



Recovery of black-tailed prairie dog colonies following a sylvatic plague epizootic
by Jeffry Dwight Fennell

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish
and Wildlife Management

Montana State University

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Abstract:

Black-tailed prairie dogs suffered a 94-99% reduction in habitat during the twentieth century. In recent decades, the introduced pathogen responsible for sylvatic plague has led to local extirpation of prairie dog colonies, reduction in colony size, and increased isolation between surviving colonies.

Consequently, plague has become the biggest challenge to prairie dog conservation. For this study I estimated prairie dog densities on the Northern Cheyenne Indian Reservation following a sylvatic plague epizootic in the 1990s. I estimated densities using mark-recapture techniques and visual counting methods. I compared variations in densities based upon a colony's plague history and colony size. I hypothesized that densities would be higher on colonies that most recently experienced the plague. In 2000, prairie dog densities ranged between 11-91 prairie dogs/ha from 21 colonies. Densities ranged between 5-90 prairie dogs/ha from 23 colonies in 2001. Prairie dog density did not differ between years. There was no significant difference in densities based upon presence or absence of past plague or colony size. Colonies that had most recently recovered from a sylvatic plague had the highest densities. I also examined factors relating to a colony's probability of having had the plague, such as nearest neighbor distances, habitat between nearest neighbor, and distance to nearest road. I predicted that colonies would be more likely to contract plague if distances between neighboring colonies were small, the habitat between colonies facilitated dispersal, or colonies were on or near migration corridors. The distances to the nearest plagued colony and nearest non-plagued colony were the best predictors of a colony's probability of having experienced sylvatic plague. For those colonies that had sylvatic plague in the 1990s, distances to other colonies with plague were shorter ($x = 3.1$ km) than to colonies that did not experience plague ($x = 19.7$ km).

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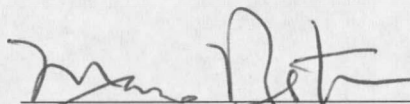
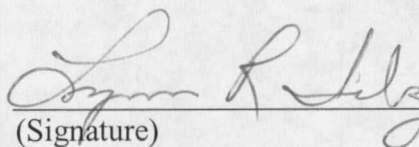
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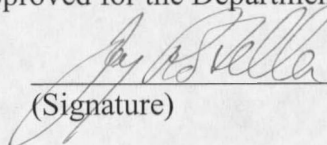
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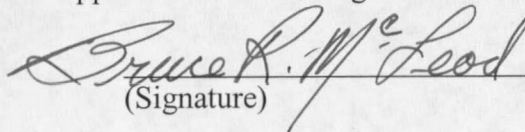
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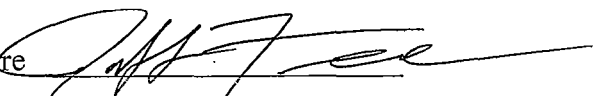
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ABSTRACT

Black-tailed prairie dogs suffered a 94-99% reduction in habitat during the twentieth century. In recent decades, the introduced pathogen responsible for sylvatic plague has led to local extirpation of prairie dog colonies, reduction in colony size, and increased isolation between surviving colonies. Consequently, plague has become the biggest challenge to prairie dog conservation. For this study I estimated prairie dog densities on the Northern Cheyenne Indian Reservation following a sylvatic plague epizootic in the 1990s. I estimated densities using mark-recapture techniques and visual counting methods. I compared variations in densities based upon a colony's plague history and colony size. I hypothesized that densities would be higher on colonies that most recently experienced the plague. In 2000, prairie dog densities ranged between 11 – 91 prairie dogs/ha from 21 colonies. Densities ranged between 5 – 90 prairie dogs/ha from 23 colonies in 2001. Prairie dog density did not differ between years. There was no significant difference in densities based upon presence or absence of past plague or colony size. Colonies that had most recently recovered from a sylvatic plague had the highest densities. I also examined factors relating to a colony's probability of having had the plague, such as nearest neighbor distances, habitat between nearest neighbor, and distance to nearest road. I predicted that colonies would be more likely to contract plague if distances between neighboring colonies were small, the habitat between colonies facilitated dispersal, or colonies were on or near migration corridors. The distances to the nearest plagued colony and nearest non-plagued colony were the best predictors of a colony's probability of having experienced sylvatic plague. For those colonies that had sylvatic plague in the 1990s, distances to other colonies with plague were shorter ($\bar{x} = 3.1$ km) than to colonies that did not experience plague ($\bar{x} = 19.7$ km).

INTRODUCTION

Prairie dogs (*Cynomys* spp.) affect a variety of ecosystem-level functions for nearly 120 vertebrate species (Miller et al. 1994, Kotliar et al. 1999). For example, prairie dogs serve as prey for such predators as the endangered black-footed ferret (*Mustela nigripes*) and golden eagle (*Aquila chrysaetos*). Their burrows provide nesting sites for the declining populations of burrowing owls (*Athene cunicularia*). Grazing by prairie dogs alters the plant community composition and creates open habitats within the prairie grasslands (Whicker and Detling 1988, Kotliar et al. 1999). Many types of avifauna, including the endangered mountain plover (*Charadrius montanus*), utilize these open areas.

Black-tailed prairie dog (*C. ludovicianus*) numbers began to decline as Europeans colonized the North American plains. Prairie dog habitat became fragmented as native grasslands were converted into pasture and agricultural fields (Hoogland 1995). Widespread poisoning campaigns further reduced prairie dog populations (Anderson et al. 1986, Cully and Williams 2001). Coupled with recurring sylvatic plague (*Yersinia pestis*) epizootics, black-tailed prairie dogs, along with the other 4 species of prairie dogs, continued to suffer population reductions during the past two decades (U. S. Department of the Interior 2000). Currently, the Mexican prairie dog (*C. mexicanus*) is listed as an endangered species while the Utah prairie dog (*C. parvidens*) is listed as a threatened species. Since European colonization, occupied prairie dog habitat has been reduced by 94-99% (U. S. Department of the Interior 2000, Roach et al. 2001).

