Factors that affect parasitism of black-tailed prairie dogs by fleas

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Abstract. Fleas (Insecta: Siphonaptera) are hematophagous ectoparasites that feed on vertebrate hosts. Fleas can reduce the fitness of hosts by interfering with immune responses, disrupting adaptive behaviors, and transmitting pathogens. The negative effects of fleas on hosts are usually most pronounced when fleas attain high densities. In lab studies, fleas desiccate and die under dry conditions, suggesting that populations of fleas will tend to decline when precipitation is scarce under natural conditions. To test this hypothesis, we compared precipitation vs. parasitism of black-tailed prairie dogs (*Cynomys ludovicianus*) by fleas at a single colony during May and June of 13 consecutive years (1976–1988) at Wind Cave National Park, South Dakota, USA. The number of fleas on prairie dogs decreased with increasing precipitation during both the prior growing season (April through August of the prior year) and the just-completed winter–spring (January through April of current year). Due to the reduction in available moisture and palatable forage in dry years, herbivorous prairie dogs might have been food-limited, with weakened behavioral and immunological defenses against fleas. In support of this hypothesis, adult prairie dogs of low mass harbored more fleas than heavier adults. Our results have implications for the spread of plague, an introduced bacterial disease, transmitted by fleas, that devastates prairie dog colonies and, in doing so, can transform grassland ecosystems.

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INTRODUCTION

Parasites can cause morbidity or mortality in hosts (Anderson and Gordon 1982, Brown and Brown 1986, 1996), thereby affecting host populations (Combes 2001, Poulin 2006) and, in some cases, the structure of ecosystems (Thomas et al. 2005, Ostfeld et al. 2008). Fleas (Siphonaptera) are hematophagous ectoparasites that remove blood from vertebrate hosts, thereby causing irritation and open sores (Hoogland 1979, Marshall 1981). Other deleterious consequences of fleas for their hosts include reduction in body mass, weakening of the immune system, and increased need for grooming (Lehmann 1993, Mooring et al. 2004,

Hawlena et al. 2006a). Moreover, many flea species transmit pathogens, some of which can be lethal to hosts (Eisen and Gage 2012). For these reasons, fleas can be important to the ecology and conservation of host species (Gage 2005, Gage and Kosoy 2006, Krasnov 2008).

The deleterious effects of fleas are sometimes difficult to detect, but other times are striking (Raveh et al. 2011, 2015). The negative effects of fleas on hosts are usually most pronounced when fleas attain high numbers (Alexander 1974, Hoogland 1979). For example, in some host species, animals lose body mass when harboring large numbers of fleas (Brown and Brown 1986, Hawlena et al. 2006b, Devevey and Christe 2009).

Furthermore, fleas are sometimes inefficient at transmitting certain kinds of pathogenic bacteria and, therefore, large numbers of fleas might be necessary to transmit sufficient numbers of bacteria to cause disease (Lorange et al. 2005, Eisen and Gage 2012).

If fleas attain high densities, the consequences can be dire for hosts. In the case of desert gerbils (*Gerbillus dasyurus*), for example, a load of 50 fleas can induce a 16% increase in daily metabolic rate (Khokhlova et al. 2002). In several species of rodents from western North America, high densities of fleas can favor outbreaks of sylvatic plague, a disease, transmitted by fleas, that devastates rodent populations (Nelson 1980, Barnes 1993, Cully et al. 2006, Wilder et al. 2008) and can kill fleas themselves (Eisen et al. 2009).

Laboratory studies demonstrate that fleas can quickly desiccate and die under dry conditions (Krasnov et al. 2001*a*, *b*, 2002). Consequently, numbers of fleas might be low during droughts under natural conditions (e.g., Parmenter et al. 1999, Enscore et al. 2002). If so, then the negative effects of fleas on hosts also should be low during droughts. However, rigorous information from hosts, fleas, and precipitation under natural conditions is elusive (Ben-Ari et al. 2011).

