3-4-2008

Spatiotemporal dynamics of black-tailed prairie dog colonies affected by plague

David J. Augustine
USDA-ARS

Marc R. Matchett
USFWS-Charles M. Russell National Wildlife Refuge

Theodore P. Toombs
Environmental Defense

Jack F. Cully
USGS-BRD Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University

Tommy L. Johnson
Montana Ecology of Infectious Disease, Division of Biological Sciences, University of Montana, Missoula, MT

See next page for additional authors

Landscape Ecol (2008) 23:255–267
DOI 10.1007/s10980-007-9175-6

RESEARCH ARTICLE

Spatiotemporal dynamics of black-tailed prairie dog colonies affected by plague

David J. Augustine · Marc R. Matchett · Theodore P. Toombs · Jack F. Cully Jr. · Tammi L. Johnson · John G. Sidle

Received: 13 June 2007 / Accepted: 15 October 2007 / Published online: 9 November 2007

Abstract Black-tailed prairie dogs (*Cynomys ludovicianus*) are a key component of the disturbance regime in semi-arid grasslands of central North America. Many studies have compared community and ecosystem characteristics on prairie dog colonies to grasslands without prairie dogs, but little is known about landscape-scale patterns of disturbance that prairie dog colony complexes may impose on grasslands over long time periods. We examined spatiotemporal dynamics in two prairie dog colony complexes in southeastern Colorado (Comanche) and northcentral Montana (Phillips County) that have been strongly influenced by plague, and compared them to a complex unaffected by plague in northwestern Nebraska (Oglala). Both plague-affected complexes exhibited substantial spatiotemporal variability in the area occupied during a decade, in contrast to the stability of colonies in the Oglala complex. However, the plague-affected complexes differed in spatial patterns of colony movement. Colonies in the Comanche complex in shortgrass steppe shifted locations over a decade. Only 10% of the area occupied in 1995 was still occupied by prairie dogs in 2006. In 2005 and 2006 respectively, 74 and 83% of the total area of the Comanche complex occurred in locations that were not occupied in 1995, and only 1% of the complex was occupied continuously over a decade. In contrast, prairie dogs in the Phillips County complex in mixed-grass prairie and sagebrush steppe primarily recolonized previously occupied areas after plague-induced colony declines. In Phillips County, 62% of the area occupied in 1993 was also occupied by prairie dogs in 2004, and 12% of the complex was occupied continuously over a decade. Our results indicate that plague accelerates spatiotemporal movement of prairie dog colonies, and have significant implications for

D. J. Augustine (✉)
USDA-ARS, Rangeland Resources Research Unit,
1701 Centre Avenue, Fort Collins, CO 80526, USA
e-mail: David.Augustine@ars.usda.gov

M. R. Matchett
USFWS-Charles M. Russell National Wildlife Refuge,
Lewistown, MT 59457, USA

T. P. Toombs
Environmental Defense, 2334 North Broadway,
Boulder, CO 80304, USA

J. F. Cully Jr.
USGS-BRD Kansas Cooperative Fish and Wildlife
Research Unit, Division of Biology, Kansas State
University, Manhattan, KS 66506, USA

T. L. Johnson
Montana Ecology of Infectious Disease,
Division of Biological Sciences, University of Montana,
Missoula, MT 59801, USA

J. G. Sidle
USDA-Forest Service, 125 N Main ST, Chadron,
NE 69337, USA

landscape-scale effects of prairie dog disturbance on grassland composition and productivity. These findings highlight the need to combine landscape-scale measures of habitat suitability with long-term measures of colony locations to understand the role of plague-affected prairie dogs as a grassland disturbance process.

Keywords Disturbance processes · Grassland · Grazing · Great Plains · Mixed-grass prairie · Semi-arid rangeland · Shortgrass steppe

Introduction

Fire and herbivores are key agents of disturbance in grassland ecosystems. While fires are temporally discrete disturbance events that can be described in terms of their frequency, intensity and extent (e.g. Wright and Bailey 1982; Anderson 1990), herbivory is a diffuse disturbance that functions over a wide range of spatial and temporal scales. Many studies have examined the landscape-scale role of large herbivores as a disturbance process in grasslands (e.g. Turner and Bratton 1985; Coughenour 1991; Frank et al. 1998; Knapp et al. 1999), and have addressed the hierarchical scaling of effects that results from their movement and selective foraging patterns (Senft et al. 1987; Bailey et al. 1996).

Black-tailed prairie dogs are also a key component of the disturbance regime in semi-arid grasslands of central North America (Whicker and Detling 1988; Detling 1998), but they differ fundamentally from large herbivores due to their coloniality, limited mobility over short time scales, and the intensity of defoliation regime they impose. Most research concerning effects of black-tailed prairie dogs in grasslands has focused on the unique community and ecosystem characteristics that occur on prairie dog colonies compared to adjacent non-colonized grassland (e.g. Whicker and Detling 1988; Kotliar et al. 1999; Kretzer and Cully 2001; Smith and Lomolino 2004). Little consideration has been given to identifying the characteristics of prairie dog colony disturbance such as frequency (number of disturbances per unit time), predictability (variance in the mean time between disturbances), and turnover rate (mean time to disturb entire area; Sousa 1984). For example, Collins and Barber (1985) described prairie dog disturbance as continuous, but did not specify a time frame. Some studies suggest prairie dogs may have a natural impetus to relocate due to changes in vegetative characteristics that develop over multiple decades of prairie dog occupancy (Garrett and Franklin 1988; Cincotta 1985; Garrett, et al 1982), but little is known about the landscape-scale dynamics of colonies prior to European settlement of central North America. This lack of information may be due in part to the wide range of anthropogenic factors which have dramatically affected prairie dog colonies since European settlement (Miller and Cully 2001; Lomolino and Smith 2001). An additional factor may be the paucity of information on non-anthropogenic factors leading to colony declines or extirpations, and the multi-decade to century time scales over which individual prairie dog colonies can persist (Garrett et al. 1982; Carlson and White 1987; Knowles and Knowles 1994).

The dynamics of prairie dog colonies in much of the shortgrass steppe and mixed-grass prairie of central North America have been dramatically altered since the introduction of plague caused by the bacterium *Yersinia pestis* from Asia in the early 1900s (Cully and Williams 2001). This disease can cause mortality rates approaching 100% within individual colonies and can spread rapidly across colony complexes covering hundreds of square kilometers in some years (Cully and Williams 2001; Stapp et al. 2004; Johnson 2005; Collinge et al. 2005a). Plague now affects approximately the western two-thirds of the black-tailed prairie dog's geographic range (Cully et al. 2006). Prairie dogs in this plague-affected region now live in dynamic metapopulations where colony locations can change over shorter time scales compared with pre-plague dynamics (Collinge et al. 2005a, b; Antolin et al. 2006).

