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## **BLACK-TAILED PRAIRIE DOG ABUNDANCE AND DISTRIBUTION IN THE GREAT PLAINS BASED ON HISTORIC AND CONTEMPORARY INFORMATION**

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**ABSTRACT**—Recorded presettlement observations of black-tailed prairie dogs (*Cynomys ludovicianus*) are not adequate to fully determine their abundance and distribution. Early naturalists and explorers made only casual reports of prairie dogs on an opportunistic basis; their written records do not represent systematic surveys. Cumulative accounts of prairie dog control efforts, together with the known current prairie dog distribution in North Dakota and Montana, clearly show that most journalists failed to record prairie dog colonies. Also, they restricted their travels to a few common routes, and as a result only a very small and select portion of the landscape was surveyed. The hypothesis that prairie dogs dramatically increased in abundance following settlement is highly speculative. It ignores the fact that the Great Plains were once populated by large numbers of native ungulates, and that prairie dog control efforts began as early as the 1880s. Many lines of evidence suggest that the black-tailed prairie dog was common prior to European-American settlement and occupied 2%-15% of large landscapes (400,000 ha or more). There are systematic accounts of prairie dogs at the time of settlement, government records concerning poisoning efforts, physical evidence of abandoned historic colonies, and contemporary information on prairie

dog ecology, dispersal, distribution, and abundance, as well as presettlement accounts of large colonies measured in miles. The association of an obligate predator (the black-footed ferret [*Mustela nigripes*]) and a commensal bird species (e.g., mountain plover [*Charadrius montanus*] and burrowing owl [*Athene cunicularia*]) with the prairie dog (*Cynomys* spp.) is considered additional evidence that prairie dogs were abundant and widespread for an extended period. The presence of black-tailed prairie dogs throughout the short- and mixed-grass regions of the Great Plains from southern Canada to northern Mexico provided an important and unique habitat to a variety of wildlife species. We conclude that the black-tailed prairie dog was more abundant than suggested by tallies of observations in the journals of early European travelers.

**KEY WORDS:** black-tailed prairie dog, historic abundance

### Introduction

The ecological importance of the black-tailed prairie dog (*Cynomys ludovicianus*) was not fully appreciated until the latter half of the 20th century, well after implementation of massive governmental eradication efforts. Early pleas to conserve small areas of prairie dogs for black-footed ferrets were largely ignored (Murie 1937). Apparently even professional wildlife biologists did not understand the importance of expansive, closely spaced prairie dog colonies to assure viable populations of associated species. However, prairie dogs were and still are commonly viewed by farmers and ranchers as destroyers of the range and competitors of domestic livestock for limited forage resources, and as such should be eradicated or severely controlled. Private landowners' negative view of prairie dogs has resulted in a pattern on the landscape of small, widely spaced colonies interspersed by areas of local extirpation. This pattern developed in the early 1900s under government-sponsored poisoning campaigns, and it has been maintained by periodic bouts of poisoning. As a result of private landowners' dislike of prairie dogs, state laws have designated prairie dogs as a pest species, and state and federal conservation agencies have aided and abetted prairie dog control. At the behest of private landowners, state wildlife management agencies have, for the most part, abdicated the authority to manage prairie dogs.

Continuing population declines resulting from sylvatic plague, poisoning, habitat loss, and shooting led to a petition to list the black-tailed prairie dog as a threatened species under the Endangered Species Act in July 1998. In February 2000 the US Fish and Wildlife Service ruled that listing

the prairie dog was warranted, but it was precluded from doing so by a backlog of other species with higher listing priorities. The Fish and Wildlife Service evaluated the petition on the basis of these five listing criteria, as required by law: (1) present or threatened destruction, modification, or curtailment of habitat, (2) overutilization for commercial, recreational, scientific, or educational purposes, (3) disease or predation, (4) the inadequacy of existing regulatory mechanisms, and (5) other natural or manmade factors affecting its continued existence (US Fish and Wildlife Service 1980). Presettlement abundance and distribution of prairie dogs was not a factor in the listing assessment. The Fish and Wildlife Service determined that (1) a significant portion of prairie dog habitat had been permanently lost to agricultural conversion of grasslands, (2) recreational shooting of prairie dogs is an unregulated and common practice, (3) sylvatic plague has impacted prairie dog numbers over a significant portion of its range, (4) state laws classify prairie dogs as a pest species and promote prairie dog control, and (5) prairie dog poisoning remains a common management practice (US Fish and Wildlife Service 2000). In its report the Fish and Wildlife Service noted that the black-tailed prairie dog is a colonial species, and that many remaining colonies throughout much of the range are small and isolated. Consequently, eradication of colonies through control efforts, plague, habitat loss, and other impacts over time may lead sequentially to local extirpations and range contractions. Since prairie dogs are a highly colonial species, the reduction in size and number of colonies represents a reduction in distribution, even though the geographic distribution has not decreased proportionately to the reduction in numbers. Although the black-tailed prairie dog still occurs over a vast region and numbers in the millions, its colonial characteristics make it vulnerable to impacts identified in the five listing criteria.

Virchow and Hygnstrom (2002) challenge the Fish and Wildlife Service's decision that the black-tailed prairie dog warrants listing; they suggest that presettlement distribution and abundance of the black-tailed prairie dog were not carefully considered. In their analysis, little evidence exists to suggest that black-tailed prairie dogs were historically "superabundant" in the Great Plains. Although presettlement abundance and distribution are not part of the listing criteria, both past and present prairie dog distribution and abundance is an important issue that needs to be addressed. Evidence suggests that the black-tailed prairie dog was once significantly more common in the Great Plains than it is today. We define "common" as occupying 2%-15% or more of large landscapes (400,000 ha or more). This would represent local populations of 200,000 to 1,000,000+ individual

prairie dogs. In this paper, we examine historical and biological literature regarding prairie dog distribution and abundance. In particular, we focus on evidence from the northern Great Plains, where domestic livestock were not introduced until the late 19th century and widespread homesteading was not initiated until the early 20th century (Howard 1959). We conclude that black-tailed prairie dogs were very common and widespread in this area and that within this region prairie dogs have been greatly reduced from their original abundance. As evidence, we cite (1) the habitats prairie dogs currently occupy and the availability of such habitat; (2) the number, distribution, and size of extant prairie dog colonies; (3) the ability of prairie dog colonies to expand into suitable habitats; (4) the dispersal abilities of prairie dogs; (5) visible remains of old abandoned prairie dog colonies; (6) historic accounts of prairie dogs at the time of settlement; and (7) records of early government efforts to eradicate prairie dogs.

### Methods

We have reviewed many of the 19th-century natural history notes for Montana and the western Dakotas (Knowles and Knowles 1993). In so doing, we determined the routes taken by early explorers and naturalists and evaluated the quantity and quality of natural history notes they recorded. Copies of the original journals were obtained whenever possible.

Recently, we have mapped prairie dog colonies in Montana (FaunaWest 1998) and in North Dakota (Knowles and Hagen 2002) by means of a systematic ground survey in Montana, and by aerial and ground surveys in North Dakota. We used a 1:150,000 scale map of prairie dog colony locations, developed by Campbell (1989), as the basis for our map of Montana. However, when federal land management agencies had current mapping information available, these data were used. For the North Dakota map we incorporated all agency records of prairie dog colonies since 1980. We then flew to each of the sites and mapped active colonies during ground surveys. Abandoned prairie dog colonies were plotted as points on 1:200,000 scale maps. The Standing Rock and Fort Berthold Reservations were not included in the ground surveys. Theodore Roosevelt National Park was not included because current prairie dog mapping data for the park was available.

For the Fort Belknap Reservation in north-central Montana, a copy of a map compiled in 1921, depicting areas where black-tailed prairie dogs and Richardson's ground squirrels (*Spermophilus richardsoni*) were poisoned on the reservation, was obtained from the National Archives in Washington, DC. We digitized this map and then compared it to a 1999 map of prairie dog

colony size and location on the reservation. Although the map did not indicate if all colonies on the reservation were poisoned, we think it is likely that the 1921 map accurately portrays the areas that were poisoned. It is possible that there were other colonies on the reservation (especially smaller ones) that were not poisoned.

