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PLANT AND BREEDING BIRD
COMMUNITIES OF BLACK-TAILED
PRAIRIE DOG COLONIES AND NON-
COLONIZED AREAS IN SOUTHWEST
KANSAS AND SOUTHEAST COLORADO

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PLANT AND BREEDING BIRD COMMUNITIES OF
BLACK-TAILED PRAIRIE DOG COLONIES AND NON-COLONIZED AREAS IN
SOUTHWEST KANSAS AND SOUTHEAST COLORADO

by

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ABSTRACT

This research was initiated to determine if plant and bird communities on black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies in southwest Kansas and southeast Colorado differed from those found on associated non-colonized areas. Vegetation height and density, and the cover and frequency of numerous plant species differed between prairie dog colonies and non-colonized areas that were co-dominated by mid-height grasses and shortgrasses. A comparison of prairie dog colonies with non-colonized areas that were dominated solely by shortgrasses did not reveal a difference in vegetation height and density. The number of species that differed in cover or frequency between prairie dog colonies and non-colonized shortgrass areas was less than when the comparison of prairie dog colonies was made with areas co-dominated by mid and shortgrasses. Plant species richness and diversity measures did not differ between prairie dog colonies and the non-colonized areas. Bird communities in 1996, following twelve months of drought conditions, were species poor relative to 1997. Fewer bird species were detected on prairie dog colonies than on non-colonized areas during both years. Burrowing owls were highly dependent on prairie dog colonies in region of this study, but there were several species for which prairie dog colonies were sub-optimal habitat. Horned lark habitat preference alternated between prairie dog colonies and non-colonized sites, probably in response to the influence of climatic variation on vegetation conditions. Fundamental differences in characteristic vegetation between semiarid shortgrass steppe and less arid regions of the Great Plains appear to contribute to regional differences in the influence of prairie dogs on plant and bird communities.

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CHAPTER 1

PRAIRIE DOGS, HERBIVORY, AND SOIL DISTURBANCE IN SHORTGRASS STEPPE

Five species of prairie dog occur in the inter-mountain western United States and Great Plains of North America (Hall 1981). The historic range of the black-tailed prairie dog (*Cynomys ludovicianus* Ord) encompassed a broad area of the western Great Plains from Montana and southern Saskatchewan, south along the front range of the Rocky Mountains to northern Mexico and southern Arizona and New Mexico, while the eastern limit of their range ran through central and eastern portions of the Dakotas, Nebraska, Kansas, Oklahoma and Texas (Hall 1981). Although black-tailed prairie dogs still occur within most of this area, cultivation of grasslands and eradication programs have severely reduced the amount of area that they occupy; by some estimates this reduction is as high as 98% (Marsh 1984, Miller et al. 1990, 1994).

Increased knowledge of the influence of prairie dogs on the environments they inhabit has suggested that ecosystems modified by prairie dogs may be important for the persistence of numerous grassland organisms (see Whicker and Detling 1988, Miller et al. 1990, 1994). This has in turn stimulated appeals for heightened protection of prairie dogs and alterations in the management of public and private rangelands (Miller et al. 1990, 1994, Davitt et al. 1996). It is hoped these results will enhance the cooperation of land managers, livestock producers, conservationists, and policy makers in ensuring the

maintenance of biotic integrity and economic vitality in North American grasslands.

When this research was initiated, and as it progressed, limitations were identified in the current state of knowledge about the influence of prairie dogs on their environments (Winter et al. In Press *a* and *b*). A review of the literature revealed that a preponderance of the research on prairie dog ecosystems had been conducted in a limited area, namely the mixed-grass prairie region of South Dakota (see Whicker and Detling 1988 for review), but the dynamics of prairie dog ecosystems in that bioregion may be different in other areas of the Great Plains. Additionally, research on vertebrate use of prairie dog colonies was primarily descriptive, with only one comparative study having been completed when this project was initiated. These and other limitations have since been elucidated by others (Stapp 1998), and hopefully further research will be undertaken in an attempt to address deficiencies in the understanding of prairie dog ecosystems.

This introductory chapter provides a backdrop against which the following chapters can be read, and it was written with the intent of providing a more thorough understanding of the ecology of prairie dogs and the shortgrass steppe biome. An understanding of how prairie dogs influence their environment requires an understanding of the functioning of the environment they occupy. Important characteristics of climate and vegetation that are relevant to the location of this study will be introduced in this chapter, and key processes such as herbivory and soil disturbances will be reviewed.

Precipitation Effects in the Western Great Plains

The semiarid region of the western Great Plains lies roughly between the Cascades and Rocky Mountains to the west and the 100th meridian to the east and is characterized by a continental climatic regime (Borchert 1950, Bailey 1995). Some of the names used to identify this region include shortgrass prairie, shortgrass steppe, Great Plains steppe, and semiarid Great Plains (Borchert 1950, Sims et al. 1978, Singh et al. 1983, Coupland 1992, Lauenroth and Milchunas 1992, Bailey 1995). The study location of this research project, Morton County, Kansas, and Baca County, Colorado, is situated in the southeastern portion of this region. In semiarid grasslands, precipitation, and its impact on soil moisture, is the primary determinant of biotic processes and attributes such as nutrient cycling and aboveground net primary productivity (Lauenroth et al. 1978, Lauenroth 1979, Sala et al. 1988, Lauenroth and Sala 1992, Sala et al. 1992, Burke and Lauenroth 1993, Milchunas et al. 1994). Precipitation amounts within the semiarid western Great Plains generally decrease from east to west, and annual amounts range from 750 mm to 250 mm (Borchert 1950, Bailey 1995). Mean precipitation (1901 - 1996) recorded at the Elkhart weather station in Morton County is 447 mm (National Weather Service Cooperative Observer Network, Personal Communication). In the southern portion of this region (Colorado, Kansas, Oklahoma, New Mexico and Texas) seventy percent of the annual precipitation occurs from April through September, and May is usually the month of maximum precipitation (Lauenroth and Milchunas 1992).

Semiarid regions like the one encompassing Morton and Baca Counties are distinguished by extreme variability in interannual precipitation (Bailey 1979, Lauenroth

and Milchunas 1992). Using data from Weins (1972, 1974) for a number of sites in the western Great Plains, Lauenroth and Milchunas (1992) reported that annual precipitation amounts deviated 50% or more from the long-term mean during an average of 9% of the years, and deviations of at least 25% occurred during an average of 44% of the years. Figure 1 illustrates annual deviations from the long term mean for precipitation measured at the Elkhart weather station in Morton County, Kansas. The high variability in annual precipitation amounts that characterize the western Great Plains is attributable to the variability in occurrence of precipitation events greater than 10 mm, and the difference in wet and dry years is often based on the presence or absence of 1 or 2 of these events (Lauenroth and Milchunas 1992, Lauenroth and Sala 1992, Sala et al. 1992). Large precipitation events (> 20 mm) may account for less than 15% of all events, but can provide more than 40% of total annual precipitation (Sala and Lauenroth 1982, Lauenroth and Milchunas 1992).

However, meteorological data indicates that the majority of rainfall events in the western Great Plains are small ones (≤ 10 mm) and there is little interannual variability in their occurrence (Sala and Lauenroth 1982, Lauenroth and Milchunas 1992, Sala et al. 1992). Precipitation events less than 10 mm can account for up to 80% of the events and 40% of total annual precipitation (Sala and Lauenroth 1982, Lauenroth and Milchunas 1992, Sala et al. 1992). Small precipitation events wet surface soils, and this moisture can quickly evaporate, while large precipitation events wet deeper soil layers where evaporation does not influence soil moisture levels (Sala and Lauenroth 1982, Lauenroth and Milchunas 1992, Sala et al. 1992). Lauenroth and Sala (1992) reported that

precipitation explained 39-45% of the variation in primary productivity in Colorado, and that large rainfall events are responsible for most of this variability.

Sala et al. (1988) identified southwest Kansas as being the center of a region within the Great Plains having the highest variability among years in aboveground net primary production. Productivity of shortgrass steppe vegetation can exhibit a time lag of several years in the ability to respond to years with normal or high precipitation when they follow drought years (Lauenroth and Sala 1992). The perennial short grass *Bouteloua gracilis* is the dominant plant in the central and southern portions of the semiarid western Great Plains and accounts for 75-90% of aboveground net primary production (Dodd and Lauenroth 1979, Lauenroth and Milchunas 1992). In spite of the great influence of large rainfall events on annual precipitation amounts and primary productivity, ecosystem dynamics in semiarid regions may be more significantly affected by the ability of *Bouteloua gracilis* to utilize small rainfall events that occur with annual consistency (Sala and Lauenroth 1982, Sala et al. 1992). At a Colorado shortgrass steppe location, 63% of rainfall events from 1950 to 1983 were ≤ 5 mm (Sala et al. 1992). Sala and Lauenroth (1982) measured the effect of 5 mm precipitation events (67% of the total number of events) on leaf water potential and leaf conductance of *Bouteloua gracilis* at a Colorado shortgrass steppe location. They demonstrated that *Bouteloua gracilis* was able to rapidly and effectively respond to these small precipitation events in less than 12 h, and that the effects lasted up to 2 days (Sala and Lauenroth 1982). Lauenroth et al. (1987) reported that the surviving roots of drought stressed *Bouteloua gracilis* plants were able to absorb enough moisture to restore leaf water potentials within one day of

receiving 0.5 mm of water.

Milchunas et al. (1994) discussed the effects that season of occurrence would have on the influence of small and large precipitation events. The effect of small events on primary productivity would be greater in warm summer months when roots are active than during cool spring months when plant growth and water uptake are minimal (Milchunas et al. 1994). Small events that only wet surface soils in March and April would be immediately utilized by only a small proportion of the plant community and most of this moisture would be lost through evaporation (Milchunas et al. 1994). Conversely, large events in March and April would wet deep soil layers below the evaporation zone, and this moisture would be available later in the season when plant growth and water uptake accelerates (Milchunas et al. 1994).

The effectiveness of *Bouteloua gracilis* in utilizing the soil moisture provided by variously sized precipitation events is likely explained by the distribution of roots within a soil profile (Coffin and Lauenroth 1991). Coffin and Lauenroth (1991) reported that *Bouteloua gracilis* roots labeled with ^{14}C extended at least 30 cm horizontally and 90 cm below individual plants. Greater than 75% of labeled roots were found directly below or within 5 cm of the edge of a plant within the upper 10 cm of soil, allowing plants to thoroughly exploit that portion of the soil profile that is influenced by small rainfall events (Coffin and Lauenroth 1991). However, the great depth at which *Bouteloua gracilis* roots extend facilitates access to the moisture provided by large rainfall events during the periods between small rainfall events (Coffin and Lauenroth 1991).

Classification of Semiarid Grasslands in the Great Plains

The spatial extent of grassland communities within the Great Plains broadly corresponds to the climatic gradient of decreasing rainfall from east to west (Borchert 1950, Coupland 1992, Kucera 1992, Lauenroth and Milchunas 1992). Weaver and Clements (1938) and Weaver and Albertson (1956) did not recognize a shortgrass vegetation type on the western edge of the Great Plains but instead classified all grasslands in the Great Plains as mixed prairie. Evidence used to support this contention included grazing exclosures and other tracts of land that were protected from grazing in the western Great Plains that were characterized by a dominant over-story of mid-height grasses (Weaver and Clements 1938, Weaver and Albertson 1956).

Because high grazing pressures caused a shift in species composition so that shortgrass species predominated and mid-height species were nearly eliminated, areas dominated by shortgrass vegetation were considered to be in a state of disturbance induced dis-climax by Weaver and Clements (1938) and Weaver and Albertson (1956), the disturbance being overgrazing by domestic livestock. However, Larson (1940) contended that because many portions of the Great Plains were characterized by high levels of herbivory from large herds of bison (*Bison bison*) before their extirpation in recent times, it would be erroneous to consider a plant community that resulted from the influence of these animals a dis-climax community caused by deviations from normal, or natural conditions. Other authors have subsequently commented on the long evolutionary history of grazing by large mammalian herbivores on the Great Plains (Stebbins 1981, Coughenour 1985, Mack and Thompson 1985).

More recent ecological treatments of Great Plains vegetation types recognize a shortgrass region in the western Great Plains, but there are disagreements over where the boundaries of this community type lie. According to Singh et al. (1983) and Lauenroth and Milchunas (1992), Morton County, KS, and Baca County, CO, lie at the border of the shortgrass steppe of the western Great Plains and the southern mixed prairie of the south-central Great Plains. Conversely, Sims et al. (1978) and Coupland (1992), identify the shortgrass steppe as entirely encompassing Morton and Baca Counties, and Kuchler (1985) designates Morton and Baca Counties as lying entirely within the region characterized by the *Bouteloua-Buchloe* vegetation type.

Classification of the vegetation of the western Great Plains and delineation of the geographical extent of these communities is complicated by the interactive effects of herbivory and climate on Great Plains vegetation. The perennial grasses *Bouteloua gracilis* and *Buchloe dactyloides* are the dominant plant species in the regions identified by Sims et al. (1978) and Lauenroth and Milchunas (1992) as shortgrass steppe. Throughout the Great Plains *Bouteloua gracilis* and *Buchloe dactyloides* tend to be very tolerant of high rates of herbivory by cattle (*Bos taurus*), while mid-height perennial grasses within the genera *Agropyron*, *Bouteloua*, *Stipa*, and *Sporobolus* tend not to be, and the relative proportions of these grasses within a plant community generally reflects past grazing pressures (Clarke et al. 1947, Lang et al. 1956, Launchbaugh 1957, 1967, Klipple and Costello 1960, Hyder et al. 1975, Sims et al 1978, Coupland 1992, Biondini and Manske 1996, Hart and Ashby 1998, Milchunas et al. 1998). Hence, the classification of a plant community as either shortgrass or mixed-grass prairie at any

given locality in many areas of the Great Plains is heavily influenced by the levels of herbivory that have occurred at those locations.

Herbivory by Prairie Dogs

Prairie dogs are known to eat a large number of different plant species, but numerous studies have determined that the bulk of their diet, from 60 - 90%, consists of graminoids (Kelso 1939 in Summers and Linder 1978, Hansen and Gold 1977, Summers and Linder 1978, Fagerstone et al. 1981, Wydeven and Dahlgren 1982, Uresk 1984). However, Fagerstone et al. (1977) showed that forbs may comprise up to 70% of the diet of prairie dogs. The consumption of *Opuntia* spp. and the digging of roots by prairie dogs has been reported during winter and drought periods (Kelso 1939 in Summers and Linder 1978, Koford 1958, Tiletson and Lechleitner 1966, Smith 1967, Fagerstone et al. 1981, Uresk 1984), and insects and seeds have been reported as minor food items (Kelso 1939 in Summers and Linder 1978, Smith 1967, Summers and Linder 1978, Fagerstone et al. 1981, Uresk 1984).

The composition of prairie dog diets has been shown to differ at various times of the year, indicating food preferences were changing, perhaps in response to seasonal changes in the nutritional quality of various plant species within prairie dog colonies (Summers and Linder 1978, Fagerstone et al. 1981, Wydeven and Dahlgren 1982, Uresk 1984). Prairie dogs can be highly selective herbivores, showing a high degree of preference for perennial graminoids such as *Agropyron smitthii*, *Bouteloua gracilis*, *Carex filifolia*, *Muhlenbergia torreyi*, *Sporobolus cryptandrus*, and *Stipa viridula*

(Summers and Linder 1978, Fagerstone et al. 1977, Fagerstone et al. 1981, Uresk 1984). Wells et al. (1990) used captive prairie dogs and food items from plants not native to the range occupied by wild prairie dogs to test the hypothesis that herbivores in temperate climates should preferentially consume C₃ plants rather than C₄ plants (Caswell et al. 1973). Wells et al. (1990) reported that the prairie dogs in the study exhibited preferences within both the C₃ and C₄ species groups, but did not demonstrate a preference for food items from C₃ plants over that of C₄ plants.

In the following discussion of the effects of prairie dogs on vegetation, previous research that reported the results of statistical analyses is identified by a statement indicating significant differences or the lack thereof. Previous research that did not report the results of statistical analyses is recounted as originally described in the literature, without the qualifier of statistical significance. Agnew et al. (1986) reported that vegetation height on prairie dog colonies was significantly lower than on adjacent mixed-grass prairie for each of three sampling periods during two years in South Dakota, but the canopy cover of forbs was significantly higher on prairie dog colonies. Total canopy cover was similar between prairie dog colonies and non-colonized mixed-grass sites during each of three sampling periods one year, but was significantly lower on prairie dog colonies during two of three sampling periods the following year (Agnew et al. 1986). Archer et al. (1987) reported that vegetation height was significantly lower on portions of a prairie dog colony that were 2-6 years old than on adjacent non-colonized mixed-grass prairie in South Dakota. Archer et al. (1987) also reported that as time of occupation by prairie dogs increased on a colony, the canopy cover of forbs and percent bare ground

increased over what was found on adjacent non-colonized mixed-grass prairie, while cover of grass decreased.

In South Dakota, Coppock et al. (1983a) reported that portions of a prairie dog colony that had been inhabited for at least 3 years were characterized by greater biomass of forbs and shrubs and less biomass of C₃ and C₄ grasses when compared to non-colonized mixed-grass prairie and younger colony portions. *Andropogon scoparius* was the dominant grass on adjacent non-colonized mixed-grass prairie, but was reduced in abundance by 30% on young colony portions, while colony portions that had been inhabited for up to 26 years were characterized by a dominance of forbs and shrubs and an almost complete absence of grasses (Coppock et al. 1983a). The number of annual species of forbs on the adjacent non-colonized mixed-grass prairie was 0, while the number of annual forbs on the young and old portions of the colony were 6 and 7, respectively (Coppock et al. 1983a). Agnew et al. (1986) reported significantly greater cover of *Buchloe dactyloides* on prairie dog colonies, while *Agropyron smithii* and *Bouteloua gracilis* cover values were significantly greater on non-colonized mixed-grass sites in South Dakota.

