ESTIMATED AREAL EXTENT OF COLONIES OF BLACK-TAILED PRAIRIE DOGS IN THE NORTHERN GREAT PLAINS

JOHN G. SIDLE,* DOUGLAS H. JOHNSON, AND BETTY R. EULISS

United States Department of Agriculture, Forest Service, Great Plains National Grasslands, 125 North Main Street, Chadron, NE 69337 (JGS)

United States Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street SE, Jamestown, ND 58401 (DHJ, BRE)

During 1997–1998, we undertook an aerial survey, with an aerial line-intercept technique, to estimate the extent of colonies of black-tailed prairie dogs (Cynomys ludovicianus) in the northern Great Plains states of Nebraska, North Dakota, South Dakota, and Wyoming. We stratified the survey based on knowledge of colony locations, computed 2 types of estimates for each stratum, and combined ratio estimates for high-density strata with average density estimates for low-density strata. Estimates of colony areas for black-tailed prairie dogs were derived from the average percentages of lines intercepting prairie dog colonies and ratio estimators. We selected the best estimator based on the correlation between length of transect line and length of intercepted colonies. Active colonies of black-tailed prairie dogs occupied 2,377.8 km$^2$ ± 186.4 SE, whereas inactive colonies occupied 560.4 ± 89.2 km$^2$. These data represent the 1st quantitative assessment of black-tailed prairie dog colonies in the northern Great Plains. The survey dispels popular notions that millions of hectares of colonies of black-tailed prairie dogs exist in the northern Great Plains and can form the basis for future survey efforts.

Key words: aerial survey, black-tailed prairie dog, colony abundance, Cynomys ludovicianus, Nebraska, North Dakota, northern Great Plains, South Dakota, Wyoming

As a keystone species, black-tailed prairie dogs modify grasslands in many ways, influencing vegetative structure, grazing by ungulates, and nutrient cycling (Kotliar 2000; Kotliar et al. 1999; Whicker and Detling 1993). Colonies of black-tailed prairie dogs provide habitat for a number of species, including the endangered black-footed ferret (Mustela nigripes—Sharps and Uresk 1990). Ferrets are obligate predators of black-tailed prairie dogs and are nearly extinct because of vast reductions of populations of black-tailed prairie dogs since 1900 (Anderson et al. 1986; Miller et al. 1996).

Some have estimated that black-tailed prairie dogs once occupied between 400,000 and 1 million km$^2$ of the Great Plains before European settlement and have declined by 98% (Mac et al. 1998; Miller et al. 1990; Mulhern and Knowles 1997). Merriam (1902) stated that 1 colony in Texas covered about 65,000 km$^2$. Conversion of grassland to cropland, poisoning and fumigation programs, and sylvatic plague (Yersinia pestis) have decimated populations of the black-tailed prairie dog (Cully 1993; Cully et al. 2000; United States Fish and Wildlife Service 2000). Most remaining colonies are <40 ha in size and are isolated from other colonies (J. G. Sidle, in litt.). Colonies of black-tailed prairie dogs declined to 6,000 km$^2$ in the Great Plains by 1960 (Anderson et al. 1986; Marsh 1984) and are estimated to occupy 3,120 km$^2$ today (P. Gober, United States Fish and Wildlife Service, pers. comm.). Most of
those estimates are based on imprecise and cursory information.

The United States Fish and Wildlife Service (1999) determined that a petition to list the black-tailed prairie dog as threatened under the Endangered Species Act presented substantial scientific information, and the agency later concluded that listing of the species as threatened is warranted (United States Fish and Wildlife Service 2000). Because of the concern about the status of the black-tailed prairie dog, the Forest Service of the United States Department of Agriculture and United States Geological Survey began planning an aerial survey of the northern Great Plains in 1996. We report the results of that survey.