Despite the reduction in their distribution over the past century, black-tailed prairie dogs are still widespread in some portions of the shortgrass steppe and mixed-grass prairie (Sidle et al. 2001; White et al. 2005; Proctor et al. 2006), and their influence on vegetation dynamics has significant implications for both livestock and the conservation of native plants and animals (Whicker and Detling 1988; Lomolino and Smith 2003; Smith and Lomolino 2004; Kretzer and Cully 2001; Derner et al. 2006).

Prairie dog effects on vegetation are typically evaluated by comparing colonized versus non-colonized grassland (e.g. Weltzin et al. 1997; Winter et al. 2002; Johnson-Nistler et al. 2004), but the time since colonization also determines vegetation changes. Studies in mixed-grass prairie of South Dakota (outside the plague zone) found that changes in species composition do not begin until 2 or more years after colonization, and that more than 15 years of prairie dog presence is required to induce the transition from grass dominance to a forb-shrub dominated community (Archer et al. 1987; Coppock et al. 1983; Whicker and Detling 1988; Detling 1998). Within the plague zone in shortgrass steppe, Hartley (2006) found that prairie dog effects on plant biomass and composition are similar to but of lower magnitude than effects in mixed-grass prairie. Furthermore, 98% of all colonies in the study area experienced a plague outbreak within 15 years of activity, and vegetation composition and biomass on plague-extirpated colonies were similar to non-colonized grassland after 1–2 years (Hartley 2006). These results indicate that the areal extent of prairie dog colonies in any given year provides an incomplete picture of the effect of prairie dogs on the landscape. An understanding of how plague affects the rate and pattern of spatial turnover of colonies through time is also needed.

The objective of this study was to quantify spatiotemporal patterns of turnover in plague-affected black-tailed prairie dog colony complexes during approximately one decade. Our analysis examines changes in colony boundaries and locations on some public lands in the western Great Plains since the 1990s. We focus on (1) a colony complex in mixed-grass prairie in Phillips County, Montana on land managed by the Bureau of Land Management (BLM), and (2) a colony complex in shortgrass steppe on the Comanche National Grassland in southeastern Colorado, both of which have been monitored for an 11-year period. We compare dynamics of these two complexes to a baseline provided by a prairie dog complex on the Oglala National Grassland in northwestern Nebraska, which has been monitored for 8 years but has not been affected by plague. We hypothesized that at the temporal scale of a decade, plague causes prairie dog colonies to fluctuate in size, but that after plague events, colonies would return to previously occupied locations. We tested this hypothesis by measuring changes in the extent and location of active prairie dog colonies in two complexes that each experienced a cycle of plague-induced colony decline and recovery over an 11 year period.

Study areas and methods

Comanche National Grassland, Colorado

This study area consisted of lands on the Carrizo Unit of the Comanche National Grassland located in southeastern Colorado in Baca and Las Animas counties (lat 37°15′N, long 102° 45′W). Our study area, which consisted of 40,700 ha of allotments on the Comanche National Grassland that were surveyed for prairie dog colonies in 1995, is centrally located in the shortgrass steppe ecosystem (Lauenroth and Milchunas 1991), and is characterized by relatively flat to gently undulating topography. Based on slopes derived from a digital elevation model, 97% of the study area is <5° slope, 2% is 5–10° slope, and 1% is >10° slope. Long-term mean annual precipitation at nearby Springfield, Colorado, is 40.3 cm. Soils are predominantly clay loams, silt loams, and fine sandy loams (Woodyard et al. 1973). Vegetation on prairie dog colonies is dominated by blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), and purple threeawn (*Aristida purpurea*), while non-colonized grassland is dominated by blue grama, sideoats grams (*B. curtipendula*), and buffalograss (Winter et al. 2002). The National Grassland allotments that we studied are intermingled with private lands, which include rangeland, Conservation Reserve Program fields with taller-structure grasses, and cropland. The allotments we studied are grazed by cattle, primarily during May 15–November 15, with permitted stocking rates of approximately 1.2–2.0 ha per Animal Unit Month (AUM). With the exception of black-footed ferrets (*Mustela nigripes*), native predators of black-tailed prairie dogs are present throughout the study area. No legal poisoning of prairie dogs occurred on public lands in the study area during the period of analysis. Recreational shooting was permitted during 1995–1999, but was prohibited during 2000–2006.

Prairie dog colonies were mapped during June–July in 1995 using a Garmin backpack GPS unit either while walking or driving along the colony perimeter (Toombs 1997). Observations in 1994 and 1995 indicated that some colonies were affected by a plague epizootic that started in 1994 and continued after 1995. Colonies were remapped in 1999 and annually during 2001–2006 using a Trimble hand-held GPS unit while following colony boundaries by vehicle. Only the active area of each colony was mapped, where active areas were identified by visually and audibly locating prairie dogs. Boundaries were determined by (1) presence of fresh prairie dog scat, (2) recent digging on and near burrow mounds, and (3) clipped vegetation, indicating foraging activity (Johnson 2005). Spatial data were differentially corrected using Trimble Pathfinder software (Trimble, Sunnydale, California, USA) and a base station in Elkhart, Kansas. GPS data were incorporated into a geographic information system (GIS: ESRI, ARCMap 9.1) to analyze changes in colony boundaries.

Phillips County, Montana

This study area consisted of BLM-managed lands in northern Phillips County, Montana (lat 47°48′N, long 107° 54′W). Topography varies from flat uplands and rolling hills to badlands and breaks. Based on slopes derived from a digital elevation model, 76% of the study area is <5°, 16% is 5–10°, and 8% is >10° slope. Soil types include a combination of deep, well-drained sandy loam-to-clay loam and shallow, well-drained clay-to-silty clay (Reading and Matchett 1997). Climate is continental with mean annual precipitation of 28–32 cm. The prairie dog complex occurred within approximately 225,000 ha of BLM parcels. BLM-administered land was intermingled with privately-owned rangeland. Vegetation consists of mixed-grass prairie and sagebrush shrubland. Grassland areas are dominated by western wheatgrass (*Pascopyrum smithii*), blue grama, needle-and-thread (*Hesperostipa comata*) and green needlegrass (*Stipa viridula*), and shrub-dominated areas contain big sagebrush (*Artemesia tridentata*) and greasewood (*Sarcobatus vermiculatus*) (Reading and Matchett 1997). Vegetation of non-colonized grassland has substantially greater abundance of cool-season perennial grasses (western wheatgrass and needle-and-thread) and sagebrush than areas colonized by prairie dogs (Johnson-Nistler et al. 2004). The area is grazed by cattle, typically during May–October, at stocking rates of approximately 2–3 ha/AUM. Less than 300 ha were affected by flea-control applications (dusting with pulicides) in 1993, 2003 and 2004 as part of management for black-footed ferret reintroduction. No legal poisoning of prairie dogs occurred during the period of analysis, but recreational shooting of prairie dogs is permitted throughout the area. Native predators of black-tailed prairie dogs are present throughout, with the exception that black-footed ferrets have only been present in small numbers on prairie dog colonies totaling <500 ha.

