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Source: *Journal of Parasitology*, 103(4):309-319.

Published By: American Society of Parasitologists

<https://doi.org/10.1645/16-195>

URL: <http://www.bioone.org/doi/full/10.1645/16-195>

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PRECIPITATION, CLIMATE CHANGE, AND PARASITISM OF PRAIRIE DOGS BY FLEAS THAT TRANSMIT PLAGUE

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ABSTRACT: Fleas (Insecta: Siphonaptera) are hematophagous ectoparasites that can reduce the fitness of vertebrate hosts. Laboratory populations of fleas decline under dry conditions, implying that populations of fleas will also decline when precipitation is scarce under natural conditions. If precipitation and hence vegetative production are reduced, however, then herbivorous hosts might suffer declines in body condition and have weakened defenses against fleas, so that fleas will increase in abundance. We tested these competing hypotheses using information from 23 yr of research on 3 species of colonial prairie dogs in the western United States: Gunnison's prairie dog (*Cynomys gunnisoni*, 1989–1994), Utah prairie dog (*Cynomys parvidens*, 1996–2005), and white-tailed prairie dog (*Cynomys leucurus*, 2006–2012). For all 3 species, flea-counts per individual varied inversely with the number of days in the prior growing season with >10 mm of precipitation, an index of the number of precipitation events that might have caused a substantial, prolonged increase in soil moisture and vegetative production. Flea-counts per Utah prairie dog also varied inversely with cumulative precipitation of the prior growing season. Furthermore, flea-counts per Gunnison's and white-tailed prairie dog varied inversely with cumulative precipitation of the just-completed January and February. These results complement research on black-tailed prairie dog (*Cynomys ludovicianus*) and might have important ramifications for plague, a bacterial disease transmitted by fleas that devastates populations of prairie dogs. In particular, our results might help to explain why, at some colonies, epizootics of plague, which can kill >95% of prairie dogs, are more likely to occur during or shortly after periods of reduced precipitation. Climate change is projected to increase the frequency of droughts in the grasslands of western North America. If so, then climate change might affect the occurrence of plague epizootics among prairie dogs and other mammalian species that associate with them.

A variety of parasites and diseases affect wildlife, sometimes causing significant problems for conservation (Binder et al., 1999; Daszak et al., 2000; Morens et al., 2004). In a recent analysis of global trends from 1940 through 2004, 60% of diseases were capable of spreading from wildlife to humans; 72% of those diseases are caused by pathogens that evolved in wildlife, including many pathogens that are transmitted—i.e., vectored—by ectoparasitic arthropods (Jones et al., 2008). More information about ectoparasites should improve efforts to reduce the spread of vector-borne diseases, thereby promoting health for both humans and wildlife (Daszak et al., 2000; Ostfeld et al., 2008; Salkeld et al., 2016).

Fleas (Insecta: Siphonaptera) are ectoparasites that feed on blood from vertebrate hosts (Marshall, 1981; Medvedev and Krasnov, 2006; Krasnov, 2008). Fleas can impose numerous costs upon vertebrates, e.g., by weakening immune systems, causing declines in body mass, and stimulating bouts of grooming that increase energy expenditures and reduce time for foraging and antipredator vigilance (Lehmann, 1993; Khokhlova et al., 2002; Neuhaus, 2003; Mooring et al., 2004; Hawlena et al., 2006; Devevey and Christe, 2009; Garrido et al., 2016). Furthermore, fleas can transmit pathogens (Gage et al., 1995; Eisen and Gage, 2012), including the plague bacterium *Yersinia pestis* that originated in Asia (Achtman et al., 1999) but has been introduced to every continent except Australia and Antarctica (Gage and Kosoy, 2006; Stenseth et al., 2008; Keim and Wagner, 2009; Antolin et al., 2010; Gage, 2012; Hinnebusch et al., 2016).

The negative effects of fleas on hosts are usually most pronounced when fleas attain high densities (Anderson and May, 1978; Hoogland, 1979; Brown and Brown, 1996; Lorange et al., 2005; Raveh et al., 2011, 2015). Consequently, many studies have tried to identify factors that affect the abundance of fleas in nature (Marshall, 1981; Krasnov, 2008). In laboratories, fleas do not survive well and their populations decline when reared under dry conditions (Silverman et al., 1981; Cooke and Skewes, 1988; Krasnov et al., 2001a, 2001b, 2002; Kreppel et al., 2016). This finding suggests that populations of fleas in terrestrial ecosystems will decline during or following dry years (Parmenter et al., 1999; Enscore et al., 2002; Ben-Ari et al., 2011).

Conversely, populations of fleas might increase during or following dry years if their herbivorous hosts suffer declines in body condition because of less succulent vegetation when precipitation is scarce. Specifically, poor body condition of hosts during or following dry years might lead to weakened defenses against fleas, so that fleas will increase in abundance (Krasnov et al., 2005; Gillespie et al., 2008; Krasnov, 2008; Facka et al., 2010; Eads, 2014). This latter hypothesis is supported by research on three herbivorous rodent species: Mongolian gerbil (*Meriones unguiculatus*), Daurian ground squirrel (*Spermophilus dauricus*; Eads et al., 2016a), and black-tailed prairie dog (*Cynomys ludovicianus* (Eads et al., 2016b; Eads and Hoogland, 2016).

