

DISSERTATION

PARASITES AND IMMUNOGENETIC DIVERSITY IN PRAIRIE DOGS

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Elizabeth M. Harp

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Doctoral Committee:

Advisor: Michael F. Antolin

Lora R. Ballweber
N. Thompson Hobbs
Ashley K. McGrew

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ABSTRACT

PARASITES AND IMMUNOGENETIC DIVERSITY IN PRAIRIE DOGS

Prairie dogs (*Cynomys* spp.) are an important component of North American grassland communities. Prairie dogs have been characterized as ecosystem engineers and keystone species because their extensive burrow systems alter ecosystem dynamics and provide homes for a variety of species. Prairie dog populations have declined dramatically over the past century as a result of eradication programs, habitat loss, and introduced plague. This research explores factors related to host-parasite ecology and immunogenetics of prairie dogs. The second chapter is a systematic review of parasites recorded from all five prairie dog species. The third chapter characterizes genetic diversity and investigates selection at the hyperdiverse MHC DRB locus in black-tailed prairie dogs. The fourth chapter uses multimodel inference to investigate host and environmental factors affecting flea aggregation on black-tailed prairie dogs.

I found host-parasite records documenting at least 104 parasite species from prairie dogs. Over 2/3 of parasite species were ectoparasites, primarily fleas. Most endoparasites were protozoa. Bacteria and viruses are essentially undescribed from prairie dogs. Potentially related to the diversity of parasites they are exposed to, the DRB gene in black-tailed prairie dogs was characterized by high levels of diversity. I also found considerable evidence for contemporary directional selection and historical balancing selection acting on the DRB gene in black-tailed prairie dogs. However, I found only weak evidence for a relationship between DRB genotype and flea parasitism in black-tailed prairie dogs. Primary drivers of flea aggregation on black-tailed prairie dogs, identified by multimodel inference of generalized linear models, were host

sex and month of capture. Males were more heavily parasitized than females, and flea loads are greatest in September and lowest in June.

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CHAPTER ONE

INTRODUCTION

Host-parasite interactions result in selective pressures on both hosts and parasites, though the exact nature of these selective pressures has not been fully resolved (Papkou *et al.* 2016). The major histocompatibility complex (MHC) family of genes encodes cell-surface molecules involved in antigen recognition and contains the most diverse region of the vertebrate genome (Bernatchez and Landry 2003). It is generally accepted that some form of balancing selection must be responsible for maintaining the considerable genetic diversity of MHC genes over evolutionary timescales (Meyer *et al.* 2018). It is not clear, however, what selective forces are responsible for the origin and persistence of specific alleles, especially at contemporary timescales (Jeffery and Bangham 2000). Additionally, balancing selection encompasses three different mechanisms, frequency-dependent selection (rare allele advantage), heterozygote advantage, and fluctuating selection. Determining which of these mechanisms best accounts for MHC diversity has been challenging (Spurgin and Richardson 2010). To complicate matters further, any of these selective mechanisms can be mediated by parasites or mate choice (sexual selection), with evidence for each of these in different taxa (Winternitz *et al.* 2013).

Studies with wild rodents investigating the relationship between parasitism and class II MHC DRB genotype (n = 11 studies¹) found evidence for allele-specific reductions in parasitism in all but one instance², and evidence for susceptibility alleles in six cases³. None of the 10

¹ (Froeschke and Sommer 2005; Harf and Sommer 2005; Meyer-Lucht and Sommer 2005; Tollenaere *et al.* 2008; Guivier *et al.* 2010; Kloch *et al.* 2010; Biedrzycka *et al.* 2011; Axtner and Sommer 2012; Froeschke and Sommer 2012; Kloch *et al.* 2013; Zhang and He 2013)

² (Froeschke and Sommer 2005; Harf and Sommer 2005; Meyer-Lucht and Sommer 2005; Tollenaere *et al.* 2008; Kloch *et al.* 2010; Biedrzycka *et al.* 2011; Axtner and Sommer 2012; Froeschke and Sommer 2012; Kloch *et al.* 2013; Zhang and He 2013)

³ (Harf and Sommer 2005; Kloch *et al.* 2010; Biedrzycka *et al.* 2011; Axtner and Sommer 2012; Kloch *et al.* 2013)

studies found evidence for heterozygote advantage. All but one study (Guivier *et al.* 2010) used multiple parasite species, with four investigating multiple groups of parasites (e.g., helminths, bacteria, and ectoparasites)⁴, including two with ectoparasites (Cutrera *et al.* 2011; 2014), while the remainder were limited to helminth species. Results from these studies provide substantial evidence for parasite-mediated selection in multiple species⁵ of rodents. Also notable is the lack of support for heterozygote advantage, which has been the dominant hypothesis for the primary mechanism of selection at MHC loci since it was proposed by Doherty and Zinkernagel in 1975 (Doherty and Zinkernagel 1975b; Hedrick 2012).

Prairie dogs are social, burrowing rodents in the family Sciuridae (Slobodchikoff *et al.* 2009). There are five species in the genus (*Cynomys gunnisoni*, *C. leucurus*, *C. ludovicianus*, *C. mexicanus*, *C. parvidens*), two of which are listed as threatened (*C. parvidens*) or endangered (*C. mexicanus*) under the United States Endangered Species Act (USFWS 2017). While prairie dogs are much reduced in numbers as a result of habitat loss, eradication programs, and the introduced plague bacterium, *Yersinia pestis*, they are widespread throughout the grasslands of North America (Antolin *et al.* 2002). Social animals, such as prairie dogs, are predicted to have a greater diversity of parasites because of increased exposure (Altizer *et al.* 2003b). Elucidating host and environmental influences on parasitism, and effects of parasites on their hosts has long been of interest to biologists, and is still an active area of research (Warburton *et al.* 2016; Ferris and Best 2018; Sackett 2018). Recognition of the importance, to both hosts and parasites, of within-host parasite-parasite interactions has grown steadily over the past two decades (Telfer *et al.* 2008; Hellard *et al.* 2015). Parasite-parasite interactions are often mediated by the host

⁴ (Tollenaere *et al.* 2008; Cutrera *et al.* 2011; Kloch *et al.* 2013; Cutrera *et al.* 2014)

⁵ *Apodemus flavicollis*, *Arvicola scherman*, *Gerbillurus paeba*, *Lasiopodomys brandtii*, *Microtus oeconomus*, *Myodes glareolus*, *Rhabdomys pumilio*, *Spermophilus suslicus*

immune system, either through direct manipulation by parasites, or by host immune system trade-offs (e.g., Wuerthner *et al.* 2017; Lehmer *et al.* 2018).

Summary of research

Though small in size, parasites can have large effects on ecosystems, hosts, and even other parasites (Poulin 1999; Marcogliese 2004). This research provides a window into the past, present, and future of interactions between prairie dogs and their parasites. Results from this effort will help us gain a better understanding of the importance of parasitism in prairie dog ecology and evolution, and aid future research by providing a comprehensive review of prairie dog parasites.

CHAPTER TWO attempts to document, for the first time, all published host-parasite records for the genus *Cynomys* (*C. gunnisoni*, *C. leucurus*, *C. ludovicianus*, *C. mexicanus*, *C. parvidens*). Locating potential references begins with a search of five academic databases using a standardized search string designed to capture as many relevant references as possible. Because some prairie dog parasites are of public health importance, particularly fleas that may transmit plague, a search of the United States Public Health Reports archive is also included. In order to capture additional articles not found in the previous sources while still maintaining a repeatable search strategy, additional records are located through the references cited of relevant articles. A variety of statistical techniques are then used to assess the completeness of the collection of host-parasite records.

CHAPTER THREE investigates genetic diversity and evolution at an immune system gene, the class II MHC DRB locus, in black-tailed prairie dogs on Pawnee National Grassland, Colorado. Methods used to determine modes and strength of selection acting on the DRB locus include: (1) analysis of non-synonymous and synonymous substitution ratios using statistical

hypothesis testing (codon-based Z-tests), model-based inference, and Bayesian identification of specific codon sites under selection, (2) examination of the frequency of derived segregating site variants (Tajima's D test), and (3) phylogenetic analysis to investigate trans-species polymorphism at the DRB locus in the family Sciuridae. I also attempt to identify functionally similar DRB alleles by means of discriminant analysis of principal components.

CHAPTER FOUR aims to identify host and environmental factors affecting flea parasitism of black-tailed prairie dogs. Previous research in rodents has revealed several biologically plausible predictors of flea abundance, including host sex, host age, season, site, and genotype (e.g., Krasnov *et al.* 2005a; Krasnov *et al.* 2006b). The relative contribution of each of these factors to flea counts on black-tailed prairie dogs is explored using generalized linear models (GLMs), with the best supported model identified using an information theoretic approach (Burnham and Anderson 2002).

Summary of results

This research has resulted in the first comprehensive review of published host-parasite records for the genus *Cynomys*. Species accumulation curves suggest we are close to discovering all flea species parasitizing prairie dogs, if we haven't already, while more effort needs to be focused on identifying viruses and bacteria. The number of parasites recorded for each species of prairie dogs appears to be positively correlated with hectares of occupied habitat, but correlations between both of these and number of records obscure this relationship. At least one bacterial species, *Francisella tularensis*, was not discovered using methods established here, indicating future research intending to exhaustively document species host-parasite records should modify these methods so that unpublished records from relevant government agencies are included. These results may be useful for future research investigating drivers and effects of parasite

diversity in prairie dogs (e.g., Johnson and Hoverman 2012; Johnson *et al.* 2015; Betts *et al.* 2018).

I found evidence for historical balancing selection and contemporary directional acting on the class II MHC DRB locus, as well as evidence of trans-species polymorphisms shared within and between *Cynomys* and *Spermophilus* species, with divergence times as great as 12 mya. This research also provides a baseline for immunogenetic diversity in black-tailed prairie dogs on Pawnee National Grassland, Colorado. As summarized previously, MHC diversity in rodents is shaped, at least in part, by parasite-mediated selection. There is also evidence that *diversity* of parasites is the most important determinant of MHC diversity (Wegner *et al.* 2003). Results from chapters two and four of this research revealed high levels of DRB diversity and potentially high parasite diversity in black-tailed prairie dogs. This is in contrast to lower DRB diversity (Cobble *et al.* 2016) and potentially lower parasite diversity chapter two) of Gunnison's prairie dogs. This observation supports the hypothesis of a positive correlation between parasite diversity and immunogenetic diversity, presumably driven by some form of parasite-mediated selection.

Fleas, many of which transmit plague, are the most common parasites of prairie dogs (see Chapter two). This chapter used GLMs to explore host and environmental factors potentially affecting flea abundance on black-tailed prairie dogs. Host sex and month of capture were the strongest predictors of flea counts. More fleas were found on prairie dogs in September than any other month, males had more fleas than females. Weak effects of host age, colony, and genotype were also found. These results agree with many similar studies in rodents, and are contrary to some others, suggesting some factors may be species-specific. A similar effort with black-tailed and Gunnison's prairie dogs, employing a variety of modeling techniques and additional

explanatory variables with larger spatial and temporal samples (Sackett 2018), was published after this research was completed. Sackett's (2018) results largely contrast with mine, finding no real effect of sex, and an opposite effect for age.

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CHAPTER TWO

A REVIEW OF THE PARASITES OF PRAIRIE DOGS (*CYNOMYS* SPP.)

Introduction

Parasites, which make up nearly 50% of the known biodiversity of animal species (Poulin 2000), exert tremendous influence on ecological communities and ecosystem functioning, and as such, are important components of communities and ecosystems (Hudson *et al.* 2006; Lefevre *et al.* 2009; Hatcher *et al.* 2012; 2014; Wood and Johnson 2015). The most obvious effects of parasites at the level of the individual host come from overt disease, but more subtle effects include changes in behavior, reductions in fecundity or growth, and increased susceptibility to predation (Marcogliese 2004). Parasites may even play a role in conservation of host species, primarily by assuring a properly functioning host immune system (Spencer and Zuk 2016), and possibly by reducing transmission rates through within-host parasite competition (Johnson *et al.* 2013). Parasites have even been called ecosystem engineers (Hatcher *et al.* 2012).

Given their importance, both numerically and functionally, it is not surprising that many have called for considering parasites in biodiversity conservation plans. Reasons for preserving parasites range from their intrinsic value as species (Gompper and Williams 1998; Gómez and Nichols 2013; Rocha *et al.* 2016), to their contribution to host species conservation (Gompper and Williams 1998; Spencer and Zuk 2016), and their often underappreciated effects on ecological systems (Gómez and Nichols 2013; Dougherty *et al.* 2016; Spencer and Zuk 2016; Weinersmith and Earley 2016). More than one study has found that parasites are major components of food webs (e.g., Huxham and Raffaelli 1995; Memmott *et al.* 2000; Thompson *et al.* 2005; Lafferty *et al.* 2006; Hernandez and Sukhdeo 2008; Amundsen *et al.* 2009; Johnson *et*

al. 2010; Poulin *et al.* 2013). If we are to have a better understanding of the role of parasites at the population, community, and ecosystem levels, and if we aim to preserve parasite biodiversity, we must first document host-parasite relationships in the wild, especially for host species of conservation concern. If we do not, we risk a situation like that of the black-footed ferret, where only five parasite species, two of them likely now extinct, were documented before black-footed ferrets were so reduced in numbers that the remaining 18 wild individuals were captured to start a captive breeding program (Boddicker 1968; Gompper and Williams 1998; Harris *et al.* 2014). Two previously unidentified species of *Eimeria*, unlikely to be native to black-footed ferrets, were discovered in the captive population (Gompper and Williams 1998). A conscious decision was made to not eliminate the newly discovered *Eimeria* spp. in order to maintain an appropriate immune response in ferrets destined for the wild (Gompper and Williams 1998). We will never know what other parasites were native to wild black-footed ferrets (Williams *et al.* 1992; Gompper and Williams 1998).

While many reasons exist to conserve parasite species, there are also valid reasons to control parasites, particularly when they threaten the long-term persistence of their host population (Stringer and Linklater 2014; Wood and Johnson 2015), or cause devastating disease in humans (Wood and Johnson 2015). Because of this, it is important to not only identify the host-parasite relationships of species of conservation concern, but also to identify the relative risk to wildlife and humans associated with each parasite (Stringer and Linklater 2014; Pacioni *et al.* 2015; Wood and Johnson 2015).

Prairie dogs, the obligate prey of black-footed ferrets, are social, burrowing rodents in the family Sciuridae that inhabit grasslands of North America. There are five species of prairie dogs: black-tailed (*Cynomys ludovicianus*), Gunnison's (*C. gunnisoni*), Mexican (*C. mexicanus*), Utah

(*C. parvidens*), and white-tailed (*C. leucurus*). Of these, Mexican and Utah prairie dogs are recognized as endangered by the International Union for Conservation of Nature and Natural Resources (IUCN 2017), while the Mexican prairie dog is listed as endangered, and the Utah prairie dog is listed as threatened by the United States Fish & Wildlife Service (USFWS 2017). According to IUCN, populations of all five species of prairie dogs are decreasing (IUCN 2017). Prairie dogs have declined from an estimated 5 billion individuals at the start of the 20th century to about 50-100 individuals million currently (Slobodchikoff *et al.* 2009). This is primarily due to the combined effects of early-1900s eradication campaigns, current habitat loss, and the introduced bacterium *Yersinia pestis*, causative agent of plague (Barnes *et al.* 1972; Ubico *et al.* 1988; Barnes 1993; Antolin *et al.* 2002; Scott-Morales *et al.* 2004; Avila-Flores *et al.* 2012; Brown *et al.* 2016).

The five species of prairie dogs fit into two evolutionary groupings, with the black-tailed and Mexican prairie dogs grouped together in a “black-tailed” group in the subgenus *Cynomys*, and Gunnison’s, white-tailed, and Utah prairie dogs grouped together in a “white-tailed” group in the subgenus *Leucocrossuromys* (Hollister 1916; Pizzimenti 1975; Goodwin 1995). Fossil and genetic evidence suggests that a Gunnison’s-like prairie dog evolved first, with current-day Gunnison’s prairie dogs evolving in the southern Rocky Mountains (Pizzimenti 1975). Of the extant species of prairie dogs, Gunnison’s, black-tailed, and white-tailed prairie dogs can be found in the fossil record as far back as the Pliocene (Goodwin 1993; Goodwin 1995). It is unclear whether white-tailed prairie dogs are more closely related to Gunnison’s prairie dogs or Utah prairie dogs; genetic evidence suggests Gunnison’s and white-tailed prairie dogs are more closely related to each other than to Utah prairie dogs (Herron *et al.* 2004), while immunological evidence suggests that white-tailed and Utah prairie dogs are more closely related to each other

than to Gunnison's prairie dogs (McCullough *et al.* 1987). Black-tailed prairie dogs likely evolved separately, with the Mexican prairie dog evolving from the black-tailed prairie dog (McCullough *et al.* 1987; Goodwin 1995; Castellanos-Morales *et al.* 2016).

All five prairie dog species live in smaller social groups within a larger colony made up of varying numbers of social groups (Slobodchikoff *et al.* 2009). Black-tailed and Mexican prairie dogs are the most social, white-tailed prairie dogs are least social, and Gunnison's and Utah prairie dogs fall somewhere in between based on the frequency of interactions within social groups (Hoogland 1979; Slobodchikoff *et al.* 2009). The number of interactions between Gunnison's prairie dogs is dependent on the distribution of food resources within a territory (Travis and Slobodchikoff 1993). Patchier food resources result in more social interactions and larger social groups, presumably to have enough individuals to defend patchy food resources (Travis and Slobodchikoff 1993). It is possible that the same mechanism explains interaction and social group-size differences observed in other prairie dog species (Slobodchikoff *et al.* 2009). In relation to parasites, one of the most important social behaviors of prairie dogs is mutual grooming, observed in black-tailed, but not in Gunnison's, white-tailed, or Utah prairie dogs; these three species engage instead in self-grooming (Slobodchikoff *et al.* 2009). Social behavior in Mexican prairie dogs is not well-studied, but it is hypothesized that their level of sociality and propensity to engage in mutual grooming is similar to black-tailed prairie dogs because of their close evolutionary relationship (Slobodchikoff *et al.* 2009).

The Great Plains of North America encompasses three different habitats: short-grass, mixed-grass, and tall-grass prairie. Prairie dogs are found most often in short- and mixed-grass prairie, with black-tailed prairie dogs occasionally found in tall-grass prairie at the eastern edge of their range (Slobodchikoff *et al.* 2009). Black-tailed prairie dogs are the most widespread

(Fig. 2.1), with a range that extends from northern Mexico across the great plains of the United States, and into Canada, though they are now rare or extinct in some areas (Hoogland 1996). Their current occupied habitat is estimated to be 8,500 km² (USFWS 2015). White-tailed prairie dogs have the second largest geographic range (Fig. 1.1), with colonies found in parts of Montana, Wyoming, Colorado, and Utah; the majority of the range found in Wyoming (Clark *et al.* 1971). The most recent estimate of occupied habitat for white-tailed prairie dogs is 3,405 km², but this is based on surveys with different methodologies in the four states where prairie dogs are found, and thus may not be accurate (Seglund *et al.* 2004; USFWS 2010). Gunnison's prairie dogs are restricted to higher elevations (1830 – 3660 m) in the southern Rocky Mountains, with their distribution centered around the Four Corners region where the borders of Arizona, Colorado, New Mexico, and Utah meet (Fig. 1; Pizzimenti and Hoffman 1973). It is estimated that Gunnison's prairie dogs currently occupy about 3,883 km² (Seglund *et al.* 2006; USFWS 2013). Utah and Mexican prairie dogs have the smallest geographic distributions. Utah prairie dogs are found in the southern half of Utah (Pizzimenti and Collier 1975), and current occupied habitat is estimated to be 134 km² (USFWS 2011). Mexican prairie dogs are found within a 600 km² region in northern Mexico (Ceballos *et al.* 1993). For the most part, ranges of each of the five species of prairie dog do not overlap, except for a zone in Wyoming where black-tailed and white-tailed prairie dog ranges overlap, and a small region in western Colorado where Gunnison's and white-tailed prairie dog ranges overlap (Johnsgard 2005).

Prairie dogs are particularly susceptible to plague, typically dying within 5-7 days of being bitten by an infected flea (Cully and Williams 2001), though there is some evidence they may be evolving resistance (Rocke *et al.* 2012). The first evidence of plague in the continental United States appeared on March 6, 1900, in a resident of San Francisco (Kellogg 1920;

Hampton 1940), and had occurred previously aboard ships docked in San Francisco and New York in 1899 (Link 1955). The first confirmed case of sylvatic plague in the United States occurred east of San Francisco in 1908 in ground squirrels in Contra Costa County, California (Hampton 1940), and from there spread north, south, and east. Through the end of 1934, sylvatic plague had only been detected in California and in a few port cities in Washington, Texas, and Louisiana (Hampton 1940). However, intensive surveillance efforts outside of California did not begin until 1935, the same year that sylvatic plague was found in ground squirrels as far west as Beaverhead County, Montana, followed in 1936 by detection of plague in several other sciurids in Idaho, Montana, Nevada, and Utah (Hampton 1940). Plague was first detected in prairie dogs in Garfield County, Utah in 1936 in Utah prairie dogs (Allred 1952). By 1940, plague had been recorded from 39 rodents, including Gunnison's, white-tailed, and Utah prairie dogs, as well as one species of rabbit (*Sylvagus nuttallii nuttallii*) in 10 out of 11 western states (Hampton 1940; Link 1949; Allred 1952). By 1946 plague had also been recorded from black-tailed prairie dogs (Cully *et al.* 2000). Plague was found in Mexican prairie dogs in 1954 (Varela and Vasquez 1954), but has not been found since (Trevino-Villarreal *et al.* 1998). Until recently, plague did not occur east of the 103rd meridian in South Dakota (Antolin *et al.* 2002). Plague outbreaks have now been reported from Pine Ridge Indian Reservation (Rocke *et al.* 2008) and Conata Basin (Griebel 2009; Abbott *et al.* 2012) in South Dakota, and infected fleas have been found in Badlands National Park, South Dakota (Mize and Britten 2016). These reports suggest plague now occurs throughout the range of prairie dogs in the United States (Mize and Britten 2016). Efforts to understand the ecology of plague and to identify important transmission patterns is ongoing, particularly in relation to prairie dogs and their fleas (e.g., Richgels *et al.* 2016; Eads and Hoogland 2017).

This review documents published records of host-parasite relationships for all five species of prairie dogs. Throughout this review I use the term parasite broadly to include any infectious organism capable of colonizing a host, utilizing host resources, and spreading to new hosts (Altizer *et al.* 2003b). This includes microparasites (viruses, bacteria, protozoa) and macroparasites (helminths and arthropods; Anderson and May 1992). Records have been taken from the scientific literature and government documents, some of which is difficult to access. This research is the first comprehensive review of host-parasite relationships for prairie dogs.

Materials and Methods

Literature Search

Using records from the published literature, I compiled a database of parasites and pathogens found naturally in and on all five species of prairie dogs (*Cynomys gunnisoni*, *C. leucurus*, *C. ludovicianus*, *C. mexicanus*, *C. parvidens*). I searched five online academic databases (CAB Abstracts Complete; Google Scholar, PubMed, Web of Science, Zoological Record Plus; last search performed October 1, 2017) using the following search string: ((*Cynomys* OR "prairie dog") AND (parasit* OR disease OR pathogen OR helminth OR fung* OR virus OR bacteria OR protozoa OR arthropod OR vector)), and then evaluated each batch of search results using the following hierarchy: title; abstract; full article. I used an extremely permissive filter for article titles and abstracts, so that if it seemed at all possible an article might contain at least one parasite record from one or more wild prairie dogs, it was passed through to the next level of consideration. I excluded records of parasites or pathogens found in captive prairie dogs (*e.g.*, research, zoo, pet trade), unless there was undeniable evidence that the infection was acquired naturally. I also did not include records of parasites found in burrows of prairie dogs, regardless of whether or not the parasite had previously been recorded from prairie

dogs. It has been suggested that the traditional dichotomy of “nest” fleas versus “body” fleas is not useful, because flea indices calculated from host body sampling are reliable indicators of flea populations (Krasnov *et al.* 2004). Additionally, because several other animals are known to inhabit prairie dog burrows (e.g., Stapp 2007; Zapata-Valdes *et al.* 2018), it is possible that not all fleas collected from prairie dog burrows actually parasitize prairie dogs. If sample collection methods indicated that host(s) had been captured in an earlier study, I only used previously unrecorded host-parasite records from that reference. If a checklist of host-parasite records referred to a published record, parasite data were recorded from the original publication, rather than the checklist, when possible. If a published reference for which I did not have a record was mentioned in the body of an article, I located that reference and followed the same protocol for inclusion described previously. Because not all host-parasite associations are documented in the published literature, and not all published records are indexed in search engines or cited in indexed literature, it is likely that some records are not included in this list (e.g., records from plague surveillance activities conducted by health departments in the western states). To minimize bias, I also searched the Public Health Reports archives (1878-2007) for the terms “*Cynomys*” and “prairie dog” (separate searches). Finally, I examined the literature cited in each article that documented host-parasite relationships for prairie dogs, and used the same criteria used for database results to locate additional references. Once all host-parasite records were entered in the database, I manually checked records by date and location, discarding records that appeared to be duplicates (e.g., same collector, date, location, or sample size).

Recorded Information

I recorded the following for each host-parasite record (when available): host name; reported parasite or pathogen name (subspecies noted if given); collection location (country,

state, locality, Global Positioning System (GPS) coordinates, elevation); host sample size; location from where the parasite or pathogen was isolated (*e.g.*, fur, blood, feces); prevalence and intensity (as defined in Margolis *et al.* 1982); how the parasite or pathogen was identified (*i.e.*, antibodies or positive identification (visual, genetic)); start and end years of field research or collection (for records without this information, publication year was used as collection year); and citation information. I used a center point from the locality information given when GPS coordinates were not provided. If location was indicated by section, township, and range, I used EarthPoint (<http://www.earthpoint.us/TownshipsSearchByDescription.aspx>) to determine GPS coordinates. I used an online converter (<http://www.geoplaner.com/>) to determine Universal Transverse Mercator (UTM coordinates) from GPS coordinates given in degrees, minutes, and seconds or decimal degrees. I used UTM coordinates to determine elevation using an online calculator (<http://www.geoplaner.com/>) when elevation was not provided.

All reported parasite names were checked for validity using published literature, expert consultation, and the following online resources:

Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>)

Catalogue of Life (<http://www.catalogueoflife.org/col/search/all>)

Encyclopedia of Life (<http://eol.org/>)

Global Species Website (<http://www.globalspecies.org/>)

Integrated Taxonomic Information System (<http://www.itis.gov/>)

NCBI Taxonomy Database (<http://www.ncbi.nlm.nih.gov/taxonomy>)

Nomina Insecta Nearctica (<http://www.nearctica.com/nomina/databases/databases.htm>)

Universal Biological Indexer and Organizer (<http://www.ubio.org/>)

Statistical Analyses

Poulin et al (2016) recommend three criteria by which to judge the completeness of host-parasite checklists: (1) compare the number of realized links to the number of potential links in the host-parasite network, (2) analyze the species accumulation curve and determine the number of parasite species not yet discovered using methods presented in Bebber et al (2007; described below), and (3) determine the correlation between the number of published records mentioning a host-parasite relationship and the time elapsed, in years, since the relationship was first reported. I used only the second and third methods to analyze completeness of the host-parasite list for prairie dogs. The first method is not appropriate here because the hosts and parasites are not all part of the same network.

I used the following generalized linear model (GLM) with quasipoisson errors described in Bebber et al (2007) to estimate the expected total number of parasite species: $E(S_t) = k(N_{tot} - N_{t-1})$, where $E(S_t)$ is the expected number of species discovered in year t , N_{tot} is the total number of existing species, N_{t-1} is the cumulative number of species discovered by year $t - 1$, and k is the fraction of undiscovered species at time $t - 1$. The value of N_{t-1} for which S_t is zero can be calculated by dividing minus the intercept by the slope (Bebber *et al.* 2007).

For the Spearman rank correlation test, the magnitude of the correlation coefficient (ρ) provided a measure of the strength of the relationship between the number of reports mentioning a particular host-parasite relationship and the time since the first publication of that relationship.

Because the number of parasites recorded for a species is partly a function of sampling effort, and sampling effort is expected to be, in part, a function of geographic range (Guegan and Kennedy 1996), I performed for (1) number of parasite species versus number of host-parasite records, (2) number of parasite species versus estimates of occupied habitat, and (3) number of

host-parasite records versus estimate of occupied habitat. A host-parasite “record” consists of a parasite species documented at a specific time and location regardless of how many individuals the parasite was recovered from.

Results

I found 160 published references documenting 841 host-parasite records for wild prairie dogs (see map, Fig. 1.2). There were 104 parasite species (excluding 12 genus records for which a species record also exists) representing 60 genera, 33 families, 20 orders, 14 classes, and 9 phyla (Table 2.1). Of these, 30 parasite species (28.8%) were endoparasites and 74 (71.2%) were ectoparasites, with 40 (54.1%) of the ectoparasite species being fleas (Table 2.1). The number of records of each host-parasite relationship ranged from one to 150 (Tables 2.2-2.9), with 48 parasite species (46.2%) having only a single host-parasite record in the literature. Of those parasite species with only a single record in the literature, the following also had genus records (number of genus records in parentheses): *Oropsylla* (n = 3), *Raillietina* (n = 1), *Bartonella* (n = 14), *Cryptosporidium* (n = 1), and *Eimeria* (n = 1).

The species accumulation curve for all parasites (Fig.1.3-A) shows that it is likely there are still species to be discovered because the line is still increasing and has not reached an asymptote (Bebber *et al.* 2007; Poulin *et al.* 2016). In contrast, the rate of discovery of all ectoparasites (Fig. 1.3-B) appears to be leveling off somewhat. However, the accumulation curves for individual ectoparasite groups (Fig. 1.3-C – 3-E) reveal that only fleas (Fig. 1.3-C) appear to be approaching an asymptote, indicating we should expend additional effort identifying ticks and mites infesting prairie dogs, but that we have likely discovered most, if not all, prairie dog fleas. None of the endoparasite species accumulation curves appear to have reached an asymptote (Fig. 1.4).

A Spearman rank correlation test revealed a significant positive association between the number of reports mentioning a particular host-parasite relationship and time since first publication of that relationship ($\rho = 0.45$, $p < 0.0001$; Fig. 1.5), suggesting prairie dogs have been well-sampled for parasites. However, with $\rho < 0.5$ the relationship was not quite what Poulin et al (2016) would consider a “strong” relationship. The estimate of the total number of parasite species that will eventually be recorded from prairie dogs had no upper bound on the confidence limit, and so cannot be reliably calculated (Bebber *et al.* 2007). This is probably because the species accumulation curve has not yet reached an inflection point, indicating there are species yet to be discovered (Bebber *et al.* 2007).

Of the 160 references, 92 references (57.5%) documented host-parasite relationships for black-tailed prairie dogs, 44 (27.5%) for Gunnison’s prairie dogs, 31 (19.4%) for white-tailed prairie dogs, 11 (6.9%) for Utah prairie dogs, 6 (3.8%) for Mexican prairie dogs, and 10 references (6.3%) documented host-parasite relationships for unknown species of prairie dogs that could not be placed into a species designation according to geography of the host-parasite record (Table 2.10). Several references documented host-parasite records for more than one species of prairie dog, and many references documented host-parasite records for multiple locations. The number of parasite species per host species was strongly associated with both the number of references for that host species ($\rho = 0.97$, $p = 0.006$) and the number of host-parasite records for that host species ($\rho = 0.91$, $p = 0.03$).

Of the 846 host-parasite records, 452 (53.4%) were classified as random surveys (i.e., prairie dogs randomly shot or trapped), while 394 (46.6%) were classified as opportunistic observations (e.g., prairie dogs found dead, museum records). Thirty-seven (8.2%) of the random surveys did not report a sample size, 15 (3.3%) had a sample size of one, 111 (24.6%) had a host

sample size between two and nine, and 289 (63.7%) had a host sample size of at least 10. The maximum sample size was 1299 (see Tripp *et al.* 2009), and the mean sample size was 91.5 (95% CI: 53.3, 129.7). Only 132 (29.2%) of the random surveys reported parasite prevalence (summary in Table 2.11), and of these, only 88 (19.5%) had a sample size of at least 10. Of the 132 records that reported prevalence, 82 (62.6%) were for ectoparasites (39 with sample size 10+), 25 (18.3%) were for protozoa (all with sample size 10+), 16 (12.2%) were for bacteria (all with sample size 10+), and 9 (6.9%) were for helminths (8 with sample size 10+; Table 2.11). *Yersinia pestis* had the lowest prevalence (0.2%), while *Oropsylla hirsuta*, *Pulex irritans*, and *P. simulans* had the highest prevalence (100%; Table 2.11).

Black-tailed prairie dogs had the highest parasite species richness (84 species), followed by white-tailed (47 species), Gunnison's (45 species), Utah (15 species), and Mexican prairie dogs (6 species; Table 2.10). Black-tailed prairie dogs also had the largest number of host-parasite records (n = 302), followed by white-tailed (n = 287), Gunnison's (n = 162), Utah (n = 64), and Mexican prairie dogs (n = 13; Table 2.10). There were 12 host-parasite records for which the species of prairie dog was not reported and could not be determined by geography (Table 2.10).

Of the 116 species of parasites (includes all genus-only records), the number of shared parasite species ranged from two shared species between Mexican and Utah prairie dogs to 32 shared parasite species between black-tailed and white-tailed prairie dogs (Table 2.12). Just two parasites, *Oropsylla hirsuta* and *Yersinia pestis*, have been recorded from all five prairie dog species (Tables 2.2 and 2.8). Black-tailed, Gunnison's, white-tailed, and Utah prairie dogs have six additional parasite species in common: two ticks (*Ixodes kingi* and *I. sculptus*; Table 2.5) and four fleas (*Oropsylla idahoensis*, *O. labis*, *O. tuberculata cynomuris*, and *Pulex simulans*; Table

2.2). Black-tailed, Gunnison's, and white-tailed prairie dogs have an additional 15 parasites in common: eight *Eimeria* species (*E. beecheyi*, *E. callospermophili*, *E. cynomysis*, *E. lateralis*, *E. ludoviciani*, *E. morainensis*, *E. spermophili*, and *E. vilasi*; Table 2.7), five flea species (*Pulex irritans*, *Rhadinopsylla fraterna*, *Oropsylla tuberculata*, *O. t. tuberculata*, and *Oropsylla* sp.; Table 2.2), one mite species (*Haemolaelaps fahrenheitzi*; Table 2.4) and one louse species (*Enderleinellus suturalis*; Table 2.3). Separating the prairie dogs into their evolutionary groupings, the black-tailed group had six shared parasite species out of a total of 84 parasite species (all six parasite species recorded from Mexican prairie dogs have also been recorded from black-tailed prairie dogs), and the white-tailed group had nine shared parasite species out of a total of 67 parasite species among them (Table 2.12).

The number of parasite species recorded from each prairie dog species was positively correlated with both the number of host-parasite records ($\rho = 0.91$, $p = 0.03$) and the estimate of occupied habitat ($\rho = 0.98$, $p = 0.003$). The number of host-parasite records was also positively correlated with the estimate of occupied habitat, but the correlation was not significant ($\rho = 0.84$, $p = 0.07$; Fig. 1.6).

Fleas

Fleas from prairie dogs represent five families (Ceratomyzidae, Ctenophthalmidae, Hystrichopsyllidae, Leptopsyllidae, and Pulicidae) and 19 genera (*Aetheca*, *Anomiopsyllus*, *Cediopsylla*, *Ceratophyllus*, *Echidnophaga*, *Eumolpianus*, *Foxella*, *Hoplopleura*, *Hystrichopsylla*, *Megabothris*, *Meringis*, *Neopsylla*, *Opisocrostis*, *Orchopeas*, *Oropsylla*, *Peromyscopsylla*, *Pulex*, *Rhadinopsylla*, and *Thrassis*). There were a total of 43 flea species, including three genus-only records (*Neopsylla* sp., *Oropsylla* sp., *Pulex* sp.) described from 75 references (Table 2.2).

The most commonly reported flea was *Oropsylla hirsuta*, generally known as the prairie dog flea, and was also the only flea found on all five prairie dog species (Table 2.2). The next most common flea species were (number of host-flea records in parentheses): *Oropsylla tuberculata cynomuris* (n = 60), *Oropsylla labis* (n = 44), *Oropsylla idahoensis* (n = 35), and *Pulex simulans* (n = 27; Table 2.2). Of these, only *P. simulans* was found on Mexican prairie dogs, while the other species were found on all prairie dog species except Mexican prairie dogs (Table 2.2). Under the criterion of plague vector competency presented in Eisen et al (Eisen *et al.* 2009), all of the most common fleas are known plague vectors, with the exception of *P. simulans* (Table 2.13; Eisen *et al.* 2009). Of the 43 species of fleas found on prairie dogs, 25 (58%) are known plague vectors (Table 2.13), including *P. irritans*, which is so closely related to *P. simulans* that the two are often mistaken for each other (Smit 1958). Strictly speaking, it appears the plague vector competency of *P. simulans*, has never been documented. However, Smit (1958) notes that at least some of the vector-capacity studies on *P. irritans* almost certainly used *P. simulans* and so it is included here as a plague vector (see Table 2.13).

Gunnison's prairie dogs had the most flea species (n = 26), followed closely by black-tailed prairie dogs (n = 24) and white-tailed prairie dogs (n = 22; Table 2.2). Mexican and Utah prairie dogs had the fewest flea species with only three species found on Mexican prairie dogs and 10 species found on Utah prairie dogs (Table 2.2). Seven species of fleas were found on unknown species of prairie dogs (Table 2.2). The number of host-parasite records for fleas was not always in proportion to the number of flea species, with white-tailed prairie dogs having the most records (n = 224), followed by black-tailed prairie dogs (n = 123) and Gunnison's prairie dogs (n = 96). Utah prairie dogs had 55 host-flea records, while Mexican prairie dogs had just 10

host-flea records. There were 12 host-flea records for which the species of prairie dog was not given and could not be determined by geography.

Lice

Lice from prairie dogs represent three families (Enderleinellidae, Hoplopleuridae, and Polyplacidae), four genera (*Enderleinellus*, *Hoplopleura*, *Linognathoides*, and *Neohaematopinus*), and seven species (including one cryptic genus; see Table 2.3 for species list). There were a total of 22 host-lice records found in 14 references (Table 2.3). All but one louse species had two or more records from the literature, with *Enderleinellus suturalis* having the most records (n = 6), followed by *Linognathoides laeviusculus* and *Linognathoides marmotae* with four records each, *Linognathoides cynomyis* with three records, and *Neohaematopinus citellinus* and *Neohaematopinus* sp. with two records each (Table 2.3). *Hoplopleura acanthopus*, a flea normally found on arvicoline rodents (Durden and Musser 1994; Kucera *et al.* 2007), had only one record from a black-tailed prairie dog in Billings County, North Dakota. Of the 14 references, eight documented species from black-tailed prairie dogs, four documented species from white-tailed prairie dogs, three documented species from Gunnison's prairie dogs, and just one reference documented a louse species from Mexican prairie dogs.

Black-tailed prairie dogs had the greatest number of louse species (n = 6; Table 2.3), followed by Gunnison's and white-tailed prairie dogs with two species each, and Mexican prairie dogs with a single species (Table 2.3). No louse species have been recorded from Utah prairie dogs. *Neohaematopinus* sp. was found on Mexican prairie dogs in El Manantial, San Luis Potosi and on black-tailed prairie dogs in Terry County, Texas. The *Neohaematopinus* sp. collected from black-tailed prairie dogs was identified as "near *citellinus*" by G. F. Ferris (Menzies *et al.*

1951), an entomologist skilled at identifying lice (Anon. 2018). *Neohaematopinus citellus* is the only species in this genus recorded from prairie dogs (Table 2.1), and so this may represent a second *Neohaematopinus* sp. found on prairie dogs.

Mites

Mites from prairie dogs represent three orders (Astigmata, Mesostigmata, and Prostigmata), four families (Ascidae, Laelapidae, Pneumocoptidae, and Trombiculidae), and 13 genera (*Androlaelaps*, *Brevisterna*, *Cheladonta*, *Dermadelema*, *Echinonyssus*, *Euschoengastoides*, *Euschongastia*, *Eutrombicula*, *Hyponeocula*, *Kayella*, *Neoschoengastia*, *Odontacarus*, and *Parasecia*). Twenty-one species of mites have been documented from prairie dogs, with all but three of these recorded from black-tailed prairie dogs (Table 2.4). Three species of mites have been found on white-tailed prairie dogs, two species on Gunnison's prairie dogs, and one species on Utah prairie dogs (Table 2.4). One mite species (*Echinonyssus cynomys*) was found only on a prairie dog whose species could not be determined by geography (Table 2.4). Of the 19 references documenting mites from prairie dogs, 14 documented mites from black-tailed prairie dogs, four from Gunnison's prairie dogs, three from white-tailed prairie dogs, and just one reference documents mites from Utah prairie dogs.

Ticks

Ticks from prairie dogs represent one order (Ixodida), two families (Argasidae, Ixodidae) and three genera (*Dermacentor*, *Ixodes*, *Ornithodoros*). Eight tick species identified to the species level, and two species identified to genus level have been documented from prairie dogs, with all but two species found on black-tailed prairie dogs (Table 2.5). Tick life stages isolated from prairie dogs are shown in Table 2.14. Including two species identified only to genus, six tick species have been found on white-tailed prairie dogs, three on Gunnison's prairie dogs, and

two on Utah prairie dogs (Table 2.5). Of the 27 references documenting ticks on prairie dogs, 18 document ticks on black-tailed prairie dogs, six document ticks on white-tailed prairie dogs, five document ticks on Gunnison's prairie dogs, three document ticks on Utah prairie dogs, and one reference documented ticks on Mexican prairie dogs. One reference documents ticks on prairie dogs whose species was not given and could not be determined by geography. The tick species with the most records was *Ixodes kingi* (24 records), followed closely by *I. sculptus* with 18 records, with both recorded from all but Mexican prairie dogs (Table 2.5). The next most prevalent tick records were of *Ornithodoros parkeri*, with eight records, and *O. turicata* with six records (Table 2.5). *Ixodes kingi* and *I. sculptus* were.

