climate change in Utah. Ecological Applications 17:101-117.

Luong, L. T., and P. J. Hudson. 2012. Complex life cycle of *Pterygodermatites peromysci*, a trophically transmitted parasite of the white-footed mouse (*Peromyscus leucopus*). Parasitology Research 110:483-487.

Marcogliese, D. J. 2008. The impact of climate change on the parasites and infectious diseases of aquatic animals. Revue Scientifique et Technique 27:467-484.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465-474.

Molnár, P. K., A. P. Dobson, S. J. Kutz. 2013. Gimme Shelter – the relative sensitivity of parasitic nematodes with direct and indirect life cycles to climate change. Global Change Biology 19:3291–3305.

Morand, S., S. Bouamer, and J. P. Hugot. 2007. Nematodes. Pp. 63-79 in Micromammals and Macroparasites: From Evolutionary Ecology to Management (S. Morand, B. R. Krasnov, and R. Poulin, eds.). Springer. Tokyo, Japan.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261-264.

Mouritsen, K. N., D. M. Tompkins, and R. Poulin. 2005. Climate warming may cause a parasite-induced collapse in coastal amphipod populations. Oecologia 146:476-483.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R.B. O'Hara, G. L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner 2016. vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Patz, J. A., T. K. Graczyk, N. Geller, and A. Y. Vittor. 2000. Effects of environmental change on emerging parasitic diseases. International Journal for Parasitology 30:1395-1405.

Pérez, J. M. M., and J. Pascau. 2013. Image processing with ImageJ. Packt Publishing Ltd.

Phillips, B. L., C. Kelehear, L. Pizzatto, G. P. Brown, D. Barton, and R. Shine. 2010. Parasites and pathogens lag behind their host during periods of host range advance. Ecology 91:872-881.

Poulin, R. 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132:143-151.

Poulin, R. 2007. Evolutionary Ecology of Parasites. 2nd ed. Princeton University Press. Princeton, New Jersey.

Poulin R., B. R. Krasnov, S. Morand. 2007. Patterns of host specificity in parasites exploiting small mammals. Pp. 233-256 in Micromammals and Macroparasites: From Evolutionary Ecology to Management (S. Morand, B. R. Krasnov, and R. Poulin, eds.). Springer. Tokyo, Japan.

Rohr, J. R., A. P. Dobson, P. T. J. Johnson, A. M. Kilpatrick, S. H. Paull, T. R. Raffel, D. Ruiz- Moreno, M. B. Thomas. 2011. Frontiers in climate change-disease research. Trends in Ecology and Evolution 26:270–277.

Sillmann, J., V. V. Kharin, F. W. Zwiers, X. Zhang, and D. Bronaugh. 2013. Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections. Journal of Geophysical Research: Atmospheres 118:2473-2493.

Smith, N. F. 2001. Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts. Oecologia 127:115-122.

Stahl, W. 1963. Studies on the life cycle of *Syphacia muris*, the rat pinworm. The Keio Journal of Medicine 12:55-60.

Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London B: Biological Sciences 270:467-473.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Webster, W. D., and J. K. Jones. 1982. *Reithrodontomys megalotis*. Mammalian Species 167:1-5.

Table 5.1. Forward (F) and reverse (R) primers and sequences for mitochondrial cytochrome c oxidase I (COI) genes that were used to split parasites into species groups.

Primer name	Parasite(s) identified	Sequence (5'– 3')
JB3F	Nematodes Cestodes Trematodes	TTTTTTGGGCATCCTGAGGTTTAT
JB5R	Nematodes	AGCACCTAAACTTAAAACATAATGAAAATG
JB4.5R	Cestodes	TAAAGAAAGAACATAATGAAAATG
TremR	Trematodes	CAACAAATCATGATGCAAAAGG
AcanthF	Acanthocephalans	AGTTCTAATCATAA(R)GATAT(Y)GG
AcanthR	Acanthocephalans	TAAACTTCAGGGTGACCAAAAAATCA

Table 5.2. Parasite species composition in the Great Basin from historical sampling and resampling. Historical sampling included 400 deer mice. Recent sampling included 382 deer mice.

Taxonomic group	Parasite species	Life cycle	Prevalence		Mean intensity ± SE	
			Historical	Recent	Historical	Recent
Nematode	*Syphacia peromysci*	Direct	0.3	0.07	31.9 ± 8.5	24.5 ± 8.2
Nematode	*Syphacia montana*	Direct	0	0.003	0	91 ± 0.0
Nematode	*Aspiculuris americana*	Direct	0.008	0.013	4.67 ± 1.8	3.4 ± 1.0
Nematode	*Heligmosomoides polygyrus*	Direct	0.015	0	1.17 ± 0.0	0
Nematode	*Heligmosomoides vandegrifti*	Direct	0	0.03	0	7.6 ± 2.1
Nematode	*Trichuris stansburyi*	Direct	0.003	0	1 ± 0.0	0
Nematode	*Brevistriata skrjabini*	Direct	0.003	0	1 ± 0.0	0
Nematode	*Protospirura numidica*	Complex	0.11	0.09	5.02 ± 0.6	5.03 ± 1.3
Nematode	*Pterygodermatites peromysci*	Complex	0.10	0.06	2.44 ± 0.3	2.04 ± 0.6
Nematode	*Mastophorus muris*	Complex	0	0.02	0	4.71 ± 1.6
Cestode	*Hymenolepis* sp.	Complex	0.033	0.039	3.08 ± 1.0	1.73 ± 0.5
Cestode	*Catenotaenia* sp. 1	Complex	0.025	0.060	2.6 ± 1.0	1.30 ± 0.2
Cestode	*Catenotaenia* sp. 2	Complex	0.015	0.003	1.0 ± 0.0	1.0 ± 0.0
Cestode	*Choanotaenia* sp.	Complex	0.003	0.003	1.0 ± 0.0	1.0 ± 0.0
Acanth.	*Moniliformis sp.*	Complex	0.008	0.02	2 ± 0.6	4.33 ± 2.5
Acanth.	*Acanth. sp. 2*	Complex	0	0.005	0	5.0 ± 3.0
Trematode	*Brachylaima microti*	Complex	0.01	0.01	2.5 ± 1.0	2.0 ± 0.6

Table 5.3. Parasite species at two sites sampling historically and resampled recently after an increase in P-J woodlands. Listed are the prevalences and abundances for both sites sampled. One hundred two mice were sampled for parasites at Stansbury A in 1968, and 49 deer mice were sampled more recently. Twenty-four mice were sampled historically at Stansbury B in 1957, and 26 were sampled recently.

Stansbury A	Prevalence		Mean intensity ± SE	
Parasite species	Historical	Recent	Historical	Recent
Syphacia peromysci	0.55	0.14	26.54 ± 4.12	27.9 ± 9.13
Aspiculuris americana	0	0.02	0	7.0 ± 0.0
Heligmosomoides vandegrifti	0	0.16	0	8.88 ± 2.37
Heligmosomoides polygyrus	0.059	0	1.17 ± 0.17	0
Protospirura numidica	0.03	0.06	1.67 ± 0.67	7.67 ± 6.17
Pterygodermatites peromysci	0.010	0	3.0 ± 0.0	0
Hymenolepis sp.	0.04	0	1.25 ± 0.25	0
Acanth. sp. 2	0	0	0	0
Brachylaima microti	0	0	0	0
Stansbury B	Prevalence		Mean intensity ± SE	
Parasite species	Historical	Recent	Historical	Recent
Syphacia peromysci	0.25	0.04	23.5 ± 6.9	104.0 ± 0.0
Aspiculuris americana	0	0.04	0	3.0 ± 0.0
Heligmosomoides vandegrifti	0	0	0	0
Heligmosomoides polygyrus	0	0	0	0
Protospirura numidica	0	0.04	0	4.0 ± 0.0
Pterygodermatites peromysci	0.13	0.04	1.33 ± 0.33	2.0 ± 0.0
Hymenolepis sp.	0	0.08	0	2.0 ± 0.0
Acanth sp. 2	0	0.04	0	2.0 ± 0.0
Brachylaima microti	0	0.08	0	1.0 ± 0.0

Table 5.4. The prevalence and total abundance of *Syphacia peromysci* from deer mice in four replicate locations at which low P-J and high P-J habitat types were sampled. Locations are shown in Fig. 5.1. Sample size is the number of deer mice sampled at each site within each location.

		Prevalence		Total abundance	
Location	Sample sizes	Low P-J	High P-J	Low P-J	High P-J
Stansbury A	Eco = 24, P-J = 49	0.21	0.14	218	195
Stansbury B	Eco = 28, P-J = 26	0.14	0.04	57	104
Oquirrh A	Eco = 25, P-J = 26	0.04	0.08	4	7
Oquirrh B	Eco = 27, P-J = 26	0	0.04	0	1

Table 5.5. Host specificity of nematode parasites found in deer mice (*Peromyscus* maniculatus) in the southwestern U.S. Host specificity refers to the number of mammal (definitive) hosts. These data include deer mice as a host.

Parasite species	Life cycle	Host specificity	References
Syphacia peromysci	Direct	2	Grundmann and Frandsen 1960; Frandsen and Grundmann 1961b
Aspiculuris americana	Direct	2	Frandsen 1960; Derrick 1971
Heligmosomoides polygyrus	Direct	2	Forrester 1971; Pfaffenberger et al. 1985
*Heligmosomoides vandegrifti**	Direct	1	Durette-Desset et al. 2007; Gritzen 2012
Trichuris stansburyi	Direct	1	Frandsen and Grundmann 1961a
Brevistriata skrjabini	Direct	1	Frandsen and Grundmann 1961b
Protospirura numidica	Complex	8	Grundmann and Frandsen 1960; Cook and Grundmann 1964; Healey and Grundmann 1974
Pterygodermatites peromysci	Complex	6	Grundmann and Frandsen 1960; Frandsen and Grundmann 1961b
Mastophorus muris	Complex	3	Pfaffenberger et al. 1985

* *H. vandegrifti* was described from *P. maniculatus* in Pennsylvania (Durette-Desset et al. 2007).

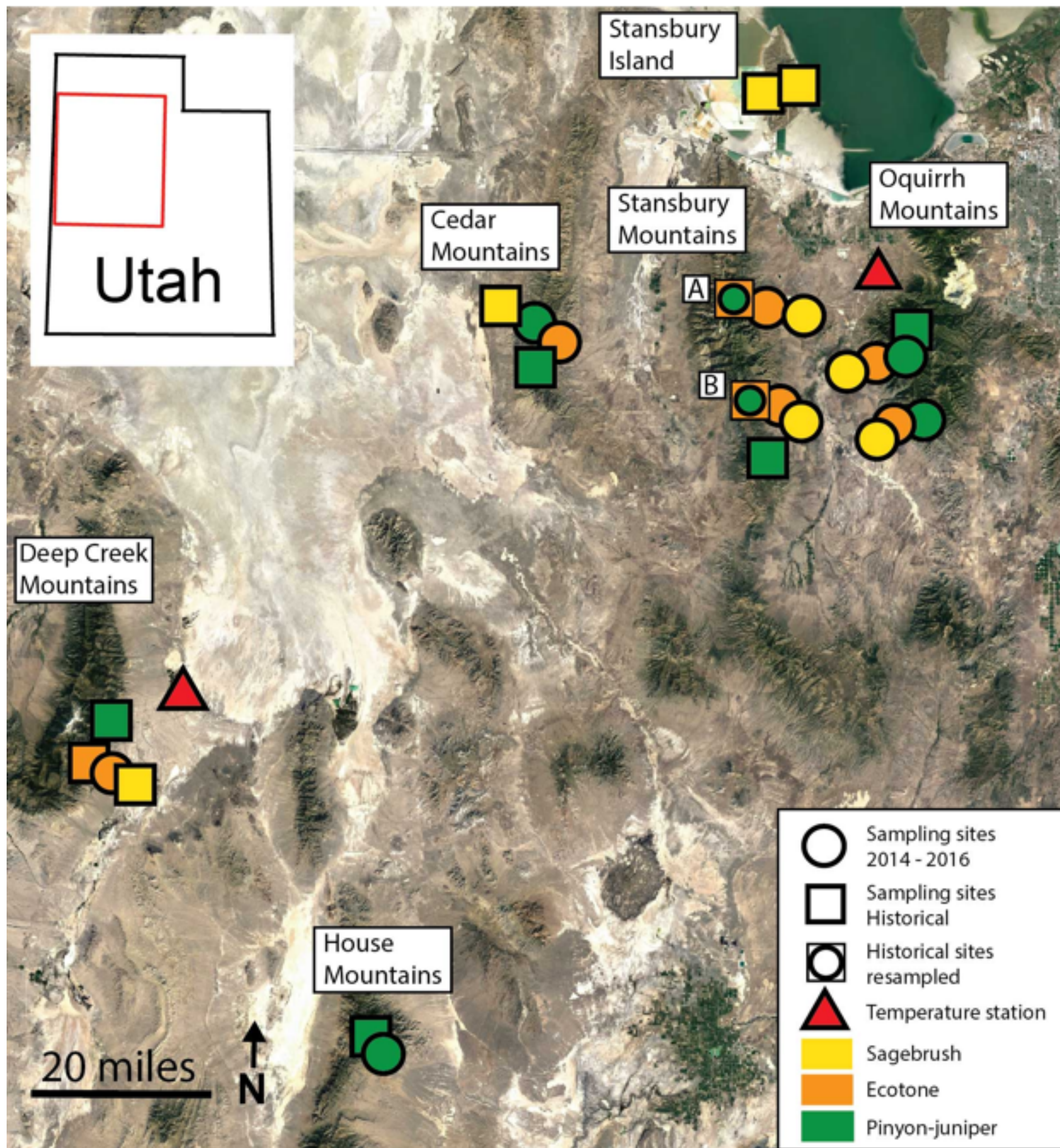

Figure 5.1. Map of current and historical parasite sampling sites in the Great Basin. Three habitats were sampled (yellow, orange, and green). Circles represent current sampling, and squares refer to historical sampling. Squares with circles inside denote sites that were resampled and the colors refer to the habitat types of the sites historically (outer square color) and currently (inner circle color). Red triangles are the locations of weather stations at which temperature data were collected.

