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BLACK-TAILED PRAIRIE DOG POPULATION DYNAMICS AT SCOTTS BLUFF NATIONAL MONUMENT, NEBRASKA: A 28-YEAR RECORD

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ABSTRACT.—Black-tailed prairie dogs, *Cynomys ludovicianus,* now inhabit a small fraction of their original range in the Great Plains. We monitored a population of black-tailed prairie dogs at Scotts Bluff National Monument, Nebraska, from colonization in 1981 until 2009 (28 years). Colony boundaries were mapped by delineating clip lines and active burrows; population densities were estimated via visual counts. Estimates of total population size revealed 4 distinct periods of changing dynamics: (1) a linear increase, (2) a decline and prolonged depression, (3) an exponential increase, and (4) a period of high variability. Area occupied revealed similar, although less-defined trends, whereas densities fluctuated greatly (8–80 individuals · ha^{-1}). Even after almost 30 years, this population remains relatively small. Decreases in the population may have been due, in part, to predation by badgers, although sylvatic plague cannot be ruled out. Black-tailed prairie dogs are recognized as keystone grassland species, and attempts are underway to reintroduce them to parts of their historic range. Our data suggest that black-tailed prairie dogs possess high potential for rapid population growth and decline, regardless of colony size. Therefore, either human-assisted or natural dispersal events may be important in establishing colonies in suitable habitat.

RESUMEN.—El perrito de pradera de cola negra, *Cynomys ludovicianus,* habita en una pequeña fracción de su distribución original en las Grandes Llanuras. Monitoreamos una población de perritos de pradera de cola negra en Scotts Bluff National Monument, Nebraska, por 28 años, desde la colonización en 1981 hasta 2009. Trazamos los límites de las colonias usando de referencia las líneas de ramoneo y las madrigueras activas, y estimamos la densidad de las poblaciones mediante un recuento visual. Los estimados de población total revelaron cuatro períodos distintos de dinámicas cambiantes: (1) un aumento lineal, (2) una disminución y depresión prolongada, (3) un aumento exponencial y (4) un período de alta variabilidad. El área ocupada reveló tendencias similares, aunque menos definidas, mientras que las densidades fluctuaron mucho (8–80 individuos · ha^{-1}). Aún después de casi 30 años, esta población permanece relativamente pequeña. Los decrementos en la población pueden haber sido provocadas en parte por la depredación por tejones, aunque no se puede descartar como causa la plaga silvática. El perrito de pradera de cola negra se considera una especie clave de la pradera, y están en proceso esfuerzos por reintroducirlos en partes de su distribución histórica. Nuestros datos indican que los perritos de pradera de cola negra tienen alto potencial de crecimiento y disminución de su población, sin importar el tamaño de la colonia. Por lo tanto, los eventos de dispersión, ya sean naturales o con asistencia humana, podrían ser importantes para establecer colonias en hábitats adecuados.

Black-tailed prairie dogs, *Cynomys ludovicianus*, (hereafter simply "prairie dogs") once inhabited hundreds of thousands of square kilometers of the Great Plains from Canada to Mexico and may have numbered close to 5 billion (Sidle et al. 2001, Knowles et al. 2002, Hoogland 2006). Although contention exists over the exact historical numbers (Miller et al. 2007), it is clear that prairie dogs now inhabit only a small fraction of their original range (Proctor et al. 2006).

Prairie dogs exhibit many ecological interactions with both flora and fauna, and, therefore, have been termed both a "keystone" and a "foundation" species (Miller et al. 1994, Kotliar et al. 2006, Davidson and Lightfoot 2007). Conservation and restoration of Great Plains ecosystems are not possible without the preservation of prairie dogs. Federal lands offer potential space for the conservation of prairie dogs, and many of the largest colonies now in existence are located on federal property (Sidle et al. 2006).

