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The Influence of Sylvatic Plague on North American Wildlife at the Landscape Level, with Special Emphasis on Black-footed Ferret and Prairie Dog Conservation

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Introduction

"Prairie-dogs are distributed over a large part of the Great Plains and Rocky Mountain regions. Their colonies often number thousands of individuals, and their destruction of grasses and other forage plants makes them of considerable economic importance. Drastic measures are frequently necessary to prevent the destruction of crops of grain and hay. The Biological Survey is exterminating these rodents in national forests and in the public domain. The information in this report, in regards to the several species and their distribution, as indicated by maps, will aid materially in efforts, national or state, to control or exterminate them," said Henry W. Henshaw in 1915 (Hollister 1916).

The short-sighted goal of exterminating or severely limiting prairie dogs (*Cynomys* spp.) may be met, but not because of the control campaigns set forth by Henshaw's call to arms. Rather, prairie dogs continue to be devastated by plague, the infectious disease caused by the bacterium, *Yersinia pestis*, whose inadvertent introduction and spread into the western United States coincided with the poisoning programs. This is the same pathogen that was primarily responsible for three known world pandemics of plague in humans, including an outbreak in the 5th century in the eastern Mediterranean region, the Black Death of medieval Europe and the last pandemic that began in China the 1870s and continues in parts of the world today (Poland and Dennis 1998). Indeed, it appears that infectious diseases of all kinds, including those caused by bacteria (plague, anthrax), viruses (human immunodeficiency virus, West Nile encephalitis), protozoans (malaria) and prions (chronic wasting disease), now rapidly move around the globe, causing morbidity and mortality in humans. The same infectious diseases that afflict humans often have devastating consequences for wildlife species because many have an animal (zoonotic) origin, infect more than a single host species and efficiently travel among hosts via arthropod vectors (Gratz 1999, Dobson and Foufopoulos 2001, Woodhouse et al. 2001). This is certainly the case for sylvatic plague, as the disease caused by *Y. pestis* is known when it cycles in natural populations of mammalian hosts and flea vectors (Barnes 1993, Poland et al. 1994, Biggins and Kosoy 2001). Sylvatic plague is now firmly established in the western United States, reported from at least 76 species of mammals (Barnes 1993).

Here, we briefly review the natural history of sylvatic plague. We consider the consequences of plague on human health and the conservation of prairie dogs and associated animals. Particularly, we examine how plague has affected population dynamics of prairie dogs and recovery of the black-footed ferret (*Mustela nigripes*) in Wyoming and Montana. Finally, we outline efforts aimed toward improving management of prairie dog populations and how management of grassland and shrubland ecosystems must consider both direct and indirect effects of sylvatic plague.

Natural History of Plague in the United States

The bacterium, *Y. pestis*, was first recorded in the United States in 1899 on ships in port in California, Washington, Delaware and New York (Dicke 1926, Link 1955), during the early stages of last worldwide pandemic that originated in China. Plague was also found on ships in Texas, Louisiana and Florida. Early human cases were associated with commensal rats (*Rattus* spp.), particularly the black rat (*R. rattus*) and its fleas. The primary flea vector implicated in human bubonic plague is the oriental rat flea, *Xenopsylla cheopis*, although, worldwide, more than 150 flea species are capable of transmitting plague (Gage 1998). Soon after, mortality from deadly pneumonic (person-to-person) transmission, rather than by flea bite,s occurred, but this form of transmission is rare in the United States (Levy and Gage 1999). The first confirmation of plague in a wild species was in California ground squirrels (*Spermophilus beecheyi*) near San Francisco in 1908, although large die-offs of ground squirrels were noted in 1903 (Eskey and Haas 1940). Afterward, plague quickly spread to its eastern boundary (Figure 1). Monitoring by scientists from the Centers for Disease Control and Prevention's Division of Vector-Borne Infectious Diseases, in Fort Collins, in addition to extensive surveys conducted by the US Public Health Service in the 1930s and 1940s, determined the eastern extent of plague to be near the 97th meridian, in Texas, extending northward to the 102nd meridian, in North Dakota (Barnes 1982). Extensive spread farther eastward is not expected. Worldwide, plague foci are found in natural rodent populations in semiarid regions, like the western United States (Poland and Barnes 1979, Poland and Dennis 1998), and introductions of plague into ports along the Atlantic and Gulf coasts of the United States failed to establish sylvatic plague in the eastern part of the country.

