

A NOVEL APPROACH FOR ASSESSING DENSITY AND RANGE-WIDE ABUNDANCE OF PRAIRIE DOGS

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Habitat loss, introduced disease, and government-sponsored eradication programs have caused population declines in all 5 species of prairie dogs. Black-tailed prairie dogs (*Cynomys ludovicianus*) currently occupy only about 2% of an extensive geographic range (160 million hectares) and were recently considered for listing under the United States Endangered Species Act. Accurate estimates of density for populations of prairie dogs would be valuable for estimating range-wide abundance and for determining threats to species persistence, yet estimates of density using robust approaches (e.g., complete enumeration or mark–recapture) are rarely undertaken. We introduce a novel approach to estimating density of prairie dogs using mark–resight methods. Using mark–resight, mark–recapture, and 3 other indices, we estimated the abundance of prairie dogs on 3 reintroduced colonies over a 3-year period (2003–2005). We show that mark–resight is a superior approach to estimating abundance of prairie dogs, that average density estimates from the southern extremity of the species' range are considerably lower (11.3 prairie dogs/ha) than estimates from more northerly climes ($\bar{X} = 18.3\text{--}90.3$ prairie dogs/ha), and that population densities can fluctuate widely in accordance with local environmental conditions. We propose that resource agencies use mark–resight methods to obtain density estimates of prairie dog populations within diverse ecoregions, and couple these estimates with an assessment of the area occupied by prairie dog colonies to determine range-wide abundance.

Key words: *Cynomys*, density, Endangered Species Act, keystone species, mark–resight, prairie dog

Effective management of prairie dogs (*Cynomys*) has become increasingly necessary because of declines in all 5 species, the listing of 2 species (Utah prairie dogs [*C. parvidens*] and Mexican prairie dogs [*C. mexicanus*]) under the United States Endangered Species Act, and the need to identify suitable habitat for reintroducing endangered black-footed ferrets (*Mustela nigripes*—Miller et al. 1996; United States Fish and Wildlife Service [USFWS] 1970, 1984, 2000, 2004). Members of the genus *Cynomys* are considered keystone species that strongly influence grassland biodiversity (Bangert and Slobodchikoff 2006; Ceballos et al. 1999; Desmond et al. 2000; Dinsmore et al. 2003; Hoogland 2006; Lomolino et al. 2004; Miller et al. 2000; Whicker and Detling 1993).

Of all 5 species, black-tailed prairie dogs (*C. ludovicianus*) have the most extensive range, which encompasses approximately 160 million hectares stretching from northern Mexico to

southern Canada including parts of 11 states in the United States (Hoogland 2006; Miller et al. 1996). Black-tailed prairie dogs may have numbered in the billions but now occupy approximately 2% of their historic range (Miller et al. 1996; Proctor et al. 2006). They were considered for listing under the Endangered Species Act but were recently removed from the candidate species list after the USFWS concluded that the area they occupied was greater than previously estimated and that threats to the species were not as serious as once believed (Manes 2006; USFWS 2000, 2004).

The range of black-tailed prairie dogs encompasses 20 ecoregions (Ricketts et al. 1999) that represent a variety of grassland systems such as southern mixed grassland, northern tall grassland, and Chihuahuan Desert grassland; climate patterns vary considerably across this range not only in temperature, but also in both the amount and timing of precipitation (Fig. 1). In some areas, rain falls primarily in the spring and early summer months when females are giving birth and lactating, a pattern expected to facilitate rearing and survival of young. In other areas, most precipitation falls in the summer, well after young would have been weaned, which means that the majority of primary production, driven by rainfall, occurs