Helminths

Helminths from prairie dogs represent three phyla (Acanthocephala, Nematoda, Platyhelminthes), four classes (Adenophorea, Archiacanthocephala, Cestoda, Secernentea), five orders (Cyclophyllidea, Moniliformida, Trichurida, Spiruria, Strongylida), eight families (Capillariidae, Davaineidae, Hymenolepididae, Moniliformidae, Physalopteridae, Subuluridae, Taeniidae, Trichostrongylidae), and nine genera (*Capillaria*, *Cladotaenia*, *Hymenolepis*, *Moniliformis*, *Physaloptera*, *Raillietina*, *Subulura*, *Trichostrongylus*, *Versteria*). Helminths have been documented only from black-tailed and white-tailed prairie dogs, with twice as many species documented from black-tailed prairie dogs ($n = 8$; Table 2.6). Including six species identified only to genus level, 12 helminth species have been documented from prairie dogs, eight of those from black-tailed prairie dogs, and five from white-tailed prairie dogs (Table 2.6). Only one helminth species, *Physaloptera sp.*, has been documented in both black-tailed and white-tailed prairie dogs (Table 2.6). Three of the helminth species identified only to genus level also have representatives of the genus identified to the species level: *Hymenolepis sp.*,

Physaloptera sp., and *Raillietina* sp. (Table 2.6). *Capillaria* sp., identified from the livers of two white-tailed prairie dogs, was probably *Calodium hepaticum* (Seville and Williams 1989). Of the eight references documenting helminths in prairie dogs, six document helminths from black-tailed prairie dogs, and two document helminths from white-tailed prairie dogs (Table 2.6). The number of records varied from one to three, with three records each for *Physaloptera massino* and *Trichostrongylus texianus*, two each for *Moniliformis clarki*, and *Physaloptera* sp., and one record each for the remaining six species of helminth (Table 2.6).

Protozoa

Protozoa from prairie dogs represent two phyla (Apicomplexa, Sarcomastigophora), two classes (Conoidasida, Lobosa), two orders (Amoebida, Eucoccidiorida), four families (Cryptosporidiidae, Eimeriidae, Entamoebidae, Sarcocystidae), and four genera (*Cryptosporidium*, *Eimeria*, *Entamoeba*, *Sarcocystis*). Fifteen species of protozoa have been isolated from prairie dogs, including 10 species of *Eimeria*, three species of *Cryptosporidium* (including one that could only be identified to genus level), one species of *Sarcocystis*, and one *Entamoeba* (Table 2.7). Protozoa have been documented from only three prairie dog species: black-tailed, white-tailed, and Gunnison's prairie dogs (Table 2.7). Of the 12 references documenting protozoa in prairie dogs, six document protozoa from black-tailed prairie dogs, five document protozoa from white-tailed prairie dogs, and two references document protozoa from Gunnison's prairie dogs. Of the 15 species of protozoa found in prairie dogs, eight (all *Eimeria* sp.) were found in all three species of prairie dogs, one *Eimeria* species was found in both black-tailed and Gunnison's prairie dogs, and the remaining six species of protozoa were found only in one species of prairie dog (5 in black-tailed, and 1 in white-tailed prairie dogs; Table 2.7). The

most commonly encountered protozoan was *Eimeria ludoviciana*, with 15 records, followed by *Eimeria callospermophili* with nine records (Table 2.7).

Bacteria

Bacteria from prairie dogs represent two phyla (Proteobacteria, Spirochaetes), three classes (Alphaproteobacteria, Gammaproteobacteria, Spirochaetes), four orders (Enterobacteriales, Pasteurellales, Rhizobiales, Spirochaetales), four families (Bartonellaceae, Enterobacteriaceae, Leptospiraceae, Pasteurellaceae), and four genera (*Bartonella*, *Leptospira*, *Pasteurella*, *Yersinia*). Five species of bacteria have been isolated from prairie dogs (Table 2.8). Of these, the most commonly encountered bacterium was *Yersinia pestis*, causative agent of plague, with 75 records from 32 references documenting plague in all five prairie dog species (Table 2.8). All five bacterial species have been found in black-tailed prairie dogs, and one species, *Pasteurella multocida*, has also been isolated from Gunnison's prairie dogs (Table 2.8). Of the 38 references documenting bacteria from prairie dogs, 18 document bacteria from black-tailed prairie dogs, 14 document bacteria from Gunnison's prairie dogs, three document bacteria from Utah prairie dogs, and one reference documents bacteria from Mexican prairie dogs. Three references document bacteria (*Y. pestis*) from prairie dogs whose species was not given and could not be determined by geography.

Viruses

Two viruses have been isolated from prairie dogs, *cynomys herpesvirus 1* (CynGHV-1) from a black-tailed prairie dog, and *Rabies lyssavirus* (RABV) from a prairie dog whose species was not given and could not be determined by geography (Table 2.9). *Cynomys herpesvirus 1* is a double-stranded DNA virus in the order Herpesvirales and the family Herpesviridae, while

Rabies lyssavirus is a single-stranded RNA virus in the order Mononegavirales and the family Rhabdoviridae.

Discussion

The importance of parasites in host ecology and evolution has long been recognized (e.g., Elton 1931; Elton *et al.* 1935; Anderson and May 1978; May 1978; Scott and Dobson 1989), but is often underappreciated. For example, interactions between parasites can influence infection and transmission dynamics in ways that can be predicted to some extent (Graham 2008; Lello *et al.* 2018). However, the usefulness of explanatory models of co-infection is reduced when entire groups of parasites, such as bacteria or viruses, are left out (Serrano and Millan 2014). A comprehensive parasite list is a first step toward understanding and predicting the consequences of multi-parasite infections. This research provides a comprehensive review of published host-parasite records for all five prairie dog species, and also reveals a bias in the literature towards ectoparasites and protozoa, with bacteria and viruses nearly undocumented for prairie dogs. This information can be used to inform research priorities, conservation plans, and programs that monitor and predict emerging zoonotic diseases.

Fleas

Fleas are small ectoparasites with piercing-sucking mouthparts that suck the blood of their host (Bush *et al.* 2001). Understanding the flea fauna of prairie dogs is especially important in relation to the plague bacterium, *Yersinia pestis*. More than half of fleas recorded from prairie dogs are capable of transmitting *Y. pestis* (Table 2.13). Different species of fleas are relatively better or worse at vectoring *Y. pestis* (Wheeler and Douglas 1945; Burroughs 1947; Kartman and Prince 1956; Eisen *et al.* 2008; Wilder *et al.* 2008a; Wilder *et al.* 2008b; Eisen *et al.* 2009; Eisen

et al. 2015), but it is important to note that determination of vector competency and vector efficiency can be highly influenced by experimental conditions (Eisen *et al.* 2009).

Included in the plague vector list are *Pulex simulans* and *P. irritans* (Table 2.13). These fleas were synonymized to *P. irritans* in 1908 (Jordan and Rothschild 1908), but the synonymy was challenged by Smit in 1958 (Smit 1958), who pointed out that many records of *P. irritans* are likely to be *P. simulans*. Smit (1958) also points out that *P. simulans* is a flea of colony-forming rodents such as prairie dogs, while *P. irritans* is more commonly found on larger carnivores and humans. Because of this, it may be that most, if not all, records of *P. irritans* from prairie dogs are actually *P. simulans*. Supporting this idea is the fact that, with two exceptions from white-tailed prairie dogs, all records of *P. irritans* on prairie dogs occur prior to 1958, while all records of *P. simulans* occur during or after 1958. Based on this supposition, it appears that all or nearly all records of *P. irritans* and *Pulex* sp. on prairie dogs are *P. simulans*. This is an important distinction in that *P. irritans* is a known plague vector, while *P. simulans* has not officially been tested.

Of all of the groups of parasites, fleas are likely to be the group for which we have near complete information based on the species accumulation curve (Fig. 1.3), number of records (Table 2.2), and the relative ease of isolating fleas. Comparatively, Mexican and Utah prairie dogs have not been nearly as well-sampled as black-tailed, white-tailed, and Gunnison's prairie dogs, but are likely to have fewer flea species overall because of their threatened and endangered status and reduced distribution (Altizer *et al.* 2007; Farrell *et al.* 2015).

Only three rodent species other than prairie dogs have been found on active Mexican prairie dog towns, *Perognathus flavus*, *Dipodomys ordii*, and *D. spectabilis* (Mellink and Madrigal 1993), which may explain, in conjunction with their reduced distribution, the paucity of

flea species found on Mexican prairie dogs. It is possible, that with 55 host-flea records in the literature, we have found all of the fleas there are to be found on Utah prairie dogs. Mexican prairie dogs, on the other hand, with only 10 published records, are likely undersampled, and may reveal additional host-flea records with increased sampling effort.

In general, relationships between prairie dogs and their fleas have been well-studied because of their role in plague dynamics. A Web of Science search for ((plague OR pestis) AND (Cynomys OR "prairie dog") AND (flea OR Siphonaptera)) conducted June 7th, 2018 yielded 100 results spanning the years 1992 – 2018, while the same search in PubMed gave 132 results spanning 1947 – 2018. Most research is focused on elucidating specific dynamics of plague transmission and discovering potential reservoir hosts, species that can carry and transmit *Y. pestis*, but are resistant to the disease. A primary question that remains unanswered is how plague persists between epizootic events.

Lice

Parasitic lice are divided into two informal groups, sucking lice and chewing lice, based on their mouthparts. Chewing lice (suborders Amblycera, Ischnocera, and Rhynchophthirina) infest mammals and birds (Galloway 2018). Sucking lice (suborder Anoplura) are exclusively ectoparasites of mammals (Galloway 2018), and were the only lice recorded from prairie dogs. Bush et al (2001) point out that lice are excellent vectors for bacterial pathogens that cause epidemic typhus (caused by *Rickettsia prowazekii*), trench fever (caused by *Bartonella quintana*), and relapsing fever (caused by *Borrelia* spp.), and are especially important vectors between humans during times of unrest and wars, when people often live in unsanitary, crowded conditions, and go for long periods without changing clothes. We know now that lice can also transmit *Yersinia pestis*, the causative agent of plague (Houhamdi *et al.* 2006), which is not

surprising, considering that *Y. pestis* was isolated from lice collected from marmots as early as 1949 (Link 1949), and was suspected to be a plague vector as early as 1665 (Drancourt *et al.* 2006). Because lice complete their entire life cycle on a single host (Bush *et al.* 2001; Galloway 2018), they are unlikely to be an important component in plague transmission dynamics.

Neohaematopinus sp. found on black-tailed prairie dogs in Texas were said to be “near *citellinus*” (Menzies *et al.* 1951), indicating that this is likely a second species of *Neohaematopinus* found on prairie dogs. An unidentified *Neohaematopinus* sp. was also found on Mexican prairie dogs in northeastern Mexico (Mellink and Madrigal 1993); this may have been the same species found in Texas, as the primary host in Texas, *Spermophilus (Citellus) pilosoma*, the spotted ground squirrel (Menzies *et al.* 1951), has a distribution that extends into parts of Mexico where the Mexican prairie dog is found (Streubel and Fitzgerald 1978). The only other species of *Neohaematopinus* found on prairie dogs, *Neohaematopinus citellinus*, is also found on *Spermophilus pilosoma* in addition to being commonly found on the following species that also have overlapping ranges with prairie dogs: *Ammospermophilus leucurus* (white-tailed antelope squirrel) and *Spermophilus variegatus* (rock squirrel) (Durden and Musser 1994). Only one species of louse, *Linognathoides cynomyis*, has been found exclusively on prairie dogs (Kietzmann 1987; Creekmore *et al.* 2002; Kucera *et al.* 2007). *Enderleinellus suturalis*, *Linognathoides laeviusculus*, and *Neohaematopinus citellinus* are commonly found on ground squirrels (*Ammospermophilus* spp., *Cynomys* spp., *Spermophilus* spp.; Durden and Musser 1994; Sanchez-Montes *et al.* 2013), while *Linognathoides marmotae* is common on marmots (Kim and Adler 1982; Van Vuren 1996; Ford *et al.* 2003), and *Hoplopleura acanthopus* is primarily found on arvicoline rodents (Ford *et al.* 2003; Kucera *et al.* 2007; Sanchez-Montes *et al.* 2013).

Mites

Mites are small arthropods in the class Arachnida that may be either parasitic or free-living (Bush *et al.* 2001). Parasitic mites fall into three groups, order Mesostigmata, order Prostigmata, and order Astigmata, all of which have representatives that parasitize prairie dogs. Mites may be either ectoparasitic, feeding on skin and blood, or endoparasitic, where they infect the respiratory tract. Of the mites that infest prairie dogs, all but one are ectoparasitic; *Pneumocoptes penrosei* is endoparasitic, having been isolated from the lungs of black-tailed prairie dogs in Texas and Nebraska (Baker 1951). Some mites are known to transmit pathogens, but mites that infest prairie dogs are not recognized as vectors for any pathogens.

Only one species of mite, *Echinonyssus neocynomys*, has been found exclusively on prairie dogs (Herrin 1970). All other species of mite recorded from prairie dogs have a fairly wide host range (Whitaker and Wilson 1974; Walters *et al.* 2011). Six mite species appear to be restricted to rodent hosts: *Dermadelema furmani*, *Echinonyssus cynomys*, *E. neotomae*, *Euschoengastia cynomicola*, *E. obesa*, and *Pneumocoptes penrosei* (Whitaker and Wilson 1974; Walters *et al.* 2011). Six species of mite can be found on various mammals: *Brevisterna morlani*, *Cheladonta micheneri*, *Euschoengastia criceticola*, *Euschoengastoides loomisi*, *Haemolaelaps fahrenheitzi*, and *Odontacarus dentatus* (Whitaker and Wilson 1974; Walters *et al.* 2011). Four mite species can be found on various reptiles, birds, and mammals: *Eutrombicula alfreddugesi*, *Hyponeocula arenicola*, *H. montanensis*, and *Parasecia gurneyi* (Walters *et al.* 2011). *Neoschoengastia americana* is found on various birds and small mammals, while *Kayella lacerta* is found on various reptiles and small mammals (Walters *et al.* 2011).

Ticks

Ticks are arthropods in the class Arachnida that are obligate parasites on a variety of terrestrial vertebrates (Bush *et al.* 2001). Ticks fall into two broad groups, the hard ticks, family Ixodidae, and the soft ticks, family Argasidae (Bush *et al.* 2001); members of both groups have been found parasitizing prairie dogs. Both hard ticks and soft ticks are capable of transmitting a variety of pathogens, many of which cause disease in humans. Of the eight species isolated from prairie dogs, three are recognized by the United States Centers for Disease Control (CDC) as vectors of zoonotic pathogens: *Dermacentor andersoni*, which can transmit pathogens that cause Colorado tick fever, Rocky Mountain spotted fever, and tularemia; *Dermacentor variabilis*, which can transmit pathogens that cause Rocky Mountain spotted fever and tularemia; and *Ixodes cookei*, which transmits the pathogen responsible for Powassan disease (Centers for Disease Control and Prevention 2017). This is not to say that other species of ticks found on prairie dogs are not vectors – it is likely some ticks capable of transmitting pathogens have not yet been tested for vectoral capacity, while others may transmit diseases the CDC may not be highly interested in. For example, *Bartonella* species that cause relapsing fever are commonly isolated from *Ornithodoros* ticks (Lopez *et al.* 2016). Ticks have also been shown to be infected with *Bartonella* spp., including a strain closely related to *Bartonella washoensis* (Chang *et al.* 2001), which has been isolated from prairie dogs (Bai *et al.* 2008b) and is known to cause disease in humans (Kosoy *et al.* 2003). *Ornithodoros* ticks can be infected with *Yersinia pestis*, but so far have not been shown to be able to transmit the pathogen (Thomas *et al.* 1990).

In general, ticks have a fairly wide host distribution, with hard ticks favoring specific groups of hosts for each life stage (larva, nymph, adult), and soft ticks tending to parasitize the same host or host family for all life stages (Bush *et al.* 2001; Donaldson *et al.* 2016). Of the hard

ticks found on prairie dogs (*Dermacentor andersoni*, *D. parumapertus*, *D. variabilis*, *Ixodes kingi*, and *I. sculptus*), the *Dermacentor* ticks tend to favor small mammals as larvae and nymphs, and medium to large mammals as adults (Bishopp and Trembley 1945). *Dermacentor parumapertus*, however, is primarily found on rabbits and hares as an adult (Bishopp and Trembley 1945). *Ixodes* ticks prefer small to medium mammals as larvae and nymphs, and medium to large mammals as adults (Bishopp and Trembley 1945). The soft ticks found on prairie dogs have a very wide host range, with *Ornithodoros turicata* found on small to medium mammals, reptiles, and burrowing owls (Donaldson *et al.* 2016), and *O. parkeri* on small mammals and burrowing owls (Davis 1941)

Helminths

Helminths comprise a polyphyletic grouping of parasitic worms that fall into three groups, phylum Platyhelminthes (flatworms), phylum Nematoda (roundworms), and phylum Acanthocephala (thorny-headed worms). In general, the life cycle of parasitic worms involves stages inside the host and stages outside the host; the stage outside the host can involve a free-living form and often involves an alternative host. Most helminth species reported from prairie dogs were Platyhelminthes or Nematoda, and all Platyhelminthes were tapeworms (Table 2.1). Only one thorny-headed worm, *Moniliformis clarki*, was found in prairie dogs.

Tapeworms typically require a minimum of two hosts to complete their life cycle, an intermediate host for the larval stage, and a definitive host for the adult stage (Bush 2001). At least four tapeworm species have been reported from prairie dogs, none of which have been reported from humans. Scott (1931) found two different undescribed species of *Cladotaenia* in the livers of white-tailed prairie dogs in Albany County, Wyoming. *Cladotaenia* have not otherwise been recovered from prairie dogs, but are commonly found in carnivorous birds

(Crozier 1946; Hwang 1961; Kocan and Locke 1974). At least one species of *Cladotaenia* (*Cladotaenia globifera*) was recovered from a prairie falcon (*Falco mexicanus*) in Wyoming, and the authors speculated that the infection resulted from ingesting immature forms with a ground squirrel (Croft and Kingston 1975). Seville and Williams (1989) found the tapeworm *Versteria mustelae* in white-tailed prairie dogs from the same town that the last wild black-footed ferrets were recovered from; *Versteria mustelae* was recovered from black-footed ferrets in 1990 (Rockett *et al.* 1990). Rodents (e.g., Kinsella 1968; Zenchak and Hall 1971) and mustelids (e.g., Barber and Lockard 1973; Rockett *et al.* 1990) are commonly infected with *V. mustelae*, with rodents as intermediate hosts and mustelids as definitive hosts (Rockett *et al.* 1990). Seville and Williams (1989) also found *Raillietina salmoni* in white-tailed prairie dogs; *R. salmoni* commonly infects rabbits and hares (Andrews *et al.* 1980; Pfaffenberger and Valencia 1988). Buscher and Tyler (1975) note that the unknown species of *Raillietina* they recovered from a prairie dog and several desert cottontails (*Sylvilagus audubonii*) in two locations in Oklahoma was not *Raillietina salmoni*, and was likely an accidental infection in the prairie dog, as the cestode was malformed, indicating developmental abnormalities within the host. *Hymenolepis citelli* was found in four white-tailed prairie dogs in Wyoming (Seville and Williams 1989), while *Hymenolepis* sp. was found in three black-tailed prairie dogs in Colorado (Hall 1912). *Hymenolepis citelli* is commonly found in ground squirrels (e.g., Buscher and Tyler 1975; Broda and Schmidt 1978; Shults and Stanton 1987; Wilber *et al.* 1996; Ubelaker *et al.* 2010) and other rodents (e.g., Simpson and Harmon 1968; Pfaffenberger *et al.* 1985), and uses beetles in the genus *Tenebrio* and *Tribolium* as intermediate hosts (Voge 1956).

Nematode life cycles are quite variable, with some releasing eggs into the environment, others releasing larvae, and some having one or more intermediate or paratenic hosts (Bush

2001). At least four nematode species have been reported from prairie dogs (Table 2.1). Seville and Williams (1989) noted that the *Calodium* sp. they found in the livers of two white-tailed prairie dogs was probably *C. hepaticum*, which has also been found in a zoo population of prairie dogs (Landolfi *et al.* 2003). *Calodium hepaticum* infects the liver of its host, and has been found in humans, though not commonly (McQuown 1954). In the United States, *C. hepaticum* more often infects rodents of many species (McQuown 1954; Rausch 1961; Fuehrer 2014b; a), and requires only one host to complete its life cycle (Centers for Disease Control and Prevention 2012). Other nematodes found in prairie dogs include *Trichostrongylus texianus* (Dikmans 1937; Rodenberg and Pence 1978), *Subulura* sp. (Pfaffenberger *et al.* 1984), *Physaloptera massino* (Vetterling 1962), and *Physaloptera* sp. (Hall 1912; Seville and Williams 1989). The only records of *Trichostrongylus texianus* are from black-tailed prairie dogs in Texas. *Physaloptera massino*, on the other hand, has also been reported from ground and tree squirrels (Morgan 1941a; Morgan 1941b; Morgan 1943; Broda and Schmidt 1978; Coyner *et al.* 1996; Ubelaker *et al.* 2010). An unknown species of *Subulura* was recovered from two black-tailed prairie dogs in Roosevelt County, New Mexico; *S. novomexicanus* has since been described from ground squirrels in nearby Socorro County, New Mexico (Ubelaker *et al.* 2007; Ubelaker *et al.* 2010).

Thorny-headed worms have an indirect life cycle that involves an invertebrate intermediate host for the larvae and a vertebrate definitive host for the adult stage, and occasionally a paratenic host (Bush 2001). Only a single species of thorny-headed worm, *Moniliformis clarki*, has been recovered from prairie dogs. *Moniliformis clarki* is commonly found in ground squirrels and other rodents (Ubelaker and Pearse 1967), and utilizes camel crickets as an intermediate host (Crook and Grundmann 1964; Grundmann and Crook 1966).

At least two other studies looked for helminths in prairie dogs, but did not find any. McKenna et al (1977) found unidentified nematode eggs that resembled hookworm eggs, but failed to find any adult or larval helminths after an examination of the internal organs of several black-tailed prairie dogs. Mellink and Madrigal (1993) found two cestodes and one oxyurid in Mexican prairie dogs, but they could not be identified. No helminths have been reported from prairie dogs since 1993.

Protozoa

Protozoans are a polyphyletic group of single-celled eukaryotes. All but one of the protozoan parasites that infect prairie dogs belong to phylum Apicomplexa, intracellular parasites that infect their host via resistant oocysts released into the environment or transferred via an intermediate host (Bush *et al.* 2001). One protozoan parasite infecting prairie dogs, *Entamoeba muris* (phylum Sarcomastigophora) also releases resistant cysts into the environment with the feces (Neal 1950), but remains extracellular inside the host (Lin 1971). Both groups parasitize the gastrointestinal tract of the host, typically causing an acute infection that, in extreme cases, can lead to severe diarrhea, resulting in dehydration and even death, but often results in a benign infection with little if any symptoms (Neal 1950; Seville *et al.* 1992; Bush *et al.* 2001).

Most protozoan prairie dog parasites belong to the genus *Eimeria*, infection with which rarely causes outward symptoms (Seville *et al.* 1992). The immune system likely eliminates *Eimeria* infections relatively quickly under normal circumstances, possibly resulting in resistance to future infections by the same species, though the length of protection may vary according to host age and occurrence of ‘booster’ challenges (Rose 1987). Long-lasting immunity may explain, in part, why juvenile prairie dogs are more likely to be infected with

Eimeria compared to adult prairie dogs (Michael Antolin and David Eads, personal communication March 2012).

Bacteria

Bacteria recorded from prairie dogs are all gram-negative intracellular bacteria capable of infecting humans (Chikeka and Dumler 2015). Of the four species isolated from prairie dogs (Table 2.8), the most well-known is the flea-vectored plague bacterium, *Yersinia pestis*. Plague has been one of the primary causes of prairie dog declines, with colony mortality rates typically >95%, and extinctions of entire colonies not unusual (Cully and Williams 2001; Antolin *et al.* 2002). Efforts are currently underway to develop a plague vaccine for prairie dogs in order to provide protection for reintroduced black-footed ferrets, obligate prairie dog predators that are highly susceptible to plague (Salkeld 2017). Plague transmission dynamics just before and during prairie dog die-offs have become increasingly well-understood over the past decade, but plague persistence between outbreaks remains enigmatic (reviewed in Salkeld *et al.* 2016). A better understanding of parasite communities in plague-affected areas could shed light on plague transmission and persistence.

Bartonella is transmitted by fleas, frequently isolated from rodents and other animals, and capable of causing disease in humans (reviewed in Bai *et al.* 2008b). First isolated from black-tailed prairie dogs in 2001 (Stevenson *et al.* 2003), it does not appear to cause overt symptoms, but its effect on prairie dog fitness has not yet been evaluated. Just one species, *Bartonella washoensis*, has been isolated from black-tailed prairie dogs and their fleas.

Pasteurella multocida and *Leptospira interrogans* have been reported from just one study each, despite being widespread zoonotic pathogens. Montiel-Arteaga (2015) isolated serovar-specific antibodies to *L. interrogans* from black-tailed prairie dogs Mexico (serovars Bratislava,

Canicola, Celledoni, and Tarassovi). Unfortunately they could not make a positive species identification (i.e., culture, PCR), because of practical challenges related to the tests (e.g., obtaining urine specimens from prairie dogs; Montiel-Arteaga *et al.* 2015).

Quan *et al.* (1979) suggested *P. multocida* was an opportunistic pathogen of mammals, observing that its pathogenicity appeared to coincide with plague outbreaks. A similar observation has been made about *Eimeria* (Foust 2007). *Yersinia pestis* upregulates the anti-inflammatory cytokine interleukin-10 (Nedialkov *et al.* 1997; Sing *et al.* 2002) and down-regulates the pro-inflammatory cytokine interferon-gamma (Gendrin *et al.* 2010). Manipulation of the inflammatory response by *Y. pestis* may explain the unusual pathogenicity of a normally benign infection (Price *et al.* 2012).

Viruses

Just two viruses have been described from prairie dogs (Table 2.9), one of which (*Rabies lyssavirus*) probably represents a spillover event, since it is well-monitored, and has only been recorded once in prairie dogs. The other virus, newly described as cynomys herpesvirus 1, was cultured in 2003 from a partially scavenged prairie dog presented to the Wyoming State Veterinary Laboratory. The prairie dog had died of an unidentified bacterial infection (tests for chlamydia, plague, and tularemia were negative), and had no outward signs of a viral infection. Nagamine *et al.* (2011) tested serum samples from 100 additional black- and white-tailed prairie dogs, but were unable to detect antibodies, so it is unclear if this virus routinely infects prairie dogs.

Viruses are a major source of evolutionary pressure for all life forms, not only through the evolutionary arms race between genes of the immune system and viral genes, but also as a source of novel genes in eukaryotic genomes (Forterre and Prangishvili 2009; Koonin and Dolja

2013; Nasir *et al.* 2014). With only two published records, viruses are almost certainly under-sampled given that at least 1168 viruses are known to infect animals (Nasir *et al.* 2014), with new viruses discovered every year (Rosenberg 2015). According to one estimate, every mammal species is expected to host, on average, 58 unique viruses (Anthony *et al.* 2013). Until recently, virus discovery has relied on cell culture or animal passage (Drewes *et al.* 2017), techniques that most wildlife researchers are not familiar with. Rapid advances in molecular techniques have made virus discovery in wild rodents (and other wildlife) more accessible, but so far research has been heavily biased in favor of just two families, Muridae and Cricetidae (reviewed in Drewes *et al.* 2017).

Other parasites

Two parasites prairie dogs are said to carry, but for which I could find no suitable published records are *Giardia* sp. and *Francisella tularensis*. I know through personal communication with M. Antolin and L. Ballweber that *Giardia* sp. has been identified from black-tailed prairie dogs on Pawnee National Grassland, Colorado, but these results have not yet been published. I repeated a variation of my original search ((*Cynomys* OR “prairie dog”) AND *Giardia*) in Web of Science, Zoological Record, PubMed, and Google Scholar on June 7, 2018, and found no records of *Giardia* sp. from wild prairie dogs.

Francisella tularensis, a tick-vectored bacterium that causes tularemia, is widely cited as being found in prairie dogs, but in every published instance I have found, the claim is either not cited, cites one or more cases from captive prairie dogs (e.g., Avashia *et al.* 2004), or cites a study from 1935 by Davis that showed wild-caught white-tailed prairie dogs to be highly susceptible to infection after being injected with a suspension of *F. tularensis* (syn. *Bacterium tularense*); all seven prairie dogs died within eight days of infection (Davis 1935). Davis (1935)

did show, by injecting a ground slurry into a guinea pig, that lice found on the same prairie dogs were infected with *F. tularensis*, but did not test the prairie dogs prior to purposefully infecting them. The other frequently cited reference, by Avashia et al (2004), may actually represent an instance of *F. tularensis* from wild prairie dogs. In that case, wild-caught black-tailed prairie dogs had been housed in an exotic pet distribution center in Texas for up to 2.5 months before approximately 250 prairie dogs died during a tularemia outbreak. The crowded facility had many free-roaming animals (including some prairie dogs), and prairie dogs were housed in 5 ft diameter open-top bins with 2.5 ft walls. In the six months previous to the outbreak, approximately 3600 prairie dogs had been transiently housed at the facility with only 25 deaths during that time. Additionally, prairie dogs collected from the trappers who originally supplied the prairie dogs all tested negative for tularemia (Avashia *et al.* 2004). Based on the information in the article, I decided not to record this as an instance of *F. tularensis* in wild prairie dogs because there was no way to know if prairie dogs were infected prior to arriving at the facility.

Another possibly valid report of tularemia in wild prairie dogs comes from a reference in a Public Health Report (Francis 1937) to *B. tularensis* (syn. *F. tularensis*) being isolated from a prairie dog in Utah, but no further information (e.g., locality, date) is given. Hubbard (1947, p.24) and Wiseman (1949) both make reference to a 1941 study in Carbon County, Wyoming where 43 fleas taken from 24 prairie dogs were able to infect guinea pigs, but it does not appear the prairie dogs were tested, and no reference is given. Most recently, a web page for Devils Tower National Monument, Wyoming states that tularemia was isolated from prairie dogs (Stimson 2015), but this information has not yet been published, and so was not included in the host-parasite records listed in this research. Lastly, a Colorado state government report (Seglund and Schnurr 2010) contains the following statement:

Most observations suggest that when tularemia is found within a colony, die-offs occur at small localized sites and do not spread throughout a colony or area (D. Biggins, USGS, personal communication 2007). In addition, tularemia is transmitted by ticks. Researchers that work with prairie dogs report finding few ticks on individuals, suggesting that ticks may not be an adequate vector to transmit the disease across large areas (D. Biggins, USGS, personal communication, 2007).

Lack of verifiable records of *Francisella tularensis* in prairie dogs appears to be a clear case of under-reporting, and also calls attention to the fact that government offices tasked with monitoring wildlife disease may not prioritize publishing parasite records, especially in cases where the infection seems unremarkable to them. In future, similar parasite reviews should include communication with appropriate government agencies in order to reduce bias associated with under-reporting in published literature.

Summary and Conclusions

With this research I have provided the first comprehensive review of parasites for the genus *Cynomys*, which includes five prairie dog species: black-tailed (*Cynomys ludovicianus*), Gunnison's (*C. gunnisoni*), Mexican (*C. mexicanus*), Utah (*C. parvidens*), and white-tailed (*C. leucurus*). From 160 references I documented 841 host-parasite records accounting for 116 parasite species (including 12 identified to genus only *and* for which there was also a species record). Forty-eight parasite species were found just once, with collection dates spanning 1912 – 2015. Analyses suggested flea species have been well-sampled enough that we are either close to or have found all flea species parasitizing prairie dogs. Conversely, if *Yersinia pestis* is excluded, bacteria have only been documented for black-tailed and Gunnison's prairie dogs. Likewise, a single record of a single virus species exists for black-tailed prairie dogs, with one other virus documented from a single unknown species of prairie dog in Wyoming. The almost complete lack of virus and bacterial species is likely a result of inadequate sampling effort for those

groups. The number of records for each prairie dog species was correlated with the extent of their occupied habitat, suggesting smaller host range plays a role in limiting the number of parasites a host species will have.

There is little doubt that prairie dogs are host to more parasites than have been described. Bacteria and viruses have been especially neglected, probably because identification can be more challenging than for many other parasites. The paucity of bacterial and viral species appears to be a function of sampling bias (i.e., few researchers are looking for bacteria and viruses in prairie dogs), although it is difficult to know this for certain, since negative results are so rarely published (Csada *et al.* 1996). On the other hand, it is likely that some of the parasites reported here resulted from occasional spillover from other hosts, and are not true parasites of prairie dogs. Without further research, it is difficult to know whether parasite species with few records are transient infections, or true prairie dog parasites that are under-reported or under-sampled. In some cases under-sampling reflects a lack of effort (e.g., viruses and bacteria), but can also be the result of biological traits of the parasite (e.g., size, geographical range, seasonality), or sampling method (e.g., capture/release vs. necropsy; Gaston 1991; Medellin and Soberon 1999; Cabrero-Sanudo and Lobo 2003; Collen *et al.* 2004; Krasnov *et al.* 2005b; Poulin and Mouillot 2005; Cook *et al.* 2016).

For studies documenting host-parasite relationships or interested in preserving parasite diversity, this research provides an indication of where additional effort would provide the biggest gains. Clearly bacteria and viruses will yield rewards in terms of new host records, or even new species records. Since most emerging human pathogens are zoonotic viruses (Carroll *et al.* 2018), effort in this area may also help protect human health. The very recent discoveries of *Cryptosporidium* and *Giardia* in prairie dogs suggest we should also not overlook protozoan

parasites. A good first step would be to add prairie dogs to the National Ecological Observatory Network (NEON) rodent-borne parasite sampling effort (Cook *et al.* 2016; Springer *et al.* 2016). Additionally, documenting host-parasite relationships for other species that inhabit prairie dog towns, especially other small mammals likely to share parasite species with prairie dogs, will give us a more complete picture of possible transmission networks (Rigaud *et al.* 2010), which could inform black-footed ferret recovery efforts, help with managing declining populations of prairie dogs, and possibly provide insight into inter-epizootic plague dynamics.

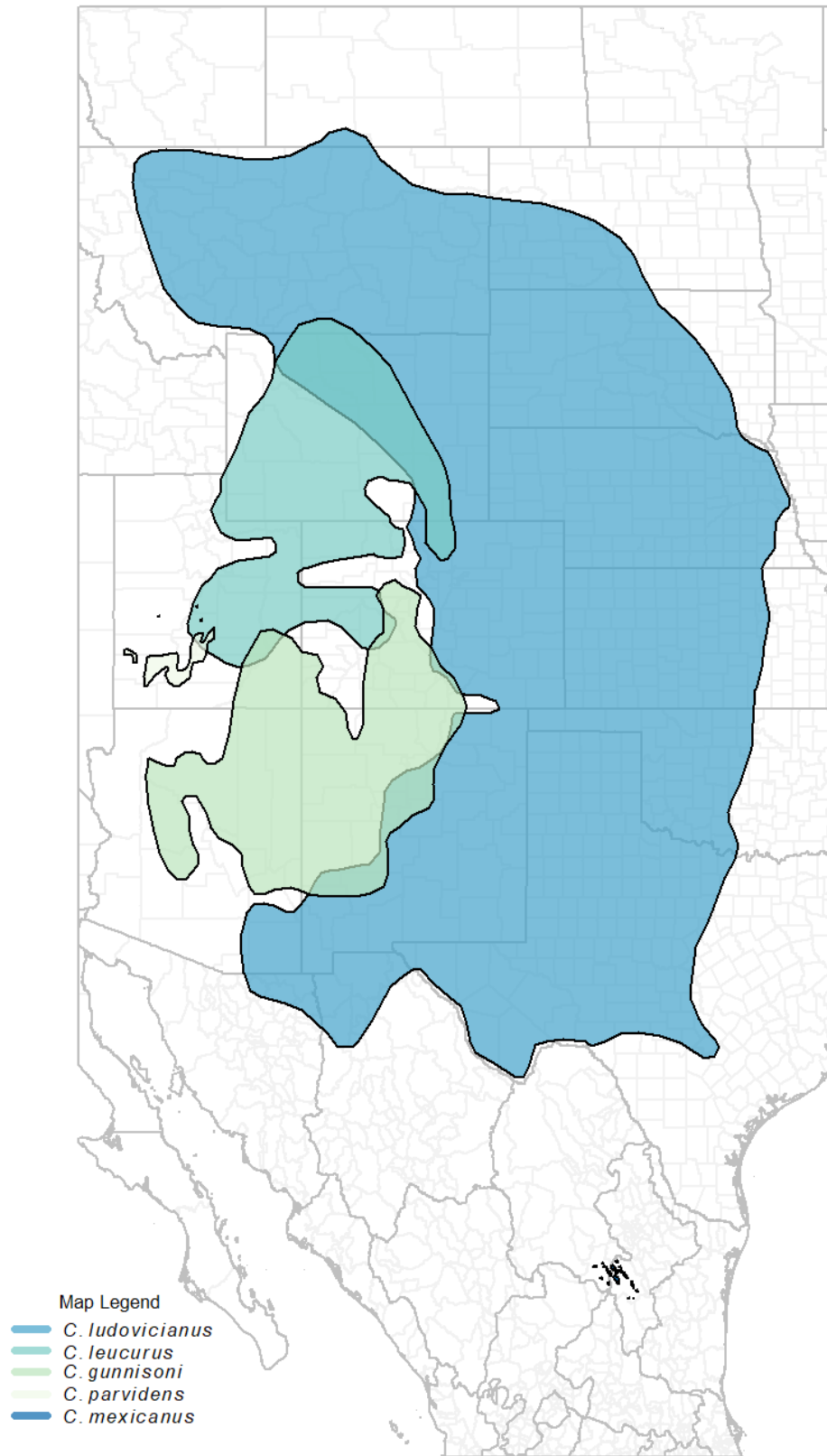


Figure 2.1 Prairie dog (*Cynomys* spp.) distributions. Recreated from spatial data downloaded from the website for the International Union of Conservation and Nature Red List of Threatened Species (IUCN 2017).

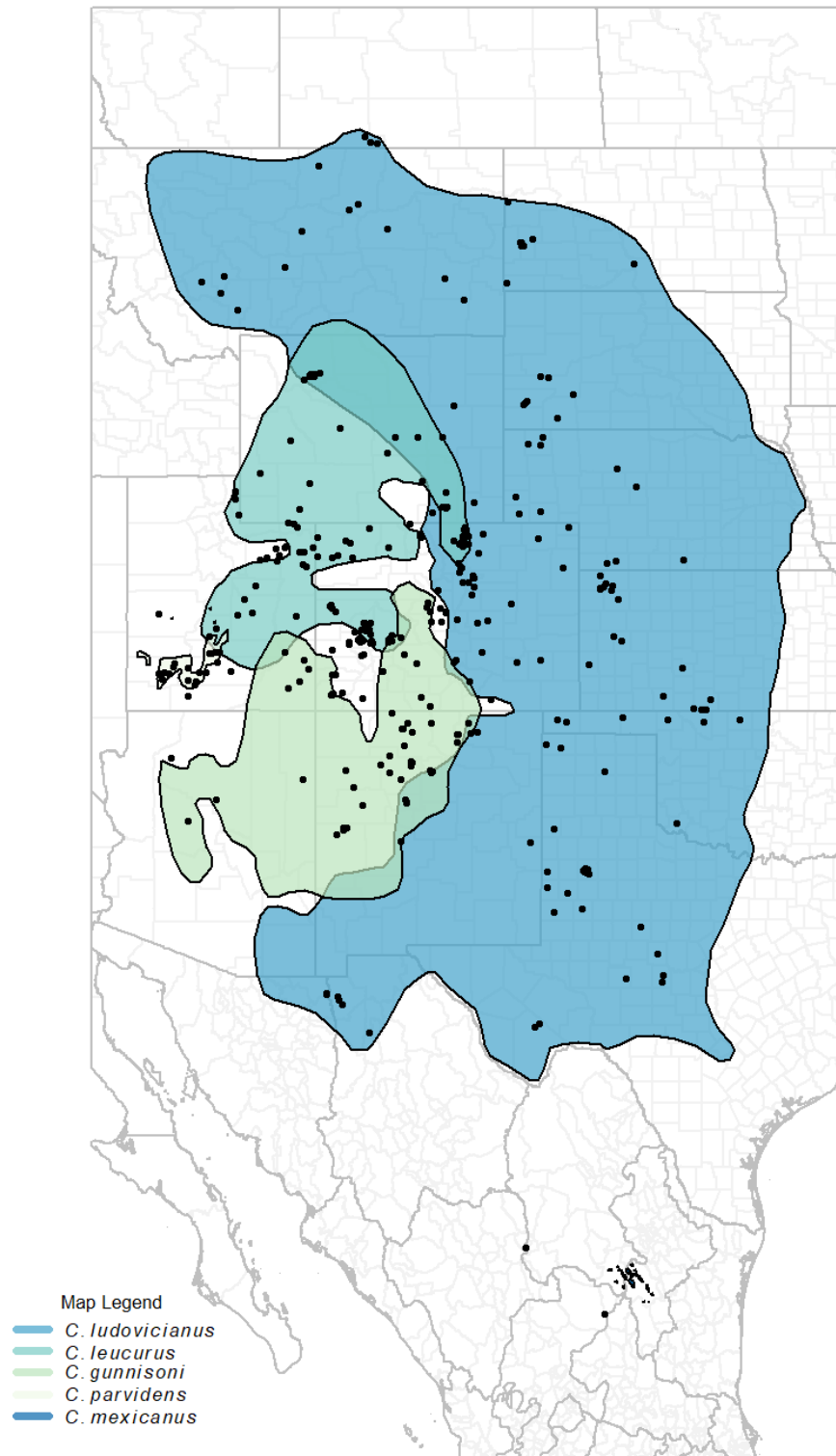


Figure 2.2 Locations (black points) of 846 host-parasite records from 160 published references shown with IUCN distributions of all five prairie dog species. Points vary in their level of geographic precision from the exact location, to the center point of a county. Records that only indicated the state the sample came from are not shown on the map. Prairie dog ranges have been recreated from spatial data downloaded from the website for the International Union of Conservation and Nature Red List of Threatened Species (IUCN 2016).

Table 2.2 All parasite species recorded from prairie dogs, including the country and locality where they were found, grouped by family within orders.