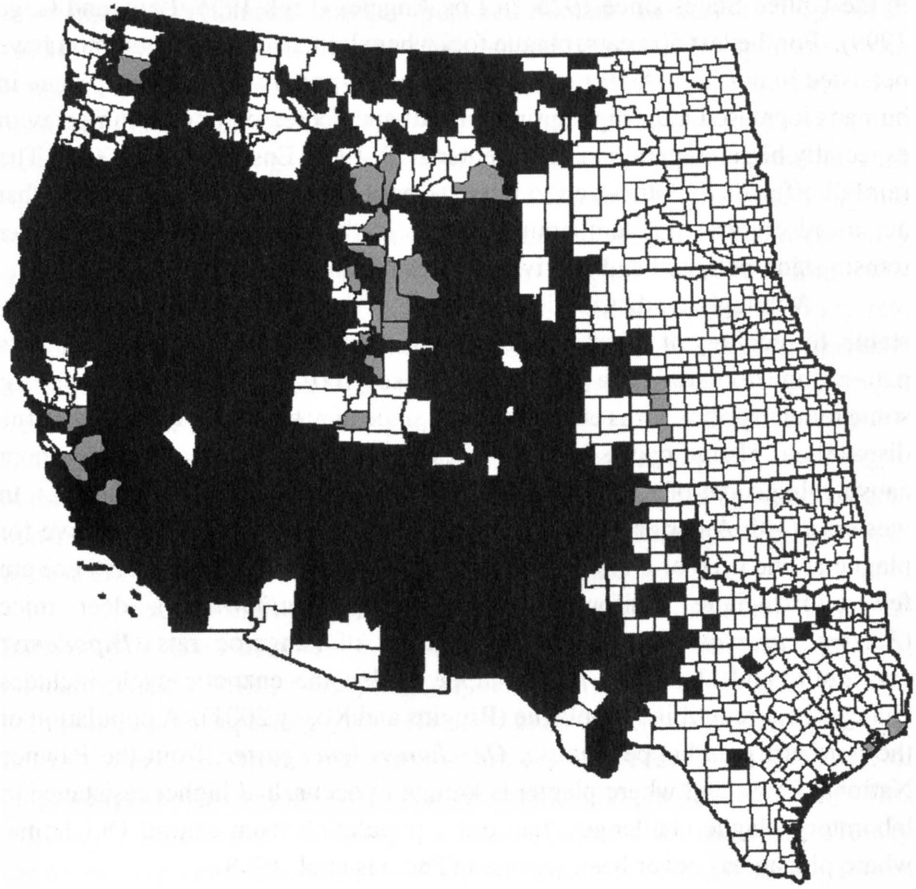

Figure 1. Geographic distribution of plague in humans and other animals in the United States by county of origin, as determined by human cases, presence of antibodies in domestic and wild animals, and plague positive fleas, between 1970 and 2001 (counties in dark gray). Some counties (light gray) had positive samples before 1970 but have no reported positives since. Map courtesy of the Division of Vector-Borne Infectious Diseases, CDC, Fort Collins, Colorado. Additional data from Link (1955) and Kartmann (1970).

In recent decades, 10 to 15 cases of plague in humans were reported each year in the United States, although deaths are uncommon as antibiotic treatment against plague is highly effective. Most human cases are of zoonotic origin, either directly or secondarily if household pets come into contact with infected rodents (Levy and Gage 1999). Although primary pneumonic cases occur, no outbreaks of plague caused by pneumonic transmission have occurred in the United States since 1925, in Los Angeles (Link 1955, Levy and Gage 1999). For the last 50 years, plague foci where human cases are common have persisted in northern Arizona and New Mexico, and, in those areas, plague in humans increased after high spring rainfall and decreased after summers with especially high temperatures (Parmenter et al. 1999, Enscore et al. 2002). The rainfall effect is hypothesized to relate to population increases of rodents that act as reservoirs; the temperature effect is thought to act through lower transmission potential and survival of fleas during hot summers.

Although the distribution of plague in the United States appears to be stable, the ecology of sylvatic plague is not completely understood, even in its native range in central Asia (Biggins and Kosoy 2001). It is clear, however, that some rodent species act as enzootic hosts, since they have high resistance to the disease and plague cycles between these hosts and their fleas exist without causing large die-offs (Barnes 1983, 1993; Biggins and Kosoy 2001). In western North America, virtually every rodent species has tested positive for plague at one time or another, but those showing high levels of resistance are few and include California voles (*Microtus californicus*), deer mice (*Peromyscus maniculatus*) and two species of kangaroo rats (*Dipodomys spectabilis* and *D. ordii*). It also appears that the enzootic cycle includes changes in susceptibility to plague (Biggins and Kosoy 2001). A population of the northern grasshopper mouse, *Onychomys leucogaster*, from the Pawnee National Grassland where plague is known to occur, had higher resistance to laboratory plague challenges than did a population from central Oklahoma, where plague has never been reported (Thomas et al. 1988).

The most dramatic effect of plague on rodents is seen in the wood rats (*Neotoma* spp.) and sciurid rodents, including ground squirrels (*Spermophilus* spp., *Ammospermophilus* spp), tree squirrels (*Sciurus*), chipmunks (*Tamias, Eutamias*), prairie dogs (*Cynomys* spp.) and marmots (*Marmota* spp.) (Poland and Barnes 1979, Barnes 1993, Biggins and Kosoy 2001). These have received more attention than most other rodents because of their involvement in human plague cases (Barnes 1993). Outbreaks in these species are explosive, with low resistance, high mortality and rapid spread of the disease in host populations. In contrast to rodents responsible for maintaining plague in its enzootic sylvatic phase, these epizootic hosts are thought to greatly amplify the pathogen in the surrounding environment and increase plague transmission back to enzootic rodent hosts, to predators like coyotes (*Canis latrans*) and to rodents that are commensal with humans, humans' pets and humans themselves (Gage et al. 1994). Complexes of epizootic host species and their fleas living in areas near human populations are implicated in maintaining human plague foci. For instance, the foci in northern New Mexico and Arizona relate to plague in Gunnison's prairie dogs (*C. gunnisoni*) in grassland habitats and in rock squirrels (*S. variegatus*) in pinon-juniper and Gambel oak woodland (Barnes 1993). Also, in contrast to enzootic host species, epizootic hosts are probably not responsible for the overall persistence of plague. It is more likely that plague epizootics break out in these susceptible hosts when they come into contact with enzootic hosts or their fleas, and conditions like temperature, moisture, flea population size and host population density favor rapid transmission of the plague pathogen (Barnes 1993, Biggins and Kosoy 2001, Cully and Williams 2001). The patchy and idiosyncratic patterns of plague outbreaks in North America over the last century are consistent with occasional transmission from resistant enzootic hosts to susceptible epizootic hosts, as opposed to large pandemics sweeping throughout the land.

The role of carnivores in plague ecology deserves mention (Poland and Barnes 1979, Gage et al. 1994, Poland et al. 1994). Mammalian predators, including canids, felids, mustelids, procyonids and ursids, can become infected with plague after ingesting infected rodent prey or being bitten by the prey's fleas. Carnivores sampled in areas where plague occurs show evidence of plague exposure in the form of antibodies to the pathogen (Barnes 1982). This evidence, together with laboratory challenges, points to the resistance of many carnivores to plague infection and to their potential role as long distance carriers of the disease. Not all carnivores are equally capable long-distance vectors. For instance, wild cats (*Lynx* spp.) in North America, suffer higher rates of mortality from plague than do coyotes, foxes (*Vulpes* spp., *Urocyon cinereoargenteus*) and badgers (*Taxidea taxus*) (Barnes 1982, Fitzgerald 1993). Further, the ability to transmit disease by the many different flea species carried by carnivores is sure to differ (Gage et al. 1994). Finally, testing carnivores for plague antibodies may provide powerful means for detecting plague in small mammal populations (Barnes 1982, Gage et al. 1994). However, when plague is prevalent in an area, carnivores show uniformly high antibody titers (Luce et al. 1997), and it remains to be seen whether carnivore surveillance will predict outbreaks in epizootic species, like ground squirrels and prairie dogs, before they occur.