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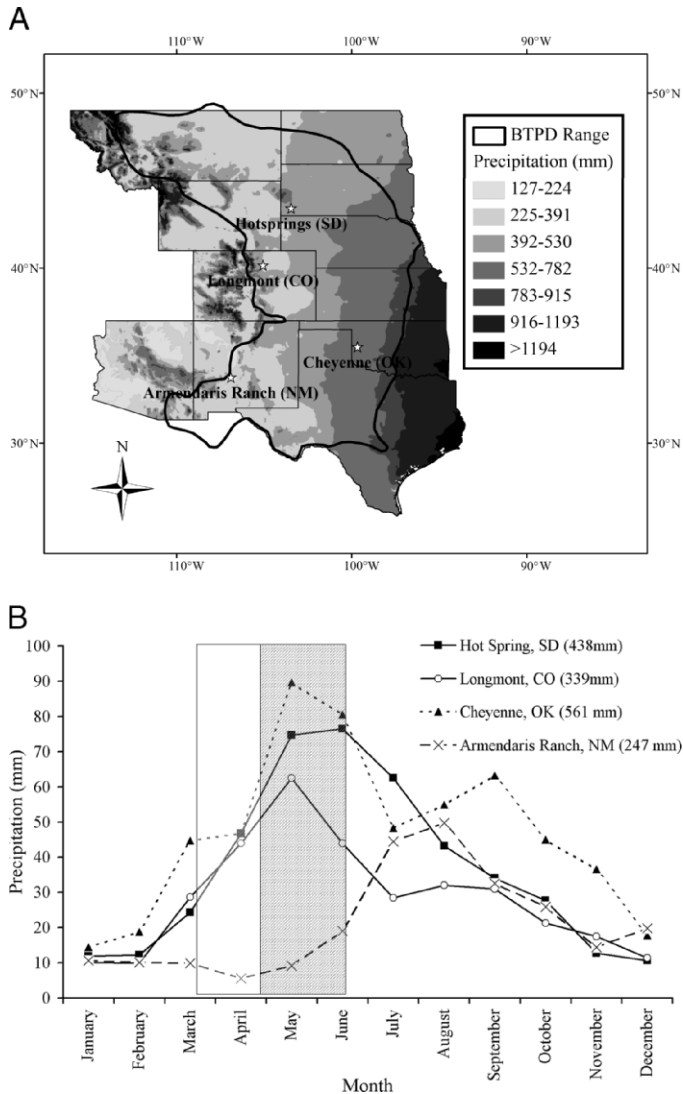


FIG. 1.—A) Average annual precipitation (mm) for regions within the historic range of black-tailed prairie dogs (*Cynomys ludovicianus*; black outline). B) Average monthly precipitation at 4 localities with variable precipitation regimes within the range of black-tailed prairie dogs. Open vertical bar and gray vertical bar represent approximate gestation and lactation periods of black-tailed prairie dogs, respectively.

after the prairie dog reproductive period (Fig. 1B). The diverse grassland ecosystems that prairie dogs occupy and the variable climates they encounter have likely contributed to differences among species in their natural history (Hoogland 1995, 2001; Tileston and Lechleitner 1966). We expect population densities of prairie dogs to vary across their range because of differences in resource quality and quantity, a pattern that has been observed in other ground-dwelling squirrels and herbivores in general (Bennett 1999; Coulson et al. 2000; Hubbs and Boonstra 1997; Van Horne et al. 1997).

Here we advocate a monitoring strategy for prairie dogs that incorporates mark–resight to estimate density of prairie dogs. We show that mark–resight is superior to other methods for estimating density and we offer a multifaceted approach to

more accurately assess the status of prairie dogs. The approach we advocate would include estimating occupied habitat on a range-wide scale using some type of remote-sensing method (e.g., estimating the areal extent of prairie dog colonies by identifying their burrows with satellite imagery or aerial photography), verifying occupancy of colonies through observation (i.e., determining if prairie dogs are present on a colony) at the regional scale, and estimating density with mark–resight at select sites stratified by ecoregion. We suggest that such an approach is necessary to accurately estimate the range-wide abundance of prairie dogs and is vital to both conservation of prairie dogs and grassland biodiversity in North America.

MATERIALS AND METHODS

Study site and populations.—Our study was conducted on the Armendaris Ranch, Sierra County, New Mexico, located at the northern end of the Chihuahuan Desert. Colonies of prairie dogs on the ranch were dominated by perennial desert grasses including alkali sacaton (*Sporobolus airoides*), burrograss (*Scleropogon brevifolius*), and tobosa (*Pleuraphis mutica*). Topography was flat and vegetation height was low, creating few features to hinder observation of prairie dogs.

A total of 19 colonies of prairie dogs have been established on the ranch in an effort to reestablish the species (Truett and Savage 1998). We studied the 3 oldest and largest colonies, all established in 1998–1999: Deep Well Colony, 9 ha in size; Red Lake Colony, 11.75 ha; and S-Curve Colony, 6 ha. At the time of study, the colonies varied in age from 4–6 years old (Deep Well Colony and S-Curve Colony) to 5–7 years old (Red Lake Colony). The colonies we studied were well within the size and age of typical present-day colonies that have experienced declines due to plague epizootics (Lomolino et al. 2004; Stapp et al. 2004), and were similar in size to other colonies where densities were estimated, including at least 1 extensive long-term study from which a large body of knowledge on the natural history of black-tailed prairie dogs has been obtained (Hoogland 1995).

