Introduced plague lessens the effects of an herbivorous rodent on grassland vegetation

Laurel M. Hartley1,2,* , James K. Detling1,2,3 and Lisa T. Savage2

1Graduate Degree Program in Ecology, Colorado State University; 2Department of Biology, Colorado State University; and 3Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA

Summary

1. Plague, introduced from Eurasia around 1900, today affects many animal species in the western part of North America, including black-tailed prairie dogs Cynomys ludovicianus, widespread colonial herbivores of the Central Plains. Most studies of introduced diseases describe how they affect susceptible individuals or populations. We examined the indirect community and ecosystem-level effects of plague to address the hypothesis that frequent plague epizootics have a mediating effect on the important role of prairie dogs in shaping grassland plant communities.

2. We used 25 years of spatially explicit monitoring data on the Pawnee National Grassland (Colorado, USA) to estimate frequency of plague epizootics in prairie dog colonies. We also examined plant community characteristics of young (3–8 years), old (~20 years) and plague-extirpated (7–12 years when extirpated) colonies intermittently to determine how colony age and status (active or inactive) influence the effects of prairie dogs on plant communities.

3. Approximately 98% of colonies experienced a plague epizootic within 15 years of continuous activity, nearly half remained inactive for at least 5 years following an epizootic, and less than half attained their pre-plague area within 10 years of an epizootic.

4. Prairie dogs lowered plant canopy height, reduced plant biomass and altered plant community composition. These effects were most pronounced for older colonies. Plague-extirpated colonies were not significantly different from their associated off-colony sites for most variables measured.

5. Synthesis and applications. Our work shows that introduced diseases can indirectly affect community- and ecosystem-level processes through their modification of host species dynamics. Frequent epizootics that lessen the effects of prairie dogs on vegetation probably affect colony-associated species and grassland food webs. Over 100 animal species are associated with prairie dog colonies because prairie dogs are an important food source and their colonies provide habitat. Prairie dogs are considered competitors with livestock for forage and are exterminated on private lands at considerable expense to ranchers. Extermination may be unwarranted and cost-ineffective where plague exists because of the high frequency of plague epizootics.

Key-words: Cynomys ludovicianus, ecosystem engineer, emerging disease, herbivory, keystone species, plant–animal interactions, prairie dogs, rangelands, shortgrass steppe, Yersinia pestis

Introduction

With the unprecedented translocations of species around the globe today, how introduced species influence ecosystem structure and function is a pressing issue in ecology. Pathogens represent an important subset of introduced species. Introduced pathogens that cause high mortality in keystone species or ecosystem engineers probably have indirect effects on other species via trophic cascades and alterations to ecosystem structure and function (Stapp 2007; Eviner & Likens 2008). We investigated how the introduction of the plague bacterium Yersinia pestis to black-tailed prairie dogs Cynomys ludovicianus Ord, burrowing, colonial rodents of the central North American grasslands, is likely to have changed: (1) the age distribution of prairie dog colonies in shortgrass steppe and (2) the role of prairie dogs in shaping plant community composition and physiognomy.

Plague was introduced from Eurasia to the USA around 1900, and the disease was first noted in prairie dogs in the late 1930s and early 1940s (Eskey & Haas 1940; Ecke & Johnson 1952). Plague causes nearly 100% mortality within infected
prairie dog colonies (Barnes 1993; Cully 1993; Stapp et al. 2004; Pauli et al. 2006). Plague occurs in the western half of the black-tailed prairie dog’s range, which mostly includes the mixed-grass prairie (Coupland 1992) and shortgrass steppe (Lauenroth & Milchunas 1992) from southern Canada to northern Mexico (Cully & Williams 2001). Prior to the introduction of plague, individual prairie dog colonies probably persisted in one location for multiple decades as they do in plague-free areas today (Carlson & White 1987; Garrett & Franklin 1988). However, where plague exists, prairie dog colonies are subject to periodic extinction events and are eventually repopulated by individuals from neighboring colonies (Roach et al. 2001; Savage 2007).

