Plague outbreaks in prairie-dog colonies associated with El Niño climatic events

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INTRODUCTION

Plague (*Yersinia pestis*) was introduced to the western U.S. in the mid-20th century and is a significant threat to the persistence of black-tailed prairie dog (*Cynomys ludovicianus)* populations. The social, colonial habits of prairie dogs make them particularly susceptible to plague, and many flea species, including known carriers of plague, are associated with prairie dogs or their extensive burrow systems. Mortality during plague epizootics, or outbreaks, is nearly 100% (Cully and Williams 2001; *J. Mammal.* 82:894), resulting in the extinction of entire colonies. In northern Colorado, prairie dogs exist in metapopulations (Roach et al. 2001, *J. Mammal.* 82:946), in which colonies naturally isolated by topography, soils and vegetation are connected by dispersal. Dispersal of either infected prairie dogs or plague-resistant reservoir species is hypothesized to spread plague among colonies. Plague outbreaks therefore may disrupt the dynamics of prairie-dog metapopulations and affect regional persistence. In the context of a century of past eradication efforts that have drastically reduced prairie-dog numbers, and increasing agricultural and urban development, plague represents a relatively new and unique threat to prairie dogs and the species that are closely associated with them.

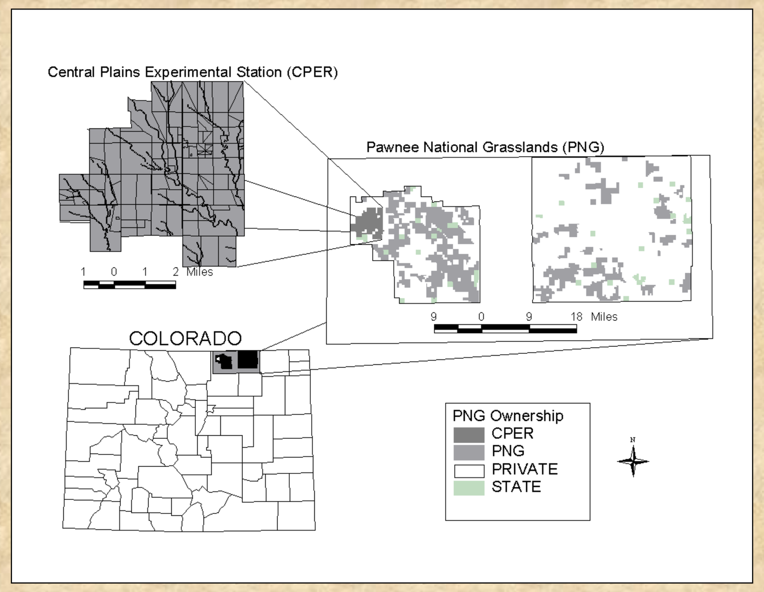
Plague is also an emerging public health issue, and human cases have been associated with weather patterns believed to be favorable to fleas, the primary vectors, or to populations of prairie dogs and other rodent hosts (Parmenter et al. 1999, *Am. J. Trop. Med. Hyg*. 61:814; Enscore et al. 2002, *Am. J. Trop. Med. Hyg*. in press). However, the link between plague outbreaks in natural rodent populations and climatic events has not been established. We took advantage of a long-term program established by the USDA Forest Service Pawnee National Grasslands (PNG) that monitors the status and size of prairie-dog colonies to study extinction and re-establishment of colonies in north-central Colorado. We examined temporal patterns of colony extinction to identify plague outbreaks and to investigate possible correlations with regional weather patterns, including those associated with El Niño Southern Oscillation climatic events. We also tested two hypotheses regarding the effects of plague in prairie-dog metapopulations: 1) that the probability of extinction decreases with population size, as estimated by colony active area; and 2) that isolated colonies are more likely to persist during plague outbreaks than closely spaced colonies.