The first GPS survey was conducted in 1993, and was guided by previous county-wide surveys during the 1980's plotted on topographic maps. The first record of sylvatic plague in Phillips County occurred in 1992, when the area occupied by prairie dogs was reduced by approximately 50% (Matchett unpublished data), and declines continued through 1996. Trimble hand-held GPS units in vehicles were used to map colony perimeters by connecting outermost active burrows during June–December. GPS data were differentially corrected using base files from Lewistown, Montana. Following the 1993 survey, colonies were subdivided into non-overlapping thirds with one-third surveyed in 1995, 1996 and 1997. These 1995–1997 surveys were combined into a single layer covering the entire study area, and are referred to hereafter as the 1996 survey. The entire study area was re-surveyed in 1998, 2000, 2002 and 2004.

Oglala National Grassland, Nebraska

The prairie dog complex under study occurred within 18,000 ha of allotments on the Oglala National Grassland in northwestern Nebraska. Topography of the area is a blend of rolling plains and badlands. Based on slopes derived from a digital elevation model, 83% of the study area is <5°, 15% is 5–10°, and 2% is >10° slope. Climate is continental with mean annual precipitation of ~38 cm in the north of the study area, increasing to ~46 cm in the south. Vegetation is mixed-grass prairie dominated by western wheatgrass, green needlegrass, blue grama, buffalograss, and sideoats grama. Allotments on the Oglala National Grassland are intermingled with private lands that consist primarily of rangeland. With the exception of black-footed ferrets, native predators of black-tailed prairie dogs are present throughout the study area. Prairie dog colonies were mapped from vehicles using hand-held Trimble GPS units in 1996, 1999, 2000, 2001, 2002 and 2004. Prairie dog colonies were controlled periodically with poisoning until the early 1990s, but neither poisoning nor plague affected this complex during 1996–2004. Recreational shooting of prairie dogs was permitted throughout the study area. The study area is grazed by cattle, primarily during May 15–November 15, with stocking rates averaging 1.8 ha per AUM during 1996–2006.

Data evaluation

Prior to data analysis, we examined the prairie dog complexes for two potential sources of error: (1) colonies that were surveyed in most years, but inadvertently missed in one of the GPS surveys, and (2) colonies that were detected after the first survey year, but which may have been present but missed in earlier years.

The study area in Phillips County, Montana was the largest of the three we examined. After creating a map that represented a composite of all active prairie dog colonies on BLM-administered land in Phillips County during 1993–2004, we visually examined polygons in which prairie dogs were active in one survey, absent in the following survey, and then active again in the third survey, for all possible sequences (1993–1998, 1996–2000, 1998–2002 and 2000–2004). While most of these polygons reflected changes in colony boundaries due to plague outbreaks or minor shifts in colony boundaries, we identified eight colonies that were missed in the 1996 survey, three colonies missed in the 1998 survey, and three colonies missed in the 2000 survey. These 14 colonies were excluded from our analysis. Second, we examined those colonies detected after the 1993 survey (i.e., new colonies) to determine (1) whether they represented expansion from a previously-mapped colony on adjacent private land, and (2) their size in the first year they were detected on BLM land. We excluded from our analysis any colonies that were not expansion from previously-known colonies, and that were >10 ha in size in the first year of detection, because these colonies likely were present but undetected in earlier years. We found no mapping errors for Oglala. Based on our criteria, we excluded 12 colonies from Phillips County and three colonies from Comanche from analysis because they were larger than 10 ha in the first year of detection, and may have been present but unmeasured in earlier surveys.

Data analysis

For each complex, we created a GIS map that represented a composite of all colonies mapped in all surveys. We used this map to calculate several spatiotemporal changes in each prairie dog colony complex: (1) total area occupied by prairie dogs at any time during the study period (referred to hereafter as the total complex footprint), (2) the proportion of the total footprint occupied by prairie dogs for varying numbers of surveys (i.e. frequency distribution of occupancy time for the total footprint), (3) trends in area occupied by prairie dogs, (4) for the area that was occupied in the first survey, trends in the amount of that area occupied in subsequent surveys, and (5) the proportion of the area occupied in the first survey that was occupied for varying numbers of surveys (i.e. frequency distribution of occupancy time for the first-survey footprint). The Comanche complex was surveyed eight times, while the Phillips County and Oglala complexes were surveyed six times. To directly compare frequency distributions for occupancy times across the three complexes, we calculated distributions for the Comanche complex using six of the eight surveys by excluding the 2002 and 2004 surveys.

Results

Comanche National Grassland, Colorado

Active prairie dog colony area fluctuated dramatically from 639 ha in 1999 to 4311 ha in 2005, with a net decline in active colony acreage over the 11-year period from 2186 to 1320 ha (Fig. 1A). The area occupied in 1995 and in subsequent years revealed the nature of prairie dog colony occupancy. First, after a plague-induced decline during 1995–1999