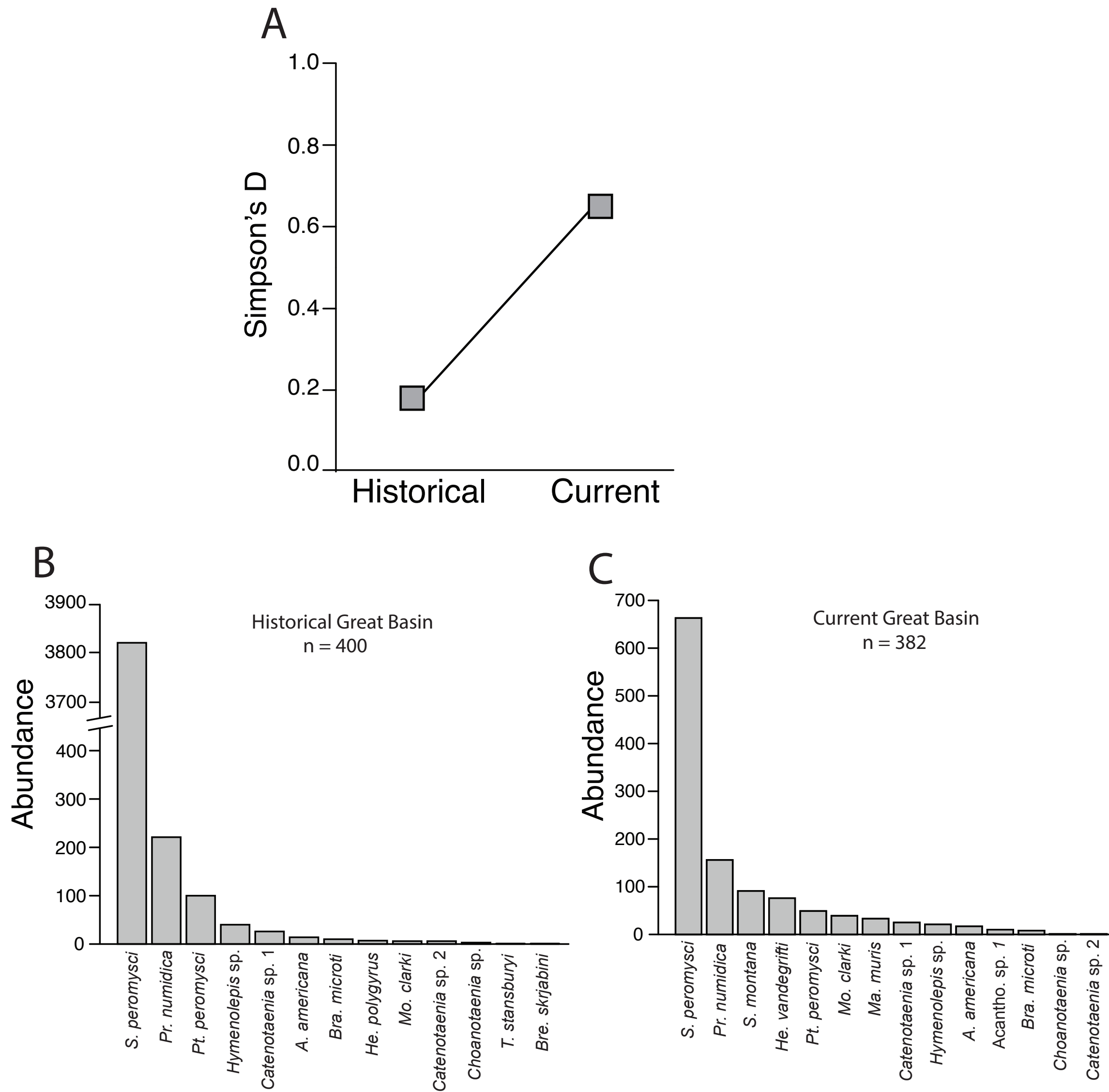

Fig. 5.2. Parasite species diversity (Simpson's D) (A) and rank abundance plots for parasites in the Great Basin historically (B) and during current sampling (C). Note the break in the axis in B.

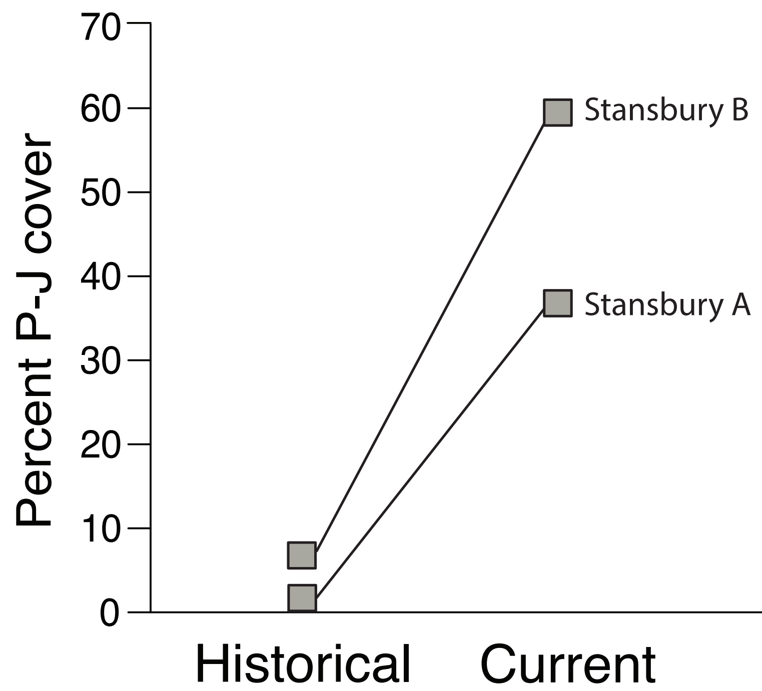

Figure 5.3. Change in P-J cover over time at the two resampled sites. Stansbury A was sampled historically in 1968 and Stansbury B was sampled in 1957.

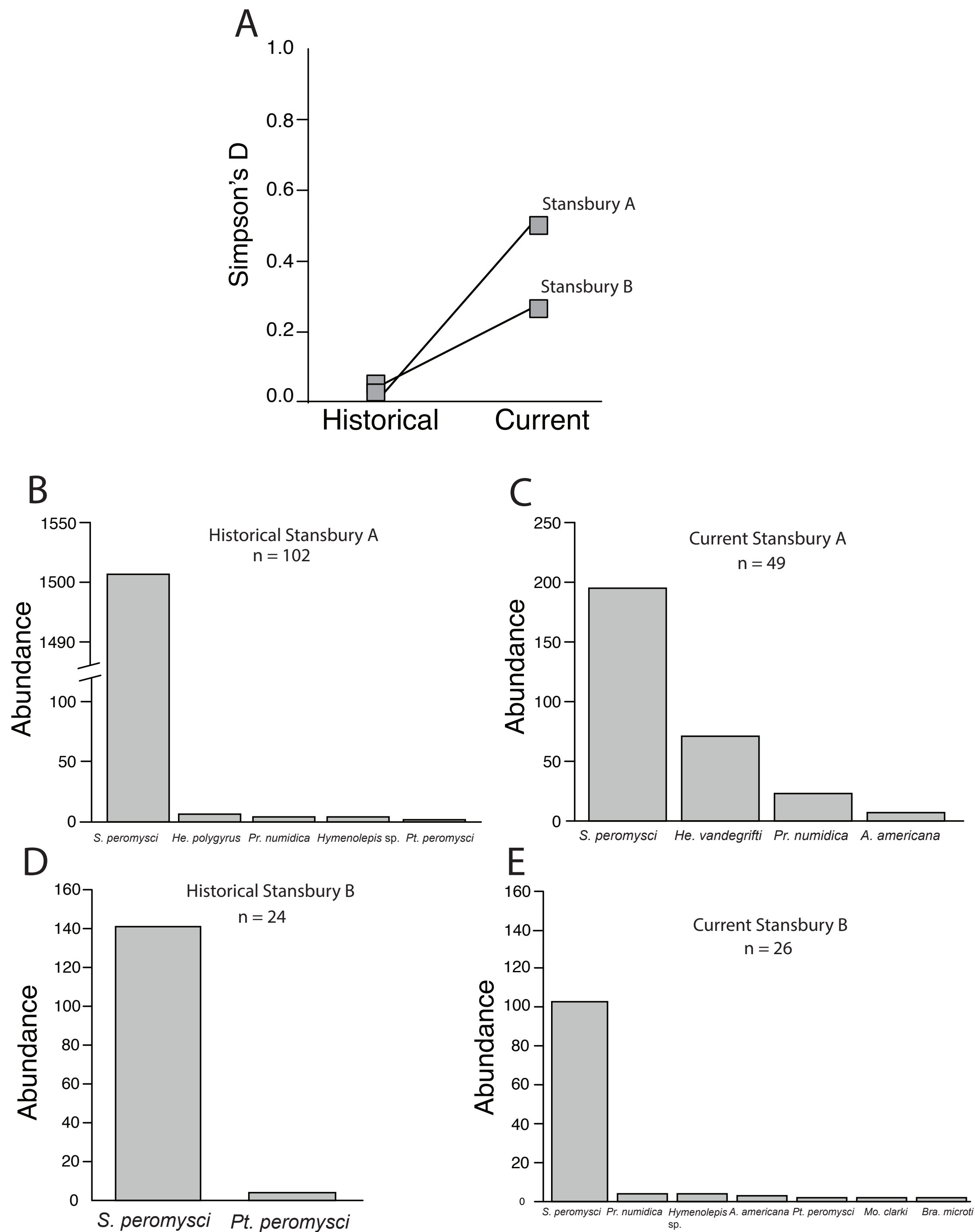

Fig. 5.4. Parasite species diversity (Simpson's D) (A) and rank abundance plots for the two resampled sites: Stansbury A (B and C) and Stansbury B (D and E). Shown are the rank abundances of each site at each time point. Sample sizes are listed. Note the break in the axis in B.

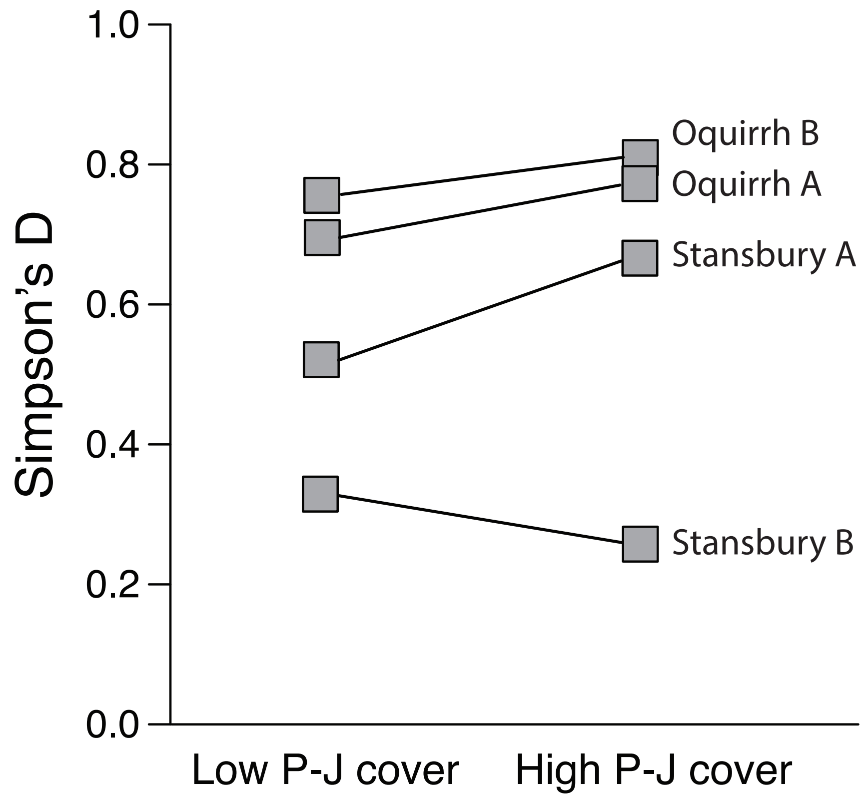

Fig. 5.5. Parasite species diversity (Simpson's D) for low P-J cover and high P-J cover sites at four replicate locations: two locations in the Stansbury Mountains and two locations in the Oquirrh Mountains.