**MATERIALS AND METHODS**

The historic range of the black-tailed prairie dog in the northern Great Plains included the Great Plains–Palouse dry steppe and Great Plains dry steppe provinces of extreme southern Saskatchewan and most of central and eastern Montana, North Dakota west and south of the Missouri River, eastern Wyoming, and most of Nebraska and South Dakota (Bailey 1995; Hoogland 1995). We surveyed the range of the black-tailed prairie dog in Nebraska, North Dakota, South Dakota, and Wyoming between 98°09'W and 107°22'W (Fig. 1). The species largely has disappeared from its range east of 98°W in Nebraska and South Dakota (United States Fish and Wildlife Service 2000).

Line-intercept sampling.—We used line-intercept sampling to estimate the area covered by colonies of black-tailed prairie dogs in the 4-state area. Line-intercept sampling often is used to estimate vegetative canopy coverage and relies on noting points along a transect line where canopy begins and ends (Bonham 1989; Daubenmire 1959; Elzinga et al. 1998; Heady et al. 1959). Lengths of canopy intercepts are divided by length of the line and the resultant is applied to the study area for an estimate of total canopy cover. The accuracy of line-intercept sampling is comparable with other sampling techniques such as quadrats and point interception (Daubenmire 1959; DeVries 1979; Floyd and Anderson 1987; Lucas and Seber 1977).

We flew an aircraft along a series of transect lines and used a global positioning system receiver to record locations where transects intersected boundaries of colonies of black-tailed prairie dogs (Sidle 1999). To reduce sampling error and increase precision, we stratified the survey area into high-density and low-density strata (Caughley and Sinclair 1994; Norton-Griffiths 1978; Thompson et al. 1998). Colonies of black-tailed prairie dogs did not occur randomly in the study area because soil types, slope, and land-use characteristics were heterogeneous and defined habitat features to which black-tailed prairie dogs were sensitive (Campbell and Clark 1981; Proctor 1998; Reading and Matchett 1997; Reid 1954; Stromberg 1975). Moreover, in North Dakota and South Dakota, most colonies occurred on and near large areas of public lands where poisoning was limited, or on tribal lands where limited resources and regulatory constraints limited poisoning and fumigation.
Stratification was based on areas of recently known colonies of black-tailed prairie dogs (high-density stratum) and areas where no colonies were known (low-density stratum). For the high-density stratum, locations of colonies reported by public agencies during 1988–1996 were entered into a geographic information system with the Map and Image Processing System (MIPS\textsuperscript{®}, MicroImages, Inc., Lincoln, Nebraska; the use of company names, software, or trademarks does not imply endorsement by the United States Government). All legal sections of land (2.59 km\textsuperscript{2}) containing known colonies were digitized to create the high-density stratum area of 10,712 km\textsuperscript{2} (Table 1). An array of north–south lines uniformly distributed at 0.86-km intervals intersected the high-density stratum polygons for a total of 7,677 km. The low-density stratum consisted of the remainder of the study area, totaling 358,199 km\textsuperscript{2}. North–south transect lines in the low-density stratum were 13.85 km apart, and lines extended across the range of the black-tailed prairie dog in the study area, excluding the high-density stratum polygons, for a total of 25,387 km.

**Table 1.---Estimates of coverage (km\textsuperscript{2}) for active and inactive colonies of black-tailed prairie dogs in the northern Great Plains. Two estimates (\(\hat{C}\)) are presented: average-density estimate (ADE) and ratio estimate (RE).**

