

Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events

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Outbreaks of many vector-borne human diseases are broadly correlated with climatic variation, but evidence of similar fluctuations in disease in natural host populations is rare. Here, we use 21 years of monitoring of black-tailed prairie dog (*Cynomys ludovicianus*) colonies to demonstrate a link between extinctions of colonies attributed to plague (*Yersinia pestis*) and climatic fluctuations associated with El Niño Southern Oscillation events that promote the growth of flea vector and rodent host populations. During epizootics, rates of extinction of the largest colonies (>16 ha) were nearly as high (>60%) as for the smallest ones (<3 ha), but only a third of intermediate-sized colonies were extirpated. The probability of extinction was influenced by the size and fate of adjacent colonies, but there was no predictable relationship between extinction probabilities and inter-colony distance, indicating that spatial isolation does not reduce the vulnerability of colonies to plague. By causing sporadic extinctions of colonies, plague creates a metapopulation structure that has altered the dynamics of prairie dog colonies as they respond to a century of human persecution and habitat loss.

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There is increasing recognition that predicting epidemics of vector-borne disease lies less in patterns of human morbidity than in the ecology of the pathogen, its vectors, and its wild hosts (Keeling and Gilligan 2000; Dobson and Fofopoulos 2001). Outbreaks of infectious disease in human populations and some natural systems are consistently related to climatic variables, which has disturbing implications for the consequences of global climate change (Gubler *et al.* 2001; Harvell *et al.* 2002). These patterns suggest that weather or related factors that influence survival and reproduction of vector and host populations will be useful in forecasting epidemics. However, what is usually missing is evidence of a correlation between climatic variation and incidence of disease in animal host populations – information that would be instrumental for identifying mechanisms by which transmission and infection rates could be influenced by climate (but see Yates *et al.* 2002).

Plague is caused by the bacterium *Yersinia pestis*, and is best known as the epidemic disease that killed millions in Europe in the Middle Ages. Plague is primarily a disease of rodents, but remains an important human health problem in many parts of the world (Keeling and Gilligan 2000). Since it was introduced to the US in the early 1900s, plague has been reported in all continental states west of the 100th meridian, and in at least 76 vertebrate species, including most rodents (Barnes 1993). Rodent species differ in their resistance to disease and, therefore, in their ability to act as sources of human infection (Barnes 1993).

Black-tailed prairie dogs (*Cynomys ludovicianus*; Figure 1) suffer high (ca 100%) mortality during epizootics (disease events that appear suddenly and spread rapidly through an animal population) (Cully and Williams 2001), probably because their high sociability increases rates of transmission as a result of individual contact and the sharing of burrow systems (Hoogland 1979). Burrows are favorable sites for the establishment of large populations of fleas, the primary disease vectors.

In the western Great Plains, prairie dogs live in colonies that are naturally isolated by topography, soils, and vegetation. Although the exact mechanism is not known, dispersal of either infected prairie dogs or other plague-resistant rodent species is hypothesized to spread plague among colonies (Cully and Williams 2001). Recent modeling studies suggest that metapopulation structure is central to the maintenance of plague in commensal rodents (Keeling and Gilligan 2000). In prairie dogs, however, dispersal among colonies may facilitate spread of the pathogen and reduce regional persistence (Hess 1996), particularly if resistant reservoir species are involved (McCallum and Dobson 2002). In the context of a century of past human activities to eradicate prairie dogs, and habitat loss resulting from agricultural and urban development, plague represents a unique threat to prairie dogs and those species of conservation concern that are closely linked to them (Kotliar *et al.* 1999).

We took advantage of a long-term program established by the USDA Forest Service that monitors the status and size of colonies in shortgrass steppe on the Pawnee National Grasslands (PNG) to study patterns of extinction and re-establishment of prairie dog colonies in north-

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Figure 1. Black-tailed prairie dogs are colonial, herbivorous rodents that inhabit the grasslands of the Great Plains of North America. Through their clipping and burrowing activities, they alter ecosystem function and provide habitat for other animals. They are also major prey for raptors and mammalian carnivores, including several species of conservation concern.

ern Colorado. We examined temporal patterns of colony extinction to identify epizootics and to investigate correlations with regional weather patterns, including those associated with El Niño Southern Oscillation (ENSO) climatic events. Cases of human plague have been associated with weather thought to be favorable to fleas or rodents (Parmenter *et al.* 1999; Enscore *et al.* 2002), but no link has been established between epizootics in wild rodent populations and climatic events. We also tested two hypotheses regarding the metapopulation consequences of plague in prairie dog colonies: first, that the probability of extinction decreases with population size, as estimated by colony area, and second, that isolated colonies are more likely to persist during outbreaks than closely spaced colonies (cf Lomolino and Smith 2001).