Because of the historical reduction of prairie dog numbers and the importance of prairie dogs to prairie ecosystems, the National Park Service has begun monitoring prairie dog populations at park units. Here we document the population dynamics of a prairie dog colony at Scotts Bluff National Monument, Nebraska, spanning a 28-year period that began with colonization of the monument in 1981. The primary goals of this monitoring were to obtain information on prairie dog density, total colony abundance, and size and location of colonies by using cost-effective procedures for tracking population trends over time (Plumb et al. 2001).

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METHODS

We conducted this study at Scotts Bluff National Monument, Nebraska (41°51′02″N, 103°43′08″W; hereafter SCBL). SCBL is located in a region of the western Great Plains that historically contained mixed- and short-grass prairie. SCBL encompasses 1215 ha, 40% of which is native mixed-grass prairie.

Prairie dogs were exterminated from SCBL in 1944. Prairie dogs naturally recolonized the northwest corner of SCBL in 1981. At the time, Nebraska state law required that prairie dogs be controlled, and in 1984, the colony was treated with diethylstilbestrol (a synthetic estrogen that inhibits reproduction). Individuals were "removed" from the colony each year from 1985 to 1988. Number of removed prairie dogs and their percentage of the total population each year were 50 (47%) in 1985, 71 (36%) in 1986, 140 (46%) in 1987, and 27 (12%) in 1988 (M.K. Cox and W.L. Franklin, unpublished report).

From 1983 to 1993, estimates of area occupied, density, and total population size were obtained (estimates of area occupied and density were not obtained in all years; no data were obtained in 1992; M.K. Cox and W.L. Franklin, unpublished reports; Scotts Bluff National Monument personnel, unpublished data). Although methods were not well documented, mark-recapture techniques were employed in 1983 and 1984. From July 1986 to August 1986, a near census was done via live capture (M.K. Cox and W.L. Franklin, unpublished report). In 1995, the law requiring the control of prairie dogs in Nebraska was repealed, and a monitoring protocol was established to ensure consistent data-collection methods over time (Plumb et al. 2001). Although data collected prior to 1995 may not be directly comparable to those collected from 1995 onward, the pre-1995 population estimates are informative for describing relatively large changes over time.

Since 1995, sampling the prairie dog population at SCBL has involved delineating the boundaries of colonies and obtaining visual counts of individuals in 4-ha (or smaller) plots. Boundaries of prairie dog colonies were delineated using a GPS in conjunction with a PC-based geographic information system, ArcGIS® 9 (ESRI 2006). Colony boundaries were determined by following active clip lines, when discernible, or by mapping the area within 5 m of active burrows. Burrows were classified as active if burrow openings were greater than 7 cm in diameter and fresh scat was observed within 0.5 m of the opening. Burrows were classified as inactive if there were spider webs across an opening or unclipped vegetation growing in or around the opening (Biggins et al. 1993, Desmond et al. 2000). The greatest extent of both active burrows and active clip lines were combined to close each colony polygon.

Eight replicate counts of individuals, with 15-minute intervals between each replicate, were made from each of 3 potential observation points (depending on colony extent). From June to August, we conducted counts on 3 consecutive mornings when possible, always between 6:30 and 9:00. Using landscape features, we defined sections of the colony for survey from each observation point to prevent counting individuals twice during a replicate. We then combined counts from each observation point to obtain a colony-wide estimate.

To estimate the density of prairie dogs from visual counts, we used the equation

$$D = ([M/A] - 3.04)/0.40 ,$$

where D is density, M is maximum visual count, and A is total area sampled. This equation was originally developed for prairie dogs inhabiting Conata Basin, South Dakota (Severson and Plumb 1998), but we subsequently applied it to prairie dogs at SCBL (Plumb et al. 2001). To calculate population size, we multiplied density estimates by the area occupied by the colony in that year. Variance calculations and 95% confidence intervals for both density and population size followed those developed by Severson and Plumb (1998).