Prairie Dogs and Their Ecosystem

Prairie dogs are an integral part of the American West and are characterized by diurnal activity, a herbivorous diet, digging of underground burrows for shelter and nesting, and living socially in towns of extended families (Hollister 1916, Pizzimenti 1975, Hoogland 1995). At one time, prairie dogs were not only numerous in North America, their historical geographic ranges defined the short grass and mixed-grass Great Plains and the relatively dry shrub-steppe valleys of the Rocky Mountains and Intermountain West (Figure 2). The accounts of early western explorers regularly included prairie dogs, and the first scientific specimens of black-tailed prairie dogs (*C. ludovicianus*) were collected during Lewis and Clark's expedition to the upper reaches of the Missouri River (Hollister 1916). During the last century, however, prairie dog populations have declined drastically as the result of four main causes: habitat loss from conversion of land for agriculture and human habitation, poisoning for population control and eradication programs, recreational shooting, and sylvatic plague (van Pelt 1999, Van Putten and Miller 1999). Consequently, the native habitat available to prairie dogs has declined from that described by Hollister (1916), and currently most prairie dog populations are reduced or fragmented, with occasional plague outbreaks that may cause local extinctions.

Even if all prairie dog habitats could be restored, and even if all controls of prairie dog populations by poisoning were to stop, it is unlikely that prairie dogs would completely regain their prominent role in the ecosystems of the Great Plains and valleys of the Intermountain West. Whether prairie dogs, especially black-tailed prairie dogs, rise to the level of keystone species is debatable (Miller et al. 1994, Stapp 1998, Kotliar et al. 1999, Kotliar 2000, Miller et al. 2000). However, we cannot ignore that prairie dogs cause landscape level effects by the disturbance of digging burrows, by clipping and eating vegetation, by the underground shelter created by burrows, and by serving as prey to a myriad of predators (Koford 1958, Whicker and Detling 1988, Hoogland 1995, Kotliar et al. 1999). Ties between prairie dogs and grassland biodiversity have been permanently changed by plague, as prairie dogs are highly susceptible epizootic hosts and suffer high mortality–nearly 100 percent in black-tailed, Gunnison's and Utah (*C. parvidens*) prairie dogs, and approximately 85 percent in white-tailed prairie dogs (*C. leucurus*) (Barnes

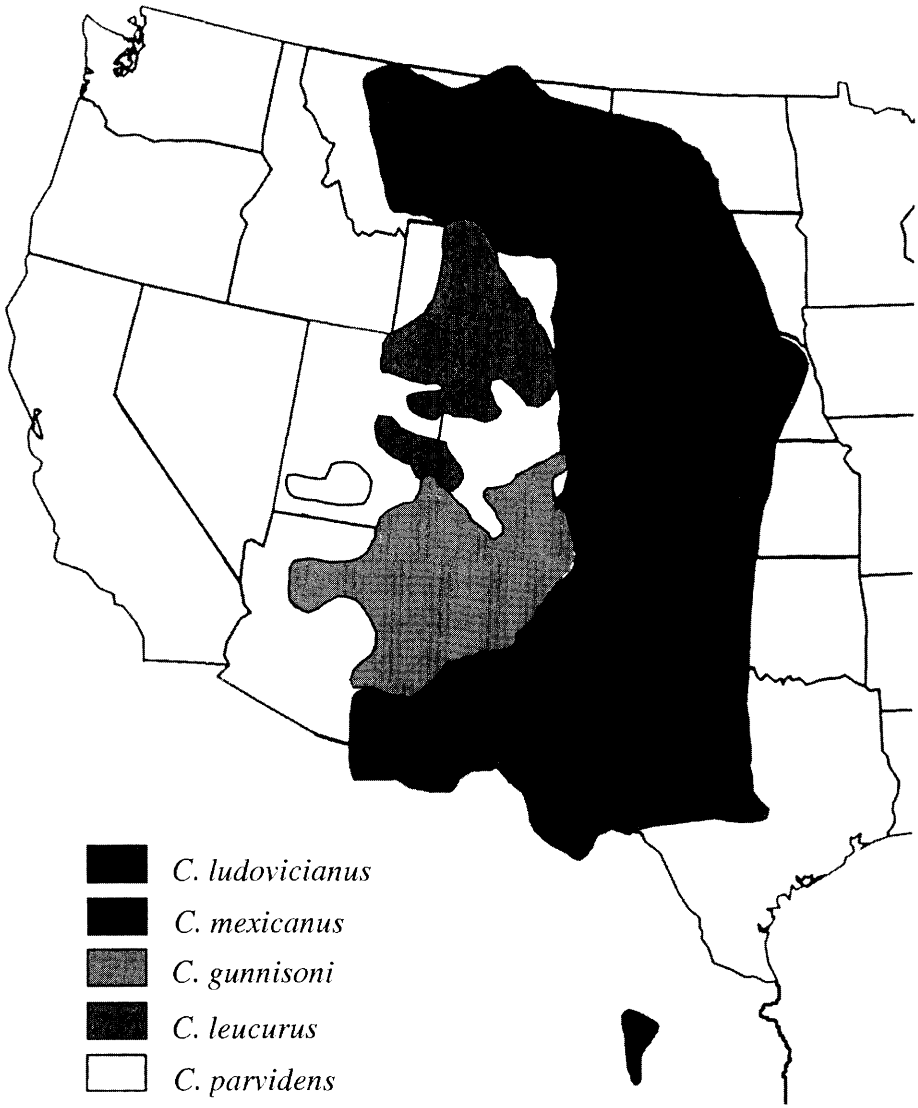

Figure 2. Historical geographic ranges of five recognized species of prairie dogs (*Cynomys*). *C. ludovicianus* = black-tailed prairie dog. *C. mexicanus* = Mexican prairie dog. *C. gunnisoni* = Gunnison's prairie dog. *C. leucurus* = white-tailed prairie dog. *C. parvidens* =Utah prairie dog. Map based on Hoffman (1981).

