NATIVE VS. NON-NATIVE GRAZERS ALTER PARASITE ASSEMBLAGES BUT YIELD FEW CHANGES IN VEGETATION STRUCTURE AND MAMMALIAN COMMUNITY COMPOSITION IN A NORTH AMERICAN SHORTGRASS PRAIRIE

By

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A Thesis Submitted in Partial Fulfillment

of the Requirements for the Degree of

Master of Science in Biology

Austin Peay State University

January 2020

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DEDICATION

For my mentors. Your unbridled patience paired with brutal honesty led me to success.

Cheers.

ACKNOWLEDGEMENTS

I would to like to acknowledge members of the Malaney lab and Philmont Scout Ranch, specifically the seasonal staff of the Wildlife Department, for their invaluable help with my summer fieldwork. Planning, logistics, and execution of my project would not be possible without their generous help. I extend gratitude to the American Society of Mammalogists and the Department of Biology at Austin Peay State University for supportive grants and scholarships that funded my travel and field equipment. A special thanks to those whose conversations lead to formation of ideas and content for my thesis.

ABSTRACT

Grasslands are deteriorating globally resulting in widespread biodiversity degradation so understanding impacts of loss, or replacement, of native megaherbivores remains a central challenge for grassland conservation. Because of their disproportionately strong functional roles I compared native (bison) versus non-native (cattle) grazers in a shortgrass prairie from a multi-year field study by sampling 1,200 vegetation locations in two habitat types (grassland, woodland) across 48 transects (19,200 trap-nights) and collecting 5,127 parasites from 509 small mammals. I tested three competing hypotheses including top-down, bottom-up, and parasite-centric models. Grazer differences appear to alter parasite community structure and composition despite lack of significant influences on vegetation and mammalian community structure and composition, thus favoring the parasite-centric hypothesis. Across parasites, nematode prevalence was significantly higher in bison-grassland sites (threefold increase, *P*=0.02) and marginally significant in bison-woodlands sites (tenfold increase, *P*=0.06). Flea prevalence was significantly higher in cattle-grasslands (twofold increase, *P*=0.03), but equivalent in woodlands. I failed to detect significant differences across treatment or habitats for cestode prevalence and all parasite intensities. These results highlight anthelmintic drugs may remain in the environment where they are encountered by nematodes.

For my second chapter, because the relative importance of host versus environmental factors for explaining prevalence and intensity of flea parasitism in small mammals remains poorly understood, I evaluated these factors at two scales; among individuals of a single host species and across the landscape, sampling hosts from two habitat types (woodland and grassland). Using generalized linear models, I found host sex was an important predictor for parasites within a host (male-bias) for predicting both prevalence and intensity. Factors across hosts showed more variation. Host density and cattle treatment had a generally consistent, positive relationship with flea prevalence and intensity, but other factors such as vegetation and year had stochastic influences. Taken together, these results have implications for wildlife disease ecology because altered host and vector population abundances and composition are known drivers of pathogen transmission. Moreover, these combined results differ from tallgrass prairies, so land managers should consider alternative approaches to conserve distinct shortgrass prairies with different megaherbivores.

CHAPTER 1

Introduction

Grasslands are deteriorating globally resulting in widespread biodiversity declines, largely due to restructuring of large-bodied herbivore populations and communities (Smith et al., 2016). Consequently, understanding the impacts of loss, replacement, and management of native and non-native herbivores weighing more than 1000 kg (hereafter, megaherbivores) remains a central challenge for grassland conservation. This is notably compelling, as immense body sizes of megaherbivores allows them to exhibit disproportionate impacts in shaping the vegetation community, structure, and function, thus resulting in altered wildlife populations that co-habit the landscape (Galetti et al., 2017). For these reasons, megaherbivores are often considered ecological keystones (Gill, 2014; Knapp et al., 1999). Due to the co-evolutionary histories of herbivores with the transcontinental formation of grasslands, using grazing as a method of conservation serves as a successful method to bolster native biodiversity, improve productivity, and alter structure and function of imperiled biomes (Allred et al., 2013; Zhu et al., 2012). Collectively, studies demonstrate the complex interactions megaherbivores have within their respective ecosystems, but broadly demonstrate top-down mechanisms across xeric savanna grasslands (Eby et al., 2014; Warui et al., 2005), steppe meadows (Derner and Hart, 2007; Zhu et al., 2012), wetlands (Holder et al., 1980; Marty, 2005), plus tallgrass, mixed-grass, and shortgrass prairies (Ahlering and Merkord, 2016; Bowen and Kruse, 1993; Schwartz and Ellis, 1981). Therefore, understanding how grazers impact landscapes remains an essential topic that informs conservation ecologists how to best implement management plans for the preservation of grazer-mediated ecosystems.

Functional mechanisms of megaherbivores include selective forging (Knapp et al., 1999) and behaviors such as wallowing (Polley and Collins, 1984), whereby large-bodied herbivores alter local landscapes by increasing heterogeneity on both large geographic scales altering entire grassland ecosystems and small localized scales by changing vegetation profiles (Gill, 2014; Smith et al., 2016). Heterogeneity from foraging includes the structural and compositional changes to vegetation by selectively foraging on certain vegetation types (*e.g.*, favoring forbs over grasses) ultimately influencing other organisms (*e.g.*, forb vs. grass specialists) occupying areas shared with the megaherbivore. Because of these important functional roles, rangeland managers are often interested in how deployment of different megaherbivores and grazers on the landscape may ultimately allow them to achieve conservation goals such as improving range conditions, altering wildlife populations, and limiting the effects of wildlife diseases and pathogens.

Because megaherbivores are often considered ecological keystones within their respective natural communities with complex interactions across trophic levels, biologists are often interested in evaluating these trophic mechanisms. Therefore, researchers have setup long-term ecological experiments that monitor change, such as the Mpala Research Center in Kenya (*see* Augustine et al., 2009; Keesing, 1998; Weinstein et al., 2017), the Long-Term Ecological Research site in Kansas (*see* Cully, 1999; Grudzinski and Daniels, 2018; Pfeiffer and Hartnett, 1995; Ricketts and Sandercock, 2016), and the Tallgrass Prairie Reserve in Oklahoma (*see* Fuhlendorf and Engle, 2001; Hamilton, 2007; Wallace and Crosthwaite, 2005). Similarly, rangeland manager are often interested in better understanding the impact of management choices and actions on native biodiversity, structure, and function of local ecosystems. Accordingly, evaluating the links between vegetation structure and composition with small mammal communities emerge as an especially valuable indicator for assessing the effects of different ecological systems and alternative management treatments (Wilford and Malaney, unpublished).

Small mammals are known for high rates of fecundity and short generation times, so they enable efficient analysis of rapid response to management practices, as well as serving as direct indicators for shifts in ecosystem structure and composition (Ricketts and Sandercock, 2016). Furthermore, small mammals serve as the primary prey base for multiple predators (Hershkovitz, 1969; Lensink et al., 1955) and some species, such as grasshopper mice (*Onychomys spp.*) are predators themselves (Sherbrooke, 1991). Small mammals also promote heterogeneity and diversity in the plant community via herbivory (Fuhlendorf et al., 2010) and seed dispersal (Weltzin et al., 1997; Williams et al., 2000). Finally, many small mammals also harbor parasites which can shape community structure and life histories of their host through antagonistic co-evolution (Combes, 2001).

Rangeland management practices can either directly or indirectly influence the survival and reproductive abilities of the parasite community thereby influencing their hosts. A large proportion of anthelminthic drugs which pass through livestock are unaltered, allowing those drugs to have maximum effect on the organisms (*e.g.* arthropods and endoparasites) that interact with feces containing the drugs (Campbell, 1985). Anthelminthic drugs range in the time they remain in the environment, and typically are influenced by a swath of conditions, such as dose administered, climate, geographical area, and the community of arthropods and bacteria present to break down the feces (Floate, 1998; Wall and Strong, 1987). Environmental responses to excreted anthelminthic drugs vary, but there is surmounting evidence these drugs remain in the feces for weeks to months and can impact the local community in and around the excrement, such as decreasing abundance and diversity of arthropods (Gover and Strong, 1996; Iglesias et al., 2006; Sommer et al., 1992). Conversely, some parasites can be indirectly influenced by different herbivores that may alter the amount of litter or litter depth. As a result of foraging, litter is often reduced with grazing, and, consequently, amount of bare ground increases (Jepson-Innes and Bock, 1989; Naeth et al., 1991; Teague et al., 2010) Litter is an essential resource to these parasites, as fleas use litter that is typically in and around host nests or burrows for egg and larval development (Krasnov et al., 2002a; Sobey et al., 1974) , and ticks use litter as habitat for molting after blood meals (Chilton and Bull, 1993). Megaherbivores whose grazing activities decrease litter and litter depth thus indirectly influence the parasite community by providing a less suitable environment for survival and reproduction.

Due to hypothesized complex interactions between vegetation, wildlife, and their parasites and pathogens across grassland ecosystems, an essential issue for conservation and management is to consider differential community responses to alternative grazing practices that span trophic levels and across geographic scales. This is especially important considering the rapid decimation of grassland ecosystems through anthropogenic activities (*e.g.*, agricultural land conversion or urban development) and climate change (Samson et al., 2004). Furthermore, changes in ecosystems often alter the spread of zoonotic diseases from parasites such as ticks (Lyme’s disease and Rocky Mountain Fever) and fleas (Bubonic plague) for which small mammals serve as vectors (Buchholz, 2016; Castellanos et al., 2016; Young et al., 2015). Therefore, my thesis aims to develop a more comprehensive understanding of how grazing practices ultimately reshape vegetation, mammalian, and parasitic communities. We choose to focus on shortgrass prairies of North America, as this ecosystem is neglected in the ecological literature (Wilford and Malaney, unpublished) and inadequately studied to determine if patterns of variation observed in tallgrass prairies mirror variation in shortgrass prairies.

In North America, bison (*Bison bison*) once numbered in the millions and had a tri-coastal distribution, but with high densities occurring within the Great Plains. However, during the late 19th and early 20th centuries, bison were nearly extirpated and likely now occupy less than 1% of their historic range (Hornaday, 1889; Sanderson et al., 2008). During this time, bison were replaced by non-native domestic cattle (*Bos taurus*). Because cattle graze differently, they reportedly reshape local landscapes in novel ways, often resulting in structural and compositional changes to vegetation and wildlife, when compared to bison (Damhoureyeh and Hartnett, 1997; Matlack et al., 2001). Due to this ecological replacement, comparisons of differential grazing by bison and cattle to evaluate alternative hypotheses about ecological responses of vegetation and wildlife remain a key focus.

The goals of this project are three-fold: evaluate how alternative grazers (native bison versus non-native cattle) 1) reshape vegetation composition and structure, 2) alter small mammal community composition and structure, and 3) impact parasite prevalence and intensity of ectoparasites (fleas) and endoparasites (nematodes and cestodes) hosted by small mammals. Consequently, we test prevailing, alternative hypotheses to evaluate how grazing practices may influence short-grass prairie communities through either top-down or bottom-up mechanisms, or if they manifest in less complex ways.

First, a top-down model (grazer-mediated hypothesis) where the megaherbivore directly reshapes vegetation and thus occupancy of other co-occurring organisms is evaluated. In tallgrass prairies, bison and cattle reportedly asymmetrically change the vegetation structure and composition due to differences in preferred diet (Towne et al., 2005) and social behaviors (Allred et al., 2011; Kohl et al., 2013). For example, Steuter and Hidinger (1999) found bison preferentially graze grasses while and avoiding forbs while cattle tend to selectively graze forbs compared to grasses. Alternative diet preferences thus transform vegetation composition and reshape vegetation structure due to direct influences by different large-bodied grazers. Consequently, according to the grazer-mediated hypothesis and because of selective diet preferences, we expect to detect a higher percentage of forb cover in bison plots and increased percentage of grass cover in cattle plots. Because small mammals often respond to vegetation differently (Rosenstock, 1996) we expect to detect greater mammalian diversity on bison (native grazer) plots compared to cattle (non-native). Correspondingly, we also expect to detect higher proportion of grass-specialist mammals on cattle plots, forb-specialist mammals on bison plots, with generalist mammals remaining unchanged between plots. Finally, because some parasites (*e.g.* fleas) are positively associated with litter cover and depth, we expect to detect greater prevalence and intensity of fleas on small mammals within the treatment that has greater litter cover and depth.

Occasionally, grazing systems fail to reflect top-down expectations (*see* Tastad 2013), which suggests alternative origins of differences, such as unsimilar management practices of bison and cattle despite maintaining similar grazing pressure (*i.e.*, grazing units). Therefore, secondly, we evaluate a bottom-up model (environmental-contaminant hypothesis) where management practices influence parasites on co-occurring small mammals through unequal deployment of anti-parasitic drugs on the megaherbivores. The use of anthropogenic management within bison and cattle livestock herds is often not equivalent, as cattle are treated with anthelminthic drugs, and bison typically lack such management. Difficulty in bison management stems from their behaviors, most notably aggression, which hinders the ability for managers to effectively and appropriately administer anthelminthic drugs (Woodbury et al., 2012). Thus, due to the use of anti-parasitic drugs, the restructured parasite communities are expected to reshape host populations and thus vegetation structure and composition through host behaviors of herbivory and seed dispersal. The environmental-contaminant hypothesis is rarely evaluated in grassland ecology literature, but it may help explain how observed ecological differences could be due to alternative anthropogenic livestock management practices, such as the administration of anti-parasitic drugs. Here we expect to detect no changes to diversity or composition of the mammal community per se, rather, increased density of all small mammals because of reduced parasite loads, if environmental contamination of anthelmintic drugs symmetrically influences endoparasites and fleas, and thus mammals, in cattle plots. This is due to patterns in the literature that demonstrate that prevalence, intensity, and composition of parasites have the ability to cause cascading changes to shape small mammal communities (Buchholz, 2016; Püttker et al., 2008). Consequently, we also anticipate increased densities of small mammals would subsequently transform the vegetation structure as many of these animals are granivores and herbivores, grazing the vegetation and dispersing seeds (Hingtgen and Clark, 1984). The local rodent populations are predominantly granivorous, therefore, we expect to detect decreased grass and forb cover with increased rodent densities (Yenni et al., 2019).

Finally, because cascading effects may be overstated in ecosystems where megaherbivores are the ecological keystones, and it is possible grazers influence one trophic level without detectable changes into other trophic levels (Halaj and Wise, 2001; Shurin et al., 2002), we evaluate an intermediate model (parasite-centric hypothesis) where vegetation and mammals fail to differentially respond to a specific grazer, but rather grazing in general, where both bison and cattle similarly influence native biodiversity (vegetation and small mammals) through grazing and social behaviors (Delaney et al., 2016; Hartnett et al., 1996; Marty, 2005; Truett et al., 2001). Here, we expect few differences between structure and composition of both vegetation and small mammal structure across sites occupied by either grazer**.** However, ranch management practices often differentially apply anthelmintic drugs to reduce parasite loads in cattle, which perhaps alters parasitic community structure in areas occupied by domesticated cattle (Strong, 1993). Consequently, we expect to detect significant differences in both prevalence and intensity for endoparasites (*e.g.*, nematodes and cestodes) contrasted by few ectoparasitic assemblage differences (*i.e.*, fleas) on small mammals occupying cattle versus bison sites.

Materials and Methods

Study Site

This multiyear field study was conducted during 2018-2019 in northeastern New Mexico (July-August for both years) at Philmont Scout Ranch. Philmont is a 567 km^2 ranch and wilderness area owned and managed by the Boy Scouts of America as a high adventure camp. The ranch is located in Colfax Co., New Mexico, USA at the transition between the mixed conifer forests of Sangre de Cristo Mountains (Rocky Mountains) and the shortgrass prairies of the High Plains (Great Plains). As an active ranch, Philmont has a livestock management program that includes bison, cattle, horses (*Equus caballus*), and burros (*Equus asinus*). The ranch location is within a xeric shortgrass prairie which provides a rare opportunity to investigate alternative grazing practices of bison and cattle because most studies evaluating grazing patterns and behaviors have occurred in tallgrass prairies of the Great Plains (Wilford and Malaney, unpublished). Moreover, Philmont has maintained an active bison herd for over 75 years, making it perhaps the longest consistently maintained bison herd suitable for ecological studies in North America.

Transects and Habitats

We identified six pastures (two bison, four cattle) and 48 transects to compare and evaluate the alternative impacts of grazing by bison and cattle (Figure 1). Because pasture sizes varied for bison and cattle, so we chose a different number of pastures to have relatively equal trapping area, and that share equal grazing pressure per treatment (Casey Meyers, personal communication). Of the 48 paired transects, 36 were in grassland habitat for bison and cattle (n = 18 each). These transects were on open, shortgrass pastureland and both grazers had similar access to available pastures through rotational grazing practices. Vegetation consisted mostly of arid-adapted grasses such as blue grama (*Bouteloua gracilis)* and Indian ricegrass (*Oryzopsis hymenoides*); forbs including sagebrush (*Artemisia spp),* desert prince's plume (*Stanleya* *pinnata*), and yarrows (*Achillea spp.*); cacti such as pincushion (*Mammillaria spp.*), hedgehog (*Echinocereus spp.*), and prickly pear (*Opuntia spp.*); with occasional conifers including junipers (*Juniperus spp.*), pinyon pine (*Pinus edulis*), or ponderosa pine (*Pinus ponderosa*). The other twelve transects were in Pinyon-Juniper woodlands (n = 6 bison and cattle respectively). The woodland habitats were on the outskirts of pastures or in large patches among grassland areas within a managed and fenced pasture. Woodlands consisted of mature ponderosa pines, junipers, with occasional spruce (*Picea spp.*), cactus, and scrub oak (*Quercus berberidifolia*). Each transect was haphazardly located using GIS data ensuring suitable sampling (approximately 500 m) in each habitat type.

Vegetation Sampling

To quantify the vegetation structure and sample habitat conditions for local wildlife, we collected vegetation data at five equidistant points (trap stations, see below) along each transect, with GPS points taken at each sampling location. Vegetation sampling locations were established at the first trap station (0 m; *see* Small Mammal Trapping below) and subsequently, systematically every 120-130 m (12th, 25th, 37th, and 50th trap station). At each vegetation sampling location, we characterized vegetation at five 1 m^2 areas using a centered point-sampled transect technique (Litvaitis et al., 1996). First, we established a central area (at the trap station) and established a random azimuth (RA) measured out 10 m, and then +90°, +180°, and +270° from the RA (*see* Figure 2) resulting in two perpendicular 20 m arm-length transects. At each of the five areas (center and terminus ends of transects), we quantified percent ground cover using a 1 m^2 Daubenmire frame (Daubenmire, 1959) for several broad vegetation classifications that are important for estimating small mammal habitat use and that may influence mammalian parasites including: grass, forb, shrub, scat, moss, coarse woody debris (CWD), rock, bare, mesic, and litter cover. The Daubenmire frame was partitioned into 10x10 decimeters (dm) to facilitate the visual estimation of percent ground cover , with 1 dm^2 equivalent to 1% of ground cover.