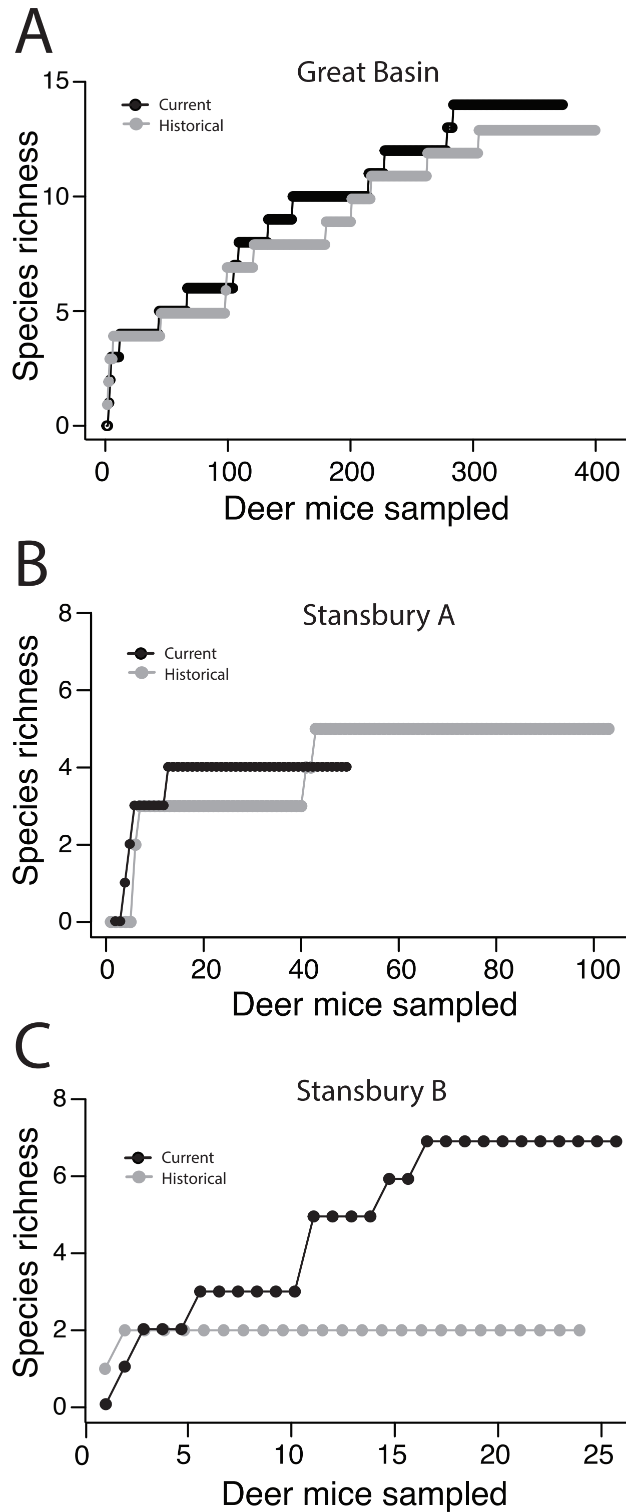

Figure 5.S1. Parasite species accumulation based on sampling individual deer mice (sample-based accumulation throughout the Great Basin (A) in two sites (B and C) that were resampled that were converted to P-J woodlands.

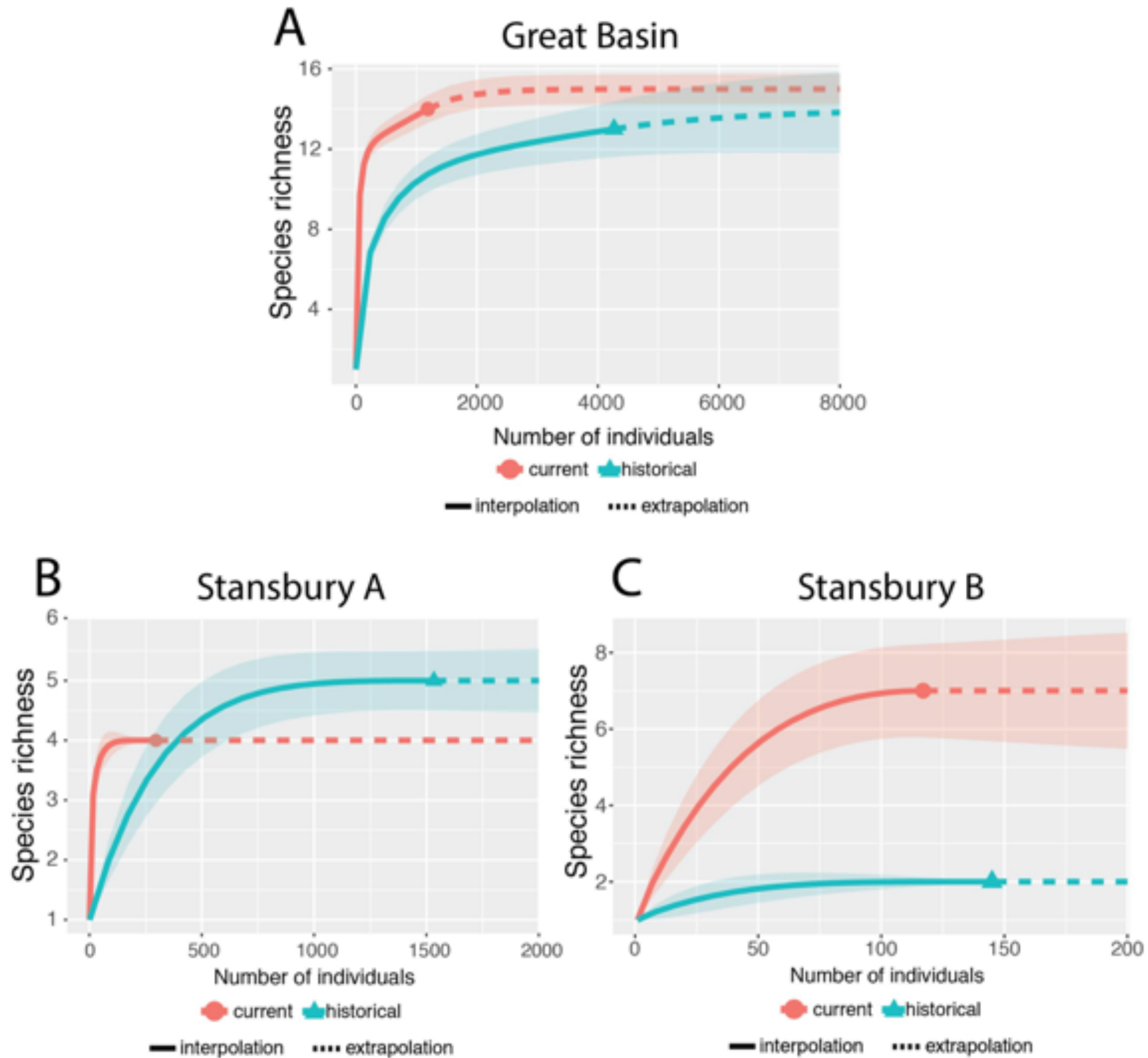

Figure 5.S2. Species accumulation curves using individual parasites (individual-based) for the Great Basin (A) and the two sites that were converted to P-J woodlands (B and C). Solid lines represent species accumulation based on number of individual parasites found. Dashed lines represent extrapolated species richness based on the Chao species richness estimator. Shaded regions around each line represent 95% confidence intervals based on bootstrapped data. Sample sizes are listed in Fig. 5.4.

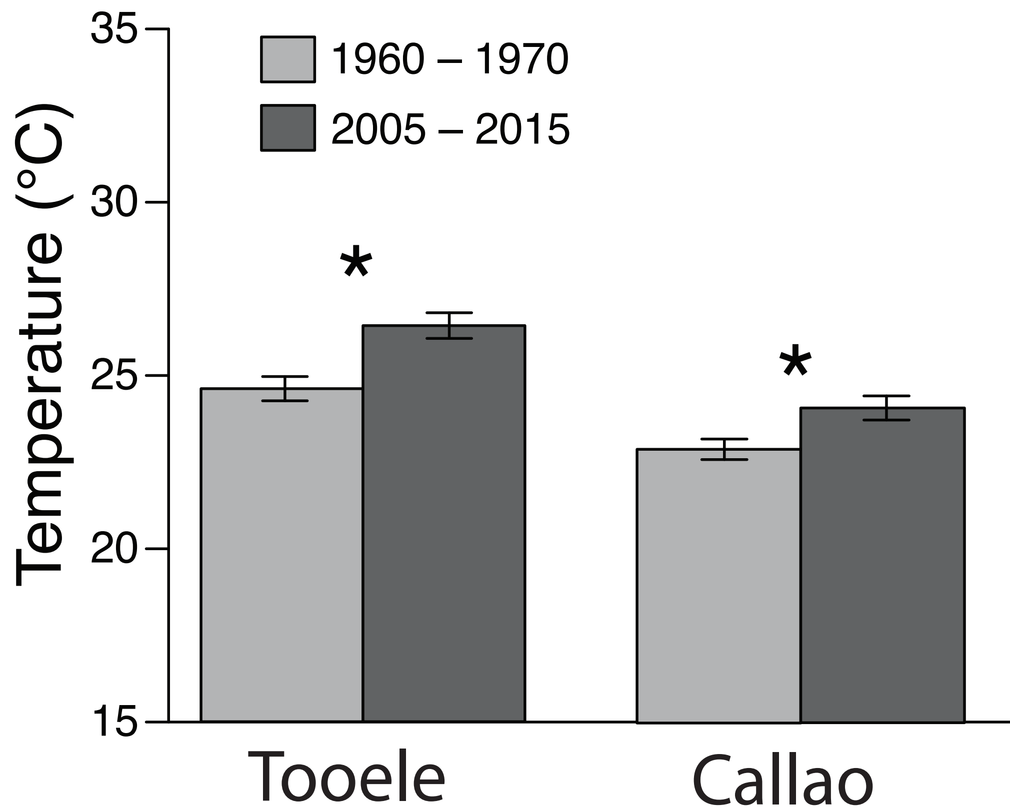

Figure. 5.S3. Mean temperature in July at two sites with temperature stations (Fig. 5.1) between two time periods, 1960-1970 and 2005 to 2010. (A) The mean temperature of Tooele, UT significantly increased between the two time periods (t-test: t = -3.53, d.f. = 19.96, P = 0.002). (B) The mean temperature of Callao, UT also significantly increased (t-test: t = -2.82, d.f. = 17.96, P = 0.017).

APPENDIX A

STABLE ISOTOPE ANALYSIS OF DEER MICE IN THE GREAT BASIN

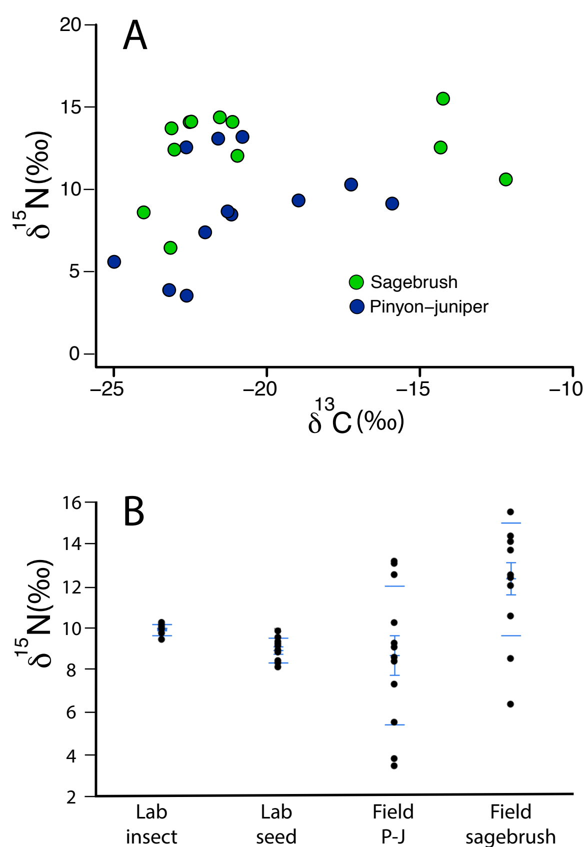

Fig. A.1. Isotope values of whiskers from deer mice. A) ^{15}N and ^{13}C values of mice caught in sagebrush habitats and pinyon-juniper (P-J) habitats. There is a significant difference between ^{15}N in sagebrush and pinyon-juniper (t-test, $t = 2.97$, $df = 21.06$, p-value = 0.007), which suggests a difference in trophic level for mice in these two habitats. Mice in sagebrush are in a higher trophic level than those in P-J, which may be due to a higher insect diet (see B). There is no significant difference between ^{13}C in mice from sagebrush and P-J habitats. B) ^{15}N values of captive deer mice and field caught mice for comparison (from A). Captive mice were fed one of two diets for two months: seed rich or insect rich. Blood was taken and ^{15}N and was measured. Mice fed insect rich diets had significantly higher ^{15}N values than mice fed seed rich diets (t-test, $t = -5.27$, $df = 15.09$, $P < 0.0001$). These results suggest that mice in sagebrush habitats are consuming more insects than mice in P-J habitats.