Over 60 years after the introduction of plague, we have little information about its effects on prairie dog colony longevity because there are few long-term, spatially explicit records of large prairie dog colony complexes. Some researchers have suggested that plague has reduced average colony size, increased distances among colonies (Cully & Williams 2001), and accelerated spatial shifting of entire colonies on the landscape (Augustine et al. 2008b). We know of no published accounts about the long-term frequency of plague epizootics on individual colonies or the average length of time colonies remain inactive following an epizootic. How long a colony is continuously grazed by prairie dogs and how long plant communities will persist without grazing pressure from prairie dogs following an epizootic could strongly influence the effects of prairie dogs on plant communities.

Black-tailed prairie dogs consume 60–80% of above-ground annual net primary production on their colonies, clear taller vegetation to facilitate communication and predator avoidance and create extensive burrow systems (Whicker & Detling 1988). They have substantial effects on plant communities (e.g. Whicker & Detling 1988; Weltzin et al. 1997; Winter et al. 2002), although their effects on vegetation have been mostly extensively studied in plague-free areas in the mixed-grass prairie. Prairie dog colonies often have higher plant species richness and diversity than off-colony sites (Bonham & Lerwick 1976; Coppock et al. 1983; Fahnestock & Detling 2002). In mixed-grass prairie, prairie dog grazing results in a lower canopy height, a decrease in litter, a decrease in above- and below-ground biomass and an increase in the ratio of live to dead standing biomass (Coppock et al. 1983; Archer et al. 1987; Weltzin et al. 1997). Prairie dogs also alter plant species composition by increasing the number, cover and biomass of forbs and decreasing those same attributes for grasses, and the magnitude of these effects increases with colony age in mixed-grass prairie (Coppock et al. 1983; Archer et al. 1987).

We conducted this study in shortgrass steppe to address unanswered questions about interactions among plague, prairie dogs and grassland plant communities. Our first objective was to estimate the frequency of plague epizootics on individual colonies and the average length of colony inactivity following an epizootic. Our next objectives were to assess how plant communities respond to release from prairie dog grazing pressure following a plague epizootic, and to assess whether effects of prairie dogs increase with colony age in shortgrass steppe as they do in mixed-grass prairie (Archer et al. 1987). We hypothesized that if the effects of prairie dogs increase with colony age, but plague reduces average colony age, then plague would effectively reduce the overall impact of prairie dogs on plant communities.

Prairie dogs are considered to be ecosystem engineers (sensu Jones et al. 1994) and keystone species (sensu Power et al. 1996) because they are a food source for other species and because their habitat alterations create unique patches within the larger grassland matrix (Ceballos, Pacheco & List 1999; Kotliar et al. 1999). They are also considered important competitors with cattle Bos taurus Linneaus for forage, and poisoning of prairie dogs on ranchland is one factor for their population decline, together with habitat loss, recreational shooting and plague (Antolin et al. 2002). Knowledge about the frequency of plague epizootics and duration of colony inactivity after an epizootic will contribute to management decisions for prairie dogs and colony-associated wildlife species, and aid in decision making about whether poisoning of prairie dogs on ranchland is warranted and cost-effective.

Materials and methods

SITE DESCRIPTION

We conducted fieldwork from 2002–2004 in north-eastern Colorado, USA, on the Shortgrass Steppe Long Term Ecological Research site on the Pawnee National Grassland (PNG), a semi-arid shortgrass steppe with cold, dry winters. Vegetation is dominated by blue grama Bouteloua gracilis and buffalo grass Buchloe dactyloides, two perennial C4 grasses and prickly pear cactus Opuntia polyacantha (McGregor 1986). Mean annual temperature is 8.6 °C and mean annual precipitation is 322 mm, with most precipitation falling during the growing season as localized thunderstorms (Lauenroth & Milchunas 1992). Total precipitation was 214 mm in 2002, 311 mm in 2003 and 286 mm in 2004 (http://sgplt.sticer.colostate.edu).