Here, we use long-term research under natural conditions to investigate the effect of precipitation on the number of fleas that parasitize Gunnison's prairie dogs (*Cynomys gunnisoni*), Utah prairie dogs (*Cynomys parvidens*), and white-tailed prairie dogs (*Cynomys leucurus*). Black-tailed prairie dogs, Gunnison's prairie dogs, Utah prairie dogs, and white-tailed prairie dogs are all herbivorous, burrowing, diurnal, colonial rodents that inhabit the grasslands of western North America (Hollister, 1916; Clark, 1977; Lechleitner, 1969; Hoogland, 1995). Precipitation negatively

Received 30 December 2016; revised 19 March 2017; accepted 23 March 2017.

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DOI: 10.1645/16-195

affects flea-counts for black-tailed prairie dogs (Eads et al., 2016b; Eads and Hoogland, 2016), but little is known about the effects that precipitation might have on flea-counts for Gunnison's prairie dogs, Utah prairie dogs, and white-tailed prairie dogs.

We considered 3 precipitation variables that might affect flea-counts from prairie dogs: (1) cumulative precipitation of the prior growing season, which correlates directly with net productivity of vegetation in the same year and the following year in grassland ecosystems (Sala et al., 1988; Knapp and Smith, 2001; Lauenroth, 2008); (2) the number of days in the prior growing season with >10 mm of precipitation, an index of the number of large precipitation events that might cause a substantial, prolonged increase in soil moisture and vegetative production (Sala et al., 1981; Lauenroth and Sala, 1992; Schwinning and Sala, 2004; Heisler-White et al., 2008); and (3) cumulative precipitation during the winter (January and February) just before flea-counts each year. This research is important because all species of prairie dogs are increasingly rare (Hoogland, 2006, 2007), plague commonly affects their populations (Clark, 1977; Rayor, 1985; Cully et al., 2006; Eads and Biggins, 2015), and an increased understanding of flea ecology is needed to better protect prairie dogs from plague (Eads et al., 2016b; Eads and Hoogland, 2016). Moreover, all 3 precipitation variables are likely to be affected by climate change (IPCC, 2007; Knapp et al., 2008), suggesting implications of our research for future prairie dog populations.

MATERIALS AND METHODS

J.L.H. and his students collected all data. We analyzed and interpreted the data. Henceforth, the term "we" is used for this collective effort. We live-trapped and collected adult fleas from prairie dogs living under natural conditions at 3 sanctuaries over 23 yr: (1) Gunnison's prairie dogs at Petrified Forest National Park, Arizona, 1989–1994; (2) Utah prairie dogs at Bryce Canyon National Park, Utah, 1996–2005; and (3) white-tailed prairie dogs at Arapaho National Wildlife Refuge, Colorado, 2006–2012. Please see Hoogland (1999, 2001, 2003) for descriptions of these areas. For each prairie dog species, annual flea-counts from the same colony over time eliminated complications from intercolonial differences that affect flea-counts for prairie dogs (Hoogland, 1979; Brinkerhoff et al., 2006; Tripp et al., 2009; Eads, 2014).

For each prairie dog species, we analyzed data from months for which we had data from every year of research. This approach minimized any confounding effects of seasonal changes in flea densities; data from March through June in 1 yr, e.g., would not be comparable to data from May through June in another year. This is an important consideration, because seasonal changes in flea populations can be substantial (Hoogland, 1979; Anderson and Williams, 1997; Wilder et al., 2008; Friggens et al., 2010; Jachowski et al., 2012; Eads and Hoogland, 2016; Tripp et al., 2016). We examined Gunnison's prairie dogs and white-tailed prairie dogs for fleas from March through June of each year. We also examined Utah prairie dogs for fleas from March through June, but, as described below, we only used data from March through May (i.e., no June) in the primary analysis.

During the intervals noted above, we detected no evidence of mortality of Gunnison's prairie dogs or white-tailed prairie dogs from plague, which can devastate populations of prairie dogs (Clark, 1977; Rayor, 1985; Cully et al., 2006; Eads and Biggins, 2015). Enzoootic, low-level plague (Biggins et al., 2010) might have

affected prairie dogs at all 3 sites, but we did not investigate this possibility. Epizootic plague devastated the study-colony of Gunnison's prairie dogs in 1995 (Hoogland, 1999), so we did not use data from that final year of research at that colony. At the study-colony of Utah prairie dogs, 2 individuals that died aboveground in June 1998 and 3 that perished aboveground in late May 2001 tested positive for plague, suggesting the disease was spreading in epizootic form (Hoogland et al., 2004). In an attempt to reduce the spread of plague, Hoogland et al. (2004) infused burrows at the study-colony with an insecticide-dust called Pyreperm (which contains permethrin) in late June 1998 and 31 May–2 June 2001. Mortality from plague appeared to stop after the infusions (Hoogland et al., 2004). We excluded Utah prairie dog data from June 1998 and June 2001 because Pyreperm kills fleas (Hoogland et al., 2004), and also because plague alters flea-counts on prairie dog by encouraging fleas to congregate on live hosts (Tripp et al., 2009; Eads, 2014). Removal of Utah prairie dog data from June 1998 and June 2001 prompted removal of data from June in other years, resulting in primary analyses with data from March through May of 10 consecutive years (see the online Supplemental Data for an analysis of Utah prairie dog data from March through June for the 8 yr with no evidence of epizootic plague: 1996–1997, 1999–2000, and 2002–2005). In the year following infusions of burrows with Pyreperm, parasitism by fleas had rebounded by the time flea-counts resumed in March 1999 and 2002, when 100% ($n = 104$) and 83% ($n = 89$) of Utah prairie dogs carried at least 1 flea, respectively (see Karhu, 1999 for a similar example of a temporal decline in the efficacy of Pyreperm with black-tailed prairie dogs). Consequently, we used flea-counts from Utah prairie dogs ≥ 9 mo after infusions with Pyreperm.

