

EFFECTS OF COLONY CONNECTIVITY ON THE SPREAD OF SYLVATIC PLAGUE IN BLACK-TAILED PRAIRIE DOGS ACROSS THE GREAT PLAINS

By Tammi L. Johnson and Jack F. Cully, Jr.

*Abstract—Sylvatic plague (*Yersinia pestis*) causes mortality rates in black-tailed prairie dogs (*Cynomys ludovicianus*) that approach 100 percent and is the only known source of large die-offs in prairie dogs. We mapped black-tailed prairie dog colonies on five national grasslands with a history of plague in 1999, 2001, 2002, and 2003, to document colony changes related to plague. Records indicate widespread, nearly simultaneous, die-off of colonies on the Comanche and Thunder Basin National Grasslands in the presence of plague. Conversely, isolated colony die-offs observed on the Cimarron each year and a gradually spreading epizootic was identified on the Kiowa and Rita Blanca in 2004. Colonies on the national grasslands did not differ significantly in size or nearest neighbor distances. Colony complex connectivity and association of colonies with drainages differed significantly in all grasslands. Dry creek drainages, identified by Roach et al. (2001), as the most likely paths followed by dispersing prairie dogs, were more associated with colonies on the Comanche and Thunder Basin. We believe the association of colonies with dry creek drainages at Comanche and Thunder Basin may facilitate the inter-colony transmission of plague. Where the infected colony is not associated with drainages, plague is less likely to spread to neighboring colonies and is therefore expected to cause only local extirpation of colonies.*

INTRODUCTION

Black-tailed prairie dogs (*Cynomys ludovicianus*) were one of the most abundant mammal species occupying the mixed- and short-grass prairie at the beginning of the 20th century; however, over the past century, prairie dog populations have declined steadily. As a result of habitat loss caused by urban sprawl and agricultural conversion of grasslands, poisoning due to perceived conflicts with farmers and ranchers, and the occurrence of sylvatic plague (*Yersinia pestis*), prairie dogs now cover only about two percent of their historic range (Miller and Cully 2001). In 1998, the U.S. Fish and Wildlife Service was petitioned by the National Wildlife Federation to list the black-tailed prairie dog as threatened under the Endangered Species Act (Graber et al. 1998). The U.S. Fish and Wildlife Service has since declared the black-tailed prairie dog as a *candidate* species under the Endangered Species Act (USDI 2000), with the higher listing of threatened being precluded by species of higher conservation risk.

Tammi L. Johnson is a Masters Student in the Division of Biology at Kansas State University Manhattan, KS, 66506

Jack F. Cully, Jr., is Associate Professor and Assistant USGS Coop Unit Leader of the Division of Biology at Kansas State University
Manhattan, KS, 66506

Since the initial petition for listing, conservation efforts have increased dramatically in order to preclude the listing in the future. Eleven states, including Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming, have joined together to form an interstate prairie dog conservation group (Colorado and North Dakota subsequently withdrew to develop their own conservation plans). Because the black-tailed prairie dog is now a *candidate* species, yearly reviews are conducted to determine if the status should be

changed. Conservation efforts have reduced or eliminated recreational shooting and poisoning of prairie dogs on public land. At this time, the most severe threat to the persistence of black-tailed prairie dogs is sylvatic plague, caused by *Yersinia pestis*. Although conservation efforts have increased significantly over past years, sylvatic plague, which typically has a within colony mortality rate of >99 percent on black-tailed prairie dogs, cannot be controlled over large areas with currently available methods.

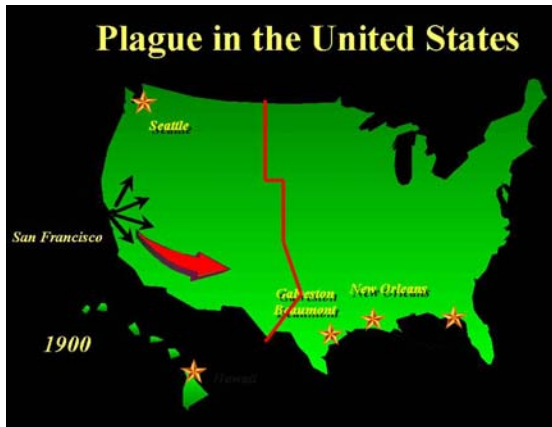


Figure 1. Plague in the United States
Plague entered the United States around 1900 in the San Francisco Bay area. Plague began a rapid eastward movement to approximately 102° longitude. Around 1950, plague reached the eastern boundary shown here.

