Plague transforms positive effects of precipitation on prairie dogs to negative effects

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ABSTRACT

Rodents characteristically benefit from increased precipitation, especially in typically dry habitats; "good years" of high precipitation improve their forage and water balance. However, *Yersinia pestis* (plague), a flea-borne pathogen of mammals that was introduced to western North America, has the greatest negative impact on at least some species of rodents during years of above-average precipitation. In the absence of plague mitigation, negative effects of plague in wet years might overwhelm the otherwise beneficial effects of increased moisture. In Montana and Utah, USA, where plague now occurs enzootically, we investigated the influence of precipitation on finite rates of annual population change (2000–2005) for 3 species of prairie dogs (*Cynomys* spp.) in replicated plots treated with deltamethrin dust and in non-treated plots for paired comparisons. There was a significant interaction between precipitation and treatment. When we reduced plague vector fleas, prairie dog visual counts tended to increase with increasing precipitation. Simultaneously, there was a negative relationship between counts and precipitation on paired plots where plague was not managed, suggesting that plague transformed and reversed the otherwise beneficial effect of increased precipitation. Are the good years gone for prairie dogs? Even if the good years are not gone, they are perhaps relatively scarce compared to historic times prior to the invasion of plague. This scenario might apply to other ecosystems and may pose broad conservation challenges in western North America.

1. Introduction

Plague, a flea-vectored disease of mammals (including humans), is caused by the bacterium *Yersinia pestis* that was introduced to North America ca. 1900. *Yersinia pestis* has caused disruptions in ecosystems of the western United States and has contributed to the precarious status of federally listed species such as the Utah prairie dog (*Cynomys parvidens*) and the black-footed ferret (*Mustela nigripes*) (Biggins and Kosoy, 2001). Plague also remains a threat to human health worldwide. Climatic factors are known to affect the incidence of human plague cases (Parmenter et al., 1999; Enscore et al., 2002), and broad-scale climate variation, such as El Niño cycles (Stapp et al., 2004), may be influential (Stenseth et al., 2006).

Precipitation likely affects the spread of plague in a variety of ways (Snäll et al., 2008; Ben Ari et al., 2011; Eisen and Gage, 2012). In general, plague seems to be more active during years of high precipitation (Parmenter et al., 1999; Enscore et al., 2002; Eads and Hoogland, 2017). Hypothesized mechanisms include trophic cascades or vortexes (Collinge et al., 2005; Ray and Collinge, 2006; Stapp, 2006) coupled with

density dependence in *Y. pestis* transmission. However, flea (Siphonaptera) abundance is a key factor in *Y. pestis* transmission rates (Lorange et al., 2005) and is also affected by precipitation at various scales from local events to broader patterns involving annual cycles and even annual lags (Eads et al., 2016a; b; Eads and Biggins, 2017). Increases in precipitation are generally correlated with decreases in mean temperatures, and changes in temperatures open additional avenues for influencing hosts, fleas, and *Y. pestis*. In particular, *Y. pestis* seems to replicate and is transmitted more efficiently by fleas in cooler temperatures (e.g., Williams et al., 2013).

Increased precipitation may produce counteracting influences, favoring rodent hosts on the one hand and plague on the other. For example, "… high precipitation and cool temperatures can enhance plague transmission through increases in host densities and *Y. pestis* replication rates, but those effects can be partly offset by improved host condition …" (Eads and Biggins, 2017:995). In this study, we assess the strength of these opposing forces using a controlled field experiment.

Four premises form the foundation for our examination: (1) Plague has the greatest negative impact on rodent hosts during years of above-

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average precipitation (Ben Ari et al., 2011; Eisen and Gage, 2012). (2) Plague seems to be maintained mainly by a variety of rodent species, most of which are primary consumers (Gage and Kosoy, 2005). (3) Populations of primary consumer rodents, including prairie dogs, respond positively to increased precipitation that directly affects their physiological water balance and improves their forage (Grassel et al., 2016; Stephens et al., 2018). (4) Precipitation is highly variable in interior continental climates (Noy-Meir, 1973; Lima et al., 2002; Letnic et al., 2011).