To handle and weigh prairie dogs, we used a conical canvas bag for adults (≥ 9 mo old) and a plastic sandwich bag for juveniles (≤ 2 mo old). Routine measurements for each captured animal included sex and body mass to the nearest gram with a Pesola (Baar, Switzerland) spring balance. We combed the sides and back of each individual 10 times (30 combings per prairie dog) and counted the number of ectoparasites that either fell to a large plywood board below or were removed from the pelage with tweezers (Hoogland et al., 2004; see also Hoogland, 1979, 1995; Eads and Hoogland, 2016). To prevent recounts, each flea was collected and submerged into alcohol. The probability of detecting ≥ 1 flea when a prairie dog harbored ≥ 1 flea was probably high (Eads et al., 2013).

We did not identify the species of fleas that we observed, but they probably included *Hoplosyllus anomalus*, *Oropsylla hirsuta*, *Oropsylla labis*, *Oropsylla tuberculata cynomuris*, *Pulex* spp., and *Thrassis francisi* (Allred, 1952; Pizzimenti, 1975; Ubico et al., 1988; Barnes, 1993; Anderson and Williams, 1997; Cully and Williams, 2001; Friggens et al., 2010; Tripp et al., 2016). Of these fleas, *O. hirsuta* and *O. t. cynomuris* are most common on prairie dogs. At a site in northeastern Colorado, *O. hirsuta* is found on prairie dogs throughout the year and often peaks in fall, and *O. t. cynomuris* peaks in March (Wilder et al., 2008). If these patterns are consistent among sites and species of prairie dogs (which is unknown), then our analysis would account for the spring period, when *O. hirsuta* can attain high densities but has not yet peaked in abundance, and March, when *O. t. cynomuris* peaks in abundance.

Using 'PROC GLIMMIX' in SAS® 9.3 (SAS Institute, Cary, North Carolina), we fit generalized linear models (GLMs) to evaluate correlations between the number of fleas observed on

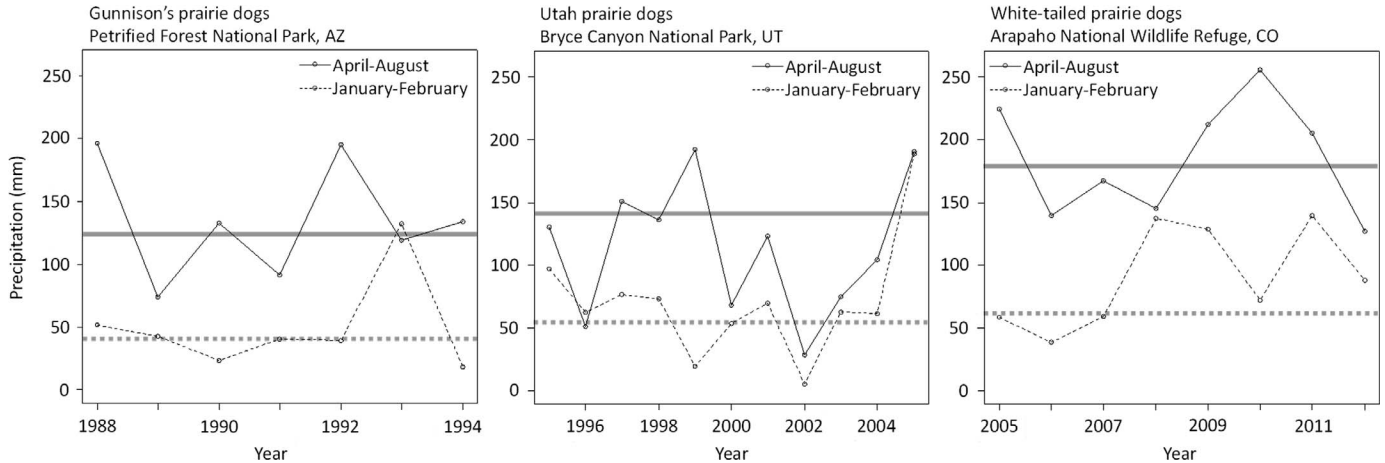


FIGURE 1. Cumulative precipitation (mm rain and melted snow) during the primary growing season April–August and just-completed winter months of January and February for colonies of Gunnison's, Utah, and white-tailed prairie dogs. These data come from the Parameter–Elevation Relationships on Independent Slopes Model (PRISM; Daly et al., 2008). Long-term average precipitation values (1950–2012) are presented as gray lines (solid = April through August, dashed = January and February). We evaluated correlations between precipitation and numbers of fleas observed on prairie dogs.

prairie dogs and 6 independent variables defined below. Because the most common flea-count for all 3 prairie dog species was 0, and because most individuals with at least 1 flea harbored <5 fleas, we implemented a SAS command that allowed the error distribution to approximate a negative binomial distribution. Negative binomial GLMs are commonly used to assess count data when counts of 0 are common (White and Bennetts, 1996; Hilbe, 2011; Warton et al., 2016) and have been used in several studies of prairie dogs and their fleas (Tripp et al., 2009, 2016; Eads, 2014; Eads et al., 2016b; Eads and Hoogland, 2016).