Plague was introduced into the United States at the beginning of the 20th century in the San Francisco Bay area. The disease spread across the western U.S. to approximately 102° longitude, its current range, by about 1950 (Figure 1). Sylvatic plague has been found to affect >200 species of mammals worldwide (Poland and Barnes 1979), 78 of which are found in North America (Barnes 1982). The lack of control encountered when attempting to regulate and manage for plague is attributed, in part, to a lack of knowledge of the spatial and temporal dynamics of sylvatic plague in the black-tailed prairie dog environment and those environments closely related to black-tailed prairie dogs. Because prairie dogs are so susceptible to plague, mortality rates in colonies often approach 100 percent. They are conspicuous diurnal mammals, so that people often notice when a colony disappears. In this context, prairie dogs serve as public health sentinels to warn people when plague is present in an area.

“Because prairie dogs are so susceptible to plague, mortality rates in colonies often approach 100 percent. They are conspicuous diurnal mammals, so that people often notice when a colony disappears. In this context, prairie dogs serve as public health sentinels to warn people when plague is present in an area.”

All prairie dog species show some level of susceptibility to sylvatic plague (Barnes 1993). Previous research demonstrates that sylvatic plague is extremely devastating in Gunnison’s (Cully et al. 1997, Lechleitner et al. 1968, Rayor 1985) and black-tailed prairie dogs (Barnes 1982, 1993, Cully et al. 2000, Miles et al. 1952). Black-tailed prairie dogs are one of the most susceptible prairie dog species to sylvatic plague, with a population mortality response approaching 100 percent; white-tailed prairie dogs show lower population mortality (~85 percent) when exposed to plague. These differences in susceptibility may be attributed to differences in density and sociality among species. Black-tailed prairie dogs are the most social species of prairie dog. The high density of black-tailed

prairie dogs, combined with high sociality, leads to high contact rates and correspondingly high rates of plague transmission in this species. This social contact provides an easy route for plague to rapidly move across a colony in a short amount of time. The mechanisms responsible for inter-colony transmission of sylvatic plague are not well understood. Both intraspecific and interspecific transmission is thought to occur during the transmission of plague; however, it is difficult to assess the probability that intraspecific transmission is responsible for inter-colony transmission.

Our research seeks new information about the spatial patterns of plague on five national grasslands. Our goal is to identify the landscape-scale dynamics of plague in complexes of prairie dog colonies on these grasslands. To accomplish this, we map prairie dog colonies to identify die-offs that are indicative of plague; locations of newly established prairie dog colonies; and rates of population recovery following extirpation by plague. Plague was first documented on the Cimarron National Grasslands in 1945, and was subsequently confirmed in 1997 and 1999 (Cully et al. 2000, Cully unpublished records). Plague was confirmed on the Kiowa National Grassland in 2004 (Johnson and Cully unpublished records). Plague was documented on Thunder Basin National Grassland in 2001 (Mary Jennings, USFWS Wildlife Biologist, personal communication). Plague has not been positively documented on the Comanche National Grassland; however an extensive die-off of colonies, which is attributed to plague, occurred there in 1994 or 1995. Plague is the only disease known to cause extensive die-offs among prairie dogs (Barnes 1993), so extensive die-offs observed on these grasslands are assumed to be due to plague.

METHODS

Colony Mapping

Colonies were mapped between late May and early October 2001-2003 on the five national grasslands: Thunder Basin National Grassland, WY; Comanche National Grassland, CO; Cimarron National Grassland, KS; Kiowa National Grassland, NM; and Rita Blanca National Grassland, OK and TX. The Kiowa and Rita Blanca National Grasslands are jointly managed as a single grassland and were, therefore, combined for analysis in our study.

To map prairie dog colonies, we used a hand-held Trimble GeoExplorer3 GPS unit set to obtain positional readings every second. Colonies were accessed and traversed during mapping with an ATV. In order to show year-to-year changes in abundance of prairie dogs, only the active areas of each colony were mapped. Active areas of colonies were identified by examining the area for active digging near and on burrow mounds, the presence of fresh prairie dog scat, and clipped vegetation indicating foraging activity or the characteristic mowing of vegetation to enhance visibility on the colony.