Also in South Dakota, Archer et al. (1987) reported that non-colonized mixed grass prairie adjacent to a prairie dog colony was co-dominated by the mid-height grasses *Stipa comata* and *Poa pratensis*, and the short grasses *Buchloe dactyloides* and *Bouteloua gracilis*. Conversely, the prairie dog colony was characterized by great reductions or elimination of *S. comata* and *P. pratensis* (Archer et al. 1987). Aerial cover values for *Buchloe dactyloides* and *Bouteloua gracilis*, and the mid-height grass *Agropyron smithii*

were higher in the adjacent non-colonized mixed-grass prairie and in the portion of the colony that was 2 years old than on portions of the colony that were 3 to 6 years old (Archer et al. 1987). The forbs *Mirabilis hirsuta*, *Conyza ramosissima*, *Oxalis stricta*, and *Sphaeralcea coccinea* were not detected in the adjacent non-colonized mixed grass prairie but were present and often abundant on various portions of the prairie dog colony, and the oldest portion of the colony was characterized by the dominance of the forbs *Tradescatia bracteata* and *Dyssodia papposa* (Archer et al. 1987).

In Texas, Weltzin et al. (1997) compared the vegetation of a prairie dog colony to the vegetation of an adjacent mixed-grass prairie co-dominated by the mid-height grasses *Sporobolus cryptandrus* and *Stipa leucotricha*, and the short grass *Buchloe dactyloides*. The prairie dog colony was characterized by significantly lower biomass of all mid-height grasses combined and C₃ mid-height grasses during each of 2 years, while biomass of perennial dicots (primarily *Ambrosia psilostachya*) and C₄ mid-height grasses were significantly lower on the prairie dog colony during 1 of 2 years (Weltzin et al. 1997b). Biomass of annual grasses was high in the non-colonized mixed-grass prairie, but annual grasses were not present in the prairie dog colony, and biomass of short grasses did not differ between the prairie dog colony and the adjacent non-colonized mixed-grass prairie (Weltzin et al. 1997). In Colorado, Bonham and Lerwick (1976) compared the vegetation of two prairie dog colonies to the vegetation of adjacent shortgrass prairie dominated by the short grass *Bouteloua gracilis*, with associate species consisting of the short grass *Buchloe dactyloides* and the mid-height grasses *Agropyron smithii*, *Oryzopsis hymenoides*, and *Stipa comata*. The prairie dog colonies were characterized by lower

cover values of *Bouteloua gracilis*, and higher cover values of the *Buchloe dactyloides*, the annual grass *Vulpia octoflora*, and annual forbs such as *Plantago patagonica*, *Aster tanacetifolius*, *Euphorbia glyptosperma*, *Oenothera albicaulis*, and various *Lappula* spp. (Bonham and Lerwick 1976).

In South Dakota mixed-grass prairie, Coppock et al. (1983a) reported higher plant species richness on old, young and edge portions of a prairie dog colony than on adjacent non-colonized mixed-grass prairie. Archer et al. (1987) also found higher plant species richness on portions of a dog town that had been colonized from 2 to 6 years than on adjacent non-colonized mixed grass prairie. Conversely, Agnew et al. (1986) found higher plant species richness on non-colonized mixed grass prairie than on prairie dog colonies. Cid et al. (1991) reported that placement of exclosures on a prairie dog colony in South Dakota did not result in a change in plant species richness after 2 years when exclosed areas were compared to occupied areas of a prairie dog colony. In Texas mixed-grass prairie Weltzin et al. (1997b) found no significant difference in plant species richness between a prairie dog colony and adjacent non-colonized mixed-grass prairie one year, but plant species richness on the non-colonized site was significantly higher than on the prairie dog colony the next year. In the shortgrass region of eastern Colorado Bonham and Lerwick (1976) reported higher plant species richness on prairie dog colonies than on non-colonized areas.

In South Dakota mixed-grass prairie, using the inverse of Simpson's index of diversity, Coppock et al. (1983a) reported that plant species diversity was greater on young and old portions of a prairie dog colony than on adjacent non-colonized mixed-

grass prairie. Also in South Dakota, Archer et al. (1987) calculated Shannon's index of diversity and described plant diversity as increasing during the first three years of colony habitation and then declining to levels that were similar to adjacent non-colonized mixed-grass prairie. In Texas, using both Shannon's index of diversity and the inverse of Simpson's index of diversity, Weltzin et al. (1997) found significantly lower diversity on a prairie dog colony than on an adjacent non-colonized mixed-grass prairie.

Prairie dog colonies can harbor distinct ecotypes of plant species relative to adjacent non-colonized mixed-grass prairie protected by a grazing enclosure (Detling and Painter 1983, Archer et al. 1987, Jaramillo and Detling 1988, Whicker and Detling 1988). Perennial plant populations on prairie dog colonies can be characterized by "grazing morphs" which are short, prostrate, or dwarf forms, in contrast to the tall forms of the same species that characterize adjacent non-colonized mixed-grass prairie (Detling and Painter 1983, Archer et al. 1987, Jaramillo and Detling 1988, Whicker and Detling 1988). Polly and Detling (1990) reported that individual *Agropyron smithii* plants from prairie dog colonies had significantly smaller tillers, more numerous tillers, and higher root biomass than plants from non-colonized areas in South Dakota. Short and prostrate grazing morphs may avoid intensive grazing on prairie dog colonies better than non-grazed plants that are tall and upright (Detling and Painter 1983, Jaramillo and Detling 1988, Whicker and Detling 1988). Populations of plants on and off prairie dog colonies that are morphologically distinct may represent phenotypic plasticity or genetic differentiation (Detling and Painter 1983, Painter 1987 in Whicker and Detling 1988, Whicker and Detling 1988, Polly and Detling 1990).

Herbivores Associated With Prairie Dog Colonies

Other mammalian herbivores that could potentially co-occur with prairie dogs include bison, domestic cattle, pronghorn antelope (*Antilocapra americana*), and various lagomorphs, sciurids and other rodents (Koford 1958, Campbell and Clark 1981, Clark et al. 1982 and Sharps and Uresk 1990, Lauenroth and Milchunas 1992). Like prairie dogs, bison and cattle both consume primarily graminoids, but the proportion of graminoids in the diet of cattle is marginally less than that of bison (Peden et al. 1974, Kautz and Van Dyne 1978, Schwartz and Ellis 1981, Van Vuren 1984, Plumb and Dodd 1993, Hartnett et al. 1997). Forbs constitute the bulk of the diet for pronghorn antelope on shortgrass range, but graminoid use can be substantial at various times of the year, and pronghorn diets show greater seasonal variation in botanical composition and diet quality than bison (Kautz and Van Dyne 1978, Schwartz and Ellis 1981, Hartnett et al. 1997). The majority of the diet of desert cottontails in Colorado shortgrass prairie is composed of graminoids during the spring and summer, while forbs and shrubs comprised the majority of the diet in winter (Hansen and Gold 1977). Hansen and Gold (1977) reported that percent similarity in the diets of prairie dogs and desert cottontails varied from 40 - 75% at various times of the year, and the mean annual percent similarity was 60%.

Several studies have suggested or demonstrated that prairie dog colonies are preferred foraging sites for some wild ungulates (Koford 1958, Coppock et al. 1983b, Wydeven and Dahlgren 1985, Coppock and Detling 1986, Krueger 1986). Research in South Dakota has demonstrated that forage on portions of prairie dog colonies that are dominated by graminoids can be characterized by higher shoot nitrogen concentrations,

due to regrowth of previously grazed plants, and lower dead:live ratios of vegetation than adjacent non-colonized mixed-grass prairie, making them highly attractive to foraging bison (Coppock et al. 1983a, Coppock et al. 1983b, Krueger 1986, Jaramillo and Detling 1988). Portions of prairie dog colonies that have been occupied for long periods of time and are dominated by forbs and shrubs have been shown to be highly attractive to pronghorn antelope (Krueger 1986). However, in South Dakota a prescribed fire in non-colonized mixed-grass prairie adjacent to a prairie dog colony induced bison to change their preference for grazing on the colony to grazing on the burned non-colonized site, illustrating how vegetation can be influenced by the interaction of herbivores with abiotic factors such as fire (Coppock and Detling 1986).

Krueger (1986) quantified bison, pronghorn and prairie dog foraging efficiency in South Dakota by measuring foraging group size, nearest neighbor distances, and by using feeding rates (number of bites per minute) and movement rates (number of steps per minute) to calculate bite:step ratios. The foraging efficiency of both bison and pronghorn antelope can be enhanced on prairie dog colonies relative to their foraging efficiency in non-colonized mixed-grass prairie (Krueger 1986). The attractiveness of prairie dog colonies to bison, and the higher foraging efficiency of bison on prairie dog colonies, may in turn contribute to higher foraging efficiency by prairie dogs, resulting in a mutually beneficial relationship driven by a positive feedback between these two species (Krueger 1986). However, Krueger (1986) concluded that the relationship between prairie dogs and pronghorn antelope may be neutral for prairie dogs and slightly negative for pronghorns. At Krueger's study location, extended occupancy of a colony by prairie

dogs creates a plant community dominated by forbs and shrubs, that is attractive to pronghorn antelope, but current foraging activities of prairie dogs reduces the foraging efficiency of pronghorns relative to pronghorn foraging efficiency in the same forb/shrub-dominated community that lacks prairie dogs (Krueger 1986).

The relationship between prairie dogs and cattle may be similar in some respects to the mutually beneficial relationship of prairie dogs and bison that was described by Krueger (1986). If graminoid forage on prairie dog colonies is characterized by high shoot nitrogen concentrations and low ratios of dead:live vegetation (Coppock et al. 1983a, Coppock et al. 1983b, Krueger 1986, Jaramillo and Detling 1988), then prairie dog colonies should be attractive foraging locations for cattle like they are for bison. Early researchers have suggested that cattle grazing may facilitate the colonization and occupation of an area by prairie dogs, as well as the expansion of colony edges, which indicates a positive effect of cattle on prairie dogs (Osborn and Allan 1949, Koford 1958, Smith 1967). Suggestive of a mutually beneficial relationship, Knowles (1986) reported that prairie dog colonies at his northeast Montana study sites were significantly closer to livestock watering developments than randomly located points, and cattle occurred significantly more often on quarter sections that contained prairie dog colonies than on quarter sections that lacked prairie dog colonies.

Because graminoids typically constitute the bulk of the diet for both prairie dogs and cattle (Peden et al. 1974, Hansen and Gold 1977, Kautz and Van Dyne 1978, Summers and Linder 1978, Fagerstone et al. 1981, Schwartz and Ellis 1981, Wydeven and Dahlgren 1982, Uresk 1984, Van Vuren 1984, Plumb and Dodd 1993), the potential

is high that these two species compete for forage resources. Hansen and Gold (1977) reported that percent similarity in the diets of prairie dogs and cattle in Colorado shortgrass prairie varied from 41 to 69% at various times of the year, and the mean annual percent similarity was 64%. Forage eaten by prairie dogs is not available to ungulate grazers, be they bison or cattle, but it has been suggested that the reduced amount of forage may offset to some degree by the higher quality of the forage that may be present (e.g. Coppock et al. 1983a, Coppock et al. 1983b, Krueger 1986, Jaramillo and Detling 1988), and the ungulate carrying capacity of rangeland containing prairie dog colonies may be related to the tradeoff between forage quality and quantity (Whicker and Detling 1988).

O'Meilia et al. (1982) reported that prairie dogs did indeed reduce the quantity of herbage present within pastures at their Oklahoma study sites, but weight gains of cattle that grazed pastures containing prairie dogs were not significantly different from weight gains of cattle that grazed pastures without prairie dogs. O'Meilia et al (1982) suggested that statistically similar cattle weight gains indicated that the lower forage quantities on the prairie dog colonies in their study may have been compensated by higher forage quality. An additional interpretation of these results is that the amount of high quality forage in the pastures containing prairie dog colonies was the same as the amount of high quality forage in the pastures lacking prairie dog colonies, because if there were a difference in the amount of high quality forage, that difference would have been reflected in a difference in the cattle weight gains (C. Owensby, pers. comm.). Cattle in both types of pastures would presumably have been consuming high quality forage in the form of

regrowth of previously grazed plants. O'Meilia et al. (1982) did not quantify where cattle in the pastures containing prairie dog colonies foraged. Cattle may consume regrowth on the prairie dog colonies, but if prairie dogs keep vegetation clipped to a level that makes it inaccessible to cattle, then cattle should create patches of regrowth in adjacent non-colonized vegetation. In either scenario, the spatial distribution of cattle herbivory and its associated influence on vegetation structure and composition would be altered by the presence of the prairie dog colonies.

The results of O'Meilia et al. (1982) should be read cautiously, because the prairie dog colonies used in their study had existed for less than 6 years, the prairie dogs having been introduced into the study area for the purposes of their study. Research in South Dakota has shown that extended occupation of a location by prairie dogs typically results in the replacement of mid-height grasses by less productive short-statured species and the displacement of many perennial grasses, and that areas occupied the longest by prairie dogs can be characterized by very low proportions of graminoids (King 1955, Coppock et al. 1983a, Krueger et al. 1986, Archer et al. 1987). Coppock et al. (1983a) reported that graminoids comprised more than 85% of peak live biomass on non-colonized mixed-grass prairie and colony edges, whereas colony portions that had been occupied by prairie dogs for at least 26 years were characterized by graminoids contributing less than 3% of peak live biomass.

Indeed, Coppock et al. (1983a) remarked that forage quality analyses were not even conducted for the portion of their study colony that had been occupied the longest by prairie dogs because graminoids were so sparse there. Portions of prairie dog colonies

that had been occupied the longest and were characterized by the dominance of forbs and shrubs have been shown to be preferred sites for resting and wallowing by bison, but these areas were in fact avoided by foraging bison (Coppock et al. 1983a, Krueger 1986). The potential for a herbivory induced increase in forage quality is irrelevant if the bulk of a herbivores diet, graminoids in the case of bison and cattle, has been eliminated from an area as a result of constant defoliation by prairie dogs and ungulate associates.

Large Mammal Herbivory and Vegetation in Shortgrass Steppe

Milchunas et al. (1988) developed a model to describe the interaction of grazers and grassland vegetation diversity for various grassland communities that was based on characteristic environmental moisture and evolutionary history of grazing. The grasses that characterize the subhumid and semiarid portions of the Great Plains have a long evolutionary history of being grazed by large mammalian herbivores (Stebbins 1981, Coughenour 1985, Mack and Thompson 1982). The model predicts that in subhumid grasslands which have a long history of grazing, plant species diversity will be highest at moderate levels of herbivory (Milchunas et al. 1988). Low herbivory levels are predicted to facilitate the domination of plant communities by a limited number of tall growth forms which exclude shorter species through competition for light resources, resulting in relatively homogenous vegetation (Milchunas et al. 1988). Moderate herbivory levels are predicted by the model to create a more heterogeneous community with a mosaic pattern consisting of heavily grazed patches of short and/or grazing tolerant species interspersed within a lightly grazed matrix of taller species (Milchunas et al. 1988). Finally, high

herbivory levels are predicted to result in a relatively homogenous community characterized by the domination of short species and the scarcity of tall species (Milchunas et al. 1988).

The grazing model for subhumid grasslands with a long evolutionary history of grazing is consistent with intermediate disturbance models which predict highest diversity at intermediate levels of disturbance (Connell 1978). Investigations of herbivory by cattle and bison in mixed-grass prairie and tallgrass prairie support the model proposed by Milchunas et al. (1988), presumably because both herbivores preferentially graze the dominant warm-season grasses, impairing their competitive effect, allowing subdominant species to experience competitive release (Collins and Barber 1985, Fahnestock and Knapp 1994, Hartnett et al. 1996, Hickman et al. 1996, Collins et al. 1998, Knapp et al. 1999).

Contrasting with the model for subhumid grasslands with a long evolutionary history of grazing, the model proposed by Milchunas et al. (1988) for semiarid grasslands which have a long evolutionary history of grazing predicts that increased grazing intensity should be correlated with no change or a slight decrease in plant species diversity. The results of research on cattle grazing reported by Klipple and Costello (1960), Hyder et al. (1966, 1975) were used by Milchunas et al. (1988) to support the model. Additional results from research on cattle grazing reported by Milchunas et al. (1989, 1998) further demonstrated that plant species diversity and richness were lower on grazed areas than ungrazed areas in Colorado shortgrass steppe. Contrarily, an analysis by Hart (In Press) of research results emanating from the same research site studied by

Milchunas et al. (1988) and Milchunas et al. (1998) showed that ungrazed sites had lower plant species diversity and evenness than grazed sites.

Semiarid grasslands with a long evolutionary history of grazing are characterized by short-statured species that are capable of rapid regrowth after herbivory or drought (Stebbins 1981, Coughenour 1985, Mack and Thompson 1982, Milchunas et al. 1988). Competition among semiarid plant species is primarily for soil resources, especially water, and because semiarid grasslands are characterized by short-statured species, defoliation does not alter competitive interactions for light resources (Milchunas et al. 1988). The response of shortgrass steppe vegetation to cattle herbivory is presumably a function of the increased dominance of the grazing tolerant perennial grass species *Bouteloua gracilis* and *Buchloe dactyloides*, as well as the elimination of rare, grazing intolerant species (Milchunas et al. 1988, 1989, 1998).

Numerous studies in the western Great Plains have demonstrated that *Bouteloua gracilis* and *Buchloe dactyloides* show no change or, especially *Buchloe dactyloides*, may actually exhibit increases in frequency, basal cover or composition with heavy cattle grazing (Lang et al 1956, Launchbaugh 1957, 1967, Klipple and Costello 1960, Hyder et al. 1966, 1975, Milchunas and Lauenroth 1989, Milchunas et al. 1988, 1989, 1992, 1998, Hart and Ashby 1998). Unlike the subhumid grasslands of the Great Plains, where cattle grazing has been shown to increase vegetation heterogeneity (Collins and Barber 1985, Fahnestock and Knapp 1994, Hartnett et al. 1996, Hickman et al. 1996, Collins et al. 1998), numerous studies, detailed below, have shown that cattle grazing in semiarid grasslands of the Great Plains can decrease the heterogeneity of vegetation (see also

Vinton and Collins (1997) for review).