In addition, for eastern Montana we developed a model to predict suitable black-tailed prairie dog habitat (Proctor 1998). By combining existing vegetation, slope, and soil data with a Geographic Information System, we created maps outlining, in varying degrees of suitability, the prairie dog habitat for large areas. The model was developed initially for Phillips and Blaine Counties in north-central Montana and later was expanded to the entire prairie dog range distribution in eastern Montana. Prairie dog presence correlated well with vegetation and slope. Soil texture correlated only minimally, and soil depth was not a significant factor. When the model was extrapolated to a much larger area of Montana, 94.5% of prairie dog colony locations fell within the higher potential habitat categories (Proctor 1998; maps available from Montana Fish, Wildlife, and Parks, Helena, MT).

## Results

### Presettlement Accounts

Prairie dogs were not mentioned repeatedly by early naturalists. Therefore, an uncritical analysis of the historical record can lead to inaccurate estimates and to the erroneous conclusion that prairie dogs did not become prevalent until the early 20th century. For example, Koford (1958) thought that prairie dogs had increased in abundance following settlement of the Great Plains because the journals of Lewis and Clark and others who crossed the region made few references to prairie dogs in places where they were abundant in the early 20th century. It is clear, however, that Lewis and Clark and other early explorers did not include their every encounter with prairie dogs in their journals. Their failure to mention prairie dogs does not mean that prairie dogs were not present. The majority of early explorers and naturalists had little interest in prairie dogs and generally filled their journal pages with accounts of hardships of travel through wilderness areas, encounters with Indians, forage conditions for horses, observations of bison (*Bison bison*) and other large mammals, and the number of animals shot for food.

A careful review of the Lewis and Clark expedition (Burroughs 1961), which recorded some of the best information on prairie dogs during the 19th

century, shows how underreported prairie dogs were. For example, in their journal entries of 7, 11, 16, and 17 September 1804, Lewis and Clark reported their first encounter with prairie dog colonies along the White River and the Missouri River in southeastern South Dakota. Their next journal entry mentioning prairie dogs came on 23 May 1805 near the Mussellshell River in Montana, where Lewis observed a large colony along the river. He noted that prairie dog colonies were located on south and southeast exposures, implying that other colonies had been seen in similar circumstances. Lewis also noted that they had found colonies 8 to 9.6 km from water, again implying the existence of unreported colonies, as all journal records were of colonies next to rivers. Two weeks later, on 5 June, Lewis reported skirting for 11 km a large prairie dog colony near the Marias River, stating that it was the largest yet seen. The next mention is on 2 August near Whitehall, Montana, when Clark reported passing prairie dog colonies. On their return trip, on 1 July 1806, Lewis provided a general description of prairie dogs while in the mountains of western Montana, outside the range distribution of prairie dogs. He stated that colonies were several hundred acres in size but gave no indication of the frequency that they were encountered. (Also, this statement ignored the large colonies reported on 17 September 1804 and 5 June 1805 that were clearly larger than several hundred acres.) The last reference to prairie dogs came on 30 and 31 August 1806 near the Niobrara River. From these accounts, it is clear that Lewis and Clark made only intermittent notations of prairie dog occurrence.

From the observations of several other early naturalists as well as from contemporary information, we know that many of the terraces of the Missouri River, from the Niobrara River in Nebraska to Holter Dam in western Montana, were suitable habitat for prairie dogs and likely were occupied at the time that Lewis and Clark traversed the area. For example, Maximilian reported a prairie dog colony on an island in the Missouri River in South Dakota, and when in North Dakota he stated that there were many villages of the prairie dog in the neighborhood (Thwaites 1966). He also reported prairie dog colonies at Beauchamp Creek (the same general area of Lewis's 23 May 1805 note) and Cow Creek in Montana. Cooper (1868, 1869) also reported seeing prairie dog colonies along the Missouri River from Fort Benton to the Dearborn River in Montana. Bailey (1926) reported a series of prairie dog colonies along the Missouri River in North Dakota from Fort Yates to the Yellowstone River.

Our recent mapping of prairie dog colonies in Montana (FaunaWest 1998) recorded a series of 18 prairie dog colonies on terraces of the Mis-

souri River along the Wild and Scenic River portion, which is still relatively pristine, and seven active and inactive colonies on the Charles M. Russell National Wildlife Refuge, located along the river above Fort Peck Reservoir. These observations document the availability of habitat for prairie dogs along a river segment where early explorers reported only one prairie dog colony. During Clark's descent of the Yellowstone River, he failed to even mention prairie dogs; yet in 1863 Stuart (1902) described terraces of this river as having many prairie dog colonies. Five prairie dog colonies still remain along the segment (Shields River to the Bighorn River) that Stuart covered (FaunaWest 1998). Thus, it is apparent that Lewis and Clark did not comprehensively report all prairie dog colonies along the Missouri and Yellowstone Rivers.

Early explorers and naturalists had limited transportation options and so they frequently restricted their travels to the same well-established trails, typically along rivers. These transportation corridors were selected for the ease of travel and safety. Because they closely followed the Missouri River through North Dakota and Montana, expeditions such as Lewis and Clark's and Maximilian's never had the opportunity to observe optimal prairie dog habitat in the upland prairie. Therefore, their descriptions cannot be used to extrapolate to upland areas in Montana and North Dakota, where the topography has permitted the development of large complexes of prairie dog colonies. Observers who did traverse the upland prairie found prairie dogs to be "quite abundant on the plains" (Grinnell 1876), described them as the characteristic mammal of the prairies (Coues 1878), or stated that they were innumerable (Mead 1899).

### **Influence of Early Settlement**

It is important to determine the date at which settlement had a major influence on prairie dogs. Virchow and Hygnstrom (2002) use 1860 as the start of the settlement period and assume that any report of prairie dogs after this period had been influenced by settlement. Although they note that settlement across the Great Plains was not uniform, they fail to take this into account when they attribute two early accounts of prairie dogs, one in South Dakota in 1859 (Hayden 1863) and another in Montana in 1871 (Messiter 1890), to the postsettlement period. The Spanish occupation of the Southwest, and their introduction of domestic livestock that could have led to overgrazing, likely dates back to the 1700s (Oakes 2000), but cattle did not come to central Montana until 1880 (Howard 1959). Interestingly, both



Hayden (1863) and Messiter (1890) reported large prairie dog colonies in Montana and South Dakota before 1880.

Coues's (1878) observations of prairie dogs north of the Milk River in Montana in 1874 also preceded settlement there. When Messiter returned to central Montana in 1882, he reported that cattle and cowboys made a poor substitute for bison and Indians, indicating that settlement was not significant during his first trip to Montana (1871-72). In western South Dakota, the Sioux tribes successfully stalled European-American settlement until the Custer expedition of 1874 into the Black Hills.

The introduction of cattle on the prairies in eastern Montana and western North Dakota did not bring about an immediate change in the intensity of land use. Early settlement in central and eastern Montana was on large ranches (Howard 1957). Establishment of these ranches often followed immediately on the heels of bison extermination, and in this case cattle were substituted for bison (Messiter 1890). It is difficult to develop a case for increased levels of grazing during the early settlement period, given the many accounts of large bison herds and reports of horses in poor condition due to lack of feed because bison had grazed the landscape so severely (Raynolds 1868; Audubon 1897; Hazlitt 1934; Burroughs 1961; Hafen and Hafen 1961). In Montana, large-scale homesteading did not begin until 1909 (Howard 1959), and stock water did not become widely available in the upland prairies until the 1930s. Thus, it is unlikely that the transition to cattle provided an environmental release for prairie dogs in the northern Great Plains.

Virchow and Hygnstrom (2002) also suggest that estimates of abundant prairie dog populations resulted from increases in geographic range distribution and increases in numbers following settlement of the Great Plains, as well as from a few grossly exaggerated reports of prairie dog abundance made to justify rodent control efforts. We disagree with Virchow and Hygnstrom, since the reports were not systematic and likely biased. Prairie dogs associate with intensively grazed areas (Koford 1958; Knowles 1986; Licht and Sanchez 1993); frequently, prairie dog colonies in Montana and North Dakota are found surrounding old homestead sites and stock water developments (Knowles 1986; Licht and Sanchez 1993). Thus, when Merriam (1902) interviewed farmers in east-central South Dakota he received reports of prairie dogs showing up around homesteads. He gave similar reports from Kansas and Arizona, where prairie dogs increased when the land was settled. However, Mead (1899) stated that in Kansas prairie dog numbers declined following extirpation of bison but recovered as domestic livestock were brought into the area. It is possible that Merriam

documented only prairie dogs reoccupying former range. None of these reports represents a systematic assessment of regional prairie dog populations and trends. All that can be concluded from these anecdotal reports is that there already were prairie dogs in these areas at the time of settlement.