We visited all previously recorded locations of prairie dogs on each grassland, many of which do not host prairie dogs at this time and appear to have been devoid of prairie dogs for some time. These areas, however, represent suitable habitat and are revisited each field season to see if they have been recolonized. These areas are placed in one of three categories: *historic colony*, which indicates a colony that is currently devoid of prairie dogs and shows little to no evidence of burrows; *old colony*, which indicates a colony where more than one half of the burrows are filled in and the colony probably has not been inhabited by prairie dogs for more than a year; or *inactive colony*, which represents a colony that has recently died out, but more than one half of the burrows are still useable.

Spatial Analysis

Files were downloaded from the GPS unit to a laptop computer using GPS Pathfinder Office. All files were differentially corrected using base-station files from the Bureau of Land Management base station in Casper, Wyoming, for colonies in the Thunder Basin, and files obtained from the U.S. Forest Service (USFS) base station in Elkhart, Kansas, for the Comanche, Cimarron, Kiowa and Rita

Blanca National Grasslands. The files were then exported to ESRI ArcView 3.2. Once in ArcView, files were combined by grassland and re-projected to NAD 1927, to be compatible with themes developed by the USFS.

Buffer analysis was completed by creating a buffer around each colony at 2, 4, 6, 8, and 10 km to assess the connectivity of colonies on each grassland. These buffers represent straight-line distances between colonies and do not account for any topographic features that may hinder or assist dispersing prairie dogs (i.e. land cover changes, slope). Movement is, therefore, assumed to be equally successful in any direction. Drainage analysis was completed using 1995 TIGER files. A theme-on-theme selection was performed to evaluate the association of individual colonies with these drainages. Colony association was calculated for colonies intersected by a drainage, and colonies within 250 and 500 m of a drainage.

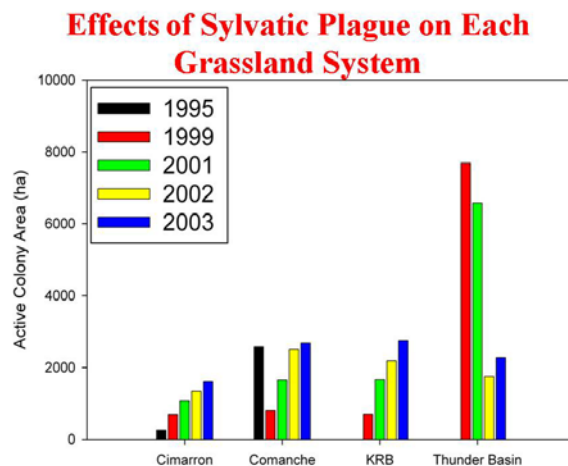
RESULTS

Colony Mapping

Active colony area on each of the four southern national grasslands exhibits steady annual increases (see Figure 2 below). The Thunder Basin National Grassland had an active colony area of 7,692 and 6,579 ha, respectively, for 1996/97 and 2001, which reflects the colony area present on the grasslands preceding the most recent plague epizootic. Despite an immense loss of active colony area following this epizootic, active colony area has increased ~30 percent annually in areas affected by plague. Active colony area on Thunder Basin National Grassland increased from 1,750 ha in 2002 to 2,321 ha in 2003, a 32 percent increase. Recolonization of the previously plagued out areas is occurring on the Thunder Basin. Newly discovered colonies as well as recolonized areas were mapped and contributed 380.19 ha of active area on Thunder Basin in 2003.

Figure 2. Effects of Sylvatic Plague on Each Grassland System

Active colony area has increased steadily each year. Mapping on the Thunder Basin National Grassland began in 2002, following the 2000 plague epizootic. The grassland staff provided area calculations for the Thunder Basin prior to 2002.



Colonies on the Comanche National Grassland have displayed continuous growth since the latest epizootic occurred in 1995. Colonies present prior to plague covered 2,574 ha (Ted Tooms, unpublished records). Post-plague colony areas in 1999, 2001, 2002, and 2003 on the Comanche National Grassland were 806; 1,649; 2,497; and 2,680 ha, respectively.