Because we predict grazers may influence structure and composition of trees and shrubs, especially in woodlands, we quantified overstory canopy cover with a convex densiometer and measured lateral foliage height and density using a Robel pole. A convex densiometer is a spherical mirror where a range canopy covers is viewed and estimated. The mirror is split into 24 ¼ inch squares and each square represents 4% overstory canopy cover (1% for each corner). Field readings were then multiplied by 1.04 to get an accurate reading of overstory density (as there are only 96 possible counts; 24 squares split into 4 corners) (Lemon, 1997). The Robel pole was 2 m tall and marked with 1 dm bands to obtain a visual reading of lateral foliage density. As described by Robel et al. (1970), readings were taken 4 m from the pole and at 1 m above ground level. Additionally, we recorded the diameter at breast height (DBH) of the nearest tree to the center of the area (if present), and data about the local habitat within the 10 m x 10 m area such as species and abundance of shrubs (classified as woody species less than 5 cm DBH), number of trees (greater than 5cm DBH), and presence of scat by the grazer or other large-bodied wildlife such as pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), or black bear (*Ursus americanus*).

Small Mammal Trapping

We evaluated small mammals and parasitic community structure and composition with specimen-based approaches. First, we sampled local populations of small mammals using straight-line trapping transects consisting of 50 trap stations set approximately 10 m apart, creating a 500 m transect. Because small mammals are trapped unequally with different trap types, we purposefully set a diversity of trap types to improve our ability to accurately capture the diversity of the small mammal community for each treatment, as utilized by Young et al. (2015). At each trap station, we set a Sherman live trap paired with a Museum Special trap or occasionally a commercial Rat trap, all baited with a mix of peanut butter and oats. We kept transects out for four consecutive nights, accumulating 400 trap nights per transect (Wilson 1996). For each trapping season (two summers), we deployed 12 trapping transects on the bison and cattle treatments respectively including 9 on grassland habitat and 3 on woodland habitat. Mammals were handled and euthanized according to protocols approved by the American Society of Mammalogists and APSU Animal Care and Use Committee (Sikes 2016; Malaney 17.001), processed using holistic specimen-based research (Galbreath et al., 2019; Hope et al., 2018), and deposited mammals along with their parasites and corresponding metadata to either the David H. Snyder Museum of Zoology (DSMZ; AT2500-AT2531) or Museum of Southwestern Biology (MSB; NK302501-NK30299, NK303751-NK304089, and NK304251-NK304504) and all data available on the Arctos database (www.arctos.org).

Parasite Screens

All host mammals underwent screens to detect parasites. Ectoparasite screens for hematophagic arthropods including fleas (Order Siphonaptera), mites (Order Mesostigmata), sucking lice (Order Anoplura), and ticks (Order Acari) were conducted after the mammal was euthanized by fully examining the exterior of the mammal. At the nape, forceps were used to part the hairs and find parasites present in the fur. The dorsal, ventral, and lateral surfaces were examined in a similar way. Each mammal was also brushed to exhume all ectoparasites onto a light-colored background. Additionally, ears, tail and near the base of the tail, between toes, and around the snout were closely inspected during screens. All ectoparasites for each individual mammal were quantified and field-preserved in 95% EtOH.

Gastrointestinal helminthic endoparasites such as round worms (Order Nematoda), tape worms (Order Cestoda), and Flukes/Flatworms (Order Trematoda) were screened by viscerating the mammal, extracting the gastrointestinal tract, and placing it in a petri dish with water. To extract contents of the small and large intestines, forceps were used to hold the end of the intestines while another set of forceps was used slice open along the length of the intestines while simultaneously squeezing out the contents (Galbreath et al., 2019). The stomach and cecum were each examined separately but using similar techniques. Water was sprayed into the dish as necessary to increase the ability to detect helminth parasites. All endoparasites were quantified by location (e.g., stomach, small intestine) and preserved in 95% EtOH immediately, apart from cestodes, which were placed in a petri dish of water to relax before placing in ethanol.

Statistical Analyses

Vegetation Composition and Structure

Sampling sites were averaged for each trap station thus, for analyses, each transect had five data points of vegetation variables representing percent cover, litter depth, vegetation height and density, and overstory canopy cover. We chose to omit moss and mesic (water, cattails, *Equisetum*, etc) percent cover categories as they were represented in only a handful of sampling locations. Correlation analyses for all sets of vegetation variables were used to determine if any paired variables were highly correlated (> |0.8|).

We analyzed vegetation structure and composition using a pair of complementary approaches. Because habitats are not central to our question, we partitioned analyses by habitat (grassland, woodland) for all analyses. First, for univariate analyses, we compared vegetation variables between bison and cattle treatments using a Mann-Whitney U test, a non-parametric alternative to a t-test (Nachar, 2008). An *a priori* Shapiro-Wilks test of normality revealed that most of the vegetation variables are not normally distributed ($P < 0.05$). All statistical analyses were conducted in R version 3.6.0 (R Core Team, 2019).

Secondly, because we are interested in the composite effect of grazers, we used a multivariate approach (Principal Components Analysis, PCA) meant to capture and summarize the totality of variation. We conducted all PCAs with package *FactoMiner* version 1.42 (Le et al., 2008). PCA is a dimension reduction technique often used to decompose sampled variation into fewer components, maximizes observed variation, and simultaneously generates a model suitable for evaluating measured variation. Moreover, PCA allowed us to detect multivariate outliers, plus quantify and evaluate how vegetation variables are clustered by treatment. We conducted two separate PCAs; one in grasslands and one in woodlands comparing and evaluating vegetation structural and compositional differences between bison and cattle treatments. PCA matrices contained eleven eigenvalues and we determined the number of significant explanatory components (axes) to retain with Horn's parallel analysis, using package *psych* version 1.8.12 (Revelle, 2018), which plots the eigenvalues of the observed data against a randomly sampled, uncorrelated distribution (Horn, 1965; Horn and Engstrom, 1979). The point where the two distributions cross indicates the maximum limit of interpretable axes for the observed data (Jackson, 1993). We depicted component scores and biplots including variable loading for each PCA, colored by treatment. From the PCA scores, we expect sampling locations to be similar between treatments by detecting great percent overlap among sampled sites and non-significant t-tests of component scores. Conversely, if treatments are different, then we expect to detect treatments to spatially separate in multivariate space and significant results of a t-test on component scores.

We used ordinary least-squares regression within a generalized linear modeling (GLM) framework to determine what relationship vegetation structure has with treatment and season (year), or their interaction. For the response variable, we used the first Principal Component scores of individual coordinates for grassland and woodland sites. Treatment was a binary variable of either of the grazers (bison or cattle) and because of differences in rainfall and temperature (*see* Table 1) between sampling years, we used year as a surrogate for seasonality. We took a three-step approach to select among the set of models which evaluates top model choice, model fit, and effect sizes (amount of variation captured in the top model).

We applied information theoretic approaches to distinguish among candidate models using Akaike Information Criterion (AIC) scores, ΔAIC, and beta coefficient weights to identify the top model. AIC is a common estimator for the predictive ability of the factors in a model and useful in GLM model comparison, as it measures model complexity and model fit to the data. The lowest AIC value is often associated with the best fitting model, therefore ΔAIC is used to facilitate comparison of differences in AIC values between close scoring models (Wagenmakers and Farrell, 2004). Conversely, models with the highest weights are indicative of top model. Typically, ΔAIC thresholds in model selections favors models with scores less than 10, and when all models (or many) have scores less than 10, a more conservative estimate of less than 2 can be used (Burnham and Anderson, 2004)**.** Standardized β coefficients were used for accurate comparison of coefficients. This facilitates comparison- as raw values are on multiple scales, but Standardized β coefficients are Z-transformed to have a mean of 0 and standard deviation of 1.

To determine the fit of the model to the data, we compared residual deviance to the residual degrees of freedom (df) and null deviance and conducted a chi square goodness of fit test. A comparison of the residual df to the residual deviance reveals the extent of overdispersion in the data, or if the variance is larger than expected (Hinde and Demétrio, 1998). Comparing the null deviance to the residual deviance provides context of how a model with no terms (intercept only) predicts the response variable and how adding terms can increase the predictive ability of the model for the response variable (Pykälä et al., 2005). A chi square goodness of fit test is another measure to evaluate model fit to the data, as the t-statistic and corresponding *P* value indicate if the fit of the model significantly differs from the data. Therefore, non-significant *P* values are indicative of good fit and significant *P* values show the fit of the model significantly differs from the data.

To evaluate effect sizes, we calculated McFadden's pseudo R^2 value. A pseudo R^2 value measures the amount of variation captured by the model and differs slightly in the interpretation of a traditional R^2 value used in ordinary least squares (OLS) regression (Hu et al., 2006). For McFadden's pseudo R^2, values of 0.2-0.4 are considered excellent (McFadden, 1979), and we used a threshold of 0.1 of amount of variation explained that was considered fair. Values below 0.1 were interpreted as not explaining a useful amount of biological variation for the model to have a meaningful impact within this study system.

Small Mammal Community

To evaluate how small mammal communities may differ between treatments (cattle versus bison) we compared sites using complementary approaches including a complementary suite of diversity and abundance measures. Small mammal community diversity was assessed using Shannon-Wiener diversity indices (H) and compared across treatments using a Hutcheson t-test (Hutcheson, 1970). Because diversity indices can be biased by small sample sizes of a few species (Barrantes and Sandoval, 2009), we removed mammals with fewer than five captures. Because we trapped two different habitats, with some species specialized to grassland (*Onchomys leucogaster, Ictidomys tridecemlineatus, Perognathus flavus*) or woodland habitats (*Peromyscus truei, P. boylii*), we calculated separate diversity indices and analyses for each habitat type as well.

To investigate how mammalian abundance may respond to alternative herbivore treatments, we determined mammalian abundances as species counts per transect in each habitat and treatment. Abundances were compared using a Mann-Whitney U tests, because a Shapiro-Wilks test suggested the abundance data were not normally distributed. We then separated small mammals into two functional populations by habitat they were captured from (grassland and woodland). Preliminary analyses indicated that no mammalian abundance values were significantly different for any species between years (2018 to 2019), so we pooled sampling years in all subsequent abundance analyses. To maintain adequate statistical power, we only evaluated species that were captured with more than 5 individuals on both treatments. Four species qualified for abundance analyses on grassland including: *Chaetodipus hispidus, Onychomys leucogaster, Peromyscus maniculatus, and P. truei*; and two species from woodland sites: *P. boylii,* and *P. truei*.

To assess the relationship between the abundance of small mammals and the vegetation structure and composition, we conducted a canonical correspondence analysis (CCA) on species abundances with package *CCA* version 1.2 (González et al., 2008). Because our trapping scheme included two habitats that resulted in two distinct vegetation and mammalian communities, we separated CCAs by habitat type. CCA is a constrained ordination technique where dominant gradients of variation in one matrix of dependent variables (*i.e.*, species abundance) are computed as linear combinations of an explanatory matrix (*i.e.*, vegetation variables). Therefore, CCA allows us to extract the joint structure in the data and evaluate both the major gradients in the mammalian abundance data that can be accounted for by the measured variation in the vegetation data, or explanatory variables (Ter Braak, 1986). Here, we constrained small mammal abundances using the same set of vegetation variables from PCAs to evaluate the influence of grazer type on vegetation structure and composition and how mammalian abundances are linearly related to those vegetation variables across the landscape. Because rarely encountered species often have an exaggerated impact on CCA, we excluded rare species (less than three captures) prior to analyses (Cao et al., 2016; Legendre and Gallagher, 2001).

For the grassland CCA we included eleven vegetation variables and ten mammalian abundances. For the woodland CCA we included eleven vegetation variables and eight mammalian abundances. We used variance partitioning to determine the amount of variation in the small mammal community explained by explanatory variables retained in the CCA respective models.

Parasite Prevalence and Intensity

We were interested in better understanding the relationship between the percentage of mammals parasitized (prevalence) and their parasitic loads (intensity) as it relates to alternative grazer treatments. We focused on two functional groups of parasites- ectoparasites and endoparasites. For ectoparasites, we examined fleas as they can be vectors for many zoonotic pathogens which impact wildlife populations and humans. For endoparasites, we focused on nematodes and cestodes because they were the most commonly encountered endoparasites and often compromise the functional health of parasitized mammals. For analyses, we used only adult hosts, considering sub-adults and juveniles typically have lower prevalence rates, probably a result of reduced exposure to potential parasitic infection (Hawlena et al., 2007; Poulin, 2007). Moreover, our analyses attempt to relate grazer effects on vegetation, mammalian community, and the corresponding parasite community, and age-related effects may manifest in different ways for younger individuals. We compared the frequency of adult mammals parasitized by cestodes, nematodes, and fleas on both bison and cattle grassland and woodland sites using chi-square tests.

To evaluate how parasitic loads may differ between bison and cattle treatment plots, we used parasite intensity. Here, intensity is defined as the abundance of parasites found on parasitized hosts. Because only a subset of individuals are included (only parasitized, adult host animals), we used a Mann-Whitney U test for non-normal parasite count data to evaluate parasite intensity of cestodes, nematodes, and fleas. Similar to the small mammal diversity tests, we first evaluated intensities across habitats and then grassland and woodland habitats separately to determine how parasite intensity compared between treatments.

Results

Vegetation Analyses

Vegetation Structure and Composition

Vegetation comparisons (Table 2) were conducted using pooled-year data for each habitat type. In the grassland, all vegetation variables were not significantly different except for CWD cover, litter depth, and shrub cover. Percent cover of CWD and litter depth was significantly higher in bison sites compared to cattle (2.4% vs. 1.3% W = 5037, $P = 0.003$; 0.5 cm vs. 0.3 cm W = 5252, $P < 0.001$, respectively). Shrub cover was significantly higher in cattle sites (7.8% vs. 6.1% W = 3279.5, $P = 0.027$). In woodland sampling sites, percent cover of forbs and rock were higher in bison sites (7.2% vs. 4.3% W = 590, $P = 0.038$; 22.9% vs. 12.4%W =

687, $P < 0.001$, respectively) and overstory canopy cover and litter cover was higher in cattle sites (34.6% vs. 13% W = 194.5, $P < 0.001$; 32.2% vs. 19.8%, W = 297, $P = 0.024$). All other vegetation variables in the woodlands were not significantly different between treatments (Table 2).

PCA

No variables for grassland or woodland sites were highly correlated, so none were removed from analyses. For both PCAs, eleven vegetation variables were used including eight for percent cover and three structural. Five axes passed the parallel analysis for the grassland PCA that captured 19.90% of the variation on the first axis (PC1), 17.02% on PC2, and 13.83% on PC3, 11.13% on PC4, and 9.73% on PC5 for a total of nearly 72% of measured variation in vegetation between grazing treatments (Figure 3a). For this analysis, we explored strong loadings |>0.40| that show, in general, a relationship of vegetation profiles contrasting open versus more densely vegetated sites. For example, PC1 represented a gradient of increasing vegetation complexity, with bare, rocky sites associated with negative scores and more dense vegetation with some overstory canopy associated with positive scores. PC2 was harder to discretely classify, but in general consisted of open grassy sites associated with negative scores and bare, rocky, sites with more shrub cover associated with positive scores. The rest of the axes were quite heterogenous in vegetation structure, thus we will not describe each here. We failed to detect spatial separation of cattle and bison treatment sites on PC1, the axis with the highest retained variation, with 96.7% of bison sites overlapping with cattle grassland sites and 100% of cattle grassland sites overlapping with bison sites. The non-parametric t-test on the five retained component axes revealed both significant and non-significant overlap in grassland sites **(**W = 4775, *P* = 0.038, W = 4707, *P* = 0.060, W = 3516, *P* = 0.127, W = 3324, *P* = 0.038, W = 4375.5, *P* = 0.353, respectively).

For the woodland PCA, almost 57% of the variation in vegetation structure and composition was accounted for with our first three axes (Figure 3b) that passed the Kaiser criterion. PC1 explained 29.2% of the variation and was characterized by open sites associated with negative scores and closed, dense sites associated with positive scores. PC2 accounted for 15.3% of the variation and represented 5a gradient of complexity, with bare, rocky sites associated with negative scores and sites with grass, forb, and shrub cover tending towards positive scores. PC3 explained 12.3% of the variation and was also heterogeneous in structure, thus we will not fully describe it here (Figure 3b). We failed to detect spatial separation of treatment type on axis PC1, with 100% of bison sites overlapping with cattle sites in multivariate space and 53.3% of cattle sites overlapping with bison sites. The non-parametric t-tests on PC scores for bison and cattle woodlands were significant and non-significant (W = 308, *P* = 0.036, W = 412, *P* = 0.582, W = 656, *P* = 0.002, respectively).

GLM

We applied PC1 scores as the vegetation response variable in GLMs and habitat (grassland and woodland) were analyzed separately. For the grassland GLM, treatment with an interaction with year was the optimal model identified ΔAIC = 0 and $\omega = 1$ (Table 3a). For this model, the null and residual deviance were 394 and 284, respectively; and the residual df was 176. The chi-square test for model fit revealed a poor fit to the data ($P < 0.001$), and the effect size indicated low explained variance ($R^2 = 0.09$). Standardized β coefficients for the interaction terms showed 2019 as the most influential term (β = -0.66; *see* Table 3b). The GLM for woodlands revealed treatment as a single predictor for the top model (ΔAIC = 0 and $\omega = 0.75$). For this model, the residual deviance was 172.04, the null deviance was 193, and the residual degrees of freedom was 58. The chi-square test for model fit indicated a poor fit to the data (P = 0.011), and the effect size revealed low ecological variation (R^2 = 0.03).

Small Mammal Analyses

We captured 509 small mammals belonging to four families and sixteen species during the trapping efforts of this study (Figure 4). Capture rates varied for each species ranging from a single individual for three species including prairie vole (*Microtus ochrogaster*), rock squirrel (*Otospermophilus variegatus),* and mountain cottontail (*Sylvilagus nuttallii*) up to 231 individuals for pinyon mouse (*Peromyscus truei*). After low captured species were removed (*M. ocrogaster*, *O. variegatus*, and *S. nuttallii*, n = 1; *Perognathus flavescens,* n = 2), twelve species had at least three total captures and were used in most analyses. Trap successes differed by treatment and habitats with bison grassland sites at 1.8%, cattle grassland at 1.2%, bison woodland at 8.4%, and cattle woodland at 3.9%. We also detected differences by year with more mammals detected in 2019 (n = 321; 3.3% trap success) compared to 2018 (n = 188; 2.0% trap success).

Mammalian Diversity

When we do not consider habitat differences, we detect small mammal diversity was significantly different between bison and cattle sites (n = 11, H = 1.78 and H= 1.56, respectively; $t_{369} = 2.34$, P value = 0.02). Likewise, when we evaluated grassland and woodland habitats separately, differences in mammalian diversity indices also emerge. In woodlands, bison pastures had significantly higher ($t = 7.29$, $P < 0.0001$) small mammal diversity $H = 0.95$ compared to cattle $H = 0.21$ ($n = 5$). Similarly, bison pastures on grassland sites had significantly ($t = 2.7$, $P = 0.007$) greater diversity $H = 1.86$ compared to cattle $H = 1.62$ ($n = 10$).