Claims have been made that early rangewide estimates of prairie dog abundance were greatly exaggerated (Virchow and Hygnstrom 2002). However, Nelson's (1919) estimate of 40,469,500 ha of prairie dog (*Cynomys* spp.) across vast areas of the Great Plains and intermountain west, which was compiled from estimates provided by field agents of the Bureau of Biological Survey and not through systematic surveys, was corroborated by a series of independent estimates. Oakes (2000) found Bureau of Biological Survey estimates of prairie dog abundance of approximately 6 million ha in New Mexico in 1921 to be fairly consistent with estimates of the areal extent of prairie dogs in 1971, minus the area poisoned during the period 1921-1971. Burnett (1919) estimated 2.8 million ha of black-tailed prairie dogs in eastern Colorado, and a total of 5.8 million ha for all three prairie dog species in the state (Burnett 1918). In Texas, Bailey (1905) estimated there were 23 million ha of prairie dogs. In Kansas, Lantz (1903) estimated there were 0.8 million ha of black-tailed prairie dogs. In South Dakota, Rose (1973) reported an early estimate (1923) for black-tailed prairie dogs on 0.7 million ha. Finally, in Montana, Flath and Clark (1986) estimated early black-tailed prairie dog abundance at 0.6 million ha. On the basis of these various independent estimates, the total for these six states alone is 37 million ha. If the area in the other six states with prairie dogs (*Cynomys* spp.) is included, it becomes apparent that the Bureau of Biological Survey estimates were well founded, and possibly conservative.

The 1919 estimates did not account for 10 to 20 years of agricultural cropland conversions and the 30+ years of control efforts that preceded organized federal poisoning programs against prairie dogs. Habitat conversion was extensive. Choate et al. (1982) estimated that two-thirds of the area within the geographic distribution of the prairie dog in Kansas was converted to cropland after settlement. Merriam's (1902) report clearly showed that cheap, effective prairie dog poisons were already available by 1902. Strychnine could be purchased in most agricultural communities, and poisoning of prairie dogs by private ranchers was already underway. Merriam (1902) listed several other control methods that were in use and effective on a limited scale. Clark (1989) found that eradication of prairie dogs began about 1880, and an organized control program in northwestern Wyoming was reported to have begun in the 1880s (Clark et al. 1986). In Kansas, the statutory requirement to control prairie dogs began in 1903 (Lantz 1903).

Carbon bisulfide, a toxic fumigant, was “popular” for use in prairie dog control by 1888 (Hubbard and Schmidt 1984). “Lee’s Peerless Gopher Killer” was a patented rodenticide in wide use at the turn of the century (Lantz 1903). In New Mexico, farmers were drowning and plowing prairie dogs in the mid-1880s (Oakes 2000). Indeed, by the time the Bureau of Biological Survey became involved with prairie dog control programs in 1915, prairie dog poisoning by private ranchers had been an ongoing process for at least two decades. As one commentator noted, “the ranch men had been poisoning prairie dogs for years and had . . . completely cleared the country of the pest” (Oakes 2000).

Under government organization and sponsorship, prairie dog poisoning became a systematic attempt at total eradication. Merriam (1902) realized that the extremely colonial nature of black-tailed prairie dogs made them highly vulnerable to such an organized extermination program. He identified cheap, effective poisons currently available, addressed the need to develop coordinated prairie dog control programs to effect large-scale extermination, and conceptually outlined how such a program could be implemented. Bailey (1926) provided records of colonies destroyed in North Dakota by 1913 and noted that the Bureau of Biological Survey and the North Dakota Department of Agriculture were investigating the prairie dog situation in North Dakota in 1915. Grondahl (1973) reported that prairie dogs had been subjected to various degrees of control for 100 years in North Dakota. Although heavily grazed areas around homesteads may have increased the amount of habitat suitable for prairie dogs, this was countered by habitat conversion to croplands and early prairie dog control efforts. Consequently, it is not possible to make generalizations about prairie dog population trends early in the settlement process.

### **Records of Prairie Dog Control Efforts**

Government reports of hectares being treated with poisons, and quantities of poisoned grain bait being applied, likely were a straightforward attempt to quantify rodent control efforts. These detailed reports provide valuable documentation of prairie dog abundance at the time of settlement. Clark (1989) reviewed information compiled by Burnett in a series of reports on annual poisonings of prairie dogs and ground squirrels (*Spermophilus* spp.) in Colorado from 1912 to 1923. Using the graph in Clark (1989), we estimated that 17,750,000 ha were treated with poisoned grain bait during this period. These records also showed that 595,926 litters of treated grain bait were applied. In eastern Colorado, Clark (1989) quoted

TABLE 1  
SUMMARY OF REPORTED PRAIRIE DOG EARLY POISONING EFFORTS  
BY STATE

State	Area poisoned (ha)	Time period	Source
Colorado	17,750,000 <sup>a</sup>	1912-1923	Clark 1986
Montana	2,832,860 <sup>b</sup>	1920	Bell 1921
Phillips Co.	72,479	1924-1939	Bureau of Land Management 1982
New Mexico	4,514,170 <sup>c</sup>	1917-1932	Hubbard and Schmitt 1984
North Dakota	2,428,166 <sup>d</sup>	1920	Bell 1921
South Dakota	400,000	1923-1939	Linder et al. 1972
Nine counties	161,133	1920	Hanson 1988
Five counties	60,729	1922	Hanson 1988
Pine Ridge Reservation	56,680	1922	Hanson 1988
Wyoming	>400,000	1915-1927	Campbell and Clark 1981
	1,120,290	1915-1923	Martley 1954

<sup>a</sup>Includes ground squirrels and Gunnison's and white-tailed prairie dogs.  
<sup>b</sup>Includes ground squirrels and white-tailed prairie dogs.  
<sup>c</sup>Includes Gunnison's prairie dogs.  
<sup>d</sup>Includes ground squirrels.

Payne's estimates (in Johnson 1912) that the abundance of black-tailed prairie dog colonies in 1903 ranged from 2% to 10% of the landscape.

Anderson et al. (1986) cited a report by Bell (1921) that documented the poisoning of prairie dogs and ground squirrels on 2,832,860 ha in Montana and 2,428,166 ha in North Dakota during 1920. By comparison, in Montana, more recently mapped prairie dog colonies totaled about 27,000 ha in 1998 (FaunaWest 1998), and in North Dakota mapped prairie dog colonies totaled about 8,000 ha in 2002 (Knowles and Hagen 2002). In Phillips County, Montana, during the three-year period 1931-33, 69,000 ha of prairie dogs were poisoned with 33,000 kg of poisoned grain bait, and 170,000 ha of ground squirrels were treated with 19,100 kg of poisoned grain bait (Table 1). In South Dakota, several reports exist of prairie dog poisonings from different areas and time periods in the early 1900s (Table 1). These records are specific for black-tailed prairie dogs, and they indicate that over 400,000 ha were poisoned during the 1920s and 1930s. In Wyoming, Anderson et al. (1986) cited Martley (1954) documenting that 1,120,290 ha of black-tailed and white-tailed prairie dogs (*Cynomys leucurus*) were poisoned between 1915 and 1923. In northeastern Wyoming

(Campbell, Niobrara, and Weston Counties), an additional 445,080 ha of black-tailed prairie dogs were poisoned from 1923 to 1928 (Day and Nelson 1929, cited in Anderson et al. 1986). One colony in this area was reported to be 160 km long.

In New Mexico, during the period 1917-1932, a large poisoning campaign was conducted against the black-tailed and Gunnison's prairie dog (*Cynomys gunnisoni*), in which approximately 4.5 million ha were treated with poisoned grain bait (Hubbard and Schmitt 1984). (No information exists on how many hectares of each species were poisoned.) Shriver (1965) estimated prairie dog abundance (both species) in New Mexico in 1919 at 4.8 million ha, or about 15.3% of the total landscape (Hubbard and Schmitt 1984). Several records from the early 1900s suggest that the black-tailed prairie dog was very abundant in New Mexico (Hubbard and Schmitt 1984). Collectively, the early reports and the detailed documents on prairie dog poisoning efforts clearly show that prairie dog poisoning occurred on a local level, began as early as the 1880s, and was conducted on a broad scale across the geographic range of the black-tailed prairie dog, starting in 1915 and continuing into the 1930s.