Black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter "prairie dogs") are colonial, burrowing, herbivorous rodents that inhabit the grasslands of western North America (King 1955). Populations of prairie dogs have decreased markedly over the past 150 years because of poisoning, recreational shooting, and destruction of habitat (Forrest and Luchsinger 2006, Proctor et al. 2006, Reeve and Vosburgh 2006). Moreover, since the 1940s, plague has killed billions of prairie dogs (Eskey and Haas 1940, Cully et al. 2006). As a result, biologists have devoted considerable attention to the ecology of fleas in prairie dog colonies (Hoogland 1979, Barnes 1993, Cully and Williams 2001, Brinkerhoff et al. 2006, Salkeld and Stapp 2006, Tripp et al. 2009, Jachowski et al. 2011, Eads et al. 2013, 2015). Some studies have suggested that high precipitation enhances growth in populations of fleas (Stapp et al. 2004, Collinge et al. 2005, Savage et al. 2011), but rigorous information about the number and density of fleas on prairie dogs has not been available for confirmation in these studies. On the contrary, prairie dog burrows might function as "climate filters," and thereby allow fleas to survive and reproduce during extended periods when conditions are dry above ground (Ben-Ari et al. 2011).

To better understand the relationship between precipitation and the number of fleas per prairie dog, we investigated the relationship between precipitation and flea loads on prairie dogs over 13 consecutive years at a single colony under natural conditions in South Dakota. We also investigated the effects of the following variables on the number of fleas: prairie dog age (adult [>1 yr old] or juvenile [≤2 months] after weaning), prairie dog sex (male or female), and time of year (May or June). Further, we evaluated a hypothesis that prairie dogs of low body mass are more susceptible to parasitism by fleas (Eads 2014, see also Krasnov 2008).

Materials and Methods

For 13 consecutive years (1976–1988), John Hoogland and his students captured and marked prairie dogs at a colony in Wind Cave National Park (Hoogland 1995). The colony occupied 6.6 ha at an elevation of ~1500 m above sea level (43°37 N–103°29 W) and in late May of 1976 through 1988 contained a mean ± SD of 123 ± 15 adult and 87 ± 26 juvenile prairie dogs (Hoogland 1995). The prairie dogs mated in mid-February through late-March. Periods of gestation and lactation were about 35 and 41 days, respectively. Nearly weaned juveniles first emerged from their natal burrows in May and early June. Litter size at weaning ranged from one to six, and most commonly was three or four (Hoogland 1995).

To handle and weigh prairie dogs, Hoogland and his students used a conical canvas bag that could be unzipped from either end; for juveniles, they used a plastic sandwich bag (Hoogland 1995). Routine measurements for each captured adult and juvenile included sex and body mass to the nearest gram with a Pesola spring balance (Baar, Switzerland). Hoogland et al. combed the back and both flanks of each prairie dog with a fine-toothed comb 10 times (30 total combings per prairie dog) and recorded the number of fleas observed during combing, handling, and marking. To

prevent double-counting, each flea was collected and submerged into alcohol. Flea species were not identified, but probably were *Oropsylla* (formerly *Opisocrostis*) *hirsuta*, *O. tuberculata cynomuris*, and *Pulex* spp. (Pizzimenti 1975, Hopla 1980, Eisen et al. 2009).

Hoogland used the same method for counting numbers of fleas on prairie dogs over the 13 years of research. For animals in general (Gómez-Díaz et al. 2010, Valença-Barbosa et al. 2014) and for prairie dogs in particular (Hoogland 1979, Eads 2014), the number of ectoparasites observed during handling is usually lower than the number of ectoparasites actually present. We assume that, as reported for other animals (Fowler and Cohen 1983, Brown and Brown 1996), the number of fleas observed during handling represented a constant proportion of the total number actually present.