EFFECTS OF PLAGUE ON COLONY LONGEVITY

From 1981 to 2005, approximately 70 prairie dog colonies, ranging in area from 1 to 253 ha, existed within the PNG (Fig. 1). We defined prairie dog colonies as locations on the landscape that were occupied by prairie dogs for one or more years between 1981 and 2005. We used annual monitoring data collected from 1981 to 2005 (US Forest Service PNG, Greeley, CO, USA) to calculate the percentage of colonies that: (1) experienced a plague epizootic within 5, 10, 15 and 20 years of continuous prairie dog activity, (2) were recolonized within 2, 5 and 10 years of an epizootic and (3) attained their pre-plague size within 2, 5 and 10 years of an epizootic. Annually, US Forest Service personnel mapped the area and recorded actively used burrows as evidenced by visual sighting of prairie dogs, fresh scent and recent digging. Prairie dog density was not estimated. Complete or nearly complete loss of prairie dogs on a colony was presumed to be the result of a plague epizootic. We are confident that extirpations of large colonies are caused by plague epizootics; however, extirpations of small colonies might result from other causes such as predation, unauthorized poisoning and demographic stochasticity (Stapp et al. 2004). To make our analysis more conservative, we did not include extinction events when records indicated that extinction probably...
resulted from poisoning (four cases) or predation (two cases). We also did not include extirpation events in very small colonies (<1 ha) that had been active for less than 2 years (six cases). Our analysis included 58 prairie dog colonies. In 2004–2005, extirpation events were examined more closely by researchers at the Centers for Disease Control and Prevention and Colorado State University. There were nine cases of colony extinction, eight of which were investigated and confirmed to be caused by plague; no other pathogen is known to cause nearly complete eradication of colonies (M. Antolin, Personal communication).

SITE SELECTION

In 2002, we chose three ‘plague-extirpated colonies’ that were 7–12 years old when plague epizootics occurred in 1999, three ‘old colonies’ that had been occupied almost continuously since 1981 and three ‘young colonies’ that were founded within the last 3–7 years. We studied plague-extirpated colonies to determine how plant communities respond to release from prairie dog grazing pressure following an epizootic. We studied young and old colonies because plague is likely to have reduced average colony age such that few colonies now persist for multiple decades. We were unable to sample more than three colonies per type because of the lack of colonies that fit our designations as young (<7 years), old (>20 years) and plague-extirpated (extinction within the last 3 years). In 1999, just prior to the plague epizootic, areas of the three plague-extirpated colonies were 68, 35 and 5 ha. In 2002, when we began this study, the old colonies occupied 160, 53 and 44 ha and the young colonies occupied 36, 15 and 7 ha. For each colony, we selected a nearby uncolonized reference site with similar slope and soil characteristics (Natural Resources Conservation Service Soil Survey Geographic data base, US Department of Agriculture). We confined sampling to historically uncultivated areas on all colonies and reference sites. Because of their similar characteristics, we assumed uncolonized sites were suitable habitat for prairie dogs and, after conclusion of the study, some colonies expanded into reference sites. All sites have been grazed by cattle during the growing season since about 1940. Within the PNG, pastures are grazed at ‘moderate’ rates averaging 1·74 ha per cow per month (Guenther & Detling 2003). Actual grazing intensity varies among pastures because cattle are privately owned and managed. Each colony was near enough to its reference site to be grazed by the same herd of cattle, and cattle appear not to prefer or avoid grazing on prairie dog colonies (Guenther & Detling 2003).

In 2004, one of the old colonies experienced a plague epizootic and was not sampled that year, and a suitable replacement site was not available.

PLANT COMMUNITY STRUCTURE AND COMPOSITION

We sampled vegetation within a 1-ha area on the oldest part of the old colonies, the youngest part of the young colonies, the centre of the plague-extirpated colonies and within a similar area on the uncolonized sites. We chose the parts of the old and young colonies to include the extremes at both ends of the age spectrum and centres of the plague-extirpated colonies because they had been occupied for the longest time prior to extirpation. We generated 25 random coordinates within each sampling area. At each coordinate, we estimated mean canopy height by balancing a light styrofoam plank (0·2 × 0·5 × 0·005 m) atop the canopy and measuring the height of the plank through a hole cut in its centre (Guenther & Detling 2003). These data were gathered both early (May/June) and late (July/August) in the growing seasons of 2002 and 2003. We also estimated mean canopy height by balancing a light styrofoam plank (0·2 × 0·5 × 0·005 m) atop the canopy and measuring the height of the plank through a hole cut in its centre (Guenther & Detling 2003). These data were gathered both early (May/June) and late (July/August) in the growing seasons of 2002 and 2003. We used canopy cover data to calculate the relative cover of graminoids and forbs, and Shannon–Weiner diversity (H') for graminoids, forbs, non-native species and total vegetation at each site (Gurevitch et al. 2002).