Parasite species	Country	State-county	Reference
FLEAS - Arthropoda, Insecta, Siphonaptera			
Ceratophyllidae			
<i>Aetheca wagneri</i>	USA	UT-emery	Stark 1958
<i>A. wagneri</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>Ceratophyllus vison</i>	USA	NM-colfax	Cully et al 1997
<i>Eumolpianus eumolpi americanus</i>	USA	NM-sandoval	Haas et al 1973
<i>Foxella ignota apachina</i>	USA	AZ-apache	Fox 1914
<i>Megabothris abantis</i>	USA	NM-sandoval	Haas et al 1973
<i>Orchopeas sexdentatus</i>	USA	TX	Cox 1950, Miles et al 1952
<i>Oropsylla bacchi</i>	USA	NM-colfax	Cully et al 1997
<i>O. bruneri</i>	USA	ND-mckenzie	McKenna et al 1977
<i>O. hirsuta</i>	MEX	CHH	Fernandez-Gonzalez et al 2016
<i>O. hirsuta</i>	MEX	COA	Trevino-Villarreal et al 1998
<i>O. hirsuta</i>	USA	AZ-apache	Hubbard 1968
<i>O. hirsuta</i>	USA	AZ-coconino	Crane 2011
<i>O. hirsuta</i>	USA	CO	Hall 1912
<i>O. hirsuta</i>	USA	CO-adams	Karhu and Anderson 2000, Seery et al 2003
<i>O. hirsuta</i>	USA	CO-boulder	Brinkerhoff et al 2006, Brinkerhoff et al 2011, Jones et al 2010
<i>O. hirsuta</i>	USA	CO-conejos	Hubbard 1968
<i>O. hirsuta</i>	USA	CO-delta	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-el paso	Hall 1912
<i>O. hirsuta</i>	USA	CO-elbert	Hall 1912
<i>O. hirsuta</i>	USA	CO-gunnison	Johnson 1962, Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-jackson	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-larimer	Baker 1895, Karami 1981, Maupin 1970
<i>O. hirsuta</i>	USA	CO-mesa	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-moffat	Pizzimenti 1975, Tripp et al 2016
<i>O. hirsuta</i>	USA	CO-montezuma	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-montrose	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-ouray	Pizzimenti 1975
<i>O. hirsuta</i>	USA	CO-park	Ecke and Johnson 1950, Fitzgerald 1970
<i>O. hirsuta</i>	USA	CO-weld	Franklin et al 2010, Tripp 2009
<i>O. hirsuta</i>	USA	KS-hamilton	Poorbaugh and Gier 1961
<i>O. hirsuta</i>	USA	KS-rawlins	PHR 65:39 1950
<i>O. hirsuta</i>	USA	MT-broadwater	Jellison 1939

Parasite species	Country	State-county	Reference
<i>O. hirsuta</i>	USA	MT-jefferson	Jellison and Kohls 1936
<i>O. hirsuta</i>	USA	MT-phillips	Holmes 2003
<i>O. hirsuta</i>	USA	ND-billings	McKenna et al 1977
<i>O. hirsuta</i>	USA	ND-mckenzie	McKenna et al 1977
<i>O. hirsuta</i>	USA	ND-morton	McKenna et al 1977
<i>O. hirsuta</i>	USA	NE-banner	Gates 1945
<i>O. hirsuta</i>	USA	NE-cherry	Gates 1945
<i>O. hirsuta</i>	USA	NE-cheyenne	Rapp and Gates 1957
<i>O. hirsuta</i>	USA	NE-dawes	Gates 1945, Hubbard 1968, Rapp and Gates 1957
<i>O. hirsuta</i>	USA	NE-harlan	Gates 1945
<i>O. hirsuta</i>	USA	NM-catron	Hubbard 1968
<i>O. hirsuta</i>	USA	NM-cibola	Crane 2011
<i>O. hirsuta</i>	USA	NM-colfax	Crane 2011, Cully et al 1997, Eads et al 2013, Eads et al 2015
<i>O. hirsuta</i>	USA	NM-colfax	O'Connor and Pfaffenberger 1987
<i>O. hirsuta</i>	USA	NM-mckinley	Hubbard 1968
<i>O. hirsuta</i>	USA	NM-rio arriba	Crane 2011, Link 1949
<i>O. hirsuta</i>	USA	NM-roosevelt	Pfaffenberger et al 1984
<i>O. hirsuta</i>	USA	NM-sandoval	Crane 2011, Friggens et al 2010, Haas et al 1973
<i>O. hirsuta</i>	USA	NM-santa fe	Crane 2011, Holdenried and Morlan 1956, Morlan 1955
<i>O. hirsuta</i>	USA	OK-cimarron	Tyler and Buscher 1975
<i>O. hirsuta</i>	USA	OK-grant	Tyler and Buscher 1975
<i>O. hirsuta</i>	USA	OK-harper	Tyler and Buscher 1975
<i>O. hirsuta</i>	USA	OK-texas	Pizzimenti 1975
<i>O. hirsuta</i>	USA	OK-woods	Tyler and Buscher 1975
<i>O. hirsuta</i>	USA	SD-custer	Easton 1982, King 1955
<i>O. hirsuta</i>	USA	SD-pennington	Creekmore et al 2002, Easton 1982, Kietzmann 1987
<i>O. hirsuta</i>	USA	SD-shannon	Larson et al 2011
<i>O. hirsuta</i>	USA	TX	Miles et al 1952
<i>O. hirsuta</i>	USA	TX-brewster	Pizzimenti 1975
<i>O. hirsuta</i>	USA	TX-dallam	PHR 65:44 1950
<i>O. hirsuta</i>	USA	TX-hutchinson	Hightower and Eads 1951
<i>O. hirsuta</i>	USA	TX-lubbock	Nascarella et al 2005
<i>O. hirsuta</i>	USA	TX-pecos	Pizzimenti 1975
<i>O. hirsuta</i>	USA	unknown	Engelthaler and Gage 2000
<i>O. hirsuta</i>	USA	UT-carbon	Stark 1958
<i>O. hirsuta</i>	USA	UT-daggett	Stark 1958
<i>O. hirsuta</i>	USA	UT-duchesne	Stanford 1944, Stark 1958

Parasite species	Country	State-county	Reference
<i>O. hirsuta</i>	USA	UT-emery	Stark 1958
<i>O. hirsuta</i>	USA	UT-garfield	Jachowski et al 2012, Standford 1944, Stark 1958
<i>O. hirsuta</i>	USA	UT-iron	Jachowski et al 2012, Pizzimenti 1975, Stark 1958
<i>O. hirsuta</i>	USA	UT-kane	Stark 1958
<i>O. hirsuta</i>	USA	UT-millard	Stark 1958
<i>O. hirsuta</i>	USA	UT-rich	Stark 1958
<i>O. hirsuta</i>	USA	UT-san juan	Stanford 1944, Stark 1958
<i>O. hirsuta</i>	USA	UT-sevier	Stark 1958
<i>O. hirsuta</i>	USA	UT-uintah	Stark 1958
<i>O. hirsuta</i>	USA	UT-wayne	Jachowski et al 2012, Pizzimenti 1975, Stark 1958
<i>O. hirsuta</i>	USA	WY-albany	Wiseman 1955
<i>O. hirsuta</i>	USA	WY-lincoln	Hubbard 1968
<i>O. hirsuta</i>	USA	WY-sweetwater	Wiseman 1955
<i>O.idahoensis</i>	USA	CO-conejos	Jellison 1945
<i>O.idahoensis</i>	USA	CO-moffat	Hubbard 1968
<i>O.idahoensis</i>	USA	CO-park	Eads 1949, Ecke and Johnson 1950, Jellison 1945, McCampbell 1931
<i>O.idahoensis</i>	USA	CO-saguache	Lechleitner et al 1968
<i>O.idahoensis</i>	USA	NM-colfax	O'Connor and Pfaffenberger 1987
<i>O.idahoensis</i>	USA	NM-sandoval	Friggins et al 2010, Haas et al 1973
<i>O.idahoensis</i>	USA	UT-sevier	Stark 1958
<i>O.idahoensis</i>	USA	WY-albany	Wiseman 1955
<i>O.idahoensis</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>O. labis</i>	CAN	SK	Holland 1949
<i>O. labis</i>	USA	CO-moffat	McCampbell 1931
<i>O. labis</i>	USA	CO-park	Ecke and Johnson 1950, Fitzgerald 1970, Hubbard 1968, McCampbell 1931
<i>O. labis</i>	USA	CO-saguache	Lechleitner et al 1968
<i>O. labis</i>	USA	MT-fergus	Hubbard 1968
<i>O. labis</i>	USA	NM-colfax	Cully et al 1997
<i>O. labis</i>	USA	UT-garfield	Jachowski et al 2012
<i>O. labis</i>	USA	UT-iron	Jachowski et al 2012
<i>O. labis</i>	USA	UT-wayne	Jachowski et al 2012, Pizzimenti 1975

Parasite species	Country	State-county	Reference
<i>O. labis</i>	USA	WY-albany	Hubbard 1968, Jellison 1939, Wiseman 1955
<i>O. labis</i>	USA	WY-carbon	Wiseman 1955
<i>O. labis</i>	USA	WY-laramie	Hubbard 1968, Jellison 1939
<i>O. labis</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>O. labis</i>	USA	WY-sweetwater	Ho 1962
<i>O. montana</i>	USA	CO-gunnison	Johnson 1962
<i>O. montana</i>	USA	CO-larimer	McC Campbell 1931
<i>O. montana</i>	USA	NM-sandoval	Haas et al 1973
<i>O. montana</i>	USA	UT-garfield	Jachowski et al 2012
<i>O. montana</i>	USA	UT-iron	Jachowski et al 2012
<i>O. montana</i>	USA	UT-san juan	Stark 1958
<i>O. montana</i>	USA	UT-wayne	Jachowski et al 2012
<i>O. rupestris</i>	CAN	SK	Holland 1949
<i>O. rupestris</i>	USA	MT-jefferson	Hubbard 1968
<i>O. tuberculata</i>	USA	CO-larimer	Maupin 1970, McC Campbell 1931
<i>O. tuberculata</i>	USA	CO-moffat	McC Campbell 1931
<i>O. tuberculata</i>	USA	CO-park	Eads 1949, Fitzgerald 1970, McC Campbell 1931
<i>O. tuberculata</i>	USA	CO-saguache	Lechleitner et al 1968
<i>O. tuberculata</i>	USA	MT-phillips	Holmes 2003
<i>O. tuberculata</i>	USA	NM-sandoval	Haas et al 1973
<i>O. tuberculata cynomuris</i>	USA	CO-adams	Karhu and Anderson 2000
<i>O. t. cynomuris</i>	USA	CO-boulder	Brinkerhoff et al 2006, Jones et al 2010
<i>O. t. cynomuris</i>	USA	CO-conejos	Jellison 1939
<i>O. t. cynomuris</i>	USA	CO-moffat	Tripp et al 2016
<i>O. t. cynomuris</i>	USA	CO-park	Ecke and Johnson 1950
<i>O. t. cynomuris</i>	USA	CO-weld	Tripp et al 2009
<i>O. t. cynomuris</i>	USA	MT-broadwater	Jellison 1939
<i>O. t. cynomuris</i>	USA	MT-custer	Jellison 1939
<i>O. t. cynomuris</i>	USA	ND-billings	McKenna et al 1977
<i>O. t. cynomuris</i>	USA	NM-colfax	Cully et al 1997
<i>O. t. cynomuris</i>	USA	NM-rio arriba	Link 1949
<i>O. t. cynomuris</i>	USA	NM-sandoval	Friggins et al 2010
<i>O. t. cynomuris</i>	USA	NM-santa fe	Morlan 1955
<i>O. t. cynomuris</i>	USA	SD-custer	Easton 1982
<i>O. t. cynomuris</i>	USA	SD-pennington	Easton 1982, Kietzmann 1987
<i>O. t. cynomuris</i>	USA	unknown	Engelthaler and Gage 2000
<i>O. t. cynomuris</i>	USA	UT-garfield	Jachowski et al 2012, Stark 1958

Parasite species	Country	State-county	Reference
<i>O. t. cynomuris</i>	USA	UT-iron	Jachowski et al 2012, Stark 1958
<i>O. t. cynomuris</i>	USA	UT-sevier	Stark 1958
<i>O. t. cynomuris</i>	USA	UT-wayne	Jachowski et al 2012
<i>O. t. cynomuris</i>	USA	WY-albany	Jellison 1939, Wiseman 1955
<i>O. t. cynomuris</i>	USA	WY-carbon	Wiseman 1955
<i>O. t. cynomuris</i>	USA	WY-fremont	Wiseman 1955
<i>O. t. cynomuris</i>	USA	WY-laramie	Jellison 1939
<i>O. t. cynomuris</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>O. t. ornata</i>	USA	CO-saguache	Fox 1940
<i>O. t. ornata</i>	USA	NM-colfax	O'Connor and Pfaffenberger 1987
<i>O. t. tuberculata</i>	CAN	SK	Holland 1949
<i>O. t. tuberculata</i>	USA	CO-delta	Pizzimenti 1975
<i>O. t. tuberculata</i>	USA	CO-gunnison	Pizzimenti 1975
<i>O. t. tuberculata</i>	USA	CO-moffat	Pizzimenti 1975
<i>O. t. tuberculata</i>	USA	CO-montrose	Pizzimenti 1975
<i>O. t. tuberculata</i>	USA	NE-cheyenne	Rapp and Gates 1957
<i>O. t. tuberculata</i>	USA	NE-dawes	Rapp and Gates 1957
<i>O. t. tuberculata</i>	USA	NE-kimball	Rapp and Gates 1957
<i>O. t. tuberculata</i>	USA	NM-sandoval	Friggins et al 2010
<i>O. t. tuberculata</i>	USA	NM-santa fe	Holdenried and Morlan 1956
<i>O. t. tuberculata</i>	USA	UT-emery	Stark 1958
<i>O. t. tuberculata</i>	USA	UT-rich	Stark 1958
<i>O. t. tuberculata</i>	USA	WY-park	Heller 1991
<i>Oropsylla</i> sp.	USA	MT-phillips	Holmes 2003
<i>Oropsylla</i> sp.	USA	UT-san juan	Stanford 1944
<i>Oropsylla</i> sp.	USA	WY-park	Heller 1991
<i>Thrassis acamantis</i>	USA	unknown	Stark 1970
<i>T. bacchi</i>	CAN	SK	Holland 1949
<i>T. bacchi</i>	USA	UT-garfield	Stark 1958
<i>T. bacchi</i>	USA	UT-san juan	Stark 1958
<i>T. bacchi consimilis</i>	USA	UT-san juan	Stark 1957
<i>T. fatus</i>	MEX	COA	Trevino-Villarreal et al 1998
<i>T. fatus</i>	USA	CO-adams	Seery et al 2003
<i>T. fatus</i>	USA	CO-weld	Tripp et al 2009
<i>T. fatus</i>	USA	ND-morton	McKenna et al 1977
<i>T. francisi</i>	USA	UT-duchesne	Stark 1958
<i>T. francisi</i>	USA	UT-emery	Stark 1958
<i>T. francisi</i>	USA	UT-garfield	Biggins et al 2010, Jachowski et al 2012, Stark 1958

Parasite species	Country	State-county	Reference
<i>T. francisi</i>	USA	UT-iron	Jachowski et al 2012, Stark 1958
<i>T. francisi</i>	USA	UT-rich	Stark 1958
<i>T. francisi</i>	USA	UT-sevier	Jellison and Good 1942, Stark 1958
<i>T. francisi</i>	USA	UT-wayne	Jachowski et al 2012, Pizzimenti 1975
<i>T. francisi</i>	USA	WY-albany	Wiseman 1955
<i>T. howelli utahensis</i>	USA	MT-fergus	Hubbard 1968
<i>T. pandorae</i>	USA	UT-daggett	Stark 1958
<i>T. pandorae</i>	USA	UT-duchesne	Stark 1958
<i>T. pandorae</i>	USA	UT-rich	Stark 1958
<i>T. pandorae</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991
<i>T. pansus</i>	USA	NM-santa fe	Morlan 1955
<i>T. petiolatus</i>	USA	CO-larimer	McC Campbell 1931
<i>T. stanfordi</i>	USA	CO-delta	Pizzimenti 1975
<i>T. stanfordi</i>	USA	NM-rio arriba	Link 1949
Ctenophthalmidae			
<i>Anomiopsyllus hiemalis</i>	USA	TX	Cox 1950, Miles et al 1952
Hystriochopsyllidae			
<i>Hystriochopsylla gigas dippiei</i>	USA	CO-park	Ecke and Johnson 1950
<i>H. g. dippiei</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>Meringis rectus</i>	USA	NM-santa fe	Morlan 1955
<i>Neopsylla inopina</i>	USA	WY-albany	Wiseman 1949
<i>N. inopina</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>N. inopina</i>	USA	MT-blaine	Hubbard 1968
<i>Neopsylla sp.</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991
<i>Rhadinopsylla fraterna</i>	USA	CO-park	Fitzgerald 1970
<i>R. fraterna</i>	USA	CO-jackson	McC Campbell 1931
<i>R. fraterna</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991, Ubico et al 1988
<i>R. fraterna</i>	USA	MT-garfield	Hubbard 1968
<i>R. fraterna</i>	USA	WY-carbon	Wiseman 1955
<i>R. sectilis</i>	USA	NM-colfax	Cully et al 1997
<i>R. sectilis</i>	USA	WY-park	Ubico et al 1988
<i>R. sectilis</i>	USA	UT-wayne	Jachowski et al 2012
<i>R. sectilis sectilis</i>	USA	UT-wayne	Jachowski et al 2012
Leptopsyllidae			
<i>Peromyscopsylla sp.</i>	USA	NM-rio arriba	Link 1949

Parasite species	Country	State-county	Reference
Pulicidae			
<i>Cediopsylla inaequalis</i>	USA	NE-dawes	Gates 1945, Rapp and Gates 1957
<i>C. inaequalis</i>	USA	NE-kimball	Rapp and Gates 1957
<i>C. inaequalis</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991
<i>Echidnophaga gallinacea</i>	MEX	CHH	Fernandez-Gonzalez et al 2016
<i>E. gallinacea</i>	USA	NM-roosevelt	Pfaffenberger et al 1984
<i>E. gallinacea</i>	USA	NM-santa fe	Morlan 1955
<i>E. gallinacea</i>	USA	TX	Miles et al 1952
<i>E. gallinacea</i>	USA	unknown	Trembley and Bishop 1940
<i>E. gallinacea</i>	USA	UT-grand	Stark 1958
<i>Hoplopsyllus anomalus</i>	USA	CO-mesa	Pizzimenti 1975
<i>H. anomalus</i>	USA	CO-montezuma	McCampbell 1931
<i>H. anomalus</i>	USA	CO-montrose	Pizzimenti 1975
<i>H. anomalus</i>	USA	NM-bernalillo	Hubbard 1968
<i>H. anomalus</i>	USA	NM-santa fe	Morlan 1955
<i>H. anomalus</i>	USA	UT-emery	Stark 1958
<i>H. anomalus</i>	USA	UT-garfield	Stark 1958
<i>H. anomalus</i>	USA	UT-iron	Jachowski et al 2012, Stark 1958
<i>H. anomalus</i>	USA	UT-rich	Stark 1958
<i>Pulex irritans</i>	USA	AZ-apache	Jellison 1939
<i>P. irritans</i>	USA	CO	Stanford 1944
<i>P. irritans</i>	USA	MT-broadwater	Jellison and Kohls 1936
<i>P. irritans</i>	USA	MT-jefferson	Jellison and Kohls 1936
<i>P. irritans</i>	USA	NE-dawes	Rapp and Gates 1957
<i>P. irritans</i>	USA	TX	Miles et al 1952
<i>P. irritans</i>	USA	unknown	Trembley and Bishop 1940
<i>P. irritans</i>	USA	WY-park	Anderson and Williams 1997, Heller 1991
<i>P.simulans</i>	MEX	COA	Trevino-Villarreal et al 1998
<i>P.simulans</i>	MEX	NLE	Pizzimenti 1975, Tipton and Mendez 1968
<i>P.simulans</i>	MEX	SLP	Mellink and Madrigal 1993
<i>P.simulans</i>	MEX	unknown	Smit 1958
<i>P.simulans</i>	USA	CO-boulder	Brinkerhoff et al 2006
<i>P.simulans</i>	USA	CO-delta	Pizzimenti 1975
<i>P.simulans</i>	USA	CO-gunnison	Pizzimenti 1975
<i>P.simulans</i>	USA	CO-moffat	Pizzimenti 1975, Tripp et al 2016
<i>P.simulans</i>	USA	CO-montrose	Pizzimenti 1975
<i>P.simulans</i>	USA	CO-ouray	Pizzimenti 1975

Parasite species	Country	State-county	Reference
<i>P.simulans</i>	USA	CO-weld	Tripp et al 2009
<i>P.simulans</i>	USA	KS-hamilton	Poorbaugh and Gier 1961
<i>P.simulans</i>	USA	MT-phillips	Holmes 2003
<i>P.simulans</i>	USA	NM-colfax	Eads et al 2013, Eads et al 2015
<i>P.simulans</i>	USA	NM-roosevelt	Pfaffenberger et al 1984
<i>P.simulans</i>	USA	TX-brewster	Pizzimenti 1975
<i>P.simulans</i>	USA	TX-lubbock	Roberts 2001
<i>P.simulans</i>	USA	TX-terry	Roberts 2001
<i>Pulex</i> sp.	MEX	CHH	Fernandez-Gonzalez et al 2016
<i>Pulex</i> sp.	USA	CO-boulder	Brinkerhoff et al 2006
<i>Pulex</i> sp.	USA	OK-cimarron	Tyler and Buscher 1975
<i>Pulex</i> sp.	USA	TX-lubbock	Nascarella et al 2005
<i>Pulex</i> sp.	USA	UT-carbon	Stark 1958
<i>Pulex</i> sp.	USA	UT-duchesne	Stark 1958
<i>Pulex</i> sp.	USA	UT-emery	Stark 1958
<i>Pulex</i> sp.	USA	UT-summit	Stark 1958
<i>Pulex</i> sp.	USA	UT-uintah	Stark 1958
<i>Pulex</i> sp.	USA	WY-park	Heller 1991
LICE - Arthropoda, Insecta, Phthiraptera			
Enderleinellidae			
<i>Enderleinellus suturalis</i>	USA	CO-park	McC Campbell 1931
<i>E. suturalis</i>	USA	CO-routt	Ferris 1916
<i>E. suturalis</i>	USA	CO-teller	Ferris 1916
<i>E. suturalis</i>	USA	unknown	Durden and Musser 1994
<i>E. suturalis</i>	USA	WY-natrona	Ferris 1919
Hoplopleuridae			
<i>Hoplopleura acanthopus</i>	USA	ND-billings	McKenna et al 1977
Polyplacidae			
<i>Linognathoides cynomyis</i>	USA	NE-thomas	Kucera et al 2007
<i>L. cynomyis</i>	USA	SD-pennington	Creekmore et al 2002, Kietzmann 1987
<i>L. laeviusculus</i>	USA	CO-jackson	McC Campbell 1931
<i>L. laeviusculus</i>	USA	CO-larimer	McC Campbell 1931
<i>L. laeviusculus</i>	USA	CO-moffat	Davis 1935
<i>L. laeviusculus</i>	USA	CO-routt	Ferris 1916
<i>L. marmotae</i>	CAN	SK	Spencer 1966
<i>L. marmotae</i>	USA	ND-billings	Kim and Adler 1982
<i>L. marmotae</i>	USA	TX-dawson	Menzies and Hightower 1951
<i>L. marmotae</i>	USA	TX-hutchinson	Hightower and Eads 1951
<i>Neohaematopinus citellinus</i>	USA	NM-santa fe	Morlan & Hoff 1957
<i>N. citellinus</i>	USA	unknown	Durden and Musser 1994

Parasite species	Country	State-county	Reference
<i>Neohaematopinus</i> sp.	MEX	SLP	Mellink and Madrigal 1993
<i>Neohaematopinus</i> sp.	USA	TX-terry	Menzies and Hightower 1951
MITES - Arthropoda, Arachnida, Astigmata			
Pneumocoptidae			
<i>Pneumocoptes penrosei</i>	USA	NE-hitchcock	Baker 1951
<i>P. penrosei</i>	USA	TX-dallam	Baker 1951
<i>P. penrosei</i>	USA	TX-parmer	Baker 1951
MITES - Arthropoda, Arachnida, Mesostigmata			
Ascidae			
<i>Proctolaelaps</i> sp.	USA	NM-roosevelt	Pfaffenberger et al 1984
Laelapidae			
<i>Brevisterna morlani</i>	USA	NM-santa fe	Strandtmann and Allred 1956
<i>Echinonyssus cynomys</i>	USA	CO-conejos	Radford 1941
<i>E. neocynomys</i>	USA	KS-barber	Herrin 1970
<i>E. neotomae</i>	USA	KS-barber	Herrin 1970
<i>Haemolaelaps fahrenheitzi</i>	USA	CO-larimer	Maupin 1970, McCampbell 1931
<i>H. fahrenheitzi</i>	USA	SD-custer	King 1955
<i>H. fahrenheitzi</i>	USA	SD-pennington	Kietzmann 1987
<i>H. fahrenheitzi</i>	USA	TX-yoakum	Eads et al 1952
<i>H. fahrenheitzi</i>	USA	unknown	Strandtmann 1949
<i>H. fahrenheitzi</i>	USA	UT-duchesne	Allred and Beck 1966
<i>H. fahrenheitzi</i>	USA	UT-uintah	Allred and Beck 1966
MITES - Arthropoda, Arachnida, Prostigmata			
Trombiculidae			
<i>Cheladonta micheneri</i>	USA	KS-barber	Lipovsky et al 1955, Loomis 1956
<i>C. micheneri</i>	USA	KS-rawlins	Lipovsky et al 1955, Loomis 1956
<i>Dermadelema furmani</i>	USA	CO-larimer	Maupin 1970
<i>Euschoengastia criceticola</i>	USA	KS-barber	Loomis 1956
<i>Euschoengastoides loomisi</i>	USA	KS-barber	Loomis 1956
<i>Euschongastia cynomyicola</i>	USA	CO-larimer	Maupin 1970
<i>E. cynomyicola</i>	USA	KS-rawlins	Crossley and Lipovsky 1954, Loomis 1956
<i>E. cynomyicola</i>	USA	NE-hitchcock	Crossley and Lipovsky 1954
<i>E. obesa</i>	USA	UT-duchesne	Brennan and Beck 1955
<i>Eutrombicula alfreddugesi</i>	USA	KS-barber	Loomis 1956
<i>Hyponeocula arenicola</i>	USA	CO-larimer	Maupin 1970
<i>H. arenicola</i>	USA	UT-garfield	Brennan and Beck 1955
<i>H. montanensis</i>	USA	CO-larimer	Maupin 1970
<i>H. montanensis</i>	USA	KS-barber	Loomis 1956
<i>H. montanensis</i>	USA	KS-rawlins	Loomis 1956
<i>H. montanensis</i>	USA	MT-wheatland	Brennan 1946

Parasite species	Country	State-county	Reference
<i>H. montanensis</i>	USA	TX-terry	Eads et al 1952
<i>H. montanensis</i>	USA	UT-duchesne	Brennan and Beck 1955
<i>Kayella lacerta</i>	USA	CO-larimer	Maupin 1970
<i>K. lacerta</i>	USA	KS-barber	Loomis 1956
<i>Neoschoengastia americana</i>	USA	TX-concho	Loomis and Crossley 1963
<i>Odontacarus dentatus</i>	USA	CO-larimer	Maupin 1970
<i>O. dentatus</i>	USA	TX-concho	Loomis and Crossley 1963
<i>Parasecia gurneyi</i>	USA	KS-rawlins	Loomis 1956
<i>Trombicula hoplai</i>	USA	KS-barber	Loomis 1971
TICKS - Arthropoda, Arachnida, Ixodida			
Argasidae			
<i>Ornithodoros parkeri</i>	USA	CO-moffat	Davis (1939b)
<i>O. parkeri</i>	USA	CO-moffat	Cooley and Kohls 1944
<i>O. parkeri</i>	USA	UT-emery	Cooley and Kohls 1944
<i>O. parkeri</i>	USA	UT-uintah	Cooley and Kohls 1944, Davis 1939a
<i>O. parkeri</i>	USA	WY-natrona	Cooley 1936, Colley and Kohls 1944
<i>O. parkeri</i>	USA	WY-sweetwater	Cooley and Kohls 1944
<i>O. turicata</i>	USA	KS-clark	Davis 1936
<i>O. turicata</i>	USA	NM-roosevelt	Pfaffenberger et al 1984
<i>O. turicata</i>	USA	TX-cochran	Eads et al 1952
<i>O. turicata</i>	USA	TX-dawson	Eads et al 1952
<i>O. turicata</i>	USA	TX-terry	Eads et al 1952
<i>O. turicata</i>	USA	TX-yoakum	Eads et al 1952
<i>Ornithodoros</i> sp.	USA	CO-moffat	Pizzimenti 1975
<i>Ornithodoros</i> sp.	USA	UT-iron	Pizzimenti 1975
Ixodidae			
<i>Dermacentor andersoni</i>	USA	CO-moffat	Pizzimenti 1975
<i>D. andersoni</i>	USA	MT-powder river	Parker and Wells 1916
<i>D. andersoni</i>	USA	SD-pennington	Kietzmann 1987
<i>D. andersoni</i>	USA	unknown	Cooley 1938
<i>D. parumapertus</i>	USA	CO-park	McC Campbell 1931
<i>D. parumapertus</i>	USA	TX-dawson	Eads et al 1952
<i>D. variabilis</i>	USA	KS-edwards	Brillhart et al 1994
<i>Ixodes cookei</i>	USA	unknown	Bishopp and Trembley 1945
<i>I. kingi</i>	USA	AZ-yavapai	Cooley and Kohls 1945
<i>I. kingi</i>	USA	CO-delta	Pizzimenti 1975
<i>I. kingi</i>	USA	CO-gunnison	Johnson 1962
<i>I. kingi</i>	USA	CO-mesa	Cooley and Kohls 1945, Pizzimenti 1975
<i>I. kingi</i>	USA	CO-moffat	Pizzimenti 1975

Parasite species	Country	State-county	Reference
<i>I. kingi</i>	USA	CO-montezuma	Burnett and McCampbell 1926, McCampbell 1931
<i>I. kingi</i>	USA	MT-gallatin	Cooley and Kohls 1945
<i>I. kingi</i>	USA	TX-cochran	Eads et al 1952
<i>I. kingi</i>	USA	TX-gaines	Eads et al 1952
<i>I. kingi</i>	USA	TX-irion	Banks 1908, Bishopp 1911
<i>I. kingi</i>	USA	unknown	Bishopp and Trembley 1945
<i>I. kingi</i>	USA	UT-daggett	Allred et al 1960
<i>I. kingi</i>	USA	UT-duchesne	Allred et al 1960
<i>I. kingi</i>	USA	UT-garfield	Allred et al 1960
<i>I. kingi</i>	USA	UT-grand	Allred et al 1960, Cooley and Kohls 1945
<i>I. kingi</i>	USA	UT-millard	Cooley and Kohls 1945
<i>I. kingi</i>	USA	UT-san juan	Allred et al 1960, Cooley and Kohls 1945
<i>I. kingi</i>	USA	UT-uintah	Allred et al 1960
<i>I. sculptus</i>	USA	AZ-yavapai	Cooley and Kohls 1945
<i>I. sculptus</i>	USA	CO-dolores	Cooley and Kohls 1945
<i>I. sculptus</i>	USA	CO-larimer	Cooley and Kohls 1945, Maupin 1970
<i>I. sculptus</i>	USA	CO-moffat	Cooley and Kohls 1945
<i>I. sculptus</i>	USA	CO-montezuma	Burnett and McCampbell 1926, Colley and Kohls 1845, McCambell 1931
<i>I. sculptus</i>	USA	CO-weld	Salkeld et al 2006
<i>I. sculptus</i>	USA	NM-rio arriba	Cooley and Kohls 1945
<i>I. sculptus</i>	USA	SD-custer	Easton 1983
<i>I. sculptus</i>	USA	SD-pennington	Creekmore et al 2002, Kietzmann 1987
<i>I. sculptus</i>	USA	unknown	Bishopp and Trembley 1945
<i>I. sculptus</i>	USA	UT-garfield	Allred et al 1960
<i>I. sculptus</i>	USA	WY-albany	Cooley and Kohls 1945
<i>I. sculptus</i>	USA	WY-sweetwater	Cooley and Kohls 1945
<i>Ixodes</i> sp.	MEX	COA	Trevino-Villarreal et al 1998
<i>Ixodes</i> sp.	USA	ND-bowman	McKenna et al 1977
<i>Ixodes</i> sp.	USA	SD-custer	King 1955
<i>Ixodes</i> sp.	USA	UT-duchesne	Allred et al 1960
HELMINTHS - Nematoda, Adenophorea, Trichurida			
Capillariidae			
<i>Calodium</i> sp.	USA	WY-park	Seville and Williams 1989
HELMINTHS - Nematoda, Secernentea, Spirurida			
Physalopteridae			
<i>Physaloptera massino</i>	USA	CO-larimer	Vetterling 1962

Parasite species	Country	State-county	Reference
<i>P. massino</i>	USA	SD-custer	Vetterling 1962
<i>Physaloptera</i> sp.	USA	CO-elbert	Hall 1912
<i>Physaloptera</i> sp.	USA	WY-park	Seville and Williams 1989
Subuluridae			
<i>Subulura</i> sp.	USA	NM-roosevelt	Pfaffenberger et al 1984
HELMINTHS - Nematoda, Secernentea, Strongylida			
Trichostrongylidae			
<i>Trichostrongylus texianus</i>	USA	TX-lubbock	Rodenberg and Pence 1978
<i>T. texianus</i>	USA	TX-nolan	Dikmans 1937
<i>T. texianus</i>	USA	TX-runnels	Dikmans 1937
HELMINTHS - Platyhelminthes, Cestoda, Cyclophyllidea			
Hymenolepididae			
<i>Hymenolepis citelli</i>	USA	WY-park	Seville and Williams 1989
<i>Hymenolepis</i> sp.	USA	CO-elbert	Hall 1912
Taeniidae			
<i>Cladotaenia</i> sp.	USA	WY-albany	Scott 1931
<i>Versteria mustelae</i>	USA	WY-park	Seville and Williams 1989
Davaineidae			
<i>Railletina salmoni</i>	USA	OK-cimarron	Buscher and Tyler 1975
<i>Railletina</i> sp.	USA	OK-jackson	Buscher and Tyler 1975
HELMINTHS - Acanthocephala, Archiacanthocephala, Moniliformida			
Moniliformidae			
<i>Moniliformis clarki</i>	USA	NM-roosevelt	Pfaffenberger et al 1984
<i>M. clarki</i>	USA	SD-custer	Vetterling 1962
PROTOZOA - Sarcocystophora, Lobosa, Amoebida			
Entamoebidae			
<i>Entamoeba muris</i>	USA	ND-billings	McKenna et al 1977
<i>E. muris</i>	USA	ND-bowman	McKenna et al 1977
<i>E. muris</i>	USA	ND-mckenzie	McKenna et al 1977
<i>E. muris</i>	USA	ND-morton	McKenna et al 1977
PROTOZOA - Apicomplexa, Conoidasida, Eucoccidiorida			
Cryptosporidiidae			
<i>Cryptosporidium rubeyi</i>	USA	ND-billings	Stenger et al 2015
<i>C. ground squirrel genotype II</i>	USA	ND-billings	Stenger et al 2015
<i>Cryptosporidium</i> sp.	USA	ND-billings	Stenger et al 2015
Eimeriidae			
<i>Eimeria beecheyi</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. beecheyi</i>	USA	WY-albany	Seville 1997, Shults et al 1990
<i>E. beecheyi</i>	USA	WY-natrona	Seville 1997
<i>E. callospermophili</i>	USA	CO-larimer	Motriuk-Smith et al 2011
<i>E. callospermophili</i>	USA	CO-weld	Foust 2007
<i>E. callospermophili</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. callospermophili</i>	USA	NM-socorro	Ryan et al 2001

Parasite species	Country	State-county	Reference
<i>E. callospermophili</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. callospermophili</i>	USA	WY-albany	Seville 1997, Todd and Hammond 1968a
<i>E. callospermophili</i>	USA	WY-natrona	Motriuk-Smith et al 2011, Seville 1997
<i>E. cynomysis</i>	USA	CO-weld	Foust 2007
<i>E. cynomysis</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. cynomysis</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. cynomysis</i>	USA	WY-albany	Seville 1997, Shults et al 1990
<i>E. cynomysis</i>	USA	WY-park	Seville and Williams 1989
<i>E. giganteos</i>	USA	CO-larimer	Vetterling 1964
<i>E. lateralis</i>	USA	CO-larimer	Vetterling 1964
<i>E. lateralis</i>	USA	CO-weld	Foust 2007
<i>E. lateralis</i>	USA	ND-billings	McKenna et al 1977
<i>E. lateralis</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. lateralis</i>	USA	WY-albany	Seville 1997, Todd and Hammond 1968b
<i>E. lateralis</i>	USA	WY-natrona	Seville 1997
<i>E. lateralis</i>	USA	WY-park	Seville and Williams 1989
<i>E. ludoviciani</i>	USA	CO-larimer	Vetterling 1964
<i>E. ludoviciani</i>	USA	ND-billings	McKenna et al 1977
<i>E. ludoviciani</i>	USA	ND-bowman	McKenna et al 1977
<i>E. ludoviciani</i>	USA	ND-mckenzie	McKenna et al 1977
<i>E. ludoviciani</i>	USA	ND-morton	McKenna et al 1977
<i>E. ludoviciani</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. ludoviciani</i>	USA	WY-albany	Todd and Hammond (1968, callospermophili)
<i>E. ludoviciani</i>	USA	WY-park	Seville and Williams 1989
<i>E. morainensis</i>	USA	CO-weld	Foust 2007
<i>E. morainensis</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. morainensis</i>	USA	WY-albany	Seville 1997, Shults et al 1990
<i>E. morainensis</i>	USA	WY-natrona	Seville 1997
<i>E. pseudospermophili</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. pseudospermophili</i>	USA	WY-natrona	Seville 1997
<i>E. spermophili</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. spermophili</i>	USA	UT-san juan	Thomas and Stanton 1994
<i>E. spermophili</i>	USA	WY-albany	Seville 1997
<i>E. spermophili</i>	USA	WY-natrona	Seville 1997
<i>E. vilasi</i>	USA	NM-bernalillo	Ryan et al 2001
<i>E. vilasi</i>	USA	NM-socorro	Ryan et al 2001
<i>E. vilasi</i>	USA	WY-albany	Seville 1997
<i>E. vilasi</i>	USA	WY-natrona	Seville 1997
<i>Eimeria</i> sp.	USA	UT-san juan	Thomas and Stanton 1994

Parasite species	Country	State-county	Reference
Sarcocystidae			
<i>Sarcocystis</i> sp.	USA	WY-park	Seville and Williams 1989
BACTERIA - Proteobacteria, Alphaproteobacteria, Rhizobiales			
Bartonellaceae			
<i>Bartonella washoensis cynomysii</i>	USA	CO-boulder	Bai et al 2008
<i>Bartonella</i> sp.	MEX	CHH	Rubio et al 2014
<i>Bartonella</i> sp.	USA	CO-adams	Stevenson et al 2003
<i>Bartonella</i> sp.	USA	CO-boulder	Ahn et al 2010, Bai et al 2008b
BACTERIA - Protobacteria, Gammaproteobacteria, Enterobacteriales			
Enterobacteriaceae			
<i>Yersinia pestis</i>	CAN	SK	Antonation et al 2014
<i>Y. pestis</i>	MEX	COA	Varela and Vasquez 1954
<i>Y. pestis</i>	USA	CO-adams	Lowell et al 2009, Stevenson et al 2003
<i>Y. pestis</i>	USA	CO-arapahoe	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-bent	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-boulder	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-chaffee	Kartman et al 1962
<i>Y. pestis</i>	USA	CO-custer	PHR 62:41 1947
<i>Y. pestis</i>	USA	CO-dolores	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-douglas	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-el paso	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-gunnison	Lowell et al 2009, Rayor 1985
<i>Y. pestis</i>	USA	CO-hinsdale	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-huerfano	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-jefferson	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-la plata	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-larimer	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-las animas	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-logan	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-mesa	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-moffat	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-montezuma	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-montrose	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-otero	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-park	Ecke and Johnson 1950, Lowell et al 2009, USPHS 1947a
<i>Y. pestis</i>	USA	CO-pueblo	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-saguache	Lechleitner et al 1968
<i>Y. pestis</i>	USA	CO-sedgwick	Lowell et al 2009
<i>Y. pestis</i>	USA	CO-weld	Lowell et al 2009. Tripp et al 2009

Parasite species	Country	State-county	Reference
<i>Y. pestis</i>	USA	CO-yuma	Lowell et al 2009
<i>Y. pestis</i>	USA	KS-scott	Cully et al 2000, USPHS 1946
<i>Y. pestis</i>	USA	KS-thomas	Cully et al 2000, USPHS 1949
<i>Y. pestis</i>	USA	MT-phillips	Biggins et al 2010
<i>Y. pestis</i>	USA	NM-catron	Byington 1940, Link 1949, USPHS 1938a, USPHS 1938b, USPHS 1938c, USPHS 1938d
<i>Y. pestis</i>	USA	NM-colfax	Cully et al 1997
<i>Y. pestis</i>	USA	NM-mckinley	Kartman et al 1967
<i>Y. pestis</i>	USA	NM-rio arriba	Link 1949, USPHS 1948a
<i>Y. pestis</i>	USA	NM-sandoval	Friggins et al 2010
<i>Y. pestis</i>	USA	TX-cochran	Miles et al 1952
<i>Y. pestis</i>	USA	TX-gaines	PHR 63:37 1948
<i>Y. pestis</i>	USA	unknown	Engelthaler and Gage 2000
<i>Y. pestis</i>	USA	UT-duchesne	Biggins et al 2010
<i>Y. pestis</i>	USA	UT-garfield	Allred 1952, Biggins et al 2010, Hoogland et al 2004
<i>Y. pestis</i>	USA	UT-uintah	Biggins et al 2010
<i>Y. pestis</i>	USA	WY-campbell	Pauli et al 2006
<i>Y. pestis</i>	USA	WY-park	Ubico et al 1988
BACTERIA - Proteobacteria, Gammaproteobacteria, Pasteurellales			
Pasteurellaceae			
<i>Pasteurella multocida</i>	USA	CO-el paso	Quan et al 1979
<i>P. multocida</i>	USA	CO-montrose	Quan et al 1979
BACTERIA - Spirochaetes, Spirochaetes, Spirochaetales			
Leptospiraceae			
<i>Leptospira interrogans</i>	MEX	CHH	Montiel-Artega et al 2015
VIRUSES - Viruses, dsDNA viruses, Herpesvirales			
Herpesviridae			
<i>cynomys herpesvirus 1</i>	USA	CO-jefferson	Nagamine et al 2011
VIRUSES - Viruses, ssRNA viruses, Mononegavirales			
Rhabdoviridae			
<i>Rabies lyssavirus</i>	USA	WY	CDC 1986

Table 2.2 Flea species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each flea species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Aetheca wagneri</i>	8	4				X		
<i>Anomiopsyllus hiemalis</i>	2	2	X					
<i>Cediopsylla inaequalis</i>	6	4	X			X		
<i>Ceratophyllus vison</i>	1	1			X			
<i>Echidnophaga gallinacea</i>	6	6	X		X	X		X
<i>Eumolpianus eumolpi americanus</i>	1	1			X			
<i>Foxella ignota apachina</i>	1	1	X					
<i>Hoplopsyllus anomalus</i>	11	6			X	X	X	
<i>Hystrichopsylla gigas dippiei</i>	6	4			X	X		
<i>Megabothris abantis</i>	1	1			X			
<i>Meringis rectus</i>	1	1			X			
<i>Neopsylla inopina</i>	26	5	X			X		
<i>Neopsylla sp.</i>	2	2				X		
<i>Orchopeas sexdentatus</i>	2	2	X					
<i>Oropsylla bacchi</i>	1	1			X			
<i>O. bruneri</i>	1	1	X					
<i>O. hirsuta</i>	150	54	X	X	X	X	X	
<i>O. idahoensis</i>	35	14	X		X	X	X	X
<i>O. labis</i>	44	15	X		X	X	X	X
<i>O. montana</i>	9	5	X		X		X	
<i>O. rupestris</i>	2	2	X					
<i>O. tuberculata</i>	10	7	X		X	X		
<i>O. tuberculata cynomuris</i>	60	20	X		X	X	X	X
<i>O. t. ornata</i>	2	2			X			
<i>O. t. tuberculata</i>	14	7	X		X	X		
<i>Oropsylla sp.</i>	3	3	X		X	X		
<i>Peromyscopsylla sp.</i>	1	1			X			
<i>Pulex irritans</i>	9	8	X		X	X		X
<i>P. simulans</i>	27	14	X	X	X	X		
<i>Pulex sp.</i>	12	6	X			X		
<i>Rhadinopsylla fraterna</i>	21	7	X		X	X		X
<i>R. sectilis</i>	3	3			X	X	X	
<i>R s. sectilis</i>	1	1					X	
<i>Thrassis acamantis</i>	1	1						X
<i>T. bacchi</i>	3	2	X		X		X	
<i>T. bacchi consimilis</i>	1	1			X			
<i>T. fatus</i>	4	4	X	X				
<i>T. francisi</i>	16	6				X	X	
<i>T. howelli utahensis</i>	1	1	X					
<i>T. pandorae</i>	8	3				X		
<i>T. pansus</i>	1	1			X			
<i>T. petiolatus</i>	1	1	X					

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>T. stanfordi</i>	2	2			X	X		
TOTAL	517	74	24	3	26	22	10	7

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.3 Louse species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each louse species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Enderleinellus suturalis</i>	6	4	X		X	X		
<i>Hoplopleura acanthopus</i>	1	1	X					
<i>Linognathoides cynomyis</i>	3	3	X					
<i>L. laeviusculus</i>	4	3	X			X		
<i>L. marmotae</i>	4	4	X					
<i>Neohaematopinus citellinus</i>	2	2			X			
<i>Neohaematopinus</i> sp.	2	2	X	X				
TOTAL	22	13	6	1	2	2	0	0

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.4 Mite species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each mite species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Brevisterna morlani</i>	1	1			X			
<i>Cheladonta micheneri</i>	4	2	X					
<i>Dermadelema furmani</i>	1	1	X					
<i>Echinonyssus cynomys</i>	1	1						X
<i>E. neocynomys</i>	1	1	X					
<i>E. neotomae</i>	1	1	X					
<i>Euschoengastia criceticola</i>	1	1	X					
<i>Euschoengastoides loomisi</i>	1	1	X					
<i>Euschongastia cynomyicola</i>	7	3	X					
<i>E. obesa</i>	1	1				X		
<i>Eutrombicula alfreddugesi</i>	1	1	X					
<i>Haemolaelaps fahrenheitzi</i>	8	7	X		X	X		
<i>Hyponeocula arenicola</i>	2	2	X				X	
<i>H. montanensis</i>	12	5	X			X		
<i>Kayella lacerta</i>	2	2	X					
<i>Neoschoengastia americana</i>	1	1	X					
<i>Odontacarus dentatus</i>	1	1	X					
<i>Parasecia gurneyi</i>	1	1	X					
<i>Pneumocoptes penrosei</i>	3	1	X					
<i>Proctolaelaps</i> sp.	1	1	X					
<i>Trombicula hoplai</i>	1	1	X					
TOTAL	52	19	18	0	2	3	1	1

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*, CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.5 Tick species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each tick species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Dermacentor andersoni</i>	4	4	X			X		
<i>D. parumapertus</i>	2	2	X		X			
<i>D. variabilis</i>	1	1	X					
<i>Ixodes cookei</i>	1	1						X
<i>I. kingi</i>	24	10	X		X	X	X	X
<i>I. sculptus</i>	18	10	X		X	X	X	X
<i>Ixodes sp.</i>	4	4	X	X		X		
<i>Ornithodoros parkeri</i>	7	3	X			X		
<i>O. turicata</i>	6	3	X					
<i>Ornithodoros sp.</i>	2	1				X	X	
TOTAL	70	27	8	1	3	6	3	3

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys sp.*

Table 2.6 Helminth species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each helminth species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Capillaria</i> sp.	1	1				X		
<i>Cladotaenia</i> sp.	2	1				X		
<i>Hymenolepis citelli</i>	1	1				X		
<i>Hymenolepis</i> sp.	1	1	X					
<i>Moniliformis clarki</i>	2	2	X					
<i>Physaloptera massino</i>	3	1	X					
<i>Physaloptera</i> sp.	2	2	X			X		
<i>Railletina salmoni</i>	1	1	X					
<i>Railletina</i> sp.	1	1	X					
<i>Subulura</i> sp.	1	1	X					
<i>Trichostrongylus texianus</i>	3	2	X					
<i>Versteria mustelae</i>	1	1				X		
TOTAL	19	8	8	0	0	4	0	0

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.7 Protozoan species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each protozoan species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Cryptosporidium ground squirrel genotype II</i>	1	1	X					
<i>C. rubeyi</i>	1	1	X					
<i>Cryptosporidium sp.</i>	1	1	X					
<i>Eimeria beecheyi</i>	4	3	X		X	X		
<i>E. callospermophili</i>	9	6	X		X	X		
<i>E. cynomysis</i>	6	6	X		X	X		
<i>E. giganteos</i>	1	1	X					
<i>E. lateralis</i>	8	7	X		X	X		
<i>E. ludoviciani</i>	15	5	X		X	X		
<i>E. morainensis</i>	5	4	X		X	X		
<i>E. pseudospermophili</i>	2	2	X		X			
<i>E. spermophili</i>	4	3	X		X	X		
<i>E. vilasi</i>	4	2	X		X	X		
<i>Eimeria sp.</i>	1	1			X			
<i>Entamoeba muris</i>	4	1	X					
<i>Sarcocystis sp.</i>	1	1				X		
TOTAL	67	12	14	0	10	9	0	0

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*, CYPA = *C. parvidens*, CYSP = *Cynomys sp.*

Table 2.8 Bacterial species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each bacterial species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>Bartonella washoensis cynomysii</i>	1	1	X					
<i>Bartonella</i> sp.	14	4	X					
<i>Leptospira interrogans</i>	1	1	X					
<i>Pasteurella multocida</i>	2	1	X		X			
<i>Yersinia pestis</i>	75	32	X	X	X	X	X	X
TOTAL	92	38	4	1	2	1	1	1

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.9 Virus species recorded from each species of prairie dog, including the number of records (# recs) and number of references (# refs) associated with each virus species.