Reductions in black-tailed prairie dog abundance prompted the National Wildlife Federation to file a petition with the United States Fish and Wildlife Service, requesting protection of the black-tailed prairie dog under the Endangered Species Act of 1973 (U.S. Department of Interior 2000). In 2000, the United States Fish and Wildlife Service determined that protection as a threatened species is warranted (U.S. Department of Interior 2000). However, listing of the species was precluded due to limited funds and the existence of higher priority species (U.S. Department of Interior 2000). This decision has allowed the 10 states with black-tailed prairie dog populations the opportunity to develop and implement management plans to avert federal listing.

Sylvatic plague, an introduced bacterial infection native to central Asia, has become the biggest challenge to prairie dog conservation (U.S. Department of Interior 2000, Cully and Williams 2001). To be effective, prairie dog management plans must cope with the unpredictability of sylvatic plague epizootics and the devastating effects that follow. Sylvatic plague is transmitted between mammals by a variety of flea species (Cully and Williams 2001). Although many North American mammals show some degree of resistance to the disease, mortality rates of infected black-tailed prairie dogs often exceeds 95% (Cully 1989). Sylvatic plague is able to spread quickly and thoroughly through black-tailed prairie dog colonies (Cully 1989). Plague epizootics often lead to local extirpation of prairie dog colonies, reduction in colony size, and increased isolation between surviving colonies (Cully and Williams 2001). Within such a highly fragmented landscape, isolated colonies that may become extirpated due to sylvatic plague stand little chance of natural recolonization.

In Montana, plague-infected fleas were found on black-tailed prairie dogs by the 1940s (U. S. Department of the Interior 2000). Possible epizootics in Montana occurred during the 1930s and 1970s, with documented epizootics taking place in the late 1980s and early 1990s (Restani et al. 2001, C. Knowles, FaunaWest, personal communication). Presently a plague epizootic is occurring on the Fort Belknap Indian Reservation and neighboring south Phillips County (M. Restani, personal communication). The Northern Cheyenne Indian Reservation, in southeastern Montana, experienced a plague epizootic from 1991 - 1996, which resulted in a large reduction in size of most prairie dog colonies.

The goal of this study was to measure the recovery of black-tailed prairie dog colonies following a sylvatic plague epizootic on the Northern Cheyenne Indian Reservation. Specific objectives were to estimate density of prairie dogs on a number of colonies that have had different recovery times since the epizootic. I examined several factors such as colony spacing, colony size, and plague history, which may be affecting variations in colony density. I hypothesized that densities of prairie dogs would be higher on colonies that are recovering from the plague, compared to colonies that escaped the plague. In addition, I also examined factors that may explain why some colonies contracted sylvatic plague when others did not. If plague was transmitted by movement of infected fleas from one colony to another via prairie dogs or other mammalian species, factors such as distance to nearest neighbors, the type of habitat between neighbors, or the existence of migration corridors between colonies would be related to the probability of a colony contracting sylvatic plague. I predicted that colonies would be more likely to

contract plague if distances between neighboring colonies were small, the habitat between colonies facilitated dispersal, or colonies were on or near migration corridors.

STUDY AREA

I conducted fieldwork in the Tongue River drainage of the Northern Cheyenne Indian Reservation in southeastern Montana ($45^{\circ}32'N$, $106^{\circ}25'W$). Forested hills confined the prairie dog colonies to the eastern half of the reservation. Vegetation on the study area was consistent with the native big sagebrush-wheatgrass plains community typical in this region of the Northern Great Plains (Johnson and Larson 1999). Several intermittent streams flowed eastward across the study area into the Tongue River. This study involved only those colonies located on tribally controlled lands, which included most of the prairie dog colonies in the area. The landscape was divided into grazing units, which were used on a rotational basis by horses and cattle. I seldom saw livestock on the prairie dog colonies included in this study.

During 2000 and 2001 all colonies were open to recreational shooting year-round by tribal members. During the course of the study, evidence of shooting was found on several colonies, but only 3 groups of shooters were actually observed. However, I found only 1 prairie dog shot in two years and <15 skeletal remains from the study colonies. In regions of the state with higher shooting pressures, dead prairie dogs were much more common, and skeletal remains more abundant than found on the study area (personal observation). Thus, I believe that the shooting pressure was insignificant as compared to other regions of the state.

The Bureau of Indian Affairs mapped prairie dog colonies on the Northern Cheyenne Reservation in 1989 and 1990 by hand-plotting colonies onto USGS 7.5 minute quadrangle maps. Each year, from 1994 – 2001, mapping personnel used a global

positioning system (GPS) to estimate the size of prairie dog colonies. Mapping of colonies took place during the summer months over a two-week period. For mapping purposes, an individual colony was defined as a continuous area of occupied burrows (those burrows with prairie dogs and/or fresh droppings, Biggins et al. 1993) in a matrix of clipped vegetation. Colony boundaries were assumed to be at the approximate margin between clipped vegetation and non-clipped vegetation.

Before 1991, the reservation had approximately 3000 - 4000 ha of active prairie dog colonies. Since the mapping techniques used in 1989 and 1990 were less accurate than in later years, I used the average estimate from these two years as an estimate of the area of prairie dog colonies present (Fig. 1). Most of the occupied area was contained in a few large colonies that were evenly distributed across the eastern half of the reservation. In 1991 sylvatic plague was detected on the northern prairie dog colonies (P. Young, University of Arizona, personal communication). From 1991 - 1996, the disease spread south, infecting nearly every colony. By 1995, the reservation's prairie dog colonies had undergone a large reduction in area and had become fragmented into smaller colonies. In that year, prairie dog colonies covered only 151 ha (Fig. 1). By 2000, many of the northern colonies had recovered in size ($\bar{x}$ = 12.9 ha, SD = 22.8, n = 76), while the southern colonies remained relatively small ($\bar{x}$ = 4.2 ha, SD = 4.9, n = 33) and isolated. In 2000, the reservation had approximately 109 prairie dog colonies, totaling 834 ha (Fig.1). Colonies ranged in size from <1 to 134 ha ($\bar{x}$ = 10.3 ha, SD = 19.6, n = 109).