We used Modified-Whittaker multi-scale sampling plots to gather data on species richness because this technique detects more plant species in grasslands than other techniques (Stohlgren et al. 1998). We established and sampled a Modified-Whittaker plot (1000 m²) on each prairie dog colony and off-colony site in June, 2002 and 2003. Using these data, we calculated species richness at each site for total vegetation, forbs, graminoids and non-native species. We also calculated species overlap between paired on- and off-colony sites for total vegetation, forbs and graminoids using Jaccard’s coefficient (Gurevitch et al. 2002).
PLANT BIOMASS

At the estimated time of peak biomass in 2002–2004, we clipped above-ground current year’s biomass by species on five randomly selected plots (0.25 m²) on each colony and off-colony site. We also collected standing dead plants and litter but did not separate them by species. We dried (55°C) and weighed samples. For statistical analysis (see below), we compared on- and off-colony biomass differences for the graminoid and forb functional groups, standing dead, litter, four key palatable graminoids (*B. gracilis*, *B. dactyloides*, *Agropyron smithii* and *Carex ehocharis*), an abundant, non-palatable bunchgrass (*Aristida longiseta*) and the most abundant forb (*Sphaeralcea coccinea*) (McGregor et al. 1986).

We used a soil core (6.35 cm diameter) to collect below-ground plant biomass samples to a depth of 20 cm, which probably includes ~75% of the root biomass in this grassland (Leetham & Milchunas 1985). At each on- and off-colony site, we collected five randomly placed cores in 2003 and eight cores in 2004. We separated soil from roots (Lauenroth & Whitman 1971) before drying (55°C) and weighing them. To correct for soil contamination, we combusted 0.5-g subsamples in a muffle furnace at 600°C for 4 h and multiplied the mass of the original samples by the % organic matter in the subsamples to obtain ash-free dry mass.

STATISTICAL ANALYSES

We used mixed model, repeated measures analyses of variance to test main effects, and interactions among main effects, of location (on- vs. off-colony), year, season (early or late), colony (site) and colony type (young, old, plague-extirpated) on each response variable. As we chose specific off-colony sites for each colony, we linked each pair together in the programming code. We examined differences between on- vs. off-colony pairs by colony type using LS mean values, and we examined on- vs. off-colony pairs by type and year using paired t-tests. If necessary, data were square-root transformed to achieve normality and reanalyzed. All figures and tables depict untransformed data. We report height, cover and biomass data as mean values of the years and seasons (early and late) sampled unless there were significant (P ≤ 0.05) interactions among the main effects. We used SAS statistical software for all analyses (SAS Institute Inc., 1999, Cary, NC, USA).

Results

EFFECTS OF PLAGUE ON COLONY LONGEVITY

Nearly all prairie dog colonies on the PNG experienced at least one plague event within 15 years of continuous active occupation and 73% experienced plague in 10 years or less (Fig. 2a). Mean length of continuous occupation before an epizootic was 6.6 years. Of the colonies active in 2005, 42% were active for less than 5 of the last 25 years. Of the colonies in existence in 2005, approximately 50% were founded more than 15 years prior to 2005. Almost half of all plague-extirpated colonies remained inactive for at least 5 years after extirpation (Fig. 2b), and most did not recover to their pre-plague area within 10 years (Fig. 2c).

![Figure 2](https://example.com/fig2.png)

**Fig. 2.** Percentage of black-tailed prairie dog colonies on the Pawnee National Grassland in Colorado, USA, (a) experiencing a plague epizootic within 5, 10, 15 or 20 years of continuous activity, (b) recolonized within 2, 5 or 10 years of a plague epizootic and (c) attaining pre-plague size within 2, 5 or 10 years of plague epizootic.
not on young or plague-extirpated colonies (Fig. 4c,d). Although all colony types showed a trend toward lower belowground biomass compared with their off-colony sites, the trend was not significant (Fig. 4e).

