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DISTRIBUTION AND ABUNDANCE OF BLACK-TAILED PRAIRIE DOGS IN THE GREAT PLAINS: A HISTORICAL PERSPECTIVE

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ABSTRACT—It is a common belief that the black-tailed prairie dog (*Cynomys ludovicianus*) was an extremely abundant species throughout the Great Plains prior to European settlement. We examined accounts from explorers, naturalists, and travelers in the Great Plains in the 19th and 20th centuries and found few that adequately document the relative abundance and distribution to support this view. Immense prairie dog colonies existed in the western Great Plains before Euro-American settlement, but it appears that the eastern Great Plains supported only localized populations. Historic accounts also indicate that the easternmost extent of the black-tailed prairie dog's range before settlement was at or west of the 98th meridian, which is largely west of the tallgrass prairie. We believe that the recent determination to list the species as threatened under the Endangered Species Act is flawed because presettlement distribution and abundance were overstated.

KEY WORDS: prairie dog, historic population, endangered species, grasslands

Introduction

In recent years prairie dogs have received national prominence, appearing on the front covers of *National Geographic* (Long 1998) and *Smithsonian* (Dold 1998) and becoming a major focus of the *National Wildlife Federation* (2002). Prairie dogs have also inspired debate within the scientific community; some arguing that the black-tailed prairie dog is a keystone species within the grassland (Miller et al. 1990; Kotliar 2000). Others have argued that its demise is imminent (Wuerthner 1997) and that its ecosystem should be preserved (Miller et al. 1990). The area occupied by colonies of black-tailed prairie dogs reportedly has been reduced by more than 98% since 1919 (Summers and Linder 1979). Knowles (1998a) suggested that a greater than 98% reduction in the original range occurred

within 50 years after Euro-American settlement on the Great Plains. Miller et al. (1990) reported “a 98% decline in the original geographic distribution of the four species of prairie dogs.”

In contrast, many people view prairie dogs as pests and advocate control of their numbers and distributions. This argument has historical precedence. Seton (1953) noted that the “war on prairie dogs” began in 1880. By 1921 “132,000 farmers and stockmen” had joined the federal government in using toxic baits on prairie dogs and ground squirrels (Bell 1921). Universities and the Division of Wildlife Services of the US Department of Agriculture–Animal and Plant Health Inspection Service (USDA-APHIS) continue to provide landowners with information and assistance in controlling prairie dogs (Hygnstrom et al. 1994), while the US Fish and Wildlife Service in the US Department of Interior has asked for the species to be protected (US Department of Interior 2000). These contrasting perspectives lead to differences in public policy and underlie the present debate.

Recent controversy in the environmental and agricultural communities was stimulated by petitions that asked the US Fish and Wildlife Service to list the black-tailed prairie dog (*Cynomys ludovicianus*) as a threatened species throughout its known historic range (US Department of Interior 1999). The historical range of the black-tailed prairie dog covered parts of eleven US states and small portions of Canada and Mexico. Today the range still includes all but one of the eleven US states. The petitions were based on perceived contractions in historic range boundaries and dramatic declines in prairie dog abundance. The federal threatened status is given to a species likely to become endangered over a significant portion of its historic range. The US Fish and Wildlife Service evaluated the petition, status information, and comments from the public and concluded that the threatened status was warranted, but precluded it because of higher priorities (US Department of Interior 2000).

One justification for the federal ruling is that the historic eastern boundary of the prairie dog has moved westward. The US Fish and Wildlife decision notes “significant range contractions [in the] eastern portion of the species’ historic range [tallgrass prairie] in Kansas, Nebraska and Oklahoma” (US Department of Interior 2000).

A second justification for the ruling was based on the perception that the black-tailed prairie dog was extremely abundant across its range before Euro-American settlement of the Great Plains. Modern historian Merrill J. Mattes (1969) noted that the prairie dog was one of the species that “domi-

nated the wildlife scene along the Platte.” Costello (1969) wrote that the prairie dog was “among the most important grazing mammals of the Great Plains.” The US Fish and Wildlife Service estimated that historically the black-tailed prairie dog could have occupied about 20% of its 159.4 million-ha range in the Great Plains (US Department of Interior 2000). The idea of a historic superabundance of the black-tailed prairie dog remains a basis for the federal management plan.

Considerable controversy exists over the validity of these perceptions and estimates. We reviewed accounts of early Euro-American explorers and other travelers in the Great Plains to determine the relative abundance and geographic distribution of the black-tailed prairie dog during the pre-settlement and postsettlement periods, from 1800 to 1860 and from 1860 to 1950.