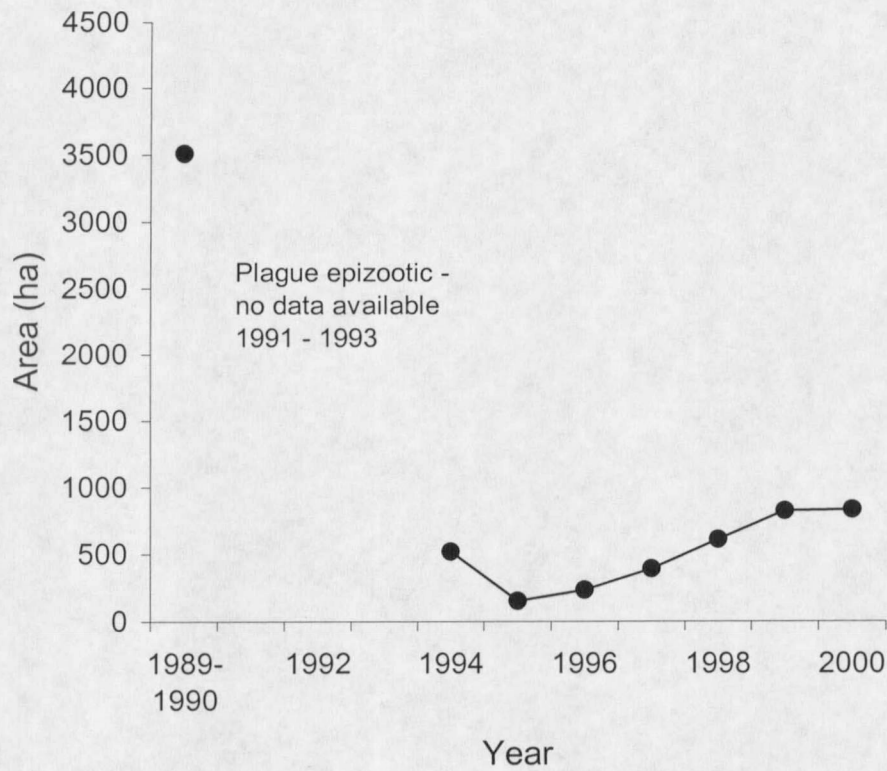


Figure. 1. Total area (in hectares) of the Northern Cheyenne Indian Reservation occupied by prairie dogs, based on Bureau of Indian Affairs mapping data. The 1989 - 1990 value is an average from the two years. Sylvatic plague moved across the reservation from 1991 to 1996.

METHODS

I designed this study to compare colony densities based on if they contracted sylvatic plague in the 1990s. Of the 109 active colonies present in 2000, 8 had not undergone a significant reduction in population size during the 1991 – 1996 plague epizootic, indicating that they had not been affected by plague (Cully 1997). I wanted to include as many of the plague-free colonies in the study as possible. In 2000, 3 of the 8 plague-free colonies were grazed by cattle or bison (*Bison bison*). However, only 2 of these colonies had livestock present in 2001. The colonies with livestock were not included in the study, as the livestock would interfere with the mark-recapture methods. The remaining colonies (5 in 2000 and 6 in 2001) with no plague history were included in the sample. Next, I randomly selected colonies from the 101 colonies with plague history. I was able to include 11 colonies exposed to past plague in 2000, and 13 colonies exposed to past plague in 2001. The length of the field season limited the number of colonies selected for the study. I selected these colonies from a set of predetermined colonies suitable for the study. Colonies needed to be of sufficient size and shape to contain the sample plots. The colonies selected ranged from 2 - 134 ha. To estimate prairie dog density, Severson and Plumb (1998) recommend that sample plots be ≥ 4 ha. However, the uneven terrain and irregular shape of the colonies on the Northern Cheyenne Indian Reservation made sample plots of this size impractical. Therefore I reduced the size of sample plots to 0.5 - 1.6 ha. Plots were square to rectangular and marked with wooden stakes.

In 2000 and 2001 I began trapping prairie dogs in early June and finished by early July. I confined trapping to a 1-month period to meet the population closure assumption required for mark-recapture techniques. Therefore, I selected only 12 colonies for trapping in 2000. I trapped at 5 colonies with no plague history and 7 colonies with plague history. Increased manpower allowed me to trap at an additional 3 colonies in 2001.

I followed the sampling guidelines provided by Severson and Plumb (1998). Twenty-five traps (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) were placed near active burrows within a given sample plot. I arranged traps to avoid clustering them near the study plot boundaries. Traps were baited daily with dry oats and locked open for 2 to 3 days prior to trapping to allow prairie dogs to become accustomed to the traps. Following the acclimation period, each sample plot was trapped for 3 consecutive warm, sunny days, to ensure maximum prairie dog activity (Hoogland 1995). Traps were baited by 0700 hrs and remained open for a minimum of 4 hours each day. I rotated the order each colony was visited during the trapping period so that the time traps remained open for each colony varied by 4 – 8 hours. I marked captured prairie dogs with a numbered, self-piercing fingerling ear tag (National Band and Tag, Newport, Kentucky, USA). The identification number of recaptured animals was recorded. For those colonies on which prairie dogs were also counted from a distance (see below), I painted the captured prairie dogs with black fur dye (Vosburgh and Irby 1998). This allowed me to determine how far marked prairie dogs moved from the sample plot during the visual counts.

I used program CAPTURE (Rexstad and Burnham 1991) to convert mark-recapture data into population estimates. I then calculated density estimates by dividing the population estimates by the area of each sample plot. Due to the relatively small sample sizes from each colony, I was unable to calculate more than one capture/recapture probability, so I therefore used the null model of program CAPTURE rather than more complex models with multiple capture and recapture probabilities.

Once trapping was finished in early July of both years, I began visual counts of prairie dogs on study plots to obtain another index of prairie dog density (Menkens and Anderson 1993). I was unable to perform the counting procedure on colonies that escaped the plague due to the uneven terrain, surrounding forests, and/or presence of cattle. In 2000, 11 sample plots were counted, 2 of which had also been trapped. Increased manpower in 2001 allowed me to count 13 sample plots, 5 of which had also been trapped. All sample plots were visible to observers at distances of 120 – 270m. Human presence at these distances did not disturb the prairie dogs (Vosburgh and Irby 1998). I counted prairie dogs from a vehicle using a 15-power spotting scope.