Regarding the six key species that we analysed, biomass of the dominant grass B. gracilis was significantly lower on than off both young and old active colonies, but not plague-extirpated colonies, and biomass of C. eleocharis was significantly lower on than off only the old colonies (Fig. 5a,b). By contrast, biomass of the unpalatable grass, A. longiseta, was greater on than off the old, active colonies, while biomass of the forb, S. coccinea, was greater on than off both the old, active colonies and the plague-extirpated colonies (Fig. 5c,d). Biomass of B. dactyloides and A. smithii did not differ on vs. off of any of the colony types (Fig. 5e,f).

Forb and total plant species richness were greater on- than off-colony for old and plague-extirpated colonies, but not for young colonies, while graminoid and non-native species richness did not differ significantly on and off any colony type (Table 1). There were also no significant differences in total, graminoid or forb species diversity (H') on vs. off any of the colony types (Table 1). We did not assess non-native species diversity because few non-native species were encountered. For all functional groups tested, Jaccard's index of similarity between on- and off-colony sites showed no significant differences among colony types (young, old and plague-extirpated). That is, young colonies were statistically no more similar to their paired off-colony sites than old or plague-extirpated colonies were to their paired off-colony sites (Table 1). However, there were trends of decreasing similarity between on- and off-colony sites with increasing age of active colonies and of increasing similarity following plague-extirpation.

**Discussion**

Understanding the possible effects of introduced pathogens on ecosystems is increasingly important as species introductions become more frequent worldwide. One way introduced pathogens can affect communities is through trophic interactions (Stapp 2007; Collinge et al. 2008). Our results suggest that the introduction of the plague bacterium Y. pestis to North America is affecting plant community composition in Central Plains grasslands through its effects on an ecosystem engineer, the black-tailed prairie dog.

Previous studies have suggested that plague has reduced the average size of prairie dog colonies, increased the distance between colonies and accelerated the rate of spatial movement of entire colonies on the landscape (Cully & Williams 2001; Augustine et al. 2008b). Our data indicate that plague has also reduced the average length of time colonies are continuously active. We found that 98% of colonies experienced a plague epizootic within 15 years of continuous occupation by prairie dogs, and that colonies were typically inactive for at least several years after an epizootic. Prior to the introduction of plague and deliberate human poisoning efforts, colonies apparently persisted in one location for multiple decades (Carlson & White 1987; Antolin et al. 2002). Because plague reduces the average number of years a colony is continuously active and colonies typically do not attain their pre-epizootic area before another epizootic occurs, we suggest that plague has also reduced average colony size. Furthermore, 36% of colonies were not recolonized within 10 years of extirpation, but other colonies were arising in previously (since 1980) uncolonized grassland. This indicates substantial spatial shifting of colony locations over time, which mitigates their impact on plant communities to an even greater degree than if they were expanding and contracting around fixed locations over time (Augustine et al. 2008b).

The major goals of our study were to determine whether there is a relationship between vegetation change and length of continuous occupation by prairie dogs and what happens to vegetation during the period of inactivity between an epizootic and recolonization. Compared with off-colony sites, prairie dog colonies generally had lower canopy height, more bare ground, greater cover and biomass of forbs, lower cover and biomass of graminoids and greater plant species richness. However, these trends were most pronounced, and often only statistically significant, for older colonies. Previous studies in the more mesic mixed-grass prairie showed that the effects of prairie dogs increase with increasing colony age (Coppock et al. 1983; Archer et al. 1987). Our results suggest that this is also the case on semi-arid shortgrass steppe, although the magnitude of the effect seems less pronounced, probably because the shortgrass steppe is dominated by shorter, more