### **Early Settlement Period Records of Prairie Dogs**

During the early settlement period, there was opportunity to record prairie dog distribution and abundance as the land was surveyed. In at least one case, prairie dogs were noted as the land was surveyed from 1908 to 1914 prior to homesteading. Flath and Clark (1986) reviewed land use classification maps for about 25% of southeastern Montana where prairie dog colonies were noted on surveyors' maps from 1908 to 1914. They looked at each 16 ha parcel, and if a surveyor noted prairie dogs in the parcel, they counted the parcel as containing 8 ha of prairie dogs. They assumed that all prairie dog colonies were recorded. They estimated that prairie dogs occupied 2.8% of the surveyed sections (1 square mile), and the percentage of surveyed sections with prairie dog colonies averaged 25%. However, for counties with more than 100 surveyed sections, the occurrence of prairie dogs ranged from 1% to 48%, indicating considerable regional variation in prairie dog abundance. Homesteading in the survey area primarily occurred later, from 1915 to 1917, after the land survey (Flath and Clark 1986). The survey excluded the Crow and Northern Cheyenne Reservations, and both reservations contain characteristic prairie dog habitat. Flath and Clark (1986) also prepared detailed maps of prairie dog distribution in the Tongue River and the Powder River areas. These maps

showed that prairie dogs were distributed primarily along the major drainages, with some colonies exceeding 16 km. They also noted that General George A. Custer reported several extensive prairie dog colonies along Rosebud Creek in 1876 (Fulton 1982, cited in Flath and Clark 1986). Physical evidence of abandoned historic colonies in these drainages is still visible (Knowles 1996-1998, personal observation). Similar maps may exist for other areas of Montana, but no systematic effort has been made to investigate this possibility.

We examined land use classification maps for Jefferson County in southwestern Montana and found one of two known historic prairie dog colonies noted on the maps. In this case the mappers indicated the colony as a "dog town" of 2-4 ha in size, consistent with Flath and Clark's (1986) observations. Both the historical colonies in Jefferson County were large (>300 ha), and it is likely that the colonies had already been poisoned when the maps were drawn in the early 1900s (exact dates unknown). The discovery of gold in this area in the 1860s led to settlement of southwestern Montana ahead of the eastern plains (Howard 1959). The available early settlement records also support a relatively high occurrence of the black-tailed prairie dog.

### **Records of Large Colonies**

Many reports of large prairie dog colonies, measured in miles, were written prior to or at the time of settlement. Some of these are listed in Virchow and Hygnstrom (2002: table 3). In Texas, one colony was estimated to be 400 km long by 160-240 km wide (or about 64,753 km<sup>2</sup>) and was mentioned by both Merriam (1902) and Bailey (1905). This colony no longer exists (Kevin Mote, Texas Game Fish and Parks, personal communication). Another large colony was reported between the North and South Wichita Rivers in what is now King and Knox Counties, Texas (Halloran 1972). Also, in southeastern Arizona, Mearns reported in 1907 (cited in Hoffmeister 1986) that burrows of prairie dogs were scattered for miles over the plains south of the Pinaleno, or Sierra Bonito. Yet the black-tailed prairie dog is now considered extirpated from Arizona. In Kansas, one colony was described as 96 km long (Baker 1889). In north-central Kansas, Mead (1899) noted that in 1859 a prairie dog colony on the divide between the Saline and Solomon Rivers, from Ellsworth County and west, was continuous for miles. He described the prairie dogs as "innumerable." In southern Logan County, Kansas, Merriam (1902) reported that about 777 km<sup>2</sup> consti-

tuted one continuous colony. In north-central Montana, between the Missouri and Milk Rivers, Messiter (1890) described prairie dog colonies as 48-64 km long. These colonies were noted by early settlers in this area (see below), even though they were not noted by the Lewis and Clark (Burroughs 1961) or Maximilian expeditions (Thwaites 1966; Thomas and Ronnefeldt 1982) when they passed just south of these colonies. Under good conditions, prairie dog colonies can be observed at a distance of 1-2 km with binoculars. Physical evidence of these colonies can still be found (see below). In this area there are currently approximately 12,000 ha of prairie dog colonies. Finally, in southeastern Montana, Flath and Clark (1986) reported many complexes along drainages extending more than 16 km, and some complexes covered more than 9,216 ha at the time of settlement.

In South Dakota, Hayden (1863) estimated that the largest colony he observed was 130 km<sup>2</sup>. Rose (1973) reported that many old timers in South Dakota spoke of prairie dog colonies extending 24-32 km along major drainages. He also noted that prairie dogs occurred in great abundance between Rapid City and Faith, South Dakota, a distance of 240 km. On the Grand River National Grassland in northwestern South Dakota, an old rancher (L. Lyon May 2002 personal communication) reported to us that his grandfather talked about a prairie dog colony between Faith and Newell that required three days to cross on horseback in one direction and two days to cross on horseback in the other direction. He specifically stated that "this was before there were towns and stuff like that." Merriam (1902) said that prairie dog colonies 32-48 km long were not rare. In Oklahoma, a virtually continuous prairie dog colony in tallgrass prairie stretched from Kingfisher Creek to Fort Reno, Oklahoma, a distance of 35 km, according to Lewis and Hassien (1973) who cited Strong (1960). In northeastern Wyoming, Anderson et al. (1986) cited Day and Nelson (1929) recording a prairie dog colony that was 160 km long. In New Mexico, Auto of Xavier in 1680 referred to the northern end of the Jornada del Muerta plain as "Paraje de las Tusas" (Place of the Prairie Dogs), implying that a large prairie dog colony existed in the broad valley (Oakes 2000). These were all significant prairie dog colonies for which there is no comparison among present prairie dog colonies in the United States.

Credible evidence suggests that large colonies existed on shortgrass and mixed-grass prairies. The question is, how many such colonies existed and what percentage of the landscape was occupied by prairie dogs. Hayden (1863), Baker (1889), Mead (1899), Messiter (1890), Merriam (1902), and Rose (1973) implied that there were more than one large colony. However, Messiter (1890) noted that the large colonies in north-central Montana were

larger than others that he had seen elsewhere. In Montana, Allen (1874), who traveled the divides between the Yellowstone and Missouri Rivers and the Yellowstone and Mussellshell Rivers during 1873, described prairie dogs as generally distributed throughout the region traversed, but nowhere very numerous. This suggests that he did not encounter extraordinarily large colonies. However, even with 2%-10% of the landscape occupied by prairie dogs, 90-98 km of each 100 km of the region transected would be free of prairie dog colonies. On the basis of the total record, it is apparent that the black-tailed prairie dog was widely distributed across the Great Plains and that in many areas it occurred in extensive colonies.

### **Evidence from Phillips and Blaine Counties, Montana**

Some of the best documentation of prairie dog abundance during the early 1900s exists for the area occupied by Phillips and Blaine Counties in north-central Montana, which includes part of the area through which Messiter (1890) traveled in 1871. In October 1974 we talked to two older men who had worked on Civilian Conservation Corps crews during the early 1930s, poisoning prairie dogs in Phillips County, Montana. They reported that a colony stretched from the base of the Little Rocky Mountains to the UL Bend on the Missouri River which was called "40-mile town." They described this "town" as a series of large colonies 65 km long as opposed to a single continuous colony, and stated that the goal of the poisoning effort here was total extermination (personal communication October 1974). The thorough nature of this effort was confirmed by Murie (1937) when he conducted a faunal survey of the area that became the Charles M. Russell National Wildlife Refuge. There is also physical evidence of a large colony that extended from the eastern portion of the Fort Belknap Reservation into central Phillips County, a distance of about 48 km (Fig. 1). This information is consistent with Messiter's (1890) observations of prairie dog colonies 48-64 km long in north-central Montana.