Evidence of plague was seen each year on the Cimarron National Grassland; however, only single or small groups of colonies die-off each year. These colony die-offs have not decreased total active colony area. In fact, increases are observed annually despite the presence of plague. Active colony areas on the Cimarron National Grassland in 1999, 2001, 2002, and 2003 were 687; 1,068; 1,344; and 1,622 ha, respectively.

Plague is currently active on the Rita Blanca National Grasslands. In 2002, five colonies were extirpated and an additional four colonies disappeared in 2003. During the spring of 2004, four more colonies disappeared. Much like we observed on the Cimarron, colony die-offs have not caused an overall decline in active colony area on these grasslands. Active colony areas on the Kiowa and Rita Blanca National Grasslands in 1999, 2001, 2002, and 2003 were 696; 1,663; 2,186; and 2,750 ha, respectively.

Colony Spatial Analyses

Buffer analysis of every colony in each grassland revealed that colonies on the Cimarron and Kiowa and Rita Blanca national grasslands exhibited connectivity at the shortest distances. The complex is fully linked with a maximum inter-colony distance of six kilometers. Colonies on the Comanche and Thunder Basin national grasslands exhibited similar connectivity at distances of eight and 10 kilometers, respectively.

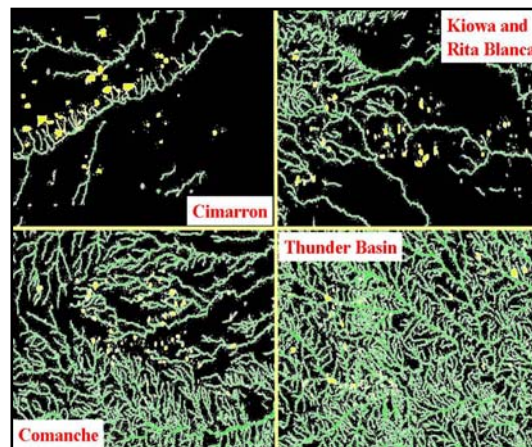


Figure 3.
Drainage Layer (Created w/ 1995 TIGER Files)
Drainages on the Comanche and Thunder Basin national grasslands are more abundant than those on the Cimarron and Kiowa and Rita Blanca. Drainages may facilitate the spread of sylvatic plague from colony to colony.

A superficial analysis of the drainage systems present on each of the five national grasslands illustrates considerable differences between grasslands (Figure 3 above). Drainage systems are much more abundant on the Thunder Basin and Comanche national grasslands than on the Cimarron and Kiowa and Rita Blanca national grasslands. Colony association with drainages was measured at three distances: 1) colonies intersected by drainages, 2) colonies within 250m of a drainage, and 3) colonies within 500m of a drainage (see Table 1 on next page). Colonies on the Thunder Basin and the Comanche national grasslands show a stronger association with drainages than colonies on the Cimarron and Kiowa and Rita Blanca national grasslands.

Table 1. Colony connectivity associated with drainages measured at three distances from the drainage. Colonies on the Thunder Basin and Comanche national grasslands are more closely associated with drainages than colonies on the Cimarron and Kiowa and Rita Blanca national grasslands.

Grassland	Intersect (% colonies)	250 m (% colonies)	500 m (% colonies)
Cimarron	2/56 4%	12/56 21%	21/56 38%
Kiowa and Rita Blanca	8/65 12%	13/65 20%	24/65 37%
Comanche	19/118 16%	50/118 42%	71/118 60%
Thunder Basin	35/142 25%	106/142 75%	130/142 92%

DISCUSSION

All five national grasslands have experienced or are currently experiencing plague epizootics; however, effects of plague on colony area varies between grasslands. Past evidence of plague epizootics has revealed a characteristic die-off pattern of affected colonies and neighboring colonies. Frequently, when a colony die-off is observed in response to a plague epizootic, extensive die-off of neighboring colonies is observed almost simultaneously (Cully et al. 1997, Cully and Williams 2001), leading to the near extirpation of entire colony complexes. This characteristic rapid and widespread colony die-off in response to plague was observed on both the Thunder Basin and Comanche national grasslands. Active colony area on the Thunder Basin National Grassland decreased from 7,692 ha to 1,750 ha following the 2000 plague epizootic. Active colony area on the Comanche National Grassland decreased from 2,574 ha in 1995, and had recovered to 540 ha when colonies were again mapped in 1999. Conversely, multiple colony die-offs have progressed more slowly on both the Cimarron and Kiowa and Rita Blanca national grasslands, where either single colony die-off occurs, as was seen on the Cimarron, or a slow progression to only a few neighboring colonies, as was seen on the Kiowa and Rita Blanca.