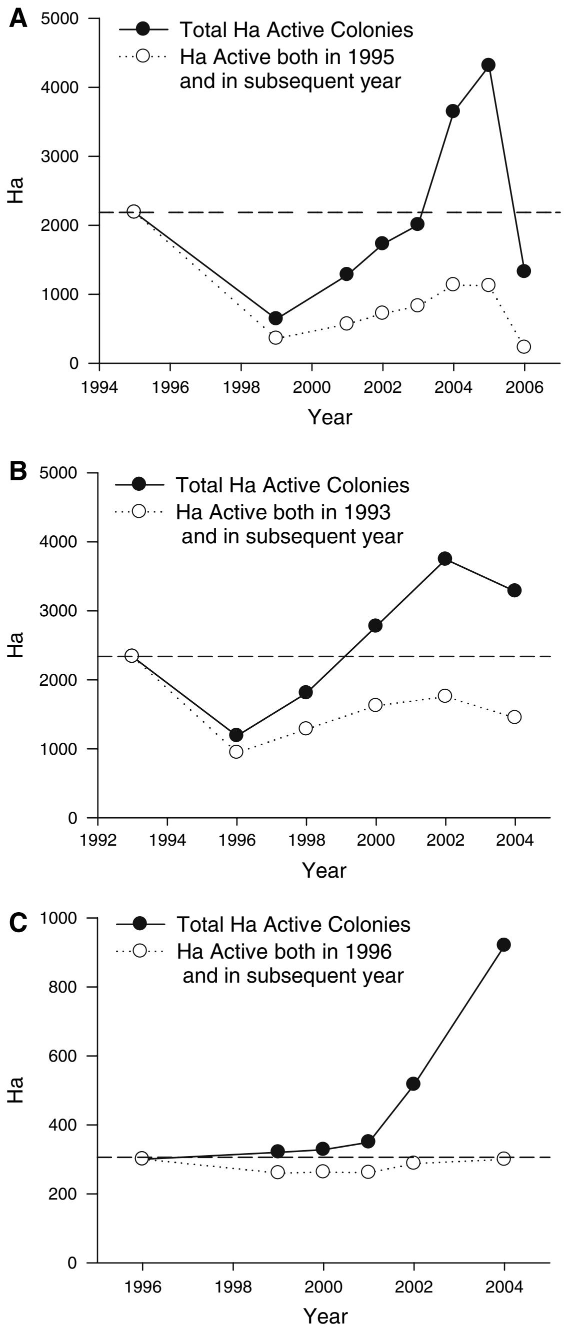


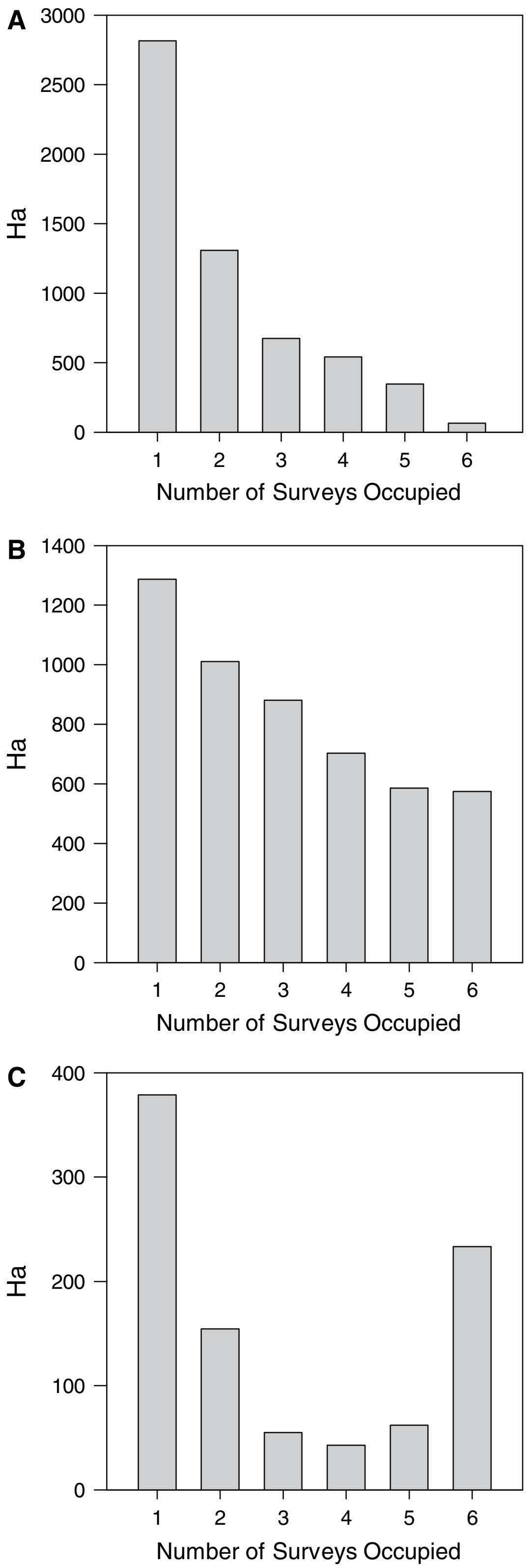
Fig. 1 Changes over time in the total area of active prairie dog colonies in each complex (solid symbols), compared with changes in area that was active colony both in the first survey and in subsequent surveys (open symbols), for (**A**) the Comanche National Grassland, Colorado (**B**) BLM-administered land in Phillips County, Montana, and (**C**) Oglala National Grassland, Nebraska. Dashed lines show the area of active prairie dog colonies in the first year surveyed at each site

followed by a recovery to similar total active area by 2003, only 825 ha or 38% of the area originally occupied in 1995 was still occupied in 2003. Second, even following the rapid expansion of prairie dog colonies during 2003–2005 to peak occupancy of 4311 ha, only 1121 ha or half of the area originally occupied in 1995 was occupied in 2005. Following another major plague-induced decline between 2005 and 2006, only 226 ha or 10% of area originally occupied in 1995 was still occupied by prairie dogs in 2006 (Fig. 1A). Conversely, in 2005 and 2006 respectively, 74 and 83% of the total area of the colony complex occurred in locations that were unoccupied in 1995.

Analysis of areal overlap of all eight surveys revealed a total footprint of 5749 ha, of which only 65 ha (1.1%) was occupied during all eight surveys. In contrast, 34% of the total footprint was occupied for just one survey. Of the area that was occupied in the first (1995) survey, 43% was occupied only in 1995, and 3% was occupied for all eight surveys. We repeated the same analysis after removing the 2002 and 2004 surveys, in order to compare the Comanche complex with the Phillips County complex when both are sampled with 6 surveys over an 11-year period. Results based on six surveys were similar to that based on eight surveys, with most of the Comanche complex's total footprint occupied for only 1 or 2 surveys (Fig. 2A). Similarly, for the area occupied by prairie dogs in the first (1995) survey, 43% (948 ha) was occupied only in 1995, and 3% (65 ha) was occupied for all 6 surveys (Fig. 3A). The temporal pattern of occupancy and re-colonization after plague epizootics reflects substantial changes in locations of active black-tailed prairie dog colonies, with few areas that were occupied in 2006 having been occupied 11 years earlier (Fig. 4).

Phillips County, Montana

Active prairie dog colony area fluctuated from 1185 ha in 1996 to 3743 ha in 2002, with a net increase over the 11-year period from 2334 to 3282 ha (Fig. 1B). Following a decline during 1993–1996 and recovery to a similar total active area by 2000, 1621 ha or 69% of the area originally occupied in 1993 was occupied in 2000. By 2004,



◀ **Fig. 2** Frequency distribution of the amount of area occupied by black-tailed prairie dog colonies for one or more surveys for (**A**) Comanche National Grassland based on 6 surveys over 11 years, (**B**) Phillips County, Montana based on six surveys over 11 years, and (**C**) Oglala National Grassland based on six surveys over 8 years