<table>
<thead>
<tr>
<th>State and stratum</th>
<th>Survey area (km\textsuperscript{2})</th>
<th>Length flown (km)</th>
<th>Number of transects</th>
<th>Active colonies, (\hat{C}) (SE)</th>
<th>Inactive colonies, (\hat{C}) (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>ADE (SE)</td>
<td>ADE (SE)</td>
</tr>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
<td></td>
<td>ADE (SE)</td>
<td>ADE (SE)</td>
</tr>
<tr>
<td>High</td>
<td>2,840</td>
<td>2,018</td>
<td>287</td>
<td>193.1 (16.8)</td>
<td>203.2 (15.5)</td>
</tr>
<tr>
<td>Low</td>
<td>138,262</td>
<td>9,908</td>
<td>35</td>
<td>126.4 (70.6)</td>
<td>144.7 (81.7)</td>
</tr>
<tr>
<td>North Dakota</td>
<td></td>
<td></td>
<td></td>
<td>38.7 (5.8)</td>
<td>69.5 (25.6)</td>
</tr>
<tr>
<td>High</td>
<td>1,048</td>
<td>777</td>
<td>129</td>
<td>89.5 (10.4)</td>
<td>103.3 (9.5)</td>
</tr>
<tr>
<td>Low</td>
<td>49,726</td>
<td>3,379</td>
<td>19</td>
<td>36.6 (19.4)</td>
<td>23.0 (11.4)</td>
</tr>
<tr>
<td>South Dakota</td>
<td></td>
<td></td>
<td></td>
<td>9.5 (9.5)</td>
<td>7.6 (7.7)</td>
</tr>
<tr>
<td>High</td>
<td>3,570</td>
<td>2,525</td>
<td>252</td>
<td>308.1 (27.2)</td>
<td>339.6 (24.0)</td>
</tr>
<tr>
<td>Low</td>
<td>107,380</td>
<td>7,748</td>
<td>27</td>
<td>236.4 (77.8)</td>
<td>261.3 (83.4)</td>
</tr>
<tr>
<td>Wyoming</td>
<td></td>
<td></td>
<td></td>
<td>114.2 (48.9)</td>
<td>126.3 (53.0)</td>
</tr>
<tr>
<td>High</td>
<td>3,254</td>
<td>2,357</td>
<td>175</td>
<td>583.6 (44.7)</td>
<td>598.8 (37.0)</td>
</tr>
<tr>
<td>Low</td>
<td>62,831</td>
<td>4,352</td>
<td>19</td>
<td>786.3 (216.6)</td>
<td>733.5 (145.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>177.3 (53.9)</td>
<td>230.5 (68.4)</td>
</tr>
</tbody>
</table>

**Aircraft operations.---**Colonies of black-tailed prairie dogs could be seen from the air because of the conspicuousness of most burrow entry mounds, which measured 2–3 m in width, were barren of vegetation, and often consisted of light colored subsoil (Cincotta 1989; Hoogland 1995). Moreover, graminoid herbivory by black-tailed prairie dogs caused significant zonation and other changes in plant cover near burrows (Bonham and Lerwick 1976; Cincotta 1985; Garrett et al. 1982; Gold 1976; Koford 1958; Whicker and Detling 1993). Bare ground and erosion increased and vegetative structure decreased, and colony appearance therefore differed markedly from that of adjacent unmodified grassland (Munn 1993; Whicker and Detling 1993). Areas of pocket gopher (Geomy\textit{s} bursarius and Th\textit{omomys} talpoides) activity lacked the grazed definition of colonies of black-tailed prairie dogs, and mounds of dirt pushed to the surface by pocket gophers were smaller than mounds in colonies of black-tailed prairie dogs and contained no entrance hole. Mounds of harvester ants (Pogonomy\textit{r}mes occidentalis) were distinguished from mounds of black-tailed prairie dogs by a ring of vegetation around the mound, absence of a burrow hole, and lack of a grazed appearance.

Low-density stratum lines were flown in Nebraska, North Dakota, and South Dakota in 1997. In Wyoming, low-density stratum lines and all high-density stratum lines were flown in 1998. Single-engine, high-wing aircraft were used at an altitude of 152 m and a speed of 145–160 km/h. A global positioning system receiver with $\pm10$ m accuracy and loaded with waypoints was used to navigate to and along high- and low-density strata lines. A computer displayed the aircraft position and high- and low-density...
strata lines on a map and recorded global positioning system coordinates at 1-s intervals (Sidle 1999). Global positioning system input to the computer was annotated to indicate portions of lines that intersected colonies and activity. We judged colonies to be active if we saw black-tailed prairie dogs, fresh burrow excavations, lack of vegetation on burrow mounds, or extensive bare ground. Colonies with heavily vegetated burrows and adjacent ground were classified as inactive.