Methods

We examined more than 70 published historic accounts, reviews, and summaries of the 19th and early 20th centuries. We also examined 17 reports of the US Bureau of Biological Survey from 1910 to 1939. The bureau was the agency responsible for controlling prairie dogs since the 1880s.

The year 1860 was used as the demarcation between presettlement and postsettlement periods on the Great Plains. We made this distinction as a generalization, knowing that some areas of the southern Great Plains were settled as early as the 1830s and others in the northern Great Plains as late as the 1890s.

We included several accounts that examined the Lewis and Clark expedition (Coues 1893; Quaife 1916; Burroughs 1961; Thwaites 1969; Moulton 1987; Cutright 1989). We also included journals of Brackenridge ([1816] 1904), Bradbury (1819), and Maximilian ([1834] 1906) and an account of Audubon’s journey (McDermott 1965) that followed the Missouri River through the northern Great Plains.

For Euro-American expeditions that traversed Kansas and Nebraska, we included historical accounts of Pike (Jackson 1966), Stuart et al. (1935), Wyeth (Thwaites 1905), Long (Fuller and Hafen 1935), Abert ([1845] 1941), Carleton (1845), and Warren (1875; Hanson 1996). The Wyeth expedition included naturalists Townsend and Nuttall and the Long expedition included naturalists James and Say. We also examined the accounts of individuals traveling the presettlement Great Plains, including DeSmet

(Chittenden and Richardson 1905), Irving (1835), Wislizenus (1839), and Sage (Hafen and Hafen 1956). We examined Baird's (1857) report to the US Congress on the zoology of the West. For the Oregon Trail period of 1840 to 1860, we examined reports by Oregon Trail travelers, relying heavily upon Mattes (1969) and Parkman ([1846] 1910).

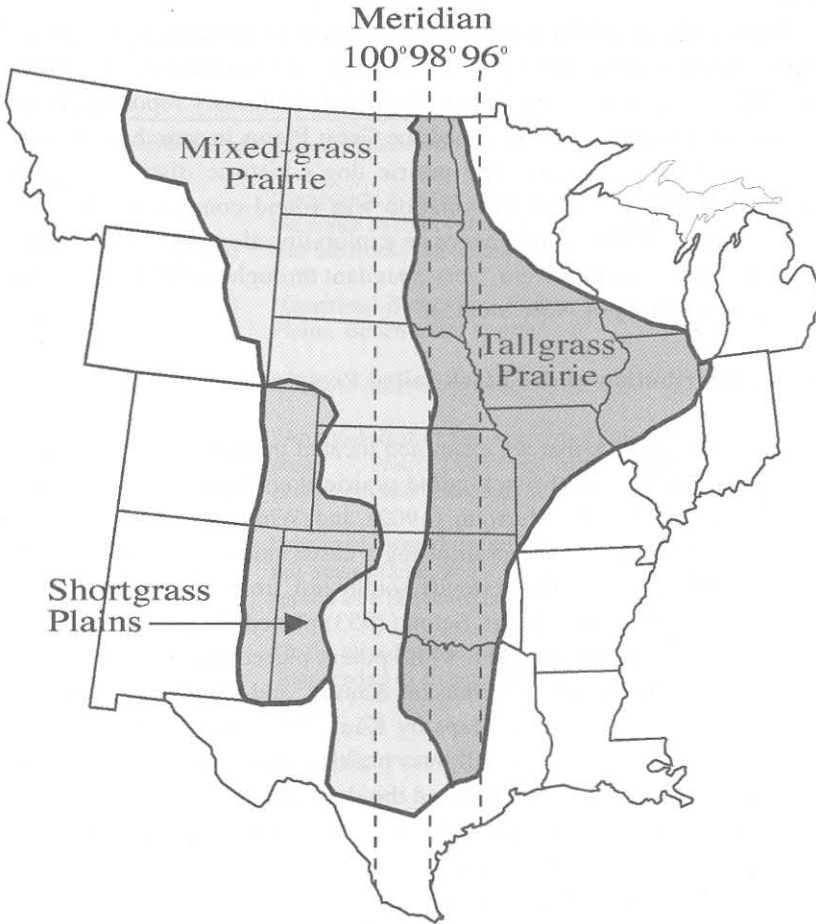
For the early settlement period of 1860 to 1900, we included the reports of topographical engineers, geologists, and naturalists that were published in transactions of scientific organizations (Hayden 1863; Brous 1877; Baker 1889; Mead 1899). We also reviewed accounts published in the popular press (Merrill 1876; *Sidney Telegraph* 1876; Messiter 1890; *Alliance Times*, 1891; *Gering Courier* 1893-95).