1993, Cully and Williams 2001). Only a relatively small portion of the range of the black-tailed prairie dog lies to the east of the plague-free line, but that part of the range is under intensive cultivation for agriculture and offers little relief.

Whether prairie dogs will gain protection from further declines under the Endangered Species Act is uncertain. In terms of protection, the status of prairie dogs differs among species. The Utah prairie dog was federally listed as an endangered species in 1973 and then changed to threatened in 1983. A recovery plan that includes translocation of Utah prairie dogs from private to public lands is being implemented (US Fish and Wildlife Service 1991). The black-tailed prairie dog was petitioned for listing as threatened in 1998 (Van Putten and Miller 1999), and it currently stands as "warranted but precluded" (US Fish and Wildlife Service 2000) with management plans being crafted in most of the 11 states that include the historic range (van Pelt 1999, Luce 2001). The black-tailed prairie dog in Mexico and Canada is protected by special statutes. Neither the white-tailed prairie dog nor Gunnison's prairie dog are currently listed or under formal petition for listing. The Mexican prairie dog (*C. mexicanus*), which has a small range near Monterey, Mexico, is listed as endangered.

In the following section, we present data showing how plague has changed population dynamics of prairie dogs, focusing on white-tailed and black-tailed prairie dogs. We also discuss how declines of prairie dogs have affected other species in the same ecosystem, especially the black-footed ferret, which is federally listed as an endangered species.

Population Trends in Prairie Dogs with Plague

Plague was first recorded in prairie dogs during the expansion of the range of the disease in the 1930s and 1940s (Eskey and Haas 1940, Ecke and Johnson 1952, Cully and Williams 2001). Few data describing changes in colonies of Utah prairie dogs related to plague outbreaks are available, and we will not mention them further here. On the other hand, several studies have detailed the effects of plague on Gunnison's prairie dogs (Barnes 1982, Rayor 1985, Fitzgerald 1993, Cully and Williams 2001), which suffer high mortality, have colonies that may not recover to pre-plague abundance and have experienced range retraction from some isolated mountain valleys. For instance, Gunnison's prairie dogs were abundant at the northern edge of their range in the large high altitude valley called South Park, which surrounds the town of Fairplay, Colorado. Along with poisoning campaigns, a series of plague epizootics in South Park, beginning in 1945, led to the extinction of Gunnison's prairie dogs from that area by the mid 1960s (Ecke and Johnson

1952, Fitzgerald 1993). A similar history of population decline and range reduction occurred in the Moreno Valley of northern New Mexico in the 1980s and 1990s (Cully and Williams 2001).

Black-tailed prairie dogs still exist in most of what constituted their original range (Luce 2001), except for Arizona where they were extirpated in 1960 (van Pelt 1999). Long-term surveys of black-tailed prairie dog towns have been conducted, in which town sizes were measured as the area that remains active, determined by ground surveys, interpretation of aerial photography and geographic coordinates recorded from Global Positioning Satellites. The amount of active area indicates relative changes of population size within an area because black-tailed prairie dog towns expand at their edges, and recolonizing prairie dogs tend to aggregate in empty habitats (Cincotta et al. 1987). Plague has changed the population dynamics of black-tailed prairie dogs; die-offs of prairie dogs have been regularly reported since the first instances in Texas and Colorado in the late 1940s (Ecke and Johnson 1952; Barnes 1982, 1993; Cully and Williams 2001; Roach et al. 2001). By contrast, in places on the east side of the plague-free line, where suitable habitats still exist, prairie dog towns have remained stable or have increased. A good example is Wind Cave National Park, near Hot Springs, South Dakota, where surveys conducted since 1938 reveal that towns remained stable over long periods of time or rapidly expanded when control programs ended (Hoogland 1995; Muenchau, personal communication 2000).

A typical pattern in areas where plague is established is seen in Philips County, in north-central Montana (Figure 3), where the area of black-tailed prairie dog towns increased during the 1970s and 1980s. The Charles M. Russell National Wildlife Refuge (CMR) became a site for reintroduction of black-footed ferrets in 1994. At approximately the same time, a plague epizootic began to decimate prairie dog towns north of the ferret release area (Matchett, personal communication 2002), and interventions to protect and increase the prairie dog population on CMR included treating prairie dog burrows with insecticides to control fleas and translocation of prairie dogs (Figure 3). The active area of prairie dog towns has increased since the first epizootics in 1992, but the increase also occurred in parts of southern Phillips County besides CMR, making it difficult to conclude that insecticide treatment and prairie dog translocation caused the increases in prairie dog numbers. Black-tailed prairie dog towns in Phillips County continue to be affected by

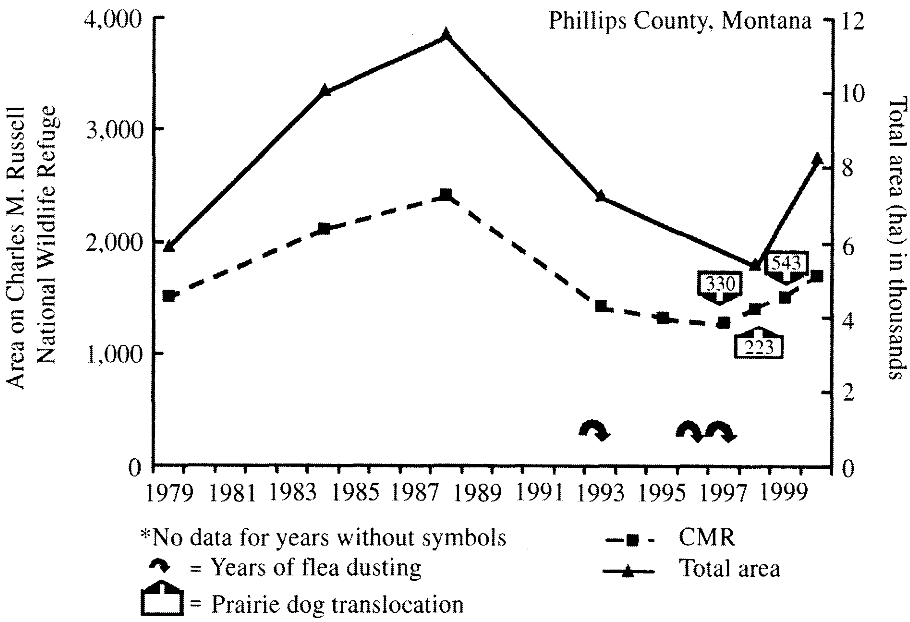

Figure 3. Area of active black-tailed prairie dog towns in southern Phillips County, Montana and the Charles M. Russell National Wildlife Refuge. Data compliments of Randy Matchett, US Fish and Wildlife Service, Lewiston, Montana.

plague, with die-offs noted during summer 2001 (Matchett, personal communication 2002).