RESULTS

Estimates of prairie dog population size at SCBL reveal 4 discrete periods (Fig. 1A): (1) From colonization in 1981, the colony grew to 303 individuals in 1987. Despite removal of individuals, the increase in numbers from 1984 to 1987 was strongly linear ($R^2 = 0.99$, $F = 231$, $P = 0.004$), with an increase of 88 individuals per year along a line of best fit as determined by a linear function. (2) The population declined rapidly from 1987 to 1989, and then declined more slowly until 1995. (3) The population grew at an exponential rate from 1995 to 2003, increasing from 17 to almost 800 individuals. This represents a doubling time of almost 1.5 years. An exponential function ($R^2 = 0.91$, $F = 70.33$,

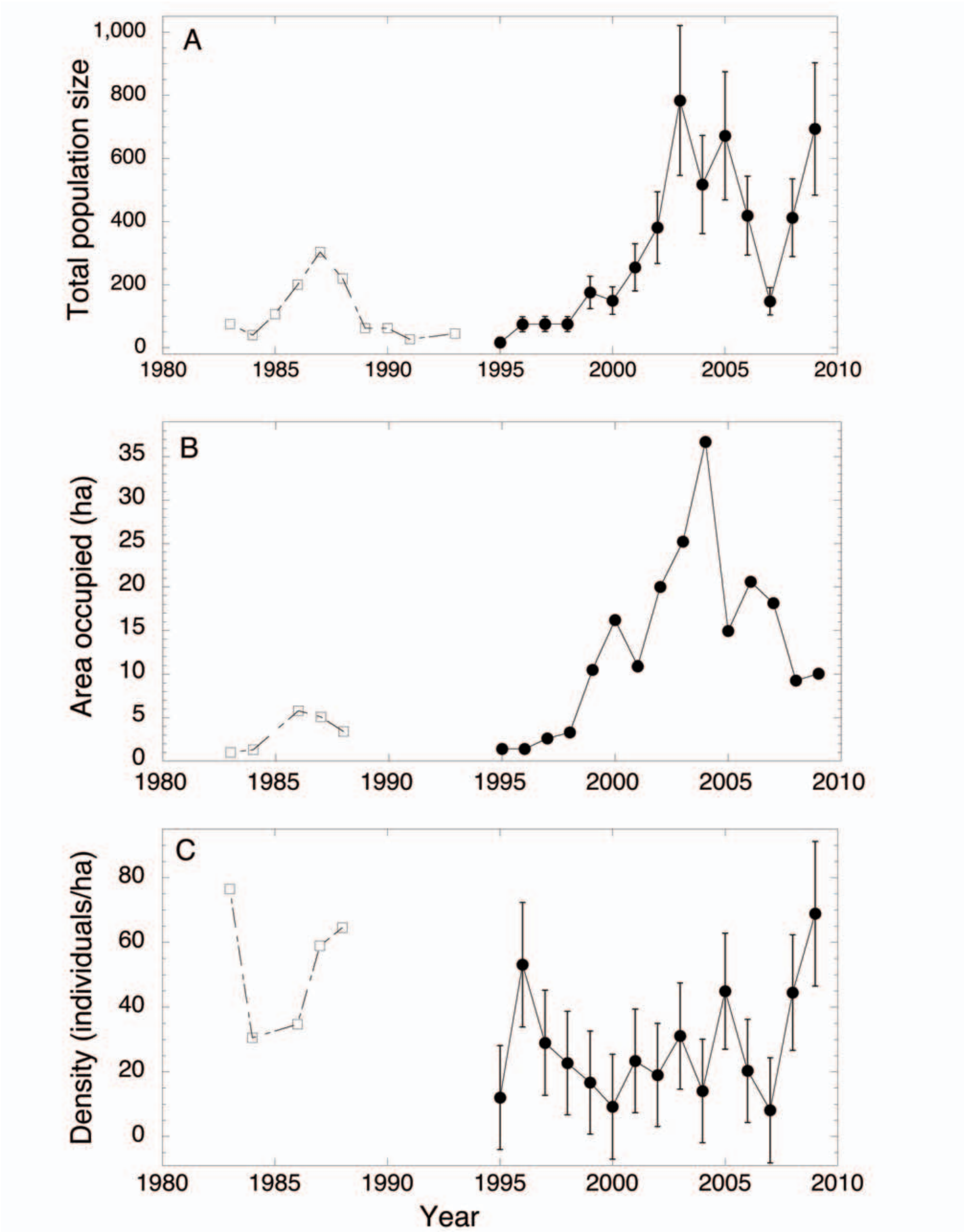

Fig. 1. Change over time in (A) total population size, (B) area occupied, and (C) density for the black-tailed prairie dog population at Scotts Bluff National Monument, Nebraska. Open squares represent data obtained before the adoption of a consistent monitoring protocol based on visual counts. Error bars represent 95% confidence intervals.

$P < 0.001$) fit the data better than a linear one ($R^2 = 0.71$, $F = 17.44$, $P = 0.004$). (4) From 2003 to 2009, the population was highly variable, declining to 147 individuals in 2007 before rebounding to almost 700 individuals in 2009.

The area occupied by prairie dogs at SCBL exhibited overall patterns of change similar to those of estimated population size (Fig. 1B). Although fewer data points were available before 1995, an increase in area is evident from colonization in 1981 to 1986, and then area decreased through the initiation of the current monitoring program. The occupied area increased dramatically from 1995 to 2004, and an exponential function (R^2 = 0.93, F = 112.98, P < 0.001) fit the data slightly better than a linear one (R^2 = 0.87, F = 54.07, P < 0.001). The occupied area declined after 2004. Occupied area was positively correlated with estimated population size from 1995 to 2009 (R^2 = 0.37, F = 7.50, P = 0.017).

During the exponential population increase from 1995 to 2004, the colony increased in area by expanding its outer boundaries (Fig. 2). However, during the decrease in aerial extent from 2004 to 2009, prairie dogs disappeared from what had been the interior regions of the largest area occupied, resulting in multiple, fragmented subcolonies. (The population was not mapped before 1995.)

Densities of prairie dogs at SCBL varied from 8 to almost 80 individuals per hectare (Fig. 1C). The magnitude of uncertainties associated with densities relative to the differences in point estimates make it difficult to distinguish systematic patterns among years. Still, some years clearly had higher densities than others. The pattern of change over time in estimated population size does not exactly match that of area occupied because of variability in density among years.