Capture and marking.—From January 2003 through October 2005 we captured and marked prairie dogs at each colony (2 or 3 traps per active burrow) using wire-mesh box traps (61 × 18 × 20 cm; Wildlife Control Supplies, Simsbury, Connecticut). The average number of traps used per day at Deep Well Colony, Red Lake Colony, and S-Curve Colony was 108 traps (*SD* = 21.6 traps), 177 traps (*SD* = 41.1 traps), and 123 traps (*SD* = 46.5 traps), respectively. Traps were prebaited for 1 week before being set with a mixture of corn and sweet feed. Animals were uniquely marked using a subcutaneous passive integrated transponder (TX1440ST; Biomark, Boise, Idaho) and externally marked with an alphanumeric code using Nyanzol-D dye (Albanil Dyestuff Manufacturers, Jersey City, New Jersey), which remains visible until they molt (King 1955). All capture and handling methods followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committee of New Mexico State University (NMSU permit 2002–06).

Resight scans.—Scans were performed from an elevated position (3 m) using a 20–60× spotting scope. Scan sessions were conducted in the morning (0700–1000 h) or evening (1600–1900 h) with 2–6 separate scans being conducted during a single session. The time it took to conduct a single scan varied with colony size and environmental conditions. Scans began and ended at predetermined points located off colony. Marked animals were identified and unmarked animals were simply counted. We counted unmarked animals only once after they passed out of the field of view to minimize double counting unmarked individuals. Resight sampling was based on the robust design (Pollock 1982). During a scan session a population was assumed to be demographically closed (i.e., no additions or subtractions to the population); scan sessions were repeated at approximately monthly intervals between which the population was assumed to be demographically open (i.e., births, deaths, immigration, and emigration could occur).

Population estimates.—We estimated population size from 33 mark–recapture and 29 resight sessions. Population estimates were made before (preemergence) and after (post-emergence) emergence of juveniles and were conducted at each colony after each marking session but before marks were lost via the molt. We assumed that between scan sessions marked animals were lost from the population at the same rate as unmarked animals. Thus, throughout our scans, the ratio of marked to unmarked animals was assumed constant. Given this assumption, an unbiased estimate of population size was possible with the Lincoln–Petersen estimator (Seber 1982). We used Chapman’s (1951) modification of the Lincoln–Petersen estimator to estimate population size.

The Chapman estimator is potentially biased when a small percentage of the population is marked or when the probability of sighting an individual is either low or heterogeneous (White and Garrott 1990; White and Shenk 2001). Thus, we compared the performance of the Chapman estimator with other estimators that work well with mark–resight data: joint hypergeometric estimator (JHE) and Bowden’s estimator as found in program NOREMARK (Bowden and Kufield 1995; White 1996).

We also compared population estimates from the mark–resight data with mark–recapture, the Severson and Plumb (1998) index (hereafter S and P index), maximum aboveground counts (MAGC), and the minimum number known alive (MNKA).

Mark–recapture population estimates were derived using program MARK (White and Burnham 1999). The Chapman estimator was used when only 2 trapping occasions were conducted, whereas the model selection procedure embodied in MARK was used to select an estimator when 3 or more trapping occasions were conducted. The S and P index was derived from a linear relationship between estimates of prairie dog density and the MAGC using a regression equation: $\hat{N} = (\text{MAGC} - 3.04)/0.4$ (Severson and Plumb 1998). The MNKA was determined by adding the total number of individually marked animals observed during any session to the maximum number of unmarked animals observed in any single scan.

Using the binomial distribution we tested the null hypothesis that a particular method produced estimates that were above the MNKA 90% of the time. The null hypothesis was rejected if $P \leq 0.05$.

Simulating the effects of a reduction in marking effort.—We examined the effect of reducing the percentage of marked animals on the bias and precision of our estimates through simulation. Simulations were constructed using a random number function (RAND) based on the hypergeometric distribution in SAS (Statistical Application Software, Cary, North Carolina). This function creates a random value with a probability distribution defined by the following 3 parameters: N (population size), R (the number of marked animals in a population), and n (the total number of animals seen during a scan [marked + unmarked]).

We simulated 2 distributions, 1 for the number of marked animals seen and another for the number of unmarked animals seen, and simulated a single scan by drawing a random value from each of these distributions. Each simulated scan was parameterized using our empirical estimates of population size as N , and the average number of animals seen during a season as n . The value for R changed depending on the percentage of the simulated population that was marked (i.e., if $N = 100$ and 10% of the population was marked, $R = 10$). Scans were simulated with 5–90% of the population marked. We then estimated mean population size with the Chapman estimator. Estimates were made with 2, 10, 50, and 100 scans to gauge how sampling effort influenced the estimate. We used nonlinear regression and a Kruskal–Wallis ranked analysis of variance to see how percent deviation and the coefficient of variation varied with the percentage of the population marked and with number of scans, respectively. We defined percent deviation as the absolute difference between the estimate of population size and the actual simulated population size times 100. We also examined the number of times estimates made with a reduced percentage of the population marked were above the MNKA based on 10 scans for each of 12 estimates using the binomial test.