Results from black-tailed prairie dog surveys conducted on the panhandle of Oklahoma (Lomolino and Smith 2001) show how these prairie dogs are affected by plague in the west and by habitat loss to the east of the plague line (Figure 4). In Oklahoma, in Beaver County, where plague has never been recorded and where intensive cultivation occurs, prairie dogs have steadily declined over the last 30 years. In the westernmost Cimarron and Texas Counties, plague epizootics beginning in the late 1940s have caused a steeper decline, especially in the 1990s. The plague has decreased overall population and reduced the sizes of prairie dog towns. The average size of towns in the non-plague is between 25 and 38 acres (10 and 15 ha) in the state and parts of the panhandle, where plague does not occur (Figure 4). On the other hand, in Cimarron County, where plague epizootics occurred regularly during the late 1990s (Cully and Williams 2001), average town size decreased from 90 acres (36 ha) to less than 38 acres (15 ha). The plague has shortened the time those

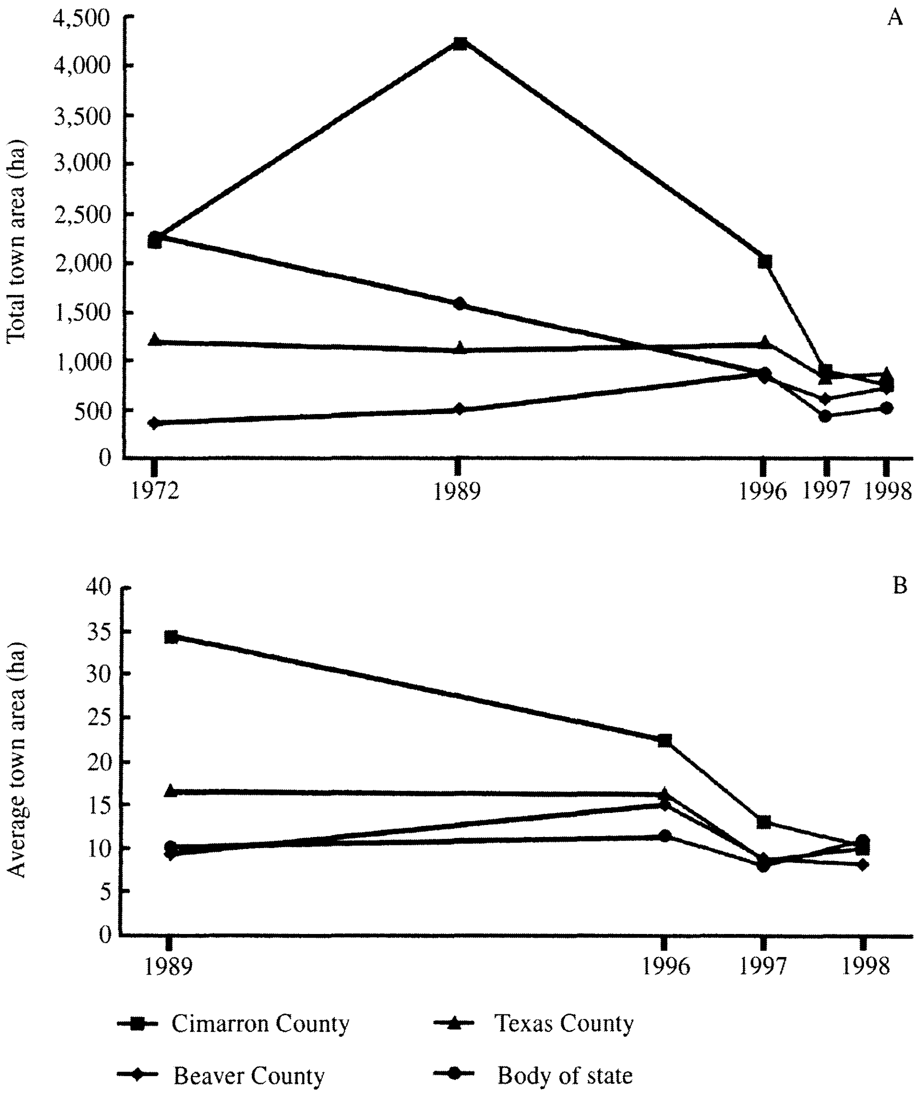

Figure 4. Area of active black tailed prairie dog towns in three western (panhandle) counties of Oklahoma, compared to towns on the remainder of the state. A. Total area of active prairie dog towns. B. Average area of individual towns. Data from Lomolino and Smith (2001).

black-tailed prairie dog towns persist, leading to population fragmentation similar to that in non-plague areas to the east, caused by cultivation of land for agriculture (Lomolino and Smith 2001).

The history of black-tailed prairie dog town occupancy on the Pawnee National Grassland (PNG) in north-central Colorado shows how much the population dynamics of these prairie dogs has changed. Sixty-two prairie dog towns have been regularly measured each year for the last 20 years. Although there was sporadic recreational shooting on the PNG during that time, there has been no poisoning of prairie dogs on the PNG since the 1960s. Overall, the areas occupied by prairie dogs increased over the 20 years (Figure 5), but most striking are the fluctuations in town size. The six representative towns graphed in figure 5 demonstrate the boom and bust cycles of town size, caused by exponential growth after recolonization, punctuated by plague epizootics. For instance, town 62 increased to approximately 100 acres (40 ha) in 1989, was struck by plague in 1990, and only now is it attaining its previous size. Town 66 increased to fill a quarter section (70 ha) in 1999, then it was decimated by plague. Other towns increased modestly before succumbing to plague in the early 1990s. The rapidity of deaths of black-tailed prairie dogs on the PNG suggests that plague is not only transmitted by fleas, but that direct transmission between prairie dogs during their various social encounters leads to deadly pneumonic plague. We have seen diseased prairie dogs on the PNG that showed classic signs of plague, including bloody froth emanating from the nasal passages (Savage and Antolin, personal communication 2000).