Parasite species	# recs	# refs	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
<i>cynomys herpesvirus 1</i>	1	1	X					
<i>Rabies lyssavirus</i>	1	1						X
TOTAL	2	2	1					1

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

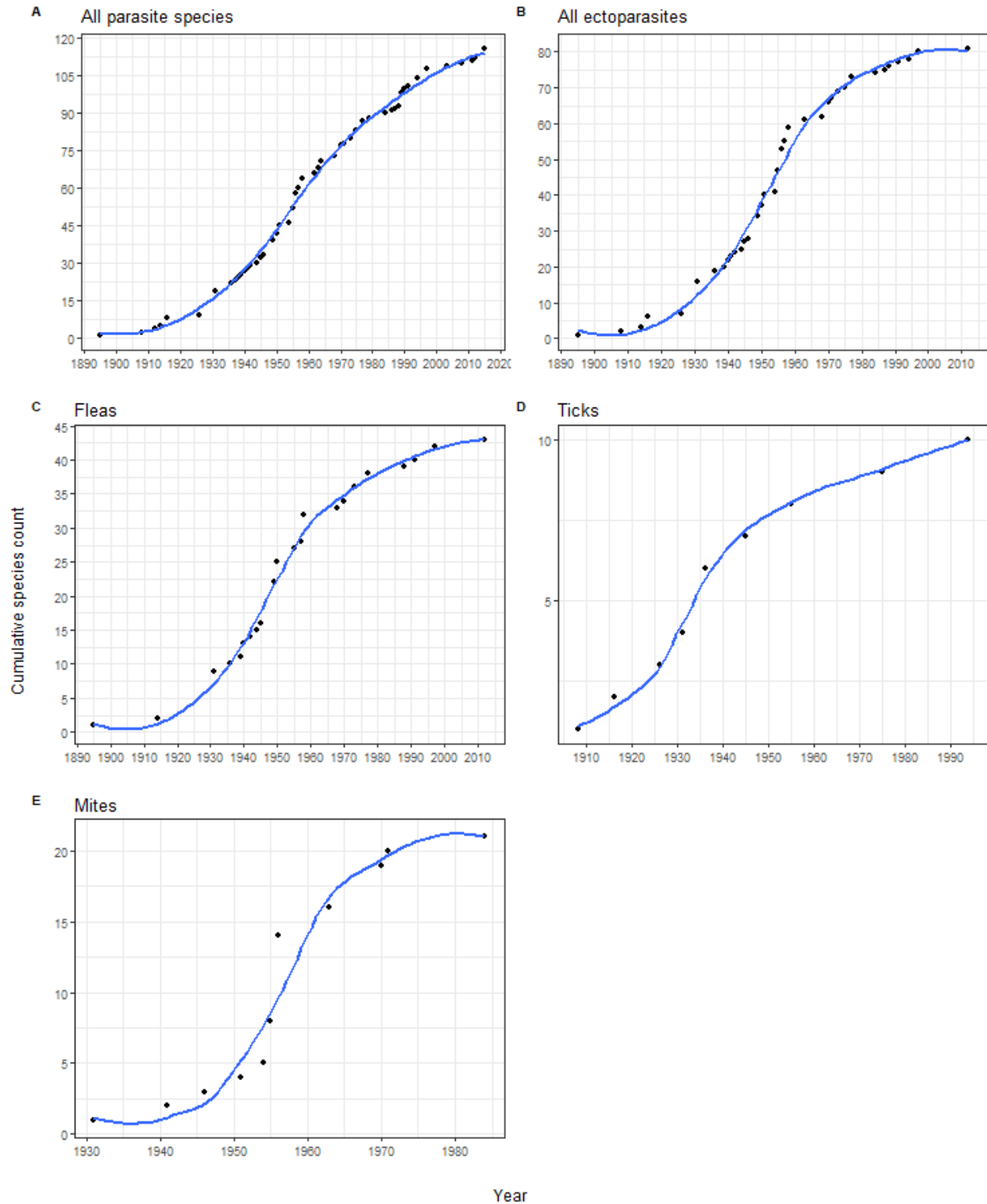


Figure 2.3 Species accumulation curves for (A) all prairie dog parasite, (B) all ectoparasites, (C) fleas, (D), ticks, (E) and mites, showing the cumulative species count plotted against year. Fitted lines show the loess smoothed curve.

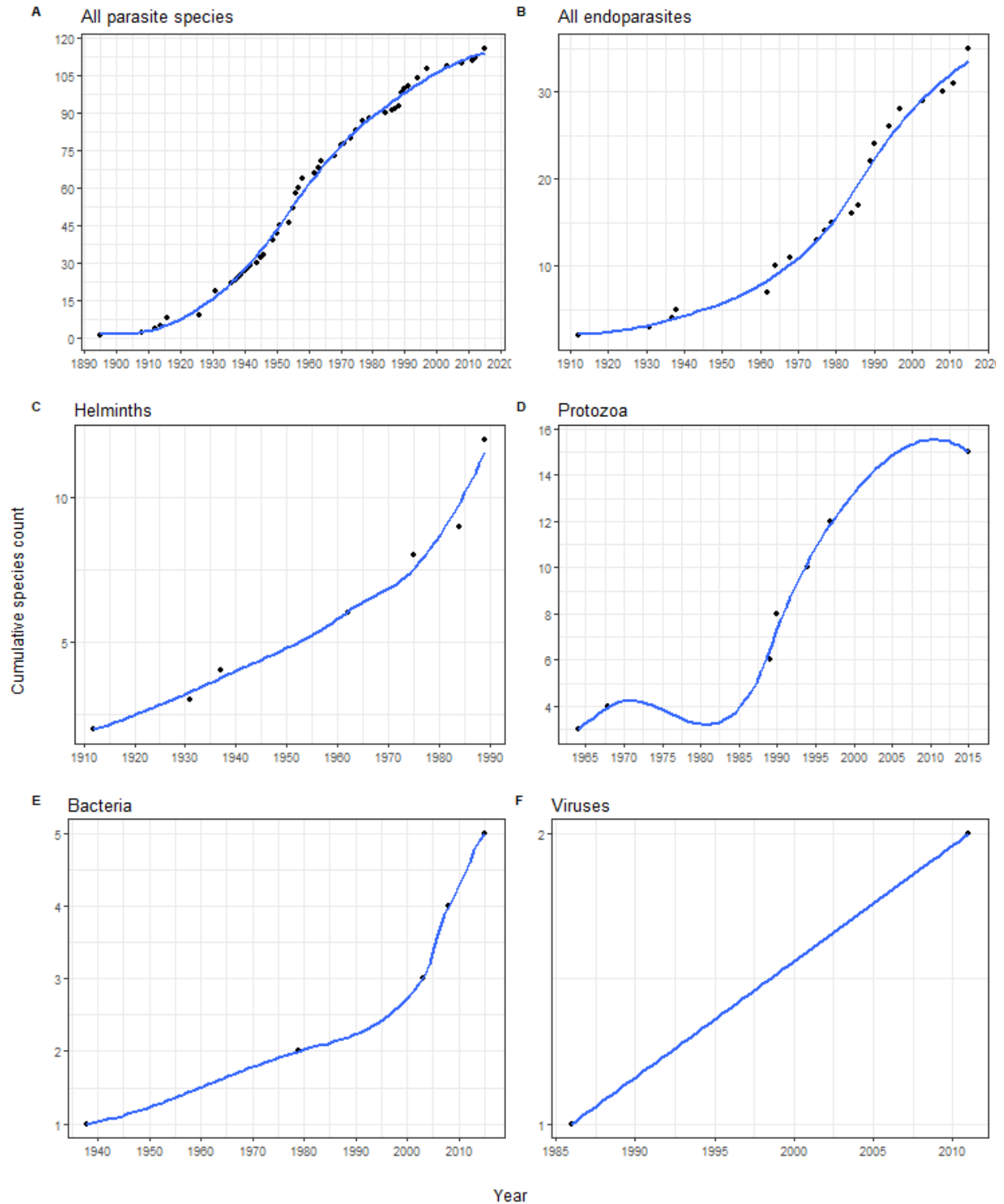


Figure 2.4 Species accumulation curves for (A) all parasites, (B) all endoparasites, (C) helminths, (D) protozoa, (E) bacteria, and (F) viruses, showing the cumulative species count plotted against year. Fitted lines show the loess smoothed curve, except for viruses, which had too few data points.

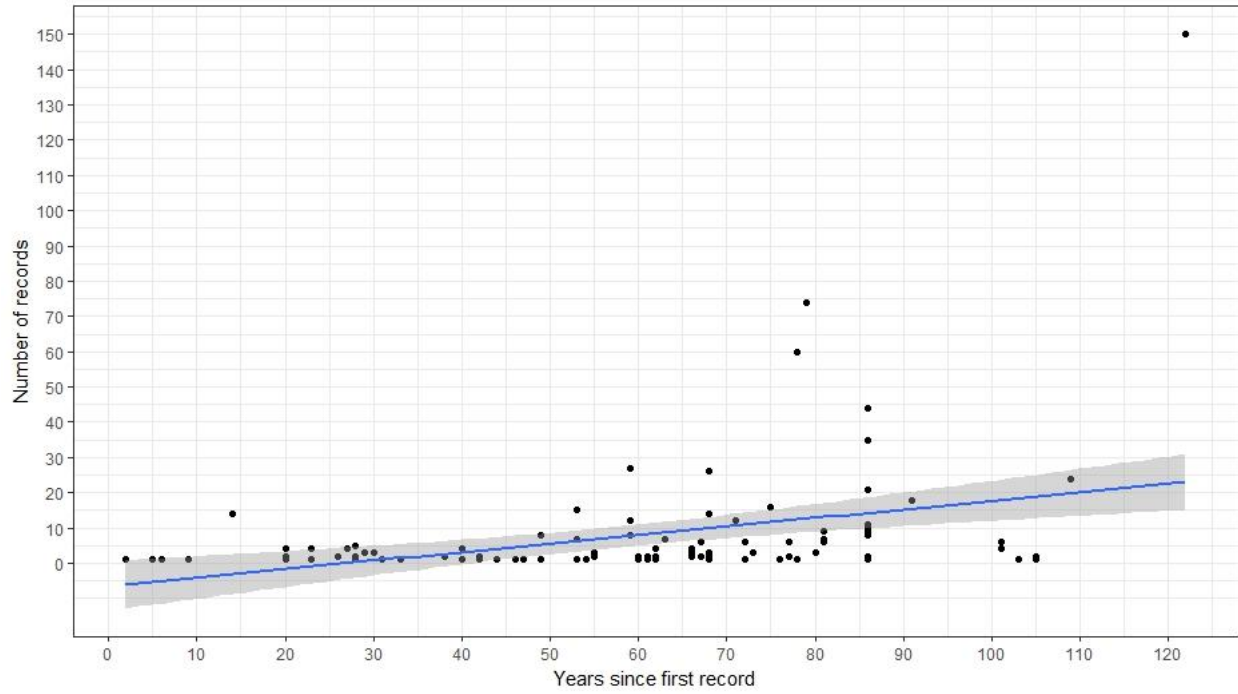


Figure 2.5 Plot of number of host-parasite records versus year since first record for parasites of all five prairie dog species. Fitted line shows a linear regression of number of records on years since first record with a 95% confidence interval.

Table 2.10 Number of parasites species (# species), number of parasite records (# recs), and number of references (# refs) for each species of prairie dog.

Host species	# species	# recs	# refs
<i>Cynomys ludovicianus</i>	84	302	92
<i>C. gunnisoni</i>	45	162	44
<i>C. leucurus</i>	47	287	31
<i>C. parvidens</i>	15	64	11
<i>C. mexicanus</i>	6	13	6
<i>Cynomys</i> sp.	13	18	10
TOTAL	116	846	160

Table 2.11 Summary of records for which parasite prevalence was reported.

Species	No. records	Mean sample size	Min sample size	Max sample size	Total sample size	Mean prev. %	Min prev. %	Max prev. %	Hosts	References
<i>Bartonella sp.</i>	12	112.8	13	219	1353	21.0	2.3	48.9	CYLU	Bai et al. 2008b, Rubio et al. 2014
<i>Dermacentor andersoni</i>	2	194.0	41	347	388	6.7	5.0	8.4	CYLU	Kietzmann 1987, Parker and Wells 1916
<i>Echidnophaga gallinacea</i>	3	66.3	13	134	199	16.1	2.0	38.5	CYGU CYLU	Fernandez-Gonzalez et al. 2016, Morlan 1955, Pfaffenberger et al. 1984
<i>Eimeria beecheyi</i>	2	70.5	18	123	141	72.8	62.6	83.0	CYGU CYLU	Shults et al. 1990, Thomas and Stanton 1994
<i>E. callospermophili</i>	3	99.7	23	222	299	37.4	16.2	61.0	CYGU CYLU	Foust 2007, Ryan et al. 2001
<i>E. cynomysis</i>	5	86.8	17	222	434	15.0	1.6	28.8	CYGU CYLU CYLU	Foust 2007, Ryan et al. 2001, Seville and Williams 1989, Shults et al. 1990, Thomas and Stanton 1994
<i>E. giganteos</i>	1	41.0	41	41	41	2.4	2.4	2.4	CYLU	Vetterling 1964
<i>E. lateralis</i>	5	84.8	17	222	424	10.6	3.3	23.5	CYGU CYLU CYLU	Foust 2007, McKenna et al. 1977, Seville and Williams 1989, Thomas and Stanton 1994, Vetterling 1964
<i>E. ludoviciani</i>	3	37.3	17	54	112	41.8	2.0	64.7	CYGU CYLU CYLU	Ryan et al. 2001, Seville and Williams 1989, Vetterling 1964
<i>E. morainensis</i>	2	120.0	18	222	240	33.5	22.0	45.0	CYLE CYLU	Foust 2007, Shults et al. 1990
<i>E. Pseudospermophili</i>	1	54.0	54	54	54	6.0	6.0	6.0	CYGU	Ryan et al. 2001
<i>E. vilasi</i>	2	38.5	23	54	77	37.0	2.0	72.0	CYGU	Ryan et al. 2001
<i>Eimeria sp.</i>	1	123.0	123	123	123	4.9	4.9	4.9	CYGU	Thomas and Stanton 1994
<i>Haemolaelaps fahrenheitzi</i>	1	41.0	41	41	42	12.0	12.0	12.0	CYLU	Kietzmann 1987
<i>Hoplopleura acanthopus</i>	1	21.0	21	21	21	4.8	4.8	4.8	CYLU	McKenna et al. 1977
<i>Hoplopsyllus anomalus</i>	1	134.0	134	134	134	1.0	1.0	1.0	CYGU	Morlan 1955

Species	No. records	Mean sample size	Min sample size	Max sample size	Total sample size	Mean prev. %	Min prev. %	Max prev. %	Hosts	References
<i>Hymenolepis citelli</i>	1	17.0	17	17	17	23.5	23.5	23.5	CYLE	Seville and Williams 1989
<i>Ixodes sculptus</i>	2	38.0	35	41	76	6.7	2.0	8.6	CYLU	Creekmore et al. 2002, Kietzmann 1987
<i>Ixodes sp.</i>	1	21.0	21	21	21	4.8	4.8	4.8	CYLU	McKenna et al. 1977
<i>Leptosira interrogans</i>	1	248.0	248	248	248	79.0	79.0	79.0	CYLU	Montiel-Artega et al. 2015
<i>Linognathoides cynomyis</i>	2	38.0	35	41	76	28.7	11.4	46.0	CYLU	Creekmore et al. 2002, Kietzmann 1987
<i>Meringis rectus</i>	1	134.0	134	134	134	2.0	2.0	2.0	CYGU	Morlan 1955
<i>Moniliformis clarki</i>	1	52.0	52	52	52	1.9	1.9	1.9	CYLU	Pfaffenberger et al. 1984
<i>Neohaematopinus citellinus</i>	1	134.0	134	134	134	1.5	1.5	1.5	CYGU	Morlan and Hoff 1957
<i>Ornithodoros turicata</i>	1	52.0	52	52	52	3.9	3.9	3.9	CYLU	Pfaffenberger et al. 1984
<i>Oropsylla hirsuta</i>	46	41.0	1	1299	1873	90.9	9.4	100.0	CYGU CYLE CYLU CYPA	Creekmore et al. 2002, Holdenried and Morlan 1956, Kietzmann 1987, Morlan 1955, Pfaffenberger et al. 1984, Pizzimenti 1975, Tripp et al. 2009, Tyler and Buscher 1975
<i>O. tuberculata cynomuris</i>	3	258.3			775	8.8	2.0	19.0	CYGU CYLU	Kietzmann 1987, Morlan 1955, Tripp et al. 2009
<i>O. tuberculata tuberculata</i>	2	71.5	9	134	143	15.2	11.0	19.4	CYGU	Holdenried and Morlan 1956, Pizzimenti 1975
<i>Physaloptera sp.</i>	1	17.0	17	17	17	35.3	35.3	35.3	CYLE	Seville and Williams 1989
<i>Proctolaelaps sp.</i>	1	52.0	52	52	52	9.6	9.6	9.6	CYLU	Pfaffenberger et al. 1984
<i>Pulex irritans</i>	1	10.0	10	10	10	100.0	100.0	100.0	CYLU	Jellison and Kohls 1936

Species	No. records	Mean sample size	Min sample size	Max sample size	Total sample size	Mean prev. %	Min prev. %	Max prev. %	Hosts	References
<i>P. simulans</i>	9	155.4	1	1299	1399	52.0	8.5	100.0	CYGU CYLU CYME	Pfaffenberger et al. 1984, Pizzimenti 1975, Tipton and Mendez 1968, Tripp et al. 2009
<i>Pulex sp.</i>	1	11.0	11	11	11	36.0	36.0	36.0	CYLU	Tyler and Buscher 1975
<i>Railleitina salmoni</i>	1	11.0	11	11	11	9.0	9.0	9.0	CYLU	Buscher and Tyler 1975
<i>Railleitina sp.</i>	1	7.0	7	7	7	14.0	14.0	14.0	CYLU	Buscher and Tyler 1975
<i>Sarcocystis sp.</i>	1	17.0	17	17	17	11.8	11.8	11.8	CYLE	Seville and Williams 1989
<i>Subulura sp.</i>	1	52.0	52	52	52	3.9	3.9	3.9	CYLU	Pfaffenberger et al. 1984
<i>Thrassis fatus</i>	1	1299.0	1299	1299	1299	4.5	4.5	4.5	CYLU	Tipp et al. 2009
<i>T. francisi</i>	1	11.0	11	11	11	9.0	9.0	9.0	CYPA	Pizzimenti 1975
<i>T. pansus</i>	1	134.0	134	134	134	2.0	2.0	2.0	CYGU	Morlan 1955
<i>Trichostrongylus texianus</i>	1	15.0	15	15	15	60.0	60.0	60.0	CYLU	Rodenberg and Pence 1978
<i>Versteria mustelae</i>	2	17.0	17	17	34	8.8	5.8	11.8	CYLE	Seville and Williams 1989
<i>Yersinia pestis</i>	3	255.0	61	574	765	5.1	0.2	9.8	CYGU CYLU	Biggins et al. 2010, Cully et al. 1997, Friggins et al. 2010

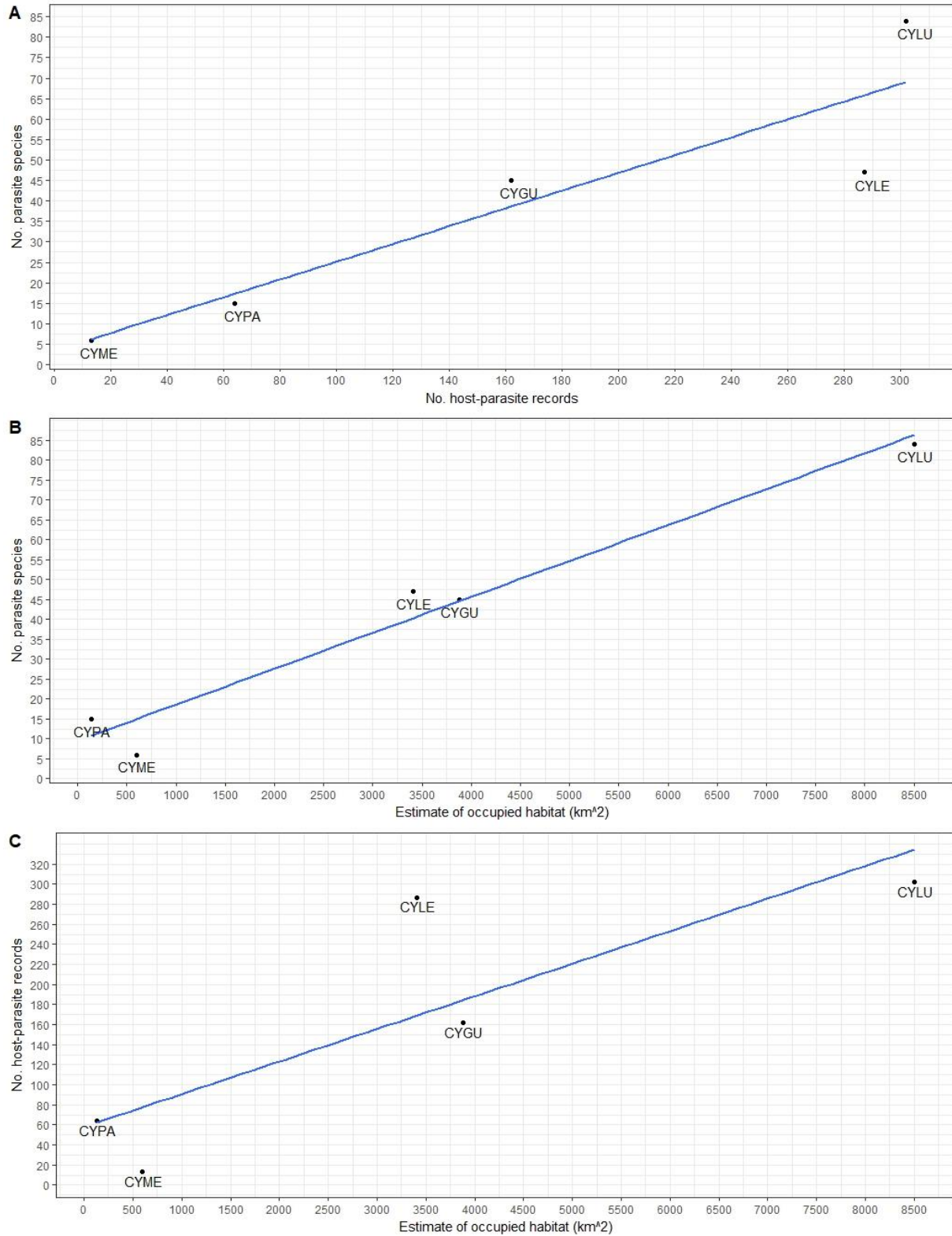


Figure 1.6 Plots of (A) number of parasite species versus number of host-parasite records, (B) number of parasite species versus estimated occupied habitat (km²), and (C) the number of host-parasite records versus estimated occupied habitat (km²) for all five species of prairie dog. Lines indicate the best fit lines from linear regressions.

Table 2.12. Number of parasite species in common between pairs of prairie dog species.

	CYLU	CYME	CYGU	CYLE	CYPA	CYSP
CYLU	84	6	29	32	10	9
CYME		6	3	4	2	2
CYGU			45	27	11	9
CYLE				47	11	8
CYPA					15	6
CYSP						13

CYLU = *Cynomys ludovicianus*, CYME = *C. mexicanus*, CYGU = *C. gunnisoni*, CYLE = *C. leucurus*,
 CYPA = *C. parvidens*, CYSP = *Cynomys* sp.

Table 2.13 Flea vectors of *Yersinia pestis*, the causative agent of plague, and their natural hosts in North America. Table adapted from Eisen et al 2009 and updated to include additional references.

Flea Species	# recs	Plague Vector?	Natural hosts	References
<i>Aetheca wagneri</i>	8	Yes	Various mice	Kartman and Prince (1956), Eisen et al (2008)
<i>Anomiopsyllus hiemalis</i>	2	Unknown		
<i>Cediopsylla inaequalis</i>	6	Unknown	Rabbits and hares	
<i>Ceratophyllus vison</i>	1	Unknown	Tree squirrels	
<i>Echidnophaga gallinacea</i>	6	Yes	Poultry	Burroughs (1947)
<i>Eumolpianus eumolpi americanus</i>	1	Yes	Chipmunks	Eskey and Haas (1939)
<i>Foxella ignota apachina</i>	1	Unknown	Pocket gophers	
<i>Hoplopsyllus anomalus</i>	11	Yes	Ground squirrels	Eskey and Haas (1939), Wheeler and Douglas (1945), Wheeler and Douglas (1941)
<i>Hystrichopsylla gigas dippiei</i>	6	Unknown	Various rodents	
<i>Megabothris abantis</i>	1	Yes	Mice, jumping mice, and voles	Kartman and Prince (1956), Burroughs (1947)
<i>Meringis rectus</i>	1	Unknown	Kangaroo rats	
<i>Neopsylla inopina</i>	26	Unknown	Ground squirrels	
<i>Neopsylla</i> sp.	2	Unknown	Ground squirrels	
<i>Orchopeas sexdentatus</i>	2	Yes	Wood rats	Eskey and Haas (1939), Burroughs (1947)
<i>Oropsylla bacchi</i>	1	Unknown	Ground squirrels	
<i>O. bruneri</i>	1	Yes	Ground squirrels	Prince (1943)
<i>O. hirsuta</i>	150	Yes	Prairie dogs	Eskey and Haas (1939)
<i>O. idahoensis</i>	35	Yes	Various rodents	Burroughs (1947)
<i>O. labis</i>	44	Yes	Ground squirrels, prairie dogs	Eskey and Haas (1939)
<i>O. montana</i>	9	Yes	Ground squirrels	Eskey and Haas (1939), Kartman and Prince (1956), Burroughs (1947), Holdenried (1952), Wheeler and Douglas (1945), Wheeler and Douglas (1941), Engelthaler et al (2000), Eisen et al (2007), Eisen et al (2006)
<i>O. rupestris</i>	2	Yes	Ground squirrels	Eskey and Haas (1939)
<i>O. sp.</i>	3	Unknown	Various rodents	
<i>O. tuberculata</i>	10	Yes	Ground squirrels, prairie dogs	Eskey and Haas (1939)
<i>O. t. cynomuris</i>	60	Yes	Ground squirrels, prairie dogs	Wilder et al (2008)
<i>O. t. ornata</i>	2	Unknown	Prairie dogs	
<i>O. t. tuberculata</i>	14	Yes	Ground squirrels	Wayson (1947)
<i>Peromyscopsylla</i> sp.	1	Unknown	Mice and wood rats	

Flea Species	# recs	Plague Vector?	Natural hosts	References
<i>Pulex irritans</i>	9	Yes	Various mammals	Wayson (1947)
<i>P. simulans</i>	27	Yes	Various mammals	Smit (1958)
<i>Pulex</i> sp.	12	Yes	Various mammals	Wayson (1947), Smit (1958)
<i>Rhadinopsylla fraterna</i>	21	Unknown	Ground squirrels	
<i>R. sectilis</i>	3	Unknown	Various rodents	
<i>R. s. sectilis</i>	1	Unknown	Various rodents	
<i>Thrassis acamantis</i>	1	Yes	Marmots	Eskey and Haas (1939)
<i>T. bacchi</i>	3	Yes	Ground squirrels	Prince (1943)
<i>T. b. consimilis</i>	1	Unknown	Ground squirrels	
<i>T. fotus</i>	4	Yes	Ground squirrels	Kartman and Prince (1956)
<i>T. francisi</i>	16	Yes	Ground squirrels	Eskey and Haas (1939)
<i>T. howelli utahensis</i>	1	Yes	Marmots	Eskey and Haas (1939)
<i>T. pandorae</i>	8	Yes	Ground squirrels	Eskey and Haas (1939)
<i>T. pansus</i>	1	Unknown	Various rodents	
<i>T. petiolatus</i>	1	Yes	Ground squirrels	Brown (1944)
<i>T. stanfordi</i>	2	Yes	Ground squirrels	Wayson (1947)

Table 2.14 Tick life stages recovered from all five species of prairie dog.

Species	Life stage found on prairie dogs					References
	L	N	I	A	U	
<i>Dermacentor andersoni</i>	L	N	I	A	U	Cooley 1938; Kietzmann 1987; Parker and Wells 1916; Pizzimenti 1975
<i>Dermacentor parumapertus</i>					U	Eads et al. 1952; McCampbell 1931
<i>Dermacentor variabilis</i>		N				Brillhart et al. 1994
<i>Ixodes cookei</i>		N				Bishopp and Trembley 1945
<i>Ixodes kingi</i>		N		A	U	Allred et al. 1960; Banks 1908; Bishopp 1911; Bishopp and Trembley 1945; Burnett and McCampbell 1926; Cooley and Kohls 1945; Eads et al. 1952; Johnson 1962; McCampbell 1931; Pizzimenti 1975
<i>Ixodes sculptus</i>		N	I	A	U	Allred et al. 1960; Bishopp and Trembley 1945; Burnett and McCampbell 1926; Cooley and Kohls 1945; Creekmore et al. 2002; Easton 1983; Kietzmann 1987; Maupin 1970; McCampbell 1931; Pizzimenti 1975; Salkeld et al. 2006
<i>Ixodes</i> sp.	L	N			U	Allred et al. 1960; King 1955; McKenna et al. 1977; Trevino-Villareal et al. 1998
<i>Ornithodoros parkeri</i>		N			U	Cooley 1936; Cooley and Kohls 1944; Davis 1939a; Davis 1939b
<i>Ornithodoros turicata</i>		N			U	Davis 1936; Eads et al. 1952; Pfaffenberger et al. 1984
<i>Ornithodoros</i> sp.					U	Pizzimenti 1975

L = larva, *N* = nymph, *I* = immature; *A* = adult, *U* = unknown

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CHAPTER THREE

DIVERSITY, SELECTION, AND THE MHC CLASS II DRB LOCUS IN BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*) FROM PAWNEE NATIONAL GRASSLAND, COLORADO

Introduction

Wildlife face ever-increasing threats from emerging pathogens, many that also cause disease in humans (Daszak *et al.* 2000; Rogalski *et al.* 2017). Host genetic diversity may play a role in buffering populations against infectious disease (Altizer *et al.* 2003a; Sommer 2005a), and genes of the vertebrate immune system, especially of the major histocompatibility complex (MHC), are the most diverse in the vertebrate genome (Wakeland and Klein 1979; Gotze *et al.* 1980; Benoist *et al.* 1983; Klein and Figueroa 1986; Edwards and Hedrick 1998; Beck and Trowsdale 2000). MHC genes are divided into three different classes, with class I and II genes encoding molecules involved in antigen presentation to T cells (Benacerraf 1978; Babbitt *et al.* 1985; Allen *et al.* 1987; Buus *et al.* 1987). Class I molecules respond to intracellular pathogens such as viruses, while class II molecules respond to extracellular parasites, such as helminths and bacteria (Klein and Figueroa 1986), including *Yersinia pestis*, the causative agent of plague (Shim *et al.* 2006). Of the three class II genes, the most diverse is the DRB locus; in particular, the second exon of the gene encoding the β 1 protein (Brown *et al.* 1993), with most variation within codons for amino acids involved directly in antigen binding (Babik *et al.* 2005; Babik 2010). Research on immunogenetic diversity in non-model organisms has therefore focused on the second exon of the DRB gene (e.g., Cobble *et al.* 2016; Zhang *et al.* 2016), partly for ongoing evolutionary interest, but also because MHC genes are relevant to conservation genetics

because of their functional importance in the immune system (Piertney and Oliver 2006; Piertney 2016).

In order to assess the genetic potential of a species to adapt to emerging disease threats, it is important to elucidate the evolutionary processes underlying functionally important genetic diversity (Eizaguirre and Baltazar-Soares 2014). How selection maintains multiple alleles at a single locus, such as a MHC gene, has been a fundamental question since the discovery of standing genetic variation in natural populations in the last century (Kimura 1956; Kimura and Crow 1964; Clarke and Kirby 1966; Hughes and Seneta 1975; Nagylaki and Lou 2006). One hypothesis for the generation and maintenance of MHC diversity is parasite-mediated balancing selection (Hughes and Yeager 1998; Bernatchez and Landry 2003) resulting from one or more of the following non-exclusive mechanisms: (1) heterozygote advantage (over-dominance), (2) negative frequency-dependent selection (rare-allele advantage), and (3) fluctuating selection in response to temporal and spatial changes in parasite species and numbers (reviewed in Spurgin and Richardson 2010). There is also evidence of MHC polymorphisms being maintained over long evolutionary time periods (Klein *et al.* 1998; Azevedo *et al.* 2015; Eimes *et al.* 2015; Tesicky and Vinkler 2015). Over 50 years of research into mechanisms behind the origin and maintenance of diversity in MHC genes has revealed many different mechanisms, with no single hypothesis rising to the top (Bernatchez and Landry 2003; Garrigan and Hedrick 2003; Lenz 2018).

Prairie dogs (*Cynomys* spp.) are social burrowing rodents in the squirrel family (Sciuridae) whose range extends from Canada into Mexico across the great plains of North America (Hoogland 1996; Slobodchikoff *et al.* 2009). Prairie dogs are an important component of North American grasslands (Kotliar 2000; Miller *et al.* 2007), but have declined throughout

their range because of the introduced pathogen *Yersinia pestis*, causative agent of plague (Antolin *et al.* 2002). There are five species in the genus, two of which are currently listed under the Endangered Species Act (*C. parvidens*, the Utah prairie dog, and *C. mexicanus*, the Mexican prairie dog; USFWS 2017). The black-tailed prairie dog (*C. ludovicianus*), while much reduced in abundance, is the most widespread of the five species. Population bottlenecks resulting from local population extinctions because of plague may result in a decrease of genetic diversity in prairie dog populations that could be compounded by genetic drift and inbreeding in small colonies (Trudeau *et al.* 2004), though this effect may be mitigated by the evolution of metapopulation dynamics in response to plague (Salkeld *et al.* 2016). There is also some evidence that prairie dogs may be evolving resistance to plague (Rocke *et al.* 2012; Sackett *et al.* 2013). In addition to *Y. pestis*, at least 83 parasite species have been documented for black-tailed prairie dogs (Chapter 2), primarily fleas and protozoa (e.g., *Eimeria* spp.). Although some records likely represent transient infections (e.g., rabies virus), it is apparent that prairie dogs face enormous parasite pressure that has the potential to apply selective pressure on immune system genes (Trowsdale and Parham 2004).

In this study we investigate mechanisms of selection and characterize genetic variation at the MHC DRB locus in three black-tailed prairie dog colonies on Pawnee National Grassland, Colorado. Exon 2 of the DRB gene was chosen because it encodes the peptide binding region of class II molecules, and because its hypervariability is thought to be maintained by balancing selection (Bernatchez and Landry 2003). This study furthers our understanding of selection mechanisms acting on MHC genes, and provides a baseline for future studies of functional genetic diversity in black-tailed prairie dogs.

Methods

Sample collection and DNA extraction

We live-trapped black-tailed prairie dogs in north-central Colorado on the western (Crow Valley) unit of the Pawnee National Grassland (PNG; Fig. 3.1). The western unit of the PNG contains large portions of contiguous federal grassland periodically interrupted by parcels of state and private land. Black-tailed prairie dogs were captured from three colonies February – November 2007 and April – November 2008. Samples from July – August 2006 were collected by Tripp (2009) using the same methods detailed here. All protocols were reviewed and approved by the Colorado State University Animal Care and Use Committee.

On each town 100 Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) were placed according to the following protocol: For each town 100 points were randomly selected using Arc/INFO 9.0, ArcView 3.3, ArcMap 8.3, or Arc9 (Environmental Research Institute, Redlands, CA), and traps were placed at the entrance to the closest active burrow within 15 meters of each point. For each trapping day, traps were opened between 5:00 AM and 7:00 AM, baited with 8% 3-way sweet feed (Manna Pro Corp, St. Louis, MO), and then checked for captures between 9:00 AM and 11:00 AM. Captured prairie dogs were brought back to a central location within the boundaries of the town and held in the shade during sample collection to avoid overheating. Empty traps were wired open to ensure prairie dogs would not be captured while traps were not being monitored.