Prairie dog colonies on the Fort Belknap Reservation were also mapped in 1921 (Fig. 2). The reservation includes some of the area crossed by Messiter in 1871. These maps were located recently in the National Archives in Washington, DC, and we have digitized and consolidated these maps. They reveal that there were approximately 16,336 ha of prairie dog colonies on the reservation in 1921, which represented about 8% of the Fort Belknap Reservation rangelands. The Fort Belknap Reservation was established in 1888, and settlement there occurred at three locations: Fort Belknap Agency, Hayes, and Lodge Pole. The latter two sites were in the Little



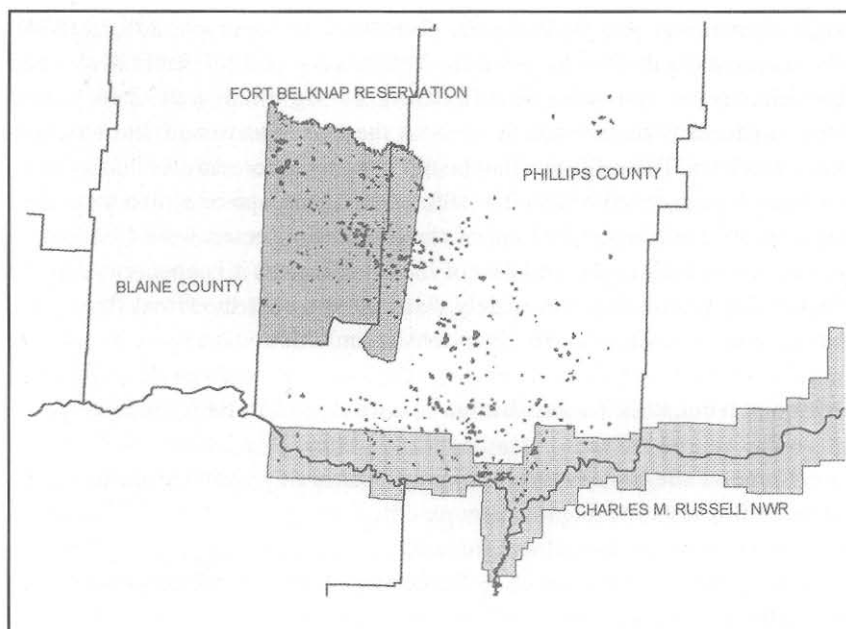


Figure 1. Map showing the current distribution of prairie dog colonies in Phillips and Blaine Counties, Montana. The current distribution can be used to estimate the location of large historic prairie dog colonies reported in this area by Messiter (1890) and by homesteaders. (Map prepared by the Charles M. Russell National Wildlife Refuge.)

Rocky Mountains, and the former site was in the Milk River bottomlands. The reservation was never opened to homesteading, but grazing by nonresidents' cattle and horses was permitted in the early years (Howard 1957). Significant conversion of grasslands to croplands did not occur until the 1970s, and development of homes outside established communities did not take place until the 1980s (personal observation). In 1999 there were approximately 6,000 ha of prairie dog colonies on the reservation (Tim Vosburgh, Fort Belknap Fish and Game biologist, personal communication), or about 38% of the mapped acreage in 1921.

Rodent control records for Phillips County, Montana, show that 72,480 ha of prairie dog colonies were poisoned from 1924 through 1939, with 68,825 ha of this total treated between 1931 and 1933 (Bureau of Land Management 1982). There were also 1.5 million ha of Richardson's ground squirrels poisoned from 1918 to 1939, which could have included some

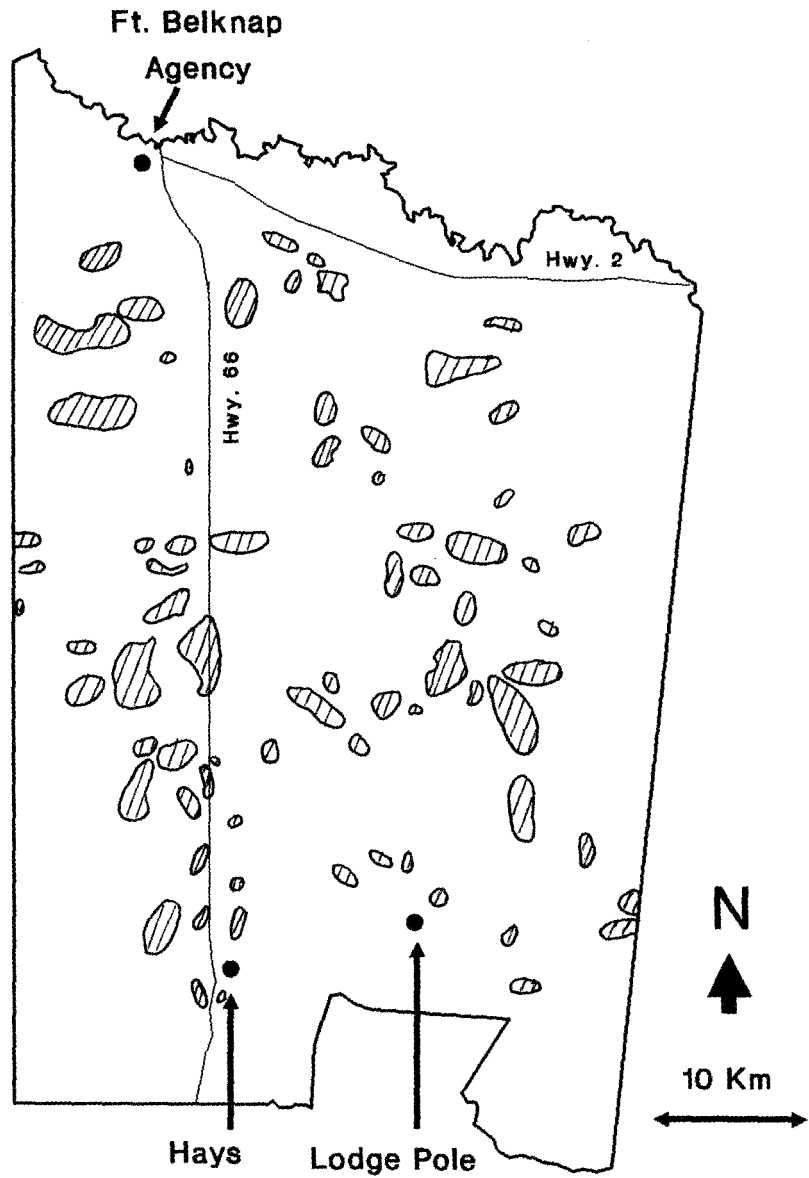


Figure 2. Map of the Fort Belknap Reservation showing the location of prairie dog colonies mapped in 1921. The 1921 distribution map is courtesy of US National Archives, Washington, DC.

prairie dog colonies. The 68,825 ha of poisoned prairie dog colonies represent about 6% of the county, which includes the areas of the Little Rocky Mountains and the Missouri River Breaks in the county that are not suitable habitat for prairie dogs. In 1998 only 5,700 ha of prairie dog colonies remained in Phillips County, or about 8% of the acres poisoned in the early 1900s. Yet Phillips and Blaine Counties currently contain Montana's largest and most extensive prairie dog colony complexes.

### **Physical Evidence of Large Prairie Dog Complexes**

Occupation of sites by prairie dogs for extended periods (perhaps centuries) can alter the appearance of the soil surface. In some cases, actual prairie dog mounds remain visible long after the prairie dogs are gone. Such evidence can be used to corroborate estimates of numbers. Bailey (1926) stated that the old burrows and mounds remain for many years, and that the sites of ancient prairie dog towns are marked by little swells of grassy turf scattered over the prairie. In northwestern Wyoming, Clark et al. (1986) reported that prairie dog mounds in abandoned white-tailed prairie dog colonies remained visible for 60+ years after the colonies were poisoned. In Montana, we have observed similar situations, especially in mountain valleys and benches in the western portion of the black-tailed prairie dog range. In native prairie sites in eastern Montana, southwestern North Dakota, and northwestern South Dakota, we frequently encounter a pattern on the soil surface of alternating raised areas that are well vegetated, and depressed areas that are less vegetated, often with pan spots. Our interpretation of these patterns is that these sites were historic prairie dog colonies, and the soil surface is a result of centuries of prairie dog activity interacting with erosional forces (wind and water). In South Dakota, Rose (1973) reported that remnants of old colonies are still evident along the Bad River between Philip and Fort Pierre. Physical evidence of abandoned prairie dog colonies is still evident near Faith and St. Onge, South Dakota, and along the Belle Fourche River near Colony, Wyoming (personal observations). Cheyenne, Wyoming, was built on the site of a large prairie dog colony (Day and Nelson 1929). Hayden (1872) mentions walking out of Cheyenne and seeing prairie dogs. Mounds of this colony are still visible 8 km east of Cheyenne off Interstate 80, as well as north of Cheyenne. When mapping current prairie dog colonies, it is not unusual to find a series of small colonies remaining in these areas that were once large prairie dog colonies (Knowles and Hagen 2002). Cultivation of rangeland sites destroys this physical evidence of past occupation by prairie dogs; however, even in areas with

limited cultivation, it is possible to plot the general distribution of former prairie dog colonies (Knowles and Hagen 2002).