■ Methods

The PNG is divided into eastern (Pawnee) and western (Crow Valley) units that differ in the amount of government and private land they encompass. PNG biologists have monitored the activity and size of colonies on federal land regularly since 1981. Colonies were surveyed once each year between July and October, and colony area was estimated by mapping the perimeter of active burrows with a compass and tape or a GPS unit, assuming a minimum convex polygon shape. We estimated nearest-neighbor distances by plotting the location of a colony on a Forest Service map, which was then digitally scanned. We used the measurement function in Adobe Photoshop 7.0 to measure the linear distance from the center of the colony to the centers of the three nearest colonies known

to be present during the same period. To estimate colony isolation, we recorded the number, combined area, and fate of colonies within 10 km, which is thought to represent the maximum dispersal distance of prairie dogs (Knowles 1985; Lomolino and Smith 2001).

Colonies were classified as extinct when PNG records indicated no activity in previously active colonies and evidence of plague. Eight colonies that had limited activity but that had declined by an average of 94% (SE = 3%) in area were also considered to have been decimated by plague. All extinctions were attributed to plague because poisoning on the PNG had ended in the 1960s, and because most records implicated plague as the likely cause of extinctions as far back as 1948 (Antolin *et al.* 2002). Similar die-offs of prairie dogs in Colorado and adjacent states have been attributed to *Y. pestis* (eg Barnes 1993; Rayor 1985; Cully and Williams 2001). Nonetheless, without serologic evidence, we cannot rule out the

possibility that a few extinctions, particularly of small colonies, may have been caused by predators or other natural mortality, or by illegal shooting or poisoning.

Probability of extinction was calculated as the proportion of colonies active in one year that were extinct the following year. To investigate how colony area and isolation influence extinction, we restricted analyses to two-year periods after five ENSO events that occurred in the winters of 1982–83, 1986–87, and 1997–98, as well as the prolonged ENSO period from 1991–95 (NOAA Climate Prediction Center 2002a). We used logistic regression to identify the area and isolation factors that best explained the probability of colony extinction. We included seven main effects: focal colony area, nearest-neighbor distance, area and fate of nearest neighbor, mean distance to the three nearest neighbors, the number of the three nearest neighbors that went extinct, and the total combined area of colonies within 10 km. We also included two interaction terms that, *a priori*, we considered might be important (neighbor-area*fate, neighbor-distance*fate). We used a stepwise model-selection procedure (PROC LOGISTIC; SAS, Version 9.0), with $\alpha=0.10$ for effects to enter and remain in the model.

■ Results

Past ENSO events in the Great Plains have been associated with warmer and, to a lesser degree, wetter winters (NOAA Climate Prediction Center 2002b). This pattern holds for our study area: December–February minimum and maximum temperatures at a nearby weather station during the five ENSO winters were 21% warmer than the

long-term means (1969–2000; $P=0.01$ and $P=0.05$, respectively, based on means of 1000 resampling runs of 5 years duration; Blank *et al.* 2001), whereas January–March precipitation was 15% higher, but not significantly so ($P=0.30$). Values of the Southern Oscillation Index (mean for December–March; NOAA Climate Prediction Center 2002a) were correlated with the deviation in winter minimum temperatures ($r=0.32$, $P=0.04$) and precipitation ($r=-0.26$, $P=0.08$), but not winter maximum temperatures ($r=-0.14$, $P=0.47$). Winters during the intervening years were not significantly warmer or wetter than expected, based on the 31-year means ($P>0.20$).