Milchunas and Lauenroth (1989) examined the influence of cattle grazing on the distribution of plant biomass in Colorado. They reported that the horizontal distribution of plant biomass (aboveground parts, crowns and roots at two depths) was much more variable in ungrazed areas than grazed areas, indicating that grazing in shortgrass steppe contributes to the homogenization of plant community structure (Milchunas and Lauenroth 1989). Milchunas et al. (1992) reported a more uniform horizontal distribution of plant biomass in cattle grazed areas compared to ungrazed areas as well. Increased uniformity in the horizontal distribution of the belowground plant parts of *Bouteloua gracilis* has been hypothesized to facilitate a more complete exploitation of a given volume of soil by this species, thus increasing its ability to compete for belowground resources, which severely limits the ability of subdominant species to colonize and occupy space in shortgrass steppe (Milchunas and Lauenroth 1989, Milchunas et al. 1989, 1992).

Milchunas and Lauenroth (1989) further reported that the horizontal distribution of biomass in grazed areas was more uniform along a topographical gradient than in ungrazed areas, indicating a homogenization of vegetation at a landscape scale (Milchunas and Lauenroth 1989). Similarly, Milchunas et al. (1989) reported that different topographic positions that were grazed by cattle were characterized by greater similarity in plant community composition than the same topographic positions that were ungrazed. Coffin and Lauenroth (1992) provided further indication of a grazing induced homogenization of vegetation when they described measures of reproductive effort (i.e.

number of flowering culms, inflorescences, seeds, etc) for *Bouteloua gracilis* on grazed and ungrazed sites in Colorado. Measures of reproductive effort for *Bouteloua gracilis* which differed significantly among different soil textures in ungrazed areas were not significantly different in grazed areas (Coffin and Lauenroth 1992).

Milchunas et al. (1989) reported that the diversity and abundance of ruderal species and introduced species were significantly lower on cattle grazed treatments than ungrazed treatments. Milchunas et al. (1992) tested the ability of plants to colonize space in Colorado shortgrass steppe by seeding opportunistic species (4 exotic and native annual species and one exotic perennial species) into areas that had been historically grazed by cattle and were grazed during the experiment (GG), areas that were historically grazed by cattle but were not grazed during the experiment (GU), and areas that were historically ungrazed and were not grazed during the experiment (UU). Few individuals of the seeded species emerged in the GG or GU treatments, and none were able to emerge and subsequently survive in the GG treatment (Milchunas et al. 1992). Germination of 2 of the species was never sufficient in any treatment to allow analyses, but densities of the remaining 3 species were consistently and significantly higher during all sampling periods in the UU treatment than in the GG and GU treatments (Milchunas et al. 1992). The poor ability of the opportunistic species to exist in the grazed treatments was attributed to the lack of "safe sites", areas where competition from neighboring, highly competitive, perennial plants was reduced sufficiently to allow colonization and persistence (Milchunas et al. 1992). Densities of opportunistic species on the UU treatment were similar to their densities on areas of disturbed soil (Milchunas et al. 1992).

Milchunas et al. (1990) examined the effects of heavy grazing by cattle, no grazing, water addition, nitrogen addition, water-plus-nitrogen addition, and root grazing by beetle larvae on various measures of vegetation composition in Colorado. Community composition measures such as density of dominant species and density and richness of opportunistic-generalist species and introduced species suggested each treatment occupied a position along a perturbation gradient (Milchunas et al. 1990). The results indicated that the most perturbed areas were those that received the water-plus-nitrogen treatment, followed by the beetle larvae treatment and the water treatment (Milchunas et al. 1990). Community composition of ungrazed areas were more similar to the water, nitrogen, water-plus-nitrogen, and beetle larvae treatments than they were to the cattle grazed areas (Milchunas et al. 1990). Furthermore, annual precipitation had less of an effect on community composition in the less perturbed areas than those areas that were classified as more perturbed (Milchunas et al. 1990). The results of this study and others demonstrates the high degree of adaptation of shortgrass steppe vegetation to large-herbivore grazing and a semiarid climate, and the authors assert that grazing should not be considered a type of disturbance in shortgrass steppe ecosystems (Milchunas et al. 1988, 1989, 1990, 1992).

Shortgrass steppe vegetation was heavily influenced in pre-Pleistocene history by a diverse mammalian grazing guild, by the Pleistocene grazing guild of bison, pronghorn antelope, and various lagomorphs and rodents, and recent history has seen the replacement of bison with domestic cattle (Stebbins 1981, Coughenour 1985, Mack and

Thompson 1982, Lauenroth and Milchunas 1992). If the shortgrass steppe was historically and is currently characterized by high rates of herbivory, and if high rates of herbivory facilitates the dominance of a few grazing tolerant grasses at the expense of other components of the vegetative community, then a valid inference might be that low diversity and heterogeneity are expected and intrinsic characteristics of shortgrass steppe vegetation. These effects on vegetation heterogeneity may further influence organisms other than plants (Weins 1976, Milchunas et al. 1998).

Research on the effect of grazing on shortgrass steppe vegetation has been conducted with cattle, and the effect of bison is open to speculation. It has been suggested that reported differences in the foraging and social ecology of bison and cattle could result in these two bovines having disparate impacts on vegetation (Peden et al. 1974, Kautz and Van Dyne 1978, Schwartz and Ellis 1981, Van Vuren 1984, Lauenroth and Milchunas 1992, Plumb and Dodd 1993, Hartnett et al. 1997, Knapp et al. 1999). However, the tolerance of grasses such as *Bouteloua gracilis* and *Buchloe dactyloides* to cattle grazing is presumed to be a result of their long evolutionary history with, and adaptations to, the grazing of bison and other herbivores (Stebbins 1981, Coughenour 1985, Mack and Thompson 1982, Lauenroth and Milchunas 1992). It is possible that the effects of management, i.e. manipulations of the spatial and temporal patterns of animal distribution, may play the largest role in determining the effect of either bovine on vegetation (Plumb and Dodd 1993, Knopf 1996, Hartnett et al. 1997, Knapp et al. 1999).

The adaptation of *Bouteloua gracilis* and *Buchloe dactyloides* to herbivory can be partly explained as an avoidance mechanism whereby much of their photosynthetic and

meristematic tissue is located below a level that is accessible to bovine grazers (Branson 1953, Coughenour 1982, Briske 1991). Conversely, the herbivory of prairie dogs should exert an effect on vegetation that is quite different from the effect of cattle or bison. The dominant plants of shortgrass steppe, *Bouteloua gracilis* and *Buchloe dactyloides*, should be much more susceptible to overutilization by prairie dogs because prairie dogs can clip plants at the ground surface, and they sometimes scratch and dig into the soil surface to expose plant tissue after aboveground parts have been removed (King 1955, Koford 1958, Smith 1967, Krueger 1986). This type of foraging thwarts the grazing avoidance mechanisms of short grasses because it removes photosynthetic and meristematic tissues down to the soil surface and into root crowns.

Additionally, prairie dog foraging activities are limited to the confines of a colony throughout the year so plants are clipped continuously during a growing season without a period of rest, and clipping occurs year after year. This contrasts with cattle, which abandon grazed patches when plants within a patch succumb to repeated herbivory and the forage quality available within a patch declines relative that available in other patches or within the surrounding matrix (C. Owensby, pers. comm.). Finally, prairie dogs also typically clip all plants within a colony to a short height, presumably to facilitate predator detection and social interaction, regardless of whether those plants are used as food items (King 1955, Koford 1958, Hoogland 1995).

Insight into the effect of close, frequent clipping by prairie dogs on vegetation is provided by research conducted in west-central Kansas (Albertson et al. 1953). The effect of defoliation height and frequency on shortgrass vegetation were examined, and

the most intense defoliation treatment consisted of clipping to the ground surface every 2 weeks from 25 May to 25 September. After 5 years, the most intense defoliation treatment was the only treatment that was distinguished by significant decreases in basal cover of *Bouteloua gracilis* and *Buchloe dactyloides* (Albertson et al. 1953). *Bouteloua gracilis* and *Buchloe dactyloides* plants within the most intense defoliation treatment were characterized by the death of portions of their crowns and fewer, more slender tillers (Albertson et al. 1953). Open spaces in the sod created by the death of crowns on the most intensely defoliated treatment resulted in surface erosion removing 1.2 - 1.9 cm of soil (Albertson et al. 1953).

The results of Albertson et al. (1953) exemplify why portions of prairie dog colonies that had been occupied for extended periods of time in South Dakota have been reported to be dominated by forbs and shrubs, were sparsely covered or lacking in graminoids, and had high percentages of bare ground (Coppock et al. 1983a, Krueger et al. 1986, Archer et al. 1987), i.e. repeated close clipping will eventually kill grasses. In addition to the unique influence of prairie dog herbivory, soil disturbances caused by the digging and mound building activities of prairie dogs may have an influence on vegetation within the shortgrass steppe that contradicts the effects of herbivory by large ungulates such as cattle and bison.

Localized, Intense Soil Disturbance by Prairie Dogs

Prairie dog colonies consist of numerous territorial family groups of individuals, and each group is called a coterie (King 1955, Hoogland 1995). The residents of each

coterie excavate numerous burrows within the territory defended by the coterie, and these burrows are used for sleeping, refuge from predators, and for sheltering of young (Hoogland 1995). Burrow entrances may be inconspicuous holes in the ground, or they may be surrounded by denuded soil or by mounds of soil (Koford 1958, Tileston and Lechleitner 1966, Hoogland 1995).

King (1955) and Hoogland (1995) described three types of burrow entrances that prairie dogs create: burrow entrances without a conspicuous mound of soil, burrow entrances surrounded by wide rounded mounds of soil, which were termed dome craters, and burrow entrances surrounded by high mounds of soil that have been molded into a distinctive rim, which were termed rim craters. Dome craters were described as having a diameter of 1.0 - 2.0 m and a height of 0.2 - 0.3 m, whereas rim craters were described as having a diameter of 1.0 - 1.5 m, and a height of up to 1.0 m (Hoogland 1995). King (1955) and Tileston and Lechleitner (1966) reported that dome mounds (mound being analogous to crater) were constructed entirely from subsoils that were brought to the surface from the burrow network, while crater mounds were constructed by mixing subsoils with surface soils which were scraped from the area around the mound.

Reported mean densities of burrows from black-tailed prairie dog colonies in various locations of the Great Plains are: 21.4 burrows/ha in in northeast Wyoming (Campbell and Clark 1981), 103.5 burrows/ha in northeast Colorado (Tileston nad Lechleitner 1966), 32.5 burrows/ha in southeast New Mexico (Clark et al. 1982), and 169.3 burrows/ha in northwest Oklahoma (O'Meilia et al. 1982). In South Dakota, Archer et al (1987) reported mean burrow densities of 123, 239 and 271 burrows/ha in

portions of a prairie dog colony that were 2, 3 and 4 - 6 years old, respectively. In their study of the relationship between aboveground counts of prairie dogs and burrow densities at 5 colonies in southwest Kansas, Powell et al. (1994) classified portions of prairie dog colonies as having low (<150 burrows/ha), medium (150-250 burrows/ha) or high (>250 burrows/ha) densities of burrows.

O'Meilie et al. (1982) estimated that the average area of denuded soil per prairie dog burrow (including burrows without conspicuous mounds of soil) was 1.1 m², and that burrows and other areas disturbed by prairie dogs digging during feeding activities resulted in the denuding of 1.9% of the area occupied by prairie dogs at their study location in Oklahoma. Based on a typical burrow system with 2 entrances, 1 - 3 m of depth, 15 m of length and a diameter of 10 - 13 cm (Sheets et al. 1971), Whicker and Detling (1988) estimated that 200 - 225 kg of soil are mixed by prairie dogs for each burrow system. Hoogland (1995) speculated that 1% or 2% of the burrows in a colony he studied in South Dakota filled in each year, but these losses were offset by new excavations. Numerous burrows at Hoogland's study colony were used for up to 14 years (Hoogland 1995). Tileston and Leichleitner (1966) reported that no new burrows were constructed during almost 2 years of observation at a prairie dog colony, but burrows were frequently plugged with soil, plugged burrows were frequently reopened, and burrow mounds were repeatedly repaired or modified, especially when soils were wet.

In addition to the bare soil represented by burrow mounds, prairie dogs disturb the soil surface in colonies in other ways as well. Soil used to construct crater mounds may be scraped from trenches radiating out from the mound, and the trenches can measure 20

cm wide, 7 to 10 cm deep, and nearly 1 m in length (Tileston and Lechleitner 1966).

Both Tileston and Lechleitner (1966) and Smith (1967) reported that prairie dogs digging for roots sometimes disturbed portions of a colony so greatly that the ground appeared as if it had been cultivated. No studies have been conducted that examine the specific influence that soil disturbances created by prairie dogs might have on vegetation, but soil disturbances by numerous other animals have been studied extensively. A review of the effects of soil disturbances by other animals should provide insight into what the effects of prairie dogs might be.

Localized, Intense Soil Disturbance by Other Animals

Numerous animals, such as pocket gophers (*Geomys* spp.), bison, badgers (*Taxidea taxus*), and ants (*Formica* spp., *Pogonomyrex* spp) can create localized, intense disturbances within grasslands that result in the mounding of subsoils on the surface or the denuding of surface soils (Platt 1975, Collins and Uno 1983, Polly and Collins 1984, Collins and Barber 1985, Coffin and Lauenroth 1989a, 1990, Huntly and Inouye 1988, Gibson 1989). Vegetation colonization and succession on localized areas of intense soil disturbance can result in localized patches of vegetation that differ in productivity and the array of species present on the patch when compared to the surrounding matrix of undisturbed vegetation (Platt 1975, Collins and Uno 1983, Polly and Collins 1984, Coffin and Lauenroth 1989a, Martinsen et al. 1990, Reader and Buck 1991). The composition and structure of vegetation may be altered substantially by the influence of the soil disturbances that occur within them (Collins and Barber 1985, Gibson 1989).

The influence of pocket gopher mounds on vegetation has been studied extensively (Laycock 1958, McDonough 1974, Foster and Stubbendieck 1980, Grant et al. 1980, Tillman 1983, Andersen and MacMahon 1985, Hobbs and Mooney 1985, Spencer et al. 1985, Inouye et al. 1987, Huntly and Inouye 1988, Gibson 1989, Martinson et al. 1990, Reichman et al. 1993, Rogers 1998). Pocket gophers are fossorial herbivores that construct extensive burrow systems below the surface of the soil, and excavated material is either backfilled into old tunnels or moved to the surface where it is deposited in mounds of loose soil (Huntly and Inouye 1988). Because pocket gopher mounds typically are initially devoid of vegetation, they may provide ideal locations for plant germination and growth, partly because competitive interactions between plants may be minimized on the sparsely vegetated mounds (Laycock 1958, Tillman 1983, Andersen and MacMahon 1985, Hobbs and Mooney 1985, Huntly and Inouye 1988). Revegetation of pocket gopher mounds occurs through germination and survival of plants on the mound, as well as the growth, through the mound, of plants that survive burial under the mound (Laycock 1958). McDonough (1974) reported that seeds were not found in the soils of mounds that had been constructed prior to the onset of the seed rain in Utah aspen rangeland, indicating that the subterranean soils that were used to construct the mounds were free of seeds.

Seasonal variation in the occurrence of new mounds can influence which plant species will colonize new mounds, because of species specific periods of seed rain (Hobbs and Mooney 1985). Annual plants are typical colonizers of pocket gopher mounds, and mounds may provide germination sites that are not available in the highly

competitive environments of undisturbed perennial vegetation (Laycock 1958, McDonough 1974, Tillman 1983). However, Gibson (1989) and Rogers (1998) reported that because burial beneath gopher mounds did not kill the roots and rhizomes of the perennial grass big bluestem (*Andropogon geardii* Vitman), regrowth through mounds by this species resulted in it being one of the most abundant plants growing on gopher mounds in Kansas tallgrass prairie.

Hobbs and Mooney (1985) studied the impact of pocket gopher soil disturbances on a serpentine annual grassland in California, and they reported that the germination opportunities provided by gopher mounds may have been crucial for the persistence of perennial grasses in that community. McDonough (1974), working in Utah aspen rangeland, reported that annual plants dominated gopher mounds initially and reached peak abundance 2 years after creation of the mound, but by the fourth year, perennial species had displaced the annuals. When species diversity was calculated using the Shannon-Wiener Index of diversity (H') in Arizona shortgrass prairie, diversity was significantly higher on intermediate age (1 - 2 years old) pocket gopher mounds than on new (< 1 year old) or old mounds (> 2 years old) (Martinsen et al. 1990). Frequency of perennial grasses was significantly lower on intermediate age mounds than new or old mounds, and frequency of perennial dicots was significantly higher on intermediate age and old mounds than on new mounds (Martinsen et al. 1990).

Levels of resources such as light, soil moisture and nitrogen on pocket gopher mounds can differ from what is found in undisturbed surface soils, and this can influence plant productivity on the mound, adjacent to the mound, and at varying distances from

the mound (Grant et al. 1980, Spencer et al. 1985, Inouye et al. 1987, Huntly and Inouye 1988, Reichmann et al. 1993, Rogers 1998). Reichman et al. (1993) reported that plant biomass exhibited fluctuating "waves" of significantly different productivity at increasing distances from pocket gopher mounds in Kansas tall grass prairie. Plant biomass was lowest on mounds, highest immediately adjacent to mounds, and intermediate at the farthest distances from the mounds (Reichmann et al. 1993). Similarly, Grant et al. (1980) reported that vegetation density was significantly higher adjacent to pocket gopher mounds than at a distances of 40 and 50 cm from mounds in Colorado shortgrass prairie.

On sandy range sites in western Nebraska, Foster and Stubbendieck (1980) reported that areas disturbed by pocket gophers had significantly higher basal cover of annual grasses, perennial forbs, and annual forbs, but lower basal cover of perennial grasses than areas undisturbed by pocket gophers. Areas disturbed by pocket gophers on silty range sites in this study were characterized by significantly lower basal cover of perennial grasses and higher basal cover of annual forbs than undisturbed areas (Foster and Stubbendieck 1980). Old fields in Minnesota that contained pocket gopher mounds were characterized by greater point to point variation in soil nitrogen, significantly greater plant species richness, significantly greater cover of annual forbs, significantly greater cover of all annual plants, and significantly greater cover of introduced species than old fields without pocket gopher mounds (Inouye et al. 1987). Martinsen et al. (1990) reported that in Arizona shortgrass prairie, plant species diversity (H') and the frequency of perennial dicots were significantly and positively correlated with the

percentage of area disturbed by pocket gophers. In Minnesota old fields pocket gophers slowed the rate of succession within fields because their mounds facilitated the persistence of early successional species within maturing vegetation, and the relative impact of pocket gophers on plant species composition was greatest within fields that had undergone succession the longest (Inouye et al. 1987).