The majority of live trappings and examinations in 1976 through 1988 occurred during May and June, so we limited our analyses of flea counts to those two months. Individual prairie dogs were examined for fleas once in either May or June of each year. Many prairie dogs were live-trapped over several consecutive years, and a few were live-trapped over as many as eight consecutive years (Hoogland 1995). In prior analyses with data collected at intervals of about one week, the number of fleas observed on a prairie dog during marking and handling did not significantly correlate with the number of fleas observed at earlier and later handlings (Eads 2014, see also Krasnov et al. 2006 for similar information from other rodent species). We therefore assumed for our statistical analysis that flea counts from the same prairie dog in different years were independent.

Throughout his research at the Wind Cave study-colony over 13 years, Hoogland (1995) detected no evidence of mortality of prairie dogs from plague. Indeed, plague was not discovered among prairie dogs anywhere in western South Dakota until 2005 (Livieri et al. 2015). Repeated, annual sampling from the same study-colony over time allowed us to concentrate on correlations between precipitation and numbers of fleas on prairie dogs, with no complications from either plague or intercolonial differences that might have affected the number and density of fleas.
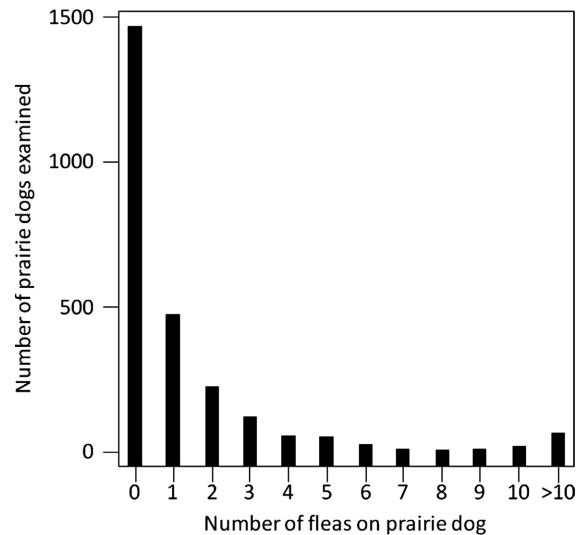

Fig. 1. Frequency of the number of fleas observed during handling and combing of black-tailed prairie dogs (*Cynomys ludovicianus*) in May or June of 1976 through 1988 at a single colony at Wind Cave National Park, South Dakota, USA.

Using "PROC GENMOD" in SAS 9.3 (SAS Institute Inc., Cary, North Carolina, USA), we fit GLMs (generalized linear models) to evaluate correlations between the number of fleas observed on prairie dogs and independent variables defined below. Most prairie dogs had 0 fleas. For prairie dogs that harbored at least one flea, most harbored ≤ 5 fleas, but a few harbored ≥ 10 (Fig. 1). We, therefore, implemented a SAS command that allowed the error distribution to approximate a negative binomial distribution (for similar examples with prairie dogs, see Tripp et al. 2009, Eads 2014).

We compared flea numbers on prairie dogs vs. precipitation during the prior growing season (year $t − 1$ April through August; King et al. 2013) and precipitation during the just-completed winter–spring (year t January through April). We estimated cumulative monthly precipitation (Fig. 2) from the Parameter-Elevation Relationships on Independent Slopes Model (PRISM; Daly et al. 2008). PRISM values correlate closely with precipitation at Wind Cave National Park (King et al. 2013). We conducted a preliminary assessment to determine if linear or nonlinear forms should be used for the precipitation variables (e.g., Franklin et al. 2000:550–551). The assessment suggested
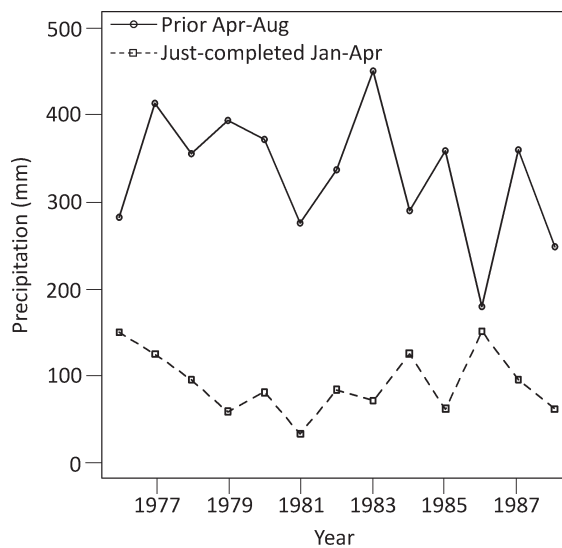
Fig. 2. Cumulative precipitation during the prior growing season, April through August, and precipitation during the just-completed winter–spring, January through April, during 1976–1988 at a single colony of black-tailed prairie dogs at Wind Cave National Park, South Dakota, USA. The two variables were not significantly correlated (linear regression: r^2 = 0.10, P = 0.292).