We included US government documents from the late 19th century (US House 1888) and early 20th century documents including two yearbook accounts from the US Department of Agriculture (Merriam 1902; Bell 1921). We did not rely heavily on the original field notes of the early explorers and travelers because of the difficulty and time involved in interpreting them. Because of time constraints we did not include a survey of research museum voucher specimens of prairie dogs.

We used the term *distribution* to mean geographic range. The use of *distribution* as a measure of abundance has caused some confusion among recent discussions in modern scientific publications. We used the definition of *superabundance*, "given to or marked by unrestrained abundance," from the *American Heritage Dictionary*, 4th ed. (2000). We used Kaul's (1975) *Native Vegetation of Nebraska* (circa 1850) to evaluate the historic distributions of the Great Plains prairie types and associated black-tailed prairie dogs (Fig. 1).

Results and Discussion

Our literature search revealed several detailed reports on the natural history of prairie dogs (Maximilian [1834] 1906; Irving 1835; Carleton 1845; Coues 1893). We were surprised, however, by how rarely the abundance and distribution of prairie dogs were mentioned among reports from early expeditions of the US West. For example, naturalists Townsend and Nuttall made no mention of prairie dogs while traveling the length of Nebraska in 1834 (Thwaites 1905). Snowden, another naturalist, described only one colony of prairie dogs in his notes while accompanying Warren and his expedition down the length of Nebraska's Niobrara River in 1855 (Hanson 1996). No other mention of prairie dogs was made in the accounts of Warren's three expeditions (1855-1857) that crossed north-central and



100th meridian	(Seton 1953)
98.5° W	(Merrill 1876)
98th - 99th meridian	(Merriam 1902; Whitaker 1997)
97th meridian	(Hollister 1916; Hall and Kelson 1959)

Figure 1. Great Plains prairie types and authors that documented the easternmost occurrence of black-tailed prairie dogs (Coupland 1992).

western Nebraska, eastern Wyoming, and southern South Dakota (Warren 1875).

During the mid-19th century the Smithsonian Institution produced a comprehensive general report of the zoology of the Great Plains (Baird 1857). The report was a compilation of the natural history reported among the several expeditions that traversed the Great Plains in search of the best route for a Pacific railroad. The prairie dog's historic distribution was mentioned (Table 1) but no information was found concerning its abundance. Kennerly (1859), a member of an exploration along the 35th parallel, says only that prairie dogs were "very abundant throughout Texas and on the Jornada del Muerto of New Mexico."

Historic Distribution of the Black-tailed Prairie Dog

All of the sources that we examined located the easternmost extent of the historic distribution of black-tailed prairie dogs between the 97th and 100th meridians (Fig.1). Merriam (1902) and Whitaker (1997) show in almost identical maps of the prairie dog's easternmost distribution a line about the 98th meridian that extends southward from the South Dakota-Nebraska border to central Texas. Seton (1953) placed the eastern boundary as far west as the 100th meridian while others placed the boundary as far east as the 97th meridian in Nebraska, Kansas, and Oklahoma (Hollister 1916; Hall and Kelson 1959). Maps by Kaul (1975) and Shelford (1963) place the western extent of the tallgrass prairie at the 98th meridian.

Prairie dogs historically inhabited the shortgrass plains (Hall 1955), or steppe, and mixed-grass prairie (Clements and Shelford 1939; Shelford 1963) (Table 1). Hall (1955) and Shelford (1963) regarded the black-tailed prairie dog as having a limited occurrence in the tallgrass prairie. Merrill (1876) and Seton (1953) specifically excluded prairie dogs from the tallgrass prairie region while Merriam (1902), Wolcott (1926), Petry and Visser (1926), and McCulloch (1926) generally excluded the tallgrass region in their description of the species' range. Perplexingly Sarvis and Switzer (1926) make no mention of prairie dogs among the original biota of any of the tallgrass or mixed-grass prairies of North Dakota. Nearly all presettlement accounts that included sightings of prairie dogs first located them west of the 98th meridian (Table 2). The one exception we found was Bradbury (1819), who reported on prairie dogs between the 97th and 99th meridians.