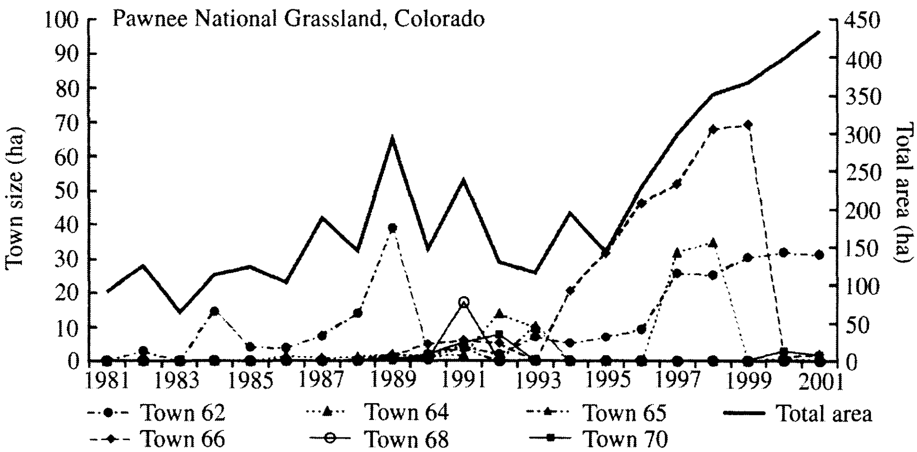

Figure 5. Area of active black tailed prairie dog towns on the Pawnee National Grassland in north-central Colorado, showing both the total area (dark line) and areas of six representative towns (broken lines). Data are from the Pawnee National Grassland, Greeley, Colorado and from Short Grass Steppe Long-term Ecological Research, Colorado State University, Fort Collins, Colorado

The overall persistence of black-tailed prairie dogs in northern Colorado, where die-offs were first reported in 1948 (Ecke and Johnson 1952), depends upon successful recolonization after local extinctions. This pattern was reported for the Cimarron National Grassland in southeastern Kansas (Cully and Williams 2001), and it may indicate a permanent change in population structure of black-tailed prairie dogs (Roach et al. 2001). A genetic study of the PNG population (Roach et al. 2001) showed that almost 40 percent of prairie dogs captured were either immigrants or the offspring of immigrants from towns other than where they were trapped. Dispersers between towns on the PNG likely moved along drainages that connect towns, and recolonization and dispersal was frequent enough to prevent great overall loss of genetic diversity. How this compares to genetic diversity on the east side of the plague line is the subject of an ongoing study (Savage and Antolin, personal communication 2002).

Populations of white-tailed prairie dogs can still be found in most parts of their historic range, but patterns of decline in white-tailed prairie dogs are different from those of black-tailed and Gunnison's prairie dogs. Long-term monitoring of white-tailed prairie dogs in Wyoming was carried out in conjunction with habitat assessment for recovery of black-footed ferrets, using methods described in Biggins et al. (1993). Plague was reported in Meeteetse in 1985 and Shirley Basin in 1987. In addition to experiencing epizootics that caused some local extinctions, overall population sizes of white-tailed prairie dogs have declined (Figure 6). However, even after plague epizootics subsided, densities of white-tailed prairie dogs have remained low. It should be noted that the low densities and diffuse burrow systems of white-tailed prairie dogs create a bias against detection of both local extinctions and recolonization after plague subsides. White-tailed prairie dogs may have fit the definition of epizootic amplifying hosts in the past when plague first spread into Wyoming in the 1930s, since they are highly susceptible and died in great numbers. The data suggest that white-tailed prairie dogs, which are the least social *Cynomys*, currently have a different relationship to plague than do other prairie dog species (Cully and Williams 2001). It is possible that plague in white-tailed prairie dogs is now maintained as an enzootic disease, primarily transmitted between individuals by fleas, and explosive die-offs seen in other ground squirrel and prairie dog species are prevented because low population density and fewer social contacts between individuals reduce transmission rates.