Other animal generated soil disturbances have been shown to facilitate the persistence of species that are otherwise rare in the surrounding undisturbed vegetation. Bison wallows are depressions created by the trampling and rolling of bison in exposed soils, and the vegetation within wallows can differ dramatically from the vegetation outside of wallows (Collins and Uno 1983, Polley and Collins 1984, Gibson 1989). Because of the water holding characteristics of wallows (topographic depression, compacted soils) the vegetation of wallows can be composed of plant species that are characteristic of more mesic soils than the vegetation surrounding the wallow (Collins and Uno 1983, Polley and Collins 1984, Gibson 1989).

The vegetation on badger mounds can also differ markedly from the vegetation of surrounding undisturbed areas (Platt 1975, Gibson 1989). In Kansas tallgrass prairie, total plant species richness and species richness of annual plants were higher on badger mounds than on undisturbed reference plots (Gibson 1989). Gibson (1989) reported that approximately 20% of the vegetation that occurred on badger mounds were annual species. Platt (1975) identified a guild of "fugitive" species, comprised of biennials and perennials, that were typically associated with badger mounds, but were uncommon in undisturbed tallgrass prairie in Iowa, and these fugitive species were consistently the

most prominent seedlings on badger mounds.

Nest sites of ants have been shown to influence vegetation dynamics in ways that are both similar to and distinct from the soil disturbances previously described. Western harvester ants (*Pogonomyrex occidentalis*) use soil and gravel to construct cone-shaped mounds on the soil surface above their nest chambers and these mounds in Wyoming have been reported to be up to 0.26 m high and 1.52 m diam at their base (Lavigne 1966, 1969, Rogers 1972). Mounds are situated within disks of bare soil and these disks have been reported to range from 0.2-5.18 m diam in Wyoming and Colorado (Lavigne 1966, Rogers 1972). Similar to the effect of pocket gopher mounds on vegetation productivity described by Reichman et al. (1993), Rogers and Lavigne (1974) reported that plant biomass on the edge of the cleared disks of western harvester ant nests in Colorado shortgrass steppe was significantly higher than that found 50 and 100 cm from the edge.

Coffin and Lauenroth (1990) also reported that total plant biomass, biomass of all perennial graminoids, biomass of the perennial grass *Bouteloua gracilis*, and biomass of all other perennials combined were all significantly higher in a ring around the nest sites of western harvester ants than in undisturbed reference plots that lacked ant nests in Colorado shortgrass steppe. The increase in plant biomass adjacent to the cleared disk of ant nests is presumably caused by the elimination of transpiring plants from within the disk, resulting in greater amounts of soil moisture being available to plants on the edge of the disc (Wight and Nichols 1966, Rogers and Lavigne 1974). Rogers and Lavigne (1974) reported that soil moisture levels inside the cleared discs of ant nests were in fact significantly higher than levels outside the discs.

Ant hills constructed by *Formica* spp. in Kansas tallgrass prairie were characterized by significantly higher abundances of the dominant perennial grass, big bluestem (Gibson 1989). Coffin and Lauenroth (1990) reported that western harvester ant nest sites in Colorado shortgrass steppe were characterized by significantly lower density and cover of perennial graminoids and total vegetation, but statistically similar density and cover of annuals and non-graminoid perennials than undisturbed reference sites. Western harvester ants are primarily granivorous, and the seeds they collect from the area around their nests are stored in chambers beneath the mounds of their nest sites (Lavigne 1969, Rogers 1974). Coffin and Lauenroth (1990) reported that seed banks present within the nest sites of western harvester ants in Colorado shortgrass steppe were composed primarily of the seeds of annual species of plants, and the number of germinable seeds of all plants combined, all annuals combined, and 3 species of annual forbs were significantly higher within the mounds of nest sites than within the cleared disks surrounding the mounds. Germinable seeds of the dominant plant species, the perennial grass *Bouteloua gracilis*, were not found stored in either the mounds or disks of nest sites (Coffin and Lauenroth 1990).

In spite of the dominance of annual species within the seed bank in the nests of western harvester ants, Coffin and Lauenroth (1990) reported that one year after the abandonment of nests, re-vegetation of nest sites was primarily by perennial species. Densities of annuals were significantly higher on abandoned nest mounds than abandoned disks, and densities of annuals were significantly higher at abandoned nest sites than in undisturbed reference vegetation for 1 of 4 sampling periods (Coffin and Lauenroth

1990). Densities of perennial graminoids were significantly lower during 4 of 4 sampling periods on abandoned nest sites, and densities of all other perennials were significantly higher during 2 of the 4 sampling periods on abandoned nest sites than in undisturbed reference vegetation (Coffin and Lauenroth 1990). Western harvester ants clear the vegetation at nest sites by clipping it belowground, and re-vegetation of abandoned mounds primarily occurs via the regrowth of plants that survived this clipping, as well as the vegetative growth of plants at the margin of nest sites (Coffin and Lauenroth 1989a, 1990). The perennial grass *Bouteloua gracilis* was not found on abandoned nest sites, even though it dominated the undisturbed reference vegetation (Coffin and Lauenroth 1990).

An effect of localized, intense soil disturbances that is highlighted by the results of many studies is a facilitation of the persistence of "pioneer" or "fugitive" species (often annuals and short-lived perennials), via the production of sites conducive for colonization and growth, within highly competitive environments dominated by perennial plants (Laycock 1958, McDonough 1974, Platt 1975, Tillman 1983, Gibson 1989, Coffin and Lauenroth 1990). Increased plant species diversity and richness can characterize landscapes where numerous localized, intense soil disturbances are present, relative to landscapes with few or none (Collins and Barber 1985, Inouye et al. 1987, Martinsen et al. 1990).

No studies have been published that have compared the vegetation on the mounds made by prairie dogs to the vegetation between the mounds within a colony, or to the non-colonized vegetation adjacent to the colony. However, studies that report increased

species richness or diversity or higher cover values, abundances, or frequencies of specific plants or groups of plants on prairie dog colonies than on non-colonized grassland suggest that prairie dog colonies do indeed represent areas where "fugitive" or "pioneer" species can maintain populations in landscapes that may otherwise be sub-optimal for them (Bonham and Lerwick 1976, Coppock et al. 1983a, Archer et al. 1987). An understanding of the effects of soil disturbances by prairie dogs on vegetation in the region of this study, the shortgrass steppe, would benefit from an expanded examination of the role of disturbances in shortgrass steppe plant community ecology.

Disturbance Ecology at Large Scales in Shortgrass Steppe

Natural recovery through secondary succession (i.e. unaided by seeding or other range improvement practices) of vegetation on abandoned farmland in the western Great Plains has been described by numerous authors (Judd and Jackson 1939, Judd 1940, 1974, Tolstead 1941, Costello 1944, Reichhardt 1982, Dormaar and Smoliak 1985, Samuel and Hart 1994, Coffin et al. 1996). Secondary succession was depicted as a four step process on abandoned farmlands in Montana (Judd 1940), south central South Dakota (Tolstead 1941), western Nebraska (Judd and Jackson 1939), and at numerous locations in the "Dust Bowl" region encompassing eastern Colorado and New Mexico and western Kansas, Oklahoma, and Texas (Judd 1974). The first stage was characterized by annual grasses and forbs (present for the first 1-5+ years post abandonment), the second stage was characterized by a mixture of annual plants and short-lived perennials (present at years 2-7+), the third stage was characterized by

perennial grasses (present at years 3-12+), and the fourth stage, appearing 8-50+ years post abandonment, was characterized by the the dominance of "climax" perennial grass species such as *Bouteloua gracilis*, *Buchloe dactyloides*, *Stipa* spp., and *Agropyron* spp. (Judd and Jackson 1939, Judd 1940, 1974, Tolstead 1941). In northeast Colorado, Costello (1944) identified 5 stages of succession following abandonment of farmland. These stages were similar to those described by Judd and Jackson (1939), Judd (1940, 1974), and Tolstead (1941) except that a stage lasting 10-20 years and characterized by the dominance of the perennial grasses *Aristida longiseta* and *Aristida purpurea* occurred between the short-lived perennial grass stage and the final stage which was classified as a mixed prairie association (Costello 1944).

The common features of these studies and others are (1) an initial dominance by annual species following abandonment, (2) a reduction in the proportion of annuals and an increase in the proportion of perennials, and (3) the dominating presence of long-lived perennial grasses, which may include a prolonged period of dominance by perennial *Aristida* spp. (Judd and Jackson 1939, Judd 1940, 1974, Tolstead 1941, Costello 1944, Hyder and Everson 1968, Samual and Hart 1994). However, another common feature of successional dynamics in shortgrass steppe regions that has been illustrated by many studies is the slow rate of recovery of the dominant perennial grass *Bouteloua gracilis* (Judd and Jackson 1939, Costello 1944, Hyder and Everson 1968, Hyder et al. 1971, Judd 1974, Samual and Hart 1994, Coffin et al. 1996). Because the rate of vegetative spreading by individual *Bouteloua gracilis* plants is very slow (Samual 1985), sexual reproduction and recruitment of seedlings provide the primary mechanism for this species

to revegetate large disturbances such as abandoned farmland (Lauenroth et al. 1994, Coffin et al. 1996).

However, seed production by *Bouteloua gracilis* can be low and variable (Coffin and Lauenroth 1992), and storage of seeds in soil seed banks may be poor (Coffin and Lauenroth 1989b). Very poor survival of *Bouteloua gracilis* seedlings also impedes revegetation of abandoned farmland (Riegel 1941, Bement et al. 1965, Hyder et al. 1971). Survival of *Bouteloua gracilis* seedlings requires the emergence and development of adventitious roots (Hyder et al. 1971, Briske and Wilson 1978, 1980, Wilson and Briske 1979). Because adventitious roots of *Bouteloua gracilis* seedlings are initiated at an average depth of 2 mm below the surface of the soil (Hyder et al. 1971), seedlings are extremely vulnerable to mortality caused by desiccated surface soils (Hyder et al. 1971, Briske and Wilson 1978, 1980, Wilson and Briske 1979). Environmental conditions that are required for seedling survival include temperatures above 15° C, and two consecutive periods of 2-4 days of continuously moist surface soils: first during the period of emergence and establishment of the seminal root, as well as 2-8 weeks later during the period that adventitious roots develop (Briske and Wilson 1977, 1978, Wilson and Briske 1979).

The specific environmental parameters that are required for the survival of *Bouteloua gracilis* seedlings are rarely met in many areas of the shortgrass steppe (Briske and Wilson 1977, Laycock 1989, 1991, Roohi et al. 1991). Precipitation in the shortgrass steppe occurs primarily as small events (Sala and Lauenroth 1982, Sala et al. 1992) which are often inadequate to insure the survival of *Bouteloua gracilis* seedlings because the

soil surface can rapidly dry after the occurrence of such an event (Briske and Wilson 1977, Sala et al. 1992). Using climate and soil temperature data from northeast Colorado, Briske and Wilson (1977) determined that the probability of 2 or more consecutive days of damp cloudy weather in consecutive seven day periods was less than 15% for most of the duration of the growing season when soil temperatures were above 15° C. Briske and Wilson (1977) reported that the period with the highest probability of 2 or more consecutive days of optimum moisture occurs in May, but temperatures at this time are marginal for seedling development, whereas optimum temperatures for seedling development occurs during mid-summer when the probability of 2 or more consecutive days of moisture is very low.

There has been speculation that *Bouteloua gracilis* may have become established as the dominant plant species in the more arid portions of the shortgrass steppe (i.e. where precipitation is < 380 mm/yr) during previous, more favorable climatic conditions, and that current climatological conditions in these regions effectively preclude *Bouteloua gracilis* from reproducing sexually (Briske and Wilson 1977, Laycock 1989,1991). However, when Lauenroth et al. (1994) used data from Colorado shortgrass steppe in a simulation model of the physiological requirements of *Bouteloua gracilis* seedlings and soil water dynamics in various soil types, their results indicated that *Bouteloua gracilis* should be capable of recruitment from seed in regions that receive less than 380 mm/yr of precipitation. Their model predicted a wide range in probability of recruitment for various soil types, varying from one recruitment event as often as once every 29 yr in silty loam soils, to less than one recruitment event every 5000 yr in sandy soils

(Lauenroth et al. 1994). In Colorado Coffin et al. (1996) examined 15 abandoned farm fields, each adjacent to unplowed shortgrass steppe vegetation, and reported that each field had *Bouteloua gracilis* present in them, indicating that this species was able to revegetate farmland that had been abandoned 53 years previously. Basal cover contributed by this species in these fields ranged from 0.4 - 9.1%, while the mean basal cover in unplowed fields was 11.7% (Coffin et al. 1996). Many of the fields examined exhibited a decrease in cover of *Bouteloua gracilis* with increased distance from the edge of the field adjoining the unplowed vegetation (Coffin et al. 1996).

It is interesting to note that the climatic characteristics (a preponderance of small precipitation events) that have been proposed as facilitating the dominance of *Bouteloua gracilis* in shortgrass steppe regions (Sala and Lauenroth 1982, see discussion above) are apparently responsible in part for the great impediment to recruitment by seed of this species. Incidentally, Morton and Baca Counties do not lie within the more arid portions of the shortgrass steppe, the mean annual precipitation recorded at the Elkhart weather station in Morton County is 447 mm (National Weather Service Cooperative Observer Network, Personal Communication).

Disturbance Ecology at Small Scales in Shortgrass Steppe

Individual *Bouteloua gracilis* plants exert a substantial competitive influence on neighboring plants, and because it is the dominant species in shortgrass steppe, competitive interactions may be greatest between neighboring *Bouteloua gracilis* than between *Bouteloua gracilis* and other species (Coffin and Lauenroth 1991, Hook et al.

1994, Aguilera and Lauenroth 1995). Coffin and Lauenroth (1991) reported that individual *Bouteloua gracilis* plants at a research site in Colorado had an average basal cover of 320 cm² and neighboring plants were separated by an average distance of 10 cm. Within the upper 10 cm of soil directly beneath an individual *Bouteloua gracilis* plant, 87% of the roots within that volume of soil belonged to that plant, but the roots of up to 4 other *Bouteloua gracilis* plants could occur in that volume of soil as well (Coffin and Lauenroth 1991).

Hook et al. (1994) estimated that less than 0.5% of the soil surface at their research site in Colorado was far enough away from *Bouteloua gracilis* plants to indicate that the soil below contained no roots of this species, but they stressed that competition between plants is dependent on the densities of roots, not just their presence or absence. They reported that root densities in the centers of small (10-12 cm), medium (20-23 cm), and large (50-85 cm) openings in the sod were 62, 33, and 4%, respectively, of root densities found directly beneath *Bouteloua gracilis* plants (Hook et al. 1994). Openings < 20 cm diameter comprised 86% of all openings at the study site, and the potential is high for a strong competitive influence of neighboring plants on seedlings within this sized opening (Hook et al. 1994). Openings > 50 cm diameter, where the competitive influence of neighboring plants is greatly reduced, comprised 2% of all openings and occupied 2% of the total area at the study site (Hook et al. 1994).

Just as revegetation by *Bouteloua gracilis* from seed may be poor in vast areas where it has been eliminated (i.e. abandoned farmland), recruitment from seed can also be poor in areas where parent plants are abundant and are able to exert a competitive

influence on seedlings (Aguilera and Lauenroth 1995). Aguilera and Lauenroth (1995) examined the influence of conspecific neighbors and patch disturbances on the emergence, survival and performance of *Bouteloua gracilis* seedlings in Colorado. *Bouteloua gracilis* caryopses were planted in bare soil adjacent to healthy adult *Bouteloua gracilis* plants, in the hummock formed by healthy adult plants, in bare soil adjacent to adult plants that had been killed with various treatments, and in the hummocks of adult plants that had been killed by various treatments, and all seedlings were watered until adventitious roots had developed (Aguilera and Lauenroth 1995). Seedlings growing in microsites where conspecific neighbors had been killed had significantly greater survival and produced significantly more tillers than seedlings growing in microsites where healthy adult plants were present (Aguilera and Lauenroth 1995). Seedlings growing in the presence of healthy adult plants usually produced only one tiller during their first growing season, and seedlings with one tiller were almost three times as likely not to survive the over-winter period as seedlings with more than one tiller (Aguilera and Lauenroth 1995).

Coffin and Lauenroth (1988) used data from fieldwork and published literature in a simulation model to examine the effects of three types of disturbance, cattle fecal pats, western harvester ant mounds, and small mammal burrows (i.e. skunks, badgers and pocket gophers), on *Bouteloua gracilis* population dynamics in Colorado. Cattle fecal pats were the smallest of the three disturbance types, but they were also the most abundant and covered the largest total area (Coffin and Lauenroth 1988). Because cattle fecal pats were approximately the same size as individual *Bouteloua gracilis* plants they

tended not to cover entire plants, so they influenced plants by killing tillers and recolonization of this disturbance patch occurred through tiller replacement (Coffin and Lauenroth 1988). Because ant mounds and small mammal burrows were always larger than individual *Bouteloua gracilis* plants they were more likely to kill entire plants than fecal pats, and recolonization of these disturbance patches would typically require the establishment of new *Bouteloua gracilis* plants (Coffin and Lauenroth 1988). *Bouteloua gracilis* is able to maintain its dominance in shortgrass steppe in part because it is capable of revegetating small, frequent disturbances such as fecal pats, while larger disturbance types, though rarer, have a larger impact per disturbance event and may have the largest potential effect on community structure (Coffin and Lauenroth 1988, 1989a).

Coffin and Lauenroth (1989a) compared the successional dynamics of western harvester ant mounds, small mammal burrows, and artificially created disturbances (all soil and plant material removed to a depth of 10 cm) that were 50, 100 and 150 cm diameter in Colorado. After one year of succession on each disturbance type, plant species composition on the natural disturbances (ant mounds and mammal burrows) were similar to each other but were different from that on the artificial disturbances (Coffin and Lauenroth 1989a). Natural disturbances were colonized by perennial species of plants while artificial disturbances were colonized by annuals (Coffin and Lauenroth 1989a). Cover values of annuals on the small artificial disturbances were significantly lower than on the large artificial disturbances while density values were not different, an indication that plants colonizing the small disturbances experienced a greater competitive effect from plants outside the disturbance than plants colonizing the large disturbances (Coffin

and Lauenroth 1989a).