Discussion

The prairie dog population at SCBL increased dramatically in both size and occupied area over the first 6 years after colonization, despite treatments with reproduction-inhibiting drugs and removal of individuals. The population also increased dramatically from 1995 to 2003—especially from 2000 to 2003, when it increased more than 5-fold. These findings are surprising, given the relatively slow reproduction rates documented for several species of prairie dogs, including black-tailed prairie dogs (Hoogland 2001). Young colonies of black-tailed prairie dogs expanding into new areas, however, exhibit higher reproductive rates than older, established colonies that have little room for expansion (Garrett et al. 1982). Additionally, reproduction may increase greatly in established colonies in the years following a population crash (Knowles 1986, 1987).

The rapid decline and sustained depression in population size from 1987 to 1995 could have been the result of unofficial shooting or poisoning. Sylvatic plague, although never documented from SCBL, has been reported from western Nebraska (Cully et al. 2010), and it is possible the colony may have been infected with this disease. Mortality in colonies infected by sylvatic plague often ranges from 85% to 100% (Cully et al. 2010). The 2005–2007 population decline did not show a pattern similar to the 1987–1995 decline, and was followed by a symmetrical rebound from 2007 to 2009. Sylvatic plague may cause shifts in the spatial distribution of prairie dog colonies (Augustine et al. 2008), and recent research indicates that plague may persist in a latent phase in prairie dog colonies during interepizootic periods (Biggins et al. 2010, Salkeld et al. 2010)

Alternatively, predators may have been partially responsible for the declines. Badgers (*Taxidea taxus*) are possibly the most significant predator of prairie dogs (Campbell and Clark 1981, Lindzey 1982), and even a single badger may have a relatively large impact on a small prairie dog colony. "High mortality" was reported due to a badger that excavated 39 burrows between 1987 and 1988 (Cox and Franklin, unpublished report), and this predation may have been, at least in part, responsible for the decline from 1987 to 1989. A badger was observed in 2004 and again in 2007, corresponding to the short-term declines in population size documented in 2003–2004 and 2005–2007. In addition to the direct effect, predation may have important indirect effects on colony size (e.g., predation on lactating females may cause coterie collapse, which can lead to increased intraspecific mortality due to cannibalism, decreasing pup survival; G. Plumb personal communication).