Abundance

We failed to detect statistically significant differences in the mammalian abundances of any species across habitat or treatment (Figure 5). Of the qualifying four species found on grasslands (at least five captures for both treatments), all had similar abundances for both bison and cattle treatments (*Chaetodipus hispidus*: $n_b = 23$, $n_c = 6$, $W = 41$, $P = 0.11$; *O. leucogaster*: $n_b = 8$, $n_c = 13$, $W = 16$, $P = 0.86$; *P. maniculatus*: $n_b = 33$, $n_c = 32$, $W = 58.5$, $P = 0.52$; *P. truei*: $n_b = 9$, $n_c = 6$, $W = 4$, $P = 1.0$). A similar pattern was observed for the two species found in woodlands (*P. boylii*: $n_b = 19$, $n_c = 5$, $W = 8$, $P = 0.09$; *P. truei*: $n_b = 134$, $n_c = 82$, $W = 12$, $P = 0.73$).

CCA

There was overlap of treatment for both habitats in our CCA plots (Figure 6 a & b). In grassland, the first axis was positively associated with grass and shrub cover, and two grassland specialist species, *O. leucogaster* and *Ictidomys tridecemlineatus*. Negative values were associated with closed canopy and denser vegetation, but no species greatly associated exclusively with that vegetation structure. The second axis was positively described by bare ground and rock, and conversely with litter, deeper litter depth, and CWD cover. *Peromyscus truei* and *P. maniculatus* were associated with positive values of the second axis and *Reithrodontomys montanus* was associated with negative values. Most species were located near the intersection the axes, indicating they were captured in a variety of vegetation structures but with a slight affinity to litter cover and more litter depth.

For the woodland CCA, the first axis was mainly positively associated with forb and grass cover with *P. maniculatus, P. leucopus,* and *R. montanus*. Negative values were characterized by shrub and litter cover, and litter depth with *P. boylii* and *Neotoma mexicana* as the primary mammals associated with these vegetation variables. The second axis was positively associated with litter depth and litter cover with *R. megalotis* and *N. mexicana* showing a strong relationship with these variables. Conversely, cover of CWD and scat were associated on the negative axis with *P. boylii* and *R. montanus* having a relationship with these variables. *Peromyscus truei,* the most common small mammal, was located near the intersection of the axes, illustrating that it was found in a variety of vegetation types within woodlands.

Parasite Prevalence

Using all adult hosts (n = 335; bison, 213 and cattle, 122), we evaluated how parasite prevalence differed between treatments (bison and cattle) across the mammalian community for cestodes, nematodes, and fleas. Preliminary exploratory analyses revealed that year was not a significantly important variable for determining parasite prevalence, so we pooled samples between years. The results for differences of 2018 vs. 2019 within the bison treatment for nematodes was 24.0% vs. 14.6% (χ^2 = 2.44, *P* = 0.12), cestodes was 4.8% vs. 3.8% (χ^2 = 7.97E-

31, $P = 1.00$), and fleas were 20.4% vs. 30.0% ($\chi^2 = 1.90$, $P = 0.17$). Likewise, for the cattle treatment between years for nematodes 10.9% vs. 3.9% ($\chi^2 = 1.25$, $P = 0.26$), cestodes 8.7% vs. 1.3% ($\chi^2 = 2.32$, $P = 0.13$), and fleas 26.1% vs 36.8% ($\chi^2 = 1.06$, $P = 0.30$).

Nematode prevalence in small mammals was nearly 3x as high ($\chi^2 = 7.93$, $P = 0.005$) within bison plots (18.3%) compared to cattle plots (6.6%). Cestode prevalence was practically identical between treatments with 4.2% of small mammals in bison plots parasitized and 4.1% in cattle plots had at least one cestode. Thus, the cestode prevalence was not significantly different between treatments ($\chi^2 = 1.8414\text{E-}31$, $P = 1.00$). We detected that fleas were not significantly different between treatments with 38.5% of mammals parasitized on bison plots and 32.8% on cattle plots ($\chi^2 = 1.23$, $P = 0.25$).

When we partition analyses by habitat, we found a significant ($\chi^2 = 5.59$, $P = 0.02$) nematode prevalence signal across mammals with 29.5% on bison grasslands compared to 11.0% on cattle grasslands. However, nematode prevalence was only marginally significantly ($\chi^2 = 3.4$, $P = 0.06$) higher on bison woodland plots (10.4%) than cattle woodland treatments (1.6%). Cestodes showed non-significant pattern ($\chi^2 = 0.09$, $P = 0.77$), with 5.7% mammals parasitized on bison grassland sites and 8.3% mammals on cattle grassland sites. Similarly, we detected no difference between mammals parasitized on bison woodland sites (3.2%) compared to mammals on cattle woodlands (0.0%) although no statistical tests were possible on these sites (Table 5). Taken together, we detected higher nematode prevalence on both habitats for bison, but only a significant difference on grassland, higher (but not statistically significant) cestode prevalence on cattle grassland and no cestode prevalence on cattle woodland. Prevalence of fleas was calculated across both habitat and treatment, and within grassland habitat there was a significantly ($\chi^2 = 4.52$, $P = 0.03$) higher prevalence of fleas on small mammals in the cattle treatments (35.0%) compared to bison (18.2%). In woodlands, flea prevalence was nearly identical between treatments (32.0% bison and 30.6% cattle; $\chi^2 = 0.0004$, $P = 0.98$).

Parasite Intensity

In general, we detected similar patterns of nematode, cestode, and flea intensities in both habitat types between both bison and cattle treatments (Table 6). For example, we found that mean intensities for nematodes in small mammals on the bison treatment of 20.46 (n = 39) was not significantly different from the cattle treatment of 22.63 (n = 8) per individual (W = 116, $P = 0.26$). Similarly, when we compared grasslands, nematodes averaged 23.46 and 20.43 within parasitized hosts on bison and cattle treatments, respectively (W = 78 $P = 0.58$). When we compared woodlands, nematodes intensities were also non-significant, with 14.46 on bison plots and 38 on cattle plots (W = 2, $P = 0.3$).

Cestode intensity was also not significantly different between treatments, with small mammals occupying bison sites (n = 9) averaging 6.33 cestodes per infected individual and compared to small mammals occupying the cattle treatment (n = 5) where mean cestode intensity was 2.2 (W = 28, $P = 0.44$). When looking within grasslands, we found cestodes were also not significantly different between bison and cattle plots (10 vs. 2.2, respectively; W = 16, $P = 0.44$). For woodlands, however, we found no small mammals on the cattle treatment parasitized by cestodes preventing intensity analyses (*see* Table 6).

Flea intensity for mammals parasitized in bison plots was 2.24 compared to 2.26 on cattle plots highlighting no significant difference between treatment (W = 980, $P = 0.26$). We also detected no significant difference between treatments for either habitat type for flea intensities. The average flea intensity in grasslands for bison and cattle was 2.9 and 3.5, respectively (W = 145.5, *P* = 0.48). Similarly, in woodland habitats, bison and cattle flea intensity was 2.02 and 2.6, respectively (W = 387.5, *P* = 0.90).

Discussion

Across the literature, evidence presented overwhelmingly indicates that bison and cattle differ in grazing preferences and behaviors resulting in measurable differences for both vegetation and co-occurring wildlife (Allred et al., 2013; Fay, 2003; Matlack et al., 2001; Steuter and Hidinger, 1999; Towne et al., 2005). However, our data and analyses seemingly contradict those broad patterns and provide an alternative perspective where bison and cattle may not result in functional differences that alter vegetation and wildlife structure and composition for shortgrass prairies. For example, we generally failed to find any significant difference between bison and cattle in either grassland or woodland habitat types in vegetation structure or composition, small mammal community or abundances, nor for most parasites. Further, our analyses of the impact of native and non-native grazers in a North American shortgrass prairie yielded low support for the downward cascading expectations of the grazer mediated hypothesis (*i.e.* cattle forage for more forbs, bison consume more grasses yielding differing mammal and parasite communities). Similarly, results for endoparasite prevalence, but not intensity, provides some initial support for the environmental contaminant hypothesis, however we failed to detect the correspondingly expected upward cascading trophic effects. Instead, we found the best support for the parasite-centric hypothesis because we detect some parasitic differences without, as expected, significant differences in vegetation or mammalian community structure and composition. Taken together, results from our study perhaps best illustrates how depauperate our understanding of shortgrass prairie ecosystems remains. Additional studies are needed, however, to unravel if indeed vegetation and wildlife respond via a series of complex interactions (*i.e.,* top-down or bottom-up) or if some grassland systems are best understood through a relatively simple (*i.e.*, parasite-centric) response to grazing practices. Each warrant further discussion.

Vegetation Composition and Structure

Vegetation composition and structure often differs when similar grazing pressures of bison and cattle are applied, especially in tallgrass prairies. For example, in a ten year study, Towne et al. (2005) found that bison occupying tallgrass prairie sites had higher percent cover of perennial forbs and lower percent cover of warm-season grasses when compared to cattle. Similarly, Peden et al. (1974), using limited sampling, found that bison diets versus cattle diets in shortgrass prairies differ, as bison primarily consume grasses and cattle ingested a larger amount of forbs. Conversely, we failed to detect vegetation compositions as significantly different for most grassland ground cover categories including, importantly, percentage of grass and forbs on our grassland sites. Although we do detect a significant difference on woodland sites for forbs, the effect sizes are small (4-7% cover), treatments were only 3% different, and both had larger SDs than means making meaningful inferences difficult. Other individual variables that significantly differed also had similar means with overlapping SD intervals, such as shrub and CWD (Table 2). We interpret these differences as not necessarily an impact of grazers, but perhaps due to either the stochastic variation between sampling sites, low overall means, or limited sampling of sites that exhibited these vegetation variables. For example, litter depth differed significantly between bison and cattle plots in grasslands, but the average was only 0.2 cm higher in the bison treatment. Similarly, rock cover was significantly higher in bison plots (22.9% ± 13.2 for bison and 12.4% ± 16.9 for cattle; $W = 687$, $P < 0.001$), but because rock is unpalatable for either grazer, this observed difference is likely due to landscape differences between treatment sites and not as a result of the grazer. Despite taking steps to sample comparably regarding vegetation structure and composition, real systems will ultimately vary in unpredictable ways (Peckarsky, 1998). However, due to the complex nature of ecological systems, studies regarding influence of grazing in active ranching pastures, as opposed to long-term research stations, yield results most applicable to land managers, wildlife conservationists, and community ecologists (Pickett and Cadenasso, 1995). Differences in overstory canopy cover are also likely due to landscape variation as available woodland sites in bison pastures were in and around the grassland habitat, whereas woodland sites on cattle plots were closer to the base of the mountains and thus denser with greater overstory canopy cover. As leaves and pine needles fall from the overstory canopy and litter accumulates, our results show the cattle treatment had a significantly higher percent litter cover than the bison treatment (Table 2).

Because grass and forb cover were similar or only marginally differ, we fail to find support for the grazer mediated hypothesis in shortgrass prairies that bison eat grasses and leave forbs and conversely for cattle. This pattern is typically reported in tallgrass and mixed-grass prairies (Steuter and Hidinger, 1999; Towne et al., 2005). Discrepancy in our data and the literature are perhaps the products of two alternatives. First, differences in floral community between tallgrass and shortgrass prairie systems provide a different suite of species for the grazer’s diets (Pearson et al., 1976; Samson and Knopf, 1996). If accurate, differing floral communities would mean a different composition of nutrients available to the grazer, thus driving an alteration in diet preferences for the megaherbivores. Our results of forb cover versus grass cover, which indicate grasses are two to four times as abundant for every treatment and habitat, describe a system which has more grasses available to the grazers. As cattle typically prefer to eat more forbs and are reportedly the more selective grazer (Hartnett et al., 1997; Schwartz and Ellis, 1981), this alteration in floral community could have driven the diets of cattle to be more similar to bison, resulting in less pronounced differences between vegetation composition than tallgrass prairies. Although we did not directly measure the diets of the grazers, the resulting floral communities are an indirect indication of this behavior. To test this hypothesis, further studies in this system should look at biomass of both megaherbivore’s diets for all vegetation groups to evaluate the validity of this claim.

Secondly, signals of ecosystem-level structural and functional differences may be emerging across different North American prairie types that may manifest in differences in behaviors and foraging selectivity of native and non-native megaherbivores. Within shortgrass prairies, data and results presented here appear to show that vegetation responds similarly to either native or non-native grazers with similar grazing pressure. Because of this contradiction within the literature, additional studies are needed, especially in shortgrass prairies and because many conservation initiatives favor native grazers to restore grassland habitats (Knapp et al., 1999; Truett et al., 2001). However, based on our data and results, some conservation initiatives, such as restoring vegetation structure and composition, may be equally achieved with non-native grazers (cattle) in shortgrass prairie ecosystems regardless of habitat (grasslands or woodlands).

The results for our GLM suggest how type of grazer is influencing how the vegetation becomes structured in both habitat types. In grassland, the model with the interaction between treatment and year was the best at explaining vegetation differences, with a weight of 1. The interaction of year and treatment with cattle is supported by other studies. For example, a behavioral study of Allred et al. (2013) found when temperatures change, cattle are less physiologically robust and thus change social and foraging behaviors more readily. With bison, thermoregulatory ability surpasses that of cattle, and so it took greater shifts in temperatures for their behaviors to be modified. As year was our proxy for temperature and rainfall seasonality, these results are congruent with patterns of variation detected in our system.

For woodland habitats, treatment was also the top model with a weight of 0.41. However, we did attribute some structural and percent cover differences to the location of the woodlands that were available to us rather than the grazers themselves. In our system, grazer might not have had as considerable influence as our model suggests, but the literature reveals use of forested or woodland habitat can be different between bison and cattle (Allred et al., 2013; Fuhlendorf et al., 2010; Steuter and Hidinger, 1999). Many authors conclude that cattle often spend more time in wooded areas compared to bison, allowing for the megaherbivore to restructure vegetation differently (Roath and Krueger, 1982; Senft and Rittenhouse, 1985; Smoliak and Peters, 1955; Steuter and Hidinger, 1999). This is likely due to changes in temperature and the grazer’s capability to thermoregulate (Allred et al., 2013). In heat of the summer, cattle often find refuge from the sun under the overstory canopy, and in the winter the dense vegetation can shield against strong, bitter winds. Bison, as the native grazers on the landscape, have likely been physiologically adapted to be more resistant against these fluctuations and extremes in climate (Plumb and Dodd, 1993).

However, despite the top models being supported in the literature, the ability of our models to accurately reflect the data is limited. The results of the Chi-square goodness of fit test indicated poor fit of top models for both habitats (grassland and woodland) to the data ($P < 0.001$ and $P = 0.011$, respectively), the residual deviances indicated overdispersion and limited improvement from the null model (Table 3a), and the pseudo R^2s (0.09 and 0.03, respectively) revealed low ability for meaningful biological interpretation with the amount of variation explained by the models. The uncertainty of our results could be due to insufficient data to accurately detect the patterns in the data, but since our data is in agreement with the literature, we suspect further data collection would help bolster the results to more confidently identify of the patterns of the grazers selectively utilizing the landscape.

Small Mammal Communities

Diversity

We detected significantly different mammalian diversity in both grasslands and woodlands between bison and cattle treatments, with bison treatments having higher small mammal diversity in both habitats (Table 4). Although this signal was expected for the grazer mediated hypothesis (top-down), where the grazer directly changes vegetation composition resulting in cascading effects for the small mammal community, we fail to detect significant evidence of vegetation differences driving differences in small mammal diversity. For example, results of the CCA demonstrate in grassland habitats the majority small mammals were captured in vegetation types similar for both grazers, with minimal exceptions. The most notable exception being *Reithrodomtomys montanus,* which appears to be influenced by differences in litter depth and cover of litter and CWD between treatment sites. The CCA for woodlands was limited by fewer transects, but still there is not a clear, fundamental separation of small mammal species based on how the grazers structured the landscape (*see* Figure 6). Like grasslands, *Reithrodontomys spp.* seem to be most influenced by select vegetation variables. If the grazers had changed the vegetation composition in such a way that it changed the spatial structure of the small mammal communities between treatments, we would have expected to see separation of treatment sampling sites with distinct clustering of small mammal species within each treatment. Despite minimal differences in the vegetation structure and small mammal species composition between bison and cattle treatments, we do not detect grazers to be fundamentally changing the landscape that, in turn, results in a trophic change in the small mammal community. We also failed to detect a strong signal of parasites reshaping mammalian diversity, as expected by the bottom-up hypothesis. This seemingly paradoxal pattern where the mammalian diversity differs but without vegetation (top-down) or parasitic (bottom-up) differences, may be the product of at least four alternatives.

First, increased diversity of small mammals may be an unconsidered response by mammals to the native megaherbivore although we know of no functional mechanism. Theoretical frameworks have been constructed to explain the concept of the key functional roles native megaherbivores can have in grasslands, but all such frameworks invoke a cascading impacts mechanism. For example, across Eastern African savannas, which contain a rich diversity of grazers (Ritchie, 1999) mammalian diversity often differs when megaherbivores are lost, but mammalian diversity is indirectly, influenced through a cascade from vegetation response. In North America, this pattern is also apparent, as Ricketts and Sandercock (2016) found bison grazing promoted higher diversity of small mammals in a pyric-herbivory tallgrass ecosystem, however tallgrass prairies are dominated by fire return frequencies that also alter vegetation and thus mammalian communities.

Second, stochastic mammalian differences, such as drift, colonization, and extinction, result in accidental diversity indices differences (Chase and Myers, 2011; May, 1972). As with other systems, stochastic processes are likely occurring within this system, but we generally discount it, as it is difficult to predict and quantify with studies that occur over short temporal scales (Armstrong and McGehee, 1980; Vandermeer, 2006). Although year-to-year differences suggest higher small mammal diversity in bison pastures, it is possible the timing of our sampling coincided with any number of stochastic processes unaccounted for within our study design, as comprehensive consideration of all conditions and possible scenarios is unrealistic (*see* Allred et al., 2011). Stochastic processes paired with abiotic influences can be just as or more influential than deterministic processes in ecological niches (Ellwood et al., 2009; Stegen et al., 2012). For instance, Chase (2007) monitored communities in ponds over time and found drought years had a considerable impact on community assembly as opposed to years with average or above average rainfall. Because one of our years was a drought year, we could be seeing the effects of compounded stochastic and abiotic influences within our small mammal diversity results. However, the temporal scale which this study was conducted limits our ability to confidently make inferences on stochastic and abiotic influences. A long-term study in this system would provide invaluable insight into how stochastic differences influences diversity indices.

Third, diversity indices can be sensitive to rare detections, and so correcting for few samples may have influenced results because we found slightly different mammalian communities in bison and cattle pastures (Figure 4). Other diversity indices may be better, such as Simpson’s index, which is more robust to the inclusion of rare species as it holds more weight to species richness and evenness (DeJong, 1975), or Jaccard’s and/or Sorenson’s similarity index, which measure the similarity of species composition between two sites (Chao et al., 2006). However, the inclusion of the Shannon-Weiner index in this study is due to it being the most widely used index, as the components of the calculation are at the intersection of historical processes that lead to species composition (richness) and current deterministic processes such as intra-and interspecific composition, predation, competition, and parasitism (relative abundances) (Barrantes and Sandoval, 2009). Additionally, a critique of the Shannon-Weiner index is the sensitivity to sampling bias, but our paired design allowed us to have adequate and even sampling of each treatment, therefore corrections for sampling bias were not necessary (Ludwig and Reynolds, 1988).