Counts were conducted on clear days between dawn and 1000 hrs or 1800 and sunset, peak activity hours for prairie dogs (Hoogland 1995). For each colony, I performed a total of 9 counts over a 3-day period. I conducted counts at approximately the same time of day for each counting day. Each day, I conducted three separate counts, each lasting approximately 10 minutes, at 30-minute intervals. I divided the maximum number counted by the sample plot area to obtain a density estimate (Severson and Plumb 1998).

To increase the number of density estimates for statistical tests, I combined density estimates obtained from the mark-recaptures and the maximum counts, to arrive at density estimates for 21 colonies in 2000, and 23 colonies in 2001. I performed a linear regression to test the correlation between the mark-recapture density estimates and the maximum count density estimates. Furthermore, to ensure that the colony densities did not differ between the two methods, I tested for differences in densities for colonies measured with both methods, using a 2-sample t test (Freund and Simon 1997). With the combined set of colony densities, I used the same 2-sample t test to check for density differences due to the presence or absence of past plague, and for differences between years. I used linear regression to test for density differences due to colony size.

Sylvatic plague moved across the reservation from north to south. From the 9 years of mapping data, I was able to determine the order in which plague infected sets of neighboring colonies based upon when the colonies decreased in size. From these data I established 5 colony groupings, based upon natural landscape features that divided the groups, as well as the length of time since the colonies became infected with the plague. For the first 4 groupings, I divided the reservation horizontally into fourths. The first group, group number (1), was the southernmost group that had the shortest length of time to recover from the plague. The last plague-positive fleas from the reservation were detected from these colonies in 1996 (P. Youngs, The University of Arizona, personal communication). Next, moving north came (2) the south-central group, where colonies had been reduced in size by 1995. A small hill, historically devoid of prairie dogs, divided this group from group number (3), the north-central group. Group number (4),

the northernmost group, was the first to contract the plague, and therefore had the longest time to recover. This group was separated from group number (3) by a large stream drainage, historically vacant of prairie dogs. The last group of colonies, group number (5), contained all the westernmost colonies that did not experience sylvatic plague. I tested the impact of this timing on colony density since the plague epizootic using a 1-way analysis of variance (ANOVA).

I used the mapping data to examine the spatial arrangement of study colonies, because distances between colonies can affect the probability of a colony contracting sylvatic plague (Cully and Williams 2001). For all colonies included in this study, I measured the distances, using the 2000 mapping data, to the nearest neighboring colony with plague and nearest neighboring colony without plague. I measured the minimum distance between the nearest edges of the 2 colonies. The shorter of these two distances was used as the nearest neighbor distance. I also classified the habitat type between nearest neighboring colonies. I created 3 habitat classes, and ordered them based on the degree to which I presumed small mammals carrying infected fleas would be able to penetrate. The three categories were (1) sagebrush/grassland prairie, (2) forest, and (3) forested hills. Knowles (1985) suggested that dispersing prairie dogs will utilize roads. Therefore, for each colony I also determined the distance to the nearest road. For each of these 5 variables I performed 2-sample *t* tests to test for significant relationships between these variables and the presence/absence of past exposure to plague.

RESULTS

Density Estimates

I used mark-recaptures and maximum counts to calculate density estimates for 21 colonies in 2000 and 23 in 2001. I captured and marked 252 prairie dogs from 12 colonies in 2000 and 289 prairie dogs from 15 colonies in 2001. Between 7 - 36 prairie dogs were captured per study plot in 2000 ($\bar{x} = 20$, $SD = 8.3$, $n = 12$) and 10 - 33 in 2001 ($\bar{x} = 19$, $SD = 6.5$, $n = 15$; Table 1). Density estimates derived using mark-recapture techniques ranged from 14 - 83 prairie dogs/ha in 2000 ($\bar{x} = 34$, $SD = 21.3$, $n = 12$), and 11 - 67 prairie dogs/ha in 2001 ($\bar{x} = 29$, $SD = 19.2$, $n = 15$; Table 1).

Following the trapping period in both years, I performed the counts of prairie dogs on sample plots. All colonies that were counted had past plague history. I counted 16 - 68 prairie dogs per sample plot ($\bar{x} = 30$, $SD = 18.4$, $n = 11$) from 11 colonies in 2000. In 2001, I counted 8 - 48 prairie dogs per sample plot from 13 colonies ($\bar{x} = 26$, $SD = 12.6$, $n = 13$). Converting these maximum counts into density estimates resulted in densities ranging from 11 - 91 prairie dogs/ha in 2000 ($\bar{x} = 33$, $SD = 23.7$, $n = 11$), and from 5 - 90 prairie dogs/ha in 2001 ($\bar{x} = 30$, $SD = 23.6$, $n = 13$; Table 2).

Table 1. Size of black-tailed prairie dog colonies in 2000 and of mark-recapture sample plots for colonies on the Northern Cheyenne Indian Reservation. Density estimates and confidence intervals from program CAPTURE.

Colony	Colony Area (ha)	Sample Plot Size (ha)	2000			2001		
			Number Marked	Density	95% CI	Number Marked	Density	95% CI
				Estimate (no./ha)			Estimate (no./ha)	
Without Plague								
Ash Creek	6.2	0.90	13	22	17-49	11	16	13-30
Buffalo Pasture	10.0	1.00	36	63	47-104	30	54	39-94
Logging Creek 1	21.7	1.50	21	19	16-31	21	27	18-55
Logging Creek 2	11.2	0.75	25	53	40-91	19	27	27-36
Soldiers Gulch	8.1	1.30	25	31	23-52	10	15	9-46
White Buffalo ^a	13.3	1.10	--	--	--	14	21	15-45
With Plague								
Ashland Flats ^a	29.1	0.40	--	--	--	17	53	45-85
Lake Creek 1	120.4	1.56	15	27	14-85	18	13	12-21
Logging Creek 4	133.9	1.25	10	20	10-84	14	14	12-27
Logging Creek 6	30.3	1.25	7	14	7-57	23	22	20-32
North Kelty Creek 3	10.5	1.50	27	36	25-71	16	11	11-15
South Logging Creek	22.1	0.38	23	83	69-131	24	67	67-85
Stebbins Creek 4	7.6	1.60	19	17	14-31	17	16	13-29
Tie Creek1 ^b	2.4	0.75	--	--	--	33	59	49-84
Two Feather 2	44.5	1.00	13	25	16-71	22	17	14-29

^a Presence of cattle in 2000 prevented trapping in that year.