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Fig. 3. (a) Mean canopy height (cm) and (b) cover of bare ground (+1 SE) off and on prairie dog colonies on the Pawnee National Grassland, Colorado, USA, averaged across 2 months (June and August) and years (2002–2003) and presented by colony type (young, old and plague-extirpated). Off- and on-colony pairs are significantly different at **P < 0.01.© 2009 The Authors. Journal compilation © 2009 British Ecological Society, Journal of Applied Ecology, 46, 861–869
grazing-tolerant grass species than the mixed-grass prairie. One highly grazing-tolerant grass, *B. gracilis*, dominates the North American shortgrass steppe and is critically important to shortgrass steppe ecosystem structure and function (Milchunas et al. 1989, 1990; Coffin et al. 1996). *Bouteloua gracilis* is a preferred forage for both prairie dogs and cattle (Detling 2006). The reduction in *B. gracilis* abundance on active colonies over time may facilitate the establishment and subsequent increase in forb abundance. This, in turn, may eventually reduce *B. gracilis*’ ability to recover from heavy grazing following plague epizootics. However, because of frequent plague epizootics, grazing pressure by prairie dogs is rarely sustained for more than 10 years, making widespread reduction in *B. gracilis* less likely now than prior to the introduction of plague.

Comparisons between on and off plague-extirpated colonies showed many of the same trends as comparisons between on and off active colonies, but the trends were statistically

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**Fig. 4.** Mean biomass (+1 SE) of (a) graminoids, (b) forbs, (c) standing dead, (d) litter and (e) below-ground standing crop (to 20 cm depth) off and on prairie dog colonies on the Pawnee National Grassland in Colorado, USA, averaged over years (2002–2004 for above-ground biomass and 2003–2004 for below-ground biomass) and presented by colony type (young, old and plague-extirpated). On- and off-colony pairs are significantly different at **P ≤ 0.01.**

**Fig. 5.** Mean above-ground biomass (+1 SE) of important plant species off and on prairie dog colonies on the Pawnee National Grassland, Colorado, USA, averaged over all years (2002–2004) and presented by colony type (young, old and plague-extirpated). On- and off-colony pairs are significantly different at *P ≤ 0.05 and **P ≤ 0.01.**
significant for only a few variables (forb and total species richness and S. coccinea biomass). Thus, changes in canopy height and standing crop biomass of important graminoid and forb species appear to be quickly reversed following extirpation of colonies. However, this interpretation must be tempered by the fact that, when our plague-extirpated colonies were abandoned, they were younger than our ‘old’ colonies and thus may not have experienced as much vegetation change as experienced by our older colonies. We expect that vegetation on colonies that have been active for 20 years or more will take longer to return to an uncolonized state than vegetation on the 7- to 12-year-old plague-extirpated colonies we studied. However, because of plague, colonies more than 20 years old have become rare on the PNG.

Previous studies have measured vegetation characteristics on colonies from which plague dogs have been removed. In tallgrass prairie, effects of plague dogs were reversed within several years following their removal (Osborn & Allan 1949). Cid et al. (1991) found that biomass increased 32–36% within 2 years following exclusion of plague dogs from mixed-grass prairie, but species diversity, similarity and dominance were not significantly affected by the exclusion of plague dogs. By contrast, Klatt & Hein (1978) and Uresk (1985) reported no reversal of the effects of plague dogs within 1–5 years of removal from shortgrass steppe and mixed-grass prairie respectively. Our results suggest that the effects of plague dogs on vegetation increase with colony age, and that colony age might be an important indicator of how quickly grasslands will return to an uncolonized state after cessation of plague dog activities. In addition to colony age, composition of the plant community at the time of the plague epizootic, colony size, weather conditions following the epizootic and grassland type (shortgrass, mixed-grass, tallgrass) were also likely to influence the rate at which vegetation on colonies recovers and explain why the previous research on extirpated colonies has produced varying results.

We examined only the variables of length of continuous activity prior to an epizootic and length of time inactive following an epizootic. Other effects of plague on prairie dogs could influence their role in structuring individual plant communities and landscapes. Grazing pressure by plague dogs could also be alleviated if their average density on individual colonies decreases because of plague. This is plausible as extirpated colonies must be recolonized by immigrants from neighbouring colonies, and a colony’s population may have less than 15 years to grow before another plague event is likely to occur. Effects of plague dogs at the landscape level could be lessened if plague reduces total area (average colony area × number of colonies) occupied by plague dog colonies at any one time. Previously, researchers have suggested that average colony area has been reduced by the introduction of plague (Cully & Williams 2001) and our work supports this idea. The total number of colonies in North American grasslands has probably decreased; however, the effects of plague are difficult to separate from the effects of reduction in suitable habitat due to land-use change and intentional large-scale eradication efforts.