In north-central Montana, physical evidence of large former prairie dog colonies is still very evident in Phillips and Blaine Counties. This is consistent with Messiter's (1890) observations, early maps of the Fort Belknap Reservation, accounts of early residents of this area, and reports of prairie dog control efforts for this area (above). It is possible to use a map of existing prairie dog colonies in this area to estimate the general outline of the large colonies that apparently once occurred in this area. Although we have observed evidence of large former prairie dog colonies in other locations in Montana, most of those areas are too fragmented by croplands to determine the full extent of the colonies, even though a few scattered prairie dog colonies remain.

In western North Dakota, while mapping prairie dog colonies along the Little Missouri River corridor and in the upper portions of the Knife, Heart, Cannonball, and North Grand Rivers, we found physical evidence at 153 sites of former prairie dog colonies. This was not a comprehensive survey of old colonies nor an attempt to determine the aerial extent of these colonies. However, it was apparent that this area at one time contained significant prairie dog colonies. The upper drainage basins from 10 km north of Belfield and Fryburg south to Amidon, a distance of approximately 53 km, appeared to have contained extensive prairie dog colonies. Some of this area is upland prairie within the Little Missouri National Grassland and has never been cultivated, but cultivation of many of the sections in this area makes it difficult to precisely trace this colony complex. Bailey (1926) stated that upland prairie was the primary habitat of prairie dogs in North Dakota. Within this area, we located 47 sites that appeared to be former prairie dog colonies. However, a 1939-1942 map of prairie dog colonies within the Medora Ranger District showed only three small colonies in this area (Bishop and Culbertson 1976), but our mapping effort in 2002 located 31 small- to moderate-sized colonies (unpublished data). It is apparent that prairie dogs were greatly reduced in this area by 1939-1942 but have recovered somewhat in recent years.

### **Prairie Dog Ecology**

Our knowledge of prairie dog ecology suggests that once a colony is established it is capable of expanding into areas with slopes up to 12% and into areas with herbaceous vegetation up to 20-30 cm in height (Knowles 1996-1998, personal observation). Although shrubs like big and silver sage-

brush (*Artemisia tridentata*, *A. cana*) can restrict prairie dog colony expansion, over a number of years these shrubs will be eliminated or modified to permit occupation of a site by prairie dogs. Prairie dogs are capable of constructing burrows in a variety of clay and clay/loam soils that are common in the Great Plains (Koford 1958). Much of the shortgrass and mixed-grass prairie is suitable habitat for prairie dog colonization because of the soils, vegetation, and slope.

We developed a map of potential habitat of prairie dogs within their range distribution in Montana, based on the data on slope, soils, and vegetation found at existing prairie dog colonies. This mapping effort identified 1.1 million ha of preferred habitat and an addition 11.3 million ha of potential habitat. This analysis excluded approximately 4.5 million ha of cultivated croplands, even though cropland sites are frequently suitable prairie dog habitat based on slope and soils (Bailey 1926). In Montana, it is apparent that the 27,000 ha of documented prairie dog colonies are not limited by habitat features; also, it is clear that prior to massive poisoning campaigns, cultivation of upland prairie, and the introduction of sylvatic plague, the available habitat would have supported a substantially greater prairie dog population. This is verified by historic accounts (Messiter 1890), early land surveys (Flath and Clark 1986), and records of early poisoning efforts (Bureau of Land Management 1982; Anderson et al. 1986).

Despite anecdotal accounts of seemingly high prairie dog colony growth rates, recorded long-term growth rates over broad areas on the northern Great Plains generally do not support these accounts (Table 2). Annual growth rates at these frequently mapped prairie dog complexes exceeded 50% only where prairie dogs were recovering from poisoning programs (Theodore Roosevelt National Park in 1947-1953 and Charles M. Russell National Wildlife Refuge in 1964-1970) and from the plague (Northern Cheyenne Reservation in 1998-1999). While mapping prairie dogs in North Dakota we encountered one 23.5 ha colony next to a ranch headquarters that the landowner reported had first appeared in the early 1960s and had never been poisoned. It is a long-term process for prairie dogs to occupy such large areas as 48- to 64-km-long colonies. This, it is doubtful that the large prairie dog colonies reported at the time of settlement could have developed in the few years from the start of homesteading to initiation of prairie dog control programs.

Prior to settlement of the Great Plains, black-tailed prairie dogs had thousands of years to invade and colonize suitable habitats. Dispersal distances of prairie dogs are normally under 10 km (Knowles 1985; Garret and Franklin 1988). Maps of the distribution of prairie dog colonies at the time

TABLE 2

## ANNUAL PRAIRIE DOG COLONY GROWTH RATES FOR ROOSEVELT NATIONAL PARK AND FOUR AREAS OF MONTANA

Area	Time period	Annual rate of change (%)	Source
Roosevelt National Park (western North Dakota)	1947-53	51	Theodore Roosevelt National Park files
	1953-56	21	
	1956-57	-26	
	1957-63	29	
	1963-65	1	
	1965-73	-7	
	1973-77	-1	
	1977-82	2	
	1982-85	12	
	1985-88	-5	
	1988-91	20	
	1991-92	9	
	1992-95	-3	
	1995-97	3	
C.M. Russell National Wildlife Refuge (north-central Montana)	1964-70	71	Knowles 1982 and C.M. Russell National Wildlife Refuge files
	1970-74	15	
	1974-79	2	
	1979-84	7	
	1984-88	5	
	1988-94	-5	
	1994-95	-20	
	1995-97	0	
Phillips County (north-central Montana)	1981-84	15	Reading et al. 1989 and Stoneberg 1993 John Grensten personal communication
	1984-88	3	
	1988-92	-10	
	1992-93	-3	
	1993-98	1	
Northern Cheyenne Reservation (south-central Montana)	1984-90	12	FaunaWest 1994 Steve Fourstar personal communication
	1990-94	-23	
	1994-95	-36	
	1995-97	25	
	1997-98	39	
	1998-99	63	
	1999-00	37	
Fort Belknap Reservation (north-central Montana)	1978-90	12	FaunaWest 1991 Bureau of Indian Affairs files Tim Vosburgh personal communication
	1990-94	-4	
	1994-96	-23	
	1996-97	22	
	1997-98	11	
	1998-99	-5	
	1999-00	-9	

of settlement (Flath and Clark 1986), and during the latter portion of the 20th century, show that colonies are typically relatively close to each other, which reflects prairie dogs' dispersal ability and the availability of suitable habitat (Fig. 1). For example, Flath and Clark (1986) reported that the mean intercolony distances for two areas surveyed from 1909 to 1914 in southeastern Montana were 3.4 and 2.9 km. On the Charles M. Russell National Wildlife Refuge following 15 years without any prairie dog control, Knowles (1982) recorded a mean intercolony distance of 2.5 km. Based on maps supplied by Reid (1954), Scheelhaase (1973), Hillman et. al. (1978), and Coppock (1981), Knowles (1982) calculated mean intercolony distances of 1.2 km for Theodore Roosevelt National Park, 2.4 km for Wind Cave National Park, 3.8 km for southern Saskatchewan, and 2.4 km for southwestern South Dakota. Thus, based on our knowledge of prairie dog colony distributions today, it is unlikely that presettlement prairie dog distribution was characterized by small isolated colonies; instead, colonies would have been within the normal dispersal range of one another.

Together, the short dispersal distances and extreme coloniality of black-tailed prairie dogs mean that establishment of a geographic range distribution throughout the Great Plains, extending from southern Canada to northern Mexico and from the Rocky Mountains to the 98th meridian, would have required the development of a large metapopulation in which colonies were relatively closely spaced within the normal dispersal range of prairie dogs. Nothing in modern prairie dog mapping data suggests that isolated small colonies are a normal pattern in prairie dog colony distributions. If accurate, Bailey's (1905) observation that colonies in Texas were separated by 16 to 32 km is a clear indication that prairie dogs had already been controlled severely in that area. In Montana and North Dakota, our observation is that prairie dog colonies are rarely found separated from other colonies by such distances.