APPENDIX B

SPECIES OF LICE COLLECTED FROM RODENTS IN THE GREAT BASIN

Table B.1. Species identifications of lice collected from rodents in the Great Basin from 2014 to 2016. Rodents were trapped, euthanized, and combed for ectoparasites. Each louse was mounted on a glass slide after first clearing the abdomen using a lysis buffer and proteinase k. All identifications were made by D. Gustafsson.

Louse species	Host species	Prevalence
Hoplopleura hesperomydis	*Peromyscus maniculatus*	144/525
Polyplax auricularis	*Peromyscus maniculatus*	1/525
Hoplopleura arboricola	*Tamias minimus* *Tamias dorsalis*	3/10 1/12
Neohaematopinus neotomae	*Neotoma lepida*	3/20
Neohaematopinus citellinus	*Ammospermophilus leucurus*	1/8
Neohaematopinus pacificus	*Tamias dorsalis*	1/12
Fahrenholzia reducta	*Perognathus parvus*	2/22
Fahrenholzia pinnata	*Dipodomys ordii*	2/10
Hoplopleura acanthopus	*Microtus longicaudus*	1/8
Hoplopleura hesperomydis	*Reithrodontomys megalotis*	1/26
Hoplopleura difficillus	*Tamias dorsalis*	1/12
Hoplopleura sciuricola	*Lemmiscus curtatus*	1/5

APPENDIX C

ANIMALS INFESTED WITH BOTFLIES AT TIME OF CAPTURE

Table C.1. Botflies from rodents captured between 2014 and 2016 in the Great Basin. The number of botflies in each host and the habitat in which the rodent was captured is listed.

Collection Number *	Host Species	Botfly species	Intensity per host	Habitat
AWB110	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB111	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB129	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB141	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB170	*Peromyscus maniculatus*	*Cuterebra*	2	P-J
AWB228	*Peromyscus maniculatus*	*Cuterebra*	2	P-J
AWB358	*Neotoma lepida*	*Cuterebra* sp.	1	P-J
AWB499	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB502	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB518	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB541	*Peromyscus maniculatus*	*Cuterebra*	1	Sagebrush
AWB568	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB571	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB575	*Peromyscus maniculatus*	*Cuterebra*	1	P-J
AWB604	*Peromyscus maniculatus*	*Cuterebra*	1	P-J

* Animals are located at the Natural History Museum of Utah in Salt Lake City, UT

APPENDIX D

HOST-PARASITE DATA FROM RODENTS IN THE GREAT BASIN

Table D.1. Host-parasite data of rodents collected in the Great Basin. Listed are all the individual rodents captured, the species, sex, and the numbers of ectoparasites (split into fleas, ticks, and lice) and helminth species. Measurements (body length, tail length, leg length, and ear length) of each animal, and site locations can be obtained from the Natural History Museum of Utah (Collection numbers AWB1-AWB683).