RESULTS

Comparative effort.—A total of 21,135 trap days yielded 2,838 captures of 549 individuals. Average recapture rate (\hat{p}) was 0.40 ($SD = 0.17$, range = 0.13–0.80) and fell below 0.20 on only 2 of 33 recapture sessions. Average number of days spent capturing prairie dogs for mark–recapture estimates was 7.2 days ($SD = 4.6$ days, $n = 17$).

Average number of days spent trapping to externally mark individuals was 6.3 days per colony ($SD = 4.6$ days, $n = 17$); however, it took only 2.8 days per colony ($SD = 1.9$ days, $n = 17$) to capture and mark 25% of the population. Total time spent scanning was 36 h with 132 scans ($\bar{X} = 16$ min/scan, $SD = 10$ min/scan) conducted. The average probability of sighting an animal was slightly lower than the recapture rate ($\bar{X} = 0.34$, $SD = 0.17$, range = 0.01–0.63) and fell below 0.20 on only 3 of 29 scan sessions. Sighting probability varied significantly across years (Kruskal–Wallis: $\chi^2 = 12.17$, $d.f. = 2$, $P = 0.002$).

TABLE 1.—A comparison of population estimates for black-tailed prairie dogs (*Cynomys ludovicianus*) using 3 mark–resight estimators: Chapman’s, Bowden’s, and joint hypergeometric estimator (JHE; with 95% confidence interval in parentheses); minimum number known alive (MNKA); Severson and Plumb index (S and P); maximum aboveground counts (MAGC); and mark–recapture (Capture) at 3 colonies, before (PRE) and after (POST) juvenile emergence, from 2003 (03) to 2005 (05). DWC = Deep Well Colony; RLC = Red Lake Colony; SCC = S-Curve Colony.

Colony	Time	Chapman’s	Bowden’s	JHE	MNKA	S and P	MAGC	Capture
DWC (9 ha)	PRE 03	37 (24–50)	— ^a	44 (30–78)	21	12	8	8 (4–17)
	PRE 04	16 (8–24)	13 (10–18)	24 (19–38)	17	20	11	17 (11–58)
	POST 04	17 (16–18)	— ^a	18 (18–19)	14	22	12	14 (14–15)
	PRE 05	18 (17–19)	17 (15–19)	19 (19–20)	16	10	7	16 (8–23)
	POST 05	54 (9–98)	61 (37–101)	65 (45–119)	35	42	20	28 (23–41)
RLC (11.75 ha)	PRE 03	91 (84–97)	117 (84–165)	91 (88–94)	81	117	50	61 (45–75)
	POST 03	106 (95–118)	110 (80–140)	110 (103–119)	75	145	61	94 (87–118)
	PRE 04	76 (67–84)	68 (60–78)	75 (71–80)	66	64	29	106 (44–168)
	POST 04	238 (230–248)	248 (175–248)	249 (194–320)	89	127	54	112 (88–158)
	PRE 05	127 (95–159)	111 (93–132)	141 (130–154)	116	82	36	101 (88–123)
SCC (6 ha)	POST 05	193 (162–230)	202 (174–243)	195 (168–235)	126	137	58	137 (121–161)
	PRE 03	86 (77–94)	94 (57–153)	82 (80–85)	77	82	36	68 (55–96)
	POST 03	170 (149–194)	194 (153–247)	173 (190–246)	117	140	59	114 (109–125)
	PRE 04	8 (8–8)	8 (8–9)	8 (8–8)	8	10	7	11 (3–30)
	POST 04	19 (17–22)	— ^a	19 (15–27)	14	10	7	10 (9–21)
	PRE 05	17 (9–24)	17 (14–20)	17 (16–22)	16	17	10	10 (10–16)
	POST 05	34 (5–62)	43 (25–76)	42 (30–75)	26	14	9	54 (42–74)

^a Estimates could not be made with Bowden’s estimator because individual animals were not identified.

Population estimates.—Populations declined at all 3 colonies from 2003 to 2004 (Table 1). The S-Curve Colony experienced the most dramatic decline (90.7%), falling from an estimated preemergence population size of 86 in 2003 to 8 animals in 2004 (Table 1). In fact, after marking 8 animals in early 2004 we never observed an unmarked animal until after the birth pulse. Population size at all 3 colonies remained stable or increased from 2004 to 2005. This pattern of population change coincided with a period of below-average precipitation in 2003 and then average precipitation in 2004 and 2005 (Western Regional Climate Center, Elephant Butte Dam Station, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nmelep>).

Generally, estimates derived from Chapman’s estimator were lower than those from either the JHE or Bowden’s estimator, and typically had larger confidence intervals (Table 1). Nevertheless, we used Chapman’s estimator in subsequent comparisons.