Independent variables for our investigation of precipitation vs. the number of fleas on prairie dogs included the following: (1) cumulative precipitation (mm rainfall and melted snow) during the prior growing season of year $t - 1$, (2) cumulative precipitation during the just-completed January and February of the current year t , (3) month of flea-counts (March, April, May, or June), (4) age of prairie dog (adult or juvenile), (5) sex of prairie dog, and (6) body mass of prairie dog at the time of combing for fleas. Previous research has shown that age, sex, body mass, and month correlate with the number of fleas on black-tailed prairie dogs (Eads and Hoogland, 2016). Month of flea-counts also correlates with the number of fleas on Gunnison's prairie dogs (Friggens et al., 2010), Utah prairie dogs (Jachowski et al., 2012), and white-tailed prairie dogs (Hoogland, 1979; Anderson and Williams, 1997; Tripp et al., 2016). Individuals of low body mass might exhibit weakened behavioral and immunological defenses against fleas (Krasnov et al., 2005; Eads, 2014; Eads et al., 2016b; Eads and Hoogland, 2016). Because adult and juvenile rodents probably differ in their ability to combat fleas by using behavioral and immunological defenses, and in the amount of surface area (i.e., habitat) they provide for fleas (Krasnov, 2008; Eads and Hoogland, 2016), we included an interaction between age and body mass. A significant interaction would justify assessments of the correlation between body mass and flea-counts for adults and juveniles separately. Conversely, no statistical significance would justify combining data from adults and juveniles, while controlling for prairie dog age (if the independent effect of prairie dog age was significant).

We estimated cumulative monthly precipitation at each colony from the parameter-elevation relationships on independent slopes model (PRISM; Daly et al., 2008). PRISM values correlate directly with precipitation in the grasslands of western North America (Di Luzio et al., 2008), where precipitation during the growing season within a given year correlates directly with net productivity of vegetation in the same year and the following year (Sala et al., 1988; Knapp and Smith, 2001; Lauenroth, 2008). The growing season (i.e., that part of the year when precipitation and temperature allow for vegetative growth) can vary with latitude and longitude. We defined the growing season as April through August, when the majority of precipitation fell and temperatures tended to remain above 0 C during our study (Smith, 1966; Thomas et al., 2003; Peterson et al., 2004). Precipitation just before flea-counts in each year t was calculated for all species of prairie dogs as the sum of precipitation during January and February (Fig. 1). For reference, we present data on historical precipitation from 1950 through 2012 (Fig. 1; see Results).

For each species of prairie dogs, the full GLM for flea-counts was represented by the following equation:

$$\begin{aligned} &\text{Number of fleas on prairie dog} \\ &= \text{Intercept} + \text{Precipitation of the prior growing season} \\ &\quad + \text{Precipitation of the just-completed January and February} \\ &\quad + \text{Month} + \text{prairie dog age} + \text{prairie dog sex} \\ &\quad + \text{prairie dog body mass} \\ &\quad + (\text{prairie dog age} \times \text{prairie dog body mass}) + \text{error}. \end{aligned}$$

Models with too few variables can result in biased inference, whereas models containing too many variables can result in poor precision or inclusion of variables with spurious effects (Burnham and Anderson, 2002). We reduced the above GLM to a parsimonious model by using backward elimination (McCullagh and Nelder, 1989) based on tests with an approximate chi-square (χ^2) distribution for the test statistic, with $\alpha = 0.050$.

As described in the Results, trends from our primary analyses sometimes changed if the variable for precipitation of the prior growing season was expressed as the number of days with >10 mm of precipitation (Daly et al., 2008) rather than as cumulative

TABLE I. Mean number of fleas (± 1 SE) vs. month (March, April, May, or June) during J.L.H.'s long-term research on black-tailed (1976–1988), Gunnison's (1989–1994), Utah (1996–2005), and white-tailed (2006–2012) prairie dogs. Data from May and June are from both juveniles (<2 mo old) and adults (>9 mo old). Data from March and April are from adults only. Data from black-tailed prairie dogs are limited to May and June, because these are the only months for which we had large sample sizes every year. Data from Utah prairie dogs exclude flea-counts from June of the 2 yr (1998 and 2001) when epizootic plague was detected (but see online Supplemental Data).