Bouteloua gracilis plants partially covered by the soil of animal burrows made an important contribution to the recolonization of this disturbance type through vegetative growth, unlike the other disturbance types where it was of minor importance in successional dynamics during the study (Coffin and Lauenroth 1989a). The results suggested that recovery times would be quickest for the natural disturbances, small mammal burrows in particular because of the recovery of *Bouteloua gracilis*, and slowest for the large artificial disturbances (Coffin and Lauenroth 1989a). In another study in Colorado that examined the effect of artificial disturbances of three sizes (50, 100, and 150 cm diameter), cover values of *Bouteloua gracilis* decreased with increasing size of disturbance, while cover values of *Buchloe dactyloides* increased (Martinez-Turanza et al. 1997).

Milchunas et al. (1992) studied the colonization of space by 4 exotic and native annual species (*Kochia scoparia*, *Salsola iberica*, *Sisymbrium altissimum*, and *Lepidium densiflorum*) and one exotic perennial species (*Cirsium arvense*) in Colorado. Seeds were planted into areas that had been historically grazed and were grazed during the experiment (GG), areas that were historically grazed but were not grazed during the experiment (GU), areas that were historically ungrazed and were not grazed during the experiment (UU), areas that had the vegetation killed by herbicide and were ungrazed during the experiment (KU), and areas that had the vegetation removed by blading with a tractor, further disturbed by hoeing, and ungrazed during the experiment (DU) (Milchunas et al. 1992). *K. scoparia*, *S. iberica* and *S. altissimum* were the only species

to emerge in numbers suitable for analyses, and the KU and DU treatments consistently had significantly higher densities of these 3 species during all sampling periods than the GG or GU treatments (Milchunas et al. 1992).

Densities in the DU treatment were significantly higher than those in the KU treatment during all sampling periods for *K. scoparia* and during 3 of 4 sampling periods for *S. iberica* (Milchunas et al. 1992). Densities of *K. scoparia*, *S. iberica* and *S. altissimum* within the UU treatment were significantly higher during all sampling periods than in the GG and GU treatments, but were often similar or higher than in the KU and DU treatments (Milchunas et al. 1992). Milchunas et al. (1992) concluded that grazed areas were depauperate of "safe sites", areas of greatly reduced competition for colonizing species, but disturbances (represented by the KU and DU treatments) were important because they create safe sites and increase heterogeneity in shortgrass steppe communities.

It should be noted that prairie dog-induced soil disturbances are unique in many ways when compared to the other types of soil disturbance that have been discussed so far. Prairie dog burrow mounds are frequently re-disturbed by prairie dogs as they add soil to the mounds and shape them (King 1955, Smith 1967, Hoogland 1995). When soils are wet prairie dogs may pack mound soils tightly using the feet, forehead and nose, and the resulting mound has a hard, pavement like surface when dry (King 1955, Smith 1967, Hoogland 1995). Prairie dogs also continuously enter and exit their burrows during the day, and they congregate on mounds and use mounds as elevated perches from which to survey their surroundings (King 1955, Smith 1967, Hoogland 1995). All of these

activities would severely limit the ability of plants to colonize the bare soil on burrow mounds. Additionally, any plants that were able to colonize disturbed soil within prairie dog colonies would then be subject to constant clipping from prairie dogs attempting to maintain the low stature vegetation that characterizes their colonies.

Conclusion: Prairie Dogs in Shortgrass Steppe Ecosystems

In summary, the shortgrass steppe in the western Great Plains is characterized by a semiarid climate where precipitation is the primary determinant of biotic processes and attributes. While large rainfall events have been shown to be responsible for most of the variability in primary production, the majority of rainfall events are small ones that occur with little interannual variability, and these small rainfall events may have the greatest effect on ecosystem dynamics in semiarid regions. The perennial grass *Bouteloua gracilis* is the dominant plant in the shortgrass steppe of the western Great Plains and its competitive influence on other plant species is formidable. The competitive influence of *Bouteloua gracilis*, and its frequent co-dominant, *Buchloe dactyloides*, are further heightened by the foraging activities of large mammalian herbivores that are ubiquitous in these environments. The effects of this interaction are evident at various spatial scales as reductions in the structural and compositional heterogeneity of vegetation. These effects on vegetation heterogeneity may further influence communities of other organisms.

The soil disturbing activities of numerous organisms have been shown to increase structural and compositional heterogeneity within North American grasslands, including

shortgrass steppe. Revegetation of both large and small scale disturbances within shortgrass steppe characteristically involves an initial period of colonization by annuals and short-lived perennials, which are typically absent or rare in mature communities dominated by the perennial grass *Bouteloua gracilis*. In shortgrass steppe soil disturbances influence plant community dynamics in a manner that counteracts the effects of herbivory by large mammals. Additionally, prairie dogs can exert herbivory pressures that are much more severe than those exerted by larger herbivores such as cattle and bison. Prairie dogs also disturb and redistribute large amounts of soil within their colonies. Because prairie dog colonies are locations of both intense herbivory and soil disturbance, the potential is great that prairie dog colonies can profoundly influence the heterogeneity of shortgrass steppe ecosystems. The following chapters detail investigations of the effects of prairie dogs on plant and bird communities in Morton County, Kansas, and Baca County, Colorado.

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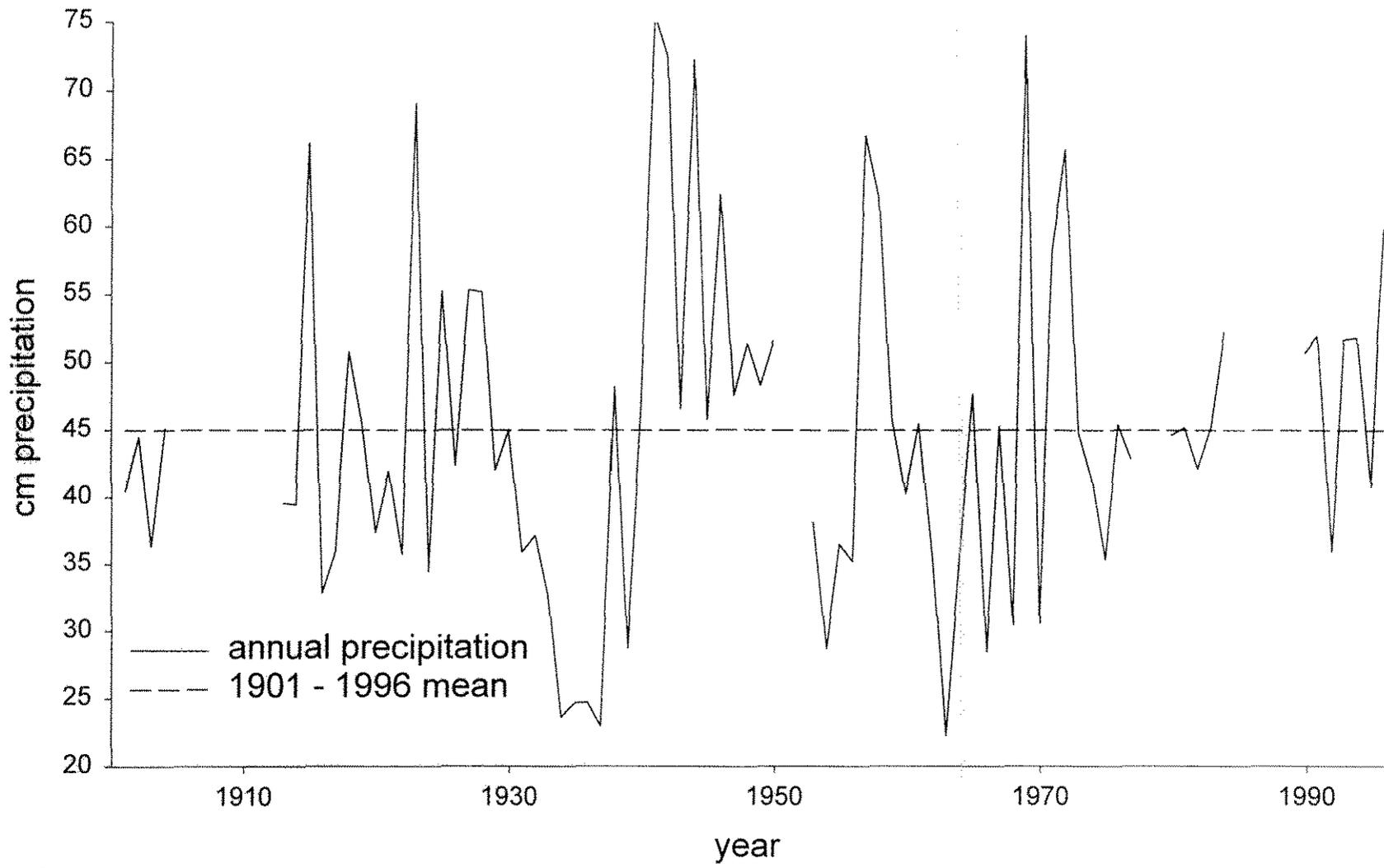
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Figure Legend

Figure 1. Annual precipitation amounts and 1901 - 1996 mean recorded at Elkhart weather station in Morton County, Kansas.



CHAPTER 2

PLANT COMMUNITIES OF BLACK-TAILED PRAIRIE DOG COLONIES AND NON-COLONIZED AREAS IN SOUTHWEST KANSAS AND SOUTHEAST COLORADO

ABSTRACT

This research sought to determine if the plant communities on black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies in southwest Kansas and southeast Colorado differed from those present on associated non-colonized grassland sites. Cover, bare ground, vegetation height and density, frequency of each species, and species richness were quantified on prairie dog colonies, non-colonized areas dominated by perennial short grasses, and non-colonized areas co-dominated by perennial short grasses and perennial mid-height grasses in 1996 and 1997. Cover of live grass was higher on non-colonized sites co-dominated by short and mid-height grasses than on prairie dog colonies or non-colonized sites dominated by short grasses in 1996, while cover of live forbs was higher on prairie dog colonies than that found on both types of non-colonized sites that year. There were no differences in cover of live grass or live forbs among any of the treatments in 1997. Vegetation height and density on prairie dog colonies were lower than that found on non-colonized sites co-dominated by short and mid-height grasses in 1997, the only year these variables were measured. Percent bare ground did not differ between prairie dog colonies and non-colonized sites during either year of the

study. Numerous species differed in frequency between the three types of sites sampled, but the results indicate that plant communities on prairie dog colonies are more similar to those found on non-colonized sites dominated by short grasses than those found on non-colonized sites co-dominated by short and mid-height grasses. Significant differences in species richness or species diversity were not detected among any of the treatments in 1996 or 1997. The results of this study contribute to an understanding of how the influence of prairie dogs on grassland vegetation may differ in various regions of the Great Plains.

INTRODUCTION

Research on the effects of black-tailed prairie dogs (*Cynomys ludovicianus* Ord) on grassland ecosystems has demonstrated that prairie dogs can alter vegetation structure and composition and ecosystem dynamics in South Dakota mixed-grass prairie (Agnew et al. 1986, Archer et al. 1987, Cid et al. 1991, Coppock et al. 1983a, Krueger 1986), Texas mixed-grass prairie (Weltzin et al. 1997b), Texas *Prosopis* savanna (Weltzin et al. 1997a), and Colorado shortgrass prairie (Bonham and Lerwick 1976). Prairie dogs influence vegetation as a result of their herbivory and by soil disturbance resulting from their mound building and digging activities (Archer et al. 1987, Cid et al. 1991). Prairie dog colonies have also been reported to be preferred foraging locations for some large herbivores, and the activities of these large herbivores may in turn influence the vegetation within and adjacent to prairie dog colonies (Koford 1958, Coppock et al. 1983b, Wydeven and Dahlgren 1985, Coppock and Detling 1986, Krueger 1986).

A substantial portion of the research on prairie dog ecosystems has been conducted in a limited area of the Great Plains, namely the mixed grass region of South Dakota (see Whicker and Detling 1988 for review), but the dynamics of prairie dog ecosystems in that bioregion may be different in areas with different climatic conditions and characteristic plant communities (Winter et al. In Press *a* and *b*, Stapp 1998). This chapter reports the results of two years of vegetation research conducted on prairie dog colonies and non-colonized areas in a shortgrass region of southwest Kansas and southeast Colorado.

STUDY SITE AND METHODS

Study sites were located at Cimarron National Grassland and adjacent private lands in Morton County, southwest Kansas, and Baca County, southeast Colorado. Cimarron National Grassland comprises more than 43,700 ha of land administered by the U.S. Forest Service. The majority of this land is characterized perennial grasses and is grazed by cattle (*Bos taurus* L.). Most of the surrounding private land is used for the production of annual crops, though some areas remain in perennial grass cover and are used for cattle grazing. Study sites occupied loamy upland range sites characterized by loamy and silty loam soils within the Richfield-Ulysses association, with slopes between 0 to 6% (Dickey et al. 1963). It was not possible to determine which of the study sites were unbroken native rangeland, and which of them may have been revegetated farmland that was abandoned in the 1930's. The proportion of short and mid-height grasses in the community of loamy upland range sites in the region of this study reflects either the seed

mixes used to reclaim abandoned farmland in the 1930's to 1950's (Schumacher and Atkins 1965), or the history of cattle grazing pressure at these locations (Lang et al 1956, Klipple and Costello 1960, Launchbaugh 1957, 1967, Hyder et al. 1975). Loamy upland range sites in excellent condition in Morton County can produce 1,400 - 2150 kilograms of air dry forage per hectare (Dickey et al. 1963).

Mean precipitation (1901 - 1996) recorded at the Elkhart weather station in Morton County is 44.75 cm (National Weather Service Cooperative Observer Network, Personal Communication). Precipitation during the twelve months preceding the 1996 sampling period was 34.35 cm, 77 % of the long term mean. Precipitation during the twelve months preceding the 1997 sampling period was 67.97 cm, 150 % of the long term mean.

In 1996 eight of the largest prairie dog colonies, five non-colonized shortgrass sites and eight non-colonized random sites were selected for study on Cimarron National Grassland. The criterion used to select non-colonized shortgrass sites was a visual determination that either or both of the perennial shortgrasses *Buchloe dactyloides* and *Bouteloua gracilis* were the dominant grass at the non-colonized sites. Non-colonized random sites were selected from a list of potential sites that had soil types and slopes that were identical to the soil types and slopes that characterized the prairie dog colonies. Selection of non-colonized random sites occurred without knowledge of what type of vegetation was growing at those sites. Study sites in 1996 varied in size from 32.4 ha to 64.8 ha. In 1997 thirteen prairie dog colonies, six shortgrass sites and the eight random sites were sampled at Cimarron National Grassland and adjacent private lands in Morton

county, KS, and Baca county, CO. One of the prairie dog colonies sampled in 1996 was not sampled in 1997, but all of the non-colonized sites sampled in 1996 were sampled again in 1997. Study sites in 1997 varied in size from 6 to 80 ha.

Cattle grazing had occurred at all study sites prior to the study. Grazing season varied for each site. Grazing during the entire growing season, rotational grazing, and fall and winter grazing were all practiced on Cimarron National Grassland and adjacent private lands. Three prairie dog colonies and two non-colonized shortgrass sites were not grazed at all during 1996 and 1997. In 1996, because of drought conditions, cattle were not put into any pastures until 17 June. In 1997 cattle were put into pastures as early as 1 May. Determination of exact grazing dates and AUM's for each study site from Forest Service grazing schedules was not possible because personal observations indicated that permittees did not rigorously adhere to grazing plans. AUM information in this study would be of questionable value because some study sites were located in large pastures that contained numerous range sites which differed greatly in plant species composition and productivity, thus potentially influencing cattle distribution.

In 1996 sampling occurred between 1 July and 18 July. In 1997 sampling occurred between 18 June and 2 July. Sampling was conducted using a 10.0 m² circular plot centered on one corner of a 0.10 m² rectangular plot. Canopy cover of live grass, live forbs, dead grass, dead forbs, canopy cover of each species, and percent bare ground were estimated within the 0.10 m² plot. Frequency of each species, species richness and species diversity were quantified using both the 0.10 m² and the 10.0 m² plot. In 1996 sampling occurred at 40 randomly located points at each study site. To facilitate the

sampling of small prairie dog colonies in 1997, the number of randomly located points sampled at each site was proportional to the area of the site, thus only 20 points were sampled at some of the smaller prairie dog colonies while up to 60 points were sampled at some of the larger random sites.

In 1997, between 27 May and 18 June, vegetation structure was measured using a visual obstruction pole modified from Robel et al. (1970) at randomly located points along transects at each study site. The number of points sampled at each site varied from 35 to 120, in proportion to the area of the site. Observations were made one meter from the pole at a height of one meter. Vegetation height was determined by recording the highest point at which vegetation crossed between the observer and the pole. Vegetation density was determined by recording the lowest point at which the pole was visible.

Species richness, Shannon's diversity index (H'), an evenness measure based on Shannon's diversity index (E), and the inverse of Simpson's diversity index ($1/D$) were calculated using frequency data from both the 0.10 m² and the 10.0 m² plots. Diversity index equations were obtained from Magurran (1988). Species richness and diversity indices for 1996 were calculated by determining the total number of species encountered at each study site. Because the number of points sampled at each site was proportional to the area of each site in 1997, species richness and diversity values generated using all plots at each site would not be comparable. Species richness and diversity indices for 1997 were calculated by determining the number of species encountered on a ten-plot basis at each study site. Plots within each study replicate were assigned to each group of ten on a random basis without replacement. Richness and diversity indices for each study

site were calculated using the mean value of the ten-plot groups within that site.