TABLE 2.—A comparison of the number (and proportion) of times population estimates were above the minimum number known alive (MNKA) at 6 levels of marking effort for a simulated population. Significance values (*P*-value) are based on a binomial distribution where the null hypothesis is equivalent to 90% of the estimates being above the MNKA.

Percent of the colony marked	Number of estimates above MNKA	Proportion of estimates above MNKA	<i>P</i> -value
5	4	0.36	< 0.001
10	4	0.33	< 0.001
25	8	0.66	0.026 ^a
50	9	0.75	0.110
75	10	0.83	0.341
90	11	0.92	0.717

^a Not significant with a Bonferroni correction (0.05/6).

Estimates of population size were less biased using mark–resight than other approaches. Population estimates were above the population threshold (MNKA) in all but 1 instance (5.9%; Table 1) and could not be rejected as estimating population size above this threshold for 90% of the sessions ($P = 0.23$, $n = 29$). In contrast, mark–recapture underestimated population size 9 (52.9%) of 17 times, which was significantly different from our null hypothesis of being above the MNKA 90% of the time across all sessions ($P < 0.001$, $n = 33$). The MAGC was never above the MNKA and estimates made using the S and P index fell below the MNKA on 6 (35.3%) of 17 occasions ($P < 0.001$, $n = 29$).

Reduced effort with mark–resight.—As the percentage of the population marked increased, the percent deviation declined ($r^2 = 0.37$ to 0.43 using 2, 10, 50, or 100 scans; $F = 21.2$ to 26.9 , $df. = 1, 70$, $P < 0.001$ for all), indicating that as more animals were marked the accuracy of the population estimate improved regardless of the number of scans employed. There also was a significant declining trend in the coefficient of variation with an increase in the percentage of the population marked ($r^2 = 0.15$ to 0.35 for all scan sample sizes, $F = 7.0$ to 20.2 , $df. = 1, 70$, $P < 0.01$). The number of scans used to make estimates did not significantly affect either the percent deviation ($\chi_{kw}^2 = 6.03$, $df. = 3$, $P = 0.11$) or the coefficient of variation ($\chi_{kw}^2 = 6.75$, $df. = 3$, $P = 0.08$), but there was a trend for greater precision as the number of scans increased.

Estimates of population size were above the MNKA 75% of the time when more than 50% of the population was marked and at least 66% of the time when 25% of the population was marked (Table 2). Because of numerous tests, the type I error rate was inflated so we used a Bonferroni adjustment (0.05/6), which suggested that even when only 25% of the population was marked we could not reject the null hypothesis that 90% of our population estimates would be above the MNKA.

Simulations indicated that precision increased with both marking effort and sighting probability (Fig. 2). Marking effort had a greater influence, but this relationship also was nonlinear and approached an asymptote. The results were similar when we compared accuracy, as measured by percent deviation (results not shown).

DISCUSSION

Despite extensive research examining the biology of black-tailed prairie dogs, there are few studies that have used robust approaches (e.g., mark–recapture) to estimate their density. We could find only 6 studies where rigorous density estimates were made: 4 were conducted in southwestern South Dakota, 1 in Montana, and another in Colorado (Table 3). Until our study, density estimates in the southern portion of the species’ range were lacking. All other published estimates of density used some form of an index (e.g., active burrow or aboveground counts). Further, of the state agency plans that have been developed, only 3 discuss the need for detecting population change and all use an index to estimate density (Colorado Department of Natural Resources 2000; Cooper and Gabriel 2005; Kansas Black-Tailed Prairie Dog Working Group 2002; Knowles 1999; Luce 2003; New Mexico Black-Tailed Prairie Dog Working Group 2001; North Dakota Game and Fish Department 2001; Texas Black-Tailed Prairie Dog Working Group 2004; Wyoming Game and Fish Department 2004). Finally, there are few studies that have estimated the density of other species of prairie dogs, including those listed under the Endangered Species Act or those recently petitioned (USFWS 1970, 1984, 2004, 2006). In sum, there are few published studies that have used robust approaches to estimate the density of any species of prairie dog.

Here we have shown that marking and sighting individuals takes less effort than marking and recapturing individuals, yet provides superior estimates of population size and density (Table 1). Our estimates of density made with mark–recapture required a much greater time commitment (> 6 days) because we trapped more than 60–70% of the total population, whereas,