This study was an outgrowth of an earlier study of plague management in prairie dogs (Biggins et al., 2010). That previous study provided the opportunity to examine the relationship between precipitation and population change in 3 species of prairie dogs (PDs hereafter) because it involved pulicide treatments to manage plague with non-treated areas for paired comparison. Reduction of the effect of plague via flea control with pulicide treatment should allow PD populations to respond to precipitation in a manner resembling historic responses prior to introduction of plague. Although *Y. pestis* may not be entirely removed from plots by killing the fleas that transmit it, vector control significantly improved survival rates of PDs (Biggins et al., 2010). In areas of Montana and Utah, where enzootic plague was presumed to be present and when epizootics did not occur, controlling the flea vectors with deltamethrin increased annual survival rates for adult PDs by >40% (Biggins et al., 2010). In years when epizootic plague became common, populations on the deltamethrin-treatment plots had significantly higher growth rates compared to their non-treated, paired counterparts (Biggins et al. 2021a). In an associated study of black-footed ferrets (*Mustela nigripes*) – endangered specialized predators of PDs – either deltamethrin treatment of burrows or treatment of ferrets with a plague vaccine improved ferret annual survival by >200% (Matchett et al., 2010).

Here, we examine relationships between plague, prairie dogs, and precipitation in grassland ecosystems. The demonstrated efficacy of plague management enabled the current assessment of precipitation and its interactions with plague and PDs. Based on the four premises above, we hypothesize a reduction of plague transmission via vector control on the treated plots will produce a positive correlation between precipitation and PD population growth. In contrast, we hypothesize the combined effects of plague and precipitation on the non-treated plots will produce PD population declines assuming plague responds positively to increased precipitation and its effects overwhelm the otherwise beneficial effects of increased moisture. Alternatively, the relationship between population growth and precipitation on the non-treated plots might be positive or neutral because the relative strengths of precipitation and plague effects are unknown (Ben Ari et al., 2011; Eisen and Gage, 2012). Regardless, the relationships between annual population growth and annual precipitation should differ for treated and non-treated plots, producing a significant statistical interaction between precipitation and treatment.

2. Materials and methods

We studied three PD species (*C. lucovicianus, C. leucurus,* and *C. parvidens*) on five study areas in Montana and Utah, USA, 2000–2005 (Fig. 1). Details of experimental design and data collection were described by Biggins et al. (2010), but the most salient features are reiterated below.

2.1. Study areas

The black-tailed PD (*C. ludovicianus*) study area included five sites in Phillips County of northern Montana, USA. Four white-tailed PD (*C. leucurus*) sites were in the Coyote Basin study area of northeastern Utah near the border of Colorado. Utah PD (*C. parvidens*) sites were split among three recovery areas occupied by this species in southern Utah. Three Utah PD sites were on the West Desert Recovery Area (Fig. 1, southwest location), three sites were on the Paunsaugunt Recovery Area
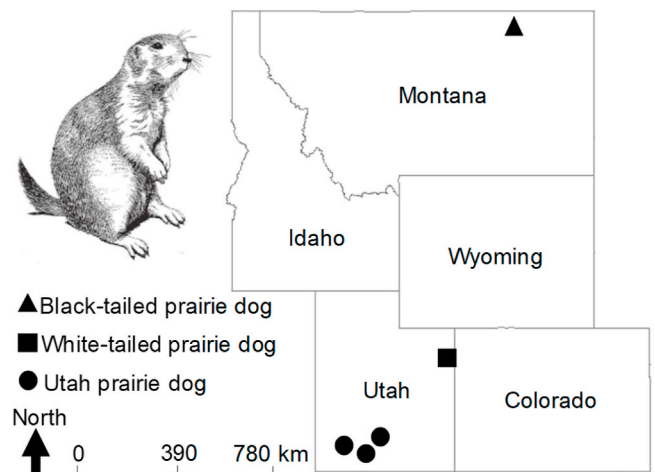

Fig. 1. Study sites in the western United States where the influence of precipitation on prairie dog population change was evaluated on paired plots with and without deltamethrin treatment to control the flea vectors of plague. Prairie dog sketch by D. Crawford.