Captured prairie dogs were anesthetized using isoflurane (Halocarbon Industries, River Edge, NJ) in a two-step process. In the first step, an individual prairie dog was isolated inside a 1 gallon container that contained a tea strainer with an isoflurane-soaked cotton ball inside; prairie dogs were closely monitored during the process to prevent an overdose. Once the prairie dog was

immobile, it was removed from the container and held inside a plastic tub while we used a fine-toothed comb to remove fleas (also anesthetized) from the animal. Fleas were immediately placed into vials containing 1.5% saline with 0.001% TWEEN 80 (ICN Biomedicals Inc., Aurora, OH) and stored on ice until returning to the lab, at which point they were transferred to a -20°C freezer. Once all fleas were removed from the prairie dog, the animal was administered isoflurane via an oxygen-driven vaporizer (Seven-Seven Anesthesia Inc., Fort Collins, CO) through a small bell-shaped cover (open at the bottom) fitted over the animal's head. Each prairie dog was weighed and then classified by sex and age (juvenile, yearling, adult; based on size, body condition, and pelage). A small tissue sample was taken from the tip of each animal's tail, placed in a vial containing 70% ethanol, and stored on ice until returned to the lab, where vials were stored in a -20°C freezer. Each animal received a tag on each ear (National Band and Tag Co., Newport, KY) to enable identification of recaptured individuals. After sample collection and tagging, animals were allowed to fully recover from the anesthesia in the shade before being returned to the point of capture.

Genomic DNA was extracted from tail tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions.

Molecular methods

Microsatellites

We amplified seven nuclear microsatellite loci specifically designed for black-tailed prairie dogs (A2, A104, C116, D1, D2, D12, D115; Jones *et al.* 2005). All microsatellites were amplified in 25 µl reaction volumes using 2 µl template DNA, 1X buffer, 0.8 mM deoxynucleoside triphosphates, 0.2 mM fluorescently labeled forward primer (Applied Biosystems), 0.4 mM reverse primer (Applied Biosystems), [2.5-3.75] mM MgCl₂, and 0.02 U

AmpliTaq Gold DNA polymerase (Applied Biosystems). All reactions were carried out in a MyCycler thermocycler (BioRad, Hercules, CA) using touchdown PCR (Korbie and Mattick 2008) and annealing temperatures (T_A) from Jones et al. (2005) under the following conditions: initial denaturing at 95°C for 10 min followed by 32 cycles of 94°C for 30 s, touchdown annealing ($T_A + 10^\circ\text{C}$ to start, stepped down by 0.5°C each cycle until T_A is reached) for 90 s, 72°C for 1 min, with a final extension step of 72°C for 10 min. All polymerase chain reactions included a negative control prepared at the same time as the samples and containing the same reagents but no DNA. For each PCR sample plate, the presence, approximate size, and relative quality of a subsample of PCR products was confirmed visually on 3% agarose gels containing GelRed (Biotium, Fremont, CA).

All PCR products were sequenced on an Applied Biosystems 3730XL Genetic Analyzer (Applied Biosystems, Foster City, CA) at the Cornell University Biotechnology Resource Center (Ithaca, NY). Samples were submitted in 96 well plates (95 individual or pooled samples, and 1 negative control), each containing 5 μl pooled PCR product, 0.5 μl LIZ 600 Size Standard (Life Technologies, Carlsbad, CA), and 14.5 μl Hi-Di formamide (Life Technologies, Carlsbad, CA). Prior to submission, we assessed the average concentration of PCR products for each microsatellite, and diluted products down to approximately 10 ng DNA per μl . After diluting individual PCR products, we aliquoted individual samples into 96 well plates with up to 4 samples per well in equal amounts. Pooled samples that used the same fluorescent primer (i.e., 6-FAM, VIC, NED, PET) did not have overlapping size ranges. All microsatellite loci were run at least twice and scored manually using Geneious v7 (Kearse *et al.* 2012). We checked all microsatellite loci for null alleles using Microchecker software (van Oosterhout *et al.* 2006).

Class II MHC DRB exon 2 – Amplification and sequencing

PCR reactions for MHC class II DRB exon 2 were prepared in a 25 µl reaction volume with 2 µl DNA taq polymerase, 0.5 µl forward primer (10 uM), 0.5 µl reverse primer (10 uM), 0.25 µl total combined dNTPs (20 mM), 2.5 µl 10x buffer with MgCl₂, 2 µl DNA template, and 19.1 µl ddH₂O, and run under the following conditions using a MyCycler thermocycler (BioRad): an initial denaturing step at 92°C for 5 min, followed by 35 cycles of 92°C for 1 min, 55°C for 1 min, 72°C for 10 min, with a final extension step of 70°C for 10 min. All PCR products were run on a 1% agarose gel to confirm presence and size of products, and sequenced bidirectionally at the University of Chicago Cancer Research Center DNA Sequencing Facility on an Applied Biosystems 3730xl sequencer. Primers for PCR and sequencing reactions were from Erlich and Bugawan (1990), GH46F (CCGGATCCTTCGTGTCCCCACAGCACG) and GH50R (CTCCCCAACCCCGTAGTTGTGTCTGCA).

Class II MHC DRB exon 2 – Haplotype determination

I used single strand conformation polymorphism (SSCP; Orita *et al.* 1989) for initial genotyping of individuals. For each sample we mixed 1 µl PCR product with 6 µl formamide stop buffer (10 mM NaOH, 95% formamide, 0.05% bromophenol blue, 0.05% xylene cyanol) and denatured for 5 minutes at 95°C followed immediately by an ice water bath. Samples were loaded into 30% acrylamide gels (30% acrylamide, 2% bis-acrylamide) and run on a vertical electrophoresis system for 14-18 hours at 350 V followed by silver staining to visualize the resulting bands.

After initial genotyping by SSCP analysis, all samples were sequenced bi-directionally, aligned using Geneious v7 (Kearse *et al.* 2012), checked manually for accuracy, and haplotypes were determined using a combination of the software PHASE v2.1 (Stephens *et al.* 2001)

implemented in DnaSP v5.10 (Librado and Rozas 2009) and manual determination using Geneious v7 (Kearse et al. 2012). Each haplotype was confirmed to be from MHC class II DRB exon 2 by performing a nucleotide BLAST search for homologous sequences (Altschul et al. 1990). Sequences were considered to be true MHC class II DRB exon 2 alleles if they were amplified at least twice in separate PCR reactions and had significant sequence similarity with other members of Sciuridae in BLASTn search results (all e-values $\leq 2e-106$).

Characterizing class II MHC DRB genetic diversity

Allelic richness, corrected for sample size using rarefaction (El Mousadik and Petit 1996; Kalinowski 2004) was calculated using the program FSTAT (Goudet 1995; 2001). Number of segregating sites (S), haplotype diversity (H_d), average number of nucleotide differences between alleles (K), and nucleotide diversity (π) were calculated for the MHC DRB locus using DnaSP v.5 (Librado and Rozas 2009). Nucleotide diversity and haplotype diversity are both measures of heterozygosity (Nei 1987). Nucleotide diversity is the average number of nucleotide differences per site between any two alleles, while haplotype diversity represents the probability that two randomly sampled alleles are different, based on the relative frequencies of the haplotypes (Tajima 1983; Depaulis and Veuille 1998).

Comparison of microsatellite and class II MHC DRB genetic diversity

For both microsatellites and the DRB locus, observed and expected heterozygosities (H_o and H_e) were calculated using the package popgenreport (Adamack and Gruber 2014) implemented in R (R Core Team 2017). The inbreeding coefficient (F_{is}) and tests of deviation from Hardy-Weinberg proportions were calculated using the package genepop (Rousset 2008) implemented in R (R Core Team 2017), with p-values corrected for multiple testing following the false discovery rate method (Benjamini and Hochberg 1995). Pairwise and global estimators

of Jost's D (Chao *et al.* 2008; Jost 2008) and Weir and Cockerham's Θ (Weir and Cockerham 1984) and their bias-corrected bootstrapped confidence intervals (10,000 replicates) were calculated using the package *diveRsity* (Keenan *et al.* 2013) implemented in R (R Core Team 2017). We chose to calculate Jost's D in addition to Θ to measure population differentiation because estimates of Θ may be skewed downward for highly variable loci, such as MHC DRB , and because Jost's D takes into account differences in allele frequencies between populations (Jost 2008). To see if physical distance between colonies or time since colonization could explain pairwise values of Θ or Jost's D, we performed Mantel tests using the package *ade4* (Dray and Dufour 2007) implemented in R (R Core Team 2017).

Analyses of natural selection at the class II MHC DRB locus

Tajima's D (Tajima 1989), which compares the frequency of derived segregating site variants to the neutral expectation, was calculated using *DnaSP v.5* (Librado and Rozas 2009). An excess of rare variants results in a negative Tajima's D value, suggesting purifying selection or population growth, while an excess of intermediate frequency variants results in a positive Tajima's D, suggesting balancing selection or population structure with sampling from many populations. Thus Tajima's D is expected to be zero in the absence of selection (neutrality), positive in the presence of balancing selection, and negative in the presence of purifying selection (Tajima 1989).

The ratio (ω) of nonsynonymous (amino-acid changing; d_N) to synonymous (silent; d_S) DNA base substitutions provides a measure of selective pressure at the amino acid level (Hughes and Nei 1988; Yang and Nielsen 2002), where a value of $\omega = 1$ ($d_N = d_S$) indicates a lack of selective pressure, while sequences with $\omega > 1$ ($d_N > d_S$) show evidence of positive (diversifying) selection, and sequences with

$\omega < 1$ ($d_N < d_S$) show evidence of purifying selection. Specific codons corresponding to amino acids within antigen binding sites (ABS) of the DRB locus were inferred based on the 3-dimensional crystallographic structure of the homologous human gene of the human leucocyte antigen complex (HLA; the human equivalent of the MHC), HLA-DR1 (Brown *et al.* 1993), ω was then calculated, using the method of Nei and Gojobori with the Jukes-Cantor correction (NEI AND GOJOBORI 1986), and a Z-test for positive selection was performed for ABS, non-ABS, and the entire sequence using MEGA 7.0 (Tamura *et al.* 2013; Kumar *et al.* 2016). The Jukes-Cantor correction accounts for multiple substitutions at a single site, such as is common in highly variable sequences (Jukes and Cantor 1969).

To further investigate selection at the MHC DRB locus, we used the CODEML program in the PAMLX package (Yang 2007; Xu and Yang 2013) to identify codons subject to positive selection using two pairs of codon-based substitution models: model M1a (nearly neutral) versus model M2a (positive selection), and model M7 (no positive selection) versus model M8 (positive selection). Model M1a assumes two site classes, with $0 < \omega_0 < 1$ (purifying selection with conserved sites) and $\omega_1 = 1$ (selectively neutral), while model M2a adds a third site class to model M1a, with $\omega_2 > 1$ (positive selection). Model M7 (β) uses a β distribution for ω approximating dN/dS variation, which does not allow for positively selected sites, while model M8 (β and ω) allows a proportion of sites to evolve with $\omega > 1$ (positive selection). For each model, CODEML calculates the log-likelihood of the data given the model, allowing the use of likelihood ratio tests (LRT) to compare each set of nested models (Yang *et al.* 2000): model M1a (null model) to model M2a (positive selection) and model M7 (null model) to model M8 (positive selection). A significant LRT indicates positive selection is likely to be acting on a proportion of sites (Yang *et al.* 2000; Yang *et al.* 2005). Because twice the log-likelihood

difference (Δ) between nested models can be compared to a chi-square distribution (Yang *et al.* 2000), we calculated $\Delta = -2*(\ln L(\text{null}) - \ln L(\text{selection}))$, and used the `pchisq` function in R (R Core Team 2017) with $df = 2$ (the number of additional parameters in the selection model) to determine the p-value for each LRT, with $p < 0.05$ suggesting a significant improvement in fit from the null model to the selection model. We then used the `getAIC` function in R (R Core Team 2017) to calculate AIC values based on $\ln L$ and the number of parameters for each model. If positive selection is inferred from a LRT, the CODEML program then uses a Bayes empirical Bayes (BEB) approach to calculate the posterior probability for each codon site that it is subject to positive selection (Yang *et al.* 2005).

Phylogenetic analysis

To infer phylogenetic relationships among alleles and to investigate the possibility of trans-species polymorphism (TSP) we used Bayesian inference of phylogeny implemented in MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The best-fit evolution model showing the relationship among DRB alleles was identified based on Akaike's information criterion (AIC) using MrModelTest 2.3 (Nylander 2004) implemented in PAUP 4.0a (Swofford 2002). In addition to alleles found in this research, we also included MHC DRB exon 2 sequences from other Sciuridae available on GenBank; sequences included 77 alleles from seven species: *C. gunnisoni* (9 alleles), *C. ludovicianus* (5 alleles), *Marmota marmota* (7 alleles), *M. monax* (15 alleles), *Sciurus vulgaris* (22 alleles), *Spermophilus citellus* (3 alleles), and *S. suslicus* (16 alleles). For the phylogenetic analysis, two separate MCMC analyses with four independent chains each (one cold, three heated) were run simultaneously for 33×10^6 generations with sampling every 100th generation, the first 25% of trees discarded as burn-in, and

a final average standard deviation of split frequencies < 0.01 . *Dipodomys spectabilis* (banner-tailed kangaroo rat) allele Disp-DRB*03 (GenBank accession # EU817481.1) was used as an outgroup because it was the most closely-related species outside of Sciuridae for which there was an MHC DRB sequence available in GenBank (Fabre *et al.* 2012). The resulting phylogenetic tree was visualized using the package ggtree (Yu *et al.* 2017) implemented in R (R Core Team 2017).

Class II MHC DRB supertype determination

To characterize functional diversity at the DRB locus, we grouped alleles into superotypes based on five physiochemical z-descriptors used to describe amino acids: z_1 (hydrophobicity), z_2 (steric bulk), z_3 (polarity), and z_4 and z_5 (electronic effects; Sandberg *et al.* 1998; Doytchinova and Flower 2005). First, we collapsed the genetic information contained in each of the 21 alleles down to two different subsets of nucleotide triplets (codons), each predicted to code for a specific amino acid: (1) codons identified as coding for antigen binding sites (ABS; $n = 18$) of the DRB molecule in humans (Fig. 2; Brown *et al.* 1993), and (2) codons identified from model M2a as being positively selected sites (PSS) according to the Bayes empirical Bayes method (Yang *et al.* 2005) with probability $> 95\%$. This resulted in two sets of alleles composed of codons located within regions hypothesized to be functionally important in antigen binding; nucleotides not located in these sites were not used in determining superotypes. We then characterized each codon using the physiochemical descriptor variables (z-descriptors) for amino acids from Sandberg *et al.* (1998) to create a matrix consisting of five numerical descriptors for each codon, so that each allele was now described by 55 or 65 numbers (ABS alleles: 13 codons*5 z-descriptors each = 65 z-descriptors; PSS alleles: 11 codons*5 z-descriptors = 55 z-descriptors). We used the adegenet package (Jombart 2008; Jombart and Ahmed 2011)

implemented in R (R Core Team 2017) to group alleles into functional clusters using discriminant analysis of principal components (DAPC; Jombart *et al.* 2010).

Results

Class II MHC DRB genetic diversity

From 137 prairie dogs we amplified 21 unique alleles of a 220-bp region (excluding primer regions) of MHC class II DRB exon 2, corresponding to a region encoding 73 amino acids (Fig. 3.2). No stop codons were detected in any of the sequences. No more than two alleles were found in any individual, suggesting no duplication of the DRB locus in black-tailed prairie dogs, consistent with most other research in ground squirrels (Biedrzycka and Radwan 2008; Biedrzycka *et al.* 2011; Ricanova *et al.* 2011; Cobble *et al.* 2016; Ferrandiz-Rovira *et al.* 2016). BLASTn search results for each allele confirmed homology with known MHC class II DRB exon 2 sequences from other sciurid species.

A nucleotide alignment of the 21 220-bp DRB alleles (Fig. 3.2) revealed 56 segregating (polymorphic) sites, with haplotype diversity of 0.82 and nucleotide diversity of 0.09 (Table 3.1). Haplotype diversity was highest on colonies 88 ($H_d = 0.81$) and 70 ($H_d = 0.80$), while nucleotide diversity was highest on colony 81 ($\pi = 0.10$; Table 3.1). A genbank search revealed that allele I, the most common allele (Table 3.2, Fig. 3.3), was identical to a previously described black-tailed prairie dog allele (Cylu-DRB1*04; GenBank accession KR338367.1), from Phillips County, Montana (Cobble *et al.* 2016).

The number of DRB alleles differed for each colony, but was consistent with sample sizes (e.g., lowest sample size yielded fewest alleles; Table 3.3). Allelic richness (A_r), rarefied to adjust for uneven samples, was highest in colony 70 ($A_r = 13.61$), and lowest in colony 88 ($A_r = 10.8$; Table 3.3).

The most common allele (allele I), had an overall frequency of 0.372, and occurred at high frequencies in all three colonies (70 = 0.39, 81 = 0.46, 88 = 0.282; Table 3.2, Fig. 3.3). The majority of alleles ($n = 17$) had overall frequency < 0.05 (Table 3.2). In colonies 70 and 81, just two alleles occurred at frequencies higher than 0.07, and in colony 88, just three alleles occurred at frequencies above 0.07 (Table 3.2, Fig 3.3). As mentioned previously, allele I occurred at high frequency in all three colonies, however the second most frequent allele was different in each colony (Table 3.2, Fig. 3.3). In fact, the second most frequent alleles in colony 70 (allele L, freq. = 0.205) and colony 81 (allele P, freq. = 0.22) were not found at all in colony 88, and the most frequent allele in colony 88 (allele Q, freq. = 0.308) was found at very low frequencies in colony 70 (freq. allele Q = 0.027) and colony 81 (freq. allele Q = 0.04; Table 2, Fig. 3.3). The two most frequent alleles in each colony accounted for over 59% of alleles in that colony. Six of the 21 alleles were found in all three colonies (alleles A, B, I, K, N, Q; Table 3.2). Only two alleles were found to occur just once across all three colonies (alleles O and R; Table 3.2). Colony 70 had four private alleles (alleles C, D, R, and X), colony 88 had one private allele (allele O), and colony 81 had no private alleles (Table 3.2). The DRB locus deviated from HWE in each of the three colonies, with observed heterozygosity consistently lower than expected ($p < 0.0001$; Table 3.2).

Class II MHC DRB supertype determination

DRB alleles clustered into two superotypes (Table 3.2) within both groups of alleles, one identified by antigen binding sites (ABS), and the other identified by positively selected sites (PSS). Clustering was not identical in the ABS and PSS superotypes, although there was some overlap (Table 3.2). Nine alleles clustered together in both ABS supertype 1 and PSS supertype 1 (alleles J, M, N, P, Q, R, T, U, and W), while just four alleles clustered together into ABS

supertype 2 and PSS supertype 2 (alleles C, F, I, and K; Table 3.2). Eight alleles diverged entirely from this pattern of shared clustering, with alleles A, B, D, E, L, O, V, and X clustering with ABS superrtype 1 and PSS supertype 2. Interestingly, the two most frequent alleles in each colony belonged to different ABS supertypes, while the most frequent alleles in colonies 81 and 88 also belonged to different PSS supertypes (Table 3.2). Of the three alleles that had a global frequency greater than 0.10 (alleles I, L, Q), alleles I and Q belonged to different ABS and PSS supertypes, while allele L clustered into ABS supertype 1 and PSS supertype 2 (Table 3.2).

Comparison of class II MHC DRB genetic diversity to neutral genetic diversity

A total of 137 individuals were genotyped at seven microsatellite loci, but analysis revealed evidence for null alleles at one microsatellite locus, C116, which was therefore not further considered in population genetic analyses. Number of alleles per colony for each locus, as well as allelic richness (A_r), observed (H_o) and expected (H_e) heterozygosity, and the inbreeding coefficient (F_{is}) are shown in Table 3.3. Microsatellite locus D1 showed evidence of deviation from Hardy-Weinberg equilibrium (HWE) in all three colonies (corrected p-value = 0.0477 for each colony), with observed heterozygosity lower than expected in colonies 70 and 81, and higher than expected in colony 88 (Table 3.3). Locus D12 had a significant heterozygote deficiency in colony 70 (corrected p-value = 0.048). There were no other significant departures from HWE for microsatellite loci ($0.146 < p < 0.9658$; Table 3.3).

Global per-locus estimates for Weir and Cockerham's Θ are shown in Table 3.4, with $0.025 < \Theta_{msats} < 0.111$, multi-locus $\Theta_{msats} = 0.064$, and $\Theta_{DRB} = 0.066$. All Θ estimates except one (microsatellite locus D12) had bootstrapped confidence intervals that did not include zero (Table 3.4), indicating genetic differentiation between these three populations. Global Jost's D estimates showed a similar pattern, with $0.022 < D < 0.324$ for microsatellite loci, multi-locus $D = 0.202$

for microsatellites, and $D = 0.292$ for the DRB locus (Table 3.4). All global estimates of Jost's D had bootstrapped confidence intervals that did not include zero (Table 3.4).

Pairwise estimates of Weir and Cockerham's Θ , comparing differentiation among individual colonies, were similar for microsatellites ($0.065 < \Theta_{\text{msats}} < 0.076$), showing a slight reduction in heterozygosity for all population pairs compared to panmixia (Table 3.5). In contrast, for the DRB locus, the pairwise estimate of Θ for colony 70 vs. 81 was low ($\Theta = 0.023$) compared to 70 vs. 88 ($\Theta = 0.078$) and 81 vs. 88 ($\Theta = 0.089$; Table 3.5). Allelic differentiation, as measured by Jost's D , was highest for the DRB locus in comparisons of colony 70 vs. 88 ($D = 0.353$) and 81 vs. 88 ($D = 0.345$), about three times the highest values for microsatellites (70 vs. 81: $D = 0.116$; 70 vs. 88: $D = 0.119$; Table 3.5). The lowest values of Jost's D were for microsatellites for colony 81 vs. 88 ($D = 0.074$) and the DRB locus for 70 vs. 81 ($D = 0.087$; Table 3.5). The only pairwise confidence intervals that included zero occurred with comparisons of colony 70 vs. 81 for the DRB locus ($-0.009 < \Theta < 0.066$; $-0.018 < D < 0.226$; Table 3.5). Mantel tests investigating correlations between values of Θ and Jost's D and either physical distance between colonies or time since colonization were not significant ($0.176 < p < 0.841$).

Evidence for selection at the class II MHC DRB locus

Tajima's D , which compares the observed distribution of derived nucleotides to neutral expectations (Tajima 1989), for the DRB locus showed support for balancing selection at all three colonies individually and combined ($2.16 < D < 3.02$; $p < 0.05$; Table 3.6). On the other hand, codon-based Z-tests for positive selection, which test for differences between non-synonymous and synonymous substitution rates, revealed a significant excess of non-synonymous substitutions compared to synonymous substitutions at putative antigen-binding sites (ABS) within colonies ($4.107 < dN/dS < 8.641$; $2.046 < Z < 3.490$; $0.0003 < p < 0.0215$) and

across all colonies (ABS; $dN/dS = 1.908$, $Z = 2.486$, $p = 0.007$), indicating effects of positive selection (Table 3.6). In contrast, non-synonymous substitution rates did not exceed synonymous rates at non-ABS sites ($0.643 < dN/dS < 0.821$; $-1.368 < Z < 0.206$; $0.4188 < p \leq 1.000$; Table 3.6). The dN/dS ratio for the entire 220-bp sequence (ABS and non-ABS combined) was significantly positive only for colony 88 ($dN/dS = 1.373$, $Z = 1.819$, $p = 0.0357$; Table 3.6).

Likelihood ratio tests of nested models implemented in the CODEML program showed significantly more support for positive selection models within and across colonies ($p < 0.0001$; Table 3.7). Both positive selection models (M2a and M8) had similar AIC values for all sets of alleles (Table 3.7). There were several cases where positively selected codon sites (PSS) were identified by model M8 but not model M2a (Table 3.7). Six codon sites (13, 37, 38, 67, 70, 71) were identified by both positive selection models (M2a, M8), with posterior probability $> 95\%$, PSS in all three colonies and for the entire set of alleles, three of which (codon sites 67, 70, 71) had posterior probability $> 99\%$ for all sets of alleles (Table 3.7). Five codon sites (13, 37, 38, 70, 71) identified as PSS with posterior probability $> 95\%$ were located in putative ABS, and the sixth (codon site 67) was adjacent to a putative ABS (Fig. 3.2). Codon site 47, located in a putative ABS, was identified by both models with $>95\%$ posterior probability as PSS for allele sets from all three colonies, but not for the entire set of alleles (Table 3.7).

Phylogenetic evidence for trans-species polymorphism

Figure 4 shows phylogenetic relationships among 77 DRB exon 2 sequences from seven species in the squirrel family (Sciuridae), including 21 alleles from this research. Only posterior probabilities less than 100% are shown in order to reduce clutter within the tree. The best fit nucleotide substitution model for the relationship between DRB alleles was the symmetrical

model (Zharkikh 1994) with gamma distributed rate variation among sites (SYM + G; AIC weight = 0.5061).

Alleles from tree squirrels (*Sciurus vulgaris*) and ground squirrels (*Cynomys* spp., *Marmota* spp., *Spermophilus* spp.) formed separate clades, with tree squirrels basal to ground squirrels. There were four cases of trans-species polymorphism (TSP), labelled TSP 1 – TSP 4 in figure 3, suggesting alleles within each group were likely derived from a common ancestor but are still identifiable after speciation (Klein *et al.* 1998). Pairwise alignments of each TSP group are shown in figure 4. TSP 1 included two nodes that formed a dichotomy at the distal end of a clade that contained mostly black-tailed prairie dog alleles. One node in TSP 1 included allele I from this research, and the identical allele, Cylu-DRB1*04, isolated by Cobble *et al.* (2016) from a black-tailed prairie dog captured in Phillips county, Montana, while the other node included two alleles, Cygu-DRB*4 and Cygu-DRB1*04, isolated by Cobble *et al.* (2016) from Gunnison’s prairie dogs sampled in Arizona.

TSP 1 was supported with 99% posterior probability and included four alleles from two prairie dog species (2 alleles each; Fig. 3.4). Both of the Gunnison’s prairie dog alleles were identical, as were the two black-tailed prairie dog alleles, and differed from the other species’ allele at two amino acid sites (3 nucleotide sites), one in a putative ABS, and the other adjacent to a putative ABS (Fig. 3.5). Even though all species in TSP 1 were prairie dogs, it is remarkable they are so alike, because they were collected from two different species in three different states (Cygu-DRB*4 and Cygu-DRB1*04 from Arizona (Cobble *et al.* 2016), allele I from Colorado, and Cylu-DRB1*04 from Montana (Cobble *et al.* 2016)).

TSP 2 was supported with 100% posterior probability and included four alleles from three species: black-tailed prairie dogs (2 alleles), Gunnison’s prairie dogs (1 allele), and

spotted suslik (*Spermophilus suslicus*; 1 allele; Fig. 3.4). There were 19 variable amino acid sites (35 variable nucleotide sites) in the TSP 2 alignment, however, Cylu-DRB1*02 and Cygu-DRB*2 differed from each other at just a single amino acid site, and Spsu-DRB*09 differed from both Cylu-DRB1*02 and Cygu-DRB*2 at just eight amino acid sites (Fig. 3.5). The spotted suslik allele, Spsu-DRB*09, was collected from southeast Poland (Biedrzycka and Radwan 2008), while the prairie dog alleles were collected in either northern Arizona (Cylu-DRB1*02, Cygu-DRB*2 (Cobble *et al.* 2016) or northern Colorado (allele P; this research).

TSP 3 was supported with 99% posterior probability and included two alleles from *Spermophilus* species, one from European ground squirrel (*S. citellus*), and one from spotted suslik (*S. suslicus*; Fig. 3.4). There were seven variable amino acid sites (11 variable nucleotide sites) in the TSP 3 alignment (Fig. 3.5). Spci-DRB*04 was collected in Czech Republic, Slovakia, or Hungary (Ricanova *et al.* 2011), while Spsu-DRB*14 was collected in southeast Poland (Biedrzycka and Radwan 2008).

TSP 4 was supported with just 63% posterior probability and included four alleles from two *Spermophilus* species, one from European ground squirrel (*S. citellus*), and three from spotted suslik (*S. spermophilus*; Fig. 3.4). If one of the spotted suslik alleles is excluded from TSP 4, support increases to 100% posterior probability (Fig. 3.4). There were 18 variable amino acid sites (25 variable nucleotide sites) in the TSP 4 alignment, however, Spci-DRB*03, Spsu-DRB*15, and Spsu-DRB*04 are identical at all but three sites; Spci-DRB*03 and Spsu-DRB*15 differ at only one site (Fig. 3.5). Collection locations were the same as for alleles in TSP 3.

Of the 21 alleles isolated in this research, nine (alleles B, C, D, E, F, I, K, P, V) clustered with previously described prairie dog alleles, two alleles (alleles O and U) formed their own

cluster, and alleles L, M, N, Q, R, and X were located at solitary nodes within the ground squirrel clade (Fig. 3.4).

Discussion

This is the first large-scale survey of genetic diversity at the functionally important class II MHC DRB locus of black-tailed prairie dogs and the first investigation into potential contemporary and historic evolutionary mechanisms shaping that diversity. We found high levels of allelic and nucleotide diversity for the DRB locus in black-tailed prairie dogs, and was able to detect signatures of selection despite limited temporal and spatial sampling, and ongoing genetic drift combined with regular disease-induced extinction and colonization. These results provide evidence that long-term balancing selection has acted historically to maintain high levels of genetic diversity, and that positive directional selection is currently acting on the DRB locus in black-tailed prairie dogs on Pawnee National Grassland. Black-tailed prairie dogs are exposed to a considerable diversity of parasites that could potentially be recognized by class II MHC molecules (Chapter 2), suggesting that selection acting on the DRB locus is mediated, at least in part, by parasites.

Class II MHC DRB genetic diversity

The number of alleles per colony (Table 3.3) was higher than is typically found in rodents at individual sampling localities (Fig. 3.6). Black-tailed prairie dogs on Pawnee National Grassland harbored a greater number of different alleles per colony (Table 3.3) than have been recorded at an individual sampling locality from non-murid rodents with an unduplicated DRB locus (Fig. 3.7), and a greater total number of alleles than most other squirrel species (Fig. 3.8). Twenty of the 21 alleles were previously undescribed for black-tailed prairie dogs, bringing the total number of black-tailed prairie dog alleles to 25 (Fig. 3.8), just over six times as many as

have been found in Gunnison's prairie dogs (Cobble *et al.* 2016). These results are consistent with low genetic diversity previously found in Gunnison's prairie dogs (Travis *et al.* 1997), and generally high levels of genetic diversity found in black-tailed prairie dogs (Antolin *et al.* 2006), despite temporary local reductions in diversity as a result of plague epizootics (Roach 1999; Trudeau *et al.* 2004).

Allelic richness at the DRB locus (Table 3.3) was also higher than current values for other squirrel species, and is at the upper end of what is typically found in wild rodents (Fig. 3.9). For samples under 65 individuals there is a trend of finding additional alleles with increased sample size for wild rodents (Fig. 3.7), while that same trend tends to level off at about 40 individuals for allelic richness (Fig. 3.9), suggesting that research studying MHC DRB allelic diversity in rodents should aim for a minimum sample size of 40 – 65 individuals. Given this information, and that the probability of finding rare alleles increases with increasing sample size (El Mousadik and Petit 1996), along with the fact that most DRB alleles occurred at low frequency (Table 2, Fig. 3.3), it is likely that the number of alleles found in colony 81, and possibly colony 88 (Table 3.3), underrepresents true allelic diversity for the DRB locus in those colonies.

Haplotype diversity at the DRB locus (Table 3.1), which represents the probability that two randomly sampled alleles are different, was similar to that reported from other rodent species (Fig. 3.10). In contrast, nucleotide diversity (Table 3.1), the average number of nucleotide differences per site in pairwise comparisons, is at the upper end of what has been reported from rodents (Fig. 3.11). Similarly, with an average of about 10% difference between alleles, the average number of nucleotide differences (Table 3.1) is also at the upper end of what

has been reported from rodents (Fig. 3.12). It is unclear how these results compare to other squirrel species, as we were unable to find published values for these genetic diversity measures.

High levels of allelic and nucleotide diversity are common for the DRB locus (Klein and Figueroa 1986; Hedrick 1998; Bernatchez and Landry 2003). The maintenance of such high levels of genetic diversity is typically attributed to some form of balancing selection, such as heterozygote advantage, negative frequency-dependent selection (i.e., rare-allele advantage), or fluctuating selection, which can be further mediated through host-parasite interactions or sexual selection (e.g., for mates that are genetically diverse or different; Hedrick and Thomson 1983; Hughes and Nei 1992; Apanius *et al.* 1997; Hedrick 1998; Sommer 2005a). The original source of genetic diversity at the DRB locus is likely either positive directional selection or diversifying selection (Hughes and Nei 1988; Ritte *et al.* 1991).

Class II MHC DRB supertype determination

Based on previous research in mammals that grouped DRB alleles according to supertype, with the fewest number of alleles ($n = 22$) being able to be grouped into seven superotypes, (e.g., Schwensow *et al.* 2007; Kaesler *et al.* 2017; Marmesat *et al.* 2017), we expected prairie dog alleles to cluster into more than just two superotypes (Table 3.2). Clustering MHC alleles into superotypes was originally suggested as a way to organize the vast number of human MHC alleles into functional groups for vaccine development (Southwood *et al.* 1998; Trachtenberg *et al.* 2003). Doytchinova and Flower (2005) found non-hierarchical k-means clustering on z-scores to be a reliable method for human MHC alleles, but consistent statistical methods among wildlife researchers have not yet been established. For example, in a random sample of seven studies that grouped alleles by supertype, two used a tree-based method (Schwensow *et al.* 2007; Ellison *et al.* 2012), two used hierarchical clustering (Meyer-Lucht *et*

al. 2010; Marmesat *et al.* 2017), one used k-means clustering (Kaesler *et al.* 2017), one used k-means clustering in combination with DAPC (Buczek *et al.* 2016), and one gave up trying to classify their alleles into supertypes using a tree-based method (Srithayakumar *et al.* 2011), as they were unable to group their 67 alleles into fewer than 62 supertypes, a result that is difficult to interpret. Discriminant analysis of principal components (DAPC) using the adegenet package (Jombart 2008; Jombart and Ahmed 2011) implemented in R (R Core Team 2017) appears to be commonly used among bird researchers (e.g., Sepil *et al.* 2012; Eimes *et al.* 2015; Gonzalez-Quevedo *et al.* 2015), and was the method we employed. In summary, while it may be that the 21 black-tailed prairie dog alleles from Pawnee National Grassland cluster into only two supertypes, there are at least two other alternatives that are not mutually exclusive: (1) reliable, consistent statistical techniques have yet to be established for wildlife research, and (2) with additional investigation into MHC class II DRB diversity and evolution in non-model organisms, we could find that the codons responsible for the functionally important antigen binding sites on MHC molecules are in different enough locations that the supertype concept in wildlife is not yet as practically useful as it is in human research.

Evidence for selection at the class II MHC DRB locus

In contrast to microsatellite loci, we found significant heterozygote deficiency at the DRB locus in all three colonies (Table 3.3). Observed heterozygosity in wild rodents has been reported for 10 species from 64 sampling localities (Fig. 3.13), with significant heterozygote excess reported for 3 species at nine sites, and significant heterozygote deficiency reported for six species at 14 sites (Fig. 3.13). Unfortunately, most studies that have reported observed heterozygosity at the DRB locus in rodents did not test for significance, and many did not compare DRB heterozygosity to neutral loci, which could provide insight into processes other

than selection that may be influencing heterozygosity (Waples 2015). Combined evidence from this research and other studies of wild rodents does not appear to support heterozygote advantage at the DRB locus in wild rodents, in contrast to research in laboratory rodents (e.g., Doherty and Zinkernagel 1975b) and some other mammals (e.g., Schaschl *et al.* 2012; Osborne *et al.* 2015; Salmier *et al.* 2016)

Heterozygote deficiency can be explained by selective pressure, demographic processes (e.g., inbreeding), or stochastic processes (e.g., genetic drift; Hedrick 2011). Since microsatellites did not consistently show a pattern of heterozygote deficiency, it seems more likely that the lower heterozygosity at the DRB locus is explained by selection. Piertney and Oliver (2006) suggest that the selection advantage of MHC heterozygosity may be more important over long evolutionary timescales. On the other hand, current selective processes, such as parasite-mediated selection for specific alleles, could cause an increase in one or a few alleles, resulting in heterozygote deficiency (Bernatchez and Landry 2003, Piertney and Oliver 2006). The pattern that we observed at all three colonies of having two high-frequency alleles and many low-frequency alleles (Table 3.2, Fig. 3.3) suggests current positive selection for one or a few specific alleles. Because of the strong selection pressure imposed by *Y. pestis*, it is tempting to attribute the high frequency of allele I to protection from plague, but at the moment this is a purely speculative idea. Cobble *et al.* (2016), found a similar pattern of allele frequencies in Gunnison's prairie dogs (but no deviation from HWE), and attempted to find a significant link between specific alleles and either laboratory plague challenge survival or colony plague history, but their results were inconclusive.

Additional evidence for selection acting at the DRB locus in black-tailed prairie dogs comes from comparing the rates of synonymous (d_s) and non-synonymous (d_N) nucleotide

substitutions. In the absence of selection, the ratio of non-synonymous to synonymous substitutions (d_N/d_S) should be one, however, under the influence of positive selection the rate of non-synonymous nucleotide changes is expected to exceed synonymous changes, while purifying selection should result in fewer non-synonymous substitutions, since they would quickly be removed from the population as a result of their deleterious effects (Edwards and Hedrick 1998; Hughes and Yeager 1998; Garrigan and Hedrick 2003). Consistent with the prediction that dN/dS should be greater than one for antigen binding sites (ABS), and less than one for non-ABS (Hughes and Nei 1988; Hughes and Yeager 1998), we found dN/dS was significantly greater than one for putative ABS sites, and less than one at non-ABS for the entire set of alleles, and for the subset of alleles isolated from each colony (Table 3.6). This is consistent with most other rodents, including three species in the squirrel family (alpine marmot, eastern woodchuck, spotted suslik; Biedrzycka and Radwan 2008; Kuduk *et al.* 2012; Moreno-Cugnon *et al.* 2015), and provides evidence that positive directional or balancing selection is acting on the DRB locus in black-tailed prairie dogs on Pawnee National Grassland. This is in contrast to results from Cobble *et al.* (2016), who found no evidence of elevated non-synonymous substitutions in separate analyses of alleles from 94 Gunnison's prairie dogs and five black-tailed prairie dogs.

Tajima's D was significantly positive in all three colonies individually and collectively, suggesting that balancing selection has acted in the past to maintain levels of genetic diversity at the DRB locus that cannot be explained by neutral evolution (Tajima 1989; Garrigan and Hedrick 2003). This is consistent with previous results from other species, including humans (Hedrick 1994; Apanius *et al.* 1997; Hedrick 1998; Hughes and Yeager 1998; Meyer and Thomson 2001; Piertney and Oliver 2006).

Codon-based selection models allowing positive selection fit my data significantly better than neutral models for the entire set of alleles and for alleles found in each colony (Table 3.7). This is consistent with what has been found in a variety of mammals (e.g., Castro-Prieto *et al.* 2011; Zhang *et al.* 2018), including rodents (e.g., Cutrera *et al.* 2014; Scherman *et al.* 2014). Bayesian analysis provided evidence of positive selection acting on 21 of the 220 nucleotide sites examined (Table 3.7), most of which were located at or adjacent to proposed antigen binding sites (ABS; Fig. 2; Brown *et al.* 1993), consistent with most studies of other rodent species (Babik and Radwan 2007; Bryja *et al.* 2007; Kuduk *et al.* 2012; Froeschke and Sommer 2014; Scherman *et al.* 2014). In contrast, similar analyses in Gunnison's prairie dogs failed to reject neutral models (Cobble *et al.* 2016).

Evidence for trans-species polymorphism at the class II MHC DRB locus

Trans-species polymorphism, the non-neutral sharing of allelic lineages across species, is a common feature of genes subject to balancing selection (Takahata and Nei 1990; Klein *et al.* 2007). Winternitz *et al.* (2013) analyzed 601 alleles from 5565 individual rodents across 31 populations and 16 species, and found considerable evidence for trans-species polymorphism. In a phylogenetic analysis of 98 alleles from seven species in the squirrel family (Sciuridae), we found evidence for four instances of trans-species polymorphism among prairie dogs and spotted suslik, and between spotted suslik and European ground squirrels (Fig. 3.4), including alleles from black-tailed prairie dogs and Gunnison's prairie dogs that differed at just two amino acid sites (Fig. 3.5), and alleles from spotted suslik and European ground squirrels that differed at just three amino acid sites (Figs. 4, 5). Black-tailed and Gunnison's prairie dogs are estimated to have diverged approximately three million years ago, while approximately nine million years separates European ground squirrels and spotted susliks from their common ancestor. The two

genera, *Spermophilus* and *Cynomys*, are estimated to have diverged approximately 12 million years ago (Harrison *et al.* 2003). These divergence times are well within the 30 – 40 million year upper limit for taxa to share alleles proposed by Takahata and Nei (1990), and are consistent with evidence of trans-species polymorphism found in other squirrel species (Ricanova *et al.* 2011; Kuduk *et al.* 2012; Ballingall *et al.* 2016; Cobble *et al.* 2016). It is worth pointing out, however, that even though the species groupings agree with previous research, many branches of the tree are not well-supported, indicating the need for DRB sequences from additional species in order to provide a more complete picture of the evolution of the DRB locus in squirrels, and maintenance of trans-species polymorphisms over millions of years. Nonetheless, this research provides further evidence for the existence of trans-species evolution in rodents, and supports the hypothesis of balancing selection acting over long evolutionary time periods to maintain genetic diversity at the DRB locus in black-tailed prairie dogs.

In summary, we have documented relatively high levels of diversity at the functionally important class II MHC DRB locus in black-tailed prairie dogs, and presented evidence consistent with a combination of historical balancing selection acting over long-term evolutionary time periods, and positive directional selection responding to contemporary pressures (Kreitman 2000; Garrigan and Hedrick 2003). Significant heterozygote deficiency at the DRB locus in the absence of a similar pattern in microsatellites (Table 3.3) provides evidence of contemporary positive selection, while high levels of genetic diversity (Tables 3.1 and 3.2), an excess of non-synonymous substitutions (Table 3.6), and evidence of a greater number of intermediate frequency variants than expected under neutral expectations (D; Table 3.6) suggests some form of balancing selection has been acting historically to maintain genetic diversity (Kreitman 2000; Garrigan and Hedrick 2003). Additionally, codon-based nucleotide substitution

models identified sites in the DRB exon 2 sequence that have likely been subject to positive selection (Table 3.7), consistent with the discovery that amino acids at specific locations in the MHC protein are responsible for identifying foreign proteins and presenting them to T-cells to initiate an adaptive immune response (Doherty and Zinkernagel 1975a; Brown *et al.* 1993; Stern 1994; McFarland and Beeson 2002). Finally, evidence for trans-species polymorphisms shared between *Spermophilus* and *Cynomys* (Figs. 3 and 4), suggests that some alleles arose in the common ancestor, and have been maintained by positive selection favoring specific alleles over long-term evolutionary time periods (Klein *et al.* 1998; Tesicky and Vinkler 2015).