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	cest.sp.1	*Hymenolepis* sp.	cest.sp.3	cest.sp.4	Number of acanthocephalans	acan.sp.1	acan.sp.2	Number of trematodes	*Brachylaima microti*
AWB1	1	*Peromyscus maniculatus*	NA	NA	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB2	2	*Peromyscus maniculatus*	M	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB3	3	*Peromyscus maniculatus*	M	17.5	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB4	4	*Peromyscus maniculatus*	F	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB5	5	*Peromyscus maniculatus*	M	18	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB6	6	*Peromyscus maniculatus*	M	20	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB7	7	*Peromyscus maniculatus*	M	20.5	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB8	8	*Peromyscus maniculatus*	F	15.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB9	9	*Peromyscus maniculatus*	F	21	0	0	2	114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB10	10	*Peromyscus maniculatus*	F	21.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB11	11	*Peromyscus maniculatus*	M	17	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB12	12	*Peromyscus maniculatus*	M	16.5	0	0	4	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB13	13	*Peromyscus maniculatus*	F	14	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB14	14	*Peromyscus maniculatus*	M	17	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB15	15	*Peromyscus maniculatus*	M	15	0	0	1	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB16	16	*Peromyscus maniculatus*	M	17.5	4	0	66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB17	17	*Peromyscus maniculatus*	M	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB18	18	*Peromyscus maniculatus*	M	17.5	0	0	28	212	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB19	19	*Peromyscus maniculatus*	M	17.5	1	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB20	20	*Peromyscus maniculatus*	M	22	0	1	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB21	21	*Peromyscus maniculatus*	M	19	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB22	22	*Peromyscus maniculatus*	F	16	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB23	23	*Peromyscus maniculatus*	F	15.5	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB24	24	*Peromyscus maniculatus*	M	16	30	0	0	1	0	0	0	0	0	0	0	1			0	0	0	0	0	0	0
AWB25	25	*Peromyscus maniculatus*	F	20	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB26	26	*Peromyscus maniculatus*	M	20.5	12	1	0	109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB27	27	*Peromyscus maniculatus*	M	23	13	2	11	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB28	28	*Peromyscus maniculatus*	F	25.5	5	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB29	29	*Peromyscus maniculatus*	F	19	0	0	3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB30	30	*Peromyscus maniculatus*	F	20.5	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB31	31	*Peromyscus maniculatus*	F	26	2	0	0	310	1	0	0	309	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB32	32	*Peromyscus maniculatus*	M	20.5	11	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB33	33	*Tamias dorsalis*	F	55.0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB34	34	*Tamias dorsalis*	M	53.0	0	0	0	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB35	35	*Tamias dorsalis*	F	50.0	2	1	7	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB36	36	*Tamias dorsalis*	M	53.0	0	0	1	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB37	37	*Tamias dorsalis*	M	55.0	2	0	0	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB38	38	*Peromyscus maniculatus*	M	21.5	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB39	39	*Peromyscus maniculatus*	M	20.5	25	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB40	40	*Peromyscus maniculatus*	M	21.5	31	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
AWB41	41	*Peromyscus maniculatus*	F	19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB42	42	*Peromyscus maniculatus*	F	23.5	4	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB43	*43*	*Peromyscus maniculatus*	M	21.5	21	1	1	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB44	*44*	*Peromyscus maniculatus*	F	24.5	5	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB45	*45*	*Peromyscus maniculatus*	M	22	3	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB46	46	*Tamias minimus*	M	33.5	4	1	4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB47	*47*	*Peromyscus maniculatus*	M	19	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB48	*48*	*Peromyscus maniculatus*	M	21	14	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB49	*49*	*Peromyscus maniculatus*	F	22	16	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB50	*50*	*Peromyscus maniculatus*	M	18.5	4	1	0	15	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB51	*51*	*Peromyscus maniculatus*	NA	NA	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB52	*52*	*Peromyscus maniculatus*	M	23.5	11	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB53	*53*	*Peromyscus maniculatus*	F	22.5	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB54	54	*Lemmiscus curtatus*	F	22.0	1	0	0	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB55	55	*Perognathus parvus*	F	23.5	1	0	0	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB56	*56*	*Peromyscus maniculatus*	M	24.5	17	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB57	*57*	*Peromyscus maniculatus*	M	18.5	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB58	*58*	*Peromyscus maniculatus*	M	20.5	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB59	*59*	*Peromyscus maniculatus*	M	19.5	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB60	*60*	*Peromyscus maniculatus*	F	21.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB61	*61*	*Peromyscus maniculatus*	M	19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB62	*62*	*Peromyscus maniculatus*	M	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB63	*63*	*Peromyscus maniculatus*	M	20.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB64	*64*	*Peromyscus maniculatus*	M	19.5	1	0	0	26	2	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB65	*65*	*Peromyscus maniculatus*	F	23.5	0	0	0	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB66	66	*Perognathus parvus*	F	16.0	0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB67	*67*	*Peromyscus maniculatus*	M	19	25	1	0	44	0	0	0	44	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB68	68	*Lemmiscus curtatus*	F	9.5	18	1	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB69	*69*	*Peromyscus maniculatus*	F	19	0	0	3	15	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB70	*70*	*Peromyscus maniculatus*	F	20	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB71	*71*	*Peromyscus maniculatus*	F	19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB72	*72*	*Peromyscus maniculatus*	F	20	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB73	*73*	*Peromyscus maniculatus*	F	17	1	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB74	*74*	*Peromyscus maniculatus*	F	26.5	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB75	*75*	*Peromyscus maniculatus*	M	26	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB77	*76*	*Peromyscus maniculatus*	NA	8.8	0	1	0	212	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB76	76	*Neotoma cinerea*	F	110.0	1	1	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB78	*78*	*Peromyscus maniculatus*	M	19.5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB79	*79*	*Peromyscus maniculatus*	F	20	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB80	*80*	*Peromyscus maniculatus*	F	25.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB81	*81*	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB82	*82*	*Peromyscus maniculatus*	F	21.5	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB83	*83*	*Peromyscus maniculatus*	M	15.5	0	0	0	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB84	*84*	*Peromyscus maniculatus*	F	19	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB85	*85*	*Peromyscus maniculatus*	F	26	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB86	*86*	*Peromyscus maniculatus*	M	18	0	1	6	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB87	*87*	*Peromyscus maniculatus*	F	16.5	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB88	*88*	*Peromyscus maniculatus*	M	20.5	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB89	*89*	*Peromyscus maniculatus*	M	21	1	0	4	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
AWB90	90	*Tamias dorsalis*	M	46.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB91	*91*	*Peromyscus maniculatus*	M	17.5	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB92	*92*	*Peromyscus maniculatus*	F	21.5	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB93	*93*	*Peromyscus maniculatus*	M	18.5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB94	*94*	*Peromyscus maniculatus*	F	15.5	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB95	*95*	*Peromyscus maniculatus*	F	16	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB96	96	*Tamias dorsalis*	F	60.0	0	0	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB97	97	*Neotoma lepida*	F	70.0	2	0	15	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB98	98	*Peromyscus truei*	M	19.0	0	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB99	*99*	*Peromyscus maniculatus*	F	24	0	1	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB100	*100*	*Peromyscus maniculatus*	M	15.5	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB101	101	*Peromyscus truei*	F	18.5	0	0	9	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB102	102	*Peromyscus truei*	F	15.5	0	3	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB103	103	*Peromyscus truei*	F	19.5	0	0	4	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB104	*104*	*Peromyscus maniculatus*	F	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB105	105	*Peromyscus truei*	F	23.5	8	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB106	*106*	*Peromyscus maniculatus*	F	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB107	*107*	*Peromyscus maniculatus*	M	22.5	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB108	108	*Peromyscus truei*	F	12.0	33	2	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB109	*109*	*Peromyscus maniculatus*	M	18	2	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB110	*110*	*Peromyscus maniculatus*	F	NA	10	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB111	*111*	*Peromyscus maniculatus*	F	16.5	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB112	112	*Tamias dorsalis*	F	50.0	2	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB113	113	*Peromyscus truei*	F	28.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB114	114	*Peromyscus truei*	M	20.0	13	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB115	*115*	*Peromyscus maniculatus*	F	16.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB116	*116*	*Peromyscus maniculatus*	M	15	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB117	*117*	*Peromyscus maniculatus*	M	17	3	0	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB118	118	*Peromyscus truei*	F	20.5	7	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB119	*119*	*Peromyscus maniculatus*	M	19	0	6	0	31	0	0	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB120	*120*	*Peromyscus maniculatus*	M	17.5	1	0	4	5	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
AWB121	*121*	*Peromyscus maniculatus*	M	20.5	0	10	0	18	0	0	0	15	0	3	0	0	0	0	0	0	0	0	0	0	0
AWB122	*122*	*Peromyscus maniculatus*	F	17.5	9	3	0	52	0	0	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB123	*123*	*Peromyscus maniculatus*	F	17	0	1	0	22	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0
AWB124	*124*	*Peromyscus maniculatus*	F	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB125	*125*	*Peromyscus maniculatus*	M	20	0	3	0	10	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB126	*126*	*Peromyscus maniculatus*	F	11.5	6	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB127	*127*	*Peromyscus maniculatus*	M	22	0	8	0	7	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
AWB128	*128*	*Peromyscus maniculatus*	F	12.5	0	0	0	69	0	0	0	69	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB129	*129*	*Peromyscus maniculatus*	M	21.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB130	130	*Micotus montanus*	F	33.0	0	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB131	*131*	*Peromyscus maniculatus*	F	12.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB132	132	*Peromyscus maniculatus*	F	11	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB133	133	*Peromyscus maniculatus*	M	17.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB134	134	*Peromyscus maniculatus*	F	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB135	135	*Peromyscus maniculatus*	M	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB136	136	*Peromyscus truei*	M	20.5	0	2	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB137	137	*Peromyscus maniculatus*	NA	15.5	2	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB138	138	*Peromyscus maniculatus*	F	11.5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB139	139	*Peromyscus maniculatus*	F	15.5	0	0	0	7	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0
AWB140	140	*Peromyscus maniculatus*	M	19.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB141	141	*Peromyscus maniculatus*	F	20	0	1	0	16	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0
AWB142	142	*Peromyscus maniculatus*	M	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB143	143	*Microtus longicaudus*	M	41.5	0	6	0	2	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB144	144	*Peromyscus maniculatus*	F	17.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB145	145	*Peromyscus maniculatus*	M	16	0	0	0	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB146	146	*Peromyscus maniculatus*	M	17.5	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB147	147	*Peromyscus maniculatus*	M	14.5	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB148	148	*Peromyscus maniculatus*	F	16	0	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB149	149	*Peromyscus maniculatus*	F	15	0	5	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB150	150	*Peromyscus maniculatus*	M	15.5	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB151	151	*Peromyscus maniculatus*	M	NA	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB152	152	*Peromyscus maniculatus*	M	17.5	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB153	153	*Peromyscus maniculatus*	M	19	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB154	154	*Peromyscus maniculatus*	F	16.5	0	1	0	27	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB155	155	*Peromyscus maniculatus*	M	16.5	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB156	156	*Peromyscus maniculatus*	F	16.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB157	157	*Peromyscus maniculatus*	M	18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB158	158	*Peromyscus maniculatus*	M	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB159	159	*Peromyscus maniculatus*	F	16.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB160	160	*Peromyscus maniculatus*	F	21	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB161	161	*Peromyscus maniculatus*	M	17.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB162	162	*Peromyscus maniculatus*	F	20.5	0	3	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB163	163	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB164	164	*Peromyscus maniculatus*	M	18	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB165	165	*Peromyscus maniculatus*	F	17.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB166	166	*Peromyscus maniculatus*	M	17.5	0	3	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB167	167	*Peromyscus maniculatus*	M	18	0	0	1	5	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
AWB168	168	*Peromyscus maniculatus*	F	15	0	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB169	169	*Peromyscus maniculatus*	M	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB170	170	*Peromyscus maniculatus*	M	18.5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB171	171	*Peromyscus maniculatus*	F	18.5	0	2	0	12	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB172	172	*Peromyscus maniculatus*	F	17	0	4	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB173	173	*Peromyscus maniculatus*	M	18.5	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB174	174	*Reithrodontomys megalotis*	M	10.0	0	0	2	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB175	175	*Peromyscus maniculatus*	F	19	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB176	176	*Reithrodontomys megalotis*	F	14.5	0	0	6	2	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB177	177	*Peromyscus maniculatus*	M	18.5	0	8	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB178	178	*Peromyscus maniculatus*	M	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB179	179	*Peromyscus maniculatus*	F	17	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB180	180	*Peromyscus maniculatus*	F	19.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB181	181	*Peromyscus maniculatus*	M	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB182	182	*Peromyscus maniculatus*	M	14	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB183	183	*Peromyscus maniculatus*	M	20	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB184	184	*Peromyscus maniculatus*	M	17	0	3	0	8	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB185	185	*Peromyscus maniculatus*	F	15.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB186	186	*Microtus longicaudus*	M	26.5	0	1	0	49	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB187	187	*Peromyscus maniculatus*	F	19	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB188	188	*Peromyscus maniculatus*	F	17	0	2	0	95	0	0	0	0	0	4	91	0	0	0	0	0	0	0	0	0	0
AWB189	189	*Peromyscus maniculatus*	M	18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB190	190	*Peromyscus maniculatus*	M	15.5	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB191	191	*Peromyscus maniculatus*	M	17	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB192	192	*Peromyscus maniculatus*	M	17	0	2	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
AWB193	193	*Peromyscus maniculatus*	F	13	0	2	10	26	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB194	194	*Peromyscus maniculatus*	F	19.5	0	1	1	5	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB195	195	*Peromyscus maniculatus*	M	19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB196	196	*Peromyscus maniculatus*	F	14.5	0	1	0	201	3	0	0	198	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB197	197	*Reithrodontomys megalotis*	M	8.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB198	198	*Peromyscus maniculatus*	F	17	0	0	0	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB199	199	*Peromyscus truei*	F	17.5	0	0	0	24	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB200	200	*Peromyscus maniculatus*	M	8	0	8	2	5	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
AWB201	201	*Peromyscus maniculatus*	F	10.5	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB202	202	*Microtus longicaudus*	F	25.5	0	0	0	50	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB203	203	*Peromyscus truei*	F	14.0	0	1	0	12	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB204	204	*Peromyscus truei*	M	17.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB205	205	*Peromyscus maniculatus*	M	15.5	1	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB206	206	*Peromyscus maniculatus*	M	16.5	0	1	8	6	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB207	207	*Peromyscus maniculatus*	M	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB208	208	*Reithrodontomys megalotis*	F	8.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB209	209	*Peromyscus truei*	F	15.5	11	2	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB210	210	*Peromyscus maniculatus*	F	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB211	211	*Peromyscus maniculatus*	M	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB212	212	*Microtus longicaudus*	F	23.5	0	1	1	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB213	213	*Peromyscus maniculatus*	F	20.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB214	214	*Peromyscus maniculatus*	F	16	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB215	215	*Tamias minimus*	F	35.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB216	216	*Tamias minimus*	M	29.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB217	217	*Peromyscus maniculatus*	F	15.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB218	218	*Peromyscus maniculatus*	F	21.5	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB219	219	*Peromyscus maniculatus*	M	17.5	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB220	220	*Peromyscus maniculatus*	M	18.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB221	221	*Peromyscus truei*	M	15.5	1	0	0	3	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB222	222	*Tamias dorsalis*	F	50.0	0	1	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB223	223	*Peromyscus maniculatus*	M	12.5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB224	224	*Peromyscus maniculatus*	M	20	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB225	225	*Peromyscus maniculatus*	F	17.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB226	226	*Peromyscus maniculatus*	M	15	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB227	227	*Peromyscus maniculatus*	F	19.5	0	6	0	9	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0
AWB228	228	*Peromyscus maniculatus*	M	13	0	0	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB229	229	*Peromyscus maniculatus*	F	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB230	230	*Peromyscus maniculatus*	M	17.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB231	231	*Peromyscus maniculatus*	M	14	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB232	232	*Reithrodontomys megalotis*	F	9.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB233	233	*Microtus longicaudus*	M	38.5	0	2	0	4	NA	NA	NA	NA	NA	NA	NA	1	NA	NA	NA	NA	0	NA	NA	0	NA
AWB234	234	*Microtus longicaudus*	F	19.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB235	235	*Sorex monticolus*	F	3.3	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB236	236	*Peromyscus maniculatus*	M	23.5	3	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 237	237	*Peromyscus maniculatus*	F	24	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 238	238	*Peromyscus maniculatus*	F	21	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 239	239	*Peromyscus maniculatus*	M	21	7	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 240	240	*Peromyscus maniculatus*	M	19	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 241	241	*Peromyscus maniculatus*	M	21	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 242	242	*Peromyscus maniculatus*	F	19	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
AWB 243	243	*Peromyscus maniculatus*	F	21	0	1	6	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
AWB 244	244	*Peromyscus maniculatus*	F	16	0	4	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 245	245	*Peromyscus maniculatus*	M	17.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 246	246	*Peromyscus maniculatus*	M	21	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	6	1
AWB 247	247	*Peromyscus maniculatus*	M	25	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 248	248	*Pocket mouse*	F	21.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 249	249	*Peromyscus maniculatus*	M	16.5	13	8	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 250	250	*Peromyscus maniculatus*	F	15	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 251	251	*Peromyscus maniculatus*	M	24	1	18	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 252	252	*Peromyscus maniculatus*	M	12.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 253	253	*Peromyscus maniculatus*	M	13	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 254	254	*Peromyscus maniculatus*	F	11	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 255	255	*Peromyscus maniculatus*	F	24	0	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 256	256	*Peromyscus maniculatus*	M	20	10	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 257	257	*Peromyscus maniculatus*	F	9	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 258	258	*Peromyscus maniculatus*	F	26.5	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 259	259	*Perognathus parvus*	F	18.0	1	2	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 260	260	*Tamias minimus*	F	33.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 261	261	*Tamias minimus*	F	36.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 262	262	*Peromyscus maniculatus*	M	12	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 263	263	*Peromyscus maniculatus*	F	10.5	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 264	264	*Peromyscus maniculatus*	M	12.5	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 265	265	*Perognathus parvus*	F	14.5	1	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 266	266	*Peromyscus maniculatus*	M	11.5	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 267	267	*Peromyscus maniculatus*	M	12.5	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 268	268	*Peromyscus maniculatus*	F	9.5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 269	269	*Pocket mouse*	F	21.0	12	0	0	36	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 270	270	*Peromyscus maniculatus*	M	15.5	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 271	271	*Peromyscus maniculatus*	M	23.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 272	272	*Lemmiscus curtatus*	F	13.5	5	8	1	0	NA	NA	NA	NA	NA	NA	NA	3	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 273	273	*Peromyscus maniculatus*	F	16	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 274	274	*Peromyscus maniculatus*	F	9	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 275	275	*Peromyscus maniculatus*	M	11.5	0	1	0	9	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 276	276	*Peromyscus maniculatus*	F	10.5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 277	277	*Peromyscus maniculatus*	M	19.5	0	5	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 279	279	*Tamias minimus*	F	36.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 280	280	*Tamias minimus*	M	35.0	1	1	7	0	NA	NA	NA	NA	NA	NA	NA	1	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 281	281	*Lemmiscus curtatus*	M	18.0	3	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 282	282	*Pocket mouse*	F	19.0	2	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 283	283	*Pocket mouse*	F	22.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 284	284	*Peromyscus maniculatus*	M	12	2	1	1	42	0	0	0	41	1	0	0	0	0	0	0	0	0	0	0	0	0
AWB 285	285	*Peromyscus maniculatus*	F	19.5	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 286	286	*Peromyscus maniculatus*	F	9	1	7	6	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 287	287	*Peromyscus maniculatus*	M	20	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 278	287	*Tamias minimus*	M	32.0	0	0	4	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 288	288	*Peromyscus maniculatus*	F	34	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 289	289	*Peromyscus maniculatus*	M	17.5	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 290	290	*Peromyscus maniculatus*	M	17.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 291	291	*Pocket mouse*	M	23.5	1	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 292	292	*Peromyscus maniculatus*	F	27.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 293	293	*Pocket mouse*	F	20.5	0	0	3	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 294	294	*Peromyscus maniculatus*	M	22.5	5	3	1	6	0	0	0	6	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 295	295	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 296	296	*Peromyscus maniculatus*	M	23	0	4	0	108	4	0	0	104	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 297	297	*Peromyscus maniculatus*	M	17	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 298	298	*Peromyscus maniculatus*	M	21.5	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 299	299	*Peromyscus maniculatus*	F	19.5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 300	300	*Peromyscus maniculatus*	F	25.5	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 301	301	*Pocket mouse*		17.5	0	1	1	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 302	302	*Tamias minimus*	F	34.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 303	303	*Pocket mouse*	M	23.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 304	304	*Peromyscus maniculatus*	M	19.5	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 305	305	*Peromyscus maniculatus*	F	10.5	1	4	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 306	306	*Peromyscus maniculatus*	M	22.5	0	2	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 307	307	*Peromyscus maniculatus*	F	22	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 308	308	*Peromyscus maniculatus*	M	23	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0
AWB 309	309	*Peromyscus maniculatus*	M	16	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 310	310	*Pocket mouse*	M	21.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 311	311	*Reithrodontomys megalotis*	M	13.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 312	312	*Tamias minimus*	F	40.0	0	5	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 313	313	*Reithrodontomys megalotis*	M	10.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 314	314	*Peromyscus maniculatus*	F	21.5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 315	315	*Peromyscus maniculatus*	M	11	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 316	316	*Peromyscus maniculatus*	M	13	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 317	317	*Peromyscus maniculatus*	M	20.5	1	7	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 318	318	*Peromyscus maniculatus*	M	21	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 319	319	*Peromyscus maniculatus*	M	23	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 320	320	*Peromyscus maniculatus*	M	18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 321	321	*Peromyscus maniculatus*	M	17.5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 322	322	*Peromyscus maniculatus*	M	14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 323	323	*Peromyscus maniculatus*	M	20.5	0	3	0	0	0	0	0	0	0	0	0	5	0	5	0	0	0	0	0	0	0
AWB 324	324	*Peromyscus maniculatus*	F	21	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 325	325	*Pocket mouse*	M	27.5	0	1	0	0	NA	NA	NA	NA	NA	NA	NA	2	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 326	326	*Reithrodontomys megalotis*	M	12.0	0	2	0	39	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 327	327	*Peromyscus maniculatus*	F	18	1	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 328	328	*Peromyscus maniculatus*	M	14.5	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 329	329	*Peromyscus maniculatus*	M	14.5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 330	330	*Peromyscus maniculatus*	F	22	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 331	331	*Peromyscus maniculatus*	M	13.5	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 332	332	*Peromyscus maniculatus*	F	15	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 333	333	*Peromyscus maniculatus*	M	18.5	13	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 334	334	*Peromyscus maniculatus*	M	15	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 335	335	*Peromyscus maniculatus*	M	20	3	4	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 336	336	*Peromyscus maniculatus*	F	11.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 337	337	*Peromyscus maniculatus*	M	15	0	3	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 338	338	*Peromyscus maniculatus*	F	8	0	0	9	40	0	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 339	339	*Peromyscus maniculatus*	F	28	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 340	340	*Peromyscus maniculatus*	M	24	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 341	341	*Peromyscus maniculatus*	M	12.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 342	342	*Reithrodontomys megalotis*		NA	0	2	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 343	343	*Peromyscus maniculatus*	M	19	3	1	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0