Epizootics were concentrated in the five ENSO periods (Figure 2a). Forty-seven of 63 observed extinction events (75%) were recorded in the 10 years associated with ENSO events, a result that was unlikely to have occurred by chance ($P<0.01$, based on 1000 random draws without replacement of five 2-year periods from the observed distribution of extinctions). During these periods, from 18–68% of the active colonies went extinct, but patterns of extinctions differed between units and epizootic periods (Figure 3). In 1982–83, most (78%) extinctions occurred on the Pawnee unit, whereas the 1997–98 epizootic was restricted primarily to Crow Valley colonies (78% of nine extinctions; 50% of 14 active colonies). Plague was widespread in both units in the 1991–95 events (55–82% of colonies). Only four colonies went extinct in the 1986–87 ENSO event (24%), and three of these were very small (<0.4 ha). Epizootics were usually followed by an increase in colony size and number through the establishment of new colonies and recolonization of extinct ones (Figure 3b). Despite frequent epizootics, the number and total area of colonies have increased significantly ($P<0.0002$) over the past 20 years, in part due to recent protection afforded prairie dogs, and at the end of 2001, colonies covered 416 ha (0.5%) of the 78 000 ha of the PNG.

Patterns of extinctions during major epizootics (Figure 3) suggest that colony area and the fate of adjacent colonies influenced the likelihood a colony went extinct. Very small and large colonies suffered disproportionately during outbreaks (Figure 4a). Extinction probabilities were highest (81%) for colonies <1 ha in area, and declined with increasing area up to about 14 ha, when extinction probability rose again to $>60\%$. Colonies <3 ha and >16 ha in area were more likely to go extinct than intermediate-sized colonies ($\chi^2=12.32$, $df=2$, $P=0.002$). A colony was also more likely to disappear if its nearest neighbor went extinct. Some 66% (31/47) of extirpated colonies also had their nearest neighbor go extinct, whereas only 31% (14/45) of colonies that survived during epizootics had their neighbor go extinct ($\chi^2=11.17$, $df=1$, $P=0.008$).

Logistic regression confirmed that colony area and the combined size and fate of adjacent colonies influenced the likelihood that a colony was extirpated. The final model selected (based on lowest AIC [84.19] and largest R^2 [0.59] values) consisted of colony area (categorized into three

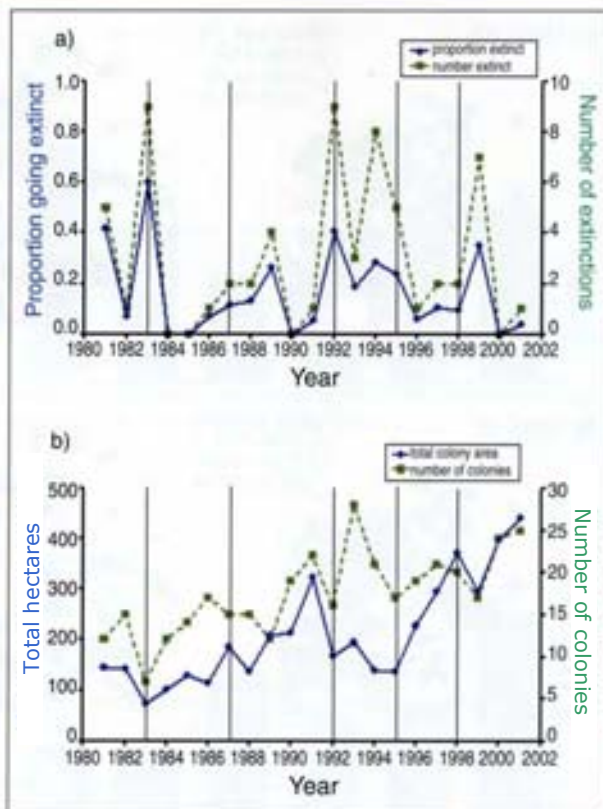


Figure 2. Temporal trends in (a) extinctions, expressed as the number and proportion of colonies active during the previous year that went extinct, and (b) the number and total area of prairie dog colonies on the Pawnee National Grasslands, Colorado. Vertical lines are drawn through the second year of the winter ENSO events, eg through 1983 of the 1982–83 event.

size classes, as above and in Figure 3), area of the nearest neighbor, and the interaction between area and fate of the nearest neighbor (Type III Wald chi-square, $P<0.018$). Overall, the probability of extinction increased with the area of the adjacent colony (Figure 4b), but the significant interaction term also indicated that, when a colony and its neighbor were large, both were highly likely to go extinct. Surprisingly, no distance or isolation measures were included in the final model, and there were no differences between extinct and surviving colonies for any of the distance or isolation variables ($P>0.48$).