(Fig. 1, southern location), and one site was on the Awapa Recovery Area (Fig. 1, northeast location).

We selected study areas because of their involvement in endangered species conservation. The black-tailed and white-tailed PD study areas supported endangered black-footed ferrets, and Utah PDs are themselves federally listed (as threatened). Although we chose these study areas without regard to their plague history, plague is likely well-established enzootically in all of them (Hanson et al., 2007; Biggins et al., 2010; Matchett et al., 2010) and epizootic eruptions also occur (Biggins et al. 2021a).

2.2. Experimental design

A key feature of the design was establishment of plots as pairs with similar ecological features on the same (split) or nearby (separate) colonies. One randomly selected plot of each pair was treated with deltamethrin dust to control the fleas that transmit *Y. pestis* and its paired plot was not treated. About 4 g of Delta Dust® (0.05% deltamethrin; Bayer Environmental Science, Carr, North Carolina, USA) was annually infused into each burrow opening on the treated plots, resulting in significant flea control over annual periods in most cases (Biggins et al., 2010; Eads and Biggins, 2019).

2.3. Visual counts of prairie dogs

We conducted visual counts annually during June–August, after young PDs were aboveground. We used binoculars and spotting scopes to systematically and repeatedly scan the plots (each plot was 3–9 ha in area), beginning just after sunrise and continuing until warming temperatures caused a decline in counts. We repeated the procedure for three days, using for analysis the highest count obtained (Fagerstone and Biggins, 1986). We counted from the same locations each year, simultaneously counting the treated and non-treated plots of each pair.

A previous report (Biggins et al., 2010) focused on individual PD survival, assessed from capture-recapture of marked animals, as the response variable, whereas the response variable here is visual counts of PDs, converted to values of annual finite population change (λ). A subset of these visual count data was used previously to examine epizootic phenomena at these sites without consideration of precipitation (Biggins et al. 2021a).

2.4. Precipitation

Precipitation data were derived from PRISM (Parameter-Elevation Relationships on Independent Slopes Model; Daly et al., 2008). Although PRISM data are interpolations, precipitation data for the period considered had the advantage of including satellite sensing in the algorithm. Precipitation (cm) was acquired from PRISM cells encompassing colony centroids from July 1 through June 30 of each annual interval, which corresponded to the typical interval between visual counts.

2.5. Statistical analyses

Data were originally in the form of two levels of repeated measures. First, data were considered as independent year pairs, with annual PD population change and total precipitation estimated for time intervals defined below. Visual counts were transformed into λ by dividing the PD count at the end of the annual interval by the count at the beginning of the interval. Re-scaling (λ + 1) assured all values were positive prior to natural log transformation, such that a complete collapse of a population had a value of zero after transformation. This procedure was done for both dusted and non-dusted plots. The visual counts at the beginning and end of each annual interval, transformed into population growth estimates, were the first level of repeated measures. The second level of repeated measures, analyzed as paired response variables in a general linear model, were the population growth estimates for the dusted and non-dusted plots of each pair.