Prairie dogs are considered ecosystem engineers (Ceballos et al. 1999) and keystone species (Miller et al. 1994; Kotliar et al. 1999; Davidson & Lightfoot 2007; but see Stapp 1998). The direct effects of plague on prairie dog populations have indirect effects on plant communities and animal species associated with colonies (Ceballos et al. 1999; Kotliar et al. 1999). The endangered black-footed ferret Mustela nigripes is dependent upon prairie dogs and has been negatively affected by plague epizootics on their colonies (Barnes 1993). Similarly, populations of nesting mountain plovers Charadrius montanus declined rapidly following plague epizootics on shortgrass steppe colonies (Augustine et al. 2008a). By contrast, Stapp (2006) found no negative effects of plague epizootics on prairie dog colonies on the populations of other rodents on the shortgrass steppe.

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<th>Table 1. Mean species richness (no. of species per 1000 m²) and Shannon–Weiner diversity (H') (± 1 SE) of plant functional groups off and on young, old and plague-extirpated (n = 3 for each) prairie dog colonies and mean species overlap (Sj) (± 1 SE) between off- and on-colony pairs for young, old and plague-extirpated colonies on the Pawnee National Grassland, Colorado, USA</th>
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Values are represented as mean ± SE. As regards species richness and diversity, off- and on-colony pairs are significantly different at *P < 0.05.
Ranching is an important industry in North American shortgrass steppe where domestic cattle long ago replaced bison *Bison bison* Linnaeus as the dominant ungulate grazers. A recent investigation near our study site demonstrated that cattle weight gains declined 5.5–13.9% when relatively young prairie dog colonies occupied 20–60% of pastures (Derner et al. 2006). How cattle weight gain is affected on old vs. young colonies is yet to be determined experimentally. Because colony age is an important determinant of the magnitude of prairie dog-induced vegetation changes, the aerial extent alone of their colonies on a landscape provides an incomplete picture. Prairie dogs have historically been viewed as competitors with cattle for forage and are often exterminated on rangelands (Detling 2006). An important management implication of our study is that expensive and labour-intensive eradication efforts may not be cost-effective on the shortgrass steppe because most colonies will experience frequent plague epizootics and subsequent periods of inactivity during which forage biomass, an important variable to ranchers, may increase quickly. Collins et al. (1984) calculated that poisoning of prairie dogs in a plague-free area of mixed-grass prairie was economically non-viable because the cost of annual maintenance via repoisoning was greater than the annual value of forage gained. We suggest extermination programs should be even less economical in a system where plague periodically extirpates colonies. By the time a colony becomes large enough after an epizootic to impose significant costs to a rancher (Derner et al. 2006), it is also increasingly likely to be extirpated by plague. Furthermore, frequent plague epizootics appear to prevent long-term declines in the production potential of the dominant forage species, *B. gracilis*.

In conclusion, our results suggest that introduced plague has affected prairie dog colony longevity and, hence, the role of prairie dogs in shaping plant community composition in North American shortgrass steppe. Specifically, in contrast to active colonies, plague-extirpated colonies did not differ significantly from their associated off-colony sites for the majority of the vegetation attributes we measured. In addition, the effects of prairie dogs on vegetation appear to increase with colony age, but because of plague, very few colonies now persist for many decades. Plague is likely to continue to be an important influence on prairie dogs and their ecosystems as there is little evidence that they are evolving significant resistance to the disease (Antolin et al. 2006).

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References


Plague lessens effects of herbivore on vegetation


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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Summary of statistical metrics (F, t, P) from Analysis of Variance for on vs. off prairie dog colony comparisons for all colonies (N=9) and for on vs. off prairie dog colony comparisons by type (young, old, and plague-extirpated colonies; N=3 for each colony type).

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