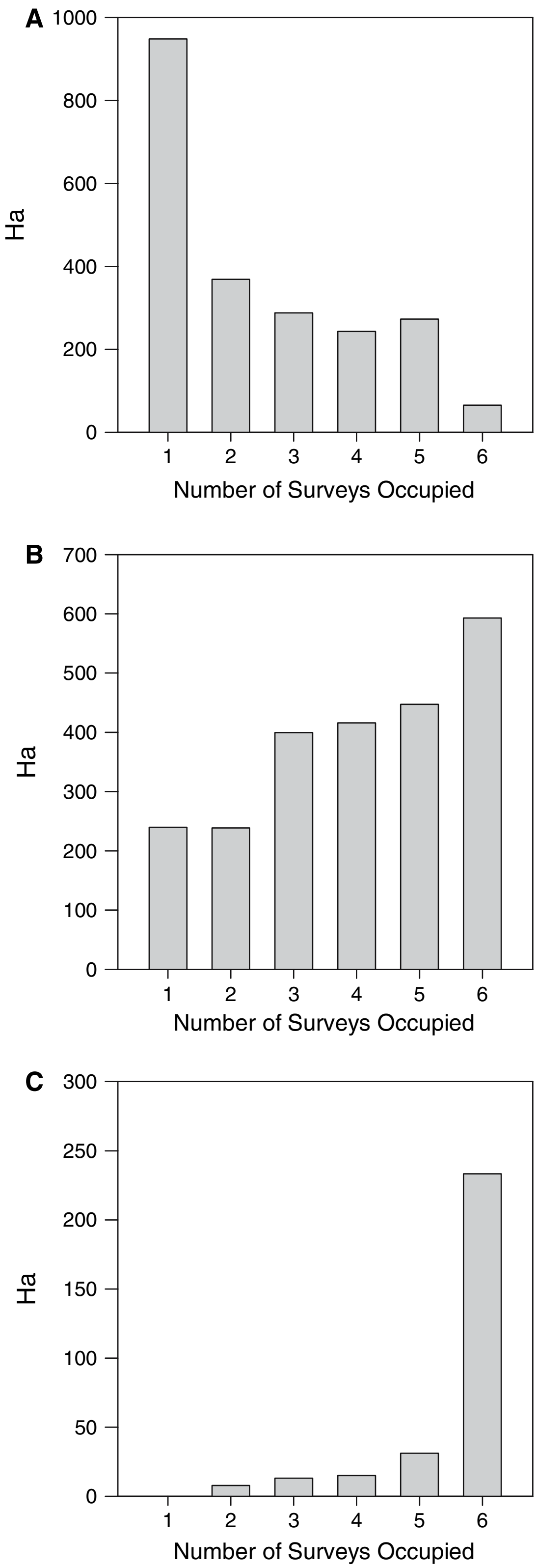
1447 ha or 62% of the area originally occupied in 1993 was still occupied by prairie dogs.

Analysis of areal overlap of all six surveys showed a total footprint of 5020 ha occupied by black-tailed prairie dogs in one or more surveys, of which 25% was occupied for only one survey and 12% was occupied for all six surveys (Fig. 2B). Of the area occupied in the first (1993) survey, nearly the opposite pattern was observed, with 10% occupied for one of the six surveys and 25% occupied in all six surveys (Fig. 3B). Patterns of occupancy and re-occupancy primarily show individual colonies expanding and contracting over time in response to plague outbreaks that are not synchronous across the landscape (Fig. 5). Following plague outbreaks, prairie dogs tended to re-colonize the same approximate area occupied previously, resulting in greater consistency in colony locations over 11 years compared with Comanche (Figs. 4 and 5).

Oglala National Grassland, Nebraska

Active prairie dog colony area was relatively stable (300–349 ha) during 1996–2001, and then increased to 919 ha by 2004 (Fig. 1C). During the period when colonies were relatively stable, 86–87% of the area originally occupied in 1996 continued to be occupied in 1999, 2000 and 2001 (Fig. 1C). This provides one estimate of the amount of spatial turnover within a prairie dog complex that may be attributable to both measurement error and non-plague factors that influence annual changes in colony boundaries. Following the period of rapid colony expansion, 99.7% of the area occupied in 1996 was also occupied in 2004.

Analysis of areal overlap of all six surveys on the Oglala revealed a total footprint of 926 ha. Forty-one percent was occupied for one year and 17% for two years, reflecting the areas colonized during the expansion from 2002 to 2004. Despite the influence of this expansion on the occupancy frequency distribution, 25% of the total footprint was occupied



◀ **Fig. 3** Frequency distribution of the amount of area occupied for one or more annual surveys, analyzed only for that subset of the colony complex that was occupied in the first year of survey for (**A**) Comanche National Grassland, (**B**) Phillips County, Montana, and (**C**) Oglala National Grassland. The area in the 1-year occupancy class for each complex represents areas that were recorded as active in the first survey, but which never supported an active colony in subsequent years, while the 6-year occupancy class shows amount of area that was occupied in the first survey and every survey thereafter

continuously for all six surveys (Fig. 2C). Of the area occupied in the first (1996) survey, 0.05% was occupied for 1 year, and 78% was occupied in all six surveys (Fig. 3C).

Discussion

While little is known about the landscape-scale dynamics of black-tailed prairie dog colonies prior to European settlement, studies conducted outside the current distribution of plague indicate that colonies can remain in the same approximate location for several decades to several centuries (Garrett et al. 1982; Knowles and Knowles 1994; Carlson and White 1987). Locations of colony boundaries may be constrained by topography and soil types (e.g. Reading and Matchett 1997), and may shift over time in response to factors such as vegetation height at colony edges (which influences predation risk) and declining forage quantity and quality in the oldest portions of colonies (e.g. Garrett et al. 1982; Cincotta 1985). However, at the temporal scale of a decade, fluctuations in colony boundaries are expected to be limited compared to the total area occupied by a prairie dog colony. Based on the 1996–2001 GPS record for the plague-free Oglala, we documented a high degree of spatial stability in colony locations. During 1999–2001, 86–87% of the area occupied in 1996 continued to be occupied by prairie dogs. This provides a baseline measurement of the amount of colony "movement" associated with non-plague factors influencing colony boundaries in combination with mapping errors. Following complex expansion in response to a series of years with below-average precipitation and low vegetation heights (2002–2004), nearly 100% of the area occupied in 1996 was still occupied in 2004.