Treatment was the paired (treated and non-treated) repeated measures variable in our general linear model, with measures of population growth (λ as described above) for all plot and consecutive year pairs. The first covariate in that model was precipitation in the annual interval during which visual count change was calculated. A second covariate in the general model was 1-year lagged precipitation, which has been influential in other analyses of precipitation, plague, and PDs (e.g., Eads and Biggins, 2017) and fleas in some cases (e.g., Eads and Hoogland, 2016; 2017; Eads et al., 2020). Lagged precipitation was total precipitation during the year before the annual interval during which visual count change was calculated. Because this data set included three PD species with differing flea communities in differing ecosystems, there could be species-specific response to precipitation and/or plague. We thus included species as a third covariate. Model parsimony was achieved with backward elimination using partial F-tests in SYSTAT 12.0 (α = 0.050). For visual illustration, we created separate graphs of the data from non-treated and treated plots without regard to the paired design used in the analysis. A least squares regression line was fit to each data set, but confidence intervals would not reflect the repeated measures analysis and, therefore, were not added. We used a Chi-square test of independence to evaluate the effect of plague management on population growth for a subset of non-paired data when precipitation was high (>15 inches).

3. Results

Visual count changes were calculated for 110 plot-intervals, representing 55 paired treatments (Biggins et al., 2010). There was little evidence that visual count changes of different PD species responded differently to precipitation ($F_{2,51} = 0.696$, $P = 0.503$), so species was not considered further. Similarly, 1-year precipitation lag did not increase explanatory power and was removed from the model ($F_{1,52} = 0.211$, $P = 0.648$).

The interactive relationship of plague management and recent precipitation was significant ($F_{1,53} = 7.439$, $P = 0.009$). When we managed plague by reducing fleas, PD visual counts tended to increase with increasing precipitation (Fig. 2). This positive relationship was accompanied by a negative relationship on paired plots where plague was not managed (Fig. 2).

Even without the increased statistical power of comparisons between treated and non-treated plots as pairs, the trends are readily apparent when recent precipitation was relatively high (Fig. 2). When recent precipitation was >15 inches (38.1 cm), visual counts increased at 8 of the 11 dusted plots within that high precipitation category but increased at only 3 of the 11 plots without plague management ($X^2 = 4.545$, $P = 0.033$).

4. Discussion

There were two noteworthy results from this assessment. First, our expectation of a significant interaction between treatment and
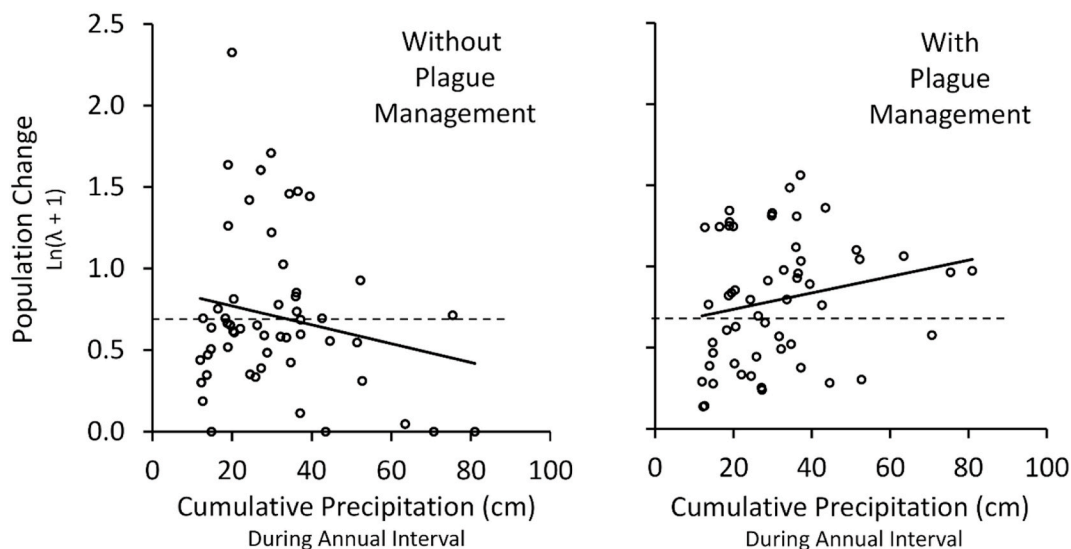