METHODS

PNG biologists have monitored the activity and size of colonies regularly since 1981. Colonies were surveyed once each year, usually between July and October. Colony area was estimated each year by mapping the perimeter of active burrows with a compass and tape or more recently, using a GPS unit. We estimated nearest-neighbor distance by plotting the recorded location of a focal colony on a USGS map and then measuring the linear distance from the colony center to the center of the nearest colony that was known to be active.

Colonies were determined to be extinct when PNG records indicated evidence of plague and no sign of activity. Eight colonies that had limited activity but that had declined precipitously (94 ± 3% SE) in size were also considered to have been decimated by plague. All extinctions were attributed to plague because poisoning on the PNG had been terminated by the start of the study period and because most records implicated plague as the cause. However, we cannot rule out other sources of mortality, e.g. predators, other diseases, illegal poisoning or shooting, that may have caused a few extinctions, particularly of small colonies.

The probability of extinction was calculated as the proportion of colonies active in one year that were extinct in the following year. To investigate how colony area and isolation influence the probability of extinction, we restricted analyses to 8 outbreak years following four El Niño Southern Oscillation events in the winters of **1982-83, 1991-92, 1994-95** and **1997-98**. We divided colonies into size classes based on their area in the year prior to extinction and then calculated the proportion of colonies in each size class that went extinct during that period. Similarly, we categorized colonies from these years by the linear distance to their nearest neighbor and calculated the proportion of colonies in each neighbor-distance class that went extinct.



STUDY AREA

The Shortgrass Steppe Long-Term Ecological Research (SGS-LTER) site is located in north-central Colorado, approximately 50 km south of Cheyenne, WY. The site consists of the USDA Agricultural Research Service Central Plains Experimental Range (CPER) and USDA Forest Service Pawnee National Grasslands (PNG). The PNG is divided into eastern (Pawnee) and western (Crow Valley) administrative units, which differ in the relative amounts of federal, state and private land.

RESULTS

Are plague outbreaks associated with El Niño events?

Past El Niño events in the Great Plains have been associated with warmer and, to a lesser degree, wetter winters (**Fig. 1**). This pattern holds for the SGS-LTER site: December-February minimum and maximum temperatures during the four El Niño winters were 22% and 25% warmer, respectively, than the 31-year means (P = 0.005 and P = 0.035, respectively, based on means of 1000 re-sampling runs of 4-years duration), whereas January-March precipitation was 14% higher but not significantly so (P = 0.275).

Outbreaks were concentrated in the four El Niño periods (**Fig. 2**). Forty-three of 63 observed extinctions (68%) were recorded in the 8 years associated with El Niño events, a result which is highly unlikely to have occurred by chance (P = **0.001** based on 1000 random 8-year draws without replacement from the observed distribution of extinctions). From 29-82% of the colonies active during these periods went extinct. In 1982-83, most (78%) extinctions occurred on the eastern Pawnee unit, where most (80%; 12/15) active colonies were located and 58% (7/12) of the colonies went extinct. The 1997-98 outbreak occurred mostly in the western Crow Valley colonies (78% of nine extinctions; 50% of 14 active colonies). Plague hit both areas in the 1991-92 and 1994-95 events (82% and 55% of colonies, respectively).

Outbreak periods were followed by an increase in colony area and number through dispersal and establishment of new colonies, and re-colonization of extinction ones (**Fig. 3**). Despite plague outbreaks, the number and total area of colonies have increased over the past 21 years and colonies currently cover some 416 ha (0.5%) of the 78,000 ha area of the PNG.

Most colonies (64%; 36/56) went extinct once in the 21-year study period; only nine colonies (1.8%) never went extinct and two-thirds (6) of these were ≤5 years old in 2001. One colony, last active in 1997, suffered four extinctions. Colonies were inactive for 1 to >21 years, but most extinctions (54%; 34/63) lasted for ≤5 years and 30% (19/63) were only 1 year in duration.