AWB 344	344	*Peromyscus maniculatus*	M	21	2	2	0	14	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 345	345	*Peromyscus maniculatus*	M	20.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 346	346	*Peromyscus maniculatus*	F	16.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 347	347	*Peromyscus maniculatus*	M	19.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 348	348	*Peromyscus maniculatus*	F	14.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 349	349	*Neotoma lepida*	F	85.0	1	3	1	3	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 350	350	*Peromyscus maniculatus*	M	20	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 351	351	*Peromyscus maniculatus*	M	21	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 352	352	*Peromyscus maniculatus*	M	19	2	3	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 353	353	*Neotoma lepida*	F	115.0	0	2	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 354	354	*Peromyscus maniculatus*	M	14.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 355	355	*Ammospermophilus leucurus*	F	110.0	0	7	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 356	356	*Peromyscus maniculatus*	M	17.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 357	357	*Peromyscus maniculatus*	M	15.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 358	358	*Neotoma lepida*	M	135.0	1	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 359	359	*Neotoma lepida*	M	105.0					NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 360	360	*Peromyscus maniculatus*	M	13.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 361	361	*Neotoma lepida*	M	40.5	1	2	2	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 362	362	*Neotoma lepida*	F	80.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 363	363	*Neotoma lepida*	M	89.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 364	364	*Neotoma lepida*	F	170.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 365	365	*Pocket mouse*	M	22.5	1	0	20	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 366	366	*Dipodomys ordii*	F	48.0	0	0	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 367	367	*Reithrodontomys megalotis*	M	10.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 368	368	*Peromyscus maniculatus*	M	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 369	369	*Peromyscus maniculatus*	M	11.5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 370	370	*Peromyscus maniculatus*	M	19.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 371	371	*Peromyscus maniculatus*	F	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 372	372	*Peromyscus maniculatus*	M	19	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 373	373	*Peromyscus maniculatus*	F	10.5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 374	374	*Peromyscus maniculatus*	F	17.5	0	0	0	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 375	375	*Peromyscus maniculatus*	M	16.5	0	2	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 376	376	*Peromyscus maniculatus*	F	14.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 377	377	*Peromyscus maniculatus*	M	13.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 378	378	*Reithrodontomys megalotis*	F	13.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 379	379	*Neotoma lepida*	M	85.0	0	6	3	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 380	380	*Neotoma lepida*	M	105.0	2	2	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 381	381	*Ammospermophilus leucurus*	F	118.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 382	382	*Peromyscus maniculatus*	M	20.5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 383	383	*Peromyscus maniculatus*	F	23.5	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 384	384	*Peromyscus maniculatus*	M	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 385	385	*Peromyscus maniculatus*	M	17.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 386	386	*Peromyscus maniculatus*	M	13	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 387	387	*Peromyscus maniculatus*	F	14.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 388	388	*Pocket mouse*	M	22.0	0	0	33	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 389	389	*Neotoma lepida*	M	94.0	1	1	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 390	390	*Neotoma lepida*	M	74.0	0	1	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 391	391	*Neotoma lepida*	M	93.0	0	0	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 392	392	*Neotoma lepida*	M	103.0	0	1	1	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 393	393	*Ammospermophilus leucurus*	M	125.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 394	394	*Peromyscus maniculatus*	M	18.5	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 395	395	*Peromyscus maniculatus*	F	21.5	0	0	4	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 396	*396*	*Peromyscus maniculatus*	M	22.5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 397	397	*Neotoma lepida*	F	100.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 398	398	*Peromyscus truei*	M	22.5	2	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 399	399	*Reithrodontomys megalotis*	M	11.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 400	*400*	*Peromyscus maniculatus*	M	13.5	0	0	1	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 401	*401*	*Peromyscus maniculatus*	M	17	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 402	*402*	*Peromyscus maniculatus*	F	23	0	0	3	10	10	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
AWB 403	*403*	*Peromyscus maniculatus*	F	12.5	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 404	404	*Peromyscus truei*	F	25.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 405	405	*Neotoma lepida*	F	14.5	NA	NA	NA		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 406	406	*Neotoma lepida*	M	110.0	NA	NA	NA		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 407	*407*	*Peromyscus maniculatus*	M	12.5	5	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 408	408	*Neotoma lepida*	M	72.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 409	409	*Neotoma lepida*	M	165.0	3	3	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 410	410	*Dipodomys ordii*	F	50.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 412	412	*Dipodomys ordii*	M	53.0	0	0	0	yes	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 413	413	*Dipodomys ordii*	F	47.0	1			0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 414	414	*Dipodomys ordii*	F	35.0	1	0	1		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 415	415	*Ammospermophilus leucurus*	F	71.0	NA	NA	NA		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 416	416	*Dipodomys ordii*	F	54.0	1	0	1		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 418	418	*Dipodomys ordii*	F	51.0	NA	NA	NA	yes	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 419	419	*Dipodomys ordii*	F	49.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 422	422	*Peromyscus truei*	M	22.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 423	423	*Peromyscus truei*	F	25.0	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 424	424	*Pocket mouse*	?	18.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 429	*429*	*Peromyscus maniculatus*	M	17	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 430	*430*	*Peromyscus maniculatus*	M	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 431	*431*	*Peromyscus maniculatus*	F	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 432	*432*	*Peromyscus maniculatus*	M	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 433	*433*	*Peromyscus maniculatus*	M	17	0	4	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 434	*434*	*Peromyscus maniculatus*	F	17.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 435	*435*	*Peromyscus maniculatus*	F	21.5	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 436	*436*	*Peromyscus maniculatus*	F	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 437	*437*	*Peromyscus maniculatus*	M	22	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 438	*438*	*Peromyscus maniculatus*	F	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 439	*439*	*Peromyscus maniculatus*	F	26.5	0	12	19	2	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
AWB 440	*440*	*Peromyscus maniculatus*	M	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 441	*441*	*Peromyscus maniculatus*	F	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 442	442	*Pocket mouse*	M	23.5	1	1	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 443	*443*	*Peromyscus maniculatus*	F	18.5	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 444	*444*	*Peromyscus maniculatus*	M	16.5	0	0	0	4	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 445	445	*Reithrodontomys megalotis*			0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 446	*446*	*Peromyscus maniculatus*	F	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 447	447	*Reithrodontomys megalotis*			0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 448	448	*Reithrodontomys megalotis*			0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 449	*449*	*Peromyscus maniculatus*	M	15	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 450	*450*	*Peromyscus maniculatus*	M	14	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 451	451	*Dipodomys ordii*			0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 452	452	*Peromyscus maniculatus*	F	22	0	7	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 453	453	*Peromyscus maniculatus*	M	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 454	454	*Peromyscus maniculatus*	M	16	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 455	455	*Dipodomys ordii*			0	1	1		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 456	456	*Peromyscus maniculatus*	F	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 457	457	*Reithrodontomys megalotis*	M	12.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 458	458	*Reithrodontomys megalotis*	M	11.0	0	1	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 459	459	*Peromyscus maniculatus*	M	18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 460	460	*Peromyscus maniculatus*	M	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 461	461	*Peromyscus maniculatus*	F	15	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 462	462	*Peromyscus maniculatus*	F	19	1	0	5	5	0	0	1	0	4	0	0	0	0	0	0	0	1	0	1	0	0
AWB 463	463	*Peromyscus maniculatus*	F	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 464	464	*Peromyscus maniculatus*	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 465	465	*Peromyscus maniculatus*	F	9	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 466	466	*Peromyscus maniculatus*	F	17	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 467	467	*Peromyscus maniculatus*	M	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 468	468	*Peromyscus maniculatus*	F	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 469	469	*Reithrodontomys megalotis*	M	9.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 470	470	*Peromyscus maniculatus*	F	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 471	471	*Peromyscus maniculatus*	F	11	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 472	472	*Peromyscus maniculatus*	M	18.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 473	473	*Peromyscus maniculatus*	M	20.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 474	474	*Peromyscus maniculatus*	F	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 475	475	*Reithrodontomys megalotis*	M	10.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 476	476	*Reithrodontomys megalotis*	F	5.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 477	477	*Peromyscus maniculatus*	M	15.5	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 478	478	*Peromyscus maniculatus*	F	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 479	479	*Pocket mouse*	F	20.0	1	1	0	2	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 480	480	*Peromyscus maniculatus*	F	18	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 481	481	*Peromyscus maniculatus*	F	12	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 482	482	*Peromyscus maniculatus*	F	16	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 483	483	*Peromyscus maniculatus*	M	7	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 484	484	*Peromyscus maniculatus*	M	19	0	2	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
AWB 485	485	*Peromyscus maniculatus*	M	19	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 486	486	*Pocket mouse*	M	13.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 487	487	*Reithrodontomys megalotis*	F	12.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 488	488	*Peromyscus maniculatus*	M	19.5	0	0	0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 489	489	*Peromyscus maniculatus*	M	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 490	490	*Peromyscus maniculatus*	M	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 491	491	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 492	492	*Peromyscus maniculatus*	M	15	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 493	493	*Pocket mouse*	M	18.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 494	*494*	*Peromyscus maniculatus*	M	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 495	*495*	*Peromyscus maniculatus*	M	16.5	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 496	*496*	*Peromyscus maniculatus*	M	17	0	1	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 497	*497*	*Peromyscus maniculatus*	M	20	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 498	498	*Reithrodontomys megalotis*	F	11.5	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 499	*499*	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 500	*500*	*Peromyscus maniculatus*	F	13.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 501	*501*	*Peromyscus maniculatus*	F	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 502	*502*	*Peromyscus maniculatus*	F	12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 503	*503*	*Peromyscus maniculatus*	M	16	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 504	*504*	*Peromyscus maniculatus*	M	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 505	*505*	*Peromyscus maniculatus*	M	23	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 506	506	*Microtus longicaudus*	M	25.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	1	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 507	*507*	*Peromyscus maniculatus*	M	26	0	3	1	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 508	*508*	*Peromyscus maniculatus*	M	17.5	0	8	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0
AWB 509	509	*Reithrodontomys megalotis*	M	8.0	0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 510	*510*	*Peromyscus maniculatus*	M	18	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 511	*511*	*Peromyscus maniculatus*	M	19	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 512	*512*	*Peromyscus maniculatus*	M	14	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 513	*513*	*Peromyscus maniculatus*	M	20.5	0	1	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0
AWB 514	*514*	*Peromyscus maniculatus*	F	17.5	0	4	0	5	0	0	0	5	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 515	515	*Tamias dorsalis*	F	71.0	0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 516	516	*Tamias dorsalis*	M	34.0	0	0	0		NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB 517	*517*	*Peromyscus maniculatus*	M	18.5	0	1	0	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 518	*518*	*Peromyscus maniculatus*	M	19	0	11	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0
AWB 519	*519*	*Peromyscus maniculatus*	F	17.5	NA	NA	NA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 520	*520*	*Peromyscus maniculatus*	M	16	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 521	521	*Reithrodontomys megalotis*	F	11.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 522	*522*	*Peromyscus maniculatus*	M	20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
AWB 523	*523*	*Peromyscus maniculatus*	M	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 524	*524*	*Peromyscus maniculatus*	M	16.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 525	*525*	*Peromyscus maniculatus*	M	14.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 526	*526*	*Peromyscus maniculatus*	M	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 527	*527*	*Peromyscus maniculatus*	F	14	0	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 528	*528*	*Peromyscus maniculatus*	M	19.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 529	*529*	*Peromyscus maniculatus*	M	20.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
AWB 530	*530*	*Peromyscus maniculatus*	F	15	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 531	*531*	*Peromyscus maniculatus*	F	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 532	*532*	*Peromyscus maniculatus*	F	10.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 533	*533*	*Peromyscus maniculatus*	M	19	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 534	*534*	*Peromyscus maniculatus*	F	17	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 535	*535*	*Peromyscus maniculatus*	M	21	0	0	1	3	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 536	*536*	*Peromyscus maniculatus*	M	12.5	4	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 537	*537*	*Peromyscus maniculatus*	F	16.5	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 538	*538*	*Peromyscus maniculatus*	F	16	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 539	*539*	*Peromyscus maniculatus*	M	20	6	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 540	*540*	*Peromyscus maniculatus*	F	19	11	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 541	*541*	*Peromyscus maniculatus*	F	20	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 542	*542*	*Peromyscus maniculatus*	F	14	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 543	*543*	*Peromyscus maniculatus*	M	17.5	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 544	544	*Reithrodontomys megalotis*	M	8.5	NA	NA	NA	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 545	*545*	*Peromyscus maniculatus*	M	16.5	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 546	*546*	*Peromyscus maniculatus*	M	17	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 547	*547*	*Peromyscus maniculatus*	F	20	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 548	*548*	*Peromyscus maniculatus*	M	19	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 549	549	*Peromyscus maniculatus*	M	15.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 550	550	*Peromyscus maniculatus*	M	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
AWB 551	551	*Reithrodontomys megalotis*	M	9.5	0	0	0	9	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 552	*552*	*Peromyscus maniculatus*	F	14	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 553	*553*	*Peromyscus maniculatus*	M	26.5	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0
AWB 554	*554*	*Peromyscus maniculatus*	M	17	11	1	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 555	*555*	*Peromyscus maniculatus*	M	11	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 556	*556*	*Peromyscus maniculatus*	M	19	0	2	1	6	0	6	0	0	0	0	0	0	0	0	0	0	24	0	24	0	0
AWB 557	*557*	*Peromyscus maniculatus*	M	14	0	0	9	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 558	*558*	*Peromyscus maniculatus*	M	20	10	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 559	*559*	*Peromyscus maniculatus*	F	15	1	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 560	*560*	*Peromyscus maniculatus*	M	20	38	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 561	*561*	*Peromyscus maniculatus*	F	19	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
AWB 562	*562*	*Peromyscus maniculatus*	M	18.5	0	2	0	6	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 563	*563*	*Peromyscus maniculatus*	M	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 564	*564*	*Peromyscus maniculatus*	M	18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 565	*565*	*Peromyscus maniculatus*	M	19.5	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 566	*566*	*Peromyscus maniculatus*	F	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 567	*567*	*Peromyscus maniculatus*	M	20	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 568	*568*	*Peromyscus maniculatus*	F	24	0	4	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 569	*569*	*Peromyscus maniculatus*	F	20.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 570	*570*	*Peromyscus maniculatus*	F	12.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 571	*571*	*Peromyscus maniculatus*	F	10	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 572	*572*	*Peromyscus maniculatus*	M	14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 573	*573*	*Peromyscus maniculatus*	M	21	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
AWB 574	*574*	*Peromyscus maniculatus*	M	14.5	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 575	*575*	*Peromyscus maniculatus*	F	23.5	0	2	0	0	0	0	0	0	0	0	0	7	5	2	0	0	3	0	3	0	0
AWB 576	*576*	*Peromyscus maniculatus*	F	15	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB 577	577	*Peromyscus maniculatus*	F	14	0	3	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 578	578	*Peromyscus maniculatus*	F	11	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 579	579	*Peromyscus maniculatus*	M	15	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 580	580	*Peromyscus maniculatus*	M	18.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 581	581	*Peromyscus maniculatus*	M	14.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 582	582	*Peromyscus maniculatus*	F	11.5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 583	583	*Peromyscus maniculatus*	F	16	0	2	0	16	0	0	16	0	0	0	0	1	0	1	0	0	8	8	0	0	0
AWB 584	584	*Peromyscus maniculatus*	M	19	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 585	585	*Peromyscus maniculatus*	F	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 586	586	*Microtus longicaudus*	M	34.0	0	1	10	0	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 587	587	*Peromyscus maniculatus*	M	22	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 588	588	*Peromyscus maniculatus*	M	12	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 589	589	*Peromyscus maniculatus*	M	21	4	1	3	27	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 590	590	*Peromyscus maniculatus*	F	16.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 591	591	*Peromyscus maniculatus*	M	11.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 592	592	*Peromyscus maniculatus*	F	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 593	593	*Peromyscus maniculatus*	M	20	0	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 594	594	*Peromyscus maniculatus*	F	14	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 595	595	*Peromyscus maniculatus*	F	18	0	1	0	13	0	13	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
AWB 596	596	*Lemmiscus curtatus*	M	16.0	0	0	0	0	NA	NA	NA	NA	NA	NA	NA	2	NA	NA	NA	NA	0	NA	NA	0	NA
AWB 597	597	*Peromyscus maniculatus*	F	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 598	598	*Peromyscus maniculatus*	M	18	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 599	599	*Peromyscus maniculatus*	M	20	0	0	0	6	2	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 600	600	*Peromyscus maniculatus*	M	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 601	601	*Peromyscus maniculatus*	F	20	0	3	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 602	602	*Peromyscus maniculatus*	M	15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 603	603	*Peromyscus maniculatus*	F	21.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
AWB 604	604	*Peromyscus maniculatus*	F	23.5	0	0	0	6	1	0	5	0	0	0	0	2	2	0	0	0	0	0	0	0	0
AWB 605	605	*Peromyscus maniculatus*	M	27.5	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB 606	606	*Peromyscus maniculatus*	F	20	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 607	607	*Peromyscus maniculatus*	F	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 608	608	*Peromyscus maniculatus*	M	18	0	6	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 609	609	*Peromyscus maniculatus*	M	14.5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB 610	610	*Tamias dorsalis*	F	52.5	0	1	1	7	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	0	NA	NA	0	NA
AWB611	611	*Peromyscus maniculatus*	F	16.5	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB612	612	*Peromyscus maniculatus*	M	17	0	10	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB613	613	*Peromyscus maniculatus*	F	25	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB614	614	*Peromyscus maniculatus*	M	20	5	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB615	615	*Peromyscus maniculatus*	F	19.5	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB616	616	*Peromyscus maniculatus*	F	9	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB617	617	*Peromyscus maniculatus*	F	9.5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB618	618	*Peromyscus maniculatus*	M	14.5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB619	*619*	*Peromyscus maniculatus*	M	19.5	2	8	0	5	5	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
AWB620	*620*	*Peromyscus maniculatus*	M	20.5	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB621	*621*	*Peromyscus maniculatus*	M	18.5	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB622	*622*	*Peromyscus maniculatus*	M	21.5	4	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB623	*623*	*Peromyscus maniculatus*	M	17.5	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB624	624	*Peromysus truei*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA		NA	NA	NA	NA	0	NA	NA	0	NA
AWB625	*625*	*Peromyscus maniculatus*	M	25	1	3	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB626	*626*	*Peromyscus maniculatus*	M	17	0	1	4	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB627	*627*	*Peromyscus maniculatus*	M	19.5	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB628	*628*	*Peromyscus maniculatus*	M	21	0	6	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB629	*629*	*Peromyscus maniculatus*	M	17	1	2	0	0	0	0	0	0	0	0	0	5	0	5	0	0	0	0	0	0	0
AWB630	*630*	*Peromyscus maniculatus*	F	26	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB631	*631*	*Peromyscus maniculatus*	M	21	3	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB632	*632*	*Peromyscus maniculatus*	M	18.5	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB633	*633*	*Peromyscus maniculatus*	F	15.5	3	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB634	*634*	*Peromyscus maniculatus*	M	9.5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB635	*635*	*Peromyscus maniculatus*	F	16	1	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB636	*636*	*Peromyscus maniculatus*	M	10.5	3	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB637	*637*	*Peromyscus maniculatus*	F	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB638	*638*	*Peromyscus maniculatus*	F	14.5	2	2	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB639	*639*	*Peromyscus maniculatus*	M	15	1	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB640	*640*	*Peromyscus maniculatus*	M	14	17	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB641	*641*	*Peromyscus maniculatus*	M	16	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB642	*642*	*Peromyscus maniculatus*	F	15	0	7	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB643	*643*	*Peromyscus maniculatus*	M	16.5	1	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB644	*644*	*Peromyscus maniculatus*	M	22	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB645	*645*	*Peromyscus maniculatus*	M	14	8	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB646	*646*	*Peromyscus maniculatus*	M	23.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB647	*647*	*Peromyscus maniculatus*	M	16.5	1	3	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB648	*648*	*Peromyscus maniculatus*	M	16	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB649	*649*	*Peromyscus maniculatus*	M	17	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB650	*650*	*Peromyscus maniculatus*	M	15	0	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB651	*651*	*Peromyscus maniculatus*	M	19.5	1	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB652	*652*	*Peromyscus maniculatus*	F	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB653	*653*	*Peromyscus maniculatus*	M	14.5	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB654	*654*	*Peromyscus maniculatus*	M	15	5	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB655	*655*	*Peromyscus maniculatus*	M	17	7	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB656	*656*	*Peromyscus maniculatus*	M	14	8	6	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB657	*657*	*Peromyscus maniculatus*	F	13.5	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB658	*658*	*Peromyscus maniculatus*	F	26	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB659	*659*	*Peromyscus maniculatus*	M	13	9	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Host Number	num	Species	sex	mass	ticks	fleas	lice	Number of nematodes	*Protospirura numidica*	*Mastophorus muris*	*Pterygodermatites peromysci*	*Syphacia peromysci*	*Aspiculuris americana*	*Heligmosomoides vandegrifti*	*Syphacia montana*	Number of cestodes	*cest.sp.1*	*Hymenolepis sp.*	*cest.sp.3*	*cest.sp.4*	Number of acanthocephalans	*acan.sp.1*	*acan.sp.2*	Number of trematodes	*Brachylaima microti)*
AWB660	*660*	*Peromyscus maniculatus*	M	18	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB661	*661*	*Peromyscus maniculatus*	M	17	2	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB662	*662*	*Peromyscus maniculatus*	M	16.5	1	4	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB663	*663*	*Peromyscus maniculatus*	F	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB664	*664*	*Peromyscus maniculatus*	F	15.5	2	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB665	*665*	*Peromyscus maniculatus*	F	24	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB666	*666*	*Peromyscus maniculatus*	M	18	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AWB669	669	*Ammospermophilus leucurus*	F	96.0	1	10	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB670	670	*Ammospermophilus leucurus*	M	73.5	0	2	34	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB671	671	*Perognathus*	M	24.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB672	672	*Ammospermophilus leucurus*	F	66.0	0	25	15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB673	673	*Ammospermophilus leucurus*	F	125.0	9	6	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB675	675	*Peromysus truei*	M	17.0	3	0	10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB676	676	*Peromysus truei*	M	19.0	6	3	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB677	677	*Peromysus truei*	F	14.0	0	0	13	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB678	678	*Peromysus truei*	M	20.0	1	2	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB679	679	*Peromysus truei*	M	17.0	6	3	2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB680	680	*Peromysus truei*	M	26.0	0	4	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB681	681	*Peromysus truei*	M	17.5	10	2	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA
AWB683	683	*Peromysus truei*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NA	NA	0	NA