Fig. 2. Relationship between visual count changes in prairie dogs (*Cynomys* spp.) and annual precipitation (cm) on plots without plague management and with plague management by treating burrows with deltamethrin dust for flea control. Population change (λ) was indexed by visual counts conducted in mid-summer of adults plus juveniles, and annual precipitation was cumulative during the 12-month period prior to the typical date of the second count (interval of 1 July-30 June). Visual counts are presented as treated in the analysis (re-scaled λ, natural log transformed), although the repeated measures analysis retained the pairings of treatments that cannot be illustrated here. Points above the dashed line indicate population increases; points below the dashed line indicate population declines with points on the zero-line indicating population collapse to 0 animals.

precipitation was supported. The relationship between precipitation and PD population growth rate differed on plague-managed plots compared to plots without plague management. Second, on plots where we attempted to reduce plague circulation, the effect of recent precipitation on PD population growth rate was positive compared to a negative growth rates as precipitation increased on plots with no plague management. These two phenomena suggest the presumed benefits of PD forage and water physiology that should accompany increased precipitation are overwhelmed by plague; potential increases or "booms" (*sensu* Dickman et al., 2010) in PD populations in wet years were transformed into declines.

The relationship between PD visual count changes and precipitation had notably high variation. Among the possible reasons are the following: (1) Visual counts can be affected by numerous sources of variation that influence PD detectability. (2) Precipitation was not directly measured at sites but was interpolated from PRISM. (3) PD populations respond to a multitude of other sources of variation including differences in plant communities, differences in predation rates, other diseases, etc. (4) The pulicide treatments are unlikely to have entirely removed plague from the treated plots, and efficiency of flea control likely varied among sites (Tripp et al., 2017; Eads et al., 2019). (5) Plague circulates at variable rates due to many factors other than precipitation (Gage and Kosoy, 2005), which doubtless contributes to the high variation noted in our non-dusted plots, at least.

Visual counts of PDs are biased low and are expected to be variable. We attempted to circumvent the high count-to-count variability by conducting multiple counts on each day and on multiple days, using the highest count overall. Even these high counts are underestimates but can be used as a population indexes, hopefully with increased precision, although they remain subject to numerous sources of variation that influence probability of detection (Fagerstone and Biggins, 1986; Menkens et al., 1990). Paired comparisons herein help to account for those multiple sources of variation by keeping biases relatively consistent within pairs. For example, variation due to spatial sources (e.g., physiography and vegetative cover) was reduced by matching paired plots according to these attributes. Variation due to temporal changes (e.g., weather) was reduced by conducting counts simultaneously on the plots of each pair. Count conditions were similar between years (mid-summer days with low wind speeds and no disturbance from predators or humans, etc.).

We must remain cautious when interpreting the results of our attempts to manage plague by using vector control (Biggins et al., 2010). Deltamethrin is a broad-spectrum insecticide that likely influences other ectoparasites and these ectoparasites might have a direct influence on their hosts. Fleas and other ectoparasites also can serve as vectors of other pathogens. Nevertheless, cumulative evidence suggests vector control is primarily influencing host population attributes through reduced plague circulation under the conditions of our field experiments. The most compelling evidence is from field experiments that have used both vector control and highly plague-specific subunit vaccines that contain the capsular protein for *Y. pestis*. For example, vaccines and vector control were used in an evaluation of black-footed ferret survival on PD habitats in Montana (Matchett et al., 2010). In that experiment, the two methods each improved ferret annual survival by a nearly identical factor (ca. 2.4-fold), and the two methods used together did not further improve survival (resulting in a significant interaction because of the non-additivity). This type of experiment using both vector control and vaccines was replicated on non-PD habitats. In an area where we presumed plague circulation was at a low level, either treatment gave only a small increase in chipmunk survival (Goldberg, 2018), and in an area where plague circulation seemed relatively high, either treatment produced a dramatic increase in woodrat survival (Biggins et al. 2021b). Because of the consistent patterns of these several cases, we believe that vector control is primarily influencing the hosts via reduction in plague circulation.

Are the good years gone for PDs? The answer cannot be unequivocal.