In 1903 Lantz described prairie dogs in Kansas as extending to the 97th meridian. He noted that prairie dogs were currently present in but not

TABLE 1

REFERENCES OR INFERENCES TO PRAIRIE TYPES ASSOCIATED WITH THE DISTRIBUTION OF BLACK-TAILED PRAIRIE DOGS

Authors	Quote
<i>Authors generally including the tallgrass prairie</i>	
Baird (1857) [speaking of the Great Plains region]	“the prairie dog has a very extensive distribution, . . . over the entire extent of the region between the Missouri River and the Rocky Mountains.”
Shelford et al. (1926)	“Grassland Biota (True Prairie, Mixed Prairie, Short-grass Plains, Bunch-grass Prairie . . .)”
<i>Authors specifically referencing the tallgrass prairie</i>	
Hall (1955) [Kansas]	“An inhabitant of the short-grass plains. In the long-grass area . . . , Prairie Dogs lived where the Bison cropped the grass short and trampled the soil.”
Jones (1964) [Nebraska]	“occurred formerly nearly to the Missouri River, where . . . tall-grass prairie, and . . . deciduous riparian . . . , evidently served as a barrier to eastward dispersal.”
Shelford (1963) [temperate prairie region]	“In the mixed prairie, extensive grazing and bison and prairie dogs tended to change <i>Andropogon</i> tall grass into short grass.”
<i>Authors generally excluding the tallgrass prairie</i>	
Merriam (1902) [Great Plains]	“ranging easterly from the arid plains toward the humid prairies . . . becomes less and less numerous, till between the ninety-seventh and nintety-eighth meridians he disappears altogether. Not even the luxurious vegetation of the prairies is sufficiently attractive to lure him into the humid belt . . . prefers . . . the dry bunch grass of the plains”
Wolcott (1926) [Kansas]	Lists as component of western Nebraska’s “plains region”
Petry and Visher (1926) [South Dakota]	Lists as component of shortgrass plains or steppe but not among biota of tallgrass prairie
McCulloch (1926) [Kansas]	“more arid grasslands of the western part ”
<i>Authors specifically excluding the tallgrass prairie</i>	
Merrill (1876) [Great Plains]	Uses 98.5° W as eastern boundary
Seton (1953) [Great Plains]	“Eastern limit was near the . . . 100th meridian; for this was the edge of the high Plains.”

TABLE 2

LOCALES OF EASTERNMOST ACCOUNT OF BLACK-TAILED
PRAIRIE DOGS AMONG EARLY WESTERN EXPLORERS

Writer/Expedition (Citation)	Year	Location	Nearest meridian
Lewis and Clark (Thwaites 1969) Ordway/Lewis and Clark (Quaife 1916)	1804	Boyd County, NE	99th
Pike (Jackson 1966)	1806	Great Bend, KS	98th-99th
Bradbury (1819)	1811	Springfield, SD	97th-98th
Brackenridge (1816)	1811	South-central SD	98th
Long/Bell (Fuller and Hafen 1935)	1820	Merrick County, NE	98th
Maximilian (1834)	1832	Southern SD.	98th
DeSmet (Chittenden and Richardson 1905)	1840	Deer Creek, NE [Platte River]	98th-99th
Wislizenus (1839)	1839	South Fork, Platte River, NE	100 th and west
Audubon (McDermott 1965)	1843	Southern SD	99th-100th
Parkman (1846)	1846	Central NE, Platte River	100th

indigenous to Douglas County, Kansas (95°-96° W). Merriam reported a colony in western Kansas that covered an area of "about 300 square miles" (75,600 ha) and implied that it was a recent phenomenon, as it was discussed under the heading "Recent Increase and Spread of Prairie Dogs" (Merriam 1902).

Merriam (1902) argued that agriculture and the concomitant control of predators caused prairie dogs to increase and move into new areas. Authors

have argued that grazing by bison (*Bison bison*) before settlement had encouraged prairie dogs to colonize tallgrass prairie (Hall 1955; Shelford 1963; Truett 2001). Others have noted that grazing by sheep (Clark 1973) and cattle (Hall 1955; Clark 1973) had similar effects during the postsettlement period.

Swenk (1907) noted that after settlement, the distribution of black-tailed prairie dogs “receded . . . west of the 100th meridian.” In contrast, Osborn and Allan (1949) stated that an eastward expansion occurred after settlement. Bailey (1905) reported that “prairie dogs are increasing and spreading over new territory” in Texas, but here, as in Merriam’s account (1902), it is unclear if range expansion or expansion within the range was implied.