Reference	Species	Month of sampling	Mean no. of fleas ± 1 SE (n)
Eads and Hoogland (2016)	Black-tailed prairie dog	May	1.49 \pm 0.1 (2,081)
		June	0.90 \pm 0.1 (440)
This study	Gunnison's prairie dog	March	23.28 \pm 1.0 (897)
		April	5.73 \pm 0.5 (454)
		May	3.27 \pm 0.2 (1,246)
		June	2.41 \pm 0.1 (2,256)
This study	Utah prairie dog	March	15.63 \pm 1.0 (901)
		April	12.05 \pm 1.3 (422)
		May	1.50 \pm 0.1 (763)
		June	0.88 \pm 0.1 (1,802)
This study	White-tailed prairie dog	March	6.07 \pm 0.8 (201)
		April	8.41 \pm 0.9 (200)
		May	2.41 \pm 0.2 (287)
		June	1.91 \pm 0.3 (820)

precipitation of the prior growing season. For comparison with data from our study periods, we present historical data from 1981 through 2012 (see Results; similar data were not available for years before 1981).

After model selection, we interpreted the effect of a variable if the 95% confidence interval of its coefficient excluded 0 (Burnham and Anderson, 2002). Significant results for precipitation are presented in figures that depict predicted values and 95% confidence intervals from model projections for adults and juveniles combined. This is similar to plotting estimates of survival from mark–recapture models (e.g., in program MARK; White et al., 2001). We present our results for correlations between precipitation and flea-counts as expected changes in flea abundance given a particular change in precipitation (Cade, 2015; Lemoine et al., 2016) by using the highest predictor value A and the lowest value B as $(A - B)/B$. Flea-counts from different months, female and male prairie dogs, and adult and juvenile prairie dogs are presented in tabular format as averages ± 1 SE. Because flea-counts from almost-weaned juveniles were in late May and early June as they emerged from natal burrows, but flea-counts from adults were from all months; we also report average flea-counts ± 1 SE for juveniles and adults in May and June.

RESULTS

Gunnison's prairie dogs, New Mexico, March–June, 1989–1994

Precipitation: Precipitation during the growing season from 1988 (the year before flea-counts began) through 1994 ranged from 74 to 196 mm (Fig. 1; \bar{x} = 135 mm), compared to 56 and 226 mm during 1950–2012 (\bar{x} = 123). The number of days with >10 mm of precipitation during the prior growing season from 1989 through

TABLE II. Mean number of fleas (± 1 SE) vs. sex of prairie dog during J.L.H.'s long-term research on black-tailed (1976–1988), Gunnison's (1989–1994), Utah (1996–2005), and white-tailed (2006–2012) prairie dogs. These data combine flea-counts from both adults and juveniles and are from May and June for black-tailed prairie dogs and March through June for the remaining 3 species (i.e., data are limited to time periods when sample sizes were large). See also legend to Table I.

Reference	Species	Mean no. of fleas ± 1 SE (n)	
		Female	Male
Eads and Hoogland (2016)	Black-tailed prairie dog	1.38 \pm 0.1 (1,934)	1.40 \pm 0.1 (1,573)
This study	Gunnison's prairie dog	4.75 \pm 0.2 (2,795)	9.58 \pm 0.5 (2,058)
This study	Utah prairie dog	4.16 \pm 0.3 (2,193)	7.53 \pm 0.6 (1,695)
This study	White-tailed prairie dog	3.15 \pm 0.2 (879)	3.81 \pm 0.4 (629)

1994 ranged from 1 to 4, compared to 0 to 6 during 1981–2012. Precipitation during the just-completed January and February ranged from 18 to 132 mm during 1989–1994 (Fig. 1; \bar{x} = 49 mm), compared to from 1 to 132 mm during 1950–2012 (\bar{x} = 40 mm).

Parasitism by fleas: The variable for precipitation of the prior growing season was insignificant and removed from the model (χ^2 = 2.54, 1 df, P = 0.111). Numbers of fleas on Gunnison's prairie dogs declined from March into June (Table I; χ^2 = 920.98, df = 3, P < 0.001). Males carried more fleas than females (Table II; χ^2 = 17.64, 1 df, P < 0.001). Adults tended to harbor more fleas than juveniles (Table III). However, in the model, the effect of age was not statistically significant (χ^2 = 1.55, 1 df, P = 0.213) because of the strong interaction between age and body mass (χ^2 = 20.44, 1 df, P < 0.001). Regarding precipitation, if precipitation of the just-completed January and February declined from the maximum to the minimum, the predicted number flea-count per Gunnison's prairie dog increased by 35% (Fig. 2; χ^2 = 20.85, 1 df, P < 0.001). The interaction between host age and body mass justified separate assessments of body mass for adults and juveniles. Body mass of adults correlated with flea-counts (χ^2 = 5.13, 1 df, P = 0.024); however, the 95% confidence interval of the coefficient nearly overlapped 0 (0.00007–0.00098). Body mass was not significantly related to flea-counts from juveniles (χ^2 = 0.14, 1 df, P = 0.705). If we define precipitation of the prior growing season as the number of days with >10 mm of precipitation and the number of days with >10 mm of precipitation declined from 4 to 1 (the observed range), the predicted number of fleas per Gunnison's prairie dog increased by 84% (P < 0.001).