Analysis.—We developed 2 estimates of coverage (C) of colonies of black-tailed prairie dogs occurring in each stratum (with area A) based on ratios (ri) of lengths of intercepts (yi) of colonies of black-tailed prairie dogs and lengths of lines flown (xi). Lines were indexed by i; i = 1, . . . , n, where n is the number of lines. One estimate, \( \hat{C}_a = \frac{A}{\sum x_i} \), is based upon a simple average of the individual line ratios (\( \frac{y_i}{x_i} \)). The variance of \( \hat{C}_a \) was estimated by \( \hat{V}(\hat{C}_a) = \frac{A^2}{\sum x_i^2} \left( \frac{1}{n(n-1)} \right) \). The ratio estimator was \( \hat{C}_r = \frac{\hat{y}}{\hat{x}} \), where \( \hat{y} = \frac{\sum y_i}{n} \) and \( \hat{x} = \frac{\sum x_i}{n} \). The variance of \( \hat{C} \) was estimated by \( \hat{V}(\hat{C}_r) = \frac{\hat{x}^2 \hat{V}(\hat{y})}{n \hat{x}^2} \), where \( \hat{V}(\hat{y}) = \frac{\hat{V}(\hat{y})}{n \hat{x}^2} \left( \frac{1}{n(n-1)} \right) \). \( \hat{V}(\hat{y}) \) was the sample covariance between \( \hat{y} \) and \( \hat{x} \), and \( \frac{\sum y_i}{n} \) was the mean of \( \hat{x} \) (Cochran 1977:155, equation 6.13). Because we ignored the finite population correction, variance estimates were biased to be high. Estimates were developed for each stratum individually, as well as combined, and the variance of that sum was the sum of the variances of estimates for each stratum. The ratio estimator is likely to be suitable for situations in which a strong positive correlation exists between the length of colony intercept and the length of line flown (Cochran 1977). Without such a strong correlation, the average-density estimator will have better properties than the ratio estimator.

RESULTS AND DISCUSSION

We estimated that 329.6 km² ± 72.3 SE, 139.9 ± 21.6 km², 576.0 ± 81.4 km², and 1,332.3 ± 149.8 km² of active colonies of black-tailed prairie dogs occurred in Nebraska, North Dakota, South Dakota, and Wyoming, respectively, for a total of 2,377.8 ± 186.7 km², and similarly, we estimated the area of inactive colonies in those states to be 122.9 ± 26.8 km², 27.8 ± 11.2 km², 152.9 ± 49.2 km², and 256.8 ± 68.5 km², respectively, for a total of 560.4 ± 89.2 km² (Table 1).

State agencies estimated the area of active colonies as 240–323 km² in Nebraska during the mid-1990s (M. Fritz, Nebraska Game and Parks Commission, pers. comm.), 85 km² in North Dakota in 1990 (Williams 1999), 745 km² in South Dakota in 1987 (Tschetter 1988), and 530–825 km² in 1987 (Oakleaf et al. 1996) and 1,465 km² in 1998 in Wyoming (R. Reichenbach, Wyoming Department of Agriculture, pers. comm.). However, previous estimates cannot be used to indicate trends in colony area because previous estimates often are cursory and incomplete and do not allow valid comparisons with our data. State agency estimates are based on limited aerial surveys, review of available aerial photographs, and collective visual estimates from weed- and pest-control staffs. Nevertheless, our estimates and state agency estimates concur that unlike popular belief, thousands of square kilometers of black-tailed prairie dog colonies do not remain in the northern Great Plains.