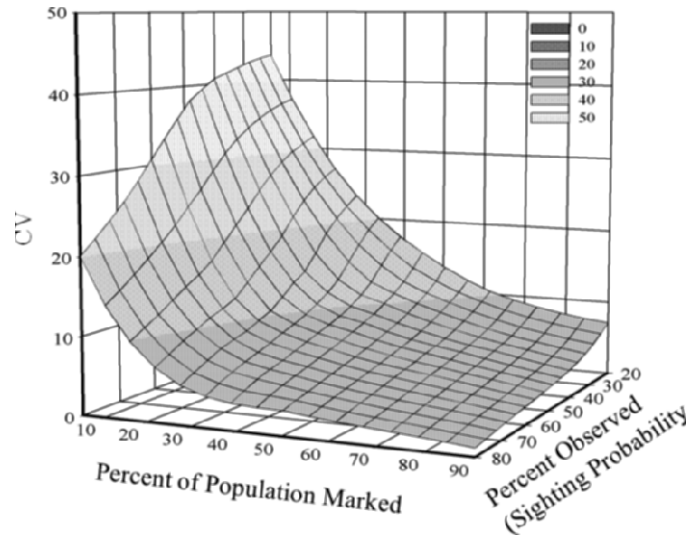


FIG. 2.—The influence of varying the percentage of the population marked and sighting probability on the precision (coefficient of variation) of population estimates of black-tailed prairie dogs (*Cynomys ludovicianus*) made with a mark–resight approach. The analysis is based on a simulated population of 100 individuals and 10 resight scans.

through simulation, we have shown that marking and resighting as little as 25% of the sampled population can still result in estimates that are both unbiased (Table 2) and precise (Fig. 2); it took us less than 3 days to trap and mark 25% of the population. In sum, mark–resight can be an economical and robust approach to estimate density of prairie dogs and it is more accurate and precise in comparison to currently used indices.

Estimating abundance of prairie dogs with indices.—Most monitoring programs use estimates of habitat occupied by prairie dogs based on the condition and number of burrows, or employ MAGCs to track population size (Biggins et al. 2006; Miller and Cully 2001). Active burrow counts maybe useful to track large changes in population size (Biggins and Kosoy

TABLE 3.—Estimates of density of black-tailed prairie dogs (*Cynomys ludovicianus*; individuals/ha) obtained from published studies. Estimates were made with complete enumeration (CE) with mark–recapture (MR) or mark–resight (MS) approaches and represent population estimates obtained after emergence of juveniles. Either the mean (*SD*) density or range is given.

Density	Sample size ^a	Colony size (ha)	Grassland type	Technique	Location	Source
20.65 (7.23)	3	2.27	Northern short grassland	MR	Wind Cave National Park, South Dakota	King 1955
6.4–31.9	1	2.8	Western short grassland	CE	Fort Collins, Colorado	Tileston and Lechleitner 1966
19.15 (8.13)	2	3.0–16.0	Northern short grassland	CE	Charles M. Russell National Wildlife Refuge, Montana	Knowles 1985
90.25 (25.81)	2	0.47–1.86	Northern short grassland	CE	Wind Cave National Park, South Dakota	Garrett and Franklin 1988
18.57 (2.24)	14	6.6	Northern short grassland	CE	Wind Cave National Park, South Dakota	Hoogland 1995
18.27 (10.45)	24	4	Northern short grassland	MR	Buffalo Gap National Grasslands, South Dakota	Severson and Plumb 1998
11.33 (9.4)	8	6–11.75	Chihuahuan Desert	MS	Armedaris Ranch, New Mexico	This study

^a King (1955): 3 annual estimates at 1 colony; Tileston and Lechleitner (1966): minimum and maximum estimates for a single colony; Knowles (1985): an estimate at each of 2 colonies; Garrett and Franklin (1988): 2 estimates at a single colony that expanded in size during the study; Hoogland (1995): 14 annual estimates at 1 colony; Severson and Plumb (1998): 24 estimates at 14 colonies over 2 years within a 4-ha plot established at each colony; this study: annual estimates made on 3 colonies over 3 years.