Most species face tremendous pressure from parasites (reviewed in Costello 2016) resulting in both long-term selection for specific alleles providing protection from common parasites (Kaesler *et al.* 2017), and maintenance of immunogenetic diversity in response to evolution of immune evasion tactics by parasites (Van Valen 1973; Borghans *et al.* 2004; Seppala and Jokela 2016). At least 84 different species of parasites have been isolated from black-tailed prairie dogs, and they likely harbor many more species, as bacteria and viruses are essentially undescribed in prairie dogs (chapter 2). While some parasite records are probably transient infections not generally found in prairie dogs (e.g., rabies virus), many are likely to be common, especially given that rodents harbor a greater diversity of parasites than other mammalian orders (Krasnov *et al.* 2006a). The most commonly found prairie dog parasites are fleas and protozoa (e.g., *Eimeria* spp.), relationships that may have persisted through speciation events (Hafner and Nadler 1988; Alcalá *et al.* 2017), while the most devastating is *Yersinia pestis*, introduced to North America in 1900 (Hampton 1940), and not found in prairie dogs until it was isolated from Utah prairie dogs in 1936 (Allred 1952). With such a variety of parasitological threats, it is not surprising to find high levels of genetic diversity in black-tailed

prairie dogs. In contrast, just 45 parasites, over half of them fleas, have been recorded for Gunnison's prairie dogs (Chapter 2). It is possible Gunnison's prairie dogs have less diversity at the DRB locus because of reduced parasite pressure (de Bellocq *et al.* 2008), resulting in a reduced genetic capacity to respond to future parasitic threats.

Wildlife reintroduction plans have typically included extensive anti-parasite treatments prior to releasing animals back into the wild (Stringer and Linklater 2014). There is growing awareness, however, that preserving native parasites may play a key role in immune system development (Stringer and Linklater 2014; Schulte-Hostedde and Mastromonaco 2015; Spencer and Zuk 2016), analogous to the hygiene hypothesis in humans (Barker *et al.* 1988; Villeneuve *et al.* 2018). In an experimental study, one day old wild Eurasian oystercatcher chicks were either treated with an anthelmintic to eradicate parasitic worm infections, or left untreated and consequently developed natural helminth infections. Contrary to the hypothesis that treated birds would perform better after fledging, survival was reduced in treated birds, even though untreated birds had higher worm burdens (Van Oers *et al.* 2002). Similarly, translocation of white rhinos from areas without tsetse flies, which transmit the protozoan parasite *Trypanosoma brucei*, to areas with tsetse flies, do not always survive *T. brucei* infection (Mihok *et al.* 1995). Parasites can also be lost during translocation events, even in the absence of anti-parasitic treatment. Six *Eimeria* species were isolated from 54 Gunnison's prairie dogs prior to their translocation from an urban to a rural area, while only two *Eimeria* species were found just three months later (Ryan *et al.* 2001). Reduced immunological competence and genetic diversity may also impair a species' ability to respond to novel parasites, such as happened to wolves that suffered parasite-induced declines when exposed to canine distemper virus and *Sarcoptes scabiei* (mange) following reintroduction to Yellowstone National Park (Almberg *et al.* 2012). As evidence

continues to mount (e.g., Vermeulen *et al.* 2016; Wait *et al.* 2017), more conservation plans may consider integrating native parasites into species management plans.

On the other hand, for species at risk of pathogen-induced extinction, such as black-footed ferrets, vaccines protecting against introduced disease may become an important wildlife conservation tool (Plumb *et al.* 2007; Salkeld 2017). A promising area of vaccine development research is focused on identifying the peptide binding specificity of MHC alleles in an attempt to formulate more effective vaccines for humans (Patronov and Doytchinova 2013; Sofron *et al.* 2016; Fleri *et al.* 2017) and domestic animals (Pandya *et al.* 2015; Obara *et al.* 2016) an approach that could be used for wildlife. Online peptide-binding prediction tools have been developed for human (Zhang *et al.* 2012; Giguere *et al.* 2013) and domestic animal (Gutierrez *et al.* 2015) MHC alleles. Such a database would be useful in wildlife conservation, as it would allow rapid sharing of information, and provide a central repository for the growing catalog of MHC alleles isolated from wildlife.

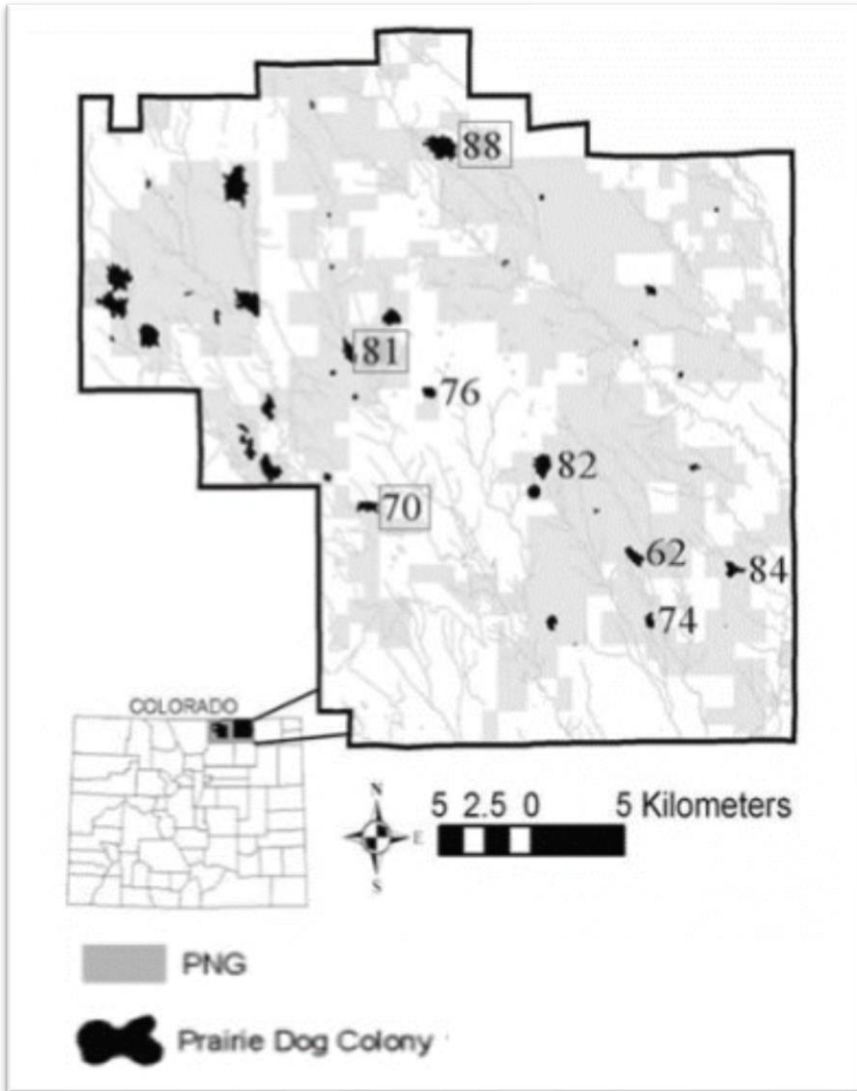


Figure 3-1
 Locations of prairie dog colonies on the western half of Pawnee National Grassland, Colorado 2007. Colonies outlined with grey boxes indicate sampling locations for this research.

Figure 3-2. Inferred amino acid alignment of 21 MHC DRB exon 2 alleles isolated from 137 black-tailed prairie dogs on Pawnee National Grassland, Colorado. Numbers correspond to common numbering of amino acid residues in human MHC DRB exon 2. A dot indicates amino acid identity with allele A. Gray shading indicates a proposed antigen binding site (ABS) in humans according to Brown et al. (1993). Circles above columns indicate sites identified by the Bayes empirical Bayes (BEB) procedure in the CODEML program implemented in PAMLX as experiencing positive selection (PSS; with probability greater than 95% that $\omega > 1$; Yang 2007), with closed circles (●) indicating sites identified by both models (M2a and M8), and open circles (○) indicating sites identified by model M8 only. Letters above columns indicate conserved sites at the 90% (b, d, f) and 100% (a, c, d) levels alleles from this research and alleles downloaded from GenBank (top 100 sequence matches for the four most frequent alleles (I, L, Q, P), with duplicates discarded, resulting in 166 GenBank sequences and 21 sequences from this research).

Table 3.1 Genetic diversity of MHC DRB exon 2 in 274 prairie dogs from three colonies (70, on Pawnee National Grassland, Colorado).

Colony	N	S	h	Hd	K	π
70	146	56	19	0.80	19.50	0.08
81	50	55	11	0.74	22.76	0.10
88	78	43	13	0.81	18.39	0.08
All	274	56	21	0.82	20.38	0.09

N= number of sequences, S = number of segregating sites, h = number of haplotypes, Hd = haplotype diversity, K = average number of nucleotide differences between two alleles, π = nucleotide diversity

Table 3.2 Allele frequencies and supertype groups for 21 alleles amplified from 137 black-tailed prairie dogs from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado. Frequencies > 0.05 are in bold, and private alleles are italicized.

Allele	ABS ST	PSS ST	n(70)	n(81)	n(88)	n(all)	freq(70)	freq(81)	freq(88)	freq(all)
I	2	2	57	23	22	102	0.390	0.460	0.282	0.372
L	1	2	30	2	0	32	0.205	0.040	0.000	0.117
Q	1	1	4	2	24	30	0.027	0.040	0.308	0.109
P	1	1	10	11	0	21	0.068	0.220	0.000	0.077
M	1	1	4	0	9	13	0.027	0.000	0.115	0.047
K	2	2	5	1	5	11	0.034	0.020	0.064	0.040
N	1	1	5	1	4	10	0.034	0.020	0.051	0.036
A	1	2	4	3	1	8	0.027	0.060	0.013	0.029
B	2	1	4	3	1	8	0.027	0.060	0.013	0.029
U	1	1	6	2	0	8	0.041	0.040	0.000	0.029
V	1	2	0	1	4	5	0.000	0.020	0.051	0.018
W	1	1	1	0	4	5	0.007	0.000	0.051	0.018
C	2	2	3	0	0	3	0.021	0.000	0.000	0.011
D	1	2	3	0	0	3	0.021	0.000	0.000	0.011
J	1	1	2	1	0	3	0.014	0.020	0.000	0.011
T	1	1	2	0	1	3	0.014	0.000	0.013	0.011
X	1	2	3	0	0	3	0.021	0.000	0.000	0.011
E	1	2	1	0	1	2	0.007	0.000	0.013	0.007
F	2	2	1	0	1	2	0.007	0.000	0.013	0.007
O	1	2	0	0	1	1	0.000	0.000	0.013	0.004
R	1	1	1	0	0	1	0.007	0.000	0.000	0.004
TOTAL			146	50	78	274	1.000	1.000	1.000	1.000

ABS ST = supertype groups based on physiochemical properties of coding regions for antigen binding sites (ABS); PSS ST = supertype groups based on physiochemical properties of coding regions for positively selected sites (PSS) as identified in CODEML analyses; n(x) = number of prairie dogs with that genotype on colony x; freq(x) = frequency of that genotype on colony x.

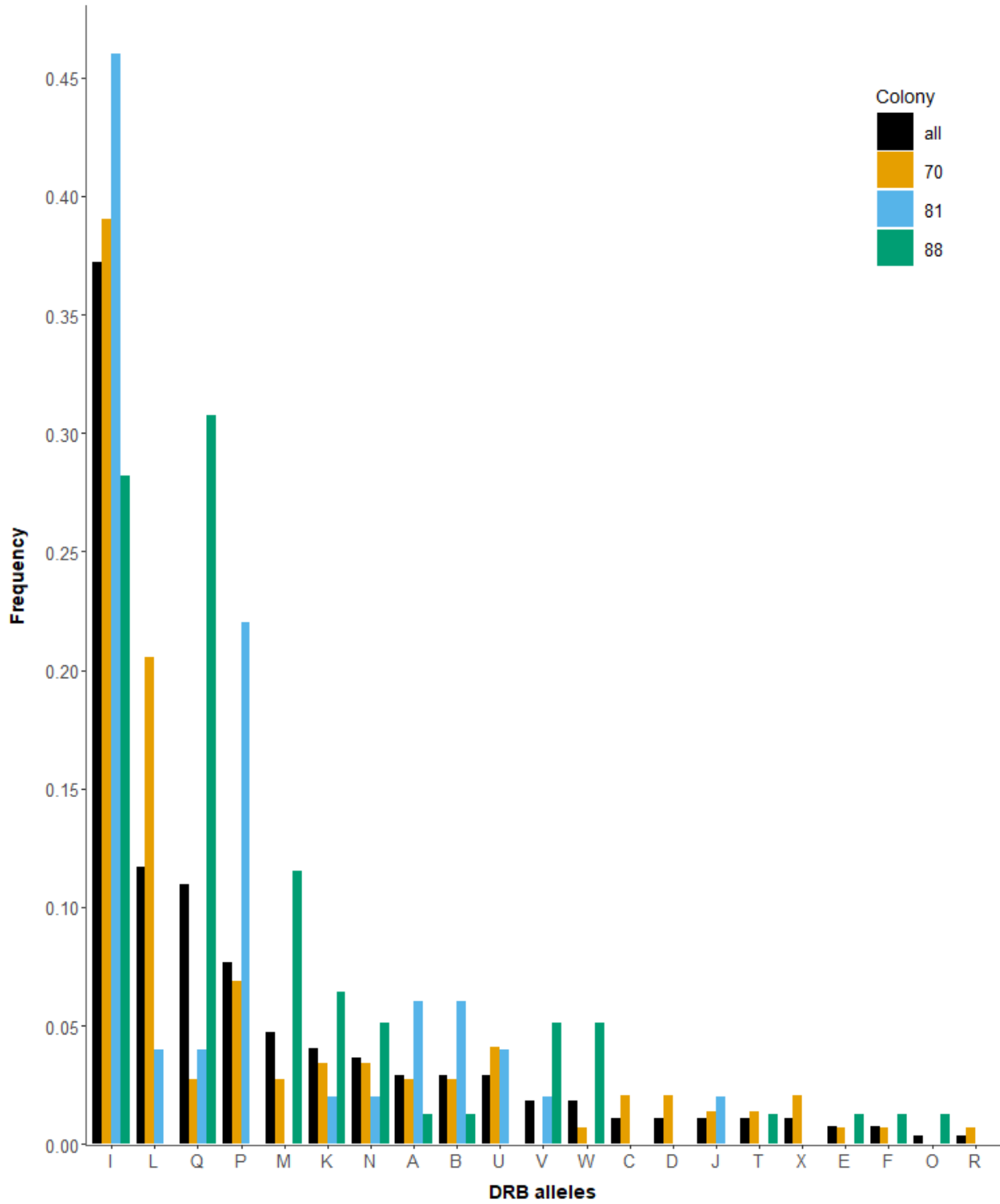


Figure 3.3 Allele frequencies for 137 black-tailed prairie dogs from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado arranged in order of decreasing overall frequency from left to right.

Table 3.3 Number of prairie dogs genotyped (N), number of alleles (A), allelic richness (Ar), observed (Hobs) and expected (Hexp) heterozygosities, and the inbreeding coefficient (Fis) for six microsatellites and MHC DRB exon 2 in black-tailed prairie dogs from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado. Significant deviations from Hardy-Weinberg equilibrium within populations are denoted by an asterisk (*). Hardy-Weinberg equilibrium was not tested across populations. N= sample size, A = number of alleles, Ar = allelic richness, Hobs = observed heterozygosity, Hexp = expected heterozygosity, p(HWE) = p-value for test of deviation from Hardy-Weinberg equilibrium, Fis = inbreeding coefficient.

Pop	Locus	N	A	Ar	Hobs	Hexp	P (HWE)	Fis
70								
	A104	70	9	6.84	0.775	0.756	0.211	-0.017
	A2	73	8	5.37	0.689	0.654	0.173	-0.047
	D1	71	7	5.28	0.694	0.688	0.048 *	-0.003
	D115	71	5	4.26	0.569	0.622	0.609	0.092
	D12	69	6	4.47	0.586	0.635	0.048 *	0.085
	D2	70	8	5.86	0.676	0.721	0.231	0.070
	MHC DRB	73	19	13.61	0.640	0.790	0.000 *	0.194
81								
	A104	23	6	5.66	0.625	0.650	0.511	0.060
	A2	25	7	6.54	0.885	0.788	0.356	-0.103
	D1	23	7	6.67	0.750	0.755	0.048 *	0.028
	D115	19	5	5.00	0.800	0.668	0.283	-0.174
	D12	21	6	5.73	0.727	0.667	0.231	-0.067
	D2	22	7	6.73	0.696	0.707	0.161	0.038
	MHC DRB	25	11	11.00	0.720	0.730	0.000 *	0.029
88								
	A104	39	5	4.87	0.744	0.691	0.966	-0.063
	A2	41	5	4.87	0.756	0.738	0.615	-0.013
	D1	40	5	4.75	0.600	0.662	0.048 *	0.106
	D115	40	5	4.58	0.450	0.598	0.146	0.259
	D12	35	4	3.81	0.600	0.588	0.966	-0.006
	D2	40	4	3.50	0.575	0.606	0.966	0.064
	MHC DRB	39	13	10.80	0.770	0.800	0.000 *	0.051
All								
	D1	134	8	5.51	0.6765	0.7371		0.0423
	A2	139	9	6.24	0.7447	0.7474		-0.0558
	A104	132	10	6.58	0.7388	0.7701		-0.0079
	D115	130	6	4.49	0.5682	0.6444		0.0510
	D12	125	8	4.47	0.6142	0.6376		0.0032
	D2	132	10	5.95	0.6493	0.7240		0.0569
	MHC DRB	137	21	13.68	0.6934	0.8208		0.1238

Table 3.4 Estimators for Weir and Cockerham's Θ and Jost's D with their 95% bias-corrected bootstrapped ($n = 10,000$) confidence intervals (CI) for six microsatellites and the MHC DRB locus for prairie dogs captured from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado.

Locus	Θ_{est} (95% CI)	D_{est} (95% CI)
D1	0.111 (0.063, 0.167)	0.287 (0.180, 0.408)
A2	0.097 (0.056, 0.145)	0.249 (0.155, 0.352)
A104	0.101 (0.054, 0.157)	0.324 (0.196, 0.458)
D115	0.062 (0.013, 0.133)	0.107 (0.040, 0.195)
D12	0.025 (-0.003, 0.067)	0.022 (0.082, 0.170)
D2	0.089 (0.046, 0.145)	0.207 (0.125, 0.308)
All msats	0.064 (0.084, 0.106)	0.202 (0.163, 0.245)
MHC DRB	0.066 (0.034, 0.106)	0.292 (0.164, 0.437)

Table 3.5 Pairwise values and 95% bias-corrected bootstrapped (n = 10,000) confidence intervals (CI) for estimators of Weir and Cockerham's Θ and Jost's D for prairie dogs captured from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado. Values for the DRB locus are shown above the diagonal, while values for microsatellites are shown below the diagonal.

Weir & Cockerham's Θ (95% CI)

	70	81	88
70		0.023 (-0.009, 0.066)	0.078 (0.041, 0.128)
81	0.068 (0.042, 0.099)		0.089 (0.036, 0.158)
88	0.076 (0.050, 0.105)	0.065 (0.036, 0.100)	

Jost's D (95% CI)

	70	81	88
70		0.087 (-0.018, 0.226)	0.353 (0.183, 0.552)
81	0.116 (0.059, 0.184)		0.345 (0.146, 0.566)
88	0.119 (0.073, 0.171)	0.074 (0.025, 0.136)	

Table 3.6 Evidence for selection acting on class II MHC DRB exon 2. Rates of synonymous (dS) and non-synonymous (dN) substitutions for putative antigen binding sites (ABS), non-antigen binding sites (non-ABS), and the entire sequence (ABS + non-ABS), results of the codon-based Z-test for positive selection (H_A : positive selection is acting on the tested sites), and results of Tajima's test (D; H_0 : all mutations are selectively neutral) for MHC DRB exon 2 sequences from black-tailed prairie dogs captured from three colonies (70, 81, 88) on Pawnee National Grassland, Colorado.

Sites	Colony	n	dN	dS	dN/dS	Z	p (Z)	D	p (D)
ABS		14							
	70	6	3.350	0.816	4.107	2.046	0.0215		
	81	50	1.848	0.441	4.188	2.181	0.0156		
	88	78	2.643	0.306	8.641	3.490	0.0003		
	All	27	4	2.171	1.138	1.908	2.486	0.0071	
non-ABS		14							
	70	6	0.811	1.261	0.643	-0.844	1.0000		
	81	50	0.430	0.636	0.677	-1.368	1.0000		
	88	78	0.515	0.627	0.821	0.206	0.4188		
	All	27	4	0.457	0.807	0.567	-0.781	1.0000	
All		14							
	70	6	1.440	1.174	1.227	0.395	0.3466	2.16	< 0.05
	81	50	0.805	0.670	1.201	-0.227	1.0000	2.16	< 0.05
	88	78	0.903	0.893	1.011	0.608	0.2722	3.02	< 0.01
	All	27	4	0.973	0.708	1.373	1.819	0.0357	2.86

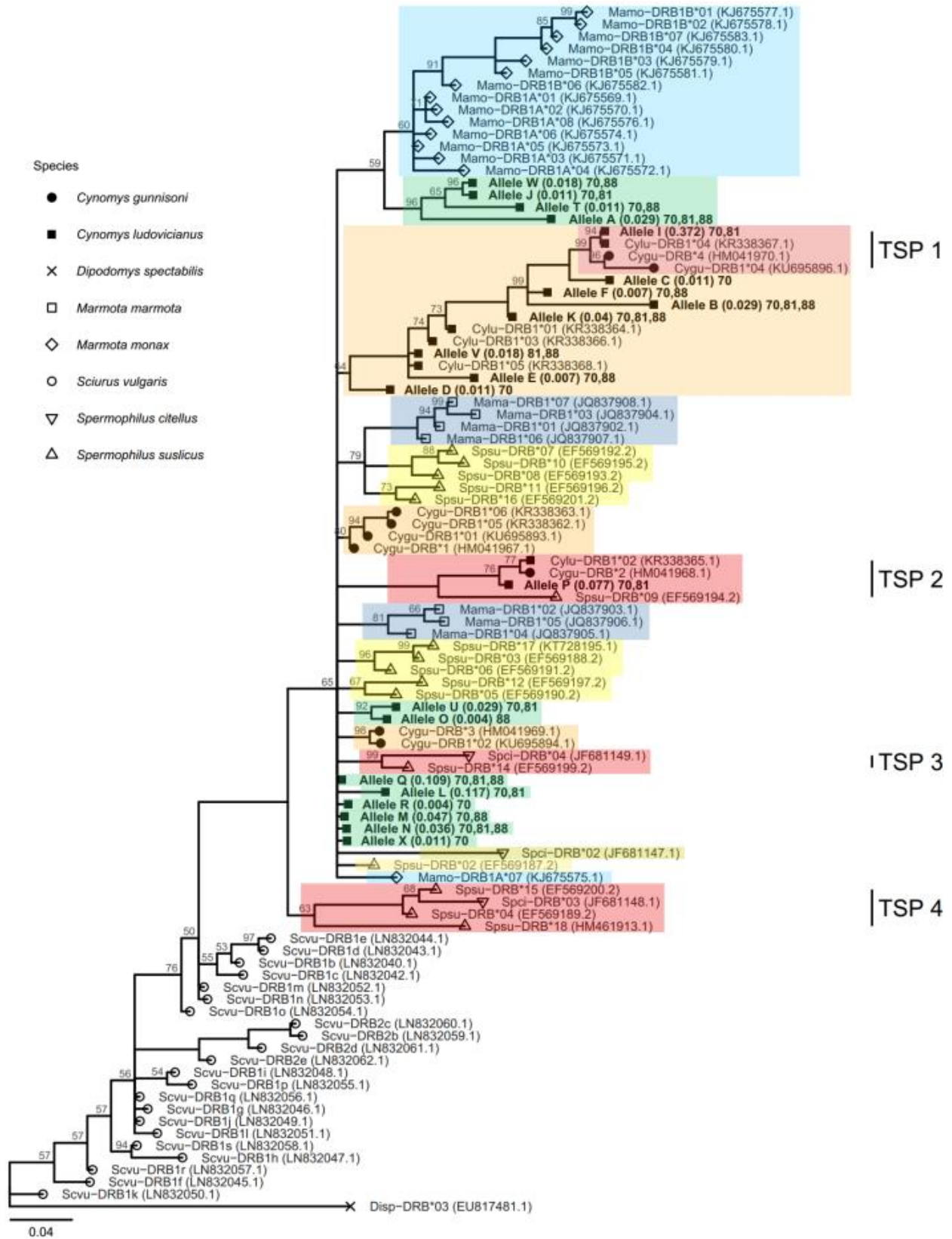
n = number of sequences considered in the analysis; P(Z) = Z-test p-value; p(D) = Tajima's test p-value

Table 3.7 Results of model-based tests of positive selection of MHC DRB exon 2 in black-tailed prairie dogs captured from three colonies on Pawnee National Grassland, Colorado. Model M1a (nearly neutral) was compared to model M2a (positive selection), and model M7 (neutral) was compared to model M8 (positive selection). In all comparisons, the model that allowed for positive selection was identified by likelihood ratio test as the best model (all p-values < 0.0001).

Colony	n	Model	lnL	np	AIC	Parameter estimates	Positively selected sites ^a
All	21	M1a	-1144	42	2372	p0 = 0.563, p1 = 0.437 $\omega_0 = 0.005, \omega_1 = 1$	not allowed
		M2a	-1115	44	2317	p0 = 0.511, p1 = 0.196, p3 = 0.293 $\omega_0 = 0, \omega_1 = 1, \omega_2 = 5.467$	<i>11, 12, 13, 37, 38, 63, 67, 70, 71, 75, 78</i>
		M7	-1144	42	2372	p = 0.010, q = 0.013	not allowed
		M8	-1115	44	2317	p0 = 0.713, p1 = 0.287 p = 0.005, q = 0.012 $\omega = 5.501$	<i>11, 12, 13, 22, 28, 30, 32, 34, 37, 38, 47, 51, 56, 60, 63, 67, 70, 71, 75, 78, 79</i>
70	19	M1a	-1078	38	2232	p0 = 0.543, p1 = 0.457 $\omega_0 = 0, \omega_1 = 1$	not allowed
		M2a	-1059	40	2198	p0 = 0.519, p1 = 0.178, p3 = 0.303 $\omega_0 = 0, \omega_1 = 1, \omega_2 = 4.251$	<i>13, 32, 37, 38, 47, 51, 57, 67, 70, 71, 75, 78</i>
		M7	-1078	38	2232	p = 0.005, q = 0.005	not allowed
		M8	-1059	40	2198	p0 = 0.673, p1 = 0.327 p = 0.005, q = 0.020 $\omega = 4.139$	<i>11, 12, 13, 28, 32, 37, 38, 47, 51, 56, 57, 60, 63, 67, 70, 71, 72, 75, 78</i>
81	11	M1a	-880	22	1804	p0 = 0.528, p1 = 0.472 $\omega_0 = 0, \omega_1 = 1$	not allowed
		M2a	-863	24	1774	p0 = 0.463, p1 = 0.303, p3 = 0.234 $\omega_0 = 0, \omega_1 = 1, \omega_2 = 5.581$	<i>11, 12, 13, 37, 38, 47, 67, 70, 71, 76</i>
		M7	-880	22	1804	p = 0.005, q = 0.005	not allowed
		M8	-863	24	1774	p0 = 0.767, p1 = 0.233 p = 0.005, q = 0.008 $\omega = 5.607$	<i>11, 12, 13, 37, 38, 47, 51, 56, 57, 60, 67, 70, 71, 74, 75, 78</i>
88	13	M1a	-885	26	1822	p0 = 0.579, p1 = 0.421 $\omega_0 = 0, \omega_1 = 1$	not allowed
		M2a	-859	28	1774	p0 = 0.672, p1 = 0, p3 = 0.328 $\omega_0 = 0.124, \omega_1 = 1, \omega_2 = 7.412$	<i>11, 12, 13, 22, 32, 37, 38, 47, 56, 67, 70, 71, 75, 78, 79</i>
		M7	-886	26	1823	p = 0.005, q = 0.005	not allowed
		M8	-859	28	1774	p0 = 0.672, p1 = 0.328 p = 14.095, q = 99.000 $\omega = 7.414$	<i>11, 12, 13, 22, 32, 37, 38, 47, 51, 56, 57, 60, 63, 67, 70, 71, 72, 74, 75, 78, 79</i>

n = number of alleles, np = number of parameters, ω_n = estimated value of dN/dS for site class n, p_n = estimated proportion of sites with ω_n , p & q are the shape parameters of the β function.

^a Positively selected sites with a Bayes empirical Bayes (BEB) posterior probability of $\geq 95\%$ that $\omega > 1.00$ are listed, and those with a BEB posterior probability $\geq 99\%$ are shown in bold. Codon sites identified by Brown et al. (1993) as antigen binding sites in the human MHC DRB are shown in italics.



[see legend on next page]

Figure 3.3 Phylogenetic tree of MHC-DRB exon 2 sequences from seven species of Sciuridae. Bayesian posterior probabilities < 100% are shown above the branches. The scale bar at the bottom shows branch length in substitutions per site. Alleles from this study are shown in bold, with overall frequency followed by the site(s) the allele was found at shown in parentheses. Accession number is shown in parentheses for alleles downloaded from GenBank.

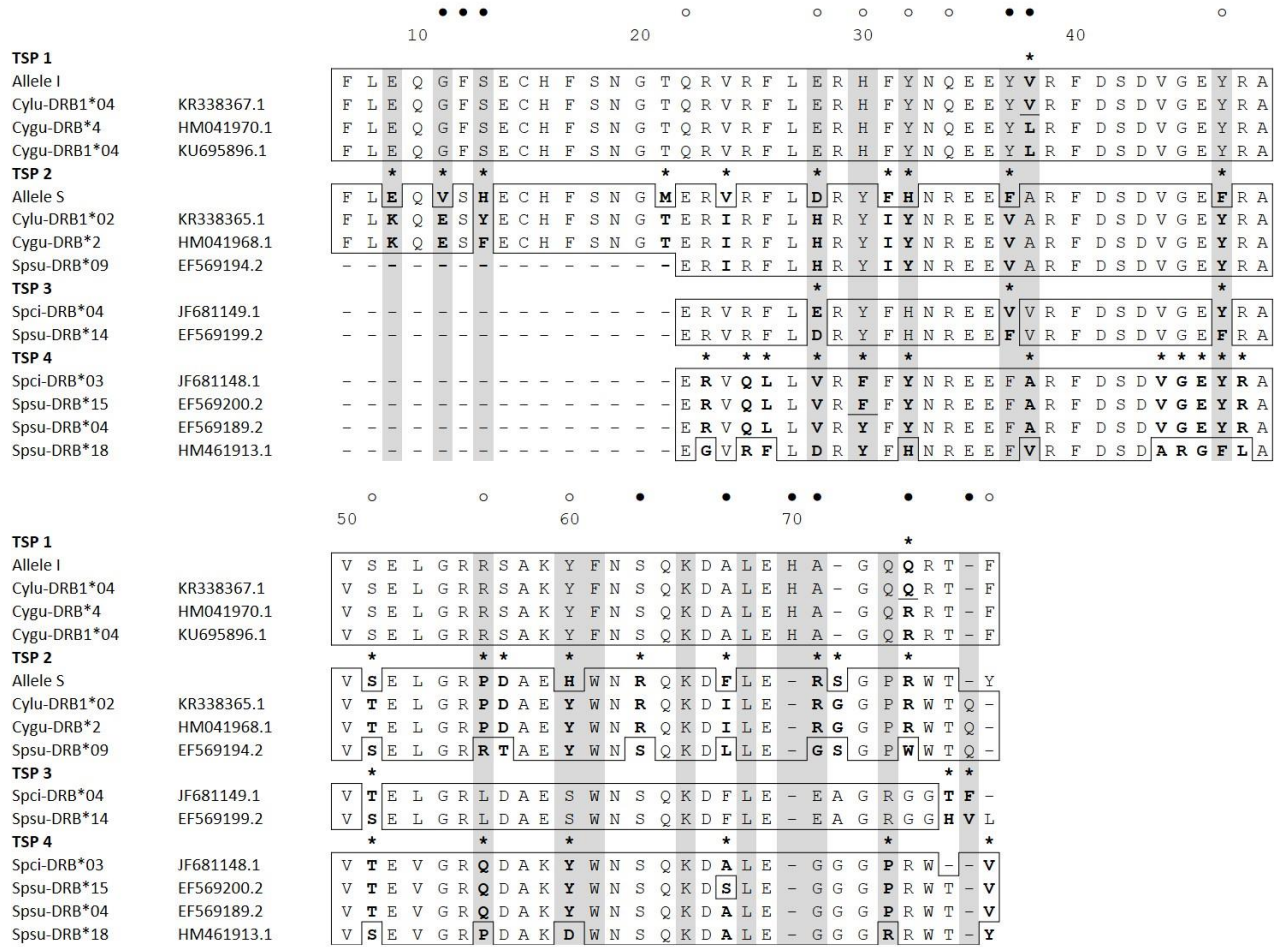


Figure 3.4 Inferred amino acid alignment of the class II MHC DRB locus for four groups (TSP 1 – 4) of species in the family Sciuridae with evidence for trans-species polymorphism (TSP) within each group (Fig. 3). Numbers correspond to common numbering of amino amino acid residues in human MHC DRB exon 2 (Brown *et al.* 1993). A dot indicates amino acid identity with allele A. Gray shading indicates a proposed antigen binding site (ABS) in humans according to Brown *et al.* (1993). Circles above columns indicate sites identified by the Bayes empirical Bayes (BEB) procedure in the CODEML program implemented in PAMLX as experiencing positive selection (PSS; with probability greater than 95% that $\omega > 1$; Yang 2007), with closed circles (●) indicating sites identified by both models (M2a and M8), and open circles (○) indicating sites identified by model M8 only. Asterisks (*) above each TSP group of alleles indicate polymorphic sites within that TSP group.

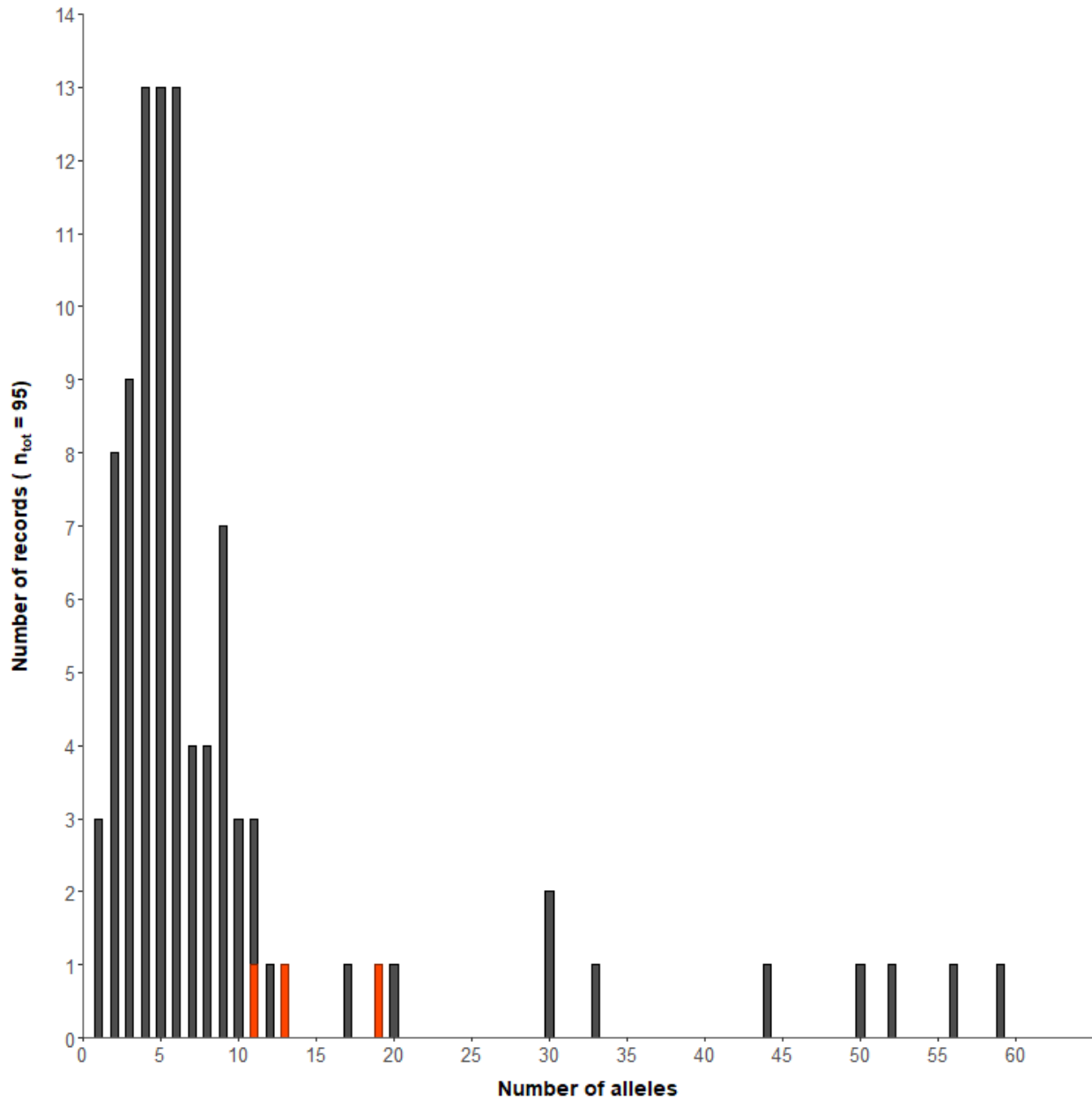


Figure 3.5 Number of class II MHC DRB alleles isolated from rodent species at individual sampling locations as determined from records published in the primary literature and from this research (red bars). Because duplication at the MHC-DRB locus may influence the number of different alleles found at an individual sampling location, species with evidence of duplication at the MHC-DRB locus were not included.

References: (Sommer et al. 2002; Sommer 2003; Froeschke and Sommer 2005; Cutrera and Lacey 2006; Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Cutrera et al. 2010; Cutrera et al. 2011; Ricanova et al. 2011; Axtner and Sommer 2012; Cutrera et al. 2012; Oliver and Piertney 2012; Cutrera et al. 2014; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017; Desvars-Larrive et al. 2017)

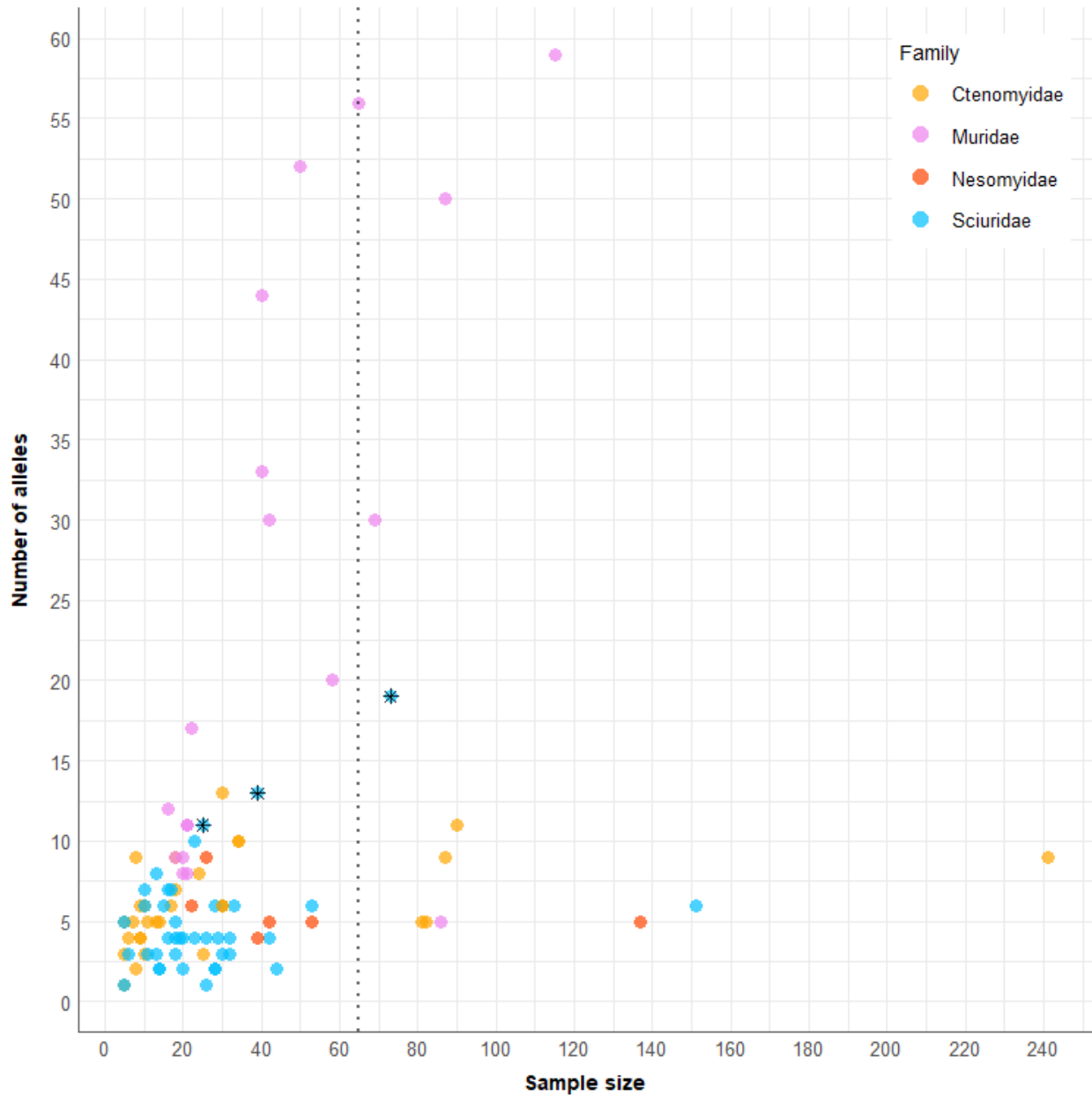


Figure 3.6 Number of class II MHC DRB alleles versus sample size at individual sampling locations for rodents as reported in published records from the primary literature, and from this research (black stars). The dotted line at $n = 65$ indicates the approximate sample size at which number of alleles found in a species does not appear to appreciably increase with increased sample size, based on currently published sample records. Because duplication at the MHC-DRB locus may influence the number of different alleles found at an individual sampling location, species with evidence of duplication at the MHC-DRB locus were not included.