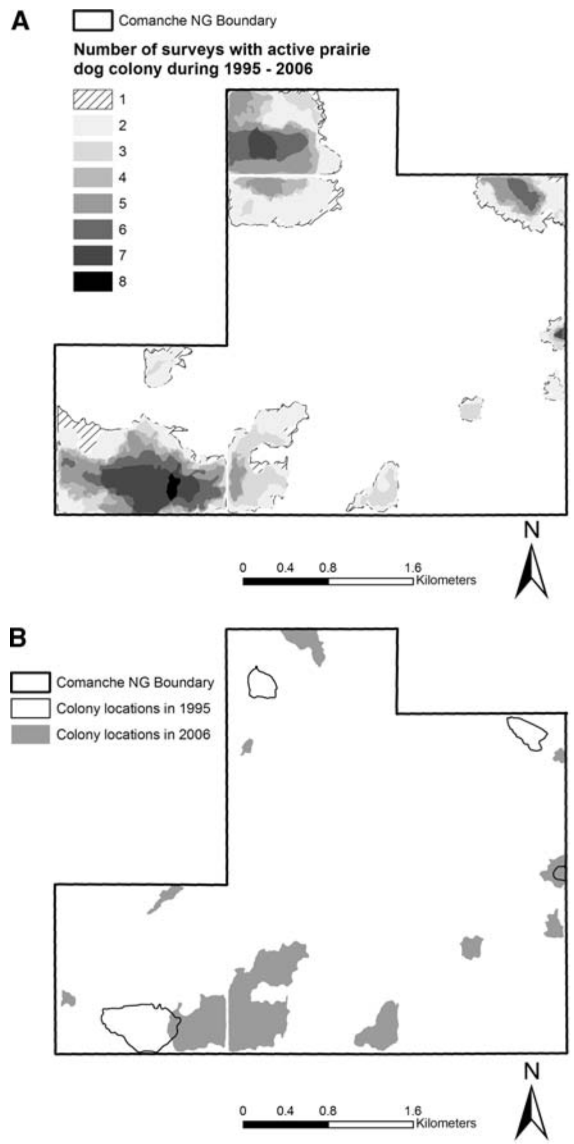


Fig. 4 Example of changes in black-tailed prairie dog colony locations over 11 years on the Comanche National Grassland. Changes are shown in terms of areas occupied for varying proportions of the eight surveys (**A**), and the net change in colony boundaries between 1995 and 2006 (**B**)

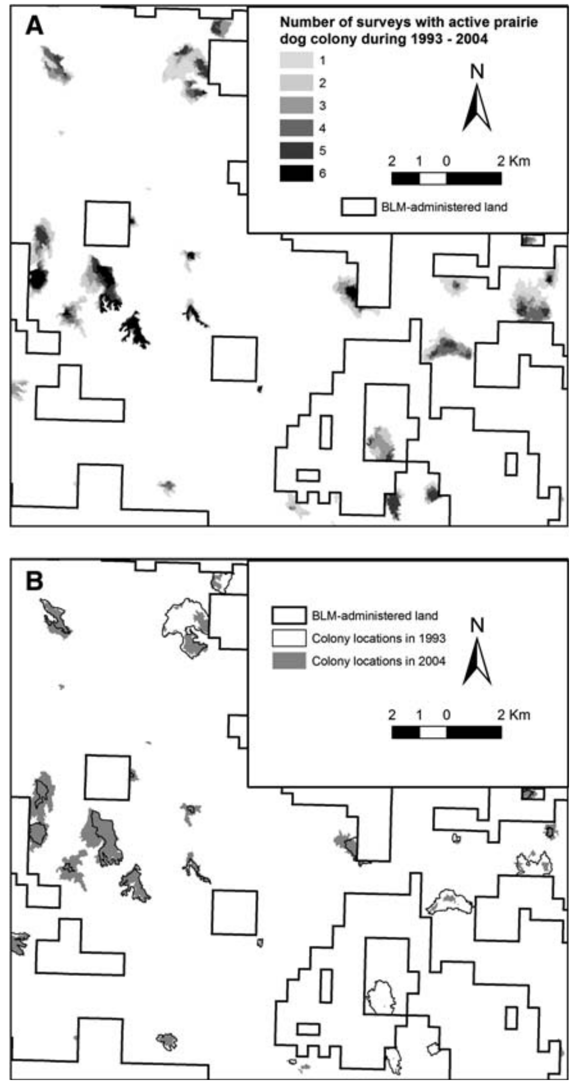


Fig. 5 Example of changes in black-tailed prairie dog colony locations over 11 years on BLM-administered land in Phillips County, Montana. Changes are shown in terms of areas occupied for varying proportions of the six surveys (**A**), and the net change in colony boundaries between 1993 and 2004 (**B**)

In contrast to the Oglala complex, we documented high spatiotemporal turnover in two large prairie dog complexes affected by plague. A key consequence is a shifting mosaic of prairie dog-affected areas within the landscape, where most areas affected by prairie dogs only remain occupied for a limited portion of a decade. Surveys were not conducted annually and hence cannot be equated directly to yearly rates of occupancy, but 72% of the Comanche complex and 45% of the Phillips County complex were occupied for one or two out of six surveys, corresponding to 1–4 years of occupancy over a decade. Conversely, in both cases only a small proportion of the complex (1 and 12% respectively) was affected by continuous prairie dog presence.

While both plague-affected complexes exhibited substantially greater spatiotemporal turnover than the Oglala complex, they also differed markedly from one another in terms of both their temporal and spatial dynamics. First, temporal fluctuations were more dramatic on the Comanche complex, where maximum colony area was seven times greater than minimum colony area over just 11 years. Temporal fluctuations were driven by plague epizootics that resulted in rapid colony declines and some colony extirpations, followed by a period of colony recovery through both expansion of existing colonies and establishment of new colonies. Lower temporal fluctuation in Phillips County, where maximum colony area was only three times greater than minimum colony area over 11 years, was associated with continued plague-induced declines in a small proportion of colonies between the widespread plague epizootics. A similar temporal pattern of plague outbreaks has been reported for the Pawnee National Grassland, northeastern Colorado, where El Niño years have a high incidence of plague, but some colonies are still affected by plague during intervening years (Stapp et al. 2004), and for the Cimarron National Grassland, southwestern Kansas, where colony area grew from 303 ha in 1989 to 526 ha in 1998 despite plague affecting dispersed individual colonies during each mapping interval (Cully and Williams 2001). Plague transmission across a large colony complex over a short time period may be related to landscape characteristics including large mean colony size, low inter-colony distances, and proximity of colonies to dry creek drainages which prairie dogs use for dispersal (Roach et al. 2001; Johnson 2005; Cully et al. 2006). Less rapid transmission among colonies and longer persistence of epizootic plague within a complex may also be related to the landscape distribution of roads, lakes and streams which can serve as barriers to dispersal and plague transmission (Collinge et al. 2005b).

In addition to the variable temporal dynamics of the plague-affected complexes, we documented two distinctly different spatial patterns of colony turnover. The Comanche complex in shortgrass steppe exhibited a high degree of colony movement, a pattern not previously reported for prairie dogs. After plague outbreaks, regrowth of colonies began near colony edges and included substantial expansion into grassland that had not been recently occupied by prairie dogs (Fig. 4). For example, much of the rapid colony expansion during 2001–2005 was into grassland with no visible evidence of old prairie dog mounds (TLJ and DJA, pers. obs.) Due to both the magnitude of plague-induced colony decline and the colonization of new areas by surviving prairie dogs, most areas within the Comanche complex have been affected by prairie dogs for only 1–2 years over the past decade; only a small component of the complex (1%) was colonized continuously for a decade. In contrast, the pattern for the Phillips County complex in mixed grass prairie and sagebrush steppe primarily consisted of colonies contracting in response to plague outbreaks, followed by re-colonization of the former colony extent. As a result, it is more likely that a given hectare within the Phillips County complex will be occupied for a longer period of time, and a higher proportion of the complex (12%) was occupied continuously for a decade.