Utah prairie dogs, Utah, March–May, 1996–2005

Precipitation: Precipitation during the growing season from 1995 through 2005 ranged from 28 to 193 mm (Fig. 1; \bar{x} = 114 mm), compared to 36 and 232 mm during 1950–2012 (\bar{x} = 141 mm). The number of days with >10 mm of precipitation during the prior growing season from 1996 through 2005 ranged from 0 to 6 (the same range from 1981 to 2012). Precipitation during the just-completed January and February ranged from 5 to 189 mm during 1996–2005 (Fig. 1; \bar{x} = 67 mm), compared to 0 to 226 mm during 1950–2012 (\bar{x} = 54 mm).

TABLE III. Mean number of fleas (± 1 SE) vs. age of prairie dog during J.L.H.'s long-term research on black-tailed (1976–1988), Gunnison's (1989–1994), Utah (1996–2005), and white-tailed (2006–2012) prairie dogs. These data include May and June for juveniles and adults (when both juveniles and adults were sampled) and March through June for adults only. See also legend to Table I.

Reference	Species	Mean no. of fleas ± 1 SE (n)		
		May and June		March–June Adult
		Adult	Juvenile	
Eads and Hoogland (2016)	Black-tailed prairie dog	1.64 \pm 0.1 (2,264)	1.09 \pm 0.1 (1,243)	
This study	Gunnison's prairie dog	4.29 \pm 0.2 (1,567)	1.43 \pm 0.1 (1,935)	10.35 \pm 0.4 (2,918)
This study	Utah prairie dog	1.19 \pm 0.1 (1,233)	0.92 \pm 0.1 (1,331)	8.08 \pm 0.4 (2,556)
This study	White-tailed prairie dog	2.10 \pm 0.2 (378)	2.01 \pm 0.3 (729)	4.75 \pm 0.3 (779)

Parasitism by fleas: The following variables did not significantly correlate with Utah prairie dog flea-counts, so we removed them from the model: the interaction between age and body mass of Utah prairie dog ($\chi^2 = 1.10$, 1 df, $P = 0.294$), body mass ($\chi^2 = 0.38$, 1 df, $P = 0.540$), and precipitation during the just-completed January and February ($\chi^2 = 2.32$, 1 df, $P = 0.128$). Fleas declined in abundance from March into May (Table I; $\chi^2 = 754.76$, 2 df, $P < 0.001$). Males harbored more fleas than females (Table II; $\chi^2 = 51.90$, 1 df, $P < 0.001$). Adults harbored more fleas than juveniles (Table III; $\chi^2 = 6.74$, 1 df, $P = 0.009$). If cumulative precipitation of the prior growing season declined from the maximum to the minimum, the predicted number of fleas per Utah prairie dog increased by 37% (Fig. 2; $\chi^2 = 6.82$, 1 df, $P = 0.009$). If the number of days with >10 mm of precipitation during the prior growing season declined from 6 to 0, the predicted number of fleas per Gunnison's prairie dog increased by 74% ($P < 0.001$).

White-tailed prairie dogs, Colorado, March–June, 2006–2012

Precipitation: Precipitation during the growing season from 2005 through 2012 ranged from 127 to 256 mm (Fig. 1; $\bar{x} = 185$ mm), compared to 102 and 281 mm during 1950–2012 ($\bar{x} = 172$ mm). The number of days with >10 mm of precipitation during

the prior growing season from 2006 through 2012 ranged from 2 to 5, compared to a range of 0 to 5 during 1981–2012. Precipitation during the just-completed January and February ranged from 39 to 139 mm during 2006–2012 (Fig. 1; $\bar{x} = 95$ mm), compared to 20 to 139 mm during 1950–2012 ($\bar{x} = 60$ mm).

Parasitism by fleas: We removed the following variables from the model because their correlations with white-tailed prairie dog flea-counts were insignificant: the interaction between age and body mass of white-tailed prairie dog ($\chi^2 = 0.10$, 1 df, $P = 0.757$), age of white-tailed prairie dog ($\chi^2 = 3.44$, 1 df, $P = 0.064$), body mass ($\chi^2 = 1.13$, 1 df, $P = 0.287$), and precipitation of the prior growing season ($\chi^2 = 3.70$, 1 df, $P = 0.054$). Fleas increased in abundance from March into April, but declined in abundance into May and June (Table I; $\chi^2 = 159.12$, 3 df, $P < 0.001$). Fleas were more abundant on males than females (Table II; $\chi^2 = 9.41$, 1 df, $P = 0.002$). If precipitation of the just-completed January and February declined from the maximum to the minimum, the predicted number of fleas per white-tailed prairie dog increased by 16% (Fig. 2; $\chi^2 = 6.01$, 1 df, $P = 0.014$).