Data quality

A number of different methodologies for estimating the abundance of prairie dogs (both black-tailed and white-tailed [*Cynomys leucurus*]) have been applied (Severson and Plumb 1998, Biggins et al. 2006). Burrow or mound counts often yield inaccurate or biased results (Powell et al. 1994, Severson and Plumb 1998, but see Johnson and Collinge 2004). Techniques involving aerial photography or satellite imagery cannot usually distinguish between active colony areas and recently deserted colonies (Biggins et al. 2006). Mark-recapture or mark-resight methods, although more accurate, are much more labor-intensive and costly, and are not free of bias (Magle et al. 2006, McClintock et al. 2009). Visual count methods, as employed here, represent a cost-effective procedure for tracking prairie dog populations over time (Fagerstone and Biggins 1986).

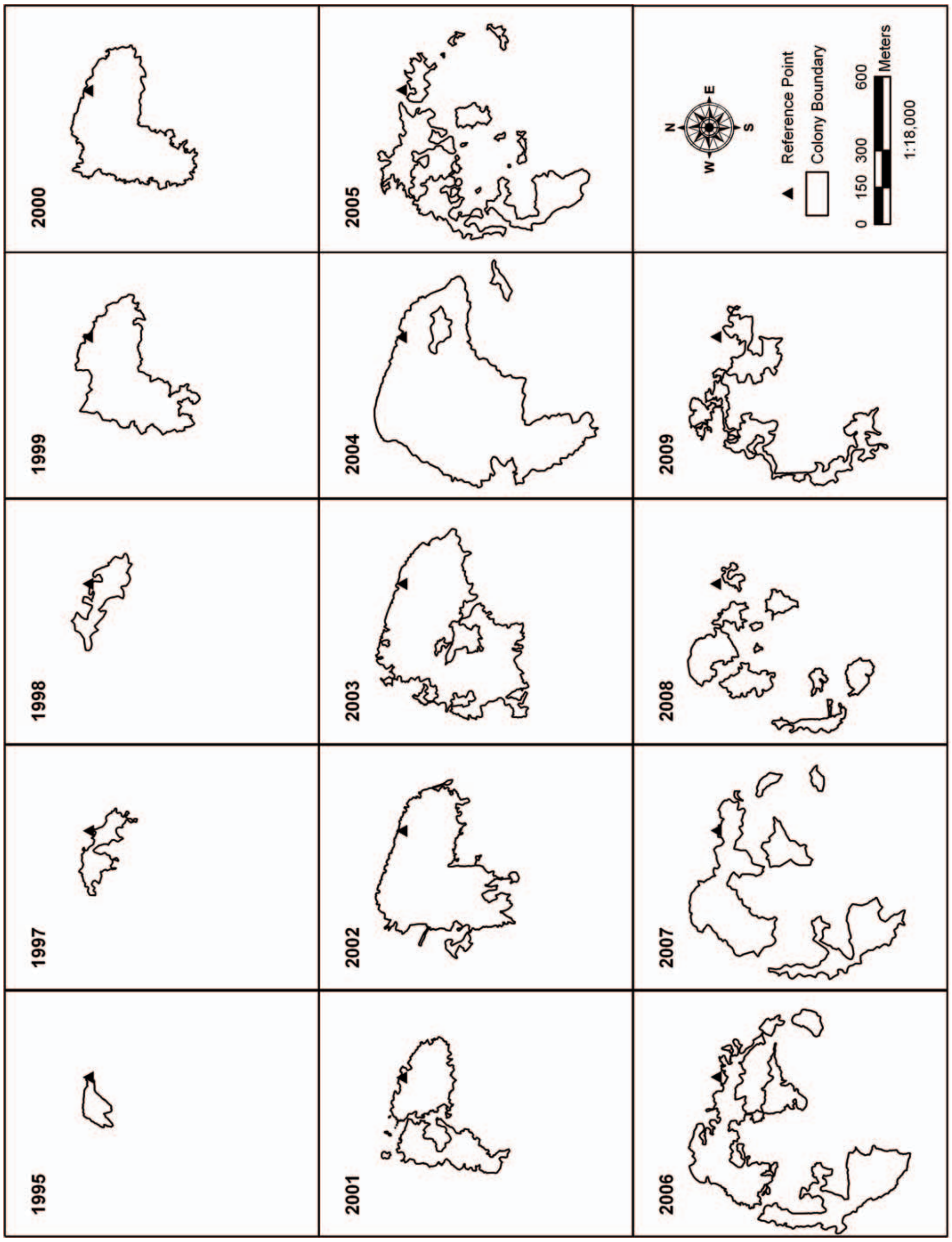

Fig. 2. Extent of black-tailed prairie dog colony boundaries at Scotts Bluff National Monument, Nebraska. An irrigation canal (not shown) limited expansion to the north.

Because the linear models developed to quantify prairie dog density from visual counts were originally developed for colonies within the Conata Basin, they are potentially affected by differing visual detectability among sites. Previous researchers have used these linear models from Conata Basin in other locations, however, or found that correction factors based on visual obstructions did not improve density estimates (Menkens et al. 1990, Severson and Plumb 1998).

The relatively large changes in population size—spanning almost 2 orders of magnitude—in the colony at SCBL over the long term are too robust to be attributed entirely to sampling error or bias. Moreover, changes in the area occupied as determined by boundaries of active burrows and vegetation clip lines, which were obtained independently of estimating the number of individuals present, revealed similar changes over time.

Barriers to expansion