Evidence of plague, in the form of colony die-offs, was observed nearly every year on the Cimarron National Grassland; however die-offs rarely spread to neighboring colonies and the overall active colony area continued to increase. Colony mapping on the Kiowa and Rita Blanca during summer 2002 revealed the extirpation of five colonies. During summer 2003, an additional four colonies were extirpated nearby, within three kilometers (km) of the nearest 2002 extirpated colony. During spring 2004, three additional colonies, also within five km of previously extirpated colonies, were void of prairie dogs and we subsequently confirmed plague; however, overall active colony area continued to grow on the Cimarron and Kiowa and Rita Blanca national grasslands.

Analyses performed on the colony complexes for all grasslands produced some counter-intuitive results. The multiple buffer analyses confirmed that maximum inter-colony distances were shorter on the Cimarron and Kiowa and Rita Blanca than on the Comanche and Thunder Basin. This leads to the expectation that plague should spread more rapidly across the Cimarron and Kiowa and Rita Blanca. However, we did not observe this on these grasslands, but rather on the Comanche and Thunder Basin, where maximum inter-colony distances are longer. When the drainages were added to this analysis, many colonies on the Cimarron and Kiowa and Rita Blanca were far from drainages, whereas on the Comanche and Thunder Basin most colonies were associated with extensive networks of drainages. These drainages may function as corridors for the spread of prairie dogs carrying plague. In the absence of drainages, plague may be less likely to spread to neighboring colonies. This may explain the slow progression and isolated incidences of plague in the Cimarron and Kiowa and Rita Blanca.

Colonies mapped on the Comanche, Cimarron, Kiowa and Rita Blanca national grasslands in 2003 represents the largest area of active prairie dog colonies documented there. Given the current size and density of prairie dog colonies on the Comanche National Grassland, if plague is present in the enzootic host community at this grassland, we may see another outbreak in the near future, which could decimate much of the existing colony complex and return to conditions similar to those existing following the plague epizootic in 1995. If the transmission of plague from colony to colony is indeed being facilitated by the presence of dry creek drainages providing connectivity between colonies, we would expect to observe widespread effects of plague on the Comanche National Grassland. If colonies on the Cimarron and Kiowa and Rita Blanca continue to increase annually, colonies may grow close to one another, altering the spatial arrangement of colonies, which may function to increase the transmission rates between colonies, despite the absence of drainages. On the other hand, if as Alan Barnes has suggested (Barnes 1982) that plague is only present episodically on the eastern short-grass prairie, colonies may continue to grow until another wave of plague spreads to this region from the east slope of the Rocky Mountains. We cannot predict when that might occur.

The differing patterns of colony die-off, attributed to plague, in these five national grasslands demonstrate the complexity of the mechanisms influencing the spread of plague across a landscape. The lack of significant differences in mean-colony-size and nearest-neighbor-distances among grasslands indicates that these colony characteristics may have little impact on the spread of sylvatic plague. However, colony location on the landscape may influence the spread of plague. Roach et al. (2001) identified dry creek drainages as the most probable route used by dispersing black-tailed prairie dogs when moving to a new colony. Colonies on the Thunder Basin and Comanche national grasslands that show strong association with dry creek drainages may be more accessible to dispersing prairie dogs than those colonies on the Cimarron and Kiowa and Rita Blanca national grasslands that show less association with these drainages. Increased accessibility may indicate a higher probability of plague transmission by prairie dogs as well as a higher recolonization rate. Therefore, isolated colony die-off on the Cimarron National Grassland and the slow proliferation of colony die-off on the Kiowa and Rita Blanca may suggest that interspecific transmission, rather than intraspecific transmission of plague may be occurring on these grasslands. Additionally, recolonization of these colonies may not occur as fast as observed on the Comanche and Thunder Basin national grasslands.