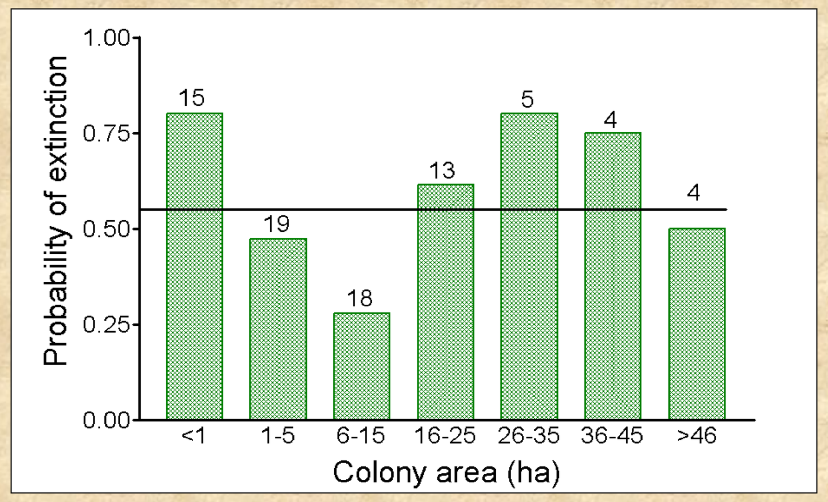


Fig. 4. Very small and large colonies were more susceptible to extinction than medium-sized (1-15 ha) colonies. The horizontal line is the proportion of all colonies that were extinct during these years (0.55).

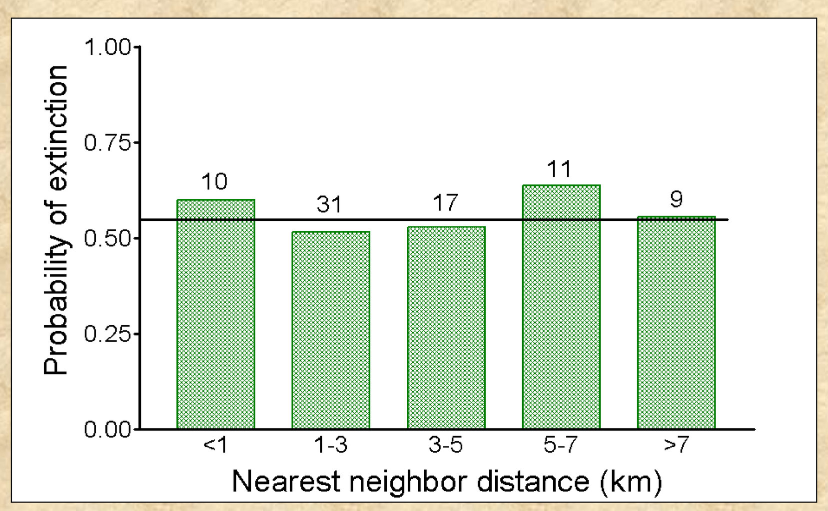
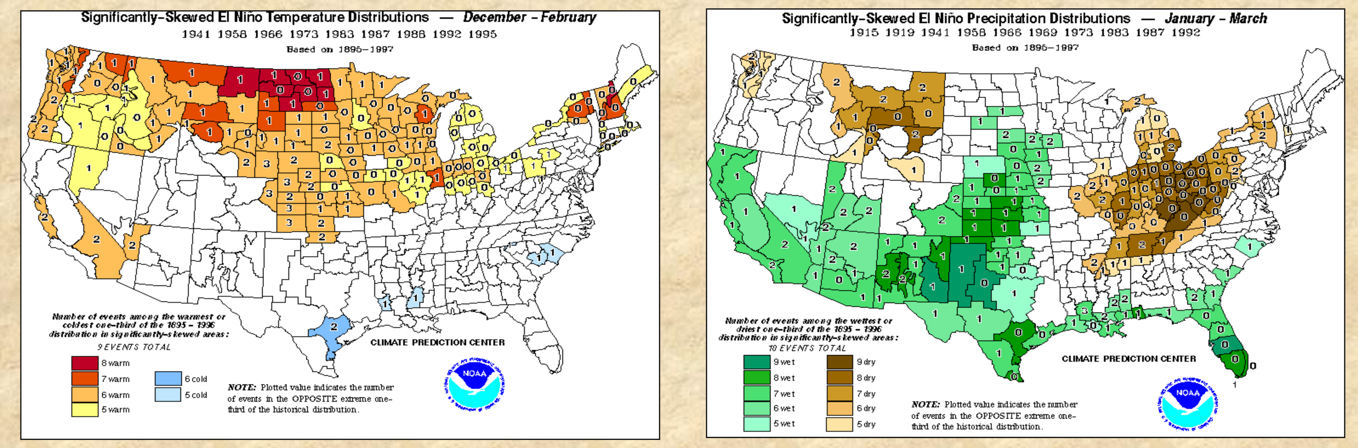