It seems likely that black-tailed prairie dogs expanded their range eastward into the newly shortened tallgrass prairie as a result of early settlement and livestock grazing during the mid- to late-1800’s. It seems likely, too, that the eastern limit of the black-tailed prairie dog during the presettlement period in Nebraska was somewhere between the 98th and 100th meridians. By the early 20th century, however, this boundary was perhaps as far east as the 96th meridian.

Jones (1964) reported that prairie dogs were “once found through a large portion of the tall-grass prairie in Nebraska . . . made suitable . . . by grazing of . . . bison.” Jones said that few prairie dog colonies occurred east of the 98th meridian but quoted Swenk, circa 1915, who noted as of 1900 the occurrence of a prairie dog town in Cuming County, Nebraska (96.5° W). Jones’s distribution map (1964) indicates an eastern boundary that undulates along a north-to-south line between the 97th and 98th meridians. A second line between 96.5° and 98° W indicates the easternmost boundary of the postsettlement (or circa 1900) distribution. Swenk (1907) noted that “formerly prairie dogs extended eastward nearly across the state, and was so noted by early explorers.” Our review of records from early explorers did not substantiate this claim.

Accounts of travelers along the Oregon Trail indicate that prairie dog colonies were present along the Platte River and its tributaries in Nebraska during the presettlement period. Today, prairie dog colonies still commonly occur wherever rangelands still exist within the Central Platte and North Platte River valleys of Nebraska. Major Stephen Long reported an attempt to drown or flood out the animals on the upper reaches of the Arkansas River in Kansas (Fuller and Hafen 1935). Lewis and Clark were near a river or creek in Nebraska when they likewise attempted to flood out prairie dog samples from a colony (Thwaites 1969).

Historic Abundance of the Black-tailed Prairie Dog

We did not find that early explorers reported on the regional abundance of black-tailed prairie dogs. We did find reports of very large colonies of prairie dogs and extensive areas of the shortgrass plains and western portions of the mixed-grass prairie inhabited by them. Most of these reports occurred after 1860 in the postsettlement period.

The presence of colonies in the mixed-grass prairie of Montana was reported by several of the early explorers of the Upper Missouri River area (1804-34), including Lewis and Clark (Thwaites 1969) and Maximilian ([1834] 1906), but only Lewis mentioned the size of a colony. Near the mouth of the Marias River in Montana, Lewis notes "we saw the largest collection of the burrowing or barking squirrels that we had ever yet seen; we passed through a skirt of the territory of this community [prairie dog colony] for about 7 miles" (5 June 1805, Moulton 1987: vol. 4: 258). Reports near the Wyoming-Nebraska border by Parkman ([1846] 1910) and Wislizenus (1839) state that there were "miles" of colonies (Table 3). Lewis's statement is noteworthy, because it provides an approximation of the relative abundance of prairie dogs that he and Clark had encountered previously along their journey across the Great Plains.

Later reports during the postsettlement period by Hayden (1863), Baker (1889), and Messiter (1890) noted very large colonies in the mixed-grass prairies of South Dakota, Kansas, and Montana. Also, Merriam (1902) reported a colony in the shortgrass plains and mixed-grass prairie of Texas that "covered over 25,000 square miles" (Table 3). He noted that colony sizes of "20 to 30 miles [were] . . . not rare" (Merriam 1902). Forrest et al. (1985) reported two historic colonies, each 100 km in length, in Wyoming and Montana. We were not able to determine if any of these extensive colonies had existed prior to settlement.

We did not find equally large colonies reported in the tallgrass prairie. Clark, Lewis, and Bradbury reported prairie dog colonies in or near the tallgrass prairie of southeastern South Dakota that were relatively small in size (Table 4). These sizes range from about 900 m (Thwaites 1969) to 1.6 km (Brackenridge [1816] 1904) in length. We found no mention by Audubon of the size of colonies in this region (McDermott 1965). On his trip up the Missouri River in 1843, he stated only that he saw "a considerable village of Prairie Dogs" just below Fort Pierre, South Dakota.