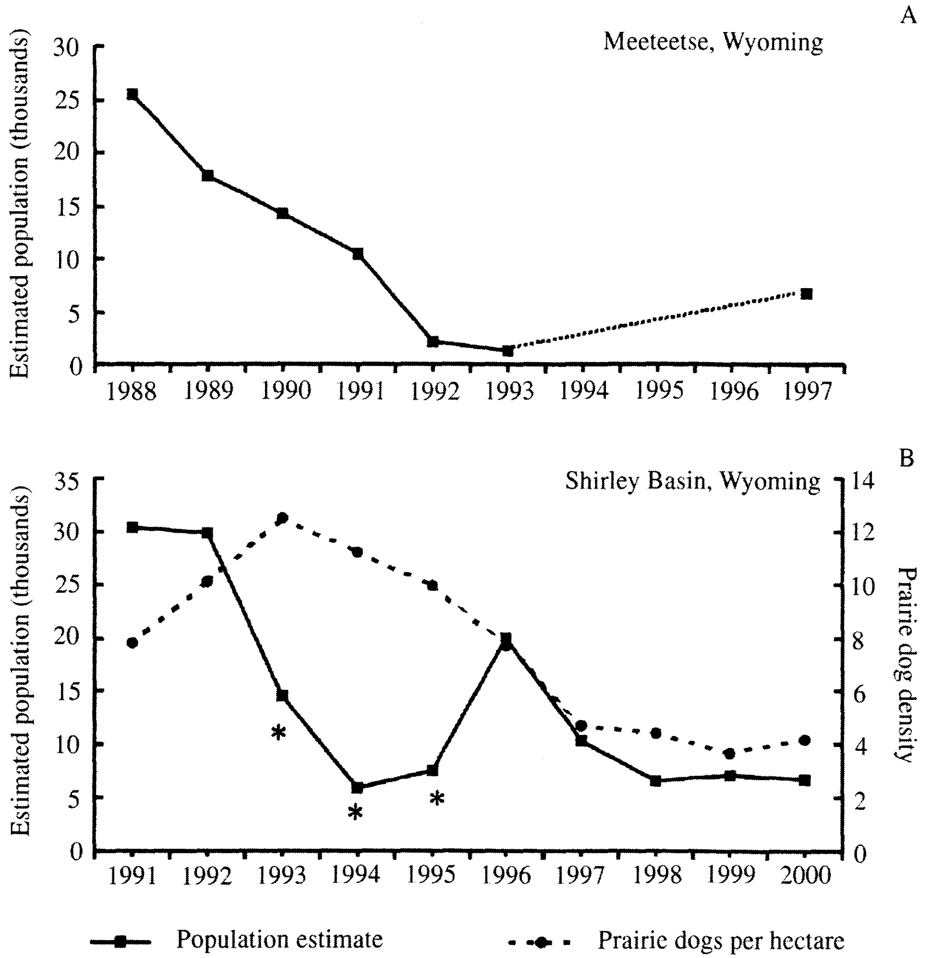

Figure 6. Population estimates of white-tailed prairie dogs. A. Meeteetse, data from Mid-Continent Ecological Sciences Center, United States Geological Service, Fort Collins, Colorado. B. Shirley Basin Primary Management Zone 1, data from Wyoming Game and Fish Department, Cheyenne, Wyoming. Fewer towns were sampled in 1993, 1994 and 1995 (marked with asterisks), so estimates of total population are artificially low for those years.

Effects of Prairie Dog Declines on Other Species

Plague's influence in western North America cascades through the ecological community that either associates with or directly depends on prairie dogs and the habitat they create. As mentioned, evidence of exposure to the disease at one time or another exists for every mammal species within the current distribution of plague (Barnes 1993). Unfortunately, we may never know how extensive plague's influence has been, as many wildlife species are not regularly monitored for disease, and data are lacking for comparisons of current abundance to that before plague was introduced. Much of the information needed to manage for biodiversity in the era of plague is not available, but we can assess how the relationship between prairie dogs and plague will influence some of the associates. The list of species that associate with black-tailed and white-tailed prairie dogs is quite extensive (Koford 1958, Campbell and Clark 1981, Miller et al. 1994, Hoogland 1995, Stapp 1998, Kotliar et al. 1999). They fall into every trophic level, from plants to scavengers to predators, and on a continuum from accidental to obligate (Kotliar et al. 1999). The majority of species sighted on prairie dog towns are simply associated; they may opportunistically use resources on prairie dog towns but are more abundant on other parts of the grasslands (Stapp 1998, Kotliar et al. 1999). Relatively few species are dependent on prairie dogs, meaning their abundance decreases in concert with decreases in prairie dog abundance.

The only vertebrate species that is known to be obligate on prairie dogs is the black-footed ferret, which will likely become extinct in the wild unless sufficient prairie dog habitats are conserved to support breeding populations (Kotliar et al. 1999). Plague has jeopardized release and recovery of black-footed ferret populations, with the exception of the program in central South Dakota, on the Buffalo Gap National Grassland and Badlands National Park, which lie to the east of the current distribution of plague. Loss of ferrets can be from lack of prey, but black-footed ferrets contract plague directly and die of the disease (Williams et al. 1994). For example, a plague outbreak on the Fort Belknap Tribal Lands, in September 1999, immediately followed the release of 33 ferrets on Peoples Creek, and, by mid-November, none of the ferrets could be found despite extensive searches (Vosburgh, personal communication 2002). Subsequent releases were diverted to Snake Butte. Plague epizootics during 2000 and 2001 on the Thunder Basin National Grassland, in eastern Wyoming, have curtailed plans for ferret releases on what were extensive black-tailed prairie dog towns. In white-tailed prairie dog habitats, the last remaining wild ferrets were removed from Meeteetse, Wyoming, in 1987, in the wake of outbreaks of both plague and canine distemper. Because of the decline of prairie dogs, this site was not considered for ferret releases from the captivebred population when the release program began in 1991. Releases in Shirley Basin, Wyoming, began in 1991, but were halted in 1995 after a series of plague epizootics began in 1992. This population of ferrets has persisted since that time.

Other dependent species, especially burrowing owls (*Athene cunicularia*), ferruginous hawks (*Buteo regalis*) and mountain plovers (*Charadrius montanus*), change in abundance as prairie dog towns expand or decline. Plague epizootics during the past 14 years on the Rocky Mountain Arsenal National Wildlife Refuge (RMA), near Denver, caused severe declines in black-tailed prairie dog populations, despite the use of insecticides to control fleas and the translocation of thousands of prairie dogs onto the site after each plague outbreak. The numbers of burrowing owls nesting on RMA tracked the fluctuations in prairie dog population size and town area (Figure 7). An extensive survey of burrowing owls on the 14 National Grasslands from Texas to North Dakota, in 1998, found burrowing owls on 307 of 444 (69 %) active black-tailed prairie dog towns, but only on 15 of 138 (11 %) towns that had experienced plague epizootics (Sidle et al. 2001). Similarly, on the RMA, the number of overwintering ferruginous hawks, but not red-tailed (*B. jamaicensis*) or rough-legged hawks (*B. lagopus*), correlated with the area of prairie dog towns (Seery and Matiatos 2000) (Figure 7). Finally, a detailed analysis of mountain plover populations, conducted from 1995 to 2000 in Phillips County, Montana, demonstrated that both recruitment of birds and population growth were related to the size of black-tailed prairie dog towns (Dinsmore 2001).