APPENDIX E

HISTOPATHOLOGY RESULTS OF RODENTS

Table E.1. Results of histopathology for rodents captured in the Great Basin. Heart, lung, kidney, and liver tissue was examined for diseases and parasites using histology. Listed are the collection numbers, species of rodent, and any parasites and pathologies found. Rodent tissues were examined and diagnosed by Dr. David Gardiner, Animal Reference Pathology.

Collection number*	Rodent species	Parasites found	Pathology
AWB7	*Peromyscus maniculatus*	None	Small amount of interstitial nephritis
AWB9	*Peromyscus maniculatus*	None	Pneumonia-cause unknown
AWB26	*Peromyscus maniculatus*	None	Small amount of interstitial nephritis
AWB27	*Peromyscus maniculatus*	None	Some mild renal mineralization
AWB28	*Peromyscus maniculatus*	None	Small amount of interstitial nephritis
AWB33	*Tamias dorsalis*	None	Mild crhronic pyelitis and rare inflammation in the liver
AWB34	*Tamias dorsalis*	None	Mild chronic pyelitis
AWB35	*Tamias dorsalis*	None	Hyperplastic bronchial associated lymphoid tissue (BALT)
AWB36	*Tamias dorsalis*	None	Both adrenal glands present. Mild chronic pyelitis
AWB38	*Peromyscus maniculatus*	None	Liver has extramedullary hematopoiesis (EMH), contains a nodule of lymphoid tissue in the perirenal soft tissue
AWB41	*Peromyscus maniculatus*	None	Abnormal adrenal gland morphology (either congenital or developmental abnormality)

Table E.1. continued

AWB43	*Peromyscus maniculatus*	None	Mild lymphocytic infiltrates present in liver
AWB44	*Peromyscus maniculatus*	None	Focal area of hepatic mineralization; focal area of interstial lymphocytic inflammation
AWB45	*Peromyscus maniculatus*	None	Mild pyelitis, hyperplastic BALT
AWB46	*Tamias minimus*	None	Mild pyelitis
AWB48	*Peromyscus maniculatus*	None	Mild EMH in liver
AWB50	*Peromyscus maniculatus*	None	Mild liver EMHand mild mineralization
AWB51	*Peromyscus maniculatus*	None	Mild BALT hyperplasia; both adrenal glands present
AWB62	*Peromyscus maniculatus*	*Capillaria hepatica*	Capillariasis
AWB64	*Peromyscus maniculatus*	*Emmonsia crescens*	Adiaspiromycosis
AWB71	*Peromyscus maniculatus*	None	Mild EMH in liver
AWB72	*Peromyscus maniculatus*	None	Hyperplastic BALT, adrenal gland present
AWB78	*Peromyscus maniculatus*	None	EMH in liver
AWB83	*Peromyscus maniculatus*	None	Hyperlastic BALT
AWB84	*Peromyscus maniculatus*	None	EMH in liver
AWB85	*Peromyscus maniculatus*	None	EMH in liver
AWB86	*Peromyscus maniculatus*	None	EMH focus in lung
AWB93	*Peromyscus maniculatus*	None	Focus of mineralization in liver; hyperplastic BALT; focus of EMH in kidney
AWB95	*Peromyscus maniculatus*	None	Small amount of EMH in kidney
AWB96	*Tamias dorsalis*	None	Abundant EMH in liver, hyperplastic BALT

Table E.1. continued

AWB97	*Neotoma lepida*	None	Focus of EMH in lung
AWB98	*Peromyscus truei*	None	Hyperplastic BALT, pyelitis, EMH in liver
AWB107	*Peromyscus maniculatus*	None	Mild EMH
AWB109	*Peromyscus maniculatus*	None	Mild liver EMH
AWB113	*Peromyscus truei*	None	Two pulmonary granulomas-cause not apparent
AWB115	*Peromyscus maniculatus*	None	Hyperplastic BALT
AWB117	*Peromyscus maniculatus*	*Emmonisa crescens*	Adiaspiromycosis
AWB120	*Peromyscus maniculatus*	None	Mild pyelitis
AWB121	*Peromyscus maniculatus*	None	Severe interstitial nephritis-cause not apparent
AWB127	*Peromyscus maniculatus*	None	Small amount of pancreas present
AWB130	*Micotus montanus*	*Emmonisa crescens*	Adiaspiromycosis
AWB133	*Peromyscus maniculatus*	None	Mild EMH in liver
AWB140	*Peromyscus maniculatus*	None	Mild EMH in liver
AWB143	*Microtus longicaudus*	*Emmonsia crescens*	Adiaspiromycosis, inflammation around bile duct

* Animals are located at the Natural History Museum of Utah in Salt Lake City, UT

APPENDIX F

SEQUENCES OF PARASITE SPECIES OF DEER MICE

Table F.1. Cytochrome oxidase I (COI) gene sequences of parasite species of deer mice collected in the Great Basin. Sequences are the sequences from one representative individual of each species.