It is commonly accepted that prairie dogs prefer sites with historical prairie dog use, particularly if existing burrows have not yet collapsed (Truett et al. 2001; Roe and Roe 2003). However, our results from Comanche suggest black-tailed prairie dogs can regularly colonize shortgrass vegetation with no visible evidence of recent occupation, and abandon previously occupied areas. The result is a shifting mosaic of areas affected by prairie dogs over a decade. Under conditions of long-term colony stability in the absence of plague, prairie dogs are capable of inducing significant changes in plant community composition, leading to increased areas of bare soil, forbs and dwarf shrubs, and reduced cover and productivity of perennial grasses (Coppock et al. 1983; Archer et al. 1987; Detling 1998). Following long-term colonization, the reversibility of plant community composition and productivity when prairie dogs are removed can be slow, with little to no changes in vegetation composition for the first 2–3 years after removal (Krueger 1986; Cid et al. 1991; Fahnstock and Detling 2002). Even 4 years after prairie dog removal in South Dakota rangeland that was also grazed by cattle, Uresk (1985) did not observe increased production of forbs or grasses. In contrast, our results show that within the plague zone, which represents a large proportion of the black-tailed prairie dog's range (Miller and Cully 2001), prairie dogs function as an intense but non-continuous disturbance within the landscape, which may have diminished long-term effects on grassland productivity and species composition (Hartley 2006). Our findings also emphasize the importance of using the types of soil and topographic characteristics outlined by Truett et al. (2001) for identification of areas suitable for black-tailed prairie dog translocations, rather than relying solely on evidence of recent or historic prairie dog occupation.

Just as fire suppression efforts during the 20th century resulted in many unintended consequences for forest ecosystems, plague-induced suppression of prairie dog disturbance and changes in spatial patterns of colony turnover could also have currently unknown consequences for grasslands. Understanding factors driving the different spatiotemporal patterns for plague-affected complexes is of particular interest because the spatial movement observed on the Comanche complex may reduce the magnitude of prairie dog effects on coexisting herbivores, particularly livestock (e.g. Derner et al. 2006; Detling 2006), but could also affect native biota that are closely tied to prairie dog disturbance (Kretzer and Cully 2001; Lomolino and Smith 2003; Smith and Lomolino 2004). While inferences drawn from a comparison of only two study areas are limited, several differences between Comanche and Phillips County study areas may be relevant to the differences in spatial turnover that we documented. The Comanche complex occurs in a landscape with little topographic variation and predominantly loamy soils. Forbs, bare ground and purple threeawn are more abundant on prairie dog colonies, but both non-colonized and colonized areas are dominated by a warm-season shortgrass, blue grama (Winter et al. 2002). In contrast, the Phillips County landscape includes greater topographic variability, a diversity of soil types, and off-colony vegetation with taller-structure, cool-season grasses and sagebrush (Reading and Matchett 1997; Johnson-Nistler et al. 2004). These differences, especially the difference in vegetation structure, likely aid prairie dog colonization or expansion into unoccupied grassland on Comanche compared to Phillips County.

The composition of private land intermingled with the public lands that we studied also varies among study sites, with unknown consequences for long-term prairie dog dynamics on the public lands. In Phillips County, most intermingled private land is rangeland, but prairie dogs occur less frequently on private compared to BLM land than expected by chance (Reading and Matchett 1997). In the Comanche landscape, prairie dog colonies are widely distributed on adjacent privately-owned rangeland (Sidle et al. 2006), but private land also includes some cropland and fields enrolled in the Conservation Reserve Program, which are generally unsuitable habitat for prairie dogs. More detailed information on prairie dog occurrence on private lands would be required to determine how the local configuration of land uses and habitat, combined with features such as roads, lakes and streams (Roach et al. 2001; Collinge et al. 2005b; Antolin et al. 2006) influences both plague and prairie dog colony movement within the landscape.

While shifts in prairie dog colony locations in response to forage conditions may have occurred in the pre-settlement landscape (e.g. Garrett et al. 1982; Cincotta 1985), plague appears to have dramatically accelerated the rate of colony turnover and movement. Our study shows that prairie dog colonies are not necessarily a static component of the landscape, and emphasizes the need for improved understanding of prairie dog colony dynamics in the absence of plague and other anthropogenic effects to provide a baseline for comparison to the colony complexes found in most of central North America today. Our results also highlight the need to combine landscape-scale measures of habitat suitability with accurate, long-term measures of colony locations to understand the role of plague-affected prairie dogs as a grassland disturbance process.

Acknowledgements We thank John Grensten and Valerie Kopcso from the Bureau of Land Management in Malta Montana, along with numerous other cooperators, interns and technicians for collecting the Phillips County prairie dog mapping data. We thank Jeff Abbeglin and Jason Brewer for collecting the Oglala National Grassland prairie dog mapping data. We thank Thomas Peters for supporting the prairie dog mapping efforts on the Comanche National Grassland. M. F. Antolin, J. L. D. Dullum and an anonymous reviewer provided helpful comments the manuscript. Funding was provided by the USDA—Forest Service, USDA—Agricultural Research Service, USDI—Bureau of Land Management, and the Kansas Cooperative Fish and Wildlife Research Unit.

References

Anderson RC (1990) The historic role of fire in the North American grassland. In: Collins SL, Wallace LL (eds), Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, pp 8–18

Antolin ML, Savage L, Eisen R (2006) Landscape features influence genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*). Landsc Ecol 21:867–875

Archer S, Garrett MG, Detling JK (1987) Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetation 72:159–166

Bailey D, Gross J, Laca E, Rittenhouse L, Coughenour M, Swift D, Sims P (1996) Mechanisms that result in large herbivore grazing distribution patterns. J Range Manag 49:386–400

Carlson D, White E (1987) Effects of prairie dogs on mound soils. Soil Sci Soc Am J 51:389–393

Cid MS, Detling JK, Whicker AD, Brizuela MA (1991) Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. J Range Manag 44:100–105

Cincotta RP (1985) Habitat and dispersal of black-tailed prairie dogs in Badlands National Park. PhD Dissertation, Department of Biology, Colorado State University, Fort Collins, CO

Collinge S, Johnson W, Ray C, Matchett R, Grensten J, Cully J, Gage K, Kosoy M, Loye J, Martin A (2005a) Testing the generality of a trophic-cascade model for plague. EcoHealth 2:1–11