References: (Sommer et al. 2002; Sommer 2003; Froeschke and Sommer 2005; Cutrera and Lacey 2006; Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Cutrera et al. 2010; Cutrera et al. 2011; Ricanova et al. 2011; Axtner and Sommer 2012; Cutrera et al. 2012; Cutrera et al. 2014; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017; Desvars-Larrive et al. 2017)

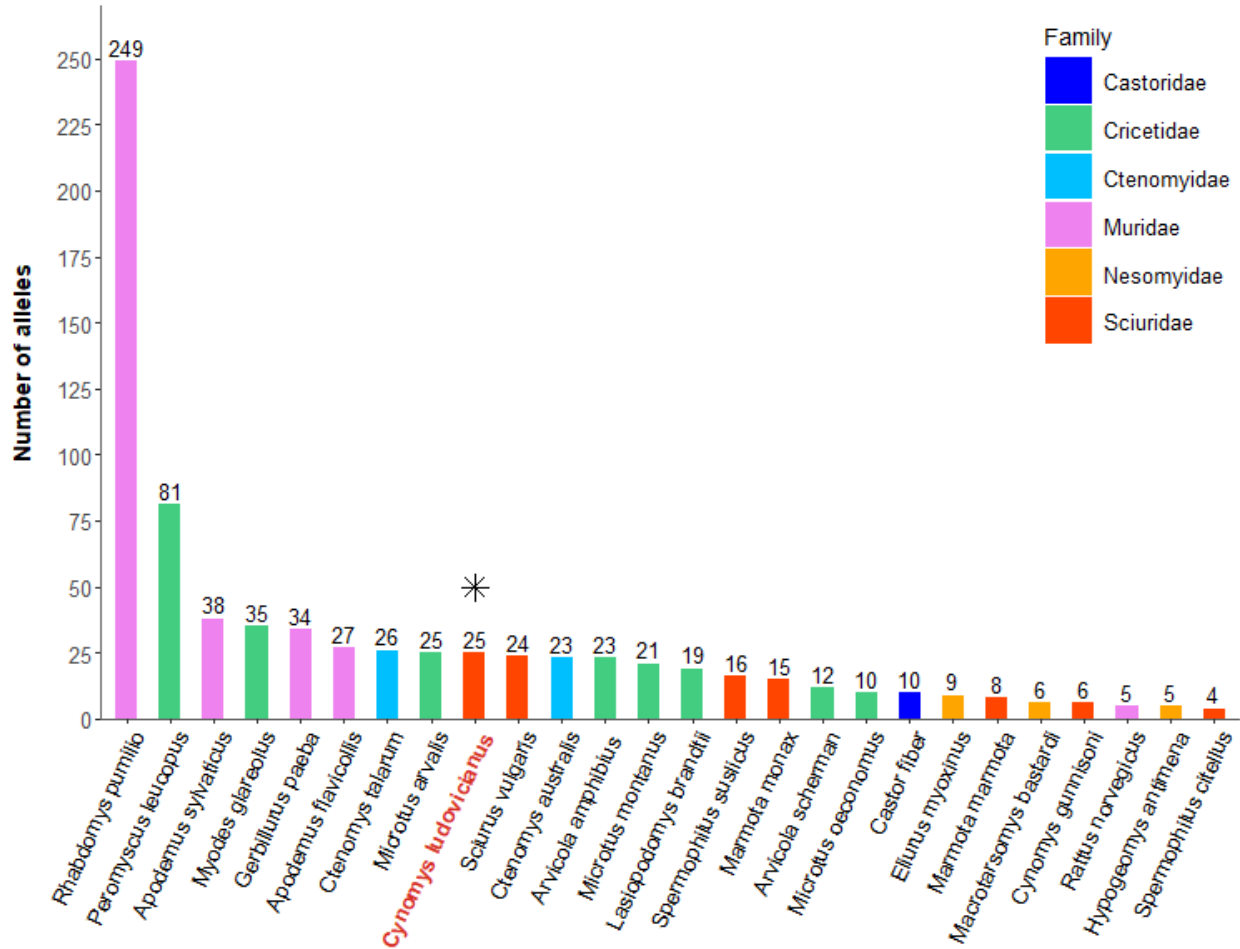


Figure 3.7 Total number of different class II MHC DRB alleles isolated from rodent species as determined from records published in the primary literature. Because duplication at the MHC-DRB locus may influence the total number of different alleles found within a single species, making comparisons to species with an unduplicated DRB locus difficult to interpret, species with evidence of duplication at the DRB locus were not included.

References: (Sommer et al. 2002; Sommer 2003; Musolf et al. 2004; Babik et al. 2005; Froeschke and Sommer 2005; Harf and Sommer 2005; Meyer-Lucht and Sommer 2005; Sommer 2005b; Cutrera and Lacey 2006; Oliver and Piertney 2006; Axtner and Sommer 2007; Babik and Radwan 2007; Bryja et al. 2007; Cutrera and Lacey 2007; Biedrzycka and Radwan 2008; Tollenaere et al. 2008; Meyer-Lucht and Sommer 2009; Oliver et al. 2009a; Oliver et al. 2009b; Cutrera et al. 2010; Guivier et al. 2010; Kloch et al. 2010; Axtner and Sommer 2011; Biedrzycka et al. 2011; Cutrera et al. 2011; Ricanova et al. 2011; Schwensow et al. 2011; Axtner and Sommer 2012; Cutrera et al. 2012; Froeschke and Sommer 2012; Kuduk et al. 2012; Oliver and Piertney 2012; Kloch et al. 2013; Winternitz and Wares 2013; Zhang and He 2013; Adnadevic et al. 2014; Cutrera et al. 2014; Froeschke and Sommer 2014; Scherman et al. 2014; Moreno-Cugnon et al. 2015; Ballingall et al. 2016; Biedrzycka and Kloch 2016; Cobble et al. 2016; Ferrandiz-Rovira et al. 2016; Schuster et al. 2016; Andre et al. 2017; Cutrera and Mora 2017; Desvars-Larrive et al. 2017)

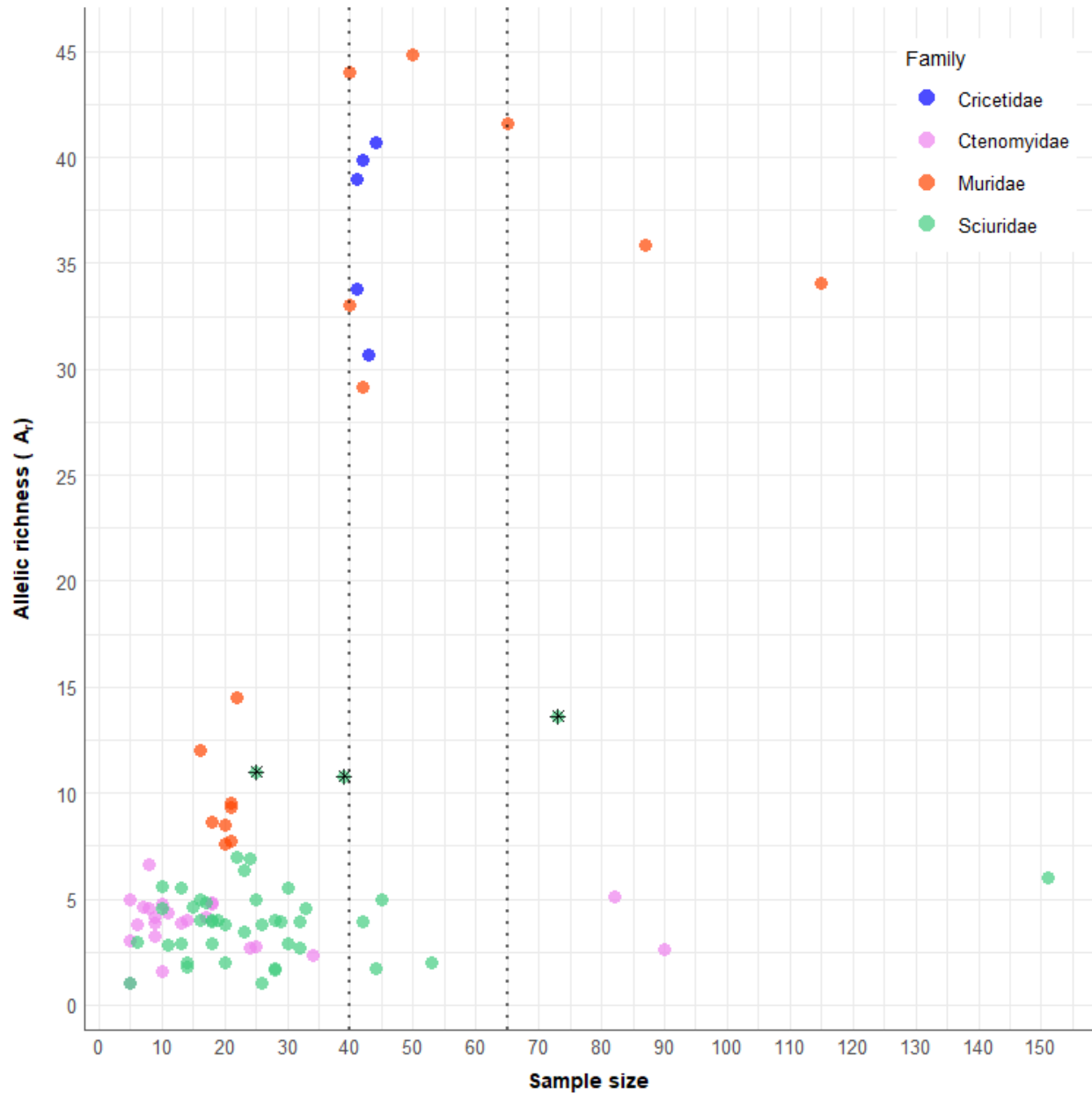


Figure 3.8 Class II MHC DRB allelic richness versus sample size at individual sampling locations for rodents as reported in published records from the primary literature, and from this research (black stars). The dotted lines at $n = 40$ and $n = 65$ indicate the approximate sample sizes at which allelic richness and number of alleles respectively does not appear to appreciably increase with increased sample size, based on currently published sample records. Because duplication at the MHC-DRB locus may influence the number of different alleles found at an individual sampling location, and number of alleles is positively correlated with allelic richness, species with evidence of duplication at the MHC-DRB locus were not included.

References: (Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Biedrzycka et al. 2011; Ricanova et al. 2011; Zhang and He 2013; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017)

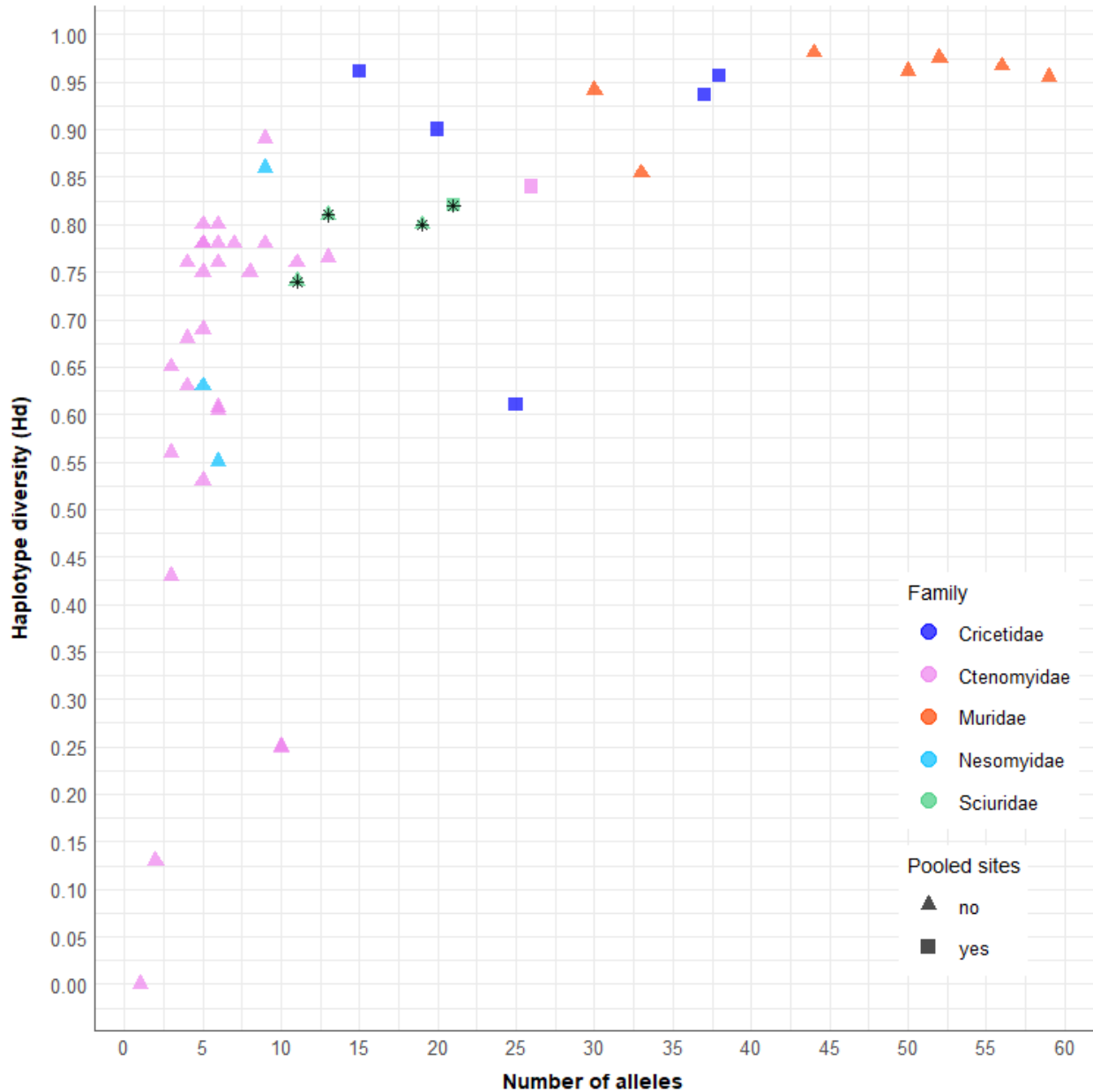


Figure 3.9 Class II MHC DRB haplotype diversity (Hd) versus number of alleles for rodent species as reported in published records from the primary literature, and from this research (black stars). Values of Hd calculated from individual sampling locations are indicated by square symbols, while values of Hd calculated from samples collected from more than one sampling location (i.e., pooled sites) are indicated by triangle symbols. Because duplication at the MHC-DRB locus influences measures of nucleotide diversity, and therefore haplotype diversity within rodents (Winternitz et al. 2013), species with evidence of duplication at the MHC-DRB locus were not included.

References: (Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Biedrzycka et al. 2011; Ricanova et al. 2011; Zhang and He 2013; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017)

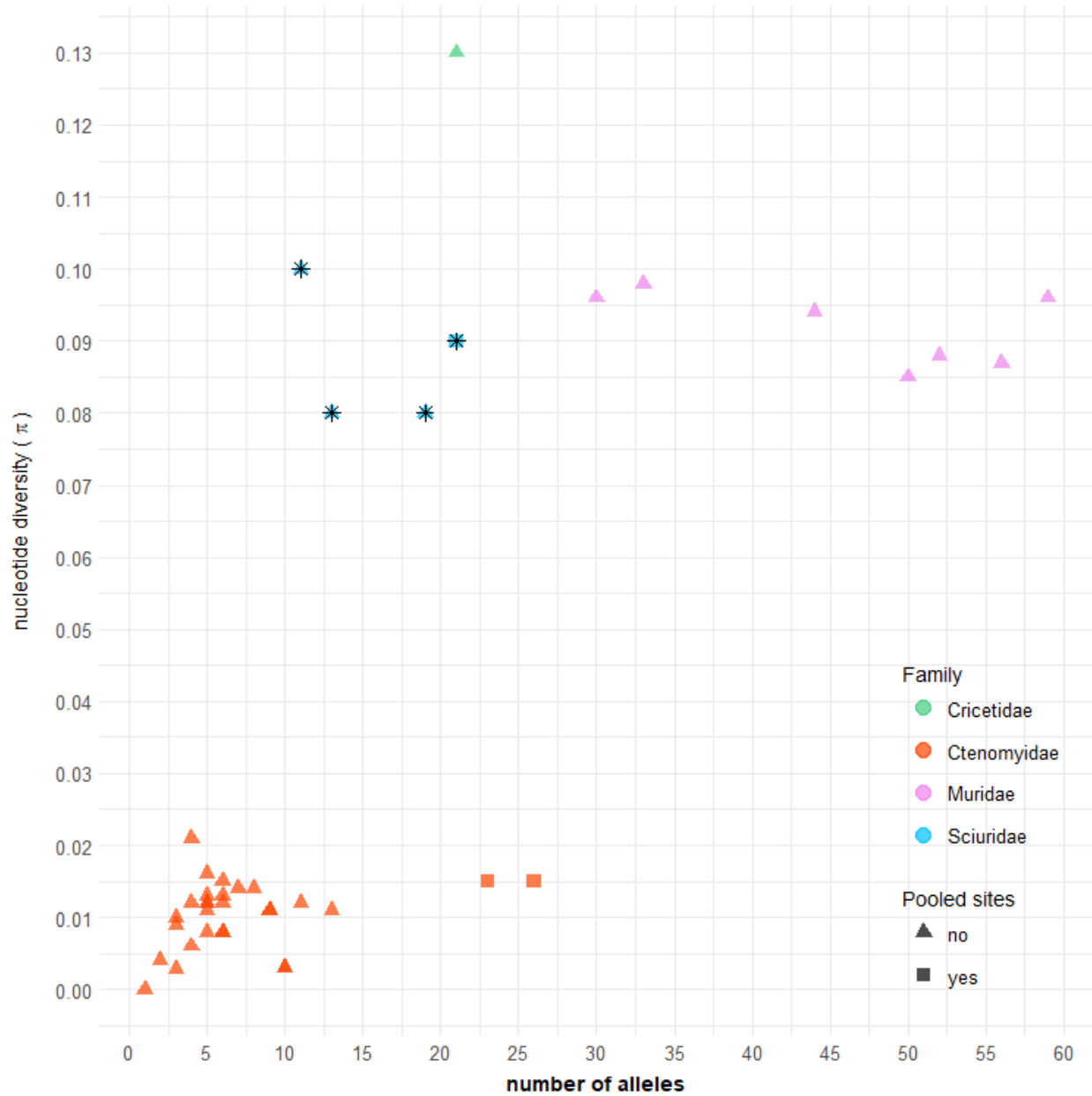


Figure 3.10 Class II MHC DRB nucleotide diversity (π) versus number of alleles for rodent species as reported in published records from the primary literature, and from this research (black stars). Values of π calculated from individual sampling locations are indicated by square symbols, while values of π calculated from samples collected from more than one sampling location (i.e., pooled sites) are indicated by triangle symbols. Because duplication at the MHC-DRB locus influences measures of nucleotide diversity within rodents (Winternitz et al. 2013), species with evidence of duplication at the MHC-DRB locus were not included.

References: (Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Biedrzycka et al. 2011; Ricanova et al. 2011; Zhang and He 2013; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017)

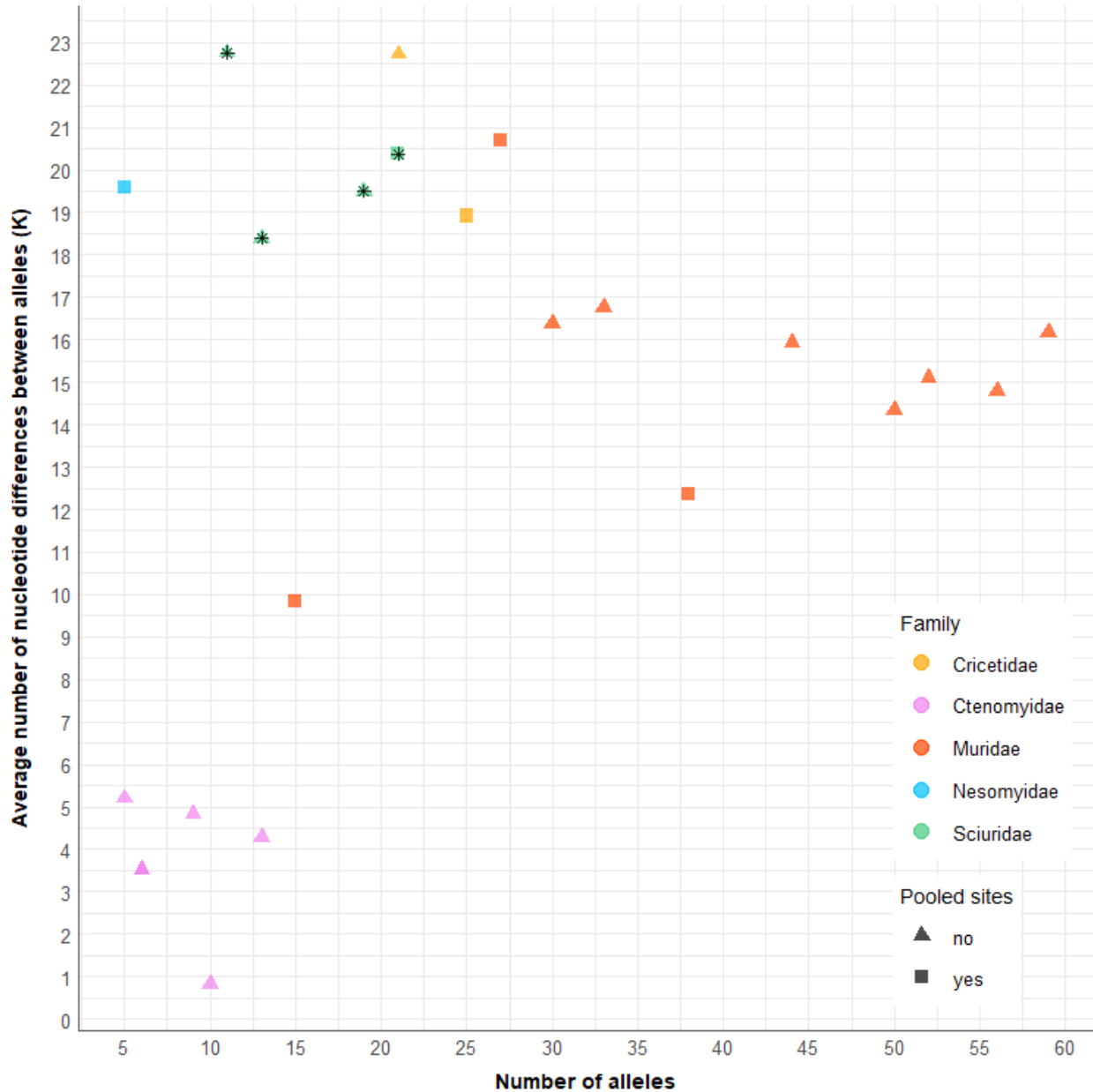


Figure 3.11 Average number of nucleotide differences between alleles (K) at the class II MHC DRB locus in rodent species as reported in published records from the primary literature, and from this research (black stars). Values of K from individual sampling locations are indicated by square symbols, while values of K from samples collected from more than one sampling location (i.e., pooled sites) are indicated by triangle symbols. Because duplication at the MHC-DRB locus influences measures of nucleotide diversity within rodents (Winternitz et al. 2013), species with evidence of duplication at the MHC-DRB locus were not included.

References: (Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Biedrzycka et al. 2011; Ricanova et al. 2011; Zhang and He 2013; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017)

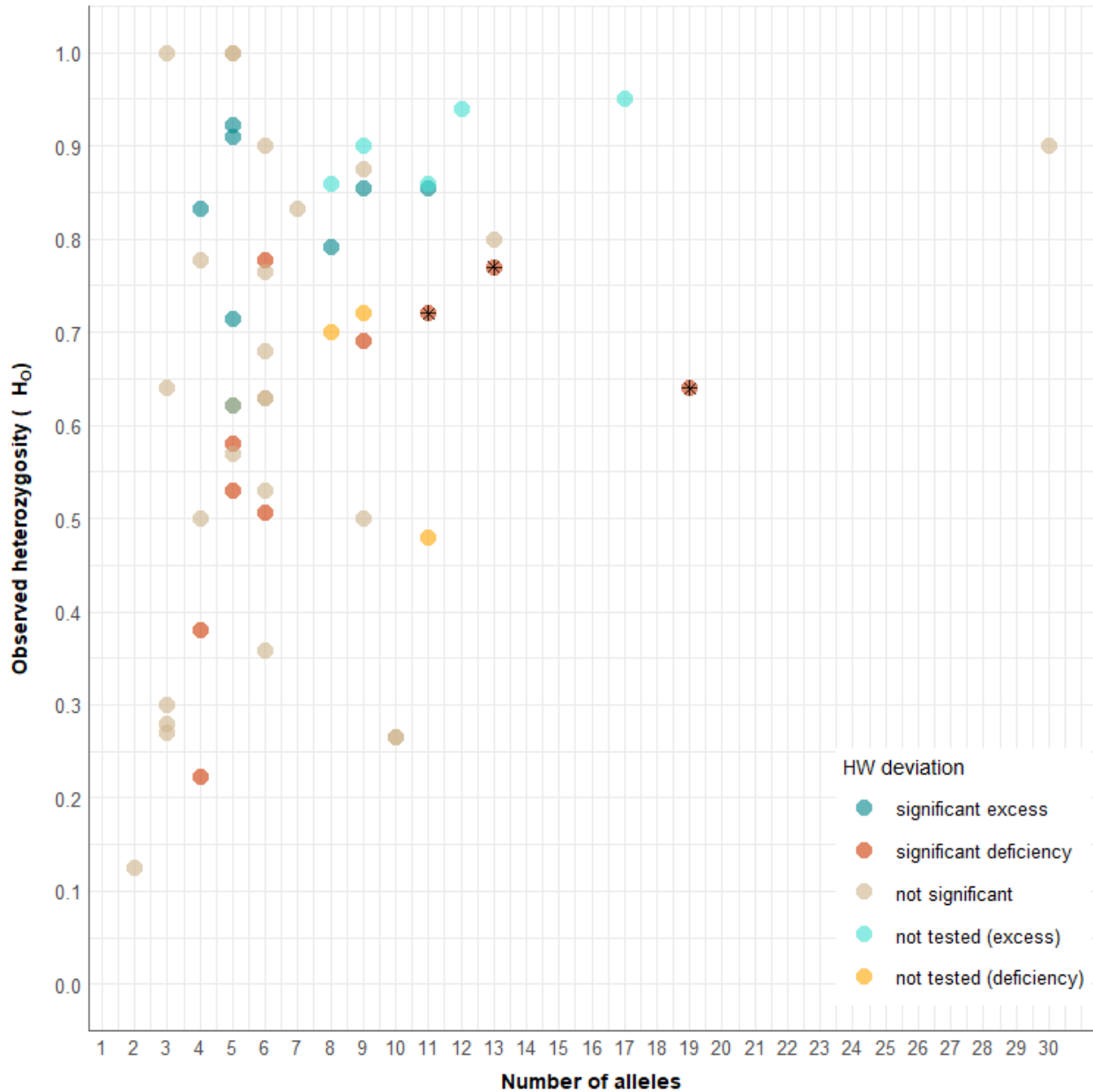


Figure 3.12 Observed heterozygosity versus number of alleles at the class II MHC DRB locus in rodent species as reported in published records from the primary literature, and from this research (black stars). All data are for species with a single unduplicated DRB locus. Colors indicate whether values of observed heterozygosity were higher or lower than expected, and whether the difference was statistically significant or not tested.

References: (Sommer et al. 2002; Sommer 2003; Cutrera and Lacey 2006; Biedrzycka and Radwan 2008; Meyer-Lucht and Sommer 2009; Cutrera et al. 2010; Biedrzycka et al. 2011; Cutrera et al. 2011; Ricanova et al. 2011; Axtner and Sommer 2012; Zhang and He 2013; Cutrera et al. 2014; Froeschke and Sommer 2014; Biedrzycka and Kloch 2016; Cobble et al. 2016; Cutrera and Mora 2017)

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CHAPTER FOURCHAPTER FOUR

FACTORS AFFECTING FLEA COUNTS ON BLACK-TAILED PRAIRIE DOGS (*CYNOMYS* SPP.) ON PAWNEE NATIONAL GRASSLAND

Introduction

Fleas are ectoparasitic insects (Insecta, Siphonaptera) that feed on the blood of their host and are transferred largely by host-to-host contact or through hosts coming into contact with infested nesting material (Marshall 1981; Krasnov and Khokhlova 2001). Fleas can have detrimental effects on their host through direct damage to the skin caused by their bites (Marshall 1981), by increasing the amount of time invested in grooming (Hawlana *et al.* 2007b; Hawlana *et al.* 2008a; Garrido *et al.* 2016), and by increasing the metabolic rate, and therefore energy expenditure, of their hosts (Khokhlova *et al.* 2002; Devevey *et al.* 2008; Kam *et al.* 2010). Fleas can also cause a decrease in the mass of their host (Khokhlova *et al.* 2002; Devevey *et al.* 2008), particularly in juveniles (Hawlana *et al.* 2006), or when food resources are limited (Hawlana *et al.* 2008b), perhaps because they spend less time foraging than individuals without fleas (Raveh *et al.* 2011). Juveniles also tend to grow more slowly when infested with fleas compared to flea-free juveniles (Hawlana *et al.* 2006; Devevey *et al.* 2008; Garrido *et al.* 2016). Additionally, fleas may decrease the ability of their host to mount an immune response to novel pathogens (Devevey *et al.* 2008).

Like many other ectoparasites, fleas are vectors for a number of disease-causing organisms, some of which infect humans (Bush *et al.* 2001; Bitam *et al.* 2010). The most well-known and devastating disease spread by prairie dog fleas is plague, caused by the bacterium *Yersinia pestis*, a zoonotic disease that can cause death if untreated. In fact, of the 43 flea species known to infect prairie dogs, 26 are known to be effective vectors of *Y. pestis* (Eisen *et al.*

2009). Prairie dog fleas are likely also vectors for *Bartonella washoensis cynomysis* (Stevenson *et al.* 2003; Brinkerhoff *et al.* 2010), a zoonotic bacterium that can cause mild to severe disease in humans (Kosoy *et al.* 2003; Probert *et al.* 2009). Eight species of fleas found on prairie dogs have been shown to harbor *Bartonella* spp. (Stevenson *et al.* 2003; Reeves *et al.* 2007; Brinkerhoff *et al.* 2010; Fernandez-Gonzalez *et al.* 2016), including the common prairie dog flea, *Oropsylla hirsuta* (Stevenson *et al.* 2003; Brinkerhoff *et al.* 2010; Fernandez-Gonzalez *et al.* 2016). Elucidating factors influencing the number of fleas found on individual hosts may inform efforts to control fleas and the diseases they transmit.

Previous research into factors affecting flea counts on hosts have uncovered several environmental and host traits associated with increased flea counts on individual hosts, but the relative importance of each factor is largely unknown. The most commonly studied factors influencing flea counts are host sex and season. Several studies have found male-biased parasitism by fleas in rodents (Morand *et al.* 2004; Krasnov *et al.* 2005a; Smith *et al.* 2005; Lareschi 2006; Matthee *et al.* 2010; Cevidanees *et al.* 2016), however the proposed mechanisms for such bias are quite varied (Krasnov *et al.* 2005a; Cevidanees *et al.* 2016), and not all studies find a difference between the sexes (e.g., Kowalski *et al.* 2015). Season is commonly found to influence flea loads on rodents, with peaks typically occurring in the spring, though the effect sometimes varies by geographic location or sex of the host (Krasnov *et al.* 2005a; Matthee 2007; Monello and Gompper 2009; Tripp *et al.* 2009; Nava and Lareschi 2012; Romeo *et al.* 2013; Archer *et al.* 2014; Fagir *et al.* 2014; Guernier *et al.* 2014; Romeo *et al.* 2014; Cevidanees *et al.* 2016).

Class II major histocompatibility complex molecules recognize extracellular foreign proteins and present them to T-cells, initiating an adaptive immune response (Klein 1982).

Research into the relationship between MHC genotype and parasitism in wild animals has focused primarily on endoparasites such as helminths and protozoa (Froeschke and Sommer 2012; Zhang and He 2013). Relatively few studies have investigated the influence of MHC genotype on parasitism by ectoparasites. However, of those that have, it is not unusual to find a connection between specific MHC genotypes and susceptibility or resistance to ectoparasites (e.g., Schad *et al.* 2012; Cutrera *et al.* 2014).

My objective was to identify the relative importance of factors influencing flea counts on black-tailed prairie dogs on Pawnee National Grassland, Colorado. Previous research at this site investigating seasonal flea counts on prairie dogs in relation to colony plague status compared mean flea abundance by age and sex and found higher average abundance on adults compared to juveniles and on males compared to females, in addition to finding peaks of flea abundance in March and September (Tripp *et al.* 2009). Other research in Colorado also found males to harbor greater numbers of fleas on average than females (Brinkerhoff *et al.* 2006). In contrast, another study in Colorado found no difference in flea parasitism between males and females (Jachowski *et al.* 2011). Most recently, researchers in South Dakota used generalized linear models (GLMs) to investigate a variety of factors affecting flea counts on black-tailed prairie dogs, and found higher flea counts on males compared to females (Eads and Hoogland 2016), however they did not report coefficients of the model, and provided no interpretation of the relative strength of these factors, as their focus was on investigating the importance of rainfall patterns on flea parasitism. I used generalized linear models (GLMs) to investigate the relative contribution of host sex, month of capture, and genotype as factors influencing flea counts on black-tailed prairie dogs on Pawnee National Grassland, Colorado. Based on previous research at this site (Tripp *et al.* 2009), I expected to find host sex and month of capture to influence flea counts on black-

tailed prairie dogs to some degree. Specifically I hypothesized that month would have the greatest effect on flea abundance because the flea life cycle should be directly tied to environmental conditions (Marshall 1981) that follow the same relative patterns from year to year (e.g., annual temperature and rainfall patterns), and that males would be more heavily parasitized than females. Because MHC molecules recognize specific parasite antigens based on the peptide-binding repertoire of individual alleles, I expected any relationship between genotype and flea counts to be allele-specific instead of being associated with general heterozygosity.

Methods

Field Methods

I conducted this research February – November 2007 and April – November 2008 at three sites (70, 81, 88) on Pawnee National Grassland (PNG) in north-central Colorado (Fig. 4.1). Pawnee National Grassland covers 78,129 hectares of shortgrass steppe habitat managed by the United States Forest Service. The shortgrass steppe is dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), and is dotted by numerous black-tailed prairie dog colonies within a patchwork of public and private land. The three colonies where I trapped prairie dogs had been in existence for varying amounts of time, with colony 81 established in 1996, colony 70 established in 1999, and colony 88 established in 2005 (Dan Tripp, pers. comm.).

I trapped prairie dogs using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with 8% three-way sweet feed (Manna Pro, St. Louis, MO). For each colony, 100 traps were placed near the entrance of an active burrow within 15m of a random point generated by the program Arc/INFO (Environmental Systems Research Institute, Redlands, CA.). Traps were baited and set at sunrise, and left open for three to four hours.

Trapping and handling protocols followed guidelines established by the Animal Care and Use Committee of the American Society of Mammalogists (Choate *et al.* 1998) and were approved by the Institutional Animal Care and Use Committee at Colorado State University. After capture, animals were placed, within their traps, in the shade to await processing. All animals were anesthetized using isoflurane (Halocarbon Industries, River Edge, NJ) administered using either an oxygen-driven vaporizer (Seven-Seven Anesthesia, Fort Collins, CO) connected to a bell-shaped cover that fit over the head of the animal, or by confining the animal in a 1 gallon plastic container with a cotton ball soaked in isoflurane (inside a round metal tea strainer). Animals were monitored closely during anesthesia for signs of distress. Distressed animals were immediately returned to their trap in the shade and allowed to recover from the anesthesia before being returned to the point of capture. While under anesthesia, animals were combed for fleas (described below), a tissue sample was taken from the tip of the tail for genetic analysis, numbered tags were attached to both ears (National Band and Tag, Newport, KY), and the sex, age (juvenile, yearling, adult based on body condition, pelage, and size; Hoogland 1995), and weight of the animal was determined. In order to recover as close to all of the fleas on an animal as possible, prairie dogs were combed over a plastic tub with a fine tooth comb over their entire body for as long as needed until no more fleas were observed coming off the animal. Because of the method of initial anesthetization (isolation in a confined area with isoflurane), the fleas were also anesthetized, and so were easy to collect from the tub during combing. All fleas were stored in vials containing 1.5% saline with 0.001% Tween 80 (ICN Biomedicals, Aurora, OH; Tripp *et al.* 2009) and kept at -20°C until identification. After processing, animals were kept in the shade within their traps until the effects of the anesthesia wore off, and were then returned to the point of capture.

Flea Identification

I identified a portion of the fleas collected using taxonomic keys from Stark (1958) and Hubbard (1968). It is not possible to distinguish between female *Pulex simulans* and female *P. irritans* (Hopla 1980), however, consistent with Tripp et al (2009), who performed field work at the same sites, all male *Pulex* sp. identified were *P. simulans*, and so, like Tripp et al (2009) I assumed that all female *Pulex* sp. were *P. simulans*.

Genotype determination

Molecular techniques for determining class II MHC DRB genotypes in black-tailed prairie dogs are described in detail in Chapter 3. Briefly, I extracted genomic DNA from tissue samples using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions. I used primers GH46F and GH50R (Erlich and Bugawan 1990) to amplify a 270 bp region in exon two of the DRB gene. Amplicons were genotyped using a combination of single strand confirmation polymorphism (SSCP) and direct sequencing. Individual alleles were determined using a combination of the software PHASE v2.1 (Stephens et al. 2001) a visual inspection using Geneious v7 (Kearse et al. 2012). Alleles were only considered valid if they were amplified at least twice in separate PCR reactions and had significant sequence similarity with other sciurid species in BLASTn search results (all e-values $\leq 2e-106$).

Data Analysis

Summary statistics

The use of the terms prevalence, intensity, and abundance follow Margolis et al (Margolis *et al.* 1982), where prevalence is the number of prairie dogs infested by fleas divided by the number of prairie dogs examined, mean intensity is the total number of fleas divided by

the number of infested prairie dogs, mean abundance is the total number of fleas divided by the total number of prairie dogs examined, and median flea abundance is the median number of fleas found on an individual prairie dog out of all prairie dogs examined.

Frequency distribution

Because the distribution of parasites on hosts can often be described by the negative binomial distribution where many hosts have few parasites and a few hosts have many parasites (Wilson *et al.* 2002), I tested whether or not the distribution of counts of fleas on prairie dogs fit a negative binomial distribution using R statistical software (R Core Team 2017). The negative binomial distribution can be described by the mean, μ , and the clumping parameter, k , such that $k = \mu^2/(\sigma^2 - \mu)$, where μ is the mean abundance of fleas on prairie dogs, σ^2 is the variance, and smaller values of k indicate a greater degree of clumping (Crawley 2007), with values of $k < 1$ consistent with a negative binomial distribution (Wilson *et al.* 2002). I estimated the value of k using maximum likelihood (Crawley 2007) and tested for goodness of fit of flea count frequencies to the negative binomial distribution using Pearson's chi-squared test (Crawley 2007).

Generalized linear modeling

To investigate the relative importance of host and environmental factors in determining the number of fleas found on prairie dogs, I fit generalized linear models (GLMs) with individual flea count as the response variable, and host colony (2 levels), month of capture (7 levels), host sex (2 levels), host age (3 levels), and class II MHC DRB genotype (5 variables with 2 or 3 levels each) as predictor variables. Age was determined by a combination of size, weight, and pelage following methods of Hoogland (Hoogland). Age classes approximately correspond to 0 – 1 yrs (juveniles), 1 – 2 yrs (yearlings), and 2+ years (adults). In order to reduce the number of

models examined, genotype predictors were limited to five variables: heterozygosity (yes, no), and number of copies (0, 1, or 2) of the four most frequent alleles (alleles I, L, P, Q). To avoid pseudoreplication, only a single capture record for each prairie dog was included in the analysis, even when the same individual was captured in multiple years. February, March, and November each had sample size < 5, and so these months were excluded from analysis. Likewise, colony 81 was excluded because no captures were made in April, May, June, or August. The final data set included 95 unique individuals characterized by two demographic variables (sex, age), two environmental variables (colony, month), and five genotypic variables (heterozygosity, 4 specific alleles).

Frequency distribution analysis of prairie dog flea counts suggested a negative binomial distribution, so I fit negative binomial generalized linear models (GLMs) using the `glm.nb` function in the MASS package (Venables and Ripley 2002) for R statistical software (R Core Team 2017). The `glm.nb` function uses maximum likelihood methods to estimate the clumping parameter (k) and coefficients (β_i) associated with terms in the model. I modeled individual flea counts, considering all possible combinations of main effects, using the following model with a negative binomial error distribution:

$$y_i = e^{(\beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i})}$$

where y_i are the flea counts from individual prairie dogs, β_1 is colony (70, 80), β_2 is month (April – October), β_3 is sex (male, female), β_4 is age (juvenile/yearling, adult), and β_5 is genotype (either heterozygosity (yes/no) or specific allele (0, 1, or 2 copies of allele I, L, Q, or P)). Each model included only one of the five possible genotype categories. Because sex and month of capture have previously been identified as factors affecting flea counts on black-tailed prairie dogs at my sites (Tripp *et al.* 2009), and in order to reduce the number of models

considered, these both sex and month were included in each of 24 models. Model performance was assessed using Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). To account for uncertainty in model selection I calculated model-averaged coefficient estimates and their 95% confidence intervals using Akaike weights (w_i) according to Burnham and Anderson (coefficient estimates; 2004) and Burnham and Anderson (confidence intervals; 2002) with the MuMIn package (Barton 2018) implemented in R (R Core Team 2017).

Results

Fleas – summary statistics

A total of 3544 fleas were collected from 330 hosts (179 individuals, 132 recaptures) captured on three colonies. Fleas were found on 87.6% (289) of prairie dogs, with a mean intensity of 12.3 (95% CI: 10.4 – 14.1) fleas per infested host (Table 4.1). Mean abundance of fleas on all hosts was 10.7 (95% CI: 9.1 – 12.4), while the median number of fleas found on all hosts was 7 (95% CI: 5.6 – 8.1; Table 4.1). The minimum number of fleas found on any one prairie dog was zero, and the maximum number of fleas was 185.

Of the 330 captured hosts, 231 were adults, 52 were yearlings, and 47 were juveniles, with a total of 179 males and 151 females (Table 4.1). Mean flea abundance was higher on adults (11.8, 95% CI: 9.5 – 14.1) than either yearlings (9.3, 95% CI: 6.6 – 12.1) or juveniles (7.1, 95% CI: 4.7 – 9.6; Table 4.1). Likewise, males had a higher abundance of fleas (13.5, 95% CI: 10.8 – 16.3) than females (7.5, 95% CI: 5.9 – 9.0; Table 4.1). Figure 2 shows flea counts separately for each age class, and Figure 3 shows flea counts separately for males and females.

Among months sampled with sample size > 5 (April – November), the highest mean abundances were in September (17.3, 95% CI: 9.9 – 24.6) and August (14.9, 95% CI: 9.2 –

20.6), and the lowest was in April (5.4, 95% CI: 2.6 – 8.2) and November (5.9, 95% CI: 2.1 – 9.7; Table 4.2). Similar trends were seen with prevalence and mean intensity, with highest prevalence occurring in August (100%), highest mean intensity occurring in September (18.8, 95% CI: 11.1 – 26.6), lowest prevalence occurring in April and July (80.8% each), and lowest mean intensity occurring in April and November (6.7 each, 95% CI: April 3.5 – 9.9, November 3.0 – 10.4; Table 4.2). Figure 4 shows flea counts by month.