We noted inconsistencies and problems with analysis of historical accounts. Observers sometimes reported the area of the colony and some-

TABLE 3

**EVIDENCE OF VERY LARGE COLONIES AND HIGH DENSITIES
WITHIN THE SHORTGRASS PLAINS AND MIXED-GRASS PRAIRIE**

Author (Citation)	Locale/Date	Quote
Merriam (1902)	Western Texas c. 1880s to 1900s	“one is known which measures about 250 miles one way by 100 to 150 miles the other, covering an area of about 25,000 square miles”
Baker (1889)	Central Kansas (c. 100° W), 1880s	“Exceedingly numerous; one ‘dog town’ being more than sixty miles in length”
Mead (1899)	Kansas, 1859	“Prairie dogs were innumerable. The divide between the Saline and Solomon in Ellsworth County and west was a continuous dog town for miles”
Wislizenus (1839)	WY-NE border, 1839	“can be spread over an area of several acres or even miles”
Sage (Hafen and Hafen 1956)	WY- NE area, 1841	“seen large settlements of them in high arid prairies”
Parkman (1846)	WY-NE border, 1846	“The number of prairie dogs was astounding . . . [the land] was thickly covered, for miles, together”
Hayden (1863)	Southwestern SD, 1863	“The largest one [prairie dog colony] I have ever seen is near the Black Hills, . . . though some times interrupted . . . covers . . . over fifty square miles.”
Messiter (1890)	Northeastern MT (Milk River), before 1890	“In this part of the country there were immense numbers of prairie dogs whose towns extend sometimes for thirty or forty miles”

times in one rather than two dimensions. Anything can be presumed about the measure of the dimension not mentioned. Both modest and enormous colonies were reported by individual travelers along the same route of the Oregon Trail but in different years. For example, Joel Palmer (1845-46) noted that prairie dog colonies along the Platte River were from 100 to 500

TABLE 4

HISTORIC QUOTES OF ACTUAL OR RELATIVE SIZE OF PRAIRIE
DOG COLONIES ON THE GREAT PLAINS

Expedition (Citation)	Date	Locale	Quote
Lewis and Clark (Thwaites 1969)	1804	Southeast SD	“970 yards long and 800 yards wide . . . those animals are <i>numerous</i> ” (Clark) “a plain . . . one mile . . . and . . . breadth of three miles . . . intirely occupied. . . this animal appears <i>here</i> in infinite numbers” (Lewis) [italics ours]
Lewis and Clark (Coues 1893)	1804	Recount of expedition	“[towns] occupy . . . several hundred acres (Lewis)
Brackenridge (1816)	1811	Southern SD	“At least a mile in length”
Bradbury (1819)	1811	Southern SD	“Numerous colonies” [in the Great Bend area]
Irving (1835)	1835	Cross Timbers, OK	“about thirty acres” [a colony described]
Parkman (1846)	1846	Horse Creek, WY-NE border	“[the land] was thickly covered, for miles, together”

acres in size (Mattes 1969). However, in 1851 James Bowen reported “prairie dog villages covering dozens of square miles, containing more inhabitants than New York City” (Mattes 1969). In 1849, R.C. Shaw recorded the plains as “completely honeycombed” with colonies (Mattes 1969), but his observations did not include scale or context.

We found that the US Department of Agriculture’s annual reports from 1901 to 1939 and the 1901 Yearbook usually included descriptions of the effort and efficacy of the federal government’s program for controlling prairie dogs rather than estimates of prairie dog abundance. The species of prairie dogs often were not identified in these reports, but considering the states mentioned, we assume that estimates mostly represented the range of

the black-tailed prairie dog. Henshaw (1912) noted that some colonies "occupy many thousand acres." Nelson (1919) estimated overall prairie dog abundance on public and private lands in the US West at 40,000,000 ha (400,000 km²). Agents of the federal government reportedly treated "1,365,429 acres of Government lands" in 1916 (Bell 1921). Nelson (1918) reported "3,500,000 acres of Government land . . . practically freed" of the rodents. In 1924 Nelson stated, "This brings the total acreage treated for control of the animals to 13,457,197 on Federal, and 124,880,786 on State and private lands." Gabrielson (1939) reported that 14,186,000 ha were treated in 1939 for all rodents, including prairie dogs.

One estimate of abundance of prairie dogs at the end of the 19th century is incredible. According to Wuerthner (1997), "Merriam calculated that prairie dogs occupied some 700,000,000 acres (2,800,000 km²) of the west in the late 1800s." This estimate presumably included all four prairie dog species in the US. By this estimate, the four species of prairie dogs in the US easily would have had colonies covering every hectare of the Great Plains!