Finally, we failed to detect vegetation and/or parasitic differences that manifest as important predictors of mammalian diversity. If so, then we may have found better support for either the top-down or bottom-up models. We measured vegetation and parasite community composition in broad categories (*e.g.* grasses, nematodes) whereas it is possible the drivers of mammalian diversity are within the family, genus, or even species-specific levels. It is common for grazing studies to describe individual plant species, however, typically vegetation is the main focus of interest, allowing for more time and resources to be invested in describing the floral community (Blydenstein et al., 1957; Cottam and Evans, 1945; Towne et al., 2005). Ultimately, our study had to forfeit species identifications for inclusion of multiple trophic level responses to grazing, as that is the overall purpose of the study. Fortunately, specimen preservation of small mammals and their parasites allows for future identification to species level, if necessary, for further analyses.

Taken together, our results suggest native grazers may support a higher diversity of small mammals than non-native grazers, but the differences are not apparently driven top-down through changes in vegetation or bottom-up through alterations via parasitism. Certainly, additional studies are required to unravel the ultimate mechanisms that result in the discrepancy of mammalian diversity between grazers in this system. Further investigation is important, as the assumptions of diversity metrics are indicative of ecosystem integrity, whereas higher diversity is linked to stable systems and lower diversity with unstable systems and likely environmental degradation in the form of anthropogenic disturbance, over-grazing, altered fire intervals, and invasive or exotic species (Hejda et al., 2009; Price et al., 2010; Ravera, 2001). As small mammals are interconnected with many other trophic levels as prey items, due to their herbivorous, granivorous and insectivorous diets, and as hosts for ecto- and endoparasites, using small mammals as a study group can inform about the quality of many levels of an ecosystem (Panzacchi et al., 2010; Ricketts and Sandercock, 2016).

Abundance

Increased mammalian abundances are attributable to key mechanisms in natural systems, such as structural variation in habitat and resource availability. Greater landscape heterogeneity can support higher abundances of species due to more variability in niches, and thus more space for burrows or nests and cover from predators (Katayama et al., 2014; Loggins et al., 2019). However, the ecological effects of habitat heterogeneity can differ depending on how the heterogeneity is synthesized, and some species are associated strongly with certain landscape features required for their overall survival (Tews et al., 2004). For example, California red-backed voles (*Myodes californicus*) are highly associated with decaying logs, as their diet typically consists of various fungi (Tallmon and Mills, 1994), and thus they would likely only benefit from habitat heterogeneity if it increased access to or amount of decaying logs containing fungi. Therefore, higher resource availability has the ability to lead to larger abundances of mammals due to lower competition and better quality diets (Ecke et al., 2001). In this study, we detected no significant differences in small mammal abundances for four species on grassland or two species in woodlands. According to the bottom-up hypothesis, we expected to see parasite prevalence and/or intensity reshaping the small mammal community structure through increased small mammal abundances, especially within the cattle treatments. However, the results do not support a strong link of parasites dictating small mammal densities within our system. Therefore, it is unlikely the parasite community is strongly influencing small mammalian abundances in this system.

From the grazer-mediated hypothesis (top-down model), two of our three expectations for small mammal abundances were not detected, which was higher proportion of grass-specialist mammals on the cattle treatment and forb-specialist mammals on the bison treatment. However, we did detect similar abundances of generalist mammals between plots, as abundance was not significantly different for any species in either habitat. These results seem to agree with the literature. For example, a study from Montana in a wet meadow habitat (Whelham et al., 2013) found an abundance of voles (*Microtus spp.*) increased with greater times of rest from grazing by cattle, indicating there was a positive link between available biomass and size of the population. Because vegetation structure did not fundamentally differ between the two treatments in both habitats, it is likely this link is also supported in our study. However, we did not quantify available biomass directly, it would be indirectly assumed to be nonsignificant different due to similarities in vegetation cover for each grazer. The results of our CCA help to support this conclusion, as abundances of small mammal species were mostly associated with vegetation shared between treatments, indicating the small mammals were utilizing relatively similar vegetation structures within each treatment (Figure 6 a & b). Therefore, the influence of grazer on the vegetation does not appear to have a detectable cascading trophic effect into the small mammal community within this particular system. On the contrary, a study on the influence of bison and cattle pyric herbivory on deer mice (*P. maniculatus*) in a tallgrass prairie found different abundances of deer mice between treatments for three consecutive sampling seasons in a tallgrass prairie (Matlack et al., 2001). The presence of fire in this tallgrass system, and absence of frequent fire in the shortgrass prairie systems, could explain incongruent results considering joint direct and indirect effects of fire often result in bison and cattle altering their foraging behaviors (Hartnett et al., 1996; Jonas and Joern, 2007; Kerns et al., 2011).

Parasite Communities

Prevalence

Parasite prevalence is an important factor to consider in ecological settings because parasites are often directly responsible for restructuring mammalian communities or directly respond to mammalian communities experiencing change. However, because different types of parasites may result in differential responses, it is often important to evaluate different parasitic responses. Consequently, we evaluated both ecto- and endoparasite prevalence and identified differences that fail to conform to expectation and found some surprises.

For ectoparasites, fleas we detected higher prevalence of fleas on small mammals in the cattle treatment in grasslands, but not woodlands (Table 5). These results are surprising, considering there was higher litter cover in woodland habitats for cattle, and litter is positively linked to flea success by providing a suitable environment for egg development (Kaal et al., 2006). Prevalence could potentially be explained by a species with higher than average flea prevalence found more abundantly on cattle grasslands. For example, 70% of *O. leucogaster* individuals on cattle grasslands with at least one flea, compared to 35% of the entire small mammal community. Taken together, host species could be more important in structuring the flea community than vegetation structure in our system, and that point is a focus of chapter 2. Regardless, there are two other possibilities we would like to discuss as possible alternatives for the pattern of flea prevalence detected between treatments.

First, it is possible the dosage of the anthelminthic drugs excreted in to the environment was not potent enough for fleas to respond. However, the industry dosage standard of anthelminthic drugs is about 0.2 – 0.5 mg per kg of animal and the majority (up to 98%) of the drug is excreted by the animal into the feces, unaltered (Horvat et al., 2012; Strong, 1992). Multiple studies have concluded that concentrations of antiparasitic drugs in cattle dung are 0.3 ppm or higher (Jackson, 1989; Sommer et al., 1992; Strong, 1992). This may not seem like much, but considering the drugs have a half-life of anywhere from one week to over seven months (Halley et al., 1989) and concentrations as low as 1 ppb have the ability to cause flea mortality (Chamberlain, 1986), the possibility for environmental contamination of these antiparasitic drugs to negatively impact non-target organisms living in the soil, feces, or nearby litter are feasible (Halley et al., 1993; Strong, 1993, 1992). Therefore, it is likely not inadequate dosage that acted as the filter to impact flea prevalence within these two treatments.

The second possibility is fleas are not encountering the fecal pats very often, resulting in the parasite being uninfected by the uneven use of anthelminthic drugs on the cattle and not bison. Because fleas are not coprophagous (Durden and Hinkle, 2019), this idea is more plausible, as the flea would have less of a reason to visit cattle feces other than a chance encounter. However, this idea by itself does not explain the higher incidence of flea prevalence on small mammals in cattle plots compared to bison plots. Previous studies report increased flea abundance in grazing systems to higher densities of small mammals (Keesing and Young, 2014; McCauley et al., 2008), but as small mammal abundances of species we were able to compare were not statistically different, this is also likely not the best reasoning we have for a discrepancy in flea prevalence between treatments. No studies have yet to investigate the influence of bison behaviors on fleas, therefore, the results from our study are novel to this geographic area and megaherbivore type. Therefore, the reason why flea prevalence is higher in cattle plots compared to bison plots remains unanswered here, and thus is a focal point of the second chapter of my thesis. Furthermore, experimental studies regarding the influence of antiparasitic drugs on fleas could prove useful to get a baseline understanding of how types of feces (bison, cattle) and treatment (treated, untreated) can potentially impact flea populations and their life cycle (Dryden et al., 2000). Although it may seem trivial to make these connections, developing management strategies to minimize the risk of resistance in parasites, not just fleas, is proving to be highly necessary (Dryden and Broce, 2000). Measures should be taken to avoid exposure of fleas to incorrect dosages of antiparasitic drugs to reduce the likelihood of reduces efficacy in the future (Bossard et al., 1998).

For endoparasites, although we detected significantly higher prevalence of nematodes on both habitat types for small mammals on bison treatment sites, the same pattern did not hold for cestodes. This observed difference between nematodes and cestodes could be the result of at least three different reasons.

First, different types of parasites are often impacted differently through the efficacy of antihelminth drugs (*i.e.,* nematodes as opposed to cestodes). More specifically, a study conducted on nine commonly administered anthelminthic drugs in cattle reported successful eradication in 10 types of gastrointestinal nematodes (abdominal, small intestinal, and large intestinal), but only one drug was effective against a single genus of cestode (Prichard, 1986). As the efficacy might differ between nematodes and cestodes, our differing results for nematode and cestode prevalence between grazers are perhaps the result of differential treatment of cattle with anthelminthic drugs compared to bison.

Second, because the effect sizes for cestodes was low, our power to detect significant differences between bison and cattle plots may have been compromised. For example, we did not detect more than a 4% difference between bison and cattle in either habitat type, and the highest prevalence for either treatment or habitat type was 8.3%. Furthermore, Chi-square tests can be sensitive to zero-inflated models (McHugh, 2013) and because only 26 animals out of 334 were parasitized by cestodes, our ability to detect differences may have been insufficient when grazers may actually influence cestode prevalence.

Third, parasites can sometimes influence other parasites through a variety of mechanisms including competitive exclusion (*i.e.* host exploitation) and interference competition. The former type of interaction typically results in greater harm to the host, as the species rapidly exploit and deplete resources from the host (Massey et al., 2004), whereas the latter interaction could potentially influence damage done onto the host as parasites utilize antagonistic mechanisms to compete with each other, reducing their overall impact on host health and fitness (Dobson, 1985)**.** Parasites are known for their robustness in competitive environments, and thus a driver of fitness and diversity in parasites is within (for endoparasites) and among (for ectoparasites) host selection (Bashey, 2015). Depending on how parasites exploit host resources or space can impact their survivability in a host where more than one species or strain co-occurs. While tests of these hypotheses were outside the scope of this study, it could be a possible explanation to the differences in nematode and cestode prevalence across habitats and between treatments. A practical way to test for if nematodes and cestodes are interacting though some sort of competitive exclusion or interference competition is through a laboratory experiment to allow for maximum control of confounding factors and extraneous conditions. However, even if this is occurring within our system, we do not expect it to have a major influence on the results, as hosts with both nematode and cestode infections were not abundant.

Because we fail to detect cascading effects for the top-down model responsible for restructuring vegetation, mammalian community, and thus parasitic prevalence, we reject the grazer mediated hypothesis for both nematodes and cestodes, although the later are likely compromised by insufficient sampling. Fleas have higher prevalence on cattle plots when compared to bison which may provide initial support for the grazer mediated hypothesis, but because perveances fail to be directly influenced through vegetation and the small mammal community we reject the top-down model. Of note, however, because of the significant differences detected between mammals and fleas predicated by either treatment or host specific factors, suggests that either extrinsic or intrinsic factors may be responsible for altering flea parasitism. Young et al. (2015) have detected that host and environmental factors may be scale-dependent for influencing flea parasitism, so we will return to this question in chapter 2.

Similarly, while our results for nematode prevalence seemingly yield initial support for the environmental contaminant hypothesis, we fail to detect cascading trophic effects up through the small mammal community and thus vegetation structure and composition and so also reject this bottom-up model. We also reject this bottom-up model for fleas, due to the only differences, detected as higher flea prevalence in the mammals within grasslands on cattle plots, were opposite of what we predicted for this interaction. Small mammals, however, are not the only hosts for endoparasites, and there are other potential hosts that are readily available in our system, such as arthropods (Biron et al., 2004; Sheridan et al., 2000). Although testing the cascading effects of endoparasites on arthropod hosts were outside the scope of our study, it could explain why we detect higher nematode prevalence on bison sites that were not paired with lower small mammal abundances. It is possible the trophic cascade does not involve small mammals, but rather another hyperabundant host in our system, such as grasshoppers. For example, Hill and Goddard (2012) reported that grasshoppers of family Acrididae are intermediate hosts for avian tapeworms *Choanotaenia infundibulum* and *Tetrameres americana* and others have investigated the antagonistic host-parasite relationship of grasshoppers and the nematomorph hairworm, *Spinochordodes tellinii* (Biron et al., 2004; Rohrscheib and Brownlie, 2013). In this study we only have anecdotal evidence that grasshoppers were hyperabundant during both seasons of trapping. Consequently, we do not have sufficient evidence to support a grasshopper hypothesis, but rather suggest it could possibly be a key aspect to be investigated in future grazing studies. To do so would require capture of grasshoppers on both treatments followed by necropsies to detect internal helminth parasites. If grasshoppers play a significant role within the trophic cascade of anthelminthic drugs on endoparasites in this system, higher prevalence and/or intensity of endoparasites would be predicted in grasshoppers in the bison treatment. Additionally, higher abundances of grasshoppers would be detected in cattle plots due to lower hinderance of parasitic infection.

Intensity

Intensity was not significantly different in either habitat or treatment for either nematodes, cestodes, nor fleas. While no known studies to date have investigated the link between grazing and endoparasite loads of small mammals, the pattern detected in this system broadly matches what others have found for fleas. For example, McCauley et al., (2008) found cattle grazing failed to have a significant effect on flea intensity of the pouched mouse (*Saccostomus mearnsi*). Although the results presented here are consistent with current literature, there is a need for more studies that focus on how grazing systems influence mammalian parasites, especially when grazing is being seriously considered as a viable management option for conservation of North American grasslands.

Additionally, our results indicate factors that drive prevalence and intensity within this system are decoupled, as differences in prevalence was not parallel with intensity, with the exception of cestodes, which we have limited data to work with. Young et al. (2015) investigated flea prevalence and intensity in Kenya and found consistent factors to predict both indices across species in the system. Additionally, they found similar drivers of prevalence and intensity at the local level and across populations within a species. Differences within this system and the Kenyan system could be due to differences in host-specific and environmental factors, and Chapter 2 of my thesis is dedicated addressing this question.

Because we failed to detect cascading effects either up or down, we reject both the grazer mediated hypothesis and the environmental contaminant hypothesis, but not necessarily the parasite centric hypothesis, as we predicted to see differences in the parasite communities between treatments that did not necessarily cascade to other levels of the ecosystem. Our conclusion does not advocate against trophic cascades within ecosystems, as there are many documented instances of this occurring, with a notable example of the reintroduction of wolves into Yellowstone (Ripple et al., 2001; Smith et al., 2003). Wolves have passively restored multi-level trophic interactions in Yellowstone from decreasing riverbank erosion, increased beaver and bison populations, reduction of elk, increased foliage cover, and higher survival rates of aspen trees (Ripple and Beschta, 2012). However, a notable distinction between that system and this system is the type of ecological keystone, predator versus megaherbivore. It is possible cascading trophic effects are more prominent in ecosystems with an apex predator, as they have direct influences on behaviors of many prey populations (*i.e.* mammals, reptiles, birds) through the selective forces of antagonistic predation (Lima and Dill, 1990). Whereas elimination or even replacement of keystone predators can destabilize entire systems by creating a detrimental cascade down trophic levels (Mittelbach et al., 1995), it appears the removal or replacement of functionally dominant megaherbivores does not have as dire of consequences. Theoretical models from Rooney et al. (2006) provide reasonable insight for this, suggesting predators can stabilize ecosystems by channeling energy in the form of productivity and turnover. Taken together, we suggest the effects of trophic cascades are likely stronger in systems with a keystone predator, and although bison or cattle are ecological keystones of their environment, the effects of grazing in this system is possibly not strong enough to detect changes in the other trophic levels we evaluated, such as the vegetation, small mammal, and parasite communities.

Conclusions

Data and results provided in this study yield a different perspective from most of the literature for vegetation and mammalian responses to native versus non-native grazing. In particular, the patterns of community-level variation we detected as a result of native versus non-native grazers differs from patterns detected across tallgrass prairies, especially for vegetation and rodent community structure and composition. In tallgrass prairies cattle and bison selectively forage for forbs or grasses, respectively (Steuter and Hidinger, 1999; Towne et al., 2005), but we failed to detect an analogous pattern in shortgrass prairies. Similarly, Matlack et al. (2001) found that rodent communities significantly differ between bison and cattle grazing, but when we compared and evaluated four small mammals from grassland and two from woodland habitats, we detected stochastic variation in both abundance and diversity with no variation attributable to alternative grazers. The implications of these results should resonate positively with land managers grazing cattle on shortgrass prairies that are often pressured to replace livestock with bison despite insufficient resources such as pastures and reinforced fencing. Consequently, if the goal of conservation is to manage the vegetation because native grazers re-structure landscapes in unique ways, cattle appear to serve similar functional roles in shortgrass prairies considering we failed to detect vegetation structural and compositional differences between treatments. Similarly, if conservation goals include managing the abundance or diversity of small mammals, there may not be a fundamental functional difference between bison and cattle when grazing shortgrass prairies.

We also present one of the first assessments of parasitic prevalence and intensity between bison and cattle grazing. Broadly, we failed to detect differences in parasite intensities between grazing treatments, but we did detect some differences in prevalence. These results suggest factors that drive parasite prevalence and intensity within small mammals may be decoupled, as we expect to see similar results if the same factors influenced intensity and prevalence collectively. Consequently, if conservation goals include managing the landscape to control parasites, as parasites often carry pathogens and spread diseases, our data and analyses suggest grazers may not result in functional differences in parasites. In fact, our data and results suggest that the application of anthelminthic drugs exclusively to cattle has an influence on the endoparasite community, especially nematodes, but may also influence ectoparasitic arthropods such as fleas. This result needs further study, but land managers may want to carefully consider how applications of anthelminthic drugs may be influencing other co-occurring organisms.

Based on our data and analyses, bison and cattle appear to serve similar functional roles in shortgrass prairies without cascading effects to vegetation, mammalian, or parasitic communities, with occasional impacts on some parasites, perhaps the result of management activities including environmental contamination by anthelminthic drugs. Therefore, in general, processes that influence changes in the structure and composition of vegetation, small mammals, and parasites are seemingly non-synonymous across prairie types. Because a bulk of the research and corresponding literature are associated with tallgrass prairies, it is intuitive to apply inferences drawn about the influence of grazers across all grassland systems, especially when planning conservation and management action. However, we urge wildlife managers and conservationists who aim to protect and maintain imperiled grasslands across North America to consider and evaluate system-specific responses and avoid temptations to extrapolate patterns of variation across all grasslands.

CHAPTER 2

VARIANCE OF FACTORS INFLUENCING FLEA (ORDER SIPHONAPTERA) PREVALENCE AND INTENSITY ACROSS TWO GEOGRAPHIC SCALES IN A NORTH AMERICAN SHORTGRASS PRAIRIE

Introduction

Despite efforts to understand host-parasite relationships, their complex and dynamic interactions remain relatively unknown. Thus, how parasites structure within host communities is typically context dependent, leaving many uncertainties for both parasitological and ecological systems. With drastic, rapid changes to global ecosystems due to climate change and anthropogenic destruction, investigating host-parasite relationships is becoming exceedingly crucial (Bitam et al., 2010), especially considering the spread and re-emergence of pathogens and diseases harbored by many types of parasites due to these shifts in ecosystem structure and function (Coura and Viñas, 2010; Hanincová et al., 2006; Haque et al., 2010; Mckenzie and Townsend, 2007).