Group	Parasite species	Sequence of representative individual
Nematode	*Protospirura numidica*	GAGGTTTATATTATTATTTTGCCGGCGTTTGGTGT TATCAGGGAGGCTGTGCTTTTTCTAACTGATAAG GAGCGTTTGTTTGGGCAAACTAGAATGACCTTTG CTTCTATTTGAATTGCTATTTTAGGTACTTCTGTA TGAGGTCATCATATATATACTGCTGGTTTGGATAT TGATACTCGTACTTATTTTAGTGCTGCTACTATGA TTATTGCTATTCCTAGGGCTGTTAAGGTTTTTAAT TGGTTGGGAACTTTATTTGGTTCTCGGCAGATTTT TCAGCCTTTGTGGTGTTGAACTTATAGTTTTATTT TATTGTTTACTGTAGGGGGGTTGAGAGGAATTAT TTTGAGTACTGCTAGTCTGGATATTGTTTTGCATG ATACTTATTATGTAGTTGCCCATTTTCATTATGTT TTAAGTTTTAGGTGCTA
Nematode	*Pterygodermatites peromysci*	CCTGAGGTTTATATTATTATTTTGCCGGCTTTTGG TATTGTGAGAGAGTGTGTTTTGCAGTTAAGTGAT AAGGAGTATTTATTTGGTCAGATAAGAATGATTT TTGCTTCTGTTTGGATTGCTGTTTTGGGCCTGACT GTGTGAGGGCATCATATGTATACAGCTGGGCTGG ATATTGATACTCGTGTGTATTTTAGTGCGGCTACT ATGATTATTGCTGTTCCTAGCGCAGTTAAGATTTT TAATTGGTTATCTACTCTTTATGGCTCTGATCAGG TTTTTCAGCCTTTATTGTGTTGGACTTATAGTTTTA TTTTGATATTTGCTACTGGTGGTATTACTGGTATT GTTTTGAGGGCGGCTAGGTTGGATGTGTTATTAC ATGATACATATTATGTGGTTGCTCATTTTCATTAT G

Table F.1. continued.

Nematode	*Mastophorus muris*	TGAGGTTTATATTATTATTTTACCTGCTTTTG GTATTATTAGTGAGTCGGTTTTGTTTTTAACT GATAAGGAGCGTTTGTTTGGTCAAACTAGGA TAACTTTCGCTTCTATTTGAATTGCTGTTTTA GGTACTTCGGTCTGGGGGCATCATATATACA CGGCTGGTTTGGATATCGATACCCGGACTTA TTTCAGGGCTGCTACTTTAATTATTGCTATCC CTAGGGCTGTAAAGGTTTTTAATTGGCTAGG GACTTTTTTTGGGTCTCATCAAAATATGCAG CCTTTGTGATGTTGAACTTATAGTTTTATTTT TTTGTTTACTTTGGGTGGTTTAAGTGGTATTA TTTTGAGTACCGCTAGTTTGGATATTATTCTT CATGACACTTATTATGTGGTGGCTCATTTTC ATTATGTTTTAAG
Nematode	*Heligmosomoides vandegrifti*	CCTGAGGTTTATATTTTGATTTTACCTGCATT TGGTATTACCAGGCAGTCAACTTTATATTTA ACAGGTAAAAAGGAGGTTTTTGGTTCATTAG GAATGGTATATGCTATTTTAAGTATTGGATT GATTGGTTGTGTGGTTTGGGCTCATCATATG TATACTGTTGGTATGGATTTGGATTCTCGTG CTTATTTTACGGCTGCTACGATAGTTATTGCT GTACCTACTGGAGTAAAAGTGTTTAGGTGAT TAGCTACTTTGTTTGGTATAAAAATGAATTT TCAACCTGTTTTGTTATGAGTTTTAGGTTTTA TTTTTTTGTTTACTATTGGTGGTTTAACTGGG GTGGTTTTATCTAATTCTAGTTTGGATATTAT TTTACATGACACTTATTATGTGGTTAGACAT TTTCATTATGTTTTAAGTTTAGGTGCTA
Nematode	*Syphacia peromysci*	CCTGAGGTTTATATTCTTATTTTGCCTGCTTT TGGAATTATTAGACATAGGATTTTGTATTTG ACTGGTAAAAAGGAAGTTTTTGGTCATGTGG GAATAATTTATGCTGTTGTTTCTATTGCTTTA ATTGGGAGAGTAGTTTGGGGGCATCATATGT TTACTGTTGGTTTTGATGTTAGTGTACGTTTA TATTTTATGGTTGCTACTATGATTATTGCTGT TCCTACAGGTATTAAGGTTTTTAGGTGGTTG TTGACTTTGTTGGGTGGTAAGTGTGTGTTTC ATCCTTTGTTGTTATGGGTTGTTGGTTTTATT TTTATGTTTACTTTGGGTGGTTTAACTGGAAT TATGGTAGCTAATCCTGTTTTGGATAATTTG TTTCATGATACTTATTTTGTAGTTGCGCATTT TCATTATGTTTTAAGTTTAGGTGCT

Table F.1. continued

Nematode	*Aspiculuris americana*	TGAGGTTTATATTCTTATTTACCGGCTTTTGG TATTATTAGTCATAGTGTGTTATATTTGACTGG TAAAAAGGAAGTTTTTGGTCATTTGGGCATGG TTTATGCTATTATTTCTATTGCTTTAATTGGGA GTGTTGTTTGAGGGCATCATATGTTTACTGTA GGTTTTGATATAAGAACTCGTTTATATTTTATG GCTGCTACTATAATTATTGCTGTGCCTACTGG GATTAAGGTTTTTAGTTGGTTGTTGACTTTGGT GGGTAATAATATAGTTTTTCAGCCTTTGCTTTT GTGGGTTATGGGGTTTATTTTTATGTTTACTTT GGGGGGTTTAACTGGTATTATGGTTGCTAATC CTGTTTTGGATAATTTGTTTCATGATACTTATT TTGTTGTTGCTCATTTTCATTATGTTTTAAGTT TAGGTGCTA
Nematode	*Syphacia montana*	TGAGGTTTATATTTTGATTTTGCCTGCTTTTGG TATTATTAGTCATAGTATTTTGTATTTAACTGG TAAAAAAGAGGTGTTTGGTCATTTAGGTATGG TTTATGCTGTTATTTCTATTGCTTTGGTTGGTA GTGTTGTCTGGGGACATCATATATTTACTGTT GGTTTTGATATGAGTACTCGTTTGTATTTTATG GCTGCTACTATAATTATTGCTGTTCCTACTGGT ATTAAGGTTTTTAGTTGATTGATAACTTTGTTG GGGGGTTATTTTGTTGTTCATCCTTTGTTGATG TGAGTGATTGGTTTTGTTTTTATGTTTACATTG GGTGGTTTGACTGGTATTATGGTTGCTAATCC
Cestode	*Hymenolepis* sp.	ATAATGAAAATGAGCCACAACAAATCACGTA TCATGCAAAACTTTATCTAAAACACAAGCAGA TAACACTATGCCCGTAACTCCACCAAAAGTAA AAAGAACTATAAAAGAAATTATTCATCATAAT ATGGGATCCATAGAACTAACCCGACATTTCAT CAGCATATATAATCAAGTAAAAACCTTAATAC CAGTGGGGACCCCTATAATCATAGTGACAGA CCTAAAAAAAACAGCCGTCTTAACATCCAAA CCAACAGTAAACATATGGTGGCCTCAAACACT ACTTCCTAAACACACTATAGAAAACATCGCAA ATAATAAACCGTAATAACCAAATACATCTGCA TTCATACTCAACCTCAAACAAATATGACTTAT AATTCCAAACCCTGGTAATATTAACACATAAA CCTCA

Table F.1. continued

Acanth.	*Moniliformis sp.1*	ACGATCCAACAGTAACATAGTCAAAGCAGCCG CCAAAACAGGTACAGTTAAAATGATCAACCCA GATGTTACAATTAAAGATCACACAAACAATGT TAATTTTTCCAACCTAATACCCATCTCCTCATA CACACACCAAACAGTAGATACAATATTAACAG AAGCCAAGATAGAAGACAAACCTGCTACATGT AAAGATAAAACTATTAAATCCACAGAAACCCC TCTTCTAAACCCATAGGACCTTAAGGGAGGGT ATATAGTTCACCCAGTACCAGCCCCGTCTACTA ACATTGACATTATCAATAATACTAATGACCCTG GAAGTAACCAAAACCTAAAGTTGTTCAAGCGA GGAAATGCCATGTCACCCACACCTAGTATTAC TGGAACCATCCAATTACCAAACCCCCCTATCAT AATAGGTATAACCAAAAAGAAAATCATCAAAA TAGCATGTGACCTTACCAGTACATTATACAGGT GATCGTCTATCAACAAAGACCCTACACATCCC AACTCCAAACGAATTACCACCCTTAAAACTAC CCCCATTAGCCCCCTCCACAAAGCAAACAGAA CATACAACACACC
Acanth.	*Moniliformis sp. 2*	CCAAAAGCAGCATCGTAAGAGCAGCCGCCAAA ACTGGCACAGTTAAAATAATCAACCCAGATGT AACAACCAAAGACCATACAAACAATGTTAGTT TTTCCAACCTGATACCCATATCCTCATACACAC ACCAAACAGTAGATACAATATTAACAGAAGCC AAAATAGAAGACAAACCTGCCACATGAAGAG ATAAAATCATTAAGTCCACAGAGACACCCCTA CTAAACCCATAAGACCTTAGGGGTGGGTACAC AGTTCACCCTGTACCCGCCCCATCTACTAGTAT TGACATCATTAACAATACTAACGATCCCGGTA ACAACCAAAATCTAAAATTATTTAATCGGGGG AATGCCATATCCCCTACACCTAGTATCACAGG AACCATCCAATTACCAAACCCCCCTATCATAAT AGGTATAACCAAAAAGAAGATCATCAAAATAG CATGTGACCTTACCAATACGTTATATAGGTGAT CGTCTATCAACAAAGACCCAACACACCCCAAC TCCAAACGAATTACCACCCTTAAGACCACCCC TATTAAACCACTCCACAAAGCAAACAAAACAT ACATGACA

Table F.1. continued

Trematode	*Brachylaima microti*	GCAAAAGGTAAGATACTTTCAGCAACCTACT TCAACACAGTCTCTCAACTTTTGAAAGCAAC CACACAGTATCAATACTTTACAAAAGTACCA TTTTACAATAAACTACACTTTCAACGCAGGG TATCATCCTCAAAACAATAATATTTAGGGCA TCCTACGTACAAACCATGATGTGGTAAAGGT ACTGTACAAACATTCACCGCTACAGAAGGTG CTCCTCATAAACCCAAAATCTTATTACCTACA ACAATTGACTCTCACAATATAAACACTAAAA AGACACCTCTTATCACAGAAATTATACCACC AAGCGATGAAATTTTTTTCATTCAATAAAAT GCAGGATCATAGCAACACACCCGCCGAGGA AGCCCATACAAACCAAGAAAATGCATTGGAA AAAAACACAGATTAAATCCAACAATAGACAC CAACCAATGCCCCTGTAGTAAATACTTATTTA AACTACATCCGGTAATCACAGGCCACCACCA AAGTAAAAAAATAACTACAGTCCTGTAAGAA CCCAACGACAAAACGTAATGAAAATGAGCC ACAACAAACCACGTATCATGAAACAACGAAT CTAAAACAGAAGCTGACAAAACAATACCAGT AACACCCCCCACAGTAAACAAAAAGATAAA AGCAATTATTCACCACACCACAGGATCGAAT ATGGAATTTCGACTACTACCCAACATGTACA ACCACGAAAAAACCTTTATCCCCGTTGGAAT ACCAATAACCATAGTTACTGATCTAAAAAAA ACAGTCGTCTTTACATCTAACCCAACAACAA ACATATGATGAACCCATACAACACTCCCAAG ACATACAATAGCCCCCATAGCAGAAACTAAA CCATAGTAGCCAAACAGAGACTCATTATTAC TCAGCCTAGAACAGATATGCCCAACAACTCC GAACCCAGGTAGGATAAGAACATAAACCTC