Results for flea-counts versus precipitation differed when we defined precipitation of the prior growing season as the number of days with >10 mm of precipitation. Specifically, flea-counts varied inversely and significantly with the number of days with

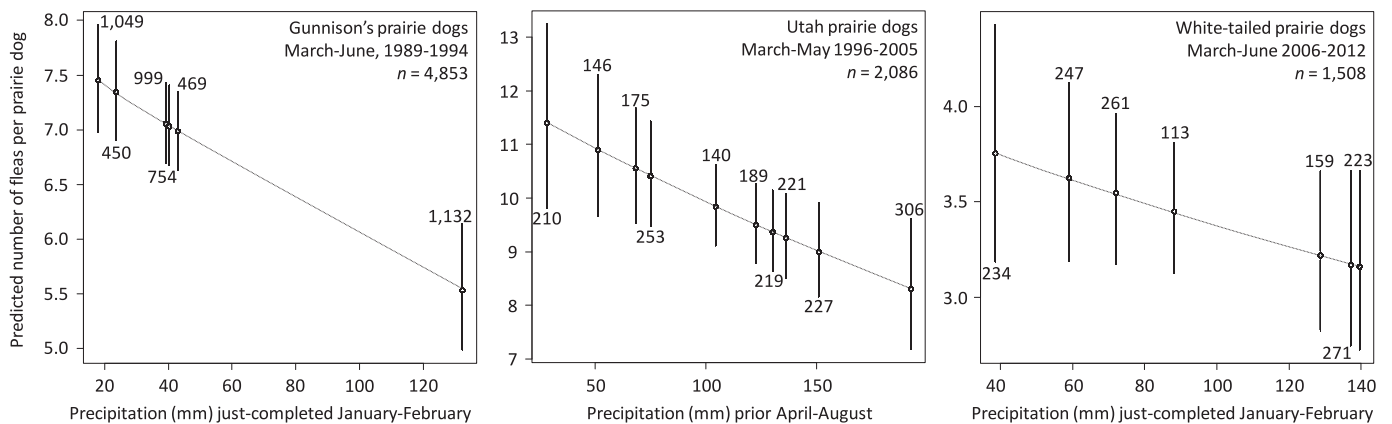


FIGURE 2. Predictions and 95% confidence intervals (dots and vertical bars) for the number of fleas on Gunnison's and white-tailed prairie dogs vs. precipitation (mm of rain and melted snow) during the just-completed January and February, and the number of fleas on Utah prairie dogs vs. cumulative precipitation during the prior growing season April–August. Individual predictions are for prairie dogs (adults and juveniles combined) during a particular year of sampling. The number above or below each confidence interval is the number of prairie dogs for which we recorded the number of fleas observed during marking and handling, and for which information from all predictor variables (in the most parsimonious multivariate model) is available. Data are from March through June for Gunnison's and white-tailed prairie dogs, and from March through May for Utah prairie dogs.

>10 mm of precipitation ($P = 0.045$). If the number of days with >10 mm of precipitation declined from 5 to 2, the predicted number of fleas per white-tailed prairie dog increased by 12%.

DISCUSSION

Three publications have now evaluated relationships between precipitation and parasitism by fleas for 4 species of prairie dogs. From 1975 through 1986 in South Dakota, the number of fleas on black-tailed prairie dogs in May and June varied inversely with cumulative precipitation of the prior growing season (March–September) and the just-completed January–April (Eads and Hoogland, 2016; for similar results, see Eads et al., 2016b). Here, we report similar trends for Gunnison's prairie dogs, Utah prairie dogs, and white-tailed prairie dogs (Fig. 2). The strength of these trends differs among prairie dog species, and is likely to depend on local factors that affect flea densities. If fleas are constrained to low densities at a prairie dog colony (e.g., because soils are not ideal for flea survival; Eads, 2014), then dry conditions might favor an increase in flea-counts, but the overall increase might be suppressed (because the fleas cannot attain high densities due to local constraints). In our study, this might have been the case with white-tailed prairie dogs (Fig. 2); the lower density of white-tailed prairie dog adults and juveniles within colonies, relative to Gunnison's prairie dog and Utah prairie dog densities (Hoogland, 1995, unpubl. data), also might have contributed to the lower white-tailed prairie dog flea-counts. Fleas were able to attain high densities on Gunnison's prairie dogs and Utah prairie dogs, and the effects of precipitation on flea counts were large for those species (Fig. 2). The overall theme for the 4 species of prairie dogs that we have studied is that dry conditions favor an increase in flea densities (see also Eads, 2014; Eads et al., 2016a, 2016b).

Annual variation in precipitation and vegetative production is high in grassland ecosystems, including those occupied by prairie dogs (Lauenroth and Sala, 1992; Knapp and Smith, 2001; Augustine, 2010; Detling, 2006). If precipitation is scarce within a grassland ecosystem, the availability of moisture and palatable forage is usually limited (Sala et al., 1988; Lauenroth and Sala, 1992; Lauenroth, 2008). Consequently, herbivorous prairie dogs can lose body mass during a drought (Cheng and Ritchie, 2006; Facka et al., 2010; Eads, 2014; see also Harlow, 1995; Pfeiffer et al., 1979). In New Mexico, black-tailed prairie dogs of low body mass devoted little time to grooming and might have exhibited weakened immunological defenses against fleas (Eads et al., 2016b). If this phenomenon also applies to Gunnison's prairie dogs, Utah prairie dogs, and white-tailed prairie dogs, it might explain why flea-counts varied inversely with precipitation of the prior growing season (Gunnison's prairie dogs and Utah prairie dogs) or just-completed January and February (white-tailed prairie dogs), and also why flea-counts varied inversely with the number of large precipitation events during the prior growing season (Gunnison's prairie dogs, Utah prairie dogs, and white-tailed prairie dogs).