Implications of understanding how host-parasite dynamics change across habitats and scales likely co-influence disease and pathogen dynamics, so it is imperative to understand the host communities they reside. Consequently, parasites have been shown to influence a swath of host characteristics such as mate choice (Vyas, 2013), altering life expectancy (Morand and Harvey, 2000; Sorenson and Minchella, 2001), changing fitness of the host and, if applicable, their offspring (Kutzer and Armitage, 2016), limiting growth (Combes 2001), and modifying social behaviors (Berdoy et al., 2000). These effects, however, are not isolated to the host population. Other organisms in the local environment such as wildlife and even humans are vulnerable to parasitic infections and parasite-borne diseases through host-switching, especially when parasites latch onto/transfer to new hosts, resulting in inter- and intraspecies transmission, or when a parasitized host infects another potential host through grooming, biting, scratching, or being consumed (Hawlena et al., 2005; Marshall, 1981; Mitzmain, 1910).

Fleas are well known for an extensive list of diseases they can harbor and transmit to other individuals or populations which includes, but not limited to, the bubonic plague, murine typhus, cat scratch disease, and Q fever (Bitam et al., 2010; Durden and Hinkle, 2019; Kramer and Mencke, 2001). Due to their relevance to public health and wildlife disease ecology, it is important to study the factors that result in flea infestations and where best to concentrate efforts of management. Empirical evidence suggests increasing flea density has a positive association with risk of human infection (Keeling and Gilligan, 2000; Samia et al., 2011), thus understanding the drivers of flea prevalence and intensity can inform management objectives to reduce spread of infectious, flea-borne diseases. For these reasons, we chose to focus on fleas as the focal group for this chapter.

A growing body of literature that investigates what influence infestation rates reveals two categories of factors: intrinsic and extrinsic (Young et al., 2015). Intrinsic factors are those of or relating to the individual host or host population. Many studies have shown a variety of intrinsic factors can be influential such as health and/or body condition (Krasnov et al., 2005a), age (Krasnov et al., 2006) and sex (Matuschka et al., 1992; Soliman et al., 2001). The second group is extrinsic traits, or those relating to the environment. Environmental factors play a functional role in parasite survival and ability to spread and reproduce. Fleas spend time on the host, but also within the host environment such as burrows or nests (Krasnov et al., 2002b) and often spend most of their life cycle off host, which makes eggs and larval forms particularly vulnerable to unfavorable conditions in the environment. These conditions can include changes in temperature (Krasnov et al., 2002c), substrate material (Krasnov et al., 2002b), and seasonality such as amount of rainfall (Stenseth et al., 2006; Young et al., 2015).

Few studies have combined investigations of intrinsic and extrinsic factors or evaluate relative influence of both factors across scales within a system. Consequently, our goal is to evaluate the relative importance of host (intrinsic) versus environmental (extrinsic) factors in determining prevalence and intensity of flea parasitism at two scales within a single system. First, we evaluate the relative influence of intrinsic and extrinsic factors and how they play a role in the prevalence and intensity of fleas across individuals within a single, dominant species and ask: 1) How do host age, sex, seasonality, and type of grazing megaherbivore (*i.e.* native vs. non-native) influence prevalence and intensity of total flea infestation? Secondly, scaling up to the landscape level we evaluate how both factors jointly influence parasitism across four common host species in two different habitats and ask: 2) How does variation across host species density and environment including vegetation cover, host density, seasonality, and type of megaherbivore explain observed variation in flea parasitism across host populations within a host species? We use prevalence and intensity as they are among the most common metrics for measuring the distribution and density of parasites (Jovani and Tella, 2006; O’Meara et al., 2007; Patterson and Ruckstuhl, 2013). Here, prevalence is defined as the percentage of hosts that are parasitized (*i.e.* > 0 parasites) and intensity is the abundance of parasites, which can also be referred to as relative intensity (Rózsa et al., 2000).

To evaluate how parasitism impacts individuals within a species, we aim to test four hypotheses related to how fleas tend to structure and aggregate within host populations. The first two hypotheses are intrinsic including the age-biased and sex-biased ideas that have been consistently demonstrated to influence prevalence and intensity (Hawlena et al., 2007; Krasnov et al., 2012; Schalk and Forbes, 1997). The age-biased hypothesis is related to how parasites tend to infect adults, which could be due to several reasons, with one example being the parasites have a reliable nutrient and resource supply with adult hosts (Hawlena et al., 2005). If the trend of adult-bias transcends ecological systems, we expect to find evidence for it in our system.

The other intrinsic hypothesis is related to biased infestation driven by sex of hosts, especially in mammals (Krasnov et al., 2005b; Patterson et al., 2008; Presley and Willig, 2008). Possible explanations for this observed pattern are different immunosuppressive abilities, home ranges, social behaviors, and body sizes (sexual dimorphism). With the sex-biased hypothesis, we expect to see a significant influence of sex, specifically higher prevalence and/or intensity of fleas on male hosts.

The last two hypotheses are extrinsic: seasonality and influence by a grazer. When we refer to season in our study, we are referring to a drought season (2018) and a wet season (2019), as a proxy for direct measures of rainfall. A handful of studies have tested the influence of rainfall on flea prevalence and intensity (*see* Olson, 1969; Young *et al.*, 2015), and the general pattern is more rainfall leads to decreased successful flea parasitism, likely stemming from the larval stages that develop in the environment. If seasonality plays a role in our system, we expect the drought season (2018) to have higher flea prevalence and/or intensity on the small mammals.

The final hypothesis for individuals within a species is whether type of grazer influences the flea structure within the small mammal community. No studies have yet to directly compare how megaherbivores influence parasitism in North American wildlife (Wilford and Malaney, unpublished). Consequently, here, we aim to evaluate how either a native grazer, bison (*Bison bison*) versus a non-native grazer, cattle (*Bos taurus*), impacts flea parasitism in short-grass prairies. We suspect to see patterns of higher prevalence and/or intensity of fleas in the non-native cattle treatment due to a native grazer hypothesis. The literature provides support for how introduced species can alter parasite structure and in instances of native grazer removal, abundance of parasites on the landscape increased. Most studies have concentrated on the impact grazers have on fleas have been conducted in Africa, as the megaherbivore populations are rapidly declining and the impacts for public health are of great concern, since aforementioned flea-borne diseases are both common and devastating in many African countries (Bitam et al., 2010). McCauley et al. (2008) found the removal of native large herbivores failed to alter flea prevalence or intensity, but doubled the density of the dominant small mammal, the pouched mouse (*Saccostomus mearnsi*), effectively doubling the amount of fleas in sites without the megaherbivore. In Canada, Bueno et al. (2012) found a higher flea intensity on meadow voles (*Microtus pennsylvanicus*) in non-native cattle plots, but the pattern was not significant for flea prevalence. Castellanos et al. (2016) also found that non-native species (of fire ants) altered arthropod parasites and pathogens hosted by small mammals across habitat types.

As the factors that determine flea intensity and prevalence might differ across spatial scales (*i.e.* within a single species in a habitat versus across species in a landscape), our second set of tests aim to evaluate the relative importance of factors at a landscape scale, across habitats. Here, we evaluate the individual or joint effects of how variation in host density, vegetation composition, type of grazer, and seasonality explain variation in flea prevalence and intensity across four common small mammalian hosts. Type of grazer (*i.e.*, treatment) and seasonality predictions were addressed within the intraspecies level (individual scale), and we suspect those to transcend to the interspecies level (landscape scale).

Because host density has a key functional role in both prevalence and/or intensity across many types of species ranging from mammals to daphnia (Arneberg et al., 1998; Bittner et al., 2002; Krasnov et al., 2002a; Mbora and McPeek, 2009), we expect to detect increased parasitism associated with increased host densities. The pattern of increased host density relating to more success in parasite transmission plays a key role in epidemiological theory (Arneberg et al., 1998). This is likely due to greater probability of the parasite being able to encounter another suitable host to infect within the same local habitat.

Vegetation structure likely has an ability to influence the flea community, as much of the flea life cycle is spent off-host (Krasnov et al., 2004). In our system, we have two distinct habitat types: open shortgrass prairie and Pinyon-Juniper woodlands (*Pinus edulis*; *Juniperus monosperma/scopulorum*). There have been few studies comparing fleas in grassland and woodland habitats, but due to environmental requirements to complete their life cycle (*see* Krasnov et al., 2002b), we predict higher prevalence and/or intensity of fleas in woodland species. Due to the off-host development of the flea typically occurs in host nests or burrows, we suspect the higher litter depth associated with woodland habitats may allow for more survival and success for fleas.

Materials and Methods

Study Site

Philmont Scout Ranch is an active bison *(Bison bison*) and cattle (*Bos taurus*) ranch in northeastern New Mexico, located near Cimarron in Colfax County. A large portion of the 567 km^2 area that Philmont covers is comprised by mountains from the Sangre de Cristos (Rocky

Mountains), and the vast pastures for bison and cattle are on plains-mesa grasslands. Colfax County is within the most western reaches of the Great Plains grasslands, and the vegetation structure is of a shortgrass prairie. The dominant grass is blue grama (*Bouteloua gracilis*), a drought-resistant plant and also an important forage grass (Allred, 2005). Our study at Philmont was conducted in two field seasons in July-August of 2018 and 2019. We used a paired design with approximately equal trapping footprints on bison and cattle treatments, with similar grazing pressures (Casey Myers, personal communication). Due to size of plots, the bison treatment had two pastures and cattle had four (*see* Figure 1).

Small Mammal Trapping

Straight-line transects were set up in each treatment to trap small mammals. Each transect consisted of 50 trap stations 10 meters apart from each other, consisting of a single Sherman live trap (8.62 x 8.89 x 22.86 cm) paired with either a single Museum Special or commercially available Rat trap. Since traps can differ in their success with certain species of mammals (Eulinger and Burt, 2011), we used three types of traps to optimally capture the diversity of small mammals on the landscape. All traps were baited with peanut butter and oats, and all transects were sampled for four consecutive nights (trap nights = 400). Traps were checked each morning, captured mammals were removed, and all traps were rebaited as needed. Treatments had equal trapping effort with 3,600 trap nights on grassland habitat and 1,200 trap nights on Pinyon-Juniper woodlands (woodland), for a total of 4,800 trap nights per treatment per season. Habitat sampling was scaled in woodlands due to available space.

To assess intrinsic and extrinsic factors within an individual species, we chose the most abundantly captured mouse, the pinyon mouse (*P. truei*), which represented 45% of total captures (n = 231). To investigate extrinsic factors across species within two different grazed habitats, we chose species that were more commonly encountered with a sufficient number of parasitized individuals to enable analyses for meaningful inferences about this shortgrass prairie system. We set criteria for each species to include at least 20 captured individuals with at least 6 parasitized individuals. We excluded *P. leucopus* (n captured= 58 and n parasitized = 14) because all parasitized individuals were detected exclusively on bison transects, negating comparisons across treatments. These criteria resulted in two species per habitat type from the following four species: *P. truei*, *P. boylii*, *P. maniculatus*, and *O. leucogaster*.

P. truei and the brush mouse, *P. boylii*, are commonly encountered small mammals in woodland ecosystems across the American Southwest and northern Mexico (Kalcounis-Rueppell and Spoon, 2008; Wilson and Ruff, 1999). The deer mouse, *P. maniculatus*, consists of both grassland and woodland forms (*see* Bowers *et al.*, 2007) and is the most widely distributed Peromyscine rodent in North America (Hall, 1981; Miller and Engstrom, 2008). These three species often have larger male home ranges than females and are common vectors for zoonotic pathogens, which makes them important focal species for monitoring public health concerns (Bedford and Hoekstra, 2015; Dragoo et al., 2006; Ribble and Stanley, 1998; Yates et al., 2002). The grasshopper mouse, *O. leucogaster*, is a unique rodent species as they readily exhibit predatory behavior, with grasshoppers being their primary prey of choice (McCarty, 1978). As is common with many small mammals, all four species have fast gestational cycles, often with multiple litters per year. Additionally, these species are known reservoir hosts for parasites and/or carriers of infectious diseases (Dragoo et al., 2006; Keegan, 1953; Tinkle, 1972; Vandegrift et al., 2008). In general, small mammals are often overlooked in management planning, despite each playing a crucial role in ecosystem processes within the grasslands and woodlands they inhabit. For example, small mammals are prey for many types of predators (Hanski et al., 2001; Maser et al., 1981) and their activities such as searching for food, caching seeds, and digging burrows, results in soil aeration and turnover allowing for greater successful germination of seeds (Rickel, 2005). The complex interactions small mammals have with their environment and other trophic levels paired with their ability to respond quickly to changes in environmental conditions due to their life histories make them an ideal host species to investigate the drivers of prevalence and intensity of fleas in this system.

Parasite Collection

Following capture, small mammals were euthanized according to protocols outlined by the American Society of Mammalogists and approved by APSU IACUC (Sikes, 2016; Malaney 17.001). All specimens were identified to species in the field and processed holistically, with methods for ectoparasite screens, tissue collection, and endoparasite screens described by Galbreath et al. (2019; *see also* Chapter 1 methods). Parasites counts were confirmed in the lab.

Vegetation Sampling

Vegetation was sampled at five equidistant stations along each trapping transect, and at five points within each sampled trap station. The five points were as follows: the origin, random azimuth (RA) 10 m away from the origin, +90º from the RA (in relation to the origin), +180º from the RA, and +270º from the RA (*see* Figure 2). At each sampling point, percent cover of vegetation and litter depth (cm) was recorded using a Daubenmire frame (Daubenmire, 1959), vegetation height and density was assessed using a Robel pole (Robel et al., 1970), and overstory canopy was calculated using a convex densiometer (Lemon, 1997; *see also* Chapter 1 methods). Vegetation data for grassland and woodland habitats were used separately for Principal Components Analyses (PCA), and the first axis for both habitats was used as a proxy for vegetation for each grazing treatment in generalized linear models (GLMs).

Statistical Analyses

All statistical analyses were completed in R v. 3.6.0 (R Core Team, 2019). To assess relative influences within a species, we applied GLMs using package *lme4* version 1.1-21 (Bates et al., 2015) with a binomial distribution and logit link for prevalence and Poisson distribution for intensity across individuals of *P. truei*, the most abundantly captured mammal species. We included two exploratory intrinsic factors (age and sex) and two extrinsic factors (year and treatment) with relevant interaction terms to address alternative hypotheses. Interactions were limited to two terms as an *a* priori power analysis indicated limitations of our dataset to have sufficient power for more than two terms. We chose treatment as the main interaction to focus on as it is integral to this study system and this project. To examine how environmental factors may influence parasitism across species in two habitat types, we used GLMs with a binomial distribution and logit link for prevalence data across four species of small mammals: *P. truei, P. boylii, P. maniculatus*, and *O. leucogaster*. The factors included in our model were host density, vegetation composition, year, and treatment. Since we did not utilize a trapping grid, we quantified host density as the abundance of captures for a species per total trap nights on a transect (n = 400 trap nights). We derived vegetation composition from PCA scores for the dominant, first axis for each corresponding habitat (*see* Chapter 1). Methods to assess intensity were repeated with the same factors but using a Poisson distribution for the GLMs. We used three criteria to determine the ability of the top model to represent the data in which we evaluated top model choice, model fit, and effect sizes, or amount of variation captured (*see* Chapter 1, Methods).

Top models for both geographic scales were further analyzed to determine McFadden's pseudo R^2 (effect size) and standardized β coefficients (only for interaction terms) using packages *jtools* version 2.0.1 and *lm.beta* verson 1.5-1, respectively (Behrendt, 2014; Long, 2019). Pseudo R^2 is relatively comparable to traditional R^2, which is used an indicator of goodness of fit in ordinary least squares (OLS) regression. McFadden's pseudo R^2 can produce values from 0.0-1.0, but practically perfect data is required to achieve higher values. Therefore, this metric is considered to be excellent from 0.2-0.4 (McFadden, 1979), and we used a cutoff value of 0.1 to describe good variance explained and anything below this threshold to have low biological meaning. Standardized β coefficients are ideal to compare estimated coefficients, as raw values are on different scales, yielding comparisons ineffective and misleading.

Results

Local Level

Using 231 *P. truei* hosts, we determined sex to be the most influential explanatory factor for both prevalence and intensity (Table 7 and 8). Males had a higher proportion of individuals parasitized (38% male and 22% female, *see* Figure 7) and higher mean abundance of fleas (0.58 for males and 0.36 for females). The top model for prevalence had a weight of 0.54, the residual deviance was 263, the null deviance 270, and the residual degrees of freedom was 215. The *P* value of the chi-square goodness of fit test was 0.01 and the pseudo-R^2 value was 0.02. The coefficient for males was 0.77. For intensity, the residual and null deviances were 95 and 99, respectively, and the residual degrees of freedom was 215. The weight was 0.54, the chi-square *P* value was 0.04 and the pseudo-R^2 value was 0.01.The coefficient for males was 0.24.

Landscape Level

The weights for top models of prevalence were 0.65 for *P. truei*, 0.31 and 0.3 for *P. boylii*, 0.49 for *P. maniculatus*, and 0.31 for *O. leucogaster*. Since *P. boylii* had two models (host density and year and treatment interaction) with similar weights and residual deviances as top models, the result of the chi-square test was used to determine the best model for prevalence (*P* = 0.06 and 0.99, respectively). Two species had similar weights for intensity top models (0.59 for *P. truei* and 0.43 for *P. maniculatus*) and two species had higher weights (*P. boylii* with 0.82 and *O. leucogaster* 0.87). Residual deviance, null deviance, and residual degrees of freedom for all top models are reported in Table 9.

Top models for flea prevalence and intensity of each species differed on their fit to the data and by the amount of variance explained. For prevalence, three species top models indicated non-significant deviation from the data: *P. truei (P* = 0.19), *P. boylii* (*P* = 0.30), and *O. leucogaster* (*P* = 0.28). The chi-square results of top models for intensity indicated two species that had good fit to the data, which were *P. boylii* (*P* = 0.82) and *O. leucogaster* (*P* = 0.20).

Overall, variance explained by top models were low (less than the 0.1 threshold) as only two of the eight GLMs had top models with pseudo-R^2 values between 0.2-0.4 (*P. boylii*, pseudo-R^2 = 0.35 and *P. maniculatus*, pseudo-R^2 = 0.23). All species had low pseudo-R^2 values for the top models of flea intensity, ranging from 0.00 for *P. boylii* to 0.07 for *P. maniculatus*. Therefore, the top models captured a small amount of biological variation.

Explanatory variables were not consistent across the four species for their predictive power of flea prevalence and intensity (Table 9). Year was least imperative to predicting flea parasitism for each species, appearing in only one top model as an interaction term for *P.boylii* prevalence. Host density was an explanatory factor that appeared in three of the eight sets of top GLMs as either a single term or as an interaction (*P. truei* prevalence, P. *truei* intensity, and *P, maniculatus* intensity), and had a positive association with prevalence or intensity in all models.

Treatment was a factor that was a part of four of the eight top models (*P. truei* prevalence, *P. boylii* prevalence, and *P. maniculatus* prevalence and intensity), but it only appeared as an interaction term and the signals were not consistent across species. For *P. truei* and *P. maniculatus* captured in the cattle treatment, there was a negative association with flea prevalence; and *P. boylii* and *P. maniculatus* in cattle plots had positive associations flea prevalence and intensity, respectively.