Mapping of prairie dog colony complexes typically reveals a characteristic pattern of colony-size class distribution. A significant portion of prairie dog colony acreage is usually contained in a few large colonies, but smaller colonies are numerically more common (FaunaWest 1998). We assume that prairie dog colony-size class distribution prior to settlement would have been similar; however, many of the smaller colonies present today are actually just remnants of colonies that were once much larger prior to control efforts. In northern Mexico, Ceballos et al. (1993) and List et al. (1997) provided information on a large prairie dog colony complex prior to control measures and agricultural land conversion. In 1986 the main colony was 34,000 ha and the entire complex contained 55,000 ha of prairie dog

colonies. During the past decade, cattle ranching and conversion of grasslands to irrigated agricultural croplands has resulted in the fragmentation of this complex. The main 34,000 ha colony has been broken into smaller colonies, and many of the smaller satellite colonies have been exterminated. This process of fragmenting large colonies into smaller colonies, and then working to exterminate the smaller colonies, was probably used in the past to break up large prairie dog complexes in the United States. This complex in northern Mexico was probably the best contemporary example of how a prairie dog colony complex would have looked prior to settlement of the Great Plains.

In the absence of poisoning and plague, it has been repeatedly demonstrated in the past 50 years that prairie dogs have the capacity to recolonize and reoccupy previously occupied habitat (Table 2). Given the centuries that this species had to colonize the Great Plains and its extensive range distribution, the black-tailed prairie dog likely expanded into most of the available suitable habitat and obtained some level of equilibrium with its environment. For example, the glaciated plains of north-central Montana (which includes Phillips and Blaine Counties) were heavily impacted by continental glaciation; however, since the end of the Pleistocene, prairie dogs appeared to be able to establish colonies in much of this area and to occupy 6%-8% of the landscape.

No one has articulated which factors likely limited prairie dog populations prior to settlement. We do not know if it was availability of suitable habitat, soils, disease, drought, severe winters, flooding, predation, interaction with large ungulates, or a combination of these factors. In much of the shortgrass and mixed-grass prairie, little in the prairie environment seems to represent a barrier to prairie dog colony growth. The topography and vegetation are generally well within the range of habitat that prairie dogs can colonize (Knowles and Hagen 2002). Thus, we hypothesize that at the time of settlement of the Great Plains, black-tailed prairie dogs were up against the habitat limitations of their environment, and that active colony sizes fluctuated in relation to environmental perturbations. The most important of these would have been fire, bison grazing patterns, extended long-term drought, and periods of excessive precipitation. The response of prairie dog populations to these perturbations may have varied across their range. For example, drought in the eastern tallgrass portion of their range would have allowed opportunities for expansion, but drought on the western semiarid portion of the prairie dog range would be met with reduced productivity (Knowles 1987). Such environmental perturbations likely influenced prairie dog numbers more than any settlement activities, exclusive of poisoning.



### **Documented Prairie Dog Declines**

In western North Dakota, Bishop and Culbertson (1976) provided an account of prairie dog decline within the Medora Ranger District. Bailey (1926) stated that prairie dog colonies within the area subsequently studied by Bishop and Culbertson (1976) were already being poisoned by 1913. The US Biological Survey and North Dakota Department of Agriculture assessed the prairie dog situation in this area in 1915. By the time of the accounting of prairie dogs in 1939-42, government-organized poisoning had gone on for at least 24 years; thus, presettlement prairie dog acreage in this area would have been considerably greater than reported by Bishop and Culbertson (1976). Within the Medora Ranger District, prairie dogs declined from 5,512 ha in 1939-42 to 404 ha in 1970-72. During this period they documented an 89% decline in the number of prairie dog colonies and a 93% decline in the area occupied by prairie dogs. A recent mapping effort found about 1,576 ha and 111 colonies in the same area (Knowles and Hagen 2002). In 1939 prairie dogs were primarily distributed along the Little Missouri River and the lower portions of some of its tributaries, and all that remained of the large colony complex between Belfield and Amidon were three small colonies. In 2002 only six prairie dog colonies remained along the Little Missouri River, and in the area encompassed by the large historic Belfield-Amidon colony complex, 31 small-to-medium colonies were located (Knowles and Hagen 2002). We updated the prairie dog population trend reported by Bishop and Culbertson (1976) with current information on prairie dogs within the Medora Ranger District (Table 3). These data suggest partial recovery since 1970, but still far short of their abundance in 1942.

In Montana, densities of prairie dog colonies have also declined. For example, Flath and Clark (1986) reported that 2.8% of the land area that they examined were occupied by prairie dog colonies. They used this information to estimate prairie dog abundances across Montana, and they calculated that there were 595,300 ha of prairie dog colonies at the time of settlement. However, their survey area did not include north-central Montana, the Crow Reservation, or the Northern Cheyenne Reservation, all of which contain areas of excellent prairie dog habitat. Thus, the area probably contained significantly more prairie dogs than estimated by Flath and Clark (1986). A better, more comprehensive statewide estimate of presettlement prairie dog abundance in Montana would be considerably higher than 600,000 ha. As of the mid-1980s, Flath and Clark (1986) reported that prairie dogs in Montana occupied only about 50,600 ha, which represented

TABLE 3

SUMMARY OF BLACK-TAILED PRAIRIE DOG COLONIES IN THE MEDORA RANGER DISTRICT, WESTERN NORTH DAKOTA, 1939-2002

Time period	Number of colonies	Area (ha)	Percentage of area occupied
1939-42	392	5,512	1.07
1957-65	91	1,217	0.23
1970-72	44	404	0.07
2002	111	1,576	0.30

Source: Data from 1939 through 1972 are from Bishop and Culbertson (1976); subsequent data collected by the authors.

a decline of 90% or more from their presettlement population estimates. In the mid-1990s a survey of prairie dogs in Montana produced a minimum estimate of about 26,720 ha of prairie dogs or 47% lower than in the late 1980s (FaunaWest 1998). In most areas within the geographic range distribution of prairie dogs in Montana, the percentage of the landscape occupied by prairie dogs was less than 0.5% (Fig. 3) (FaunaWest 1998).

Contractions of the prairie dog's distributional range are apparent in both North Dakota and Montana. In North Dakota, Bailey (1926) noted that black-tailed prairie dogs occurred along the Missouri River bottomlands, from the Standing Rock Reservation to the confluence of the Yellowstone River near Montana. This same area today is devoid of prairie dogs (Knowles and Hagen 2002). Moreover, prairie dogs have been virtually eliminated from a large agricultural area in the central portion of their range distribution in North Dakota. Prairie dog distribution in North Dakota is now limited to the Little Missouri River corridor and the Standing Rock Reservation and adjacent areas north of the reservation (Knowles and Hagen 2000).

In Montana, prairie dogs have been greatly reduced on the northern and western portions of their range. For example, Coues (1875) described the prairie dog as common as he crossed the northern Montana between the Milk River and the Canadian border. This same area today contains only about a dozen colonies. Similarly, in the western range distribution of prairie dogs in Montana, from Shelby south to Whitehall, less than 20 prairie dog colonies remain. Cooper (1868, 1869) described prairie dog colonies along the Missouri River from Fort Benton to the Dearborn River, while the Lewis and Clark expedition reported prairie dogs along the Jefferson River near Whitehall (DeVoto 1953). Now prairie dogs are entirely gone from

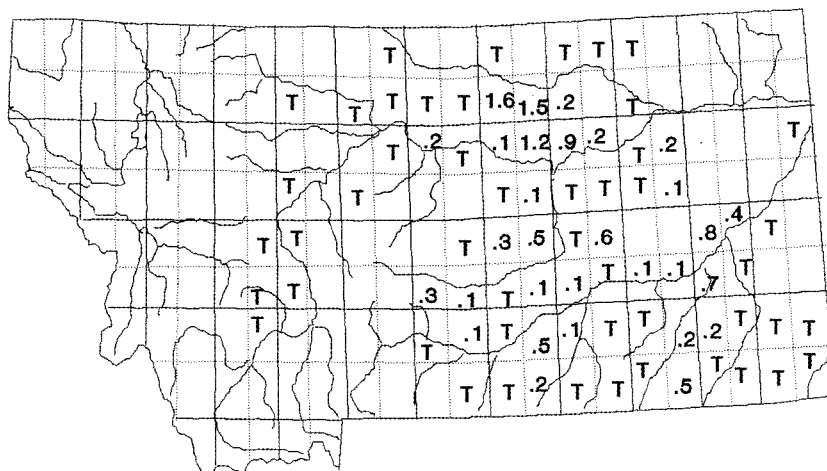


Figure 3. Map of Montana showing the quarter latilong (area encompassed by a half degree of latitude and a half degree of longitude) distribution of the percentage of land area occupied by prairie dogs (data from FaunaWest 1998). (T = less than 0.1%. Other figures represent the percentage of land area occupied rounded to nearest tenth percent.)

these areas of the Missouri and Jefferson Rivers. Additionally, on his trip down the Yellowstone River to the Bighorn River, Stuart (1902) used the words “many” and “plenty” to describe prairie dogs. Today there are only five known colonies in this same reach of the Bighorn River, and another five colonies are known to exist on the Yellowstone River bottomlands, from the Bighorn River to the Missouri River (FaunaWest 1998). As in North Dakota, the best prairie dog habitat in Montana is now used for agricultural croplands. There can be little question that Flath and Clark’s (1986) estimate of a 90% or greater reduction in prairie dogs is accurate and likely conservative.