Within our small plots, *Y. pestis* may even have become temporarily and locally absent, even in a larger landscape where plague was maintained enzootically (Lowell et al., 2015; Kosoy et al., 2017). During those site-years of low or no *Y. pestis* circulation, the population response of PDs on non-managed plots might have been similar to responses on plots where plague was managed. Indeed, the variation in the relationship between PD visual count change and precipitation seems higher in the plots where plague was not managed than in the treated plots (Fig. 2). Also, efficacy of flea control varied on the dusted plots (Eads and Biggins, 2019). Nevertheless, the significant difference in slopes of the precipitation and population trend data is not encouraging. If the good years for PDs are not gone, they are likely relatively scarce compared to years prior to the invasion of plague.

A weakness of this study is the short time series of just 5 years. Broad conclusions will require much more data from a wider range of sites and species. We acknowledge that these relationships might differ in portions of the PD range that have higher average precipitation (e.g., eastern portions). However, long-term data from manipulative field experiments are not easily obtained and we believe these data were adequate to provide preliminary support for our expected interaction. The novel set of trade-offs resulting from introduction of this pathogen-predator, *Y. pestis*, to North America offer yet another example of how *Y. pestis* becomes a transformer species (Eads and Biggins, 2015, 2017). High precipitation no longer seems to portend good times for PDs or associated organisms that depend on them, including endangered black-footed ferrets. In a sense, the good years for PDs are not only tending to be gone, but have been potentially transformed into bad years. Encouragingly, deltamethrin dust and other tools for flea control, and perhaps future vaccines, can be used to dampen such ecological transformations. However, they come with significant costs, logistical considerations and questionable sustainability (Biggins et al., 2010; Eads et al., 2019).

Does the relationship between precipitation and plague herein apply to other rodent species and ecosystems? Food web interactions and feedbacks under the influence of varying precipitation have been discussed in the context of vertebrate predators (e.g., Lima et al., 2002; Letnic et al., 2011). The tension and shifts between bottom-up and top-down controls is similar to the phenomenon we discuss here if we consider the highly lethal *Y. pestis* as a "predator" (Raffel et al., 2008; Biggins and Eads, 2017). A key difference might be the lag effect of vertebrate predators is expected to be quite short with *Y. pestis* because populations of the bacterium and its flea vectors can respond comparatively quickly to favorable conditions (Biggins and Eads, 2019).

The wider ecological ramifications of the relationships between precipitation, plague, and rodents likely extend to other rodent species and to higher trophic levels in the western United States. Relatively long-lived predators might have relied historically on "boom" years of prey abundance to efficiently reproduce–waiting out years of low prey availability. An example of such a species of conservation concern in North America might be the spotted owl (*Strix occidendtalis*). In this example, the food web complexity increases, with several species of rodents as primary consumers and two presumably competing predators (*Y. pestis* and the owl). Prey abundance seems to be a key driver of nesting success of spotted owls (Rosenberg et al., 2003). Through trophic relationships, the spotted owl's rodent prey are thought to respond positively to increased primary production during years of abundant precipitation (Cade et al., 2017). It thus seemed counterintuitive that nesting success of these owls was inversely related to precipitation during the prior year (Cade et al., 2017) or during the nesting season (North et al., 2000). The latter two studies were done in the Sierra Nevada of California, an area noted for high plague activity. Perhaps plague has reversed the relationship between precipitation and rodent abundance, thereby suppressing or eliminating rodent population booms and, consequently, reversing precipitation effects on predators.

CRediT authorship contribution statement

Dean E. Biggins: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Visualization; Writing-Original draft preparation, Reviewing and Editing.

David A. Eads: Data curation; Investigation; Methodology; Supervision; Writing-Original draft preparation, Reviewing and Editing.

Jerry L. Godbey: Data curation; Investigation; Methodology; Resources; Supervision; Writing-Original draft preparation, Reviewing and Editing.

Declaration of competing interest

The authors declare no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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