Four of the eight top models had an interaction term, thus Standardized β coefficients were calculated for *P. truei* prevalence (0.98), *P. boylii* prevalence (-26.5), *P. maniculatus* prevalence (-1.8) and *P. maniculatus* intensity (0.39) (*see* Table 10).

Discussion

Our results indicate how flea prevalence and intensity are scale dependent and variable across four focal species between two habitat types and grazers in shortgrass prairie ecosystems. Importantly, at the individual scale, sex appears to be a driving factor determining flea parasitism, while a more complex combination of both intrinsic and extrinsic factors appear to influence flea parasitism across species. In particular, host density, vegetation profiles, and type of grazer consistently determine both flea prevalence and intensity regardless of habitat type. Taken together, these new insights into the variance of factors that influence flea parasitism across geographic scales in North American shortgrass prairies warrants further scale-specific discussion.

Local Level

Of our four explanatory factors (age, sex, year, and treatment), sex was the best predictor for increased flea prevalence and intensity within *P. truei* hosts. Despite top models showing low fit to the data, low effect sizes, and in some cases, overdispersion (Table 9), sex appeared as term in the top model for prevalence and intensity, indicating there is some influence of sex-bias in our system. Parasitized hosts showing a male-bias is commonly found in systems where parasites are detectable and measurable (Krasnov et al., 2012). For example, Hillegass et al. (2008) found male Cape ground squirrels (*Xerus inauris*) harbor three times as many ectoparasites as their female counterparts, and that bias is seen in many systems (Krasnov et al., 2005b; Matthee et al., 2010; Morand et al., 2004; Poulin, 1996). There are many potential reasons for this pattern, and we will discuss three common reasons used to explain male-biased parasitism.

First, disparity in sex hormones drive different rates of infection between males and females. This idea is common in epidemiological studies, yet controversial in the mechanism by which it occurs (Moore and Wilson, 2002; Penn and Potts, 1998; Schalk and Forbes, 1997). One possible explanation is that sex hormones are driving sexual dimorphism in immunity, thus resulting in sex-biased parasitism. Estrogen, which is higher in concentration within females, has been shown to enhance immune system function through certain pathways and cell responses (Cutolo et al., 2006; Grimaldi et al., 2006; Taneja, 2018), whereas males have higher levels of testosterone, regulated by androgens, which has been shown to suppress immune system function by down-regulating certain cellular responses (Bouman et al., 2004; Giron-Gonzalez et al., 2000). A manipulative study in mice demonstrated external administration of estrogen paired with castration of a male mice increased expression and of certain genes such as the major histocompatibility complex (MHC), which bolsters immunocapabilities (Behrens et al., 2010), thus supporting the established idea of sex hormones being a direct causal factor of directing and facilitating responses of immunity. Differing ability for the host immune system to respond to foreign infection or parasitic attack can thus aid in higher rates of parasitism in males (Zuk, 1996). It is plausible this is occurring within this study system, as studies have shown bites from fleas can elicit immune response by the host (García et al., 2004; Khokhlova et al., 2004). However, we did not directly measure this idea, therefore we can only postulate the viability of this occurring within this system. If this were to be tested, we would measure immune system responses (*e.g.* MHC expression) in males and females infested with fleas, and we would predict to see more immune system function in females than males due to their increased immunocapability from estrogen. Conversely, insignificant differences in immune system responses to flea infestations or bites would provide lack of support for this being a main contributor to the male-biased parasitism detected in this system.

Another explanation regarding how sex hormones drive sex-biased infection is females have the ability to detect parasitic loads of males through mating rituals (*i.e.* displays and dances) and scent marking. A study by Hamilton and Zuk (1982) supports the idea that species of birds with most evident sexual selection (*e.g.* striking plumage, songs) were those that have greatest susceptibility to parasitic infection. Therefore, females are required to be more choosy to find mates that reduce their risk of contracting diseases, increase resistance of their offspring to parasites, and assure more parental investment (Penn and Potts, 1998). This hypothesis has been coined parasite-mediated sexual selection (PMSS) and has been the subject of debate ever since. Clayton (1991) reviewed the results of the literature and evaluates a number of studies evaluating the PMSS hypothesis, and found support for the hypothesis with some studies and a lack of support in others. It appears the PMSS hypothesis could be more apparent in some species than others, like the rock dove or barn swallow, and could be absent in some species altogether, such as tree frogs (Clayton, 1991). As for the likelihood of PMSS driving the sex-bias in *P. truei* within this system, we think it is not a likely explanation. *P. truei* are not sexually dimorphic, therefore the need for showy displays, striking pelts, and elaborate mating dances are not necessary.

Females of many mammalian species also choose mates based on scent marking (Ralls, 1971). Therefore, a choosy female should be able to detect between a healthy male and one that is parasitized to ensure the safety of herself and her offspring, which was detected by Kavaliers and Colwell (1993). Parasitized males are hypothesized to exhibit an altered chemical profile in urine or other pheromones used to attract female mates as an immune response to fighting parasitic infections (Willis and Poulin, 2000). This is possibly due to three reasons, all of which can be detected by females, even if in currently unknown ways: 1) infection alters microbes that shape odor, 2) parasites trigger immune responses in males that up-regulate MHC expression, or 3) immune system responses could create by-products in the body (*i.e.* corticosterone or lower androgens) (Penn and Potts, 1998). Detection of neuromodulatory mechanisms was outside the scope of our study, but alteration of chemical odor profiles as a result of parasitic infection is a plausible explanation for why we detected sex-bias in this system. *Peromyscus* rodents and other closely related species alter behaviors based on scent (Daly et al., 1978; Kavaliers and Colwell, 1993), thus changes in odors could be detected by females to inform their choice for mates. If parasitized males are being actively avoided by females, it reduces the exposure fleas have with females, and helps maintain male-bias. Laboratory studies would be useful for determining this association to test for olfaction-based choice while controlling for potential confounding factors such as risk of predation, scents from other species, and availability of resources.

The second reason that could drive sex-bias in rates of parasitic infection is males often have larger home ranges than females. Indeed, Ribble and Stanley (1998) detected males of *P. truei* to have larger home ranges in northeastern New Mexico. This is likely due to the disparity in strategies for mating between sexes, referred to as Bateman’s principle, where females choose the best mate to ensure maximum survival of their progeny and males attempt to mate with as many females as possible to spread their genes to the next generation (Bateman, 1948; Rolff, 2002). Consequently, larger home ranges in males allows them to encounter more parasite-infested areas in the environment and other infected hosts (Skorping and Jenson, 2004). It is possible for this to be occurring within this system, however we did not take steps to measure home ranges of captured hosts. However, home range size can be tested by comparing the results presented here (*i.e.* a species with documented larger male home ranges) to a species which females have larger home ranges, such many species of birds (Greenwood, 1980). If home range size is a crucial driving factor to sex-biased parasitism, females the focal bird species should have higher rates of parasitic infections than males.

Finally, males typically have larger body sizes than females which creates a bigger target for parasites (Moore and Wilson, 2002). A study by Soliman et al. (2001) found a positive association between ectoparasite loads and body size which they attributed to greater carrying capacity for parasite populations on larger hosts. More space and resources provided by the host allows for a larger sustained population of parasites, which in turn facilitates transmission to other hosts. Other studies have suggested larger hosts are less active, thus fleas have less possibility of falling off the host (Otten, 1924) or have more surface area which increases probabilities of parasites lurking in the local environment to attack the host (Smith et al., 1944). More recently, Krasnov et al. (2006a) reported on parasite specialization within two broad geological scales spanning South Africa and northern North America. In general, they found evidence for parasites to be associated with increasing body mass and hypothesize patterns in host preference are due to larger hosts representing a more predicable source of resources. However, they only detected a weak association between body size and flea host specificity, which led them to the conclusion that resource predictability is likely only one of possible several drivers of the sex-bias detected in flea parasitism. Because *P. truei* are not known to be sexually dimorphic for body size/mass, it is not likely this explanation is the driver behind sex-biased parasitism in this system. Conversely, we detected females to have significantly larger body weights than males (24.84 g v.s. 22.36 g, respectively, $P = 0.009$), but that was likely due to a number of pregnant females we captured, as the time we trapped is during their breeding and gestational time frame (Ribble and Stanley, 1998). For instance, the heaviest female *P. truei* we captured was 44.6 g containing five almost fully developed embryos, with crown rumps (CR) of 23 mm. Therefore, if we were able to ignore influence of gestational weight on female mass, there would have likely been little to no difference in body weight between sexes, thus negating the likelihood of larger body mass causing sex-biased parasitism.

Taken together, the most plausible drivers of host specificity of fleas in this system is likely changes in scents as a result of immune system response and/or discrepancy in home ranges. Though the detection of male-bias in our system is rather weak, it does appear sex is a factor that results in some hosts obtaining more parasites than others, consistent with the results of many other studies (Hillegass et al., 2008; Isomursu et al., 2006; Moore and Wilson, 2002; Poulin, 1996). Though empirical tests for reasons behind sex-bias were outside the scope of this study, we suspect the drivers of host specificity are likely an heterogenous combination of these factors and possibly even other factors we failed to consider.

Although age-bias is common in the study of ecological parasitology, we failed to detect strong evidence for it in our system (*see* Figure 7). For example, Hawlena et al. (2005) found conditional support for the age-biased hypothesis for fleas on a desert rodent, but only in instances of high flea density. The aim of their study was to evaluate the validity of the "wellfed host" hypothesis, which states that adults are better source of resources, and therefore chosen by fleas. This is similar to the reasoning behind one of the hypotheses behind what drives parasites to choose hosts with higher body mass (*see* Krasnov et al., 2006a), which makes sense as age and body mass are often colinear. However, conditional support as a function of flea density suggest there are more aspects of age-bias than just body size and/or mass, such as host and parasite distributions and abiotic factors (Hawlena et al., 2005). Furthermore, Hawlena et al. (2007) concluded fleas can learn to choose adult jirds but not juveniles, despite having higher reproductive success and survival on juveniles. Again, the results from this study suggest that there is another underlying factor that causes adult-bias and it is quite complex- possibly as a result of stimulus received from adults, predictability of adult behavior and resource availability, and/or evolutionary mechanisms that result in adult host preference by fleas (Hawlena et al., 2007; Krasnov et al., 2006).

Therefore, it is possible the underlying drivers that result in appearance of age-bias in fleas is not as influential in this system, though it is difficult to confirm as the exact causes of age-bias parasitism remains unknown. In populations where age-bias is not detected, some suggestions have been made to explain the discrepancy in results across studies. Christe et al. (2003) suggested this trend could be due to fleas infecting more hosts with good body condition without regard for age. Therefore, age could be what appears to drive parasite preference, but it could be that more adult hosts are in better condition than juveniles as they have escaped mortality and have enhanced behaviors for resource acquisition. If more juveniles in this New Mexican system happen to be in better body condition than adults, possibly due to adults fighting over territory or mates, this could result in the lack of adult-bias we detected in *P. truei*.

Additionally, Hawlena *et al.*, (2007) found fleas to have greater fitness on juvenile hosts, but because juveniles more vulnerable to predation, they pose a higher risk as a host. It is possible fleas have adapted to choose fitness over potential risks associated with juvenile hosts for *P. truei*, and therefore creating a more homogeneous rate of parasitism across age classes, as we detected. Taken together, the results and explanations from these studies may help to explain the lack of adult-bias in this shortgrass prairie system.

The remaining two extrinsic factors (year and treatment) are not frequently evaluated in the literature. Nevertheless, even with depauperate literature, it appears drier conditions may lead to higher flea parasitism (Olson, 1969; Young et al., 2015), but we failed to detect this signal in this system, despite considerable differences in rainfall between years (1.6 cm in 2018 and 11.6 cm in 2019), and actually see higher (but not significant) flea prevalence and intensity in 2019, though year does not appear in prevalence or intensity top models and likely has little to contribute to explain rates of flea parasitism in *P. truei*. A study by Stenseth et al. (2006) suggests wetter summers to correlate with higher survivability of fleas, associating two main factors: 1) a significant, inverse relationship of temperature and rainfall, where hot, dry conditions are deleterious and cool, wet conditions are beneficial for the flea population and 2) higher humidity (as a result of cool, wet conditions) facilitates flea reproductive conditions, allowing for higher abundances of fleas and thus more transmission to hosts. It is possible there were counteracting environmental effects by year in our system, where the drier season allowed for moderate flea success, but the wet season provided higher humidity to assist the development of fleas off host, resulting in the detection of higher flea prevalence and intensity (Young et al., 2015). Though our results agree with Stenseth et al. (2006), they are not in agreement with Olson

(1969) or Young et al. (2015), and this discrepancy warrants more studies to be conducted on this subject, as little attention has been focused on the sensitivity of fleas to the environment and the impact season plays on the ability of fleas to survive. Laboratory experiments could prove useful to gain more insight on this subject and control for more factors that are confounding in ecological studies such as ours. In natural systems, holistic control of all biotic and abiotic variables is not practical and there could be something else driving year to year differences that we failed to consider in our models, such as relative humidity, temperature, or even presence of other groups of ectoparasites.

A comparison of the influence bison and cattle have on flea prevalence and intensity has not yet been studied (Wilford and Malaney, unpublished). We expected to detect lower flea prevalence and/or intensity on the sampled plots occupied by native bison, and we do see that pattern. However, the treatment term does not appear as top model for either prevalence or intensity, indicating treatment likely does not have much driving force behind flea parasitism. Although the signal was weak, the data suggests some slight influence of type of grazer on flea parasitism rates, specifically that cattle grazing may increase flea prevalence and intensity on small mammals. The trend we detect could be an indicator of stability and healthier systems associated with native grazers, as higher rates of parasitism can be an indicator of destabilized systems or many individuals in poor health (Schalk and Forbes, 1997). More individuals handicapped by parasitism can lead to greater selection from predation and higher vulnerability to mortality (Poulin, 1994; Yuill, 1987), thus altering stable energy dynamics and flow within the system. However, a lack of other studies impairs our ability to compare our results, allowing us to only speculate on the impact of bison and cattle grazing in relation to this system.

Additionally, though cattle are frequently treated with anti-parasitic drugs that can protect them against flea infestation (Prichard, 1986), these drugs do not appear to be an environmental contaminant that reaches to the flea community. Some studies have shown the influence of these drugs can have on the environment, specifically with coprophagous beetles (Floate, 1998; Iglesias et al., 2006; Sommer et al., 1993; Strong and Brown, 1987), but we do not detect any significant effect with fleas, and actually see the opposite of what we would predict for the contamination of those drugs into the environment at a level that can influence the flea community. We are not discrediting the ability for anti-parasitic drugs to influence other trophic levels such as parasites and arthropods (*see* Chapter 1), but rather insist their impact is likely not synonymous across all groups due to differences in life histories, feeding habits, life cycle requirements, and mobility.

Landscape Level

In addition to testing intrinsic and extrinsic factors across individuals within a single species, we investigated the influence of vegetation, host density, year, and treatment across four species of small mammals found in two distinct habitat types: *P. maniculatus* and *O. leucogaster* in grasslands and *P. truei* and *P. boylii* in woodlands. There was considerable variation between factors that best predicted flea prevalence across the four species, indicating of the four hypotheses we proposed, there was not one that consistently explained flea prevalence and/or intensity within mammalian species in this system, and there were also some interesting patterns that emerged that could be explained by species-specific factors such as behavioral traits and life histories.

First, we expected increase in vegetation density of woodlands, (*i.e.* higher PC scores) would increase the survivability of fleas and thus lead to higher rates of parasitism. This is because the local environment near the host is important to the flea life cycle, as fleas spend a considerable amount of time off host (*i.e.* in nests or burrows) laying eggs and developing into larvae and pupae (Krasnov et al., 2002a; Krasnov, 2008). However, there are conflicting signals within the sets of GLMs where vegetation appeared as the top model. For prevalence rates, vegetation appeared as top model for one of the four species, *P. maniculatus,* with an interaction term of cattle treatment. Here, open, grassy vegetation (*i.e.* Principle Component scores that were lower/negative) resulted in lower prevalence rates in small mammals (Standardized β Coefficient = -1.84). Models for flea intensity revealed vegetation as the best term for two species, *P. boylii* and *O. leucogaster*, in which flea intensity increased with more open and more dense vegetation, respectively.

These seemingly disparate signals begin to tell a story when the life histories of these species are considered. Both *P. maniculatus* and *O. leucogaster* are grassland specialist species and flea prevalence and intensity, respectively, increased as these species were captured in more dense, forested vegetation. Additionally, *P. boylii* is a forest adapted species, and intensity of fleas tended to increase as hosts of this species were caught in grassy, open areas. Therefore, it appears that host behavior is likely the driver of changes in prevalence and intensity, but it manifested in our dataset within the vegetation structure, probably with the inclusion of two habitat types with species specialized to grasslands and woodlands. Though the exact mechanisms behind this pattern are currently unknown, and investigating it was outside the scope of this study, we have hypothesized a reasoning for what is causing flea abundance to increase on small mammals that leave habitats most suitable for them. These species are adapted to specific environments, thus creating a co-evolutionary relationship with hosts and fleas and hosts within a specific structural habitat. Disruption of these co-evolutionary histories could be why hosts that leave their specialized habitat, such as *O. leucogaster* and *P. maniculatus* moving away from open, grass covered habitat and conversely with *P. boylii* in densely covered habitat, are becoming infected with higher abundances of fleas. As for why *P. truei* is the only species that did not adhere to this pattern, we suspect the species is more of a vegetation-generalist within the woodland habitat, as a CCA we conducted (*see* Chapter 1) shows *P. truei* mice were captured in a heterogenous mixture of vegetation types (Figure 6), with no obvious preference for a specific vegetation structure. If this species is not adapted to have distinct habitat requirements within woodlands, it could explain why moving into more open, grassy areas did not impact the flea prevalence and/or intensity as much as the other three species. Indeed, Tylianakis et al. (2007) suggest a similar pattern with modified landscapes (*i.e.* by agricultural conversion) in a tropical system, where higher modified sites were associated with higher rates of parasitism in bees and wasps. Similarly, McKenzie (2007) suggested land conversion of forests to pastures may influence the abundances of amphibian parasite.

Although this pattern only weakly supported by our data, as the models either do not fit the data well, do not have a very large effect size, or are overdispered (Table 9), all species we tested demonstrate consistent trends for vegetation, suggesting it is something that should be investigated further. Taken together, this pattern predicts a potentially alarming consequence of anthropogenic destruction to landscapes (deforestation, land conversion for agriculture, urbanization) which drives species to shift their specialized habitats to structurally different vegetation profiles (McKenzie, 2007; Mckenzie and Townsend, 2007), and potentially altering parasitism rates of hosts and possibly transmission to other wildlife populations and humans.

Secondly, we predicted higher host density would be associated with higher rates of parasitism, as increasing available hosts in an area may increase the probability the flea will find a suitable host (Stringer and Linklater, 2015). This has been empirically tested in a limited number of studies, and generally the observed pattern of parasitism supports this predicted outcome (Arneberg et al., 1998; Bittner et al., 2002; Krasnov et al., 2002a; Mbora and McPeek, 2009). Our results show three of the eight sets of GLMs had host density as a term within the top model (Table 9). In each of these models, there was a positive association with host density and prevalence and/or intensity, though prevalence for *P. truei* being the only species whose model was not significantly different from the data. This suggests that host density has a link to flea community structure within our system, whereas higher host densities lead to greater prevalence and intensities of flea infestation, but host density is not consistent as a predictive factor across all species.