^b Trapped in 2001 to confirm unusually high counting estimate from 2000.

Table 2. Size of black-tailed prairie dog colonies in 2000 and of maximum count sample plots for colonies on the Northern Cheyenne Indian Reservation. All colonies below had sylvatic plague in the 1990s.

Colony	Colony Area (ha)	Sample Plot Size (ha)	2000				2001			
			$\bar{x}$	Maximum Number Counted	Sample Variance	Density Estimate (no./ha)	$\bar{x}$	Maximum Number Counted	Sample Variance	Density Estimate (no./ha)
Cow Creek 2	20.0	0.50	10	18	27	36	10	12	4	24
Kelty Creek 1	8.1	1.25	14	17	14	14	15	20	15	16
Lake Creek 2	26.7	0.75	11	17	17	23	23	31	12	41
Logging Creek 6 ^a	30.3	0.94	12	16	10	17	17	29	62	31
North Kelty Creek 1	10.2	0.75	17	23	23	31	8	11	10	15
North Kelty Creek 3 ^a	10.5	1.50	46	53	35	35	7	17	27	11
Reservation Creek 2	8.7	0.94	19	24	16	26	21	28	29	30
Stebbins Creek 3	49.0	1.50	11	17	9	11	6	8	3	5
Stebbins Creek 4 ^{a,b}	7.6	1.60	--	--	--	--	27	34	18	21
Tie Creek 1 ^a	2.4	0.75	59	68	45	91	40	48	55	64
Tie Creek 3	2.2	0.50	29	31	4	62	35	45	110	90
Two Feather 2 ^a	44.5	1.88	--	--	--	--	29	32	8	17
Two Feather 4	26.1	0.94	13	20	13	21	15	19	8	20

^a Colonies that were both trapped and counted.

^b Counts not performed in 2000.

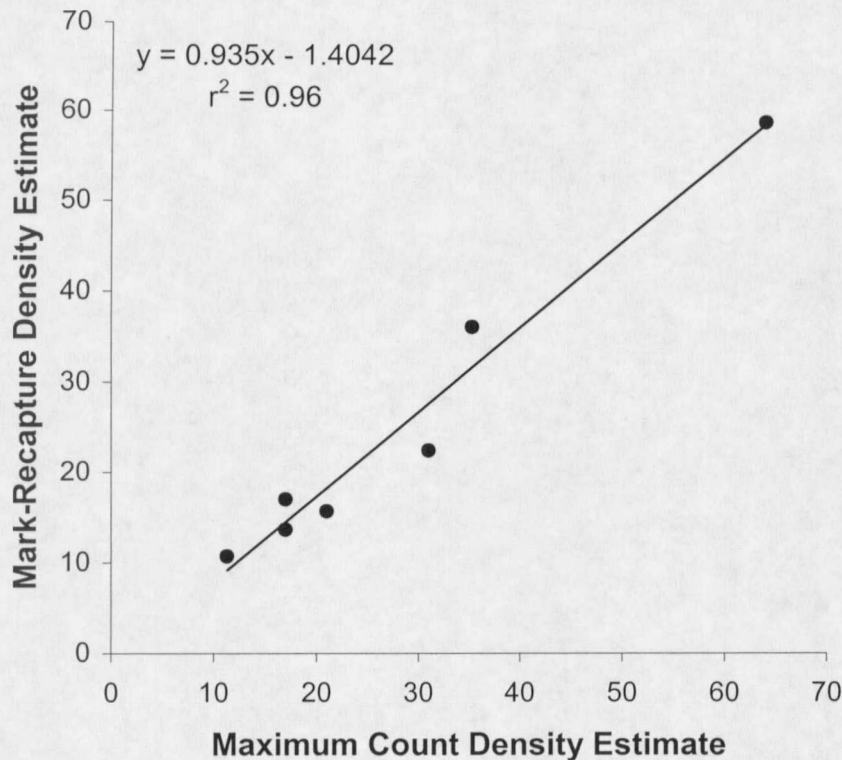


Figure. 2. Relationship between black-tail prairie dog density estimates using maximum count data and mark-recapture techniques on the Northern Cheyenne Indian Reservation during 2000 and 2001.

Seven colonies had both mark-recapture density estimates and maximum count density estimates, so I correlated the 2 density estimators. I found a very strong correlation between the mark-recapture density estimates and maximum count density estimates ($r = 0.98$, $P < 0.001$, $df = 6$; Fig. 2). Therefore, I used the maximum number counted/ha as the density estimate for the prairie dog colonies (Table 2). I next compared all the maximum count density estimates with the set of mark-recapture density estimates from colonies with past plague histories. There was no significant difference in either year (2000: $t = 0.5$, $P = 0.61$, $df = 15$; 2001: $t = 0.4$, $P = 0.72$, $df = 11$). I, therefore, combined the mark-recapture density estimates and maximum count density estimates for

each year. I had densities estimates for a total of 21 colonies in 2000 and 23 colonies in 2001. In the combined set, I used the mark-recapture density estimates for those 7 colonies that had both estimation techniques performed.

Variations in Density

The mark-recapture density estimates varied among colonies (Fig. 3). To compare the variation in the maximum count density estimates, I used the mean number of prairie dogs counted/ha, rather than the maximum number counted/ha, in order to calculate more easily confidence intervals. It was apparent that densities also varied among colonies in which I estimated density based on maximum counts of prairie dogs (Fig. 4). I used a 2-sample t test to determine if past plague history or colony size could explain differences in density. Past exposure to plague did not explain differences in prairie dog density (2000: $t = 0.73$, $P = 0.49$, $df = 8$; 2001: $t = -0.14$, $P = 0.89$, $df = 14$). In addition, the variation in density could not be explained by the size of the colony, based upon 1999 mapping data (2000: $F = 1.71$, $P = 0.21$, $df = 20$; 2001: $F = 2.28$, $P = 1.46$, $df = 22$).