More recently, naturalist Mathieson (1987) noted that the "Chisholm Trail [was] . . . surrounded by one huge town . . . from south Saskatchewan and North Dakota to southeast Arizona and Texas." Another estimate at the end of the 20th century by the US Fish and Wildlife Service seems as incredible as Merriam's estimate, a finding that black-tailed prairie dogs historically covered 1,554,000 km² in the Great Plains (US Department of Interior 2000). This estimate is equivalent to a colony of black-tailed prairie dogs covering the entire state of Nebraska and 70% of Oklahoma.

The problem of estimating prairie dog populations that existed prior to or shortly after Euro-American settlement is made more difficult by estimates that do not have references and by misrepresentations of prior estimates. For instance, Bonham and Lerwick (1976) give no reference to the statement "prairie dog populations . . . during the 1870's was estimated to be five billion." The figure may have come from Seton (1953) who said "we probably had in round number 5,000,000,000 of the Blacktailed species . . . during the latter part of the last [19th] century." Also, Summers and Linder (1979) assumed that Nelson's (1919) estimate of "100,000,000 acres" only included black-tailed prairie dogs rather than all US species of prairie dog.

We postulate that the late 20th century perspective of such historical superabundance is biased by inflated estimates in the annual reports of the US Department of Agriculture. In particular, Nelson's (1924) annual report indicated that efforts to control prairie dogs occurred on an area almost 16,000,000 ha greater than the area he earlier estimated to be inhabited by

prairie dogs! (Nelson 1919) It is true that control may have been repeated on some areas more than once, but this still does not explain what appears to be an exorbitant estimate of the area under control.

Wuerthner (1997), in making a case for threatened status, contrasted the immense historic colonies in the shortgrass plains and mixed-grass prairie of Texas and Montana with their occurrence in today's landscape, where "you can travel hundreds of miles of potential prairie dog habitat, and never see a single individual [prairie dog]." Distribution patterns of prairie dog colonies in the Great Plains are difficult to determine from the historical record. However, Bailey (1905) noted that prairie dogs in Texas occurred in "scattered colonies" and that colonies existed "perhaps 10 to 20 miles [apart]." Lacking historic accounts to the contrary, we argue that the distribution of black-tailed prairie dog colonies was largely heterogenous and that distances between colonies were most often greater than distances across a colony. Bailey (1926) reported that North Dakota was "not fully occupied" by prairie dogs and those found were "mostly west of the Missouri River." He also noted that it is "fortunate that they [prairie dogs] are colonial . . . and have scattered distribution, so that the country [North Dakota] is not fully occupied" (Bailey 1926). Both statements suggest a relatively uneven distribution pattern.

Wuerthner (1997) implied that Lewis and Clark found an "infinite" number of prairie dogs along their entire journey, stating that "Lewis crossed a town [of prairie dogs] more than 7 miles wide. The expedition leaders described prairie dog numbers encountered along their journey as 'infinite' (Coues 1893)." Yet this appears to misstate Coues in reporting the expedition's findings, as we found no such quote in Coues (1893). However, in Thwaites (17 September 1804, 1969), Lewis noted that "this animal [sic] appears here in infinite numbers" between Corvus Creek and the Missouri River in southeastern South Dakota (Table 4). Thus, the comment was in regard to a single colony rather than in the context of the entire journey.

We did find in Coues (1893) an apparent reference to prairie dog abundance on that historic route. Lewis wrote that prairie dogs "occupy in this manner several hundred acres of ground." Clark, in Thwaites (1969), also reported "noumerous" prairie dogs (Table 4). Both comments could be interpreted either in terms of a single colony or of an entire journey. Pike noted "innumerable hosts" of prairie dogs in reference to a particular colony that extended "over two and three miles square" and not to a larger geographic area (Jackson 1966).

One reason for the preponderance of reports in the Upper Missouri River area may be that Lewis and Clark, Brackenridge, Bradbury, and Maximilian each traced the same route up the Missouri River and may have observed the same colonies of prairie dogs. Another reason may be that explorers, scientists, and travelers were more likely to report prairie dog colonies observed first rather than those colonies observed later as the novelty of the animal's appearance wore off. In reviewing the fastidious and detailed notes of Maximilian, Lewis, Clark, Hayden, and others, however, we believe this to be an unlikely bias.

Later, Hayden (1863) reported that prairie dogs were "very abundant from the mouth of the Niobrara [northeastern Nebraska] to the mountains [Rockies]." Swenk (1907) also mentioned that reach of the Niobrara River and indicated that prairie dogs had receded westward in Nebraska "except in the Niobrara valley where it extends eastward to the mouth of that river."