Classical F-test analysis of variance computed by SAS v. 6.11 (1996) was used when the assumptions of the F-test were approximately satisfied. When the assumptions of the F-test were not satisfied, the Kruskal-Wallis non-parametric test computed by SAS v. 6.11 (1996) and a Tukey-type non-parametric multiple comparison (Zar 1996) were used. Two-tailed tests were used to test the null hypothesis that there was not a significant difference between the means of treatments. When the null hypothesis was rejected, the results are discussed in terms of higher or lower values of the variable being examined. The probability of type I error was accepted at $\alpha = 0.05$ for tests. A test statistic value of $Q > 2.39$ generated by the Tukey-type test indicated significant differences. The tables that accompany the results section provide P-values from analysis of variance and Kruskal-Wallis tests. When data from three treatments were used in statistical tests, significant Q and P-values from pair-wise comparisons are provided in the text in the results section. Results from F-tests and Kruskal-Wallis tests that approached significance ($0.05 \leq P \leq 0.10$) are indicated in the results section for the two treatments in which the mean \pm SE differed the most. In instances where individuals of a particular species were not detected at any study replicates of a treatment, that treatment was not included in statistical tests. However, in instances where frequency of a species in one treatment is 0, and the mean - 2SE frequency for another treatment is greater than 0, those species are termed "species of interest" and discussed accordingly.

Distinct species that were difficult to differentiate in the field were grouped into single taxonomic groups for data analysis. For example, the species *Chamaesaracha*

coniodes and *Solanum triflorum* were grouped together for analysis and are identified in tables as Solanacea. Members of taxonomic groups are identified in footnotes for each table. Nomenclature follows Great Plains Flora Association (1986) and Wilson and Reeder (1993). Authorities of plant species are provided within the tables accompanying the results section. When the results of published research are referred to, the nomenclature used in the literature being cited is retained. Voucher specimens are deposited in the Division of Biology Herbarium at Kansas State University. A list of all specimens collected in Morton and Baca Counties is provided in the Appendix.

RESULTS

Table 1 lists mean \pm SE cover of live grass, dead grass, live forbs, dead forbs, percent bare ground, and cover of each species in 1996. Cover of live forbs ($P = 0.002$) and *Euphorbia* spp. ($P = 0.003$) were higher on prairie dog colonies than on non-colonized random sites. Cover of live forbs ($P = 0.008$), *Euphorbia* spp. ($P = 0.013$) and *Aristida purpurea* ($P = 0.013$) were higher on prairie dog colonies than on non-colonized shortgrass sites. Cover of live grass ($P = 0.001$), dead grass ($P = 0.0001$) and cover of *Bouteloua curtipendula* ($Q = 3.11$) were higher on non-colonized random sites than on prairie dog colonies. Cover of live grass ($P = 0.001$), dead grass ($P = 0.0001$), and *Bouteloua curtipendula* ($Q = 2.47$) were higher on non-colonized random sites than on non-colonized shortgrass sites.

Table 2 lists the mean \pm SE frequency of each species detected within 0.10 m² plots in 1996. Frequencies of *Amaranthus* spp. ($P = 0.016$), *Euphorbia* spp. ($P = 0.0004$),

and *Aristida purpurea* ($P = 0.023$) were higher on prairie dog colonies than on non-colonized random sites. Frequency of *Aristida purpurea* was also higher on prairie dog colonies than on non-colonized shortgrass sites ($P = 0.005$). *Bouteloua curtipendula* occurred more frequently on non-colonized random sites than on prairie dog colonies ($Q = 3.15$) or on non-colonized shortgrass sites ($Q = 2.44$). *Bouteloua gracilis* occurred more frequently on non-colonized shortgrass sites than on prairie dog colonies ($P = 0.033$). *Euphorbia* spp. ($P = 0.021$) and *Bouteloua gracilis* ($P = 0.005$) occurred more frequently on non-colonized shortgrass sites than on non-colonized random sites. The difference in the frequencies of *Euphorbia strictospora* between prairie dog colonies and non-colonized shortgrass sites approached significance. Frequency of *Amaranthus* spp. on prairie dog colonies was 0.09 ± 0.04 but this species was not detected on non-colonized shortgrass sites.

Table 3 lists the mean \pm SE frequency of each species detected within 10.0 m² plots in 1996. *Euphorbia* spp. occurred more frequently on prairie dog colonies than on non-colonized random sites ($Q = 2.66$). *Astragalus lotiflorus* ($P = 0.042$) and *Bouteloua curtipendula* ($Q = 3.25$) occurred more frequently on non-colonized random sites than on prairie dog colonies. *Ambrosia confertifolia* ($Q = 2.65$) and *Buchloe dactyloides* ($Q = 2.46$) occurred more frequently on non-colonized shortgrass sites than on non-colonized random sites. Differences in the frequencies of *Amaranthus* spp., *Portulaca oleracea*, and *Aristida purpurea* between prairie dog colonies and non-colonized random sites approached significance.

Using the data from the 10.0 m² plots in 1996 (Table 3), 84 species or taxonomic

groups were detected on prairie dog colonies, 91 were detected on non-colonized random sites, and 75 were detected on non-colonized shortgrass sites. Table 4 lists the species richness and diversity indices and P-values using data from both the 0.10 m² and the 10.0 m² plots in 1996.

Table 5 lists mean \pm SE vegetation height and density, cover of live grass, dead grass, live forbs, dead forbs, percent bare ground and cover of each species for 1997. Vegetation height (Q = 3.66) and density (Q = 3.39) were higher on the non-colonized random sites than on the prairie dog colonies. Cover of *Schedonnardus paniculatus* was higher on prairie dog colonies than on non-colonized random sites (P = 0.02). Cover of *Sphaeralcea coccinea* (P = 0.014), *Aristida purpurea* (Q = 2.92) and *Schedonnardus paniculatus* (P = 0.009) were higher on prairie dog colonies than on non-colonized shortgrass sites. Cover of *Astragalus* spp. (Q = 2.72), *Psoralea tenuifolia* (Q = 2.66), *Bouteloua curtipendula* (Q = 3.84), and *Sporobolus cryptandrus* (Q = 2.52) were higher on non-colonized random sites than on prairie dog colonies. Cover of *Bouteloua gracilis* (P = 0.002) and *Hordeum pusillum* (P = 0.0004) were higher on non-colonized shortgrass sites than on prairie dog colonies. Cover of *Bouteloua gracilis* (P = 0.006) and *Hordeum pusillum* (P = 0.001) were higher on non-colonized shortgrass sites than on non-colonized random sites.

Table 6 lists the mean \pm SE frequency of all species detected within 0.10 m² plots in 1997. *Aristida purpurea* (Q = 2.68) and *Schedonnardus paniculatus* (P = 0.017) occurred more frequently on prairie dog colonies than on non-colonized random sites. *Sphaeralcea coccinea* (P = 0.005), *Aristida purpurea* (Q = 2.76) and *Schedonnardus*

paniculatus ($P = 0.009$) occurred more frequently on prairie dog colonies than on non-colonized shortgrass sites. *Astragalus* spp. ($Q = 2.64$), *Psoralea tenuifolia* ($Q = 2.73$), *Bouteloua curtipendula* ($Q = 3.69$), and *Sporobolus cryptandrus* ($P = 0.003$) occurred more frequently on non-colonized random sites than on prairie dog colonies. *Bouteloua gracilis* ($P = 0.004$) and *Hordeum pusillum* ($P = 0.002$) occurred more frequently on non-colonized shortgrass sites than on prairie dog colonies. Frequencies of *Bouteloua gracilis* ($P = 0.015$) and *Hordeum pusillum* ($P = 0.001$) were higher on non-colonized shortgrass sites than on non-colonized random sites. Differences in the frequencies of *Kochia scoparia*, *Sophora nuttalliana*, *Agropyron smithii*, and *Buchloe dactyloides* between prairie dog colonies and non-colonized random sites approached significance. The difference in the frequency of *Plantago patagonica* between non-colonized random sites and non-colonized shortgrass sites approached significance.

Table 7 lists the mean \pm SE frequency of all species detected within 10.0 m² plots in 1997. *Kochia scoparia* ($Q = 3.33$), *Euphorbia strictospora* ($Q = 3.15$), *Aristida purpurea* ($Q = 2.89$), *Buchloe dactyloides* ($P = 0.016$), and *Schedonnardus paniculatus* ($P = 0.0001$) occurred more frequently on prairie dog colonies than on non-colonized random sites. Frequency of *Schedonnardus paniculatus* was also higher on prairie dog colonies than on non-colonized shortgrass sites ($P = 0.0002$). *Psoralea tenuifolia* ($P = 0.004$), *Gaura coccinea* ($P = 0.006$), *Asclepias latifolia* ($Q = 2.78$), *Convulvulus equitans* ($Q = 3.49$), *Thelesperma* spp. ($Q = 3.32$), *Trapopogon dubius* ($Q = 3.07$), *Bouteloua curtipendula* ($Q = 3.86$), and *Sporobolus cryptandrus* ($P = 0.008$) occurred more frequently on non-colonized random sites than on prairie dog colonies. Frequencies

of *Psoralea tenuifolia* ($P = 0.046$), *Gaura coccinea* ($P = 0.003$), and *Convolvulus equitans* ($Q = 2.64$) were higher on non-colonized random sites than on non-colonized shortgrass sites. *Oenothera triloba* ($Q = 2.79$) and *Sporobolus cryptandrus* ($P = 0.019$) occurred more frequently on non-colonized shortgrass sites than on prairie dog colonies. Frequencies of *Buchloe dactyloides* ($P = 0.013$) and *Hordeum pusillum* ($Q = 2.68$) were higher on non-colonized shortgrass sites than on non-colonized random sites.

Differences in the frequencies of *Amaranthus* spp., *Astragalus plattensis*, *Euphorbia marginata*, *Lithospermum incisum*, and *Erigeron divergens* between prairie dog colonies and non-colonized random sites approached significance. Differences in the frequencies of *Euphorbia marginata*, *Lithospermum incisum*, and *Bouteloua gracilis* on prairie dog colonies and non-colonized shortgrass sites approached significance.

Differences in the frequencies of *Mirabilis linearis*, *Astragalus* spp., *Plantago patagonica*, and *Conyza canadensis* between non-colonized random sites and non-colonized shortgrass sites approached significance. Frequency of *Cryptantha minima* on prairie dog colonies was 0.14 ± 0.04 but this species was not detected at non-colonized random sites or non-colonized shortgrass sites. Frequencies of *Dalea enneandra* and *Bromus japonicus* were 0.06 ± 0.03 and 0.16 ± 0.06 , respectively, at non-colonized random sites, but these species were not detected on prairie dog colonies.

Using the data from the 10.0 m^2 plots in 1997 (Table 7), 92 species or taxonomic groups were detected on prairie dog colonies, 96 were detected on non-colonized random sites, and 87 were detected on non-colonized shortgrass sites. Table 8 lists the species richness and diversity indices and P-values using data from both the 0.10 m^2 and the 10.0

m² plots in 1997.

Using the data from the 10.0 m² plots in 1996 and 1997, six species (*Cucurbita foetidissima*, *Astragalus pectinatus*, *Asclepias pumila*, and *Cryptantha minima*) and 2 taxonomic groups (*Lappula* spp., and Cyperaceae) were detected only on prairie dog colonies. Twenty-three species were detected only on non-colonized sites. Nine of these species were encountered only on non-colonized random sites (*Delphinium virescens*, *Hibiscus trionum*, *Astragalus missouriensis*, *Lipsea cuneifolia*, *Aster falcatus*, *Ambrosia grayii*, *Artemisia filifolia*, *Muhlenbergia arenicola*, and *Setaria viridis*), while seven species were encountered only on non-colonized shortgrass sites (*Tidestromia lanuginosa*, *Eriogonum annuum*, *Chrysopsis villosa*, *Helianthus ciliaris*, *Cenchrus longispinus*, *Elymus canadensis*, and *Hilaria jamesii*).

Using the data from the 0.10 m² and 10.0 m² plots in 1996 and 1997, Table 9 lists the number of perennial grasses, annual grasses, perennial forbs, and annual forbs on prairie dog colonies and non-colonized random sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest. Table 10 lists the number of perennial grasses, annual grasses, perennial forbs, and annual forbs on prairie dog colonies and non-colonized shortgrass sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest. Table 11 lists the number of perennial grasses, annual grasses, perennial forbs, and annual forbs on non-colonized random sites and non-colonized shortgrass sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest.

DISCUSSION

Research on prairie dog ecosystems throughout the Great Plains has demonstrated that the activities of prairie dogs influence plant community composition. Characteristic responses of vegetation in the Great Plains to colonization by prairie dogs include a shift from mid-height species of grasses to grazing tolerant short grasses, a displacement of many perennial species, and an increase in the abundance and cover of forbs, especially annuals (Bonham and Lerwick 1976, Coppock et al. 1983a, Agnew 1986, Archer et al. 1987, Cid et al. 1991, Weltzin et al. 1997b).

In this study there was no difference in species richness or any of the calculated diversity indices between prairie dog colonies and non-colonized sites during either year of the study (Tables 4 and 8). This study also found no differences in the amount of bare ground when prairie dog colonies were compared to non-colonized sites, which is unlike the findings of Archer et al. (1987) from South Dakota mixed-grass prairie. In this study it is possible that the spaces between burrows and their associated denuded areas had high vegetative cover that offset the lack of cover on the burrow mounds and associated denuded areas. Perhaps the horizontal arrangement of patches of bare ground and patches of vegetation was different on prairie dog colonies than it was on non-colonized areas, but the total amount of bare ground, which is what was measured in this study, was the same. Consistent with this speculation, Bonham and Lerwick (1978) reported significant differences in the clump and patch size of *Bouteloua gracilis* and *Buchloe dactyloides* within a prairie dog colony than what was found in adjacent non-colonized shortgrass prairie in Colorado.

The results of this study suggest prairie dog colonies are more similar to the non-colonized shortgrass sites than they are to the non-colonized random sites. Cover of live grass on prairie dog colonies was not significantly different from that found on non-colonized shortgrass sites in 1996 or 1997. In 1996 prairie dog colonies had significantly greater cover of live forbs than non-colonized shortgrass sites, but there was no significant difference in 1997. When vegetation height and density were measured in 1997, there was no significant difference between these two treatments. Non-colonized shortgrass sites were characterized by very high frequencies of the perennial shortgrass *Bouteloua gracilis* and high frequencies of the perennial shortgrass *Buchloe dactyloides*. Prairie dog colonies had similar frequencies of *Buchloe dactyloides*, but frequencies of *Bouteloua gracilis* were lower while frequencies of the perennial grass *Aristida purpurea* were higher. There were only seven species for which frequencies differed significantly between prairie dog colonies and non-colonized shortgrass sites in 1996 and 1997 (Table 9). There is a suggestion that both perennial and annual forbs are favored by the conditions found on prairie dog colonies relative to non-colonized shortgrass sites when species that approach significance and species of interest are considered for the comparison of prairie dog colonies to non-colonized shortgrass sites (Table 10).

When comparing vegetation height and density, cover of live grass, and cover of live forbs on prairie dog colonies to non-colonized random sites in this study, many of the results are similar to what was reported by Agnew et al. (1986) and Archer et al. (1987) from South Dakota mixed-grass prairie. This study found significantly higher cover of live grass on non-colonized random sites than on prairie dog colonies in 1996, whereas

the cover of live forbs was significantly higher on prairie dog colonies than on non-colonized random sites. In 1997 vegetation height and density were significantly higher on non-colonized random sites than on prairie dog colonies. Non-colonized random sites were characterized by the presence of the mid-height grass *Bouteloua curtipendula* as a co-dominant with *Bouteloua gracilis*, and always higher in frequency than *Buchloe dactyloides*. Frequencies of another mid-height grass, *Sporobolus cryptandrus*, were also significantly higher on non-colonized random sites than on prairie dog colonies.

Likewise, studies in South Dakota (Coppock et al. 1983a, Agnew et al. 1986, Archer et al. 1987) and Texas (Weltzin et al. 1997b) have consistently reported lower cover values, frequencies or biomass of mid-height grasses on prairie dog colonies relative to non-colonized mixed-grass prairie.

There were 16 species or taxonomic groups that differed significantly in frequency between prairie dog colonies and non-colonized random sites during 1996 and 1997 (Table 9). There is a conspicuous division among perennial and annual forbs that differed in frequency between prairie dog colonies and non-colonized random sites. Seven species of perennial forbs were significantly more frequent on non-colonized random sites, while the number for prairie dog colonies was 0. Conversely, 4 species of annual forbs were significantly more frequent on prairie dog colonies, while the number for non-colonized random sites was 0. When species that approach significance and species of interest are considered, these trends are further enhanced. Similarly, Weltzin et al (1997b) reported that prairie dog colonies were characterized by significantly lower biomass of perennial forbs than non-colonized mixed-grass prairie in Texas, whereas

research in South Dakota mixed-grass prairie (Archer et al. 1986) and Colorado shortgrass prairie (Bonham and Lerwick 1976) reported higher frequencies or cover of annual forbs on prairie dog colonies.

Two annual grasses (*Bromus japonicus* and *Hordeum pusillum*) occurred solely or significantly more frequently on non-colonized sites than on prairie dog colonies. There were no annual grasses that occurred more frequently on prairie dog colonies than on non-colonized sites. Significantly lower biomass of annual grasses on prairie dog colonies relative to mixed grass prairie has also been reported from Texas (Weltzin et al 1997b). The perennial grasses that occurred more frequently on prairie dog colonies in this study were characterized by traits that should help them avoid herbivory, such as a short stature (*Buchloe dactyloides*), a sprawling habit (*Schedonnardus paniculatus*), or sharp-tipped awns (*Aristida purpurea*). *Buchloe dactyloides* has also been shown to be very tolerant of high rates of cattle herbivory (Lang et al 1956, Klipple and Costello 1960, Launchbaugh 1957, 1967, Hart and Ashby 1998).

This study detected six species (*Cucurbita foetidissima*, *Astragalus pectinatus*, *Asclepias pumila*, and *Cryptantha minima*) and 2 taxonomic groups (*Lappula* spp., and Cyperaceae) that were found only on prairie dog colonies. Only one of these, the annual forb *Cryptantha minima*, occurred frequently enough to warrant the designation "species of interest". However, it is possible that this species is abundant on roadsides, around stock-tanks, and at the edges of agricultural fields. This may be the case for many of the species which these results suggest might be positively influenced by prairie dogs.