use of a curvilinear, asymptotic form of prior-year precipitation (x + log[x]) and a linear form of precipitation during the just-completed winter–spring.

Previous research has shown that age of prairie dog (adult or juvenile), sex of prairie dog (female or male), and month (May or June) correlate with the number of fleas on prairie dogs (Hoogland 1979, Wilder et al. 2008, Tripp et al. 2009, Eads 2014), so we included binary variables for host age, host sex, and month-of-sampling. Because individuals of low body mass exhibit weakened behavioral and immunological defenses against ectoparasites in many species (Lochmiller and Deerenberg 2000, Krasnov 2008), we also included body mass as a variable for our analysis with prairie dogs. Adult and juvenile rodents probably differ in their ability to combat fleas using behavioral and immunological defenses, and in the amount of surface area (habitat) they provide for fleas (Krasnov 2008). Therefore, we also included an interaction between host age and body mass to determine if the correlation between body mass and flea numbers differed between adults

and juveniles; support for the interaction would justify separate assessments for adults and juveniles.

To examine potential effects of the aforementioned variables on the number of fleas observed on prairie dogs, we used the following negative binomial GLM:

Number of fleas on prairie dog
= Intercept + (Precipitation in the previous April through August + log[Precipitation in the previous April through August]) + Precipitation of the just-completed January through April + Month + Prairie dog age + Prairie dog sex + Prairie dog mass + (Prairie dog age × Prairie dog mass).

To evaluate variables and reduce the full model to the most parsimonious form, we used likelihood ratio (LR) tests with an approximate chi-square (χ^2) distribution for the test statistic (α = 0.050; McCullagh and Nelder 1989). To investigate the relative importance of the effects of precipitation in April through August of the prior year and precipitation in January through April of the just-completed winter–spring (the variables of primary interest), we evaluated changes in Akaike's information criterion for small sample sizes (i.e., AICc). The period of precipitation that caused the greater reduction in AICc when included in the most parsimonious model was considered more important (Burnham and Anderson 2002).

We evaluated predictive capabilities of the most parsimonious GLM using k-fold cross-validation (Boyce et al. 2002). We divided the data into k = 5 random subsets, each comprised of a training set (80% of data) and a testing set (20%). We iteratively withheld one of the five subsets, fit the GLM using the respective training data, and used estimated coefficients to predict values for the training and testing data sets. We separated predicted values into 14 equal-interval bins, scaled between the minimum and maximum values, and simplified the bins to those with values >0. Using a Spearman rank correlation (r_S), we compared the frequencies, by bin, of predicted

values for the test data to the frequencies, by bin, of predicted values for the training data; significant, positive correlations indicate good model performance (Boyce et al. 2002).

Results for categorical variables reported below include the mean number of fleas per prairie dog ± 1 SD. Results for continuous variables (precipitation and prairie dog mass) are presented in figures depicting predicted values from the most parsimonious GLM, which considered the sex and age structure of the study population. Using predicted values for continuous variables allows for presentation of results that account for correlations between multiple variables (e.g., time of year, prairie dog age, prairie dog sex, prairie dog mass) and the number of fleas on prairie dogs.