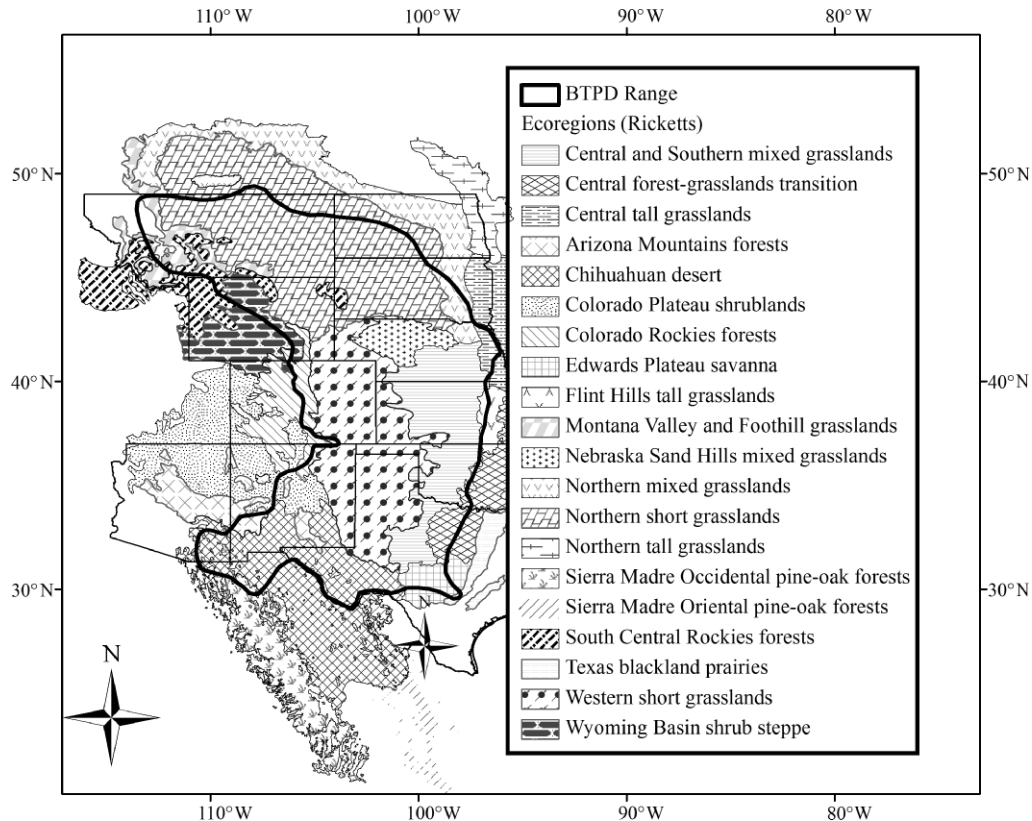


FIG. 3.—An outline of the historic range of black-tailed prairie dogs (*Cynomys ludovicianus*) within North America and the ecoregions (based on Ricketts et al. 1999) it encompassed.

2001), but they can be biased and also may miss population declines because presence of burrows may not reflect changes in populations (Biggins et al. 2006; Menkens et al. 1988; Powell et al. 1994; Severson and Plumb 1998). More importantly, active and total burrow counts are uncorrelated with mark–recapture estimates (Severson and Plumb 1998).

In contrast to burrow indices, MAGCs are correlated with mark–recapture estimates of population size (Menkens and Anderson 1993; Menkens et al. 1990; Severson and Plumb 1998). We also found MAGCs to be significantly correlated with our population estimates over all years ($r^2 = 0.82$, $F = 73.2$, $df = 1, 16$, $P < 0.001$); however, detection probability varied annually. Thus, for MAGC to be a valid index, it should be corrected annually based on a more robust estimation method such as mark–resight (Anderson 2001, 2003).

How is occupied habitat determined?—Occupied habitat is typically determined by assaying for the presence of prairie dog burrows. This was how the most recent estimate of habitat occupied by black-tailed prairie dogs in the United States (745,400 ha) was determined (USFWS 2004), but it was not apparent if attempts were made to assess whether prairie dogs were present on those colonies. At least 2 studies have shown that remote-sensing approaches (e.g., satellite imagery or aerial photography) overestimate occupied habitat by including areas that no longer contain prairie dogs or that never contained them. In an assessment of nearly 3 million hectares of colonies of prairie dogs across 4 states, 19.1% of all colonies did not

harbor prairie dogs (Sidle et al. 2001). In a critique of another study that estimated the area of “active” colonies of prairie dogs in Colorado to be 255,398 ha (White et al. 2005a), Miller et al. (2005) estimated that 25.4% of the area never had prairie dogs and that 50.3% represented inactive colonies; only 24.3% of the area actually had active colonies (but see White et al. [2005b] for a reply). Such disconnect between a determination of occupied habitat by remote-sensing approaches and the abundance of small mammals has been observed in other systems (Wheatley et al. 2005) and is a major issue in predicting species occurrence and abundance using remote-sensing approaches (Scott et al. 2002).

Estimating abundance of prairie dogs throughout their range.—Estimating abundance of prairie dogs is a matter of scale; what works at the landscape level is not appropriate at the population level and vice versa. We suggest that a sound monitoring program for prairie dogs requires at least 3 pertinent scales of assessment: range-wide estimates of potentially occupied habitat coupled with regional, landscape-scale assessments of colony occupancy and persistence, which are augmented by population-scale assessments of density that can be used to estimate range-wide abundance, model population dynamics, and infer causal factors. A rigorous sampling design that includes areas throughout the geographic range of a species and across numerous and diverse ecoregions it represents is needed (Figs. 1 and 3).