A few travelers from of the Oregon Trail period reported large areas occupied by prairie dogs along the Platte River (Mattes 1969), whereas explorers and travelers from earlier periods recorded far smaller areas, both along the river corridors and elsewhere. One explanation of this contradiction may be the disturbance associated with travelers along the Oregon Trail. Trampling and overgrazing by livestock have been hypothesized as encouraging prairie dogs (Koford 1958). During the Oregon Trail period, the Platte River valley in Nebraska was home to the travel lanes and encampments of hundreds of thousands of travelers and livestock. About 19,000 travelers crossed the Plains between 1840 and 1848, and 234,000 people traveled the Oregon Trail between 1849 and 1860 (Unruh 1979). In 1854 Zilhart noted records that showed 1,000 people and 31,000 livestock had traveled through Fort Kearny by May 22 of that year alone (Mattes 1969). It is our assessment that these travelers left an indelible mark along the Oregon Trail, making it more conducive to prairie dog colonization.

Conclusions and Implications

We conclude that: (1) the historic range of the black-tailed prairie dog extended only to the 98th meridian; (2) historically, the black-tailed prairie dog was much more abundant in the shortgrass plains and mixed-grass prairie within the western portion of the Great Plains than it was in the more eastern tallgrass prairie region; (3) colonies of black-tailed prairie dogs were unevenly distributed across the Great Plains; and (4) little evidence exists for the historic superabundance of the black-tailed prairie dog in the Great Plains.

Recent petitions to the US Fish and Wildlife Service and that agency's subsequent determination of "threatened but precluded" status has impelled nine states within the Great Plains to consider developing management plans for the black-tailed prairie dog. These groups were directed to base their targets and outcomes on presettlement populations and distributions of prairie dogs. Given the poor historical record, only vague determinations can be made. We suggest that the practice of developing management plans on an inadequate historical record is unwise because it can lead to inappropriate conclusions and expectations. We think that some, in their enthusiasm to build a case for threatened status, have exaggerated presettlement estimates or have used postsettlement accounts as presettlement estimates of prairie dog numbers.

Lacking direct evidence on the historic abundance of the prairie dog, the US Fish and Wildlife Service (2000) attempted to estimate the percentage of the potentially suitable habitats historically occupied by prairie dogs. Such models are best analyzed in the context of firsthand historical observations such as those reported here. One report that was submitted to the US Fish and Wildlife Service to support threatened status for the black-tailed prairie dog included a table representing estimates of "historical acreage" of prairie dogs in each of 11 states (C.J. Knowles 1998b, unpublished report). A footnote for 5 of the 11 states read that "no presettlement figure [is] available; estimate based on the *assumption* that the current acreage represents only 1% of presettlement acreage" [italics ours]. This backward extrapolation is a questionable method of generating historical estimates. It is particularly regrettable when such documentation is used to establish state and national population levels for prairie dogs across the Great Plains.

We also found no estimates of the abundance of black-tailed prairie dogs across their range during the presettlement period. The US Fish and Wildlife Service did not include rangewide trends in numbers of black-tailed prairie dogs that span the 19th to 21st centuries. Moreover, estimates of abundance across the 20th century indicate that the rate of rangewide decline of prairie dogs has reversed or slowed dramatically. For example, in 1919, 40 million ha were estimated for all US species of prairie dogs (Nelson 1919). Sixty years later, Summers and Linder (1979) estimated 600,000 ha. We calculate the decline between 1919 and 1979 averaged 656,600 ha lost per year.

By contrast, historically recent range-wide population estimates of the black-tailed prairie dog have ranged between 364,000 in 1961 to 1,686,000 in 1998 (US Department of Interior 2002). Moreover, the most recent range-wide population estimates were 677,000 in 1998, 676,000 and 1,041,000 in

2000, and 1,383,000 in 2001 (US Department of Interior 2002). Granting that differences in survey technique and level of effort were responsible for most of the differences between these most recent estimates, it still seems likely that prairie dog population declines have slowed in recent years.

The Endangered Species Act requires management based upon an understanding of the historical abundance and distribution of a species. We suggest that the presettlement accounts can only be used as background and not as supporting evidence on which to base today's management decisions over such a broad geographic scale. Objectives of a federal plan should be based on comparisons of known long-term population trends with recent trends. Consideration should be given to differences in trends that are currently occurring within each state within the black-tailed prairie dog's historic range.

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