RESULTS

We had information on fleas from the handling and marking of 1142 juvenile (532 females, 610 males) and 1379 adult prairie dogs (868 females,

511 males) from 1976 through 1988 (194 ± 60.1 prairie dogs per year). Results stem from the negative binomial GLM approach discussed above. Similar numbers of fleas were found on females (1.38 ± 3.6, n = 1934 fleas collected) and males (1.40 ± 4.0, n = 1573 fleas) (P = 0.639, LR χ^2 = 0.22, df = 1), so the variable for host sex was removed from analysis. Remaining variables were retained. Cross-validation indicated good model performance for the five k-fold sets (all $r_S \geq 0.829$ and $P \leq 0.042$).

Fleas were more abundant on adults (1.64 ± 4.3, n = 2264 fleas collected) than juveniles (1.09 ± 2.9, n = 1243 fleas), and this difference was significant (P = 0.002, LR χ^2 = 9.88, df = 1). Fleas were more abundant in May (1.49 ± 4.0, n = 2081 combing events, 3111 fleas) than in June (0.90 ± 2.1, n = 440 combing events, 396 fleas), and the difference was significant (P < 0.001, LR χ^2 = 25.18, df = 1).

The number of fleas on prairie dogs decreased with increasing precipitation during April through August of the prior year (Fig. 3A;
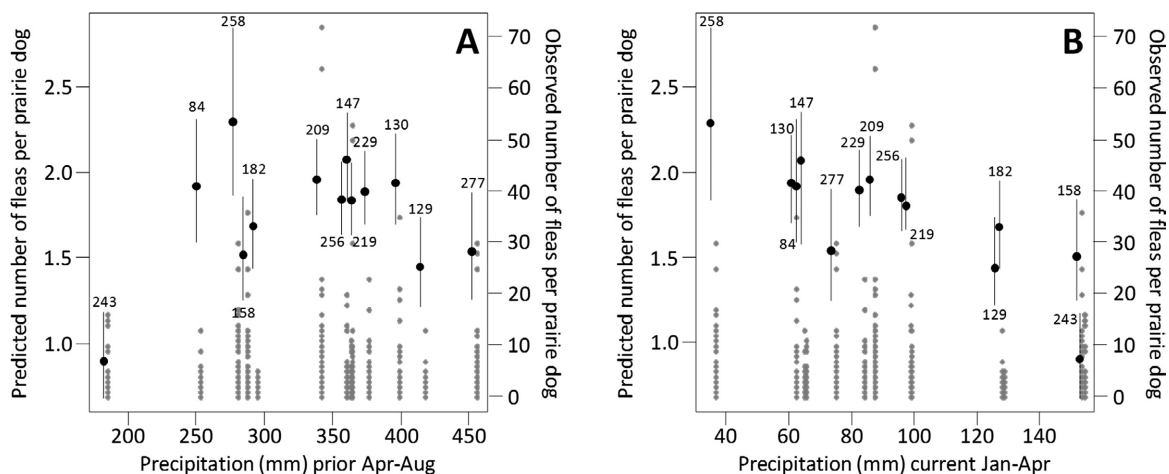