In the framework of this strategy all levels of monitoring would augment one another to provide a detailed and rigorous appraisal of populations of prairie dogs. Potentially occupied habitat, determined from remotely sensed data, could be sampled in a manner to estimate the probability of detecting an occupied colony (MacKenzie et al. 2003; MacKenzie and Royle 2005). This could be accomplished by simply verifying the presence of prairie dogs by observing them or actually sampling colonies by recording the MAGC. Mark–resight could then be conducted at a subset of these randomly selected sites every year to obtain estimates of density and sighting probability, which could be used to correct indices, increase precision, or increase sample size (Eberhardt and Simmons 1987; Nichols et al. 1981). For example, estimates of sighting probability could be used to adjust MAGC to obtain population estimates at random plots representative of a larger colony or complex. In this way, accurate estimates of density could be obtained across relatively large areas in a cost-effective manner. Further, because there is a threshold of marking effort after which the precision of estimates improves little, most animals need not be marked (Fig. 2). Together these approaches would provide a means to assess the geographic extent, occupancy, and abundance of prairie dogs at multiple scales across ecoregions. Here we outline a potential approach for use by managers:

1. Use satellite imagery or aerial photography to estimate the area potentially occupied by prairie dogs by identifying the presence of burrows.
2. Randomly select a subset of those locations identified by remote sensing, visit these sites, and document the presence or absence of prairie dogs through observation.
3. During observation of randomly selected sites, count the number of prairie dogs observed and record the MAGC.
4. Of the observed sites, select another random subset and trap and mark prairie dogs on those sites. Initially trap each site for 2 days and then scan the colony and tally the number of marked and unmarked animals observed. Assuming that marked and unmarked animals behave similarly, use the proportion of marked animals observed (i.e., number of marked animals observed/total animals marked = m_2/M_1) to estimate the total number of unmarked animals left in the population, U_1 , by simply multiplying M_1/m_2 times the number of unmarked animals observed, u_2 (i.e., $U_1 = (M_1/m_2) \times u_2$).
5. When $M_1 \sim 25\%$ of the total estimated population ($M_1 + U_1$), stop trapping.
6. Monitor colonies that contain marked animals using the mark–resight approach and estimate density using the Bowden’s estimator or JHE.
7. Regress density estimates on MAGC to correct other measures of MAGC determined from colonies where prairie dogs were not marked to estimate densities across all randomly selected and observed sites.

Conservation implications.—Burrowing mammals are widely recognized as ecosystem engineers that influence biodiversity (Machciote et al. 2004; Zhang et al. 2003) and prairie

dogs create communities that many species benefit from or are entirely dependent upon (Bangert and Slobodchikoff 2006; Ceballos et al. 1999; Desmond et al. 2000; Dinsmore et al. 2003; Lomolino and Smith 2003; Miller et al. 2000; Whicker and Detling 1993). Prairie dogs are in jeopardy: 2 species are listed under the Endangered Species Act, and white-tailed (*C. leucurus*), Gunnison’s (*C. gunnisoni*), and black-tailed prairie dogs were recently petitioned for listing; the latter currently occupies approximately 2% of its range as a result of habitat loss, government-sponsored eradication programs, recreational shooting, and plague (USFWS 1970, 1984, 2000, 2004, 2006).

Black-tailed prairie dogs were recently removed from the candidate species list based on a reappraisal of occupied habitat (745,400 ha) determined by remotely sensing burrows coupled with an average density of 24.71 prairie dogs/ha (USFWS 2004). Not only is estimating occupied habitat problematic, but densities of prairie dogs clearly vary across their range (Table 3). Our estimates of density were the 1st from the southern extremity of the species’ range and they averaged 11.33 prairie dogs/ha ($SD = 9.4$ prairie dogs/ha) and ranged from 1.8 to 28.3 prairie dogs/ha (Table 1), a lower average than in more northerly climes. These results collectively call for more sampling across the species’ range to determine the variation in densities that could be encountered across ecoregions.

The extirpation of populations of black-tailed prairie dogs across a vast geographic range may have made them “functionally extinct,” and most certainly has contributed to the decline in dependent species such as the black-footed ferret (Antolin et al. 2002; United States Department of Agriculture Forest Service 2005). The recent decision by the USFWS to remove black-tailed prairie dogs from the candidate species list has left resource agencies with a potential quandary regarding their future conservation (Sidle et al. 2006). If black-tailed prairie dogs are no longer considered a species of concern, are resource agencies obligated to consider potential impacts and develop strategies for conservation? Here we have outlined a multifaceted approach to monitoring prairie dogs that incorporates mark–resight and that can provide more accurate estimates of abundance than approaches currently used. Most resource agencies already employ a method to estimate area occupied and some determine the percentage of habitat that is actually occupied, but rigorous density estimates for most, if not all, species of prairie dogs are lacking. Until comprehensive, cost-effective monitoring programs that accurately estimate density are in place, the status of species of prairie dogs is truly unknown.

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