Our survey results indicate only a weak correlation between length of line flown and length of colonies intercepted in the low-density stratum of each state, except for Wyoming (Table 2). That correlation was true for both active and inactive colonies. In contrast, correlations were strong and positive in the high-density stratum of each state, except for inactive colonies in North Dakota (Table 2). Because of this disparity between strata, the ratio estimator of

<table>
<thead>
<tr>
<th>State</th>
<th>Active colonies</th>
<th>Inactive colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nebraska</td>
<td>0.48</td>
<td>0.18</td>
</tr>
<tr>
<td>North Dakota</td>
<td>0.64</td>
<td>−0.33</td>
</tr>
<tr>
<td>South Dakota</td>
<td>0.60</td>
<td>0.24</td>
</tr>
<tr>
<td>Wyoming</td>
<td>0.63</td>
<td>0.62</td>
</tr>
</tbody>
</table>
active colonies is preferred in the high-density stratum of each state and the low-density stratum of Wyoming. The average-density estimator is recommended for the low-density stratum in all states except Wyoming. Accordingly, we computed a composite estimator, which for each state except Wyoming is the sum of average-density estimates for the low-density stratum and the ratio estimate for the high-density stratum. For Wyoming, the composite estimator is the sum of both ratio estimates. Variances of the composite estimates were calculated as the sum of the variances of the 2 constituent estimates. Composite estimates capitalize on correlations between length of line flown and length of colony intercept when they are strong but do not use those correlations when they are weak. Accordingly, composite estimates, along with their standard errors, are best estimates of the area of active colonies of black-tailed prairie dogs in the surveyed portion of each state.

In the area of inactive colonies, the correlation between length of colonies intercepted and length of flight line was minimal, except in the high-density strata of Nebraska and South Dakota and in both strata in Wyoming (Table 2). Use of ratio estimates for those strata, and average-density estimates for the other strata, led to our general estimates of inactive colony area of black-tailed prairie dogs (Table 1). Stratification was successful in distinguishing between areas with relatively abundant active colonies of black-tailed prairie dogs and those without colonies. Percentage of high-density strata covered by colonies ranged from 6.9% in Nebraska to 17.9% in Wyoming. In contrast, values for the low-density strata ranged from only 0.1% in North Dakota to 1.3% in Wyoming. These comparisons were based on average-density estimates, but analogous conclusions were true for ratio estimates.

The low-density strata contributed substantially to the total estimated area. Colonies in those strata were sparse, but because of the great extent of the low-density strata, colonies in them constituted an appreciable area. Estimates for the high-density strata were more precise, often markedly so, than those for the low-density strata (Table 1). That disparity was due mainly to the higher sampling intensity in the high-density strata (transects were 0.86 km apart there versus 13.85 km separating transects in the low-density strata). Most of the uncertainty, as reflected in the standard errors, derived from the low-density strata.

The area of inactive colonies divided by the sum of active and inactive colonies was 27.2% for Nebraska, 19.9% for North Dakota, 21.0% for South Dakota, and 16.2% for Wyoming. Several years may pass before an inactive colony is no longer discernible from the air (Uresk and Schenbeck 1987). Inactive colonies likely are sites recently poisoned and fumigated or affected by plague epizootics, factors that can eliminate populations of black-tailed prairie dogs (Cully 1993; Fagerstone and Ramey 1996). Recreational shooting of black-tailed prairie dogs usually only limits rather than eliminates populations (Vosburgh and Irby 1998).

Because any colony of black-tailed prairie dogs known to us was included in a high-density stratum, colonies estimated for the low-density strata represent previously unknown colonies. For that reason, if no other, any comparisons of areas of colonies estimated at an earlier time to those included here could be misleading. However, our survey revealed that the general distribution of colonies of black-tailed prairie dogs in the 4-state area was similar to that reported by others (North Dakota Game and Fish Department 1990; M. Fritz, pers. comm., Oakleaf et al. 1996; Tschetter 1988).

In North Dakota, the black-tailed prairie dog largely occurs on Standing Rock Indian Reservation, which borders the Missouri River and lies south of the Cannonball River and extends into South Dakota, and in the badlands in the southwestern part of the state. The intervening area is largely crop-
land. Regions where colonies of black-tailed prairie dogs occur are largely grassland with a significant element of public (Little Missouri National Grassland and Theodore Roosevelt National Park) and tribal ownership. However, control efforts have eliminated vast areas of colonies of black-tailed prairie dogs in the southwestern area (Bishop and Culbertson 1976). Only 1,157 ha of colonies exist on the 462,705-ha Little Missouri National Grassland, although 296,000 ha are potential habitat for black-tailed prairie dogs (United States Department of Agriculture Forest Service 2001). Colonies likely persist on tribal lands because of changing policies and a lack of resources to poison and fumigate the species.