Fig. 3. (A) Predictions and 95% confidence intervals (block dots and bars) and observed values (gray dots) for the number of fleas on black-tailed prairie dogs in May and June vs. cumulative precipitation during the prior growing season, April through August. (B) Predictions and 95% confidence intervals (black dots and bars) and observed values (gray dots) for the number of fleas on prairie dogs in May and June vs. precipitation during the just-completed winter–spring, January through April. For both (A) and (B), the number of prairie dogs examined for fleas is indicated by the number above the 95% confidence interval. To examine the effects of age, sex, time of year (May or June), body mass, precipitation in the previous April through August, and precipitation in the just-completed January through April, we used a generalized linear model in SAS, with the option of specifying the error distribution as negative binomial. Observed values do not account for the negative binomial distribution of flea counts from prairie dogs or our multivariate analysis, and therefore do not clearly represent the effect of precipitation on the observed number of fleas per prairie dog. Each observed value (gray dot) represents the number of fleas observed on an individual at a specific level of precipitation.
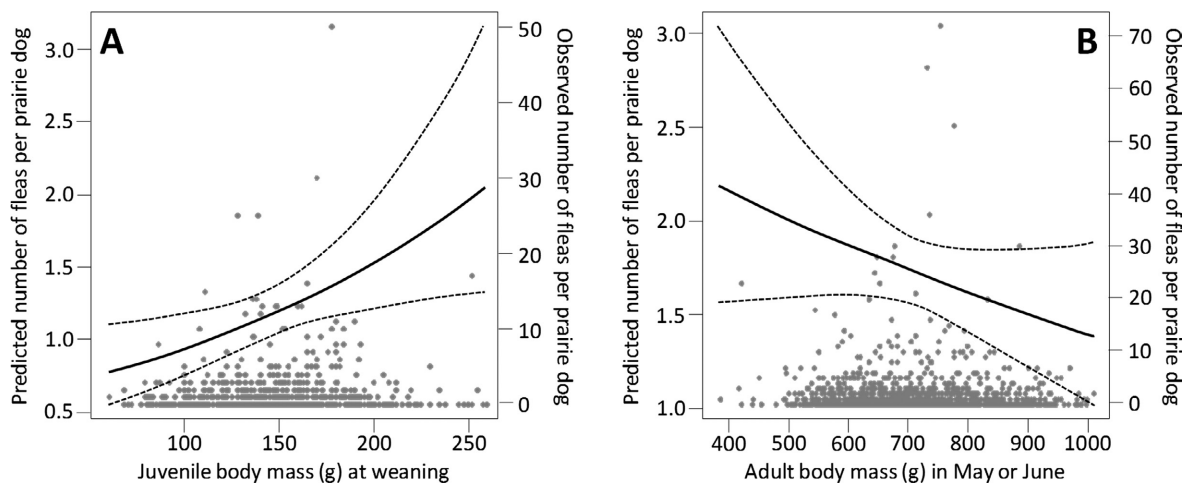
Fig. 4.   Predictions and 95% confidence intervals (black lines) and observed values (gray dots) for numbers of fleas on juvenile (A) and adult (B) black-tailed prairie dogs during May and June vs. body mass. See text and legend to Fig. 2 for details about collection of data, sample sizes for number of prairie dogs examined for fleas, and the statistical analysis. Observed values (gray dots) do not account for the negative binomial distribution of flea counts from prairie dogs or our multivariate analysis, and therefore do not clearly represent the effect of precipitation on the observed number of fleas per prairie dog. Each observed value (gray dot) represents the number of fleas observed on an individual at a specific body mass.

$P = 0.002$, LR $\chi^2 = 12.70$, df = 2). The number of fleas also decreased with increasing precipitation during January through April of the just-completed winter–spring (Fig. 3B; $P = 0.001$, LR $\chi^2 = 10.09$, df = 1). Inclusion of the variable for precipitation of April through August of the prior year reduced AICc by 5.33 units, whereas inclusion of the variable for precipitation of January through April of the just-completed winter–spring reduced AICc by 10.98 units. Thus, precipitation during the just-completed winter–spring (January through April) was a better predictor of the number of fleas on prairie dogs than prior-year precipitation (April through August).

The interaction between age and body mass justified separate assessments for adults and juveniles ($P = 0.008$, LR $\chi^2 = 6.97$, df = 1). Heavy juveniles carried more fleas than juveniles of lower body mass (Fig. 4A; $P = 0.012$, LR $\chi^2 = 6.41$, df = 1). In contrast, adult prairie dogs of low body mass carried more fleas than heavier adults (Fig. 4B; $P < 0.001$, LR $\chi^2 = 62.99$, df = 1).