Discussion

The association between colony extinctions, which we attributed to plague, and ENSO events suggests that abiotic factors such as temperature and soil moisture that influence survival and reproduction of flea vectors contribute substantially to plague epizootics. Mild winter weather may also increase food availability, and thus survival of prairie dogs and other rodent hosts, allowing victim populations to reach the high densities that facilitate transmission. In the southwestern US, incidence of

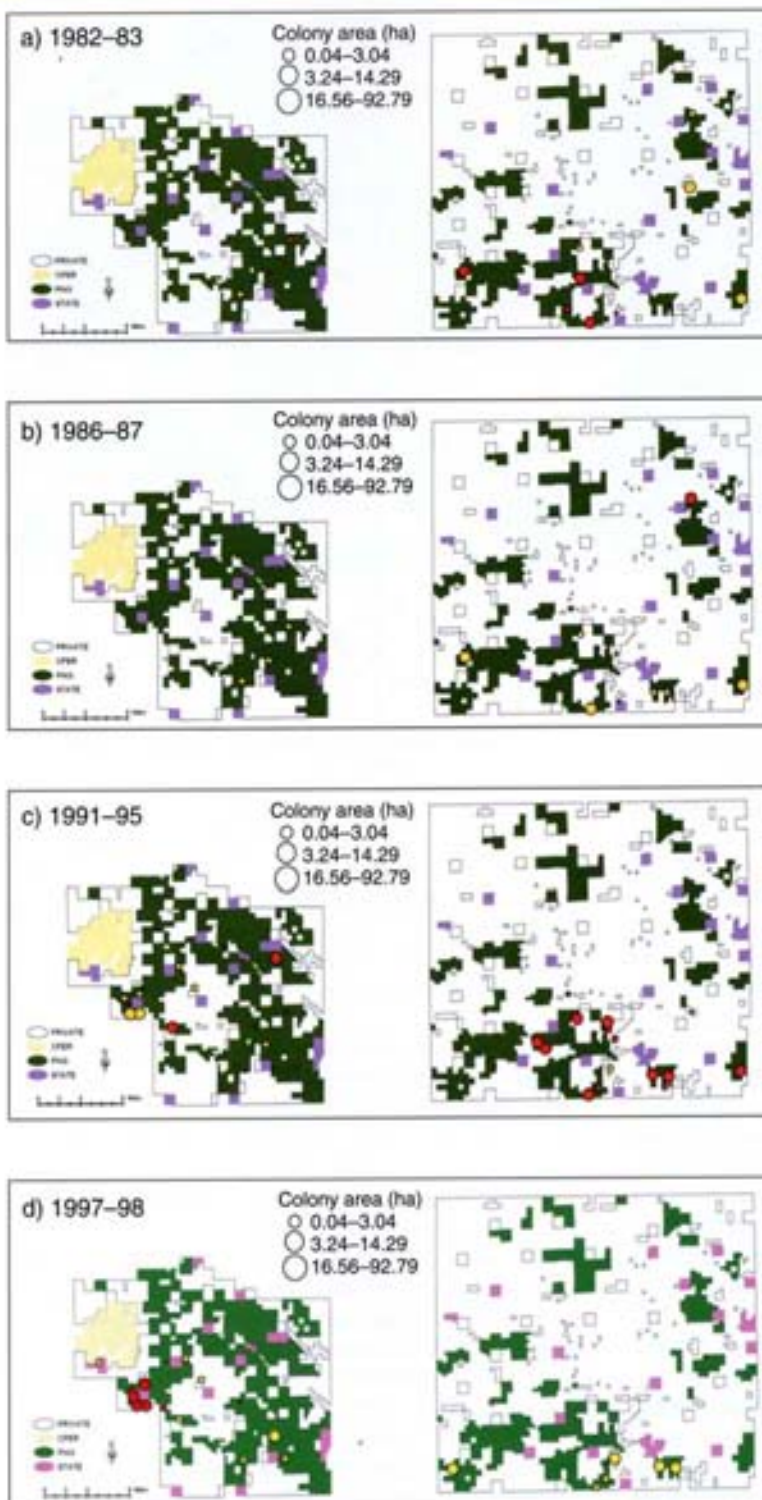


Figure 3. Locations and sizes of prairie dog colonies on the western Crow Valley (left) and eastern Pawnee Units (right) of the PNG during plague outbreaks associated with ENSO events in (a) 1982–83; (b) 1986–87; (c) the extended event from 1991–95; and (d) 1997–98. Colonies in red went extinct in those periods, whereas those in yellow survived. The locations of colonies are approximate and the size of the circles, which denote the approximate active area, are disproportionately large relative to the scale of the map.

human plague increases following periods of higher spring precipitation (Parmenter *et al.* 1999; Ensco *et al.* 2002), but are lower after periods of high summer temperatures (Ensco *et al.* 2002), which may reduce flea survival and transmission rates (Rayor 1985). Extinctions occurred in non-ENSO years, however, and most colonies survived the moderate 1986–87 event, which suggests that other factors decouple local plague dynamics from broad-scale weather patterns.

We expected that the smallest colonies would suffer high rates of extinction, perhaps from plague, but also as a result of demographic or environmental stochasticity. Large colonies were also highly vulnerable, however, presumably because higher prairie dog numbers supported larger flea populations, leading to rapid transmission via flea bites and direct animal–animal contact. Intermediate-sized colonies (3–14 ha), which include most PNG colonies (mean \pm SE area = 11.9 ± 0.9 ha, $n=21$ years), were much less likely to disappear during outbreaks. Although this suggests some area or density threshold in susceptibility, we note that the relationship between colony area, the variable that is most easily measured in the field, and actual population density could not be quantified in our study. The susceptibility of colonies of different sizes and ages may depend on whether outbreaks are driven by densities of prairie dogs and fleas, or by contact with reservoir hosts, whose populations may be related to colony area.