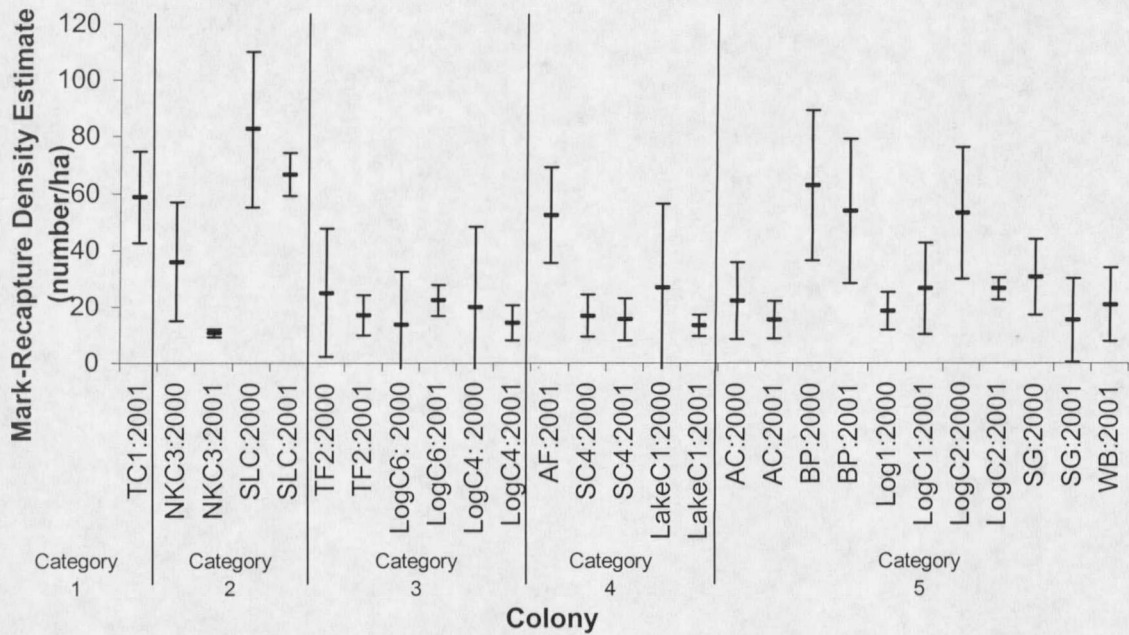


Figure 3. Mark-recapture density estimates (number/ha) and 95% confidence interval of black-tailed prairie dog colonies on the Northern Cheyenne Indian Reservation in 2000 and 2001. Divisions correspond to colony categories, relating to the time since sylvatic plague infection. Category 1 colonies were infected with sylvatic plague by 1996 while category 4 colonies were infected in 1991. Category 5 colonies were not exposed to plague.

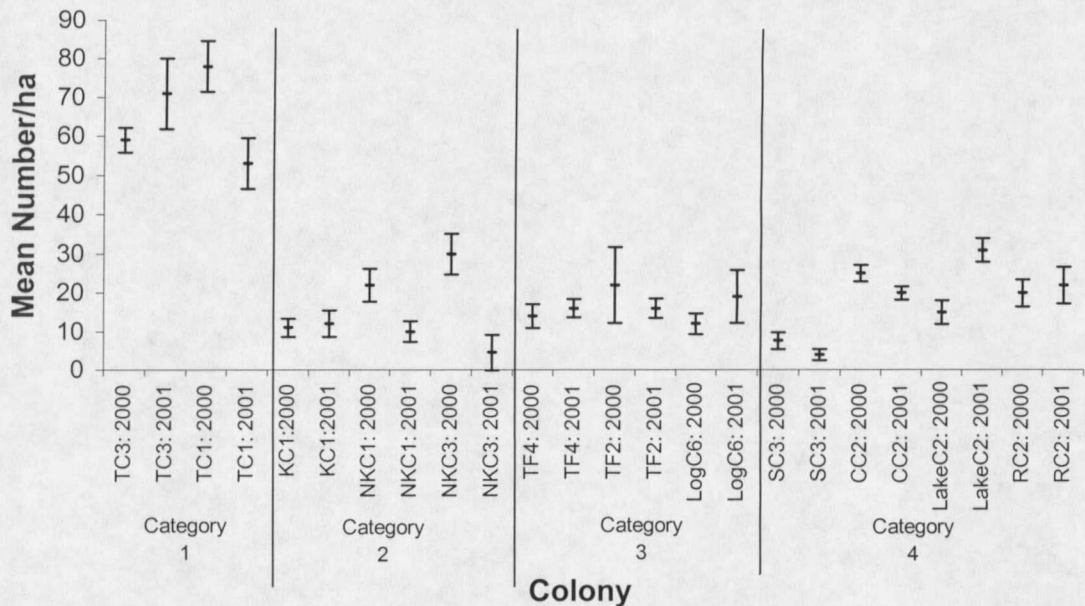


Figure 4. Mean number of black-tailed prairie dogs counted (mean number/ha) and 95% confidence interval on the Northern Cheyenne Indian Reservation in 2000 and 2001. Divisions correspond to colony categories, relating to the time since sylvatic plague infection. Category 1 colonies were infected with sylvatic plague by 1996 while category 4 colonies were infected in 1991.

Because presence or absence of plague in a colony did not explain differences in densities among colonies, I tested to see if the time since a colony was infected with plague correlated with colony density. Colony grouping did explain the density differences (2000: $F = 4.11$, $P = 0.02$, $df = 20$; 2001: $F = 3.55$, $P = 0.03$, $df = 22$). However, Tukey's pairwise comparisons showed that density estimates for many of the colony groupings were not significantly different (Table 3 and 4). When colony group (1) was removed from the sample, and the effects of colony grouping retested against colony densities, the colony groupings become insignificant (2000: $F = 2.09$, $P = 0.15$, $df = 18$; 2001: $F = 0.24$, $P = 0.87$, $df = 20$).