Our investigations with long-term data from 4 prairie dog species might provide insights into the ecology of plague, which was introduced to North America in the early 1900s and invaded the geographic ranges of prairie dogs by the 1930s–1940s (Eskey and Haas, 1940; Gage and Kosoy, 2006; Keim and Wagner, 2009). During epizootics within colonies, the disease can cause sudden, far-reaching die-offs, sometimes killing >95% of prairie

dogs (Clark, 1977; Rayor, 1985; Barnes, 1993; Hoogland et al., 2004; St. Romain et al., 2013; Salkeld et al., 2016). Single fleas are often inefficient at transmitting the plague bacterium. Consequently, high densities of fleas might be necessary to initiate and sustain epizootics (Lorange et al., 2005; Wilder et al., 2008; Eisen et al., 2009; Richgels et al., 2016). Dry conditions favor increases in the number of fleas on prairie dogs (Eads et al., 2016b; Eads and Hoogland, 2016; this study). This trend might help to explain why epizootics of plague tend to occur at some prairie dog colonies during time intervals that are dry, or during wet periods recently preceded by dry conditions (e.g., black-tailed prairie dogs in Colorado; Collinge et al., 2005; Savage, 2007). Fleas do not survive well under dry conditions in labs (Krasnov, 2008), but prairie dog bodies and burrows might help to reduce the detrimental effects of dry conditions on fleas under natural conditions (Eads et al., 2016b; Eads and Hoogland, 2016).

Climate change might increase the frequency of prolonged droughts in the grasslands of western North America (IPCC, 2007; Knapp et al., 2008). prairie dogs consume many grass species that are highly responsive to directional changes in precipitation (Alward et al., 1999; Knapp and Smith, 2001), suggesting that prairie dogs might suffer from a higher risk of droughts in the future (but see Wilcox et al., 2016). Results here and published previously (Eads, 2014; Eads et al., 2016b; Eads and Hoogland, 2016) suggest that during or shortly after droughts, when succulent plants are scarce, prairie dogs are at increased risk to parasitism by fleas. If the current trend for global warming continues, then the frequency of widespread epizootics of plague among prairie dogs might increase.

If the frequency of plague epizootics among prairie dogs increases in the future, the ramifications will be profound. Prairie dogs are keystone species of their grassland communities (Whicker and Detling, 1988; Miller et al., 1994, 2000; Bangert and Slobodchikoff, 2000; Kotliar et al., 2006; Davidson et al., 2012; Miller and Reading, 2012; Martínez-Estévez et al., 2013; Sierra-Corona et al., 2015). The black-footed ferret (*Mustela nigripes*) feeds almost exclusively on prairie dogs and therefore suffers when plague kills prairie dogs, and ferrets themselves also are directly susceptible to plague (Miller et al., 2000; Kotliar et al., 2006; Miller and Reading, 2012). Birds that preferentially nest at prairie dog colony-sites (e.g., burrowing owls, *Athene cunicularia*; and mountain plovers, *Charadrius montanus*) lose vital habitat when plague kills prairie dogs (Eads and Biggins, 2015). By killing prairie dogs, plague can cause ecological disruptions that alter competitive and trophic relationships (Biggins and Kosoy, 2001), reduce biodiversity (Antolin et al., 2002), and transform grassland ecosystems (Eads and Biggins, 2015). We should be optimistic for prairie dogs and their ecosystems, however, because prairie dogs are such resilient animals (Hoogland, 2006, 2007), and biologists are discovering more and better ways to manage plague and reduce its effects on prairie dog populations (Biggins et al., 2010; Matchett et al., 2010; Rocke et al., 2010; Abbott et al., 2012).

One current method to minimize plague within prairie dog colonies is to infuse insecticide-dusts such as DeltaDust® into burrows (Seery et al., 2003; Hoogland et al., 2004; Biggins et al., 2010; Matchett et al., 2010; Jones et al., 2012; Tripp et al., 2016). Infusions probably can provide good protection against plague but are costly and time-consuming; therefore, they are sometimes feasible at a few selected colonies each year (Hoogland et al., 2004). Another method of management involves the use of

vaccine-laden baits that might protect prairie dogs from plague (Rocke et al., 2010; Abbott et al., 2012). Our results for precipitation vs. flea-counts from prairie dog might help wildlife and conservation managers to predict which colonies are likely to have high densities of fleas—and thus a higher probability of an epizootic of plague—each year. Weather stations and PRISM, e.g., should help wildlife managers to quantify precipitation and to make better predictions about when and where to infuse burrows or vaccinate hosts. Furthermore, attempts to decrease flea-numbers via infusions with insecticide-dusts or to vaccinate prairie dogs might be more valuable if precipitation is scarce during the primary growing season. More research is necessary for a better understanding of the effects of precipitation, flea densities, and other factors on the spread of plague within and between colonies of prairie dogs. More information will lead to better management of plague, and better conservation of prairie dogs and the many species that associate with them.

ACKNOWLEDGMENTS

For financial assistance, J.L.H. thanks Colorado Parks and Wildlife, Denver Zoological Foundation, Environmental Defense, National Geographic Society, National Science Foundation, Ted Turner Foundation, and University of Maryland Center for Environmental Science. D.A.E. thanks the U.S. Geological Survey and Colorado State University for financial support through cooperative agreement G14AC00403 and D. Biggins, P. Stevens, M. Antolin, K. Gage, and J. McAllister for professional support.

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