We also expected that isolated colonies would be less susceptible to plague, but none of the distance or isolation measures properly explained patterns of extinction. The likelihood that a colony went extinct was more obviously related to the size of the adjacent colony, not its proximity. Neighboring colonies had similar fates, however, and, in some years, extinctions were largely restricted to only one PNG unit (Figure 3), indicating some spatial component to plague occurrence. Our colonies were not very isolated compared to the dispersal abilities of prairie dogs (<10 km; Knowles 1985): nearest-neighbor distances ranged from 1.0 to 21.5 km, but the median neighbor–distance was short (3.6 km), and only 12 colonies

(13%) were >10 km from another colony (six of these went extinct). Intercolony movement therefore may be relatively frequent, a conclusion that is supported by the rapid rates of colony re-establishment (1–5 years) and by recent genetic studies (Roach *et al.* 2001). In the laboratory, prairie dogs (*C. leucurus*) do not succumb to plague until 5–7 days after infection (Cully and Williams 2001), which may provide an opportunity for dispersers to infect neighboring colonies. This mode of spread might explain our results, especially if individuals tend to disperse to the neighboring colony, regardless of distance, and if the intervening habitat provides few barriers to movement, as would be expected in shortgrass steppe. To date, however, there is no conclusive evidence that intraspecific dispersal is the primary mechanism by which infection spreads to new colonies.

The fact that isolation did not reduce plague occurrence may also indicate that *Y. pestis* is maintained at low levels between outbreaks by fleas, reservoir hosts, or plague survivors. If this were the case, however, one might expect that colonies extirpated by plague would have suffered plague within the recent past, yet only 11% (5/47) of extirpated colonies went extinct within the previous 5 years. Despite >30 years of study of plague in prairie dogs, the mechanisms by which it moves among colonies and persists between epizootics remain a mystery.