Krasnov et al. (2002) suggest burrow/nest material is integral in the host density-parasitism relationship, and expectations for host density and infection rates can change based on preferred nest material of the host. Since fleas use the materials in the burrows and nests to feed on and develop from eggs to adults (Bitam et al., 2010; Krasnov, 2008), these materials can directly influence the ability for the flea to survive off-host. Furthermore, Bitam et al. (2010) states mammals species that do not create dens, but rather have large home ranges, often have less flea parasitism than species that commonly occupy nests or burrows. The two species in this system where host density is positively associated with flea prevalence and/or intensity, *P. truei* and *P. maniculatus*, have been documented to have burrows made of vegetation and litter (Hall and Morrison, 1997; Reynolds and Wakkinen, 1987), which could benefit off-host flea development. Conversely, *P. boylii,* which did not have host density as a term in prevalence or intensity top models, burrows in rock crevices and bases of trees, which are insufficient habitats for flea larvae and pupae (Thomas, 1988). The only species that we do not detect with this pattern is *O. leucogaster*, which does not have host density as a term in either top model, but have documented burrows in vegetation and litter (Ruffer, 1965). A possibly reasoning for this patter is that most *O. leucogaster* were trapped in areas adjacent to prairie dog towns which may have spill-over effects that we failed to account for. While we avoided trapping within the boundaries of prairie dog towns, mice likely traverse between areas and may face altered encounter rates with fleas within prairie dog town boundaries. Altered flea abundances occur during plague outbreaks associated with prairie dogs, but it remains unclear if abundances carry over to other co-occurring species (Tripp et al., 2009). Therefore, more research is essential to fully understand the link between host, parasite, and vegetation relationships, as this explanation is only partially supported by the patterns observed in this system and could be influenced by other confounding factors.

Third, we predicted the drier year (2018) to result in higher rates of parasitism across species and habitats, as some studies have shown drier seasons lead to less flooding and higher flea success (Makundi and Kilonzo, 1994; Olson, 1969; Young et al., 2015). However, year is the least influential factor, appearing in only one top model (with an interaction of treatment) for prevalence in *P. boylii,* suggesting that the other factors (*i.e.* vegetation, host density, and type of grazer) are better suited for predicting flea prevalence and intensity. Furthermore, the signal we detect is opposite of what we predicted, as 2019 has higher flea prevalence in *P. boylii* hosts, which is the same signal we detect at the local level of *P. truei* for both prevalence and intensity (*see* Table 9).

Taken together, we have support across geographic scales that wet conditions paired with decreasing temperatures can potentially benefit fleas, which is contrary to the results of some studies. One reason for this discrepancy could be species-specific responses to seasonality by some fleas in this system. Schwan (1986) detected different rates of parasitism in certain fleas by season, indicating some species are more prevalent in wetter seasons and others in drier seasons. It is possible there are more fleas adapted to the wet season in this system, as during the time we were trapping (July-August) is the monsoon season in New Mexico (Bowen, 1996). However, we did not ID fleas down to species level and instead focused on the overall parasitism rates of fleas, making this difficult for us to evaluate. The holistic specimen-based approach we used to collect and deposit all flea specimens into museums allows this hypothesis to be investigated in the future.

Another potential reason for why the patterns detected in this system do not agree with patterns detected by others could be the way seasonality was measured/defined. We define seasonality as during the time we trapped mammals, which was July and a few days in August. Therefore, our seasonality has no lag to account for generational times of fleas, but rather the conditions affecting the generation of fleas we collected. Young et al. (2015), however, defines seasonality as thirty days before their time of capturing small mammals, as those conditions were what would influence egg, larval, and pupae development of the fleas they collected from mammals. Additionally, though Stenseth et al. (2006) detect the same pattern as we do, they measure seasonality of the previous season to predict flea success (*i.e.* spring temperatures/rainfall for fleas captured in the summer months). Therefore, our classification of seasonality is a potential reason why there are discrepancy in results for seasonality between our study and results from other studies.

Lastly, the fourth hypothesis was the impact of grazer on rates of flea parasitism. Understanding the impact of native and non-native grazers was a central objective of this project, thus treatment was used within most interaction terms for the prevalence and intensity models. We detect four top models across three species that have treatment as an explanatory factor (Table 9), but these models have treatment interacting with another term, and when we further analyzed the standardized coefficients, we found no distinct pattern (Table 10). For *P. truei*, and *P. maniculatus*, the interaction of host density and cattle treatments had a positive influence on flea prevalence and but on *P. boylii* and *P. maniculatus*, there was a negative interaction with year (2019) and vegetation, respectively. The prevalence and intensity models for *P. maniculatus*, however, did not fit the data well, as they both had *P* values for the Chi-Square goodness of fit test below than 0.05. Taken together, this suggests the influences for flea structure within small mammals are likely species-specific, although cattle treatments do also appear to have a moderate, yet complex, influence on flea prevalence. Additionally, as is true with any ecological study in a natural system, it is possible there are factors we failed to consider within our models. These factors could also interact with treatment, resulting in differences we detect by species. Currently, there is a lack of literature which compares the impact bison and cattle have on flea parasitism on small mammals, but it is becoming an essential subject to investigate, especially when grazing management is being used for grassland conservation, and the way bison and cattle are anthropogenically managed may influence their impact on the local landscape (*see* Chapter 1).

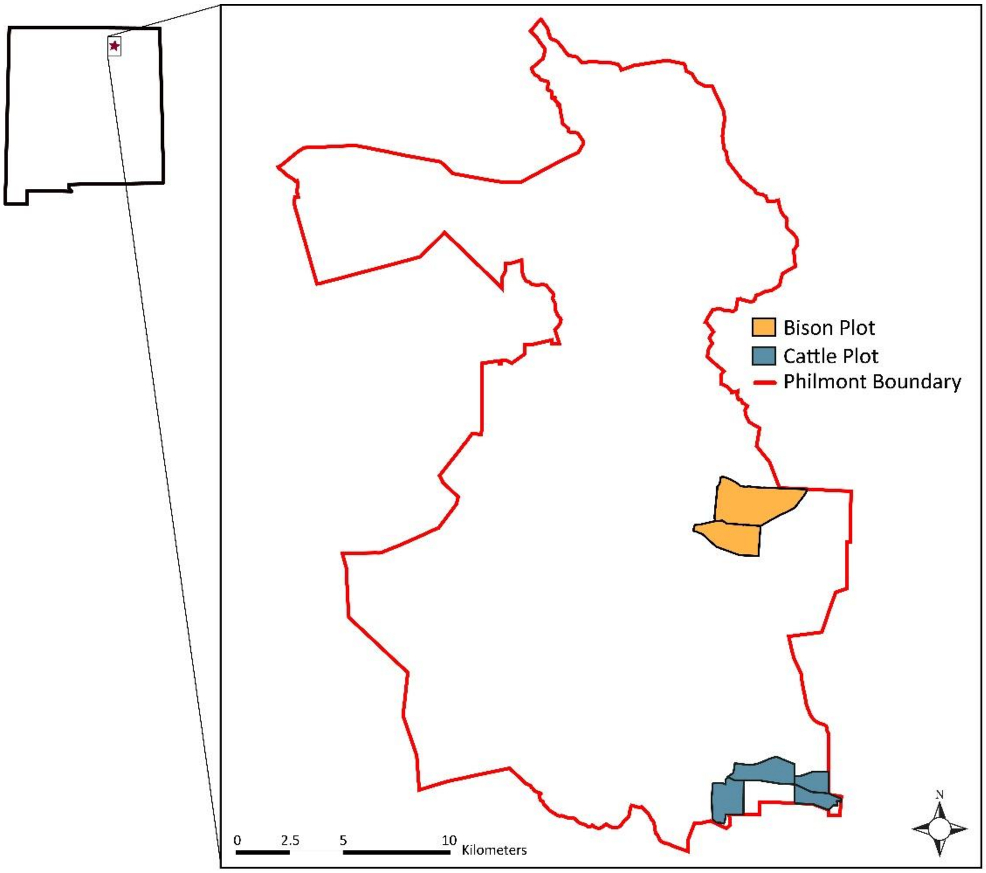
Conclusion

Host parasite relationships may be incongruent across scales and systems. Within a single species, we observed sex, specifically males, as an affluent driving factor of prevalence and intensity, providing support for the sex-biased hypothesis. We failed to detect evidence of an age-bias within *P. truei* in this shortgrass prairie system, nor a difference in seasonality, despite many occurrences within other systems (Hawlena et al., 2005; Isomursu et al., 2006). We are among the first to compare native and non-native grazers and their influences on flea structure in small mammals, and we did not detect consistent differences across four species in two habitat types. However, it does appear there is a moderate, complex effect of treatment as it did appear as an interaction in many top models.

Altogether, our results contribute to a growing body of literature attempting to decouple host-parasite interactions in ecological systems. We found that drivers of prevalence and intensity do not necessarily transcend geographic scales, which is an important point for considering the use of management ideas to control zoonotic diseases and pathogens spread by fleas. Our models do not show strong predictive power, with low effect sizes and often significantly different fit to the data and overdispersion, but this is likely a result of stochasticity in flea prevalence and intensity, whose structure within small mammals is perhaps more complex than captured by factors considered in this study. These results also indicate potential detrimental effects of anthropogenic influence in natural systems, which includes 1) the destruction of landscapes, causing species to shift from preferred habitat and potentially alters rates of parasitism and 2) management of livestock, though mechanisms not fully understood, likely influences flea prevalence and intensity. As small mammal communities shift and change across temporal scales, our results show system-specific factors require measurement before conservation plans can considered and implemented.

APPENDIX I

Figures



Bison Plot
Cattle Plot
Philmont Boundary
0
2.5
5
10
Kilometers
N

Figure 1. Map of the study area within the Philmont Scout Ranch, Colfax County, New Mexico, USA. Yellow areas indicate bison plots and blue areas indicate cattle plots used for vegetation surveys and small mammal trapping in July-August 2018 and 2019.

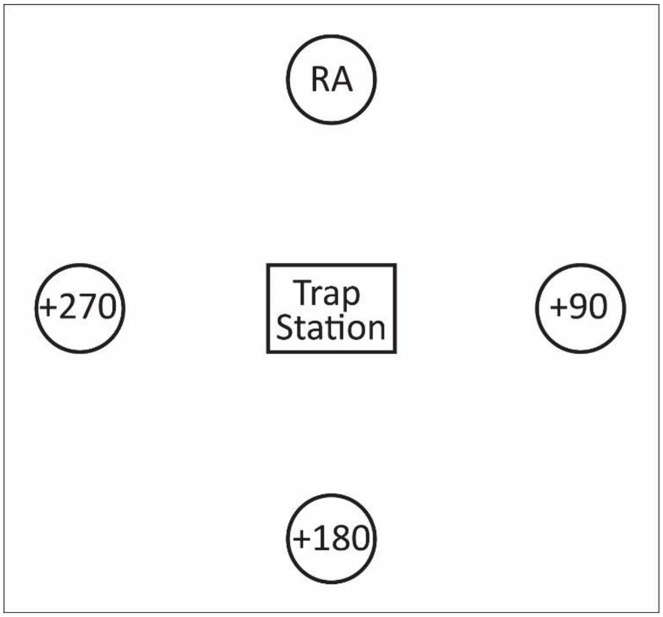


Figure 2. A bird's eye view of a trap station used for vegetation sampling. The center/trap station was the first sampling location followed by the random azimuth (RA) and then the rest- moving clockwise 90 degrees from the previous spot in relation to the trap station. At all five points, the vegetation was characterized using a $1m^2$ Daubenmire frame, Robel pole, convex densiometer, and litter depth (cm).

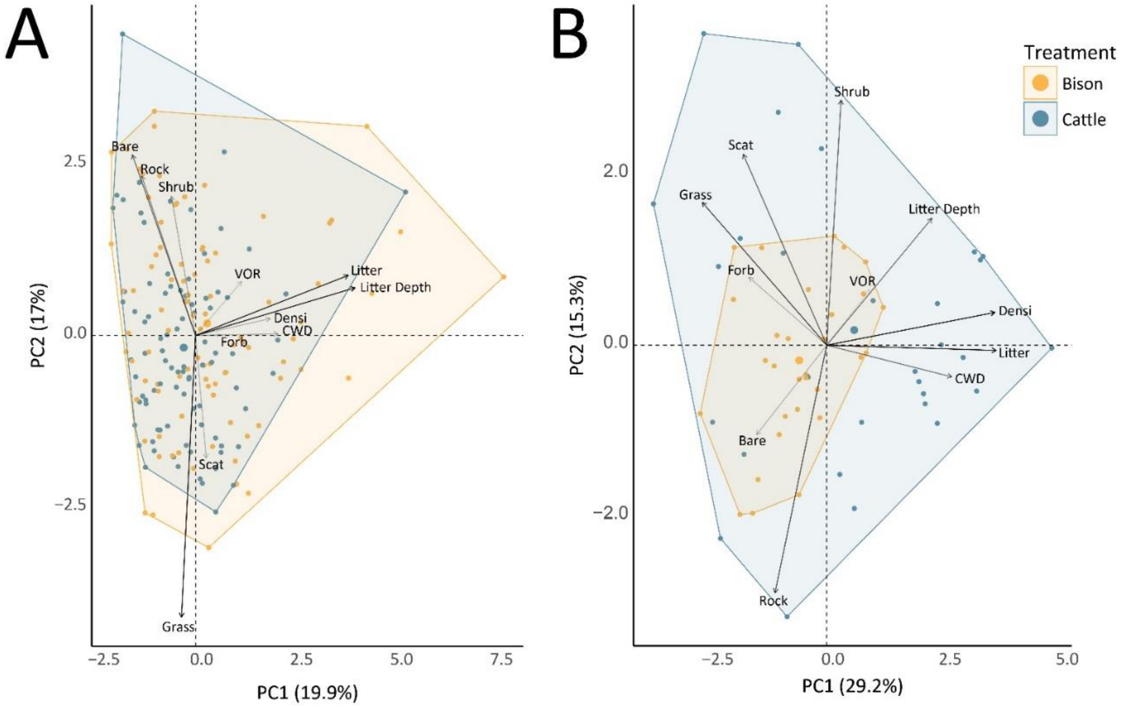


Figure 3. Principle Components Analyses (PCA) for grassland (A) and woodland (B) habitats between bison and cattle grazing treatments in Colfax Co., New Mexico, USA. Vegetation sampling points are projected, and convex polygons encompass the totality of sampling points within the two principle axes. Strength of vegetation sampling categories to in their contribution to each axis correlate to direction and length of corresponding vectors.

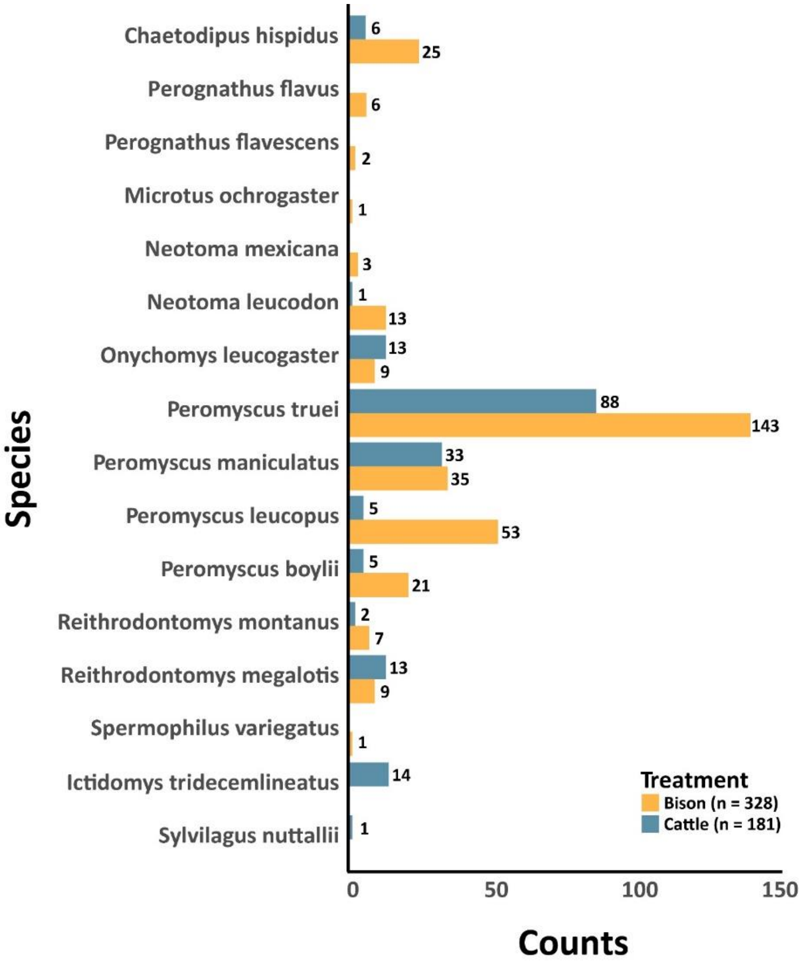


Figure 4. Overall capture abundances across years for small mammals in bison (n = 328) and cattle (n = 181) treatments in Colfax Co., New Mexico, USA Total trap nights for each treatment was 9,600 across two habitat types (not depicted).

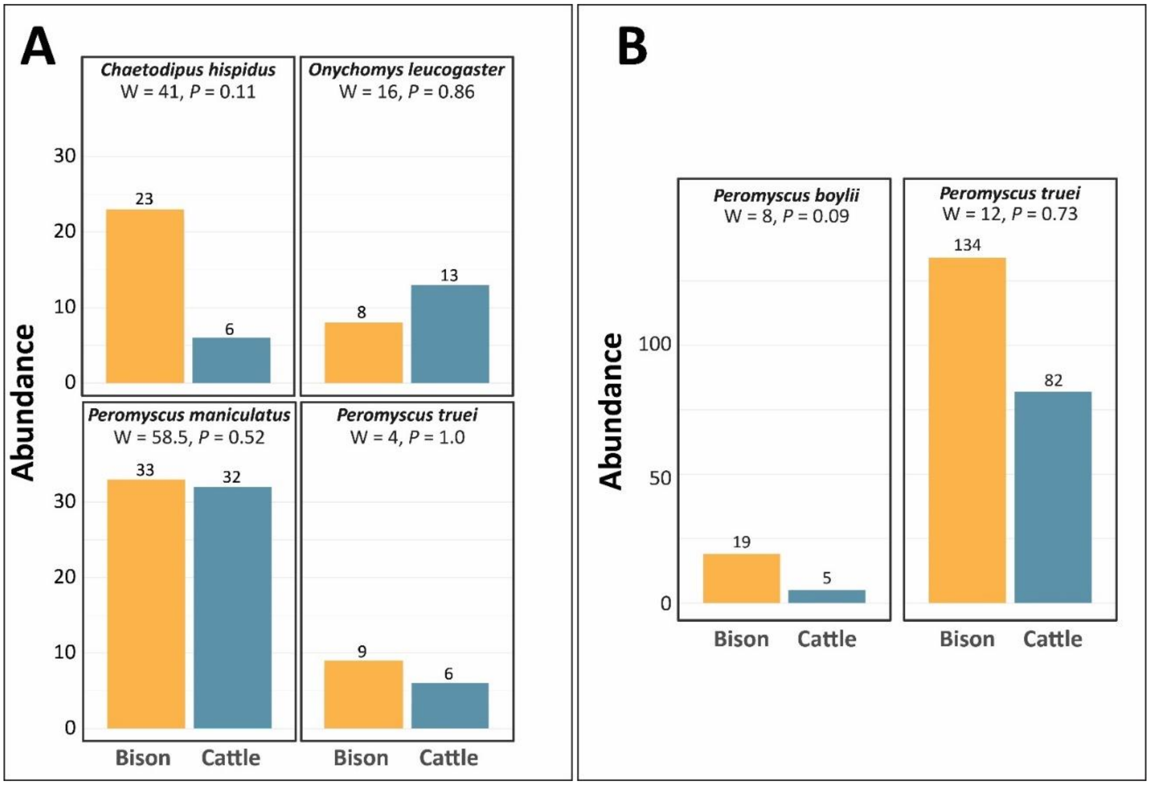


Figure 5. Species abundances by grazing treatment within grasslands (A) and woodlands (B) in Colfax Co., New Mexico, USA. Four species were used in grassland comparisons and two were used in woodlands. Mann-Whitney U tests were conducted to determine significant difference (W) with *P* values indicated.