Fig. 5. Probability of extinction was independent of colony isolation. The horizontal line is the proportion of all colonies that were extinct during these years (0.55).

Fig. 1. In the central U.S., El Niño events are characterized by warmer Dec-Feb temperatures and, to a lesser extent, higher Jan-Mar precipitation. Source: NOAA Climate Prediction Center.



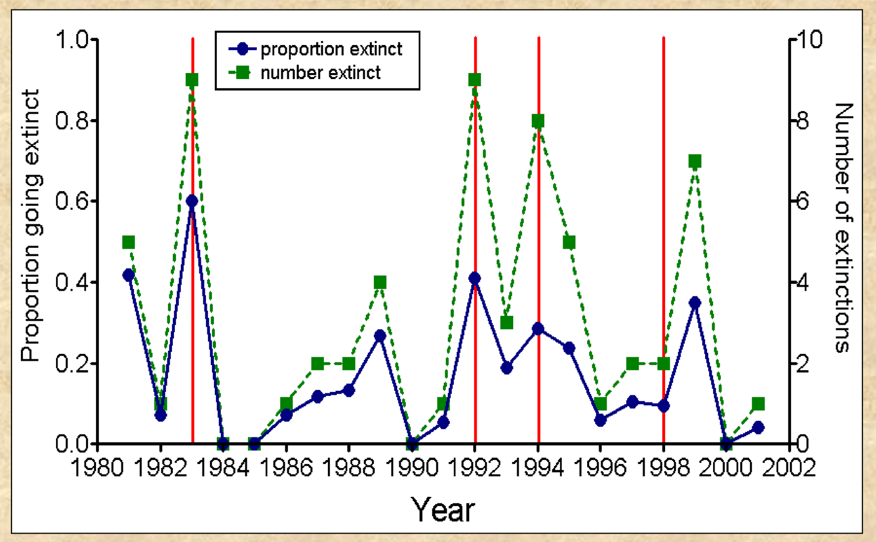


Fig. 2. Extinctions, expressed as the number and proportion of colonies that went extinct, were concentrated in years following El Niño winters. Vertical lines indicate El Niño years.

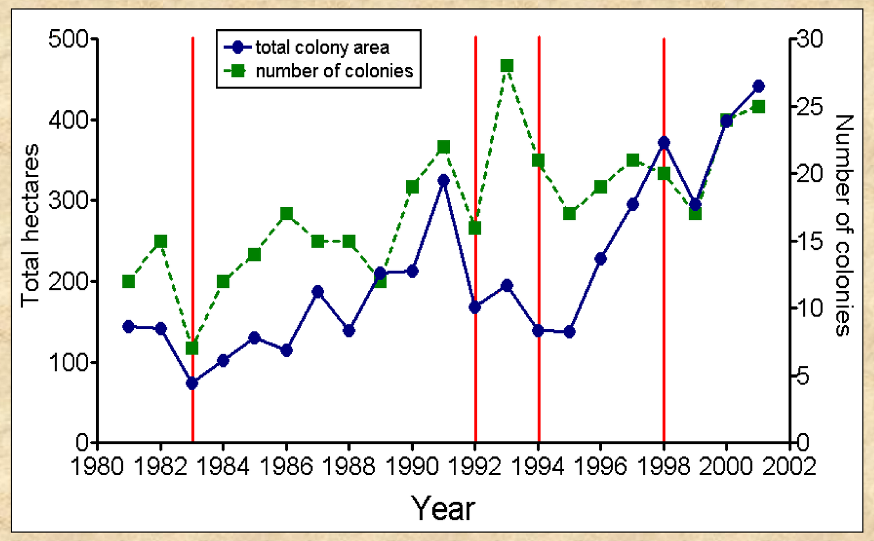


Fig. 3. Plague outbreaks reduced the number and total area of prairie-dog colonies on the Pawnee National Grasslands, Colorado. Vertical lines indicate El Niño years.