Plague is not native to North America and therefore represents a novel problem for prairie dogs, for several reasons. First, large colonies suffer higher rates of extinction than intermediate-sized ones, the opposite of what we would have predicted in the absence of plague. Furthermore, large colonies, which might normally rescue nearby small colonies as a result of dispersal, may actually increase the likelihood of local extinction by sending infected dispersers to adjacent colonies (Hess 1996). Both of these factors represent dramatic shifts in dynamics of prairie dog populations which, in the past, persisted as distinct populations or, perhaps, as complexes of large and small colonies in a mainland-island metapopulation (Stapp and Van Horne *in press*). Finally, our results suggest that 50–82% of active colonies go extinct during outbreaks, which increases the temporal synchrony of extinctions compared to pre-plague conditions, and to areas of the eastern Plains where plague is still absent. All of these complications may reduce the probability of regional persistence of metapopulations, with important implications for conservation and management of prairie dogs in the face of increasing habitat loss and fragmentation (Antolin *et al.* 2002). Moreover, because of the unique functional role of prairie dogs (Kotliar *et al.* 1999), a reduction in size and number of colonies may alter the diversity and functioning of

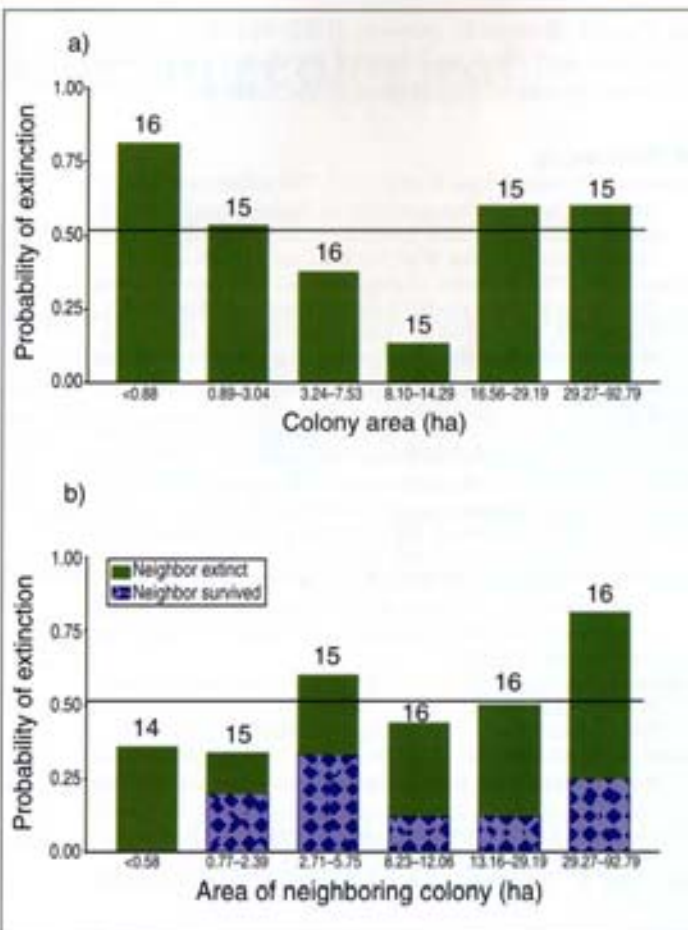


Figure 4. Probability of extinction of prairie dog colonies during epizootic years is a function of (a) colony area and (b) the area and fate of the nearest colony. Colonies were assigned to classes based on their area (or in b, the area of their nearest neighbor) in the year prior to extinction, which were then used to calculate the proportion of colonies in each size class that went extinct during that period. Numbers over bars are the numbers of colonies in each size class; in some cases, sample sizes were unequal among classes to account for tied values. The horizontal lines represent the proportion of all active colonies that went extinct during epizootic years (0.51, or 47/92 colonies).

grassland ecosystems, especially if the suitability of colonies for associated species, eg black-footed ferrets (*Mustela nigripes*), is a function of colony area. Ecological studies aimed at establishing the relationship between colony area, isolation, and extinction rates, identifying environmental factors that drive vector and host population dynamics, and elucidating the role of reservoir hosts offer the greatest opportunities for predicting the long-term consequences of plague and reducing risk of infection to nearby human populations.

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