Flea identification

I identified fleas from 73 of 282 infested hosts. These 73 hosts had a total of 905 fleas, of which 68.2% (617) were *Oropsylla hirsuta*, 31.6% (286) were *Pulex simulans*, 0.1% (1) were *O. tuberculata cynomuris*, and 0.1% (1) was *Thrassis fatus* (Table 4.3). Most hosts (91.8%) harbored *O. hirsuta*, and 47.9% harbored *P. simulans*. All hosts from which fleas were identified were caught in either summer (June, July, August) or fall (September, October). In the summer, 96% of 50 hosts harbored *O. hirsuta*, while just 38% harbored *P. simulans*, while in the fall 82.6% of 23 hosts harbored *O. hirsuta* and 69.6% of hosts harbored *P. simulans* (Table 4.3).

Frequency distribution and generalized linear modeling

Results from analysis of the distribution of flea counts on 95 prairie dogs was consistent with a negative binomial distribution ($k = 0.7473$), with most hosts harboring few, if any, fleas, and just a few hosts harboring a great many fleas (Fig. 4.5). Half of the 24 models considered accounted for 92% of the total Akaike weight (w_i) for all models Table 4.4). The top three models contributed over half of total weight, and included colony and two genotypic predictor variables (heterozygosity, allele L) in addition to month and sex (included in every model; Table 4.4).

Model-averaged coefficient estimates suggest sex has the greatest influence on flea parasitism, with males predicted to have three times as many fleas as females (Table 4.5). Month of capture was also a strong predictor of flea counts, with twice as many fleas expected on prairie dogs in September compared to April (Table 4.5). Being heterozygous in general, and specifically for allele L, was associated with greater numbers of fleas, though the effect was relatively weak, with a predicted increase of 10% compared to homozygotes (Table 4.5).

Variables associated with having fewer fleas included being captured from colony 88, and being homozygous for alleles L or Q (Table 4.5). Individuals from colony 88 had approximately 38% fewer fleas than prairie dogs from colony 70 (Table 4.5). Genotype had a smaller effect; having two copies of either the L allele or the Q allele was associated with 20% and 10% fewer fleas respectively (Table 4.5). Age appeared in a third of the top models (Table 4.4), however its predicted effect on flea parasitism appears small when averaged over all models (Table 4.5). On the other hand, when estimated only from models that included age, adults were predicted to have approximately 13% more fleas than juveniles (Table 4.5). Based on the models considered here, alleles I and P have the least predictive power of all variables considered (Table 4.5).

Confidence intervals for coefficient estimates from the top 12 models were relatively wide, and overlapped one (Fig. 4.6). Confidence intervals for model averaged coefficient estimates were much narrower, and three of the estimates did not overlap zero (sex = male, month = September, month = June). Box and whisker plots of the data used to fit the models also had wide confidence intervals for most predictor levels, with frequent high flea count outliers (Fig. 7).

Discussion

My aim in this study was to elucidate host and environmental factors associated with flea parasitism in black-tailed prairie dogs. I found prairie dogs were most heavily parasitized in September, least parasitized in June, and males were more heavily parasitized than females. Host age had a weak effect, with adults tending to harbor more fleas than juveniles. Associations between genotype and number of fleas were mixed, with some evidence for a protective effect of being homozygous for two of the four class II MHC DRB alleles investigated. General heterozygosity at the DRB locus was associated with higher flea loads, but the effect was small.

Several factors have been shown to affect flea abundance on rodent hosts, including host sex (e.g., Morand *et al.* 2004; Matthee *et al.* 2010; Cevidaneš *et al.* 2016), host age (e.g., Krasnov *et al.* 2006b; Hawlena *et al.* 2007a; Garrido *et al.* 2016), and season of capture (e.g., Monello and Gompper 2009; Tripp *et al.* 2009; Romeo *et al.* 2014); however, the magnitude and direction of the effect varies among studies. At my study sites, males were more heavily parasitized than females, and adults were more heavily parasitized than juveniles (Table 4.1). Average prevalence and intensity, as well as median flea abundance were nearly identical to a study by Tripp *et al.* (Tripp *et al.* 2009), whose sample locations were in close proximity to colonies sampled for this research. Mean flea abundance of my samples was slightly lower, but confidence intervals from both studies overlapped (Table 4.1; Tripp *et al.* 2009). Seasonal patterns of flea species found on black-tailed prairie dogs were similar to those found by Tripp *et al.* (2009).

The finding of male-biased parasitism, with males carrying more fleas than females, is consistent with much research into flea parasitism of rodents (e.g., Monello and Gompper 2009; Kowalski *et al.* 2015), though female-biased parasitism has also been documented (Matthee

2007). The two most commonly proposed hypotheses for male-biased parasitism are (1) males have lower immunocompetence because of the immunosuppressive effects of androgens and because of a trade-off between investing energy into immune responses and investing energy into competition for and courtship of females (Folstad and Karter 1992), and (2) males are more likely to encounter parasites because they are more mobile and have larger home ranges than females. These two hypotheses, increased susceptibility and increased exposure, are not mutually exclusive – both could be acting simultaneously to increase the parasite load of males compared to females. Additionally, it is expected that there will be a greater chance of male-biased parasitism in polygynous species compared to monogamous species, as the former are subject to greater forces of sexual selection (Zuk and McKean 1996).

The next most significant predictor variable was month = September, similar to other studies of black-tailed prairie dogs in Colorado (e.g., Tripp *et al.* 2009), but contrary a spring peak in mean abundance seen with many rodents (e.g., Matthee 2007; Monello and Gompper 2009). Seasonality is often found to be important in predicting patterns of flea abundance on rodents, but is often confounded by host traits such as sex or age (Krasnov *et al.* 2005a). One explanation for the conflicting seasonal patterns could be timing of favorable conditions for specific flea species coinciding with seasonal effects on life history traits that impact an individual's ability to mount an effective immune response, such as increased testosterone in males during breeding season or reduced body condition in the early spring as a result of limited food resources (Krasnov *et al.* 2012; Kiffner *et al.* 2014; Cevitanes *et al.* 2016). Out of 40 published records of *Oropsylla hirsuta* collected from prairie dogs (see Chapter 2) that identified month or season of capture, 33 were summer or late summer, suggesting environmental conditions favorable for *O. hirsuta*.

Age was also found by GLM analysis to be important, with adults more heavily parasitized than juveniles. Perhaps the simplest explanation for increased parasitism with age is based on habitat size – adults are larger, and therefore have more space for fleas to colonize (Hawlena *et al.* 2006; Sanchez *et al.* 2014; Young *et al.* 2015). Another possibility is transfer of immunity from mother to offspring (Khokhlova *et al.* 2004), a phenomenon that has also been found in humans (Niewiesk 2015).

Immune responses to parasites are varied and complex, making it difficult to uncover specific connections between genotype and parasite resistance or susceptibility (Ardia *et al.* 2011). I found a weak relationship linking one allele to reduced flea counts, and one allele to reduced flea counts when homozygous, and increased flea counts when heterozygous. It is possible that particular DRB alleles present at higher frequency on individual colonies could confound interpretation of colony or genotype effects (Oliver *et al.* 2009b). Additionally, the existence of a large number of alleles in the population makes it difficult to uncover a genotype effect on flea loads without a much larger sample size. The cryptic nature of the genotype-flea associations found in this research are certainly intriguing, but are difficult to interpret. It is likely that larger sample sizes and a broader spatial and temporal approach will yield more fruitful results.

In summary, I found overall indices of flea parasitism consistent with previous research on Pawnee National Grassland. Seasonality was also shown to be important, with peak flea abundance in September, perhaps related to ecology of the primary flea species, *Oropsylla hirsuta*. Flea counts were also influenced by host traits, with adult males being more heavily parasitized than either females or juveniles. The most important factors influencing flea parasitism were host sex and month of capture. Model predictions were not significantly

different than observed data, suggesting my model has captured at least some factors accounting for higher flea loads for some individuals. Future research should incorporate additional parasites in order to uncover possible effects of co-infection. Prairie dogs are known hosts of several species of *Eimeria*, a protozoan parasite that does not appear to have a significant impact on prairie dogs (Seville 1997). Additionally, there is evidence of a possible interaction between *Eimeria* and *Yersinia pestis* (Foust 2007), suggesting future analysis of dynamics and consequences of co-infection in black-tailed prairie dogs in relation to plague dynamics.

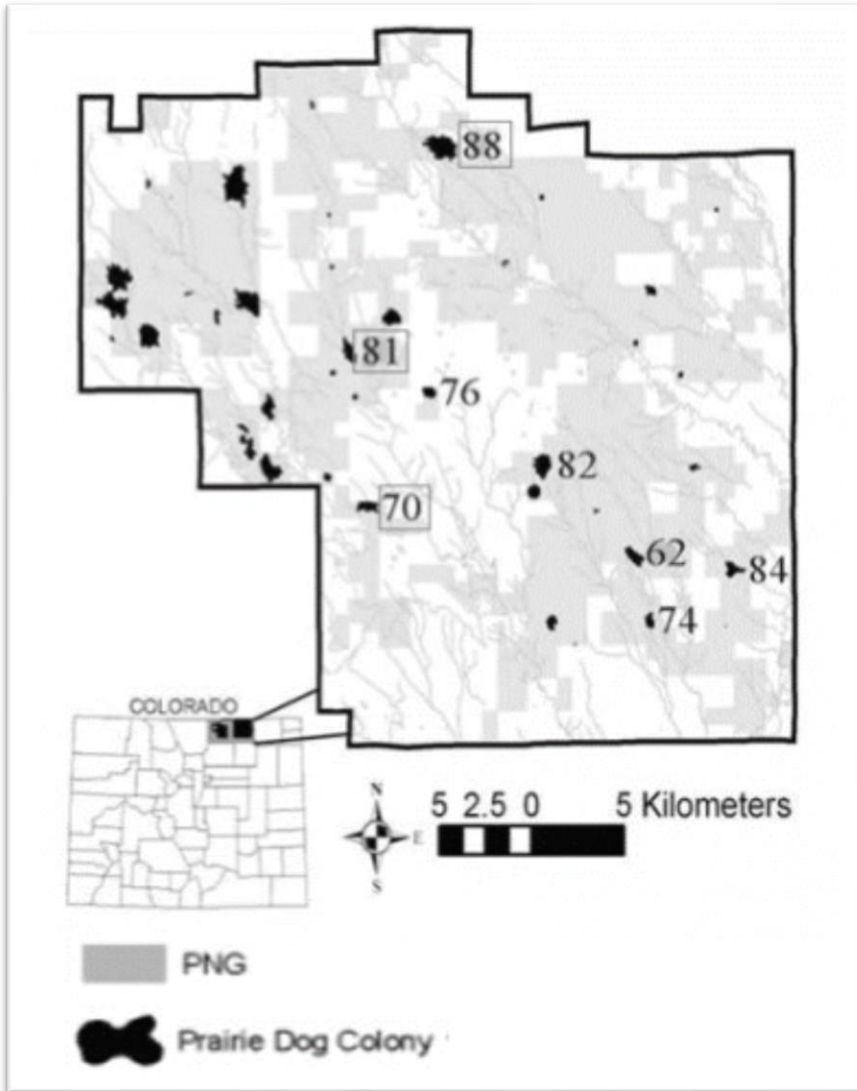


Figure 4.1 Locations of prairie dog colonies on the western half of Pawnee National Grassland. Colonies outlined with grey boxes indicate sampling locations for this research.

Table 4.1 Summary of flea counts by age and sex for fleas collected from black-tailed prairie dogs February – November 2007 – 2008 on three colonies on Pawnee National Grassland, Colorado.

Host category	Total fleas (no. hosts examined)	Maximum intensity	Mean abundance (95% CI)	Median abundance (95% CI)	Prevalence % (no. hosts infested)	Mean intensity (95% CI)
Juveniles	336 (47)	40	7.1 (4.7, 9.6)	4 (1.3, 6.7)	76.6 (36)	9.3 (6.5, 12.2)
Yearlings	485 (52)	40	9.3 (6.6, 12.1)	7 (4.5, 9.5)	88.5 (46)	10.5 (7.5, 13.6)
Adults	2723 (231)	185	11.8 (9.5, 14.1)	7 (5.6, 8.4)	87.6 (207)	13.2 (10.8, 15.5)
Females	1125 (151)	71	7.5 (5.9, 9.0)	4 (2.9, 5.1)	83.4 (126)	8.9 (7.2, 10.7)
Males	2419 (179)	185	13.5 (10.8, 16.3)	8 (6.4, 9.6)	91.1 (163)	14.8 (11.9, 17.8)
All hosts	3544 (330)	185	10.7 (9.1, 12.4)	7 (5.6, 8.1)	87.6 (289)	12.3 (10.4, 14.1)

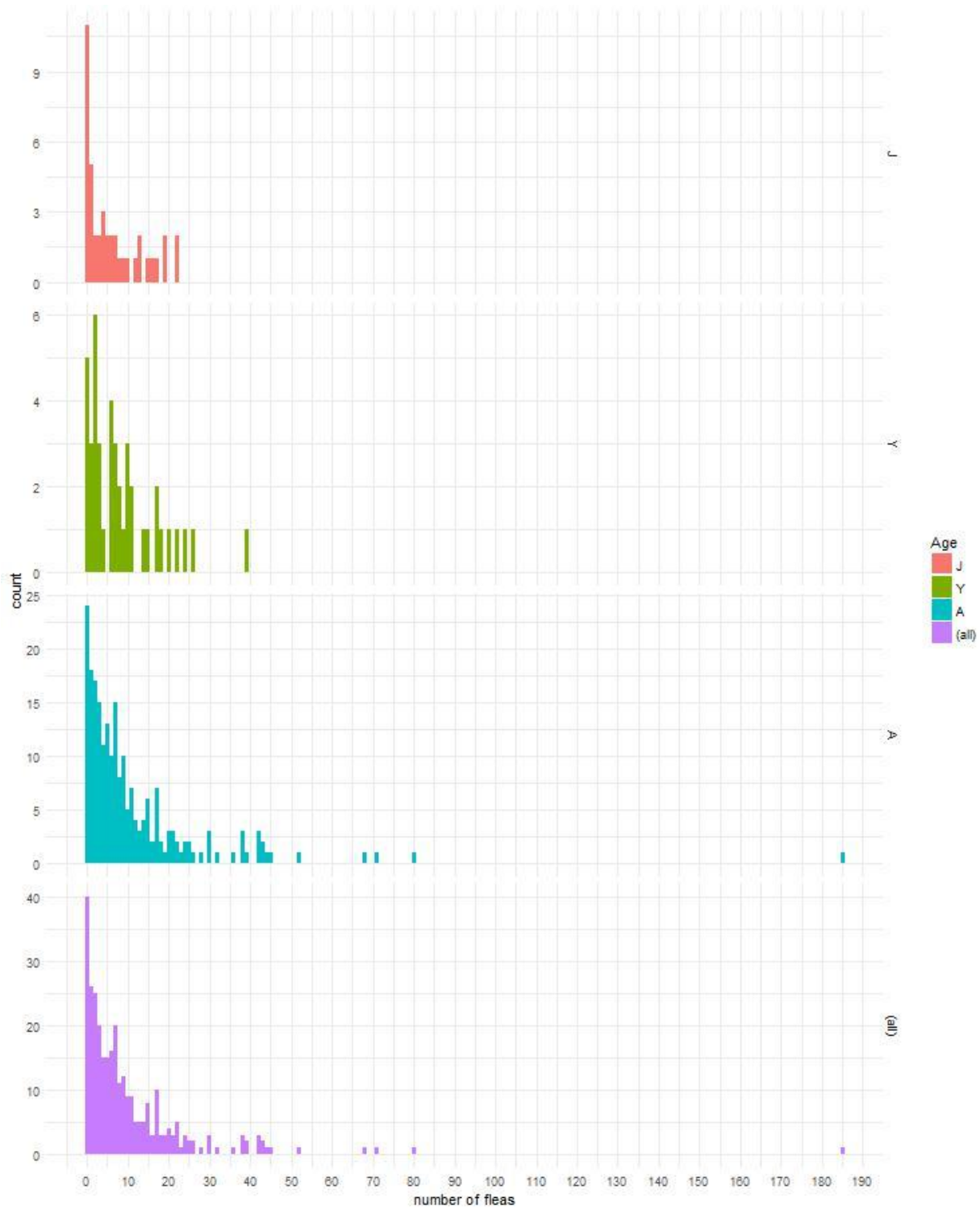


Figure 4.2 Flea counts on black-tailed prairie dogs (n = 303) by host age for three colonies on Pawnee National Grassland, Colorado, April – October 2007 – 2008. J = juvenile, Y = yearling, A = adult.

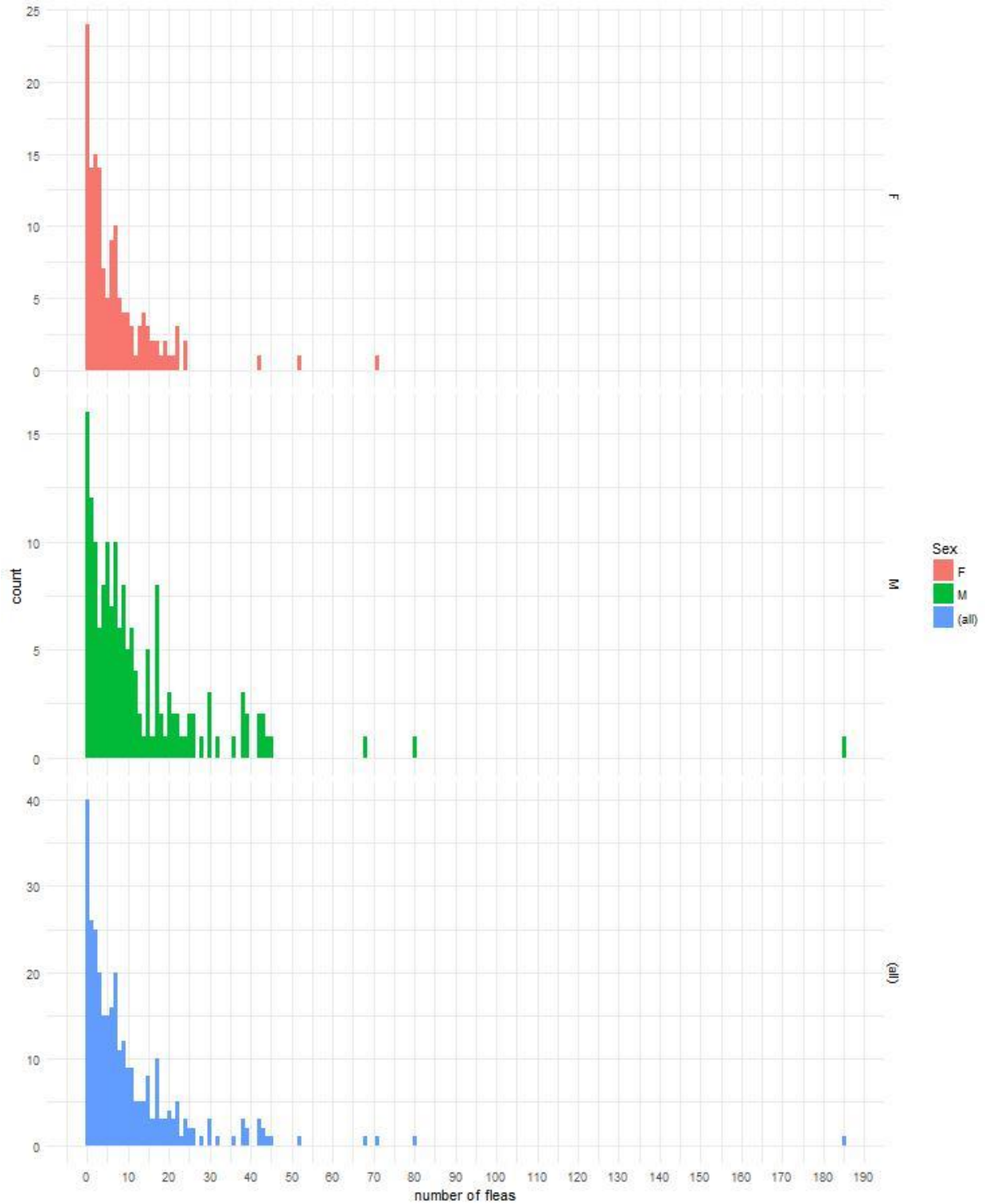


Figure 4.3 Counts of fleas on black-tailed prairie dogs (n = 303) by host sex for three colonies on Pawnee National Grassland, Colorado, April – October 2007 – 2008.

Table 4.2 Summary of monthly flea counts for fleas collected from black-tailed prairie dogs from three colonies on Pawnee National Grassland, Colorado 2007 – 2008.

Month	No. hosts	Max abundance	Mean abundance (95% CI)	Median abundance (95% CI)	Prevalence % (no. hosts infested)	Intensity (95% CI)
Feb	1	17	17 13.3	17 14	100 (1)	17 13.25
Mar	4	23	(-3.2, 29.7) 5.4 ((1.6, 26.4) 2	(4) 80.8	(-1.1, 27.6) 6.7
Apr	26	20	2.6, 8.2) 9.4	(-0.6, 4.6) 7	(21) 88.2	(3.5, 9.9) 10.2
May	34	42	(6.1, 12.7) 7.8	(4.5, 9.2) 5	(30) 86.3	(6.8, 13.5) 9.3
Jun	51	71	(4.5, 11.2) 11.0	(3.4, 6.6) 7	(44) 80.8	(5.6, 13.0) 13.5
Jul	78	60	(8.0, 13.9) 14.9	(4.5, 9.5) 11.5	(63) 100	(10.2, 16.8) 14.9
Aug	22	43	(9.2, 20.6) 17.3	(6.6, 16.4) 10	(22) 91.1	(9.2, 20.5) 18.8
Sep	56	185	(9.9, 24.6) 8.9	(6.7, 13.3) 5	(51) 92	(11.1, 26.6) 9.5
Oct	50	80	(5.2, 12.5) 5.9	(3.0, 7.0) 5.5	(46) 87.5	(5.6, 13.3) 6.7
Nov	8	14	(2.1, 9.7) 10.7	(2.7, 8.3) 7	(7) 87.6	(3.0, 10.4) 12.3
All months	330	185	(9.1, 12.4)	(5.6, 8.1)	(289)	(10.4, 14.1)

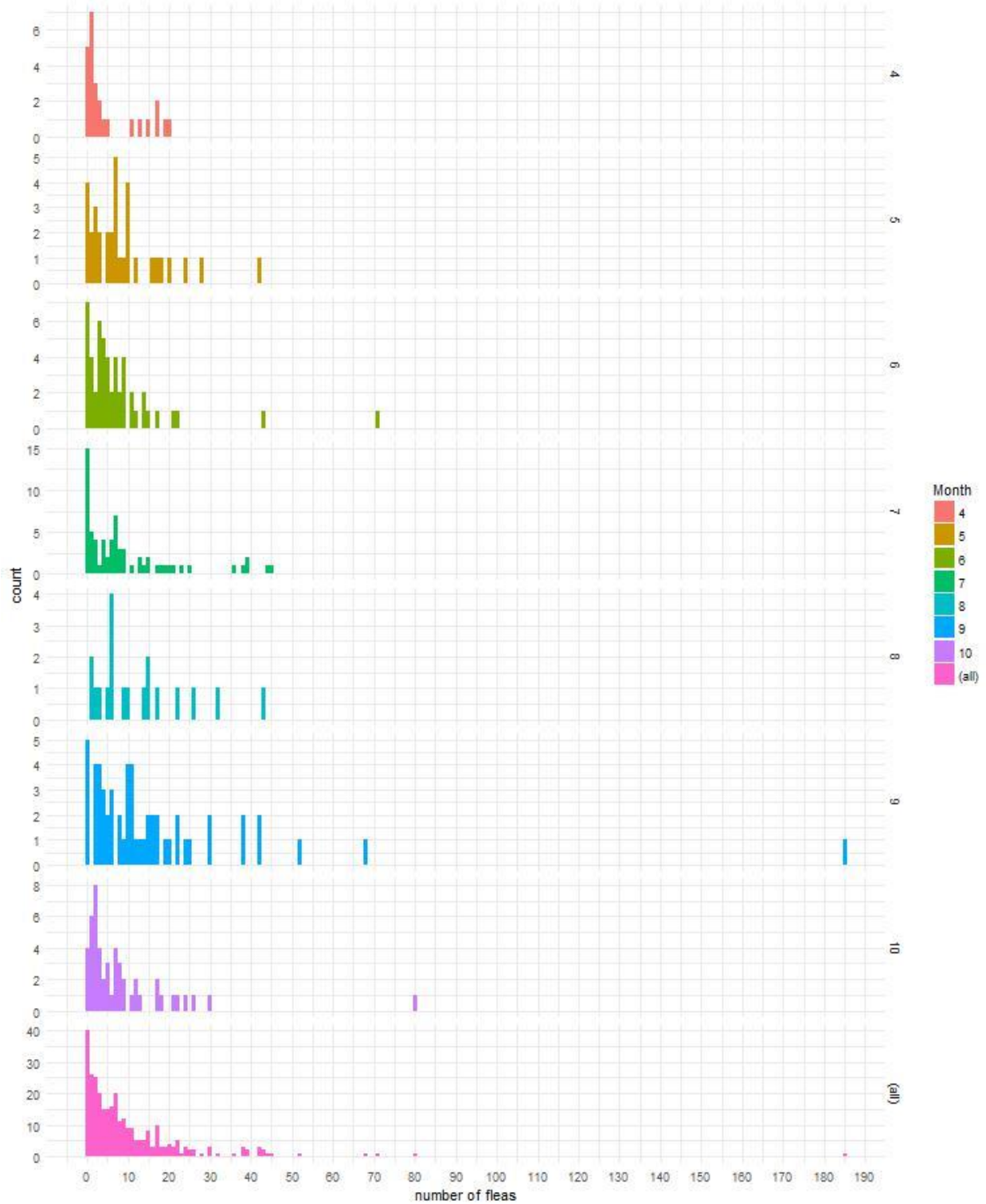


Figure 4.4 Counts of fleas on black-tailed prairie dogs (n = 303) by month for three colonies on Pawnee National Grassland, Colorado, April – October 2007 – 2008.

Table 4.3 Summary of fleas from 73 infested hosts (out of 289 infested) from three colonies on Pawnee National Grassland in summer and fall of 2007 and 2008.

Species	Total no. (% ttl fleas)	Max. no.	Mean abundance (95% CI)	Median abundance (95% CI)	Summer prevalence % (no. hosts examined)	Fall prevalence % (no. hosts examined)	Total prevalence % (no. hosts examined)
<i>Oropsylla hirsuta</i>	617 (68.2)	37	8.9 (6.9, 11.0)	7 (4.9, 9.1)	96.0 (50)	82.6 (23)	91.8 (73)
<i>O. tuberculata</i>	1 (0.1)	1	1	1	2.0 (50)	0 (23)	1.4 (73)
<i>Pulex simulans</i>	286 (31.6)	45	8.1 (4.5, 11.7)	5 (4.1, 9.9)	38.0 (50)	69.6 (23)	47.9 (73)
<i>Thrassis Fotus</i>	1 (0.1)	1	1	1	2.0 (50)	0 (23)	1.4 (73)
All fleas	905 (100)	45	12.2 (9.5, 14.8)	7 (5.0, 9.0)	100 (50)	100 (23)	100 (73)

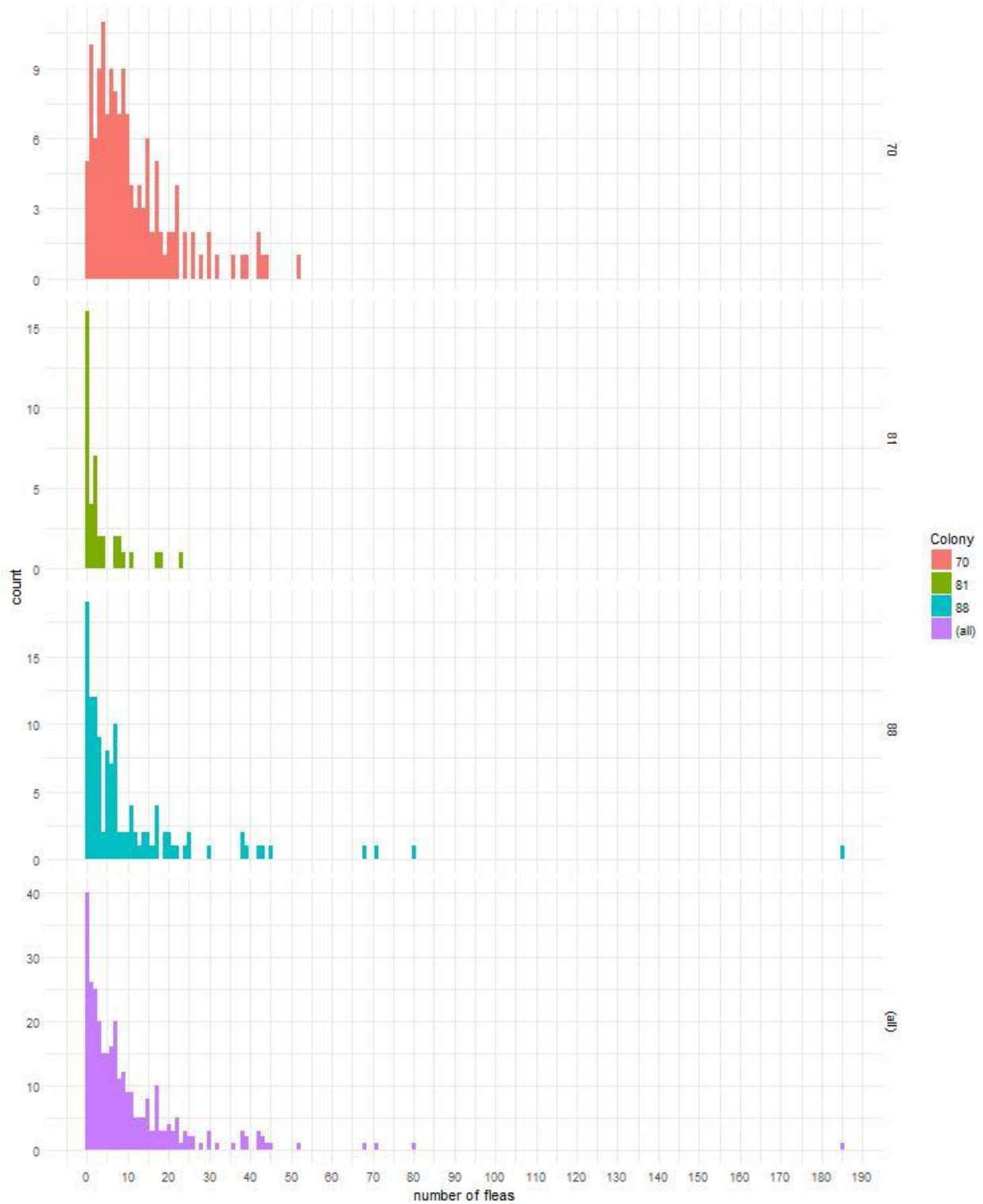


Figure 4.5 Counts of fleas on black-tailed prairie dogs (n = 303) for each of three colonies on Pawnee National Grassland, Colorado, April – October 2007 – 2008.

Table 4.4 Top 12 of 24 negative binomial generalized linear models predicting flea counts on black-tailed prairie dogs on Pawnee National Grassland, CO. These twelve models account for the top 92% of total Akaike weight (w_i) of all models considered.

Coefficients	K	logL	AICc	Δ AICc	w_i
month, sex, colony	10	-304.7	632.0	0.0	0.25
month, sex, colony, allele L	12	-302.5	632.9	0.9	0.16
month, sex, colony, heterozygosity	11	-303.8	632.9	0.9	0.16
month, sex, colony, allele P	12	-303.6	635.1	3.1	0.05
month, sex, allele L	11	-305.0	635.1	3.1	0.05
month, sex, age, colony	12	-303.7	635.2	3.2	0.05
month, sex, age, colony, allele L	14	-301.1	635.4	3.4	0.05
month, sex, colony, allele I	12	-304.0	635.8	3.8	0.04
month, sex	9	-308.0	636.1	4.1	0.03
month, sex, age, colony, heterozygosity	13	-302.9	636.4	4.4	0.03
month, sex, age, allele L	13	-303.0	636.4	4.4	0.03
month, sex, colony, allele Q	12	-304.4	636.7	4.7	0.02

K = number of estimated parameters; $LogL$ = log likelihood; Δ AICc = the difference between model AICc and the model with the lowest AICc; w_i = Akaike weight for each of the competing models.

Coefficient importance (no. containing models): month = 1.00 (24); sex = 1.00 (24); colony = 0.83 (12); allele L = 0.29 (4); heterozygosity = 0.21 (4); age = 0.19 (4) (remaining coefficients importance ≤ 0.07)

Table 4.5 Summary of model averaged coefficients for negative binomial model predicting flea counts as a function of month of capture, sex, age, colony, and genotype for black-tailed prairie dogs from two colonies on Pawnee National Grassland, Colorado, April – October 2007 – 2008 (n = 95). Coefficients have been back-transformed to allow biological interpretation.

Coefficient	Full avg.	CI, 2.5%	CI, 97.5%	Cond. avg.	CI, 2.5%	CI, 97.5%
Intercept	4.82	2.30	10.13			
May	1.41	0.63	3.14			
June	0.35	0.16	0.80			
July	1.42	0.64	3.14			
August	1.27	0.51	3.18			
September	2.13	1.07	4.24			
October	0.89	0.45	1.78			
Sex (male)	3.06	2.03	4.59			
Age (yearling)	0.94	0.65	1.37	0.74	0.38	1.45
Age (adult)	1.02	0.79	1.33	1.13	0.64	1.97
Colony 88	0.62	0.34	1.12	0.56	0.36	0.87
Heterozygosity (yes)	1.06	0.80	1.41	1.31	0.87	1.97
Allele L (1 copy)	1.09	0.74	1.62	1.36	0.80	2.31
Allele L (2 copies)	0.79	0.33	1.92	0.45	0.17	1.17
Allele Q (1 copy)	1.01	0.81	1.27	1.22	0.58	2.58
Allele Q (2 copies)	0.91	0.38	2.17	0.25	0.04	1.77
Allele P (1 copy)	1.01	0.88	1.16	1.25	0.78	1.98
Allele P (2 copies)	1.00	0.89	1.11	0.94	0.58	1.51
Allele I (1 copy)	0.99	0.86	1.15	0.86	0.44	1.69
Allele I (2 copies)	1.01	0.74	1.39	1.40	0.36	5.48

Full avg. = full average: coefficients averaged over all 24 models; Cond. avg. = conditional average: coefficients averaged only over models in which they occur. Averages are based on AICc weights.

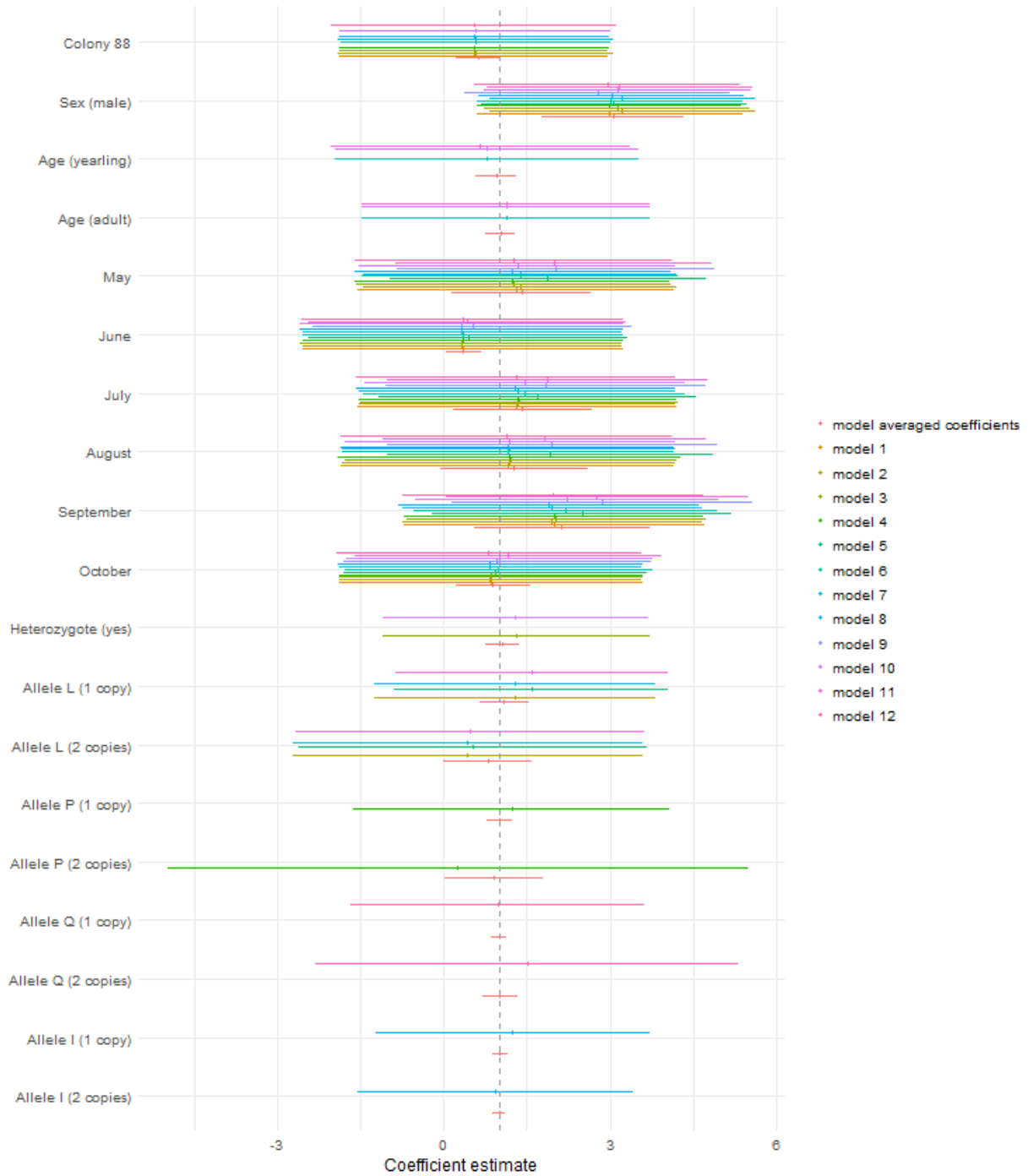


Figure 4.6 Coefficient estimates (and 95% CI) for the top twelve negative binomial models predicting counts of fleas on black tailed prairie dogs as determined by Akaike weight (w_i). The twelve best models accounted for 92% of total w_i . Also shown are the model-averaged coefficient estimates averaged across all 24 models according to w_i , and their 95% confidence intervals. Models 1 – 12 correspond, in order, to the 12 models shown in Table 4. Coefficients shown here have been back-transformed to allow biological interpretation.

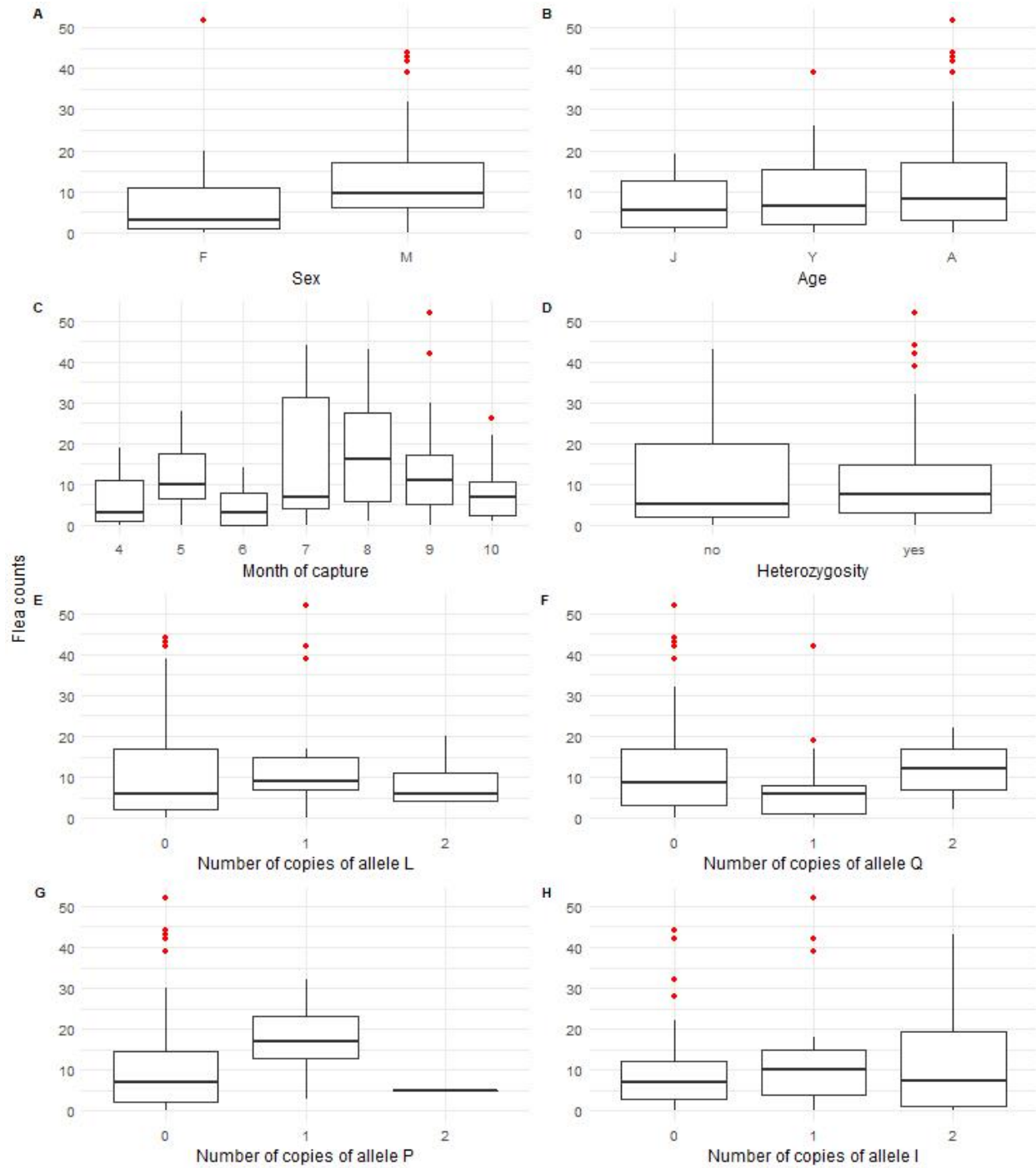


Figure 4.7 Actual flea counts from black-tailed prairie dogs on Pawnee National Grassland grouped by predictor variables included in 24 GLMs with individual flea counts as the response variable. The data represented in these figures is the same as that used to fit the models.

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