RESULTS

How does colony size and isolation affect probability of extinction?

Very small colonies and large colonies suffered disproportionately during plague outbreaks (**Fig. 4**). Colonies <1 ha and >15 ha in area were more likely to go extinct than colonies 1-15 ha in area ($\chi^2 = 9.33$, df = 2, P = 0.009). Once a colony reached this threshold size (15 ha), the probability of extinction increased dramatically to >65%. Colony area averaged 11.9 ± 0.9 (SE) ha over the 21-year study period.

The probability of extinction appeared to be independent of colony isolation; colonies that were close together were not any more likely to go extinct than isolated colonies (**Fig. 5**). However, a colony was more likely to go extinct if its nearest neighbor also went extinct. Approximately 58% (25/43) of colonies wiped out by plague also had their nearest neighbor go extinct, whereas only 34% (12/35) of colonies that persisted during outbreaks had their nearest neighbor go extinct ($\chi^2 = 4.40$, df = 1, P = 0.036). There was no correlation between nearest-neighbor distance and colony area for either plague-affected or persistent colonies (Pearson r<0.01).

CONCLUSIONS

The association between plague epizootics and El Niño climatic events suggests that abiotic factors such as temperature and soil moisture that influence survival and reproduction of flea vectors may be largely responsible for outbreaks. Mild winter weather may also increase food availability and thus survival of prairie dogs and other potential rodent hosts, allowing victim populations to reach high densities that facilitate transmission. Although the exact mechanism by which *Y. pestis* persists and moves among colonies is still not known, this information may help forecast plague outbreaks and minimize risk of human exposure.

We expected high extinction rates in very small colonies, which, in addition to plague, are probably very susceptible to other sources of mortality and stochastic events that could have been attributed erroneously to plague. However, large colonies were also highly susceptible to plague extinction, presumably because the high densities that we expect in these colonies support larger flea populations, leading to rapid transmission via flea bites and direct animal-animal contact. Population studies are needed to establish the relationship between colony area and density, but the threshold in the probability of colony extinction occurred at about 15 ha, slightly larger than the long-term average size of PNG colonies.

We predicted that spatial isolation would reduce vulnerability to plague, but isolated and closely spaced colonies went extinct at similar rates. Neighboring colonies had similar fates (i.e., went extinct or persisted) during outbreak periods, however, suggesting some spatial component to plague transmission and susceptibility. Linear nearest-neighbor distance may be less useful as an index of colony isolation than other, more ecologically relevant measures that incorporate dispersal ability, landscape connectivity or the movement of reservoir hosts (e.g., Roach et al. 2001).

Plague is not native to this system and epizootics represent a novel problem for prairie-dog metapopulations. Large colonies seem to suffer *higher*, not lower, rates of extinction, the opposite of what we would predict in the absence of plague or a similar, density-dependent mortality agent. Moreover, these large colonies, which might normally serve as sources of dispersers that rescue nearby colonies, may actually *increase* the likelihood of local extinction by sending plague-infected dispersers to adjacent colonies. Finally, our results suggest that 50-82% of active colonies go extinct during local outbreaks, which presumably *reduces* the temporal asynchrony of local extinctions compared to pre-plague conditions or to areas where plague is still absent. All of these complications would be expected to reduce regional persistence. Further analysis of these patterns, combined with ongoing monitoring programs and new, intensive studies of the ecology of plague, will improve our understanding and ability to predict the long-term consequences of plague in prairie-dog populations.

ACKNOWLEDGMENTS

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