Table 3. Colony groupings, sample size within groupings, and mean density estimates for the groupings for 2000 from the Northern Cheyenne Indian Reservation. For Tukey's pairwise comparison, groups joined by the same letter are not significantly different from each other.

Colony Group	n	Mean Density		Tukey's pairwise comparison
		(no./ha)	SD	
1	2	69.97	19.65	a c
2	4	40.42	37.45	b c
3	4	21.27	6.04	b
4	6	17.39	7.18	b
5	5	37.60	19.58	b c

Table 4. Colony groupings, sample size within groupings, and mean density estimates for the groupings for 2001 from the Northern Cheyenne Indian Reservation. For Tukey's pairwise comparison, groups joined by the same letter are not significantly different from each other.

Colony Group	n	Mean Density		Tukey's pairwise comparison
		(no./ha)	SD	
1	2	70.71	17.03	a c
2	4	25.80	27.27	b c
3	4	17.83	3.34	b
4	7	22.06	17.81	b
5	6	26.53	14.36	b

Susceptibility of a Colony to Plague

I used a paired t test to test the effects that nearest neighboring distances had on the probability of a colony contracting plague. For colonies that had plague in the 1990s, distances to the nearest neighboring colony with a plague history were lower ($\bar{x} = 3.1$ km, $SD = 1.5$, $n = 17$) than distances to colonies without past plague ($\bar{x} = 19.6$, $SD = 5.4$, $n = 17$; $t = 2.1$, $P < 0.001$, $df = 18$; Table 3). For colonies that did not have plague in the 1990s, nearest neighbor distances to colonies with plague ($\bar{x} = 18.0$, $SD = 8.7$, $n = 6$) and without plague ($\bar{x} = 6.7$, $SD = 4.7$, $n = 6$) were significantly different ($t = 2.3$, $P = 0.02$, $df = 8$). The distance to the nearest neighbor was not significant ($t = 1.91$, $P = 0.12$, $df = 5$),

as was the distance to the nearest road ($t = -0.36$, $P = 0.73$, $df = 12$). The type of habitat between colonies was also not significantly related to the presence/absence of past plague ($t = 1.80$, $P = 0.13$, $df = 5$).

Table 5. Distances (km) to nearest neighboring black-tailed prairie dog colony that (1) did not have plague and (2) did have plague in the 1990s on the Northern Cheyenne Indian Reservation. Distances were based on year 2000 mapping data.

Colony	Nearest Colony without Plague (km)	Nearest Colony with Plague (km)
Without Plague		
Ash Creek	14	15
Buffalo Pasture	5	22
Logging Creek 1	3	13
Logging Creek 2	2	8
White Buffalo	6	17
Soldiers Gulch	10	33
Mean	6.7	18.0
With Plague		
Ashland Flats	18	3
Cow Creek 2	16	2
Kelty Creek 1	30	4
Lake Creek 1	18	3
Lake Creek 2	25	3
Logging Creek 4	10	2
Logging Creek 6	17	2
North Kelty Creek 1	20	2
North Kelty Creek 2	21	2
Reservation Creek 2	30	3
South Logging Creek	17	7
Stebbins Creek 3	17	3
Stebbins Creek 4	18	3
Tie Creek 1	17	5
Tie Creek 3	26	5
Two Feather 2	13	2
Two Feather 4	21	1
Mean	19.6	3.1

DISCUSSION

Colony Density

There was no difference in prairie dog densities, based upon the presence/absence of past exposure to the plague. Assuming that the densities in the colonies with no plague history were similar to the densities in the plagued colonies before the epizootic, then the densities in the plagued colonies had recovered to pre-plague levels.

Published literature on black-tailed prairie dog densities is sparse because it is more economical to measure colony size rather than density of animals (Miller and Cully 2001). However, the ranges of densities that are published are similar to the ranges I measured. Vosburgh and Irby (1998) reported early summer densities from 8 non-hunted colonies varied from 8 – 40 prairie dogs/ha, which are similar to density estimates I calculated for the Northern Cheyenne Indian Reservation's colonies. Smith (1958) reports black-tailed prairie dog densities of 55 – 56 prairie dogs/ha. Hoogland (1995), in studying a single colony for 15 years, found densities varied 13.9 – 21.6 prairie dogs/ha. Garrett et al. (1982) had summer densities from 2 colonies that were 30.6 and 82.6 prairie dogs/ha. Over the course of their study, the two colonies varied in density by more than 64 prairie dogs/ha. This variation was attributed to dispersal, mortality, natality, and colony expansion during their study. Cully (1989) hypothesized that the rate of transmission of plague in prairie dogs is density dependent. White-tailed prairie dogs (*C. leucurus*), the least social of the prairie dog species, have densities commonly <7/ha, the lowest for any prairie dog species (Hoogland 1995). Because of these low densities, their

colonies are capable of maintaining sylvatic plague for years without becoming extirpated. This occurs despite white-tailed prairie dogs exhibiting nearly 100% mortality once infected, as do all other species of prairie dogs (Cully and Williams 2001). However black-tailed prairie dogs, the most social prairie dog species, can occur at densities 10 times as high as white-tailed prairie dogs (Cully and Williams 2001). There is no published record of a black-tailed prairie dog colony maintaining a plague epizootic.

The amount of time since plague exposure, categorized into the 5 colony groupings, related to density. My data suggest that colonies reach some maximum density during their recovery from sylvatic plague and then densities begin to decrease to a stable level. It is possible that prairie dog densities for the colonies in the first colony grouping, which have had the shortest recovery time since the plague, are near that maximum density. However, density estimates would need to be conducted during the entire recovery period following the plague to determine if this hypothesis were valid.

The forage on colony edges is preferable to forage within the interior of a colony (Garrett et al. 1982). Smaller, newly founded colonies have a greater edge:area ratio, and may therefore support a higher density of prairie dogs (Garrett et al 1982). This may explain why two of the highest density colonies on the Northern Cheyenne Indian Reservation were <3 ha in size (Fig. 3 and Fig. 4).