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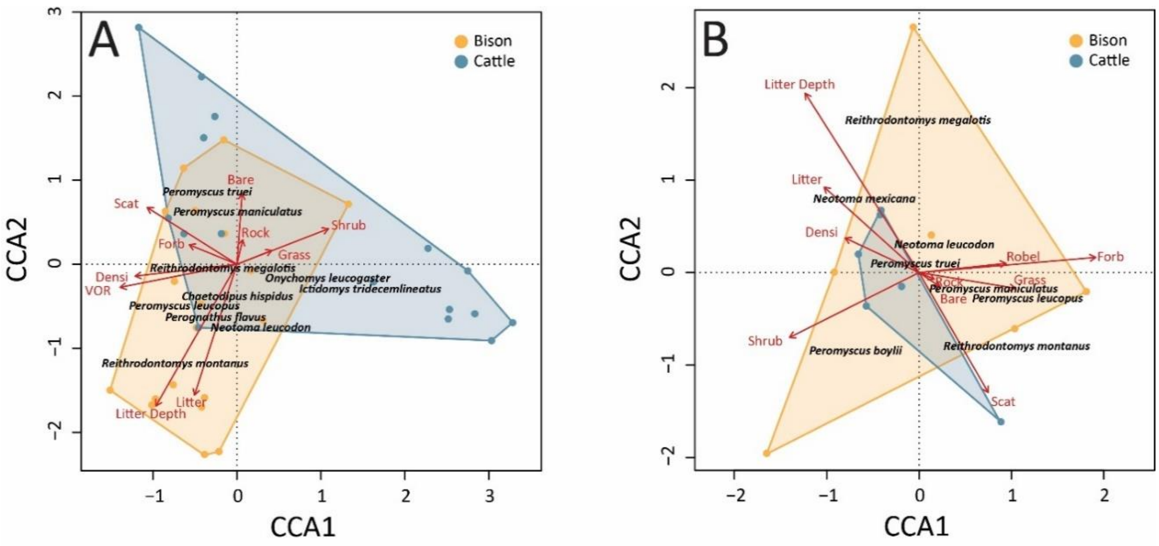


Figure 6. Canonical Correlation Analyses (CCA) for spatial distribution of small mammals within the environment for grasslands (A) and woodlands (B) in Colfax Co., New Mexico, USA. Species are projected into the matrix based on the vegetation they were commonly trapped in and vegetation variables are represented as vectors. Length of vectors signifies strength of variables within the habitat.

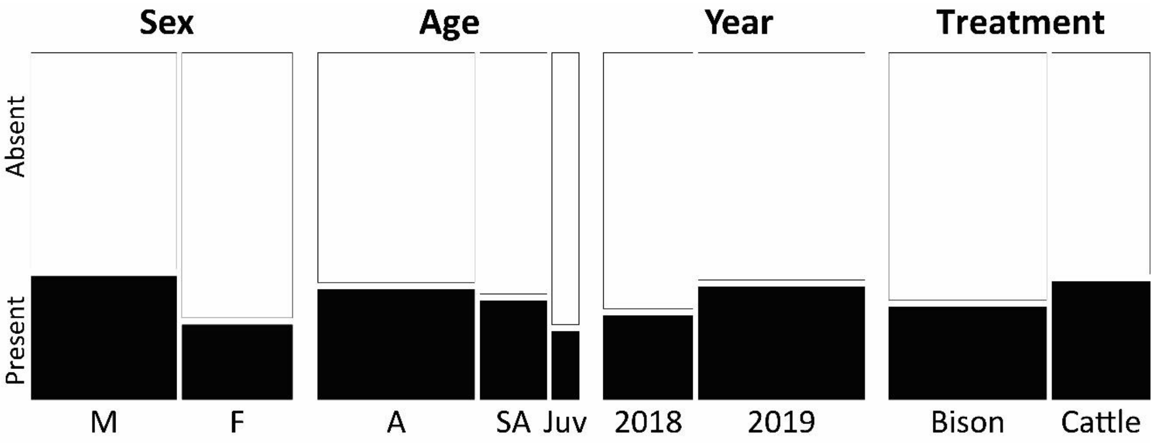


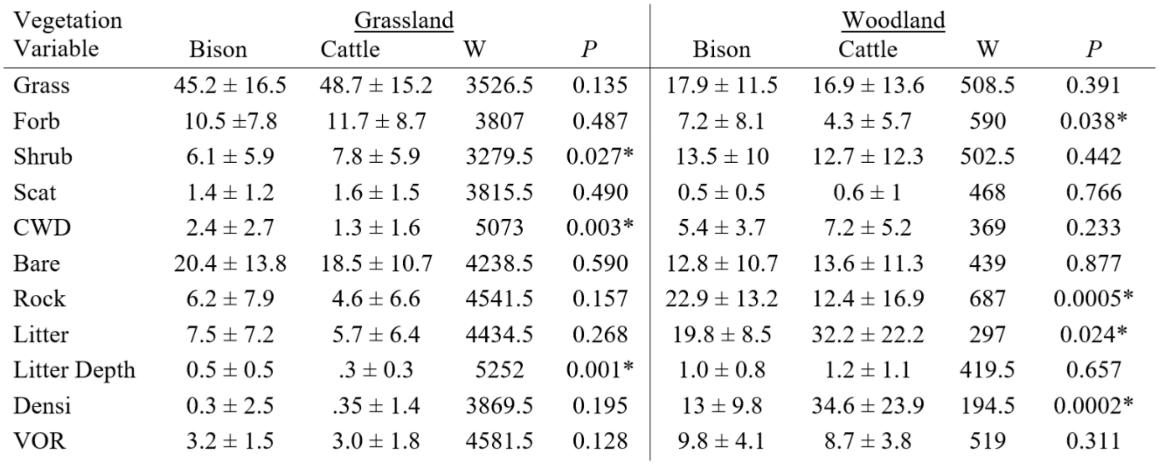
Figure 7. Flea prevalence for *P. truei* across four factors: sex, age, year, and treatment in Colfax Co., New Mexico, USA. M = male, F = female, A = adult, SA = sub-adult, J = juvenile. Width of bars is scaled to sample size, height corresponds to percent sampled mammals parasitized with fleas. Males = 36% prevalence (n = 132) and females = 22% (n = 100). Adults = 32% (n = 143), subadults = 29% (n = 62), and juveniles = 20% (n = 25). 2018 = 25% (n = 81) and 2019 = 33% (n = 151). Bison = 27% (n = 143) and cattle = 35% (n = 89).

Tables

Table 1. Average monthly climate variables for July 2018 and 2019 in Colfax Co., New Mexico, USA. Values shown are averages derived from the U.S. Climate Data database.

Climate Factor	2018	2019
Temperature (°C)	30.4	27.4
Rainfall (cm)	1.6	11.6

Table 2. Comparison of vegetation composition between bison and cattle treatments in Colfax Co., New Mexico., USA Grassland and woodland sampling sites were pooled for 2018 and 2019. Mean values ± SD are given for each treatment in each habitat type. Litter depth was measured in cm, W is the test statistic for a Mann Whitney U Test, CWD = coarse woody debris, VOR = visual obstruction reading from Robel pole, and * denotes significance.



Vegetation Variable	Grassland Bison	Grassland Cattle	Grassland W	Grassland *P*	Woodland Bison	Woodland Cattle	Woodland W	Woodland *P*
Grass	45.2 ± 16.5	48.7 ± 15.2	3526.5	0.135	17.9 ± 11.5	16.9 ± 13.6	508.5	0.391
Forb	10.5 ±7.8	11.7 ± 8.7	3807	0.487	7.2 ± 8.1	4.3 ± 5.7	590	0.038*
Shrub	6.1 ± 5.9	7.8 ± 5.9	3279.5	0.027*	13.5 ± 10	12.7 ± 12.3	502.5	0.442
Scat	1.4 ± 1.2	1.6 ± 1.5	3815.5	0.490	0.5 ± 0.5	0.6 ± 1	468	0.766
CWD	2.4 ± 2.7	1.3 ± 1.6	5073	0.003*	5.4 ± 3.7	7.2 ± 5.2	369	0.233
Bare	20.4 ± 13.8	18.5 ± 10.7	4238.5	0.590	12.8 ± 10.7	13.6 ± 11.3	439	0.877
Rock	6.2 ± 7.9	4.6 ± 6.6	4541.5	0.157	22.9 ± 13.2	12.4 ± 16.9	687	0.0005*
Litter	7.5 ± 7.2	5.7 ± 6.4	4434.5	0.268	19.8 ± 8.5	32.2 ± 22.2	297	0.024*
Litter Depth	0.5 ± 0.5	.3 ± 0.3	5252	0.001*	1.0 ± 0.8	1.2 ± 1.1	419.5	0.657
Densi	0.3 ± 2.5	.35 ± 1.4	3869.5	0.195	13 ± 9.8	34.6 ± 23.9	194.5	0.0002*
VOR	3.2 ± 1.5	3.0 ± 1.8	4581.5	0.128	9.8 ± 4.1	8.7 ± 3.8	519	0.311

Table 3a. Generalized Linear Models (GLMs) in grassland and woodland habitats in Colfax Co., New Mexico, USA. Explanatory factors of treatment and year were used to assess differences in vegetation structure and composition, provided by the first principle components (PC1) axis of each habitat type. McFadden's pseudo R^2 for the top grassland model of treatment*year was 0.09 and for the woodland top model of treatment it was 0.03.

Model	Residual Df	Residual Dev	AIC	ΔAIC	ω
Grassland					
Null	179	393.9915	655.83	52.7	0
Year	178	319.9564	620.33	17.2	0
Treatment	178	378.4842	650.63	47.5	0
Treatment*Year	**176**	**284.3625**	**603.13**	**0**	**1**
Woodland					
Null	59	192.6689	244.28	4.8	0.07
Year	58	191.1951	245.78	6.3	0.03
Treatment	**58**	**172.0426**	**239.48**	**0**	**0.75**
Treatment*Year	56	169.7168	242.68	3.2	0.15

Table 3b. Estimated β Coefficients and transformed standardized β Coefficients for the top model for predictors of vegetation differences in grassland habitat in Colfax Co., New Mexico, USA.

Term	Estimated β Coefficient	Standardized β Coefficient
Null	1.27	0.00
Cattle	-1.26	-0.43
2019	-1.95	-0.66
Cattle*2019	2.33	0.39

Table 4. Shannon-Wiener Diversity (H) comparisons between bison and cattle treatment sites within two habitat types in Colfax Co., New Mexico, USA. Diversity values are given with 95% CI. A comparison between diversity values was conducted using a Hutcheson t-test (t-statistic).

Habitat	Bison	Cattle	t	*P*
Grassland	1.86 ± 0.12	0.22± 0.13	2.71	0.007
Woodland	0.95 ± 0.14	0.58 ± 0.24	7.29	4.3E-12

Table 5. Prevalence of parasite infestation in small mammals between grazing treatments and habitat types in Colfax Co., New Mexico, USA. Binomial (1 = presence, 0 = absence) factors were used for Chi Square analyses (χ^2), with reported *P* values. Significance is denoted with an *.

	Grassland				Woodland			
Parasite	Bison	Cattle	χ^2	*P*	Bison	Cattle	χ^2	*P*
Nematode	29.5	11	5.59	0.02*	10.4	1.6	3.44	0.06
Cestode	5.7	8.3	0.09	0.77	3.2	0	--	--
Flea	18.18	35	4,52	0.03*	32	30.64	0.0004	0.98

Table 6. Intensity of parasites in small mammals between grazing treatments and habitat types in Colfax Co., New Mexico, USA. Count data of parasites within infected hosts was analyzed using a Mann-Whitney U test (W).

	Grassland				Woodland			
Parasite	Bison	Cattle	W	*P*	Bison	Cattle	W	*P*
Nematode	23.46	20.43	78	0.58	14.46	38	2	0.3
Cestode	10	2.2	16	0.44	1.75	0	--	--
Flea	2.9	3.5	145.5	0.48	2.02	2.6	3.87.5	0.90

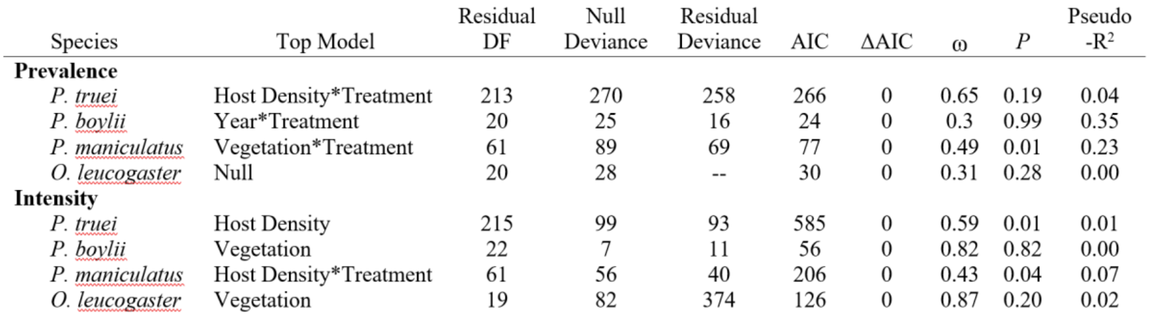
Table 7. Generalized linear models (with Binomial distribution) for flea prevalence of *P. truei* explained by four factors (age, sex, year, and treatment) and some relevant interactions. Mammals were captured in Colfax Co., New Mexico, USA. The top model (bolded) is based on weight and ΔAIC. *P* value is the result of a Chi-Square goodness of fit test and pseudo-R^2 is McFadden's statistic.

Model	Resid. Df	Resid. Dev	AIC	ΔAIC	ω	*P*	Pseudo-R^2
Null	216	269.8464	271.87	4.4	0.06		
Age	214	268.5269	274.57	7.1	0.02		
Sex	**215**	**263.4744**	**267.47**	**0**	**0.54**	**0.01**	**0.02**
Year	215	267.331	271.37	3.9	0.08		
Treatment	215	269.0408	273.07	5.6	0.03		
Sex*Age	211	261.237	273.27	5.8	0.03		
Age*Treatment	211	266.7359	278.77	11.3	0		
Sex*Treatment	213	261.252	269.27	1.8	0.22		
Year*Treatment	213	266.3604	274.37	6.9	0.02		

Table 8. Generalized linear models (with Poisson distribution) for flea intensity of *P. truei* explained by four factors (age, sex, year, and treatment) and some relevant interactions. Mammals were captured in Colfax Co., New Mexico, USA. The top model (bolded) is based on weight and ΔAIC. *P* value is the result of a Chi-Square goodness of fit test and pseudo-R^2 is McFadden's statistic.

Model	Resid. Df	Resid. Dev	AIC	ΔAIC	ω	*P*	Pseudo-R^2
Null	216	99.26318	588.93	2.3	0.13		
Age	214	98.46314	592.13	5.5	0.03		
Sex	**215**	**94.97662**	**586.63**	**0**	**0.41**	**0.04**	**0.01**
Year	215	96.57976	588.23	1.6	0.19		
Treatment	215	99.24813	590.93	4.3	0.05		
Sex*Age	211	93.65119	593.33	6.7	0.01		
Age*Treatment	211	98.32854	598.03	11.4	0		
Sex*Treatment	213	93.06104	588.73	2.1	0.15		
Year*Treatment	213	96.17919	591.83	5.2	0.03		

Table 9. Generalized linear models for flea prevalence and intensity across four species (*P. truei*, *P. boylii*, *P. maniculatus*, and *O. leucogaster*) captured in Colfax Co., New Mexico, USA in two habitat types (grassland and woodland) and four factors (vegetation, host density, year, and treatment). Prevalence models were conducted using Binomial distributions and intensity models were conducted using Poisson distributions. *P* value is the result of a Chi-Square goodness of fit test and pseudo-R^2 is McFadden's statistic.



Species	Top Model	Residual DF	Null Deviance	Residual Deviance	AIC	ΔAIC	ω	*P*	Pseudo -R^2
Prevalence									
P. truei	Host Density*Treatment	213	270	258	266	0	0.65	0.19	0.04
P. boylii	Year*Treatment	20	25	16	24	0	0.3	0.99	0.35
P. maniculatus	Vegetation*Treatment	61	89	69	77	0	0.49	0.01	0.23
O. leucogaster	Null	20	28	--	30	0	0.31	0.28	0.00
Intensity									
P. truei	Host Density	215	99	93	585	0	0.59	0.01	0.01
P. boylii	Vegetation	22	7	11	56	0	0.82	0.82	0.00
P. maniculatus	Host Density*Treatment	61	56	40	206	0	0.43	0.04	0.07
O. leucogaster	Vegetation	19	82	374	126	0	0.87	0.20	0.02

Table 10. Estimated β Coefficients and transformed standardized β Coefficients for the top model for predictors of variation from sets of generalized linear models containing vegetation, host density, year, treatment and relevant interactions for flea prevalence (binomial distribution) and intensity (poisson distribution). Species included are *P. truei, P. boylii,* and *P. maniculatus* hosts from Colfax Co., New Mexico, USA. P and I are abbreviations for prevalence and intensity.

Species	P/I	Term	Estimated β Coefficient	Standardized β Coefficient
P. truei	P			
		Null	-1.75	0.00
		Host Density	0.13	0.71
		Cattle	-0.30	-0.31
		Host Density*Cattle	0.17	0.99
P. boylii	P			
		Null	-19.57	0.00
		2019	18.72	23.04
		Cattle	20.26	20.26
		2019*Cattle	-38.98	-26.53
P. maniculatus	P			
		Null	-1.06	0.00
		Vegetation	0.40	0.86
		Cattle	1.12	1.13
		Vegetation*Cattle	-1.50	-1.84
P. maniculatus	I			
		Null	0.72	0.00
		Host Density	-0.31	-0.20
		Cattle	-0.13	-0.04
		Host Density*Cattle	0.49	0.40

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