### Obligate and Commensal Species

Finally, perhaps some of the strongest evidence of biological ubiquity for prairie dogs is the presence of obligate species. The black-footed ferret (*Mustela nigripes*) is a specialized prairie dog predator, and the mountain plover (*Charadrius montanus*) is a shorebird adapted to dryland areas with extremely short vegetation and an abundance of bareground such as that found in prairie dog colonies. To have an obligate predator (Hillman and

TABLE 4  
COUNTIES WITHIN THE RANGE OF BLACK-TAILED PRAIRIE DOGS AND  
COUNTIES WITH DOCUMENTED BLACK-FOOTED FERRET SPECIMENS

State	Number of counties within the black-tailed prairie dog range	Number of counties with ferret specimens	Percentage
Arizona	2	0	0
Colorado	29	10	34
Kansas	66	12	18
Montana	39	16	41
Nebraska	79	17	22
New Mexico	22	3	14
Oklahoma	38	4	11
South Dakota	32	20	63
Texas	107	7	7
Wyoming	14	8	57
Total	428	97	23

Source: Data from Anderson et al. (1986).

Clark 1980) and commensal bird species (Knowles et al. 1982) associated with a rodent community is truly remarkable. The test for dependence of these two species on prairie dogs has already been performed: Remove the prairie dogs and see what happens. The black-footed ferret was taken to the brink of extinction (Clark 1989), and the mountain plover was reduced from a common (Coues 1878; Silloway 1903; Saunders 1911) to a rare (Leachman and Osmundson 1990) grassland bird species. Moreover, ferrets require large prairie dog complexes (>4,500 ha) to maintain viable populations (Forrest et al. 1988; Harris et al. 1989). Specimens of ferrets have been collected throughout the range of the black-tailed prairie dog (Anderson et al. 1986), indicating that areas surrounding these collection sites at one time supported large prairie dog complexes. Nearly a quarter of the counties within the range of the black-tailed prairie dog has one or more recorded ferret specimens (Table 4). This represents a minimum estimate of black-footed ferret distribution by county, since the presence of this species was not easily detected and no systematic effort was made to document its distribution prior to widespread extirpation. We consider specialization to prairie dogs as prey and specialization to unique habitat provided by prairie dog colonies as additional evidence supporting the early estimates of prairie

dog abundance made by Merriam (1902), Burnett (1918), Nelson (1919), Flath and Clark (1986).

### Discussion

Virchow and Hygnstrom (2002) mischaracterize the existing evidence, leading to an inaccurate picture of prairie dog distribution and abundance prior to European-American settlement of the Great Plains. Their assertion (Virchow and Hygnstrom 2002) that the lack of historical accounts of prairie dog abundance, together with only a few accounts of large colonies, can be taken as evidence that prairie dogs were not abundant prior to settlement of the Great Plains is not accurate. Our studies suggest that they have focused on a limited number of early accounts of prairie dog abundance, and that they have not considered a much wider range of available information that is available and that clearly shows that prairie dogs were a widespread and common species on the Great Plains.

Nothing about early explorations can be represented as a systematic survey for prairie dogs. Virchow and Hygnstrom (2002) state that Lewis and Clark, Maximilian, and Hayden took meticulous notes and would not have failed to record prairie dog colonies. However, it is apparent that these naturalists encountered many prairie dog colonies and failed to note their existence once the novelty of the species wore off. Moreover, there are sufficient accounts of large colonies throughout the range of the black-tailed prairie dog prior to or at the time of settlement to conclude that prairie dog colonies had the potential to grow to expansive sizes given the appropriate habitat.

There is little evidence to suggest that prairie dogs actually increased with the settlement process; cattle only replaced large herds of native ungulates that, by numerous historic accounts, created overgrazed conditions at least as extensive as those produced later by cattle (Hart 2001). Prairie dog control with poisons was already in practice by the 1880s, before much of the range had been settled. Merriam's (1902) interview of a few ranchers claiming a dramatic increase in prairie dogs and hearsay evidence of an increase in prairie dogs in one location in Kansas falls far short of a rangewide systematic survey of prairie dogs that could reliably estimate prairie dog populations and trends following settlement of the Great Plains. The Fort Belknap Reservation represents a large block of prairie habitat not influenced by homesteading; and the accounting of prairie dogs in 1921 on the reservation showed 8% of the rangelands occupied by prairie dog colonies. Similarly, land surveys immediately prior to homesteading in southeastern

Montana (Flath and Clark 1986) documented that prairie dogs were widespread and occurred in extensive colonies. Government records of prairie dog poisoning during the early 1900s provide at least some quantitative estimate of the abundance of prairie dogs at the time of settlement. These records are consistent with other estimates of prairie dog abundance. In some areas of the northern Great Plains, physical evidence of expansive prairie dog colonies remains visible on the landscape, and remnant prairie dog colonies outline what were once much larger colonies.

Our knowledge of prairie dog ecology suggests that, in the absence of poisoning and plague, prairie dog colonies expand to fill suitable habitat, that dispersing individuals can colonize suitable sites up to 10 km from existing colonies, and that small colonies can merge into larger colonies. Prior to the introduction of plague in black-tailed prairie dogs on the Great Plains in 1946 (Cully 1989), we are unaware of any disease pathogen in prairie dogs that would have significantly limited prairie dog populations over a broad area. Also, prior to the 1880s, prairie dog poisoning was not significant. Prairie dogs had thousands of years to seek out and fill suitable habitats in the Great Plains, and they eventually developed an extensive geographic range distribution covering more than 160,000,000 ha. In combination with the other prairie dog species, black-tailed prairie dogs provided sufficient habitat for development of an obligatory mammal predator and a commensal bird species.

Three conspicuous North American wildlife species were originally characterized by extreme biological success and abundance. These were the passenger pigeon (*Ectopistes migratorius*), the bison (*Bison bison*), and the black-tailed prairie dog (*Cynomys ludovicianus*). The passenger pigeon was hunted to extinction by 1914 (Terres 1991). The bison was reduced to less than 1,000 individuals by the late 1800s (McHugh 1972). And the black-tailed prairie dog was reduced to a fraction of its former range by the mid-1900s (Koford 1958; Clark 1989). Each of these species was highly successful biologically, and the collapse of their populations was related to unregulated "take." Like the bison, the black-tailed prairie dog was specifically targeted for extinction by the federal government. The effort to exterminate prairie dogs is well documented.

The exact presettlement abundance and distribution of prairie dogs will never be known, because the people who had opportunity to observe prairie dogs prior to settlement of the Great Plains did not have the means or interest to quantify them. However, multiple lines of evidence make it clear that prairie dog numbers are significantly below those of the late 1800s.

Also, it is apparent that the prairie dog's failure to reestablish multiple large complexes has left at least two associated species facing a real threat of extinction and other more broadly adapted associated species, such as the burrowing owl (*Athene cunicularia*) and ferruginous hawk (*Buteo regalis*), with greatly depleted populations on the Great Plains. These obligate and associate species could not have evolved and thrived over the course of several thousand years without abundant prairie dogs as hosts. Their decline is testimony to the fact that prairie dogs no longer occur in numbers that function on an ecosystem level as they once did. The real question now is not how far prairie dogs have fallen, but how we should restore them to numbers that will conserve their important ecosystem role in the future.

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