Plague Dispersal

The distance between colonies and from colonies to roads appears to influence the spread of plague. All colonies that were at least 7 km from plague-positive colonies

remained plague free during the epizootic. These distances may be acting as a barrier to the organisms responsible for dispersing plague among colonies. The nearest neighbor distances I report between plagued colonies ($\bar{x} = 3$ km) are half the dispersal range of black-tailed prairie dogs, which is typically < 7 km (Garret and Franklin 1988). It is therefore possible that infected prairie dogs could transmit plague between nearby colonies (Cully and Williams 2001). Dispersal of infected prairie dogs over longer distances is unlikely, in part due to the lethality of sylvatic plague. Once infected, prairie dogs begin to show symptoms of illness in 2 – 3 days, and usually die within 7 days (Cully and Williams 2001).

Because virtually all black-tailed prairie dogs die when exposed to plague, colonies must be infected with sylvatic plague from beyond the colony boundaries (Cully and Williams 2001). In order for sylvatic plague to move across the reservation as it did, many colonies across the reservation would have to have been infected from colonies to their north. Many of these northern neighboring colonies were > 7 km away. Such distances make it unlikely that prairie dogs transferred the plague to these distant colonies (Cully and Williams 2001). More likely, some other species was responsible for the transfer. Cully and Williams (2001) suggest that coyotes (*Canis latrans*), badgers (*Taxidea taxus*) and raptors, all of which were common on the study area, may be responsible for transmitting infected fleas to distant colonies. Those colonies that did not get the plague were an average of 18 km from a colony with sylvatic plague. Although coyotes and raptors are capable of traveling these larger distances, I suspect that the probability of transferring the plague to other colonies decreased with greater distances.

MANAGEMENT IMPLICATIONS

The colonies present on the Northern Cheyenne Indian Reservation reestablished themselves following the sylvatic plague epizootic without human intervention. Although the total area occupied by prairie dogs is much less than prior to the plague, it is increasing yearly. Densities of prairie dogs appear to have recovered as well. The colonies that escaped the plague are too far away to serve as a source of naturally dispersing prairie dogs. Therefore, the founding populations for these expanding colonies most likely originated from individuals that survived the epizootic. These founding prairie dogs either survived the plague on their present colony, or else survived on a nearby colony. This reestablishment of colonies suggests that prairie dog colonies with close neighboring colonies are capable of recovering following a devastating reduction in colony size.

Those colonies that were isolated from infected colonies by distances > 7 km escaped the plague. Land managers may desire to have some colonies isolated to reduce the chance of a sylvatic plague epizootic striking a colony. However, such isolated colonies are not immune to the plague. When isolated colonies become infected, they stand little chance of natural recolonization from outside the colony. Transplants from other colonies would be needed to reestablish these isolated colonies. When colonies are not isolated, the plague often infects many colonies in a short time span. However, the likelihood of recolonization increases.

The issue of isolation becomes more complicated when other species dependent on prairie dog colonies are considered. Species that depend on colonies can be affected

by changes to the ecosystem during and after an epizootic. Predatory species may be dislocated, as sources of prey, either the prairie dogs themselves or another associated species, vanish. Following sylvatic plague, the unique short-grass habitat prairie dogs create may be lost as tall vegetation grows within the colony, and burrows begin to fill in. Species dependant on these habitats would be forced to either adapt to the new situation or, more likely, find more suitable habitat elsewhere. Although extirpated colonies often recover, they usually do not reach their pre-plague sizes before the next epizootic. On the other hand, isolated colonies that escape the plague can continue to provide the prey base and habitat attributes associated with prairie dog colonies.

REFERENCES CITED

- Anderson, E., S. C. Forrest, T. W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes*. Great Basin Naturalist Memoirs 8:11-63.
- Biggins, D. E., B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. United States Fish and Wildlife Service Biological Report 13:73-88.
- Cully, J. F., Jr. 1989. Plague in prairie dog ecosystems: importance for black-footed ferret management. Pages 47-55 in T. W. Clark and T. Rich, editors. The prairie dog ecosystem: managing for biological diversity. Montana Bureau of Land Management Wildlife Technician Bulletin 2.
- _____. 1997. Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic. Journal of Mammalogy 78:146-157.
- _____, and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.
- Freund, J. E., and G. A. Simon. 1997. Modern elementary statistics. Ninth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Garrett, G. G., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy 69:236-250.
- Garrett, M. G., J. L. Hoogland, and W. L. Franklin. 1982. Demographic differences between old and a new colony of black-tailed prairie dogs. The American Midland Naturalist 108:51-59.
- Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago, Illinois, USA.
- Johnson, J. R., and G. E. Larson. 1999. Grassland Plats of South Dakota and the Northern Great Plains. South Dakota State University, Brookings, South Dakota, USA.
- Knowles, C. J. 1985. Observations on prairie dog dispersal in Montana. The Prairie Naturalist 17:33-40.

- Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management* 24:177-192.
- Menkens, G. E., Jr., and S. H. Anderson. 1993. Mark-recapture and visual counts for estimating population size of white-tailed prairie dogs. Pages 67-72 in J. L. Oldemeyer, D. E. Biggins, and B. J. Miller, editors. *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret*. U.S. Fish and Wildlife Service Biological Report 13.
- 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. *Journal of Mammalogy* 82:889-893.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. *Applied Linear Statistical Models*. WCB/McGraw-Hill, Madison, Wisconsin, USA.
- Restani, M., L. R. Rau, and D. L. Flath. 2001. Nesting ecology of burrowing owls occupying black-tailed prairie dog towns in southeastern Montana. *Journal of Raptor Research* 35:296-303.
- Rexstad, R. J., and K. Burnham. 1991. Users guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Unit, Colorado State University, Fort Collins, USA.
- Roach, J. L., P. Stapp, B. Van Horne, and M. F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. *Journal of Mammalogy* 82:946-959.
- Severson, K. E., and G. E. Plumb. 1998. Comparison of methods to estimate population densities of black-tailed prairie dogs. *Wildlife Society Bulletin* 26:859-866.
- United States Department of the Interior, Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the black-tailed prairie dog as threatened. *Federal Register* 65:5476-5488.
- Vosburgh, T. C., and L. R. Irby. 1998. Effects of recreational shooting on prairie dog colonies. *Journal of Wildlife Management* 62:363-372.
- Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778-785.

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