Collinge S, Johnson W, Ray C, Matchett R, Grensten J, Cully J, Gage K, Kosoy M, Loye J, Martin A (2005b) Landscape structure and plague occurrence in black-tailed prairie dogs on grasslands of the western USA. Landsc Ecol 20:941–955

Collins SL, Barber SC (1985) Effects of disturbance on diversity in mixed-grass prairie. Vegetation 64:87–94

Coppock DL, Ellis JE, Detling JK, Dyer MI 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics. Oecologia 56:10–15

Coughenour M (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. J Range Manag 44:530–542

Cully JF, Williams ES (2001) Interspecific comparisons of sylvatic plague in prairie dogs. J Mammal 82:894–905

Cully JK, Biggins DE, Seery DB (2006) Conservation of prairie dogs in areas with plague. In: Hoogland JL (ed), Conservation of the blacktailed prairie dog. Island Press, Washington, pp 157–168

Derner JD, Detling JK, Antolin MF (2006) Are livestock weight gains affected by black-tailed prairie dogs? Front Ecol Environ 4:459–464

Detling JK (2006) Do prairie dogs compete with livestock? In: Hoogland JL (ed), Conservation of the black-tailed prairie dog. Island Press, Washington, pp 65–88

Detling JK (1998) Mammalian herbivores: ecosystem-level effects in two grassland national parks. Wildl Soc Bull 26:438–448

Fahnestock J, Detling JK (2002) Bison-prairie dog-plant interactions in a North American mixed-grass prairie. Oecologia 132:86–95

Frank DA, McNaughton SJ, Tracy BF (1998) The ecology of the earth's grazing ecosystems: comparing the Serengeti and Yellowstone. BioScience 48:513–521

Garrett MG, Franklin WL (1988) Behavioral ecology of dispersal in the blacktailed prairie dog. J Mammal 69: 236–250

Garrett MG, Hoogland JL, Franklin WL (1982) Demographic differences between an old and new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). Am Midl Nat 108:51–59

Hartley LM (2006) Plague and the black-tailed prairie dog: an introduced disease mediates the effects of an herbivore on ecosystem structure and function. PhD Dissertation, Department of Biology, Colorado State University, Fort Collins, CO

Johnson TL (2005) Spatial dynamics of a bacterial pathogen: sylvatic plague in black-tailed prairie dogs. MS Thesis, Department of Biology, Kansas State University, Manhattan, KS

Johnson-Nistler CM, Sowell BF, Sherwood HW, Wambolt CL (2004) Black-tailed prairie dog effects on Montana's mixed-grass prairie. J Range Manag 57:641–648

Knapp A, Blair J, Briggs J, Collins S, Hartnett D, Johnson L, Towne E (1999) The keystone role of bison in North American tallgrass prairie. BioScience 49:39–50

Knowles CJ, Knowles PR (1994) A review of black-tailed prairie dog literature in relation to rangelands administered by the Custer National Forest. U. S. Dep. Agric. For. Serv. 61p

Kotliar NB, Baker BW, Whicker AD, Plumb GE (1999) A critical review of assumptions about the prairie dog as a keystone species. Environ Manag 24:177–192

Kretzer JE, Cully JF (2001) Effects of black-tailed prairie dogs on reptiles and amphibians in Kansas shortgrass prairie. Southwest Nat 46:171–177

Krueger KA (1986) Feeding relationships among bison, pronghorn and prairie dogs: an experimental analysis. Ecology 67:760–770

Lauenroth W, Milchunas D (1991) Short-grass steppe. In: Coupland R (ed), Ecosystems of the world. Elsevier, New York, pp 183–226

Lomolino MV, Smith GA (2001) Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. J Mammal 82:937–945

Lomolino MV, Smith GA (2003) Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. Biol Conserv 115:89–100

Miller SD, Cully JF (2001) Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*). J Mammal 82:889–893

Proctor J, Haskins B, Forrest SC (2006) Focal areas for conservation of prairie dogs and the grassland ecosystem. In: Hoogland JL (ed), Conservation of the black-tailed prairie dog. Island Press, Washington, pp 232–247

Reading RM, Matchett R (1997) Attributes of black-tailed prairie dog colonies in north-central Montana. J Wildl Manag 61:664–673

Roach JL, Stapp P, Van Horne B, Antolin MF (2001) Genetic structure of a metapopulation of black-tailed prairie dogs. J Mammal 82:946–959

Roe K, Roe C (2003) Habitat selection guidelines for black-tailed prairie dog relocations. Wildl Soc Bull 31:1246–1253

Senft RL, Coughenour MB, Bailey DW, Rittenhouse L (1987) Large herbivore foraging and ecological hierarchies. BioScience 37:789–799

Sidle JG, Johnson DH, Euliss BR (2001) Estimated areal extent of colonies of black-tailed prairie dogs in the northern Great Plains. J Mammal 82:928–936

Sidle, JG, Schenbeck, GL, Lawton, EA, Licht, DS (2006) Role of federal lands in the conservation of prairie dogs. In: Hoogland JL (ed), Conservation of the black-tailed prairie dog. Island Press, Washington, pp 218–231

Smith G, Lomolino M (2004) Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia 138:592–602

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Stapp P, Antolin MF, Ball M (2004) Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Front Ecol Environ 2:235–240

Toombs TP (1997) Burrowing owl nest-site selection in relation to soil texture and prairie dog colony attributes. M.S. thesis. Colorado State University, Fort Collins, Colorado. 73 p

Truett J, Dullum J, Matchett M, Owens E, Seery D (2001) Translocating prairie dogs: a review. Wildl Soc Bull 29:863–872

Turner MG, Bratton SP (1985) Fire, grazing and the landscape heterogeneity of a Georgia barrier island. In: Turner MG (ed), Landscape heterogeneity and disturbance. Springer-Verlag, New York, pp 85–102, 239

Uresk DW (1985) Effects of controlling black-tailed prairie dogs on plant production. J Range Manag 38:466–468

Weltzin JF, Dowhower SL, Heitschmidt RK (1997) Prairie dog effects on plant community structure in southern mixed-grass prairie. Southwest Nat 42:251–258

Whicker A, Detling JK (1988) Ecological consequences of prairie dog disturbances. BioScience 38:778–785

White GR, Dennis PF (2005) Area of black-tailed prairie dog colonies in eastern Colorado. Wildl Soc Bull 33:265–272

Winter SL, Cully JF, Pontius JS (2002) Vegetation of prairie dog colonies and non-colonized shortgrass prairie. J Range Manag 55:502–508

Wright HA, Bailey AW (1982) Fire ecology: United States and Canada. John Wiley and Sons, New York

Woodyard SO, Preator RE, Moreland RE, McCullough MB (1973) Soil survey of Baca County, Colorado; United States Department of Agriculture, Soil Conservation Service. US Government Printing Office, Washington