It is important to continue monitoring these populations in order to begin to understand the large-scale dynamics of plague on the western Great Plains. Continued monitoring of these systems will provide valuable insight into the mechanisms that start plague epizootics in black-tailed prairie dogs. Recolonization of areas in Thunder Basin that were devastated by the recent plague epizootic provides valuable information on recolonization patterns and rates. Prairie dogs are extremely important to the prairie ecosystem and have been identified as a keystone species (Miller et al 1994, Kotliar et al.1999, Kretzer and Cully 2001). Numerous prairie-dwelling species depend on prairie dogs to provide shelter and as a food source. Some species such as the black-footed ferret (*Mustela nigripes*) feed exclusively on prairie dogs. Understanding the spread of plague will be beneficial to conservation planners as well as to the conservation efforts concerning the black-footed ferret. Additionally, documenting the spread of plague in areas that are undergoing epizootics, such as areas of the Rita Blanca National Grassland, provide new insight on how plague is maintained and spread among colonies in a prairie dog complex.

ACKNOWLEDGMENTS

We would like to thank Tim Byer, Thunder Basin National Grassland; Dave Augustine, Comanche and Cimarron National Grasslands; and Dan Garcia, Kiowa and Rita Blanca National Grasslands for contributing financial assistance. We thank Ted Tooms for contributing data from the Comanche National Grassland, and we would especially like to thank the private landowners surrounding the national grasslands for allowing us to cross their private land to access areas of the national grasslands.

Additionally, we would like to thank the National Science Foundation, Environmental Protection Agency, United States Geological Survey, and Kansas Department of Wildlife and Parks for funding assistance.

REFERENCES

- Barnes, A. M. 1982. Surveillance and control of bubonic plague in the United States. Symposium of the Zoological Society of London. 50:237-270.
- Barnes, A.M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp 28-37 in Oldemeyer et al. eds. Management of prairie dog complexes for the reintroduction of the black-footed ferret. US Fish and Wildlife Service, Biological Report 13.
- Cully, J. F., Jr., A. M. Barnes, T.J. Quan, and G. Maupin. 1997. Dynamics of plague in a Gunnison's prairie dog colony complex from New Mexico. *Journal of Wildlife Diseases*. 33: 706-719.
- Cully, J. F., Jr., L. G. Carter, and K. L. Gage. 2000. New records of sylvatic plague in Kansas. *Journal of Wildlife Diseases*. 36:389-392.
- Cully, J. F., Jr., E.S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. *Journal of Mammalogy*. 82(4):894-905.
- Graber, K., T. France, and S. Miller. 1998. Petition for rule listing the black-tailed prairie dog (*Cynomys ludovicianus*) as threatened throughout its range. [Http://www.nwf.org/nwf/grasslands/ptition1.html](http://www.nwf.org/nwf/grasslands/ptition1.html).
- Lechleitner, R. R., L. Kartman, M. I. Goldenberg, and B. W. Hudson. 1968. An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado. *Ecology*. 49:734-743.
- Kotliar, N. B., B. W. Baker, A. D. Whicker, G. Plumb. 1999. A critical review and assumptions about the prairie dog as a keystone species. *Environmental Management*. 24:177-192.
- Kretzer, J. E., and J. F. Cully, Jr. 2001. Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. *Southwestern Naturalist*. 46:171-177.
- Miles, V. I., M. J. Wilcomb, and J. V. Irons. 1952. Plague in Colorado and Texas. II. Texas. Rodent plague in Texas south plains. *Public Health Monographs*. 6:39-53.
- Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. *Conservation Biology*. 8:677-681.
- Miller, S. D. and J.F. Cully, Jr. 2001. Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy*. 82(4):889-893.
- Poland, L. D., and A. M. Barnes. 1979. Plague. In *CRC Handbook series in zoonoses, Section A: Bacterial, rickettsial, and mycotic diseases*. 1:515-556. Steele, J. F. (Ed.). Boca Raton, FL.: CRC Press.
- Rayor, L. S. 1985. Dynamics of a plague outbreak in Gunnison's prairie dog. *Journal of Mammalogy*. 66:194-196.
- Roach, J.L., P. Stapp, B. Van Horne, and M.F. Antolin. Genetic structure of a metapopulation of black-tailed prairie dogs. *Journal of Mammalogy*. 82(4):946-959.
- U.S.D.I. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants: Twelve-month finding for a petition to list the black-tailed prairie dog as threatened. *Federal Register*. 64:14424-14428.