The distribution of colonies of black-tailed prairie dogs in South Dakota follows a similar pattern as in North Dakota. Most colonies occur on and in the vicinity of public and tribal lands. From the airplane, the boundary of areas rich in colonies of black-tailed prairie dogs and poor in colonies often was signaled by passage into and out of tribal lands and public lands such as Buffalo Gap National Grassland and Badlands National Park. Surprisingly, large areas of South Dakota dominated by privately owned rangeland such as the region west of the Standing Rock and Cheyenne River Indian Reservations, harbor very few colonies of black-tailed prairie dogs.

Nebraska has very little public land and no tribal lands are found within the range of the black-tailed prairie dog. Colonies were found primarily in the western panhandle region and the southwestern region. However, colonies occurred throughout the surveyed area. Colonies were observed on small patches of grassland surrounded by cropland for miles, and near housing developments in eastern and central Nebraska. Even in the heavily cropped Platte River valley, an occasional colony occurs, attesting to the adaptability of the species. In central and western Nebraska, colonies were observed more commonly in a landscape of cropland and rangeland, such as in the vicinity of the cities of Alliance and Scottsbluff, than in large areas of contiguous rangeland in the Nebraska panhandle.

We observed few colonies in the extensive Sandhills region, a large area of nearly uniform grassland. Very sandy substrate probably accounts for few colonies of black-tailed prairie dogs. Moreover, many valleys between dunes have been converted to hay fields.

Many colonies of black-tailed prairie dogs in Wyoming occur on Bureau of Land Management public land and the Thunder Basin National Grassland. However, substantial areas of colonies occur on private land and in the vicinity of roads and other developments.

Although substantial areas of grassland have been converted to cropland in the northern Great Plains (Samson and Knopf 1994), we observed vast areas of suitable habitat for colonization and expansion of black-tailed prairie dogs on public, private, and tribal lands. This visual impression is consistent with analyses of National Grasslands (United States Department of Agriculture Forest Service 2001) and analyses in Montana (Proctor 1998; J. Proctor, Predator Conservation Alliance, pers. comm.), where hundreds of thousands of hectares and millions of hectares, respectively, are viewed to be potential habitat for colonies of black-tailed prairie dogs. Little need probably exists for habitat restoration, but rather the need is to reestablish colonies of black-tailed prairie dogs. Given the negative attitude of many people toward black-tailed prairie dogs (Reading et al. 1999), expanding populations of black-tailed prairie dogs on public lands should be a priority in any conservation strategy.

Our survey provided the only unbiased estimates of the areal extent of colonies of black-tailed prairie dogs over an extensive area. The survey also suggests a sampling plan for future monitoring of the species. Conducting the survey described herein required 600 h of flying. Future monitoring
could repeat a fraction of the original survey every year. For example, surveying 20% of the region each year for 5 years could provide reasonably current estimates of the extent of colonies and detailed information about where changes are occurring.

Standardized survey techniques are important as Great Plains states implement conservation strategies for the black-tailed prairie dog (Van Pelt 2000). Working groups comprising private landowners, state and federal agencies, tribes, and others have been established throughout the Great Plains to plan for conservation of the species. Monitoring is an important facet of conservation planning. Although millions of black-tailed prairie dogs and thousands of colonies probably exist, the ongoing threats of plague and eradication efforts only can be assessed by adequate monitoring throughout the Great Plains.

Remote sensing may prove valuable in monitoring colonies of black-tailed prairie dogs. However, aerial photography larger than the 1:24,000 scale recommended for black-tailed prairie dog monitoring (Best et al. 1983; Cheatheam 1973; Dalsted et al. 1981; Schenbeck and Myhre 1986; Tietjen et al. 1978) was not available for the study area. Resolution of satellite imagery at the time of the aerial survey was not adequate, although new orbital space sensors now provide adequate resolution.

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