Discussion

To our knowledge, only four other studies have evaluated the hypothesis that parasitism of rodents by fleas varies with precipitation. Three of the studies did not involve prairie dogs and are difficult to interpret because plague affected hosts and fleas at many of the sites under investigation (Stenseth et al. 2006, Reijniers et al. 2014, Xu et al. 2015). The fourth study involved prairie dogs over three consecutive summers (June–August) in areas of northeastern New Mexico evidently unaffected by plague. Fleas were most abundant on prairie dogs in the second summer (Eads 2014; Eads et al. 2016), which was preceded by the driest February through July on record during 113 years of monitoring in the short-grass prairies of northeastern New Mexico (NOAA 2011). These counterintuitive results encouraged our investigation using Hoogland's 13-year data set. Our results show that the number of fleas per prairie dog varies inversely with both precipitation during the prior growing season and precipitation of the just-completed winter–spring. Results from Hoogland's (1995) long-term research are therefore consistent with shorter term results from Eads (2014).

When precipitation is scarce in grassland ecosystems, vegetative production is reduced, thus limiting the availability of moisture and

Table 1. Studies that have compared host mass, host sex, host age, time of year, and precipitation with parasitism of black-tailed prairie dogs (*Cynomys ludovicianus*) by fleas; to our knowledge, these are the only studies that address these issues.

Reference	Location	Time period	Variable	Findings
Brinkerhoff et al. (2006)	Boulder County, Colorado	February and March 2004	Prairie dog mass	More fleas on heavy individuals than on individuals of lower body mass (age not accounted for)
			Prairie dog sex	More fleas on males than on females
Wilder et al. (2008)	Pawnee National Grassland, Colorado	June 2004–May 2007 (December and January excluded)	Time of year	*Oropsylla hirsuta* more abundant in June than in May; *O. tuberculata cynomuris* more abundant in May than in June
Tripp et al. (2009)	Pawnee National Grassland, Colorado	June 2004–May 2007 (December and January excluded)	Prairie dog age	*O. hirsuta*, *O. tuberculata cynomuris*, and *Pulex simulans* more abundant on adults than on juveniles
			Prairie dog sex	*O. hirsuta*, *O. tuberculata cynomuris*, and *P. simulans* more abundant on males than on females
Jachowski et al. (2011)†	Rocky Mountain Arsenal National Wildlife Refuge, Colorado	June through September 2009	Prairie dog age	More fleas on adults than on juveniles
			Prairie dog mass (condition index)	No relationships between flea parasitism and body mass for adults and juveniles
Eads (2014)	Vermejo Park Ranch, New Mexico	June through August 2010–2012	Prairie dog age	*O. hirsuta* and *P. simulans* more abundant on adults than on juveniles
			Prairie dog mass (condition index)	Both *O. hirsuta* and *P. simulans* more abundant during a year with dry February through July conditions, relative to 2 years with more spring–summer precipitation
			Precipitation	Both *O. hirsuta* and *P. simulans* more abundant on adults of low mass than on heavier individuals during the dry year
This study	Wind Cave National Park, South Dakota	May and June 1976–1988	Prairie dog mass	More fleas on adults of low body mass than on heavier adults; more fleas on heavy juveniles than on juveniles of lower body mass
			Prairie dog sex	More fleas on males than on females
			Prairie dog age	More fleas on adults than on juveniles
			Time of year	More fleas in May than in June
			Precipitation	More fleas following drier, prior growing seasons (April through August of prior year); more fleas in years with drier conditions during just-completed winter–spring (January through April)

Notes: Some of the studies used indices of host condition (instead of host mass) as a variable during analysis. In those studies that identified fleas to the species level, flea species included two prairie dog specialists (*Oropsylla hirsuta* and *O. tuberculata cynomuris*) and one generalist (*Pulex simulans*).

† In the study of Jachowski et al. (2011), an insecticide affected fleas in seven of the 11 colonies studied.

palatable forage for herbivorous prairie dogs (Sala et al. 1988, Lauenroth 2008). Consequently, prairie dogs might lose body mass in dry years (Eads 2014; Eads et al. 2016). Prairie dogs of low mass might have weaker behavioral and immunological defenses against ectoparasites (Eads et al. 2016; see Krasnov 2008 for information with other rodents), especially during dry years when prairie dogs cannot compensate for low mass by consuming more water and nutrients in succulent vegetation (Hawlena et al. 2008). Recent field data from New Mexico suggest that with low precipitation during February through July of the current year, prairie dogs of low body mass devote little time to self-grooming in July–August (Eads 2014:138–139; Eads et al. 2016). Less grooming might increase their susceptibility to parasitism by fleas (see Rust and Dryden 1997 for relevant information from domestic cats).