The Outlook for Management

If management of grassland and shrubland ecosystems is to be conducted on the level of landscapes, with conservation of both prairie dogs and their associated biodiversity as a goal, then spatial context of prairie dog towns must be taken into account. This is the basis of designating complexes of prairie dogs, where complexes comprise the towns lying within a polygon in which no town is more than 7 kilometers (4.4 mi.) from any one of the other towns. The rule is meant to include average distances that dispersing prairie dogs are likely to travel, but also refers to the longest nightly movements by black-footed ferrets at Meeteetse, Wyoming (Biggins et al. 1993, Luce 2001). With plague epizootics causing local extinctions of prairie dogs, management must account

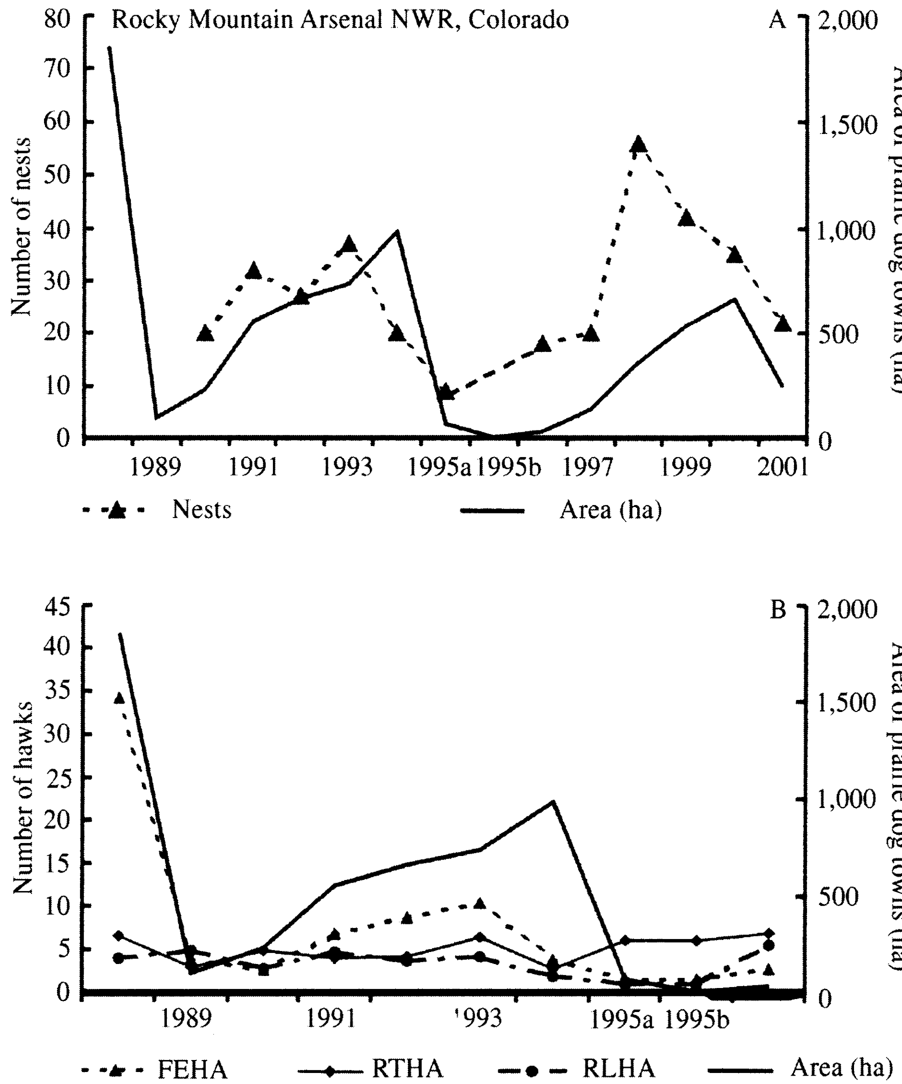

Figure 7. Relationships between black-tailed prairie dogs birds on RMA. A. Burrowing owls. B. hawks at the RMA near Denver, Colorado. FEHA = Ferruginous hawk (*Buteo regalis*), RTHA = Red-tailed hawk (*B. jamaicensis*), RLHA = Rough-legged hawk (*B. lagopus*). Burrowing owl data from the Rocky Mountain Arsenal National Wildlife Refuge, US Fish and Wildlife Service, Commerce City, Colorado.

for both the distances between towns that will allow recolonization and the landscape attributes that prairie dogs are likely to use for dispersal. Potential dispersal corridors, such as drainages, need to be maintained to ensure recolonization of unoccupied colonies and continuous dispersal among towns by prairie dogs (Roach et al. 2001). Additionally, we must have an understanding of the responses of other species to fluctuations in prairie dog numbers and whether their movements will allow recruitment to occupied towns when the towns they regularly use are lost in plague epizootics.

Unfortunately, plague makes management decisions less certain. It is possible that sylvatic plague outbreaks are more likely in large and dense prairie dog towns because greater densities provide more opportunities for the exchange of plague-infected fleas and increase the rate with which plague moves through towns (Barnes 1993, Cully and Williams 2001, Lomolino and Smith 2001). Further, predicting which towns will persist is difficult because we do not understand how plague moves from potential enzootic hosts near towns or how plague moves long distances between towns. Managing for uncertainty may mean expanding beyond the current concept of prairie dog complexes; in the wake of plague no large complex has recovered to numbers originally censussed (US Fish and Wildlife Service 2000). Successful management of biodiversity in the West will almost certainly have to include the large areas needed to assure long-term persistence of prairie dogs.

Management of prairie dogs to increase regional persistence, rather than on a town-by-town basis, will be difficult in the face of plague. Possible management interventions include use of insecticides to destroy fleas in burrows and on the animals themselves, translocation of prairie dogs back into decimated areas, and use of vaccines. However, interventions like these are intense and expensive, and they may not encompass an area large enough to control plague. One hope for management lies in the ability of mangers to break plague-amplifying epizootics in prairie dogs and ground squirrels. If the persistence of plague in the environment depends upon local amplification that increases the amount of plague cycling back to resistant enzootic hosts, then a program that includes monitoring and surveillance with local intervention when plague begins to increase may reduce plague to lower levels overall. This management scheme depends on the supposition that plague persists as a rare enzootic disease of reservoir rodents, and that plague surveillance can be aided by predictive models that include broad weather patterns, as is the case for human plague (Parmenter et al. 1999, Enscore et al. 2002). Understanding the dynamics of plague may be crucial not only for survival of prairie dogs, but for maintaining biodiversity and functioning of grassland ecosystems.

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