Compositional differences between prairie dog colonies and non-colonized

vegetation may be explained by differences in herbivory pressures and the amount of soil disturbance that is present at the two locations. Herbivory pressures on prairie dog colonies should be intense relative to non-colonized grassland. Prairie dogs can clip plants at the ground surface, and they sometimes scratch and dig into the soil surface to expose plant tissue after aboveground parts have been removed (King 1955, Koford 1958, Smith 1967), and this thwarts the grazing avoidance mechanisms of short species. Additionally, prairie dogs forage within the confines of the colony throughout the year, so plants may be continuously clipped throughout a growing season without a period of rest, and clipping can occur year after year. The extreme herbivory pressures on prairie dog colonies likely reduces the competitive influence of many species within a colony, allowing species which are exceptionally adept at avoiding or tolerating herbivory to experience competitive release.

The burrowing, digging and scratching of prairie dogs may also benefit species that may be poor competitors. Small-scale soil disturbances in shortgrass steppe, such as small mammal diggings, have been described as "safe sites" where the overwhelming competitive effects of perennial grasses are greatly reduced (Coffin and Lauenroth 1988, 1989, Milchunas et al. 1992, Aguilera and Lauenroth 1995). Even though small disturbances such as ant nest sites, gopher mounds, small mammal diggings, and areas infested with root feeding beetle larvae readily influence shortgrass steppe vegetation (Coffin and Lauenroth 1988, 1989, 1990, Martinsen et al. 1990, Milchunas et al. 1990), their relatively small size may limit the degree to which they influence animal communities. Conversely, prairie dog colonies occur at a scale that could profoundly

influence animal communities. Bare and disturbed soils within prairie dog colonies may provide abundant "safe sites" for ruderal species that avoid or tolerate herbivory as well as further digging, scratching and trampling by prairie dogs.

The contrast between the vegetation of prairie dog colonies and adjacent non-colonized grasslands depends on the contrast between the composition of vegetation within the colony, and that in the surrounding non-colonized grassland. The non-colonized random sites in this study were characterized by taller grasses than that found on the shortgrass sites, and the contrast between a prairie dog colony and non-colonized vegetation would be much higher if a prairie dog colony were situated within a non-colonized random site than if it were situated within a non-colonized shortgrass site. Similarly, the potential contrast between a prairie dog colony and non-colonized mixed-grass prairie would be much greater than the potential contrast between a colony and non-colonized shortgrass steppe, where the dominant grasses maintain a short stature even in the absence of herbivory. However, high grazing pressure by large herbivores in mixed-grass regions that cause a shift in vegetation composition, so that short grasses predominate (Sims et al. 1978, Coupland 1992), would diminish the ability of prairie dogs to create distinct patches of vegetation.

The interaction of prairie dogs with large herbivores results in contrasting implications for how prairie dog colonies might influence grassland landscapes in different regions of the Great Plains. In less arid regions of the Great Plains such as mixed-grass and tallgrass prairie, large herbivore grazing tends to increase vegetation heterogeneity (Collins and Barber 1985, Fahnestock and Knapp 1994, Hartnett et al.

1996, Hickman et al. 1996, Collins et al. 1998, Knapp et al. 1999), and the effects of prairie dogs would be complementary. In shortgrass steppe cattle grazing tends to homogenize vegetation (Milchunas et al. 1988, 1989, 1990, 1992, 1998, Milchunas and Lauenroth 1989, Coffin and Lauenroth 1992), and the effects of prairie dogs on vegetation would counter the effect of cattle. The importance of prairie dogs in promoting heterogeneity in shortgrass landscapes has been asserted by others (Knopf and Sampson 1997). In this study prairie dog colonies were distinct from non-colonized grassland, and had characteristics of earlier successional stages relative to non-colonized vegetation. Prairie dog colonies have the potential to contribute to vegetation heterogeneity at a scale that is unmatched, with the exception of agricultural conversion, by other disturbances characteristic of this region. The role that prairie dogs play in contributing to vegetation heterogeneity at a landscape scale in shortgrass steppe may have profound implications for higher trophic levels in this ecosystem.

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Table 1. Mean \pm SE canopy cover of live grass, dead grass, live forbs, dead forbs, percent bare ground, and cover of each species for prairie dog colonies (n = 8), non-colonized random sites (n = 8) and non-colonized shortgrass sites (n = 5) in 1996. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Live Grass	30.71 \pm 1.79 ^a	44.29 \pm 2.19 ^b	32.84 \pm 1.23 ^a	0.0001
Dead Grass	21.96 \pm 2.25 ^a	41.38 \pm 3.64 ^b	17.29 \pm 1.49 ^a	0.0001
Live Forb	18.31 \pm 2.96 ^a	7.11 \pm 1.73 ^b	7.63 \pm 1.47 ^b	0.004
Dead Forb	0.47 \pm 0.23	0.59 \pm 0.27	0.61 \pm 0.29	0.736
Bare Ground	30.11 \pm 3.17	32.10 \pm 3.08	28.25 \pm 1.95	0.703
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0.02 \pm 0.01	0	0.02 \pm 0.02	0.842

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Cactaceae				
<i>Coryphantha vivipara</i> (Nutt.) Britt. & Rose	0	0.02 ± 0.01	0	
<i>Opuntia macrorhiza</i> Engelm.	0.58 ± 0.33	0.54 ± 0.32	0.29 ± 0.19	0.836
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.01 ± 0.01	0.05 ± 0.05	0.03 ± 0.03	0.913
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.35 ± 0.13	0.02 ± 0.01	0.03 ± 0.03	0.097
<i>Chenopodium pratericola</i> Rydb.	0.23 ± 0.09	0.22 ± 0.17	0.23 ± 0.10	0.375
<i>Kochia scoparia</i> (L.) Schrad.	1.07 ± 0.56	0.24 ± 0.11	0.68 ± 0.44	0.433
<i>Salsola</i> spp. ¹	0.32 ± 0.17	0.14 ± 0.11	0.78 ± 0.66	0.224
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.66 ± 0.29	0.08 ± 0.05	0	0.062
Portulacaceae				
<i>Portulaca oleracea</i> L.	0.27 ± 0.13	0.02 ± 0.01	0.15 ± 0.08	0.122
Malvaceae				
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	1.69 ± 0.48	1.05 ± 0.42	0.86 ± 0.15	0.381

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Brassicaceae				
<i>Descurainia pinnata</i> (Walt.) Britt.	0	0.01 ± 0.01	0	
<i>Erysimum asperum</i> (Nutt.) DC.	0.05 ± 0.04	0.01 ± 0.01	0.02 ± 0.02	0.779
Brassicaceae				
<i>Lepidium densiflorum</i> Schrad.	0	0	0.02 ± 0.02	
Caesalpiniaceae				
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.03 ± 0.03	0	0.02 ± 0.02	0.816
Fabaceae				
<i>Astragalus lotiflorus</i> Hook.	0.01 ± 0.01	0	0	
<i>Astragalus mollisimus</i> Torr.	0.02 ± 0.02	0	0	
<i>Astragalus nuttallianus</i> DC.	0	0	0.05 ± 0.05	
<i>Melilotus</i> spp. ³	0.01 ± 0.01	0.33 ± 0.22	0.02 ± 0.02	0.728
<i>Psoralea tenuifolia</i> Pursh	0.06 ± 0.06	0.18 ± 0.16	0	0.300
<i>Sophora nuttalliana</i> B. L. Turner	0.23 ± 0.11	0.43 ± 0.18	0.83 ± 0.44	0.517
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.03 ± 0.02	0.01 ± 0.01	0.02 ± 0.02	0.779

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Onagraceae				
<i>Oenothera triloba</i> Nutt.	0	0	0.02 \pm 0.02	
Euphorbiaceae				
<i>Croton texensis</i> (Kl.) Muell. Arg.	0	0	0.12 \pm 0.10	
<i>Euphorbia dentata</i> Michx.	0.09 \pm 0.08	0.08 \pm 0.05	0.17 \pm 0.15	0.822
<i>Euphorbia lata</i> Engelm.	0.02 \pm 0.01	0.02 \pm 0.02	0.02 \pm 0.02	0.895
<i>Euphorbia marginata</i> Pursh	0.02 \pm 0.01	0	0.08 \pm 0.08	1.00
<i>Euphorbia stictospora</i> Engelm.	1.53 \pm 0.56	0.32 \pm 0.16	0.15 \pm 0.08	0.194
<i>Euphorbia</i> spp. ⁴	10.86 \pm 2.41 ^a	2.54 \pm 1.16 ^b	3.29 \pm 0.79 ^b	0.006
Zygophyllaceae				
<i>Tribulus terrestris</i> L.	0.09 \pm 0.09	0	0	
Asclepiadaceae				
<i>Asclepias latifolia</i> (Torr.) Raf.	0.06 \pm 0.06	0	0	
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.02 \pm 0.01	0.01 \pm 0.01	0	0.535
Solanaceae				
<i>Solanum elaeagnifolium</i> Cav.	0.06 \pm 0.06	0.02 \pm 0.02	0	0.927

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Solanaceae				
<i>Solanum rostratum</i> Dun.	0.12 \pm 0.05	0.01 \pm 0.01	0.03 \pm 0.02	0.225
Convulvulaceae				
<i>Evolvulus nuttalliana</i> R & S.	0.01 \pm 0.01	0	0	
Verbenaceae				
<i>Verbena bipinnatifida</i> Nutt.	0.02 \pm 0.02	0.08 \pm 0.08	0.05 \pm 0.05	0.913
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.01 \pm 0.01	0	0.02 \pm 0.02	0.726
Pedaliaceae				
<i>Proboscidea louisianica</i> (P. Mill.) Thell. *	0	0	0.02 \pm 0.02	
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.17 \pm 0.12	0.01 \pm 0.01	0.09 \pm 0.04	0.229
<i>Ambrosia psilostachya</i> DC.	0	0.02 \pm 0.01	0	
<i>Cirsium ochrocentrum</i> A. Gray	0.01 \pm 0.01	0.05 \pm 0.05	0	0.927
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.09 \pm 0.03	0.12 \pm 0.07	0.62 \pm 0.60	0.889
<i>Erigeron divergens</i> T. & G.	0	0.01 \pm 0.01	0	

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asteraceae				
<i>Gaillardia pulchella</i> Foug.	0	0.01 \pm 0.01	0	
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.26 \pm 0.26	0	0	
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.01 \pm 0.01	0.01 \pm 0.01	0.08 \pm 0.08	0.863
<i>Helianthus annuus</i> L.	0.07 \pm 0.05	0.32 \pm 0.17	0.36 \pm 0.16	0.356
<i>Helianthus ciliaris</i> DC.	0	0	0.09 \pm 0.09	
<i>Kuhnia eupatorioides</i> L.	0.01 \pm 0.01	0.28 \pm 0.18	0	0.214
<i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb.	0	0.06 \pm 0.05	0	
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0	0.09 \pm 0.06	0	
<i>Ratibida tagetes</i> (James) Barnh.	0.05 \pm 0.05	0.26 \pm 0.26	0	0.927
<i>Senecio riddellii</i> T. & G.	0	0.12 \pm 0.12	0	
<i>Thelesperma</i> spp. ⁵	0	0.05 \pm 0.02	0	
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.09 \pm 0.06	0.16 \pm 0.11	0.24 \pm 0.24	0.948
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.24 \pm 0.24	2.12 \pm 2.12	0.02 \pm 0.02	0.926
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	0.58 \pm 0.57	0.28 \pm 0.17	0.29 \pm 0.27	0.854

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Poaceae				
<i>Aristida adscensionis</i> L.	0	0.46 \pm 0.46	0.08 \pm 0.08	0.816
<i>Aristida purpurea</i> Nutt.	8.53 \pm 1.86 ^a	4.29 \pm 1.62 ^{ab}	1.67 \pm 0.47 ^b	0.034
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.13 \pm 0.12 ^a	16.38 \pm 4.64 ^b	0.09 \pm 0.07 ^a	0.004
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	14.28 \pm 4.60	13.18 \pm 2.69	22.99 \pm 3.08	0.215
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	7.16 \pm 1.53	5.08 \pm 2.98	7.62 \pm 1.74	0.219
<i>Chloris verticillata</i> Nutt.	0.25 \pm 0.22	0.06 \pm 0.06	0.02 \pm 0.02	0.528
<i>Munroa squarrosa</i> (Nutt.) Torr.	0.03 \pm 0.03	0.04 \pm 0.03	0	0.589
<i>Panicum capillare</i> L.	0.33 \pm 0.17	0.23 \pm 0.11	0.09 \pm 0.06	0.681
<i>Panicum virgatum</i> L.	0	0.05 \pm 0.05	0	
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.24 \pm 0.23	0.02 \pm 0.02	0	0.538
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L. Hitc.	0.01 \pm 0.01	0.02 \pm 0.02	0	0.927
<i>Sporobolus asper</i> (Michx.) Kunth	0	0	0.08 \pm 0.08	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.92 \pm 0.65	2.97 \pm 1.45	0.63 \pm 0.37	0.327
<i>Tridens pilosus</i> (Buckl.) Hitc.	0.23 \pm 0.22	0	0	

Table 1. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Agavaceae				
<i>Yucca glauca</i> Nutt.	0	0.12 ± 0.12	0	

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau

² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

³ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.

⁴ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

⁵ *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 2. Mean \pm SE frequency of all species detected within 0.10 m² plots for prairie dog colonies (n = 8), non-colonized random sites (n = 8), and non-colonized shortgrass sites (n = 5) in 1996. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0.01 \pm 0.01	0	0.01 \pm 0.01	0.348
Cactaceae				
<i>Coryphantha vivipara</i> (Nutt.) Britt. & Rose	0	0.01 \pm 0.01	0	
<i>Opuntia macrorhiza</i> Engelm.	0.05 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.02	0.729
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.863
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.05 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.136
<i>Chenopodium pratericola</i> Rydb.	0.08 \pm 0.03	0.04 \pm 0.02	0.08 \pm 0.03	0.285
<i>Kochia scoparia</i> (L.) Schrad.	0.13 \pm 0.05	0.06 \pm 0.02	0.11 \pm 0.07	0.465

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Chenopodiaceae				
<i>Salsola</i> spp. ¹	0.07 ± 0.02	0.04 ± 0.02	0.10 ± 0.08	0.203
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.09 ± 0.04 ^a	0.01 ± 0.01 ^b	0	0.016
Portulacaceae				
<i>Portulaca oleracea</i> L.	0.04 ± 0.02	0.01 ± 0.01	0.03 ± 0.01	0.146
Malvaceae				
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	0.25 ± 0.06	0.19 ± 0.06	0.19 ± 0.03	0.673
Brassicaceae				
<i>Descurainia pinnata</i> (Walt.) Britt.	0	0.01 ± 0.01	0	
<i>Erysimum asperum</i> (Nutt.) DC.	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.779
<i>Lepidium densiflorum</i> Schrad.	0	0	0.01 ± 0.01	
Caesalpiniaceae				
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.01 ± 0.01	0	0.01 ± 0.01	0.494
Fabaceae				
<i>Astragalus lotiflorus</i> Hook.	0.01 ± 0.01	0	0	

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Fabaceae				
<i>Astragalus mollisimus</i> Torr.	0.01 \pm 0.01	0	0	
<i>Astragalus nuttallianus</i> DC.	0	0	0.02 \pm 0.02	
<i>Melilotus</i> spp. ³	0.01 \pm 0.01	0.04 \pm 0.03	0.01 \pm 0.01	0.728
<i>Psoralea tenuifolia</i> Pursh	0.01 \pm 0.01	0.02 \pm 0.02	0	0.242
<i>Sophora nuttalliana</i> B. L. Turner	0.04 \pm 0.02	0.07 \pm 0.02	0.14 \pm 0.08	0.529
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.779
<i>Oenothera triloba</i> Nutt.	0	0	0.01 \pm 0.01	
Euphorbiaceae				
<i>Croton texensis</i> (Kl.) Muell. Arg.	0	0	0.02 \pm 0.02	
<i>Euphorbia dentata</i> Michx.	0.02 \pm 0.02	0.01 \pm 0.01	0.04 \pm 0.03	0.822
<i>Euphorbia lata</i> Engelm.	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.895
<i>Euphorbia marginata</i> Pursh	0.01 \pm 0.01	0	0.01 \pm 0.01	0.348
<i>Euphorbia stictospora</i> Engelm.	0.11 \pm 0.03	0.03 \pm 0.02	0.03 \pm 0.01	0.062
<i>Euphorbia</i> spp. ⁴	0.72 \pm 0.07 ^a	0.23 \pm 0.09 ^b	0.56 \pm 0.09 ^a	0.001

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Zygophyllaceae				
<i>Tribulus terrestris</i> L.	0.01 \pm 0.01	0	0	
Asclepiadaceae				
<i>Asclepias latifolia</i> (Torr.) Raf.	0.01 \pm 0.01	0	0	
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.01 \pm 0.01	0.01 \pm 0.01	0	0.466
Solanaceae				
<i>Solanum elaeagnifolium</i> Cav.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.719
<i>Solanum rostratum</i> Dun.	0.02 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.281
Convulvulaceae				
<i>Evolvulus nuttalliana</i> R & S.	0.01 \pm 0.01	0	0	
Verbenaceae				
<i>Verbena bipinnatifida</i> Nutt.	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.02	0.913
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.01 \pm 0.01	0	0.01 \pm 0.01	0.476

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	
	mean ± SE	mean ± SE	mean ± SE	P-value
Pedaliaceae				
<i>Proboscidea louisianica</i> (P. Mill.) Thell.	0	0	0.01 ± 0.01	
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.02	0.114
<i>Ambrosia psilostachya</i> DC.	0	0.01 ± 0.01	0	
<i>Cirsium ochrocentrum</i> A. Gray	0.01 ± 0.01	0.01 ± 0.01	0	0.719
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.03 ± 0.01	0.02 ± 0.01	0.07 ± 0.06	0.670
<i>Erigeron divergens</i> T. & G.	0	0.01 ± 0.01	0	
<i>Gaillardia pulchella</i> Foug.	0	0.01 ± 0.01	0	
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.04 ± 0.04	0	0	
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.920
<i>Helianthus annuus</i> L.	0.01 ± 0.01	0.02 ± 0.01	0.04 ± 0.02	0.277
<i>Helianthus ciliaris</i> DC.	0	0	0.01 ± 0.01	
<i>Kuhnia eupatorioides</i> L.	0.01 ± 0.01	0.02 ± 0.01	0	0.194
<i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb.	0	0.01 ± 0.01	0	
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0	0.02 ± 0.01	0	