Data from Eads et al. (2016) indicate that prairie dogs provided with supplemental food and

water had fewer fleas than prairie dogs in control areas. Perhaps the added food and water allowed the prairie dogs to devote more time to grooming themselves, thereby improving their efforts to combat fleas. Moreover, the supplemental food contained vitamins A, C, and E, which can improve a host's acquired immune system to detect an ectoparasite's saliva, and then to stimulate a swift immune response that reduces a flea's ability to acquire a blood meal (Jones 1996). The combination of supplemental food and vitamins to hosts therefore can reduce survivorship and reproduction among fleas (Krasnov 2008).

Results from Hoogland's long-term research provide insight into the potential effect of precipitation on the number and density of fleas within prairie dog colonies. Some scientists predict that global warming will disrupt the hydrological cycle in the grasslands of western North America, thereby causing an increased occurrence of prolonged droughts, with occasional short periods of intense precipitation (IPCC 2007, Knapp et al. 2008). Such extreme events are likely to affect wildlife populations (Parmesan et al. 2000), including those of ectoparasites (Jones et al. 2016). More research is needed to assess the impact of extreme climate events on prairie dogs and their fleas.

In our examination of 13 years of data, adult prairie dogs of low body mass harbored more fleas than heavier adults. Brinkerhoff et al. (2006) and Eads et al. (2016) observed the same trend, but Jachowski et al. (2011) found no relationship between flea counts and body mass (Table 1). Our results from a multivariate analysis of long-term data support the hypothesis (Eads 2014) that adult prairie dogs of low mass exhibit weakened defenses against fleas. Weakened host defenses would improve survivorship and reproduction of fleas, allowing them to increase in abundance (Krasnov 2008, St. Juliana et al. 2014).

Contrary to our results for body mass of adult prairie dogs, heavy juveniles had more fleas than juveniles of lower body mass. Factors related to acquired resistance (which can reduce survivorship and reproduction of fleas; Krasnov 2008) are seemingly not implicated, because juvenile prairie dogs had only recently emerged from their natal burrows, and their immune systems probably were not yet fully developed. As for other species of rodents (Hawlena et al.

2008, Krasnov 2008), juvenile prairie dogs might require repeated exposure to the saliva of fleas in order to develop acquired resistance to the fleas. Perhaps heavy juveniles have more fleas than juveniles of low body mass because their larger bodies provide more habitat for ectoparasites; this factor evidently did not apply to parasitism of adult prairie dogs by fleas, however. Another possibility is that heavy juveniles spent less time self-grooming than juveniles of lower body mass, or that adult prairie dogs spent less time allogrooming juveniles of low mass; we did not evaluate these possibilities.

The absence of plague during Hoogland's (1995) research facilitated interpretation of the flea data, and thereby, paradoxically, allows new insights into the role of fleas in the transmission of plague in colonies of prairie dogs. Plague persists throughout much of the prairie dog's range (Cully et al. 2006, Lowell et al. 2015, Mize 2015) and causes relatively low, chronic rates of mortality within colonies during enzootic periods (Biggins et al. 2010) and occasional sudden, far-reaching die-offs during epizootic outbreaks (Eads and Biggins 2015). Our results support a hypothesis (Eads 2014) that dry conditions within the current year can favor increases in the number of fleas on prairie dogs, and thereby increase the probability of plague epizootics when (1) moisture returns, (2) prairie dog densities increase, and (3) mild temperatures facilitate the rate at which fleas transmit *Y. pestis*. More research is needed for a better understanding of those factors that affect the spread of plague within and among colonies of prairie dogs.

Acknowledgments

is for descriptive purposes and does not imply endorsement by the U.S. Government.

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