The prairie dog colony originated in 1981 in the northwest corner of the monument, close to an irrigation canal that represents a barrier to expansion to the north. Consequently, colony expansion has been primarily to the south (Fig. 2), and apparently much more grassland is available for colonization south and east of the current colony limits. In 2002, a new colony was established across the irrigation canal to the north. The area colonized is relatively small and is surrounded by barriers to further dispersal (approximately 2.5 ha), and the estimated population size has ranged between 70 and 180 from 2004 to 2009. This new colony was not included in the analyses presented here, because additional expansion is extremely limited by geographical barriers and land-use practices.

Implications

Although prairie dogs are recognized as a keystone species, it has been estimated that a colony or complex of colonies must encompass a minimum area of 4000 ha to support a "fully functional grassland ecosystem" that would provide suitable habitat for black-footed ferrets (*Mustela nigripes*) and other species dependent on prairie dogs for survival (Proctor et al. 2006). The grassland area at SCBL falls far below this threshold, and colonization of the necessary surrounding private lands seems unlikely due to current land-use practices. Thus, the prairie dog population in the SCBL region may never grow large enough to allow for the survival of other, prairie dog–dependent species.

Other regions of the Great Plains would provide larger areas for such fully functional ecosystems (Proctor et al. 2006), and experimental work has shown that prairie dog colonies may be reestablished through translocations (Truett et al. 2001, Dullum et al. 2005). The record of the SCBL prairie dog population's growth and survival over the past 3 decades demonstrates the potential for rapid population growth from a small colony size, as well as the potential for dramatic declines, almost to extinction. Yet, after almost 30 years, the population is still relatively small (although this is in part due to geographical barriers to expansion).

Translocations (or natural dispersal events) have the potential to result in large, established colonies, and any inducement to colony growth should be considered. Manipulative studies indicate that mowing and burning treatments have significant positive effects on colony expansion (Milne-Laux and Sweitzer 2006, Northcott et al. 2008).

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