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Asteraceae				
<i>Ratibida tagetes</i> (James) Barnh.	0.01 ± 0.01	0.01 ± 0.01	0	0.718
<i>Senecio riddellii</i> T. & G.	0	0.01 ± 0.01	0	
<i>Thelesperma</i> spp. ⁵	0	0.02 ± 0.01	0	
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.02 ± 0.01	0.03 ± 0.02	0.02 ± 0.02	0.923
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.01 ± 0.01	0.07 ± 0.07	0.01 ± 0.01	0.926
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	0.05 ± 0.04	0.02 ± .01	0.02 ± 0.02	0.872
<i>Aristida adscensionis</i> L.	0	0.02 ± 0.02	0.01 ± 0.01	0.494
<i>Aristida purpurea</i> Nutt.	0.55 ± 0.09 ^a	0.28 ± 0.08 ^b	0.16 ± 0.04 ^b	0.012
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 ± 0.01 ^a	0.46 ± 0.12 ^b	0.01 ± 0.01 ^a	0.004
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.54 ± 0.12 ^a	0.41 ± 0.08 ^a	0.89 ± 0.05 ^b	0.017
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.35 ± 0.06	0.17 ± 0.09	0.43 ± 0.08	0.087
<i>Chloris verticillata</i> Nutt.	0.05 ± 0.04	0.01 ± 0.01	0.01 ± 0.01	0.528
<i>Munroa squarrosa</i> (Nutt.) Torr.	0.01 ± 0.01	0.01 ± 0.01	0	0.488
<i>Panicum capillare</i> L.	0.09 ± 0.04	0.07 ± 0.03	0.03 ± 0.02	0.681

Table 2. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Poaceae				
<i>Panicum virgatum</i> L.	0	0.01 ± 0.01	0	
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.02 ± 0.02	0.01 ± 0.01	0	0.468
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L.	0.01 ± 0.01	0.01 ± 0.01	0	0.718
Hitchc.				
<i>Sporobolus asper</i> (Michx.) Kunth	0	0	0.01 ± 0.01	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.12 ± 0.07	0.24 ± 0.09	0.09 ± 0.04	0.512
<i>Tridens pilosus</i> (Buckl.) Hitchc.	0.03 ± 0.02	0	0	
Agavaceae				
<i>Yucca glauca</i> Nutt.	0	0.01 ± 0.01	0	

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.³ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.⁴ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.⁵ *Thielerma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 3. Mean \pm SE frequency of all species detected within 10.0 m² plots for prairie dog colonies (n = 8), non-colonized random sites (n = 8), and non-colonized shortgrass sites (n = 5) in 1996. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0.07 \pm 0.02	0.07 \pm 0.03	0.02 \pm 0.01	0.289
Cactaceae				
<i>Coryphantha vivipara</i> (Nutt.) Britt. & Rose	0.04 \pm 0.01	0.02 \pm 0.01	0.03 \pm 0.01	0.316
<i>Opuntia macrorhiza</i> Engelm.	0.48 \pm 0.08	0.34 \pm 0.11	0.54 \pm 0.05	0.339
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.19 \pm 0.07	0.05 \pm 0.03	0.15 \pm 0.09	0.291
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.23 \pm 0.08	0.06 \pm 0.05	0.11 \pm 0.05	0.149
<i>Chenopodium pratericola</i> Rydb.	0.44 \pm 0.13	0.22 \pm 0.11	0.60 \pm 0.11	0.119
<i>Kochia scoparia</i> (L.) Schrad.	0.52 \pm 0.11	0.32 \pm 0.12	0.48 \pm 0.12	0.335
<i>Salsola</i> spp. ¹	0.38 \pm 0.10	0.34 \pm 0.14	0.38 \pm 0.14	0.639

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.46 ± 0.12	0.18 ± 0.07	0.23 ± 0.06	0.082
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	0	0	0.01 ± 0.01	
Portulacacaceae				
<i>Portulaca oleracea</i> L.	0.26 ± 0.09	0.07 ± 0.02	0.21 ± 0.04	0.063
Malvaceae				
<i>Hibiscus trionum</i> L.	0	0.01 ± 0.01	0	
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	0.70 ± 0.06	0.67 ± 0.08	0.66 ± 0.08	0.901
Violaceae				
<i>Hybanthus verticillatus</i> (Ort.) Baill.	0	0.01 ± 0.01	0.01 ± 0.01	0.726
Cucurbitaceae				
<i>Cucurbita foetidissima</i> H. B. K.	0.01 ± 0.01	0	0	
Brassicaceae				
<i>Descurainia pinnata</i> (Walt.) Britt.	0.01 ± 0.01	0.02 ± 0.01	0.01 ± 0.01	0.813
<i>Erysimum asperum</i> (Nutt.) DC.	0.08 ± 0.05	0.04 ± 0.01	0.03 ± 0.01	0.671
<i>Lepidium densiflorum</i> Schrad.	0.02 ± 0.01	0.01 ± 0.01	0.08 ± 0.06	0.148

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Caesalpiniaceae				
<i>Caesalpinia jamesii</i> (T. & G.) Fisher	0.01 ± 0.01	0	0	
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.02 ± 0.02	0	0.01 ± 0.01	0.816
Fabaceae				
<i>Astragalus lotiflorus</i> Hook.	0.02 ± 0.01 ^a	0.11 ± 0.04 ^b	0	0.042
<i>Astragalus missouriensis</i> Nutt.	0	0.02 ± 0.02	0	
<i>Astragalus mollissimus</i> Torr.	0.01 ± 0.01	0.01 ± 0.01	0	0.644
<i>Astragalus nuttallianus</i> DC.	0.01 ± 0.01	0.03 ± 0.03	0.03 ± 0.03	0.913
<i>Astragalus pectinatus</i> Dougl. ex G. Don	0.01 ± 0.01	0	0	
<i>Dalea enneandra</i> Nutt.	0.01 ± 0.01	0.05 ± 0.02	0.01 ± 0.01	0.179
<i>Melilotus</i> spp. ³	0.01 ± 0.01	0.16 ± 0.09	0.02 ± 0.02	0.340
<i>Psoralea tenuifolia</i> Pursh	0.06 ± 0.03	0.17 ± 0.09	0.05 ± 0.03	0.373
<i>Sophora nuttalliana</i> B. L. Turner	0.21 ± 0.09	0.29 ± 0.10	0.32 ± 0.18	0.670
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.05 ± 0.02	0.09 ± 0.03	0.02 ± 0.01	0.186
<i>Oenothera triloba</i> Nutt.	0.03 ± 0.01	0.04 ± 0.03	0.04 ± 0.02	0.894

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Euphorbiaceae				
<i>Argythamnia humilis</i> (Engelm. & Gray) Muell. Arg.	0.01 ± 0.01	0	0	
<i>Croton texensis</i> (Kl.) Muell. Arg.	0	0	0.06 ± 0.04	
<i>Euphorbia dentata</i> Michx.	0.10 ± 0.07	0.07 ± 0.03	0.09 ± 0.06	0.735
<i>Euphorbia lata</i> Engelm.	0.06 ± 0.04	0.04 ± 0.04	0.01 ± 0.01	0.587
<i>Euphorbia marginata</i> Pursh	0.14 ± 0.06	0.07 ± 0.05	0.07 ± 0.04	0.591
<i>Euphorbia stictospora</i> Engelm.	0.26 ± 0.06	0.19 ± 0.08	0.19 ± 0.09	0.657
<i>Euphorbia</i> spp. ⁴	0.93 ± 0.03 ^a	0.50 ± 0.12 ^b	0.93 ± 0.05 ^{a,b}	0.025
Linaceae				
<i>Linum rigidum</i> Pursh.	0	0.01 ± 0.01	0	
Zygophyllaceae				
<i>Kallstroemia parviflora</i> Norton	0.01 ± 0.01	0.01 ± 0.01	0	1.00
<i>Tribulus terrestris</i> L.	0.02 ± 0.01	0.02 ± 0.01	0.01 ± 0.01	0.755
Asclepiadaceae				
<i>Asclepias engelmanniana</i> Woods.	0	0.01 ± 0.01	0.01 ± 0.01	0.726
<i>Asclepias latifolia</i> (Torr.) Raf.	0.03 ± 0.02	0.03 ± 0.01	0.01 ± 0.01	0.520

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asclepiadaceae				
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.02 \pm 0.01	0.01 \pm 0.01	0	0.300
Solanaceae				
<i>Physalis hederifolia</i> A. Gray	0	0.01 \pm 0.01	0.01 \pm 0.01	0.726
<i>Quincula lobata</i> (Torr.) Raf.	0.01 \pm 0.01	0	0.01 \pm 0.01	0.816
<i>Solanum elaeagnifolium</i> Cav.	0.04 \pm 0.04	0.06 \pm 0.04	0	0.159
<i>Solanum rostratum</i> Dun.	0.21 \pm 0.07	0.25 \pm 0.08	0.15 \pm 0.08	0.726
Solanaceae ⁵	0.04 \pm 0.02	0	0.02 \pm 0.02	0.471
Convolvulaceae				
<i>Convolvulus arvensis</i> L.	0.01 \pm 0.01	0	0	
<i>Convolvulus equitans</i> Benth.	0	0.01 \pm 0.01	0	
<i>Evolvulus nuttalliana</i> R & S.	0.03 \pm 0.03	0	0.01 \pm 0.01	0.816
<i>Ipomea leptophylla</i> Torr.	0	0.01 \pm 0.01	0	
Boraginaceae				
<i>Cryptantha minima</i> Rydb.	0.01 \pm 0.01	0	0	
<i>Lappula</i> spp. ⁶	0.01 \pm 0.01	0	0	

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Boraginaceae				
<i>Lithospermum incisum</i> Lehm.	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.854
Verbenaceae				
<i>Lippia cuneifolia</i> (Torr.) Steud.	0	0.01 \pm 0.01	0	
<i>Verbena bipinnatifida</i> Nutt.	0.09 \pm 0.04	0.10 \pm 0.08	0.16 \pm 0.09	0.447
<i>Verbena bracteata</i> Lag. & Rodr.	0	0.01 \pm 0.01	0.01 \pm 0.01	0.726
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.01 \pm 0.01	0	0.01 \pm 0.01	0.842
Pedaliaceae				
<i>Proboscidea louisianica</i> (P. Mill.) Thell.	0.06 \pm 0.02	0.04 \pm 0.01	0.03 \pm 0.03	0.337
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.05 \pm 0.03 ^{a,b}	0.01 \pm 0.01 ^a	0.11 \pm 0.06 ^b	0.029
<i>Ambrosia psilostachya</i> DC.	0.02 \pm 0.01	0.04 \pm 0.01	0	0.142
<i>Aster falcatus</i> Lindl.	0	0.02 \pm 0.01	0	
Asteraceae ⁷	0.06 \pm 0.02	0.02 \pm 0.01	0.04 \pm 0.01	0.344

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asteraceae				
<i>Cirsium ochrocentrum</i> A. Gray	0.06 \pm 0.03	0.08 \pm 0.04	0.05 \pm 0.04	0.801
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.22 \pm 0.06	0.17 \pm 0.05	0.24 \pm 0.11	0.779
<i>Erigeron divergens</i> T. & G.	0	0.01 \pm 0.01	0	
<i>Gaillardia pulchella</i> Foug.	0.02 \pm 0.01	0.01 \pm 0.01	0	0.213
<i>Grindelia squarrosa</i> (Pursh) Dun.	0	0.01 \pm 0.01	0.01 \pm 0.01	0.816
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.12 \pm 0.09	0.02 \pm 0.01	0.02 \pm 0.01	0.477
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.05 \pm 0.03	0.14 \pm 0.07	0.03 \pm 0.02	0.426
<i>Helianthus annuus</i> L.	0.33 \pm 0.09	0.42 \pm 0.06	0.61 \pm 0.06	0.085
<i>Helianthus ciliaris</i> DC.	0	0	0.02 \pm 0.02	
<i>Hymenopappus tenuifolius</i> Pursh.	0	0.01 \pm 0.01	0.01 \pm 0.01	0.726
<i>Hymenoxys odorata</i> DC.	0.01 \pm 0.01	0	0.01 \pm 0.01	0.816
<i>Kuhnia eupatorioides</i> L.	0.08 \pm 0.02	0.15 \pm 0.06	0.05 \pm 0.02	0.283
<i>Leucelene ericoides</i> (Torr.) Greene.	0	0.01 \pm 0.01	0	
<i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb.	0	0.01 \pm 0.01	0	
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0.09 \pm 0.05	0.17 \pm 0.06	0.03 \pm 0.01	0.220

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Asteraceae				
<i>Ratibida tagetes</i> (James) Barnh.	0.01 ± 0.01	0.02 ± 0.02	0.01 ± 0.01	0.994
<i>Senecio douglassii</i> DC. Var. <i>longilobus</i> (Benth.) Benson	0.01 ± 0.01	0.01 ± 0.01	0	
<i>Senecio riddellii</i> T. & G.	0.04 ± 0.03	0.03 ± 0.01	0	
<i>Taraxacum officinale</i> Weber	0.01 ± 0.01	0.01 ± 0.01	0	
<i>Thelesperma</i> spp. ⁸	0.02 ± 0.02	0.09 ± 0.04	0.01 ± 0.01	0.118
<i>Trapogon dubius</i> Scop.	0	0.01 ± 0.01	0.01 ± 0.01	0.726
Cyperaceae	0.01 ± 0.01	0	0	
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.04 ± 0.02	0.09 ± 0.07	0.06 ± 0.05	0.727
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.04 ± 0.03	0.10 ± 0.09	0.01 ± 0.01	0.952
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	0.11 ± 0.08	0.14 ± 0.06	0.10 ± 0.04	0.562
<i>Aristida adscensionis</i> L.	0.01 ± 0.01	0.03 ± 0.03	0.02 ± 0.01	0.444
<i>Aristida purpurea</i> Nutt.	0.86 ± 0.05	0.58 ± 0.11	0.70 ± 0.09	0.092
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 ± 0.01 ^a	0.62 ± 0.14 ^b	0.04 ± 0.02 ^{a,b}	0.004
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.68 ± 0.12	0.67 ± 0.09	0.95 ± 0.02	0.155

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Poaceae				
<i>Bromus japonicus</i> Thunb. ex Murr.	0	0.01 \pm 0.01	0	
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.68 \pm 0.07 ^{ab}	0.39 \pm 0.14 ^a	0.88 \pm 0.05 ^b	0.048
<i>Chloris verticillata</i> Nutt.	0.14 \pm 0.09	0.08 \pm 0.04	0.02 \pm 0.01	0.563
<i>Eragrostis cilianensis</i> (All.) E. Mosher	0.01 \pm 0.01	0.01 \pm 0.01	0	0.927
<i>Hilaria jamesii</i> (Torr.) Benth.	0	0	0.01 \pm 0.01	
<i>Muhlenbergia arenicola</i> Buck.	0	0.01 \pm 0.01	0	
<i>Munroa squarrosa</i> (Nutt.) Torr.	0.03 \pm 0.02	0.07 \pm 0.05	0	1.00
<i>Panicum hillmanii</i> Chase	0.01 \pm 0.01	0	0	
<i>Panicum capillare</i> L.	0.42 \pm 0.13	0.34 \pm 0.12	0.34 \pm 0.08	0.851
<i>Panicum virgatum</i> L.	0	0.01 \pm 0.01	0	
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.09 \pm 0.04	0.06 \pm 0.04	0.01 \pm 0.01	0.123
<i>Setaria viridis</i> (L.) Beauv.	0	0.01 \pm 0.01	0	
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L. Hitchc.	0.08 \pm 0.03	0.08 \pm 0.04	0.08 \pm 0.04	0.893
<i>Sporobolus asper</i> (Michx.) Kunth	0	0	0.01 \pm 0.01	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.28 \pm 0.09	0.45 \pm 0.12	0.41 \pm 0.10	0.493

Table 3. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Poaceae				
<i>Tridens pilosus</i> (Buckl.) Hitchc.	0.09 ± 0.06	0.04 ± 0.02	0	0.856
Agavaceae				
<i>Yucca glauca</i> Nutt.	0	0.02 ± 0.01	0.01 ± 0.01	0.471

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau

² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

³ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.

⁴ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

⁵ *Chamaesaracha coniodes* (Moric. ex Dun.) Britt. and *Solanum triflorum* Nutt.

⁶ *Lappula redowskii* (Hornem.) Greene. and *L. texana* (Scheele) Britt.

⁷ *Baccharis wrightii* A. Gray, *Lygodesmia juncea* (Pursh) Hook., and *Stephanomeria tenuifolia* (Torr.) Hall.

⁸ *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 4. Species richness (S), Shannon's diversity index (H'), evenness (E'), the inverse of Simpson's diversity index (1/D), and P-values using data from 0.10 m² and 10.0 m² plots for prairie dog colonies (n = 8), non-colonized random sites (n = 8) and non-colonized shortgrass sites (n = 5) in 1996. P-values are from F-tests and Kruskal-Wallis tests.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
0.10 m² plots				
S	20.25 ± 1.05	18.13 ± 1.83	18.60 ± 2.52	0.636
H'	2.36 ± 0.05	2.20 ± 0.13	2.20 ± 0.17	0.508
E	0.79 ± 0.02	0.77 ± 0.02	0.76 ± 0.02	0.546
1/D	8.06 ± 0.50	7.21 ± 1.04	7.14 ± 1.41	0.746
10.0 m² plots				
S	41.38 ± 2.28	44.63 ± 1.99	41.2 ± 2.08	0.457
H'	3.18 ± 0.05	3.21 ± 0.07	3.12 ± 0.04	0.632
E	0.86 ± 0.01	0.85 ± 0.01	0.84 ± 0.01	0.387
1/D	19.91 ± 0.81	19.68 ± 1.75	18.37 ± 1.06	0.737

Table 5. Mean \pm SE cover of live grass, dead grass, live forbs, dead forbs, percent bare ground, vegetation height and density, and cover of all species for prairie dog colonies (n = 13), non-colonized random sites (n = 8) and non-colonized shortgrass sites (n = 6) in 1997. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Live Grass	51.85 \pm 3.10	51.41 \pm 0.68	60.01 \pm 2.90	0.134
Dead Grass	33.24 \pm 4.04	33.51 \pm 1.75	40.55 \pm 4.96	0.442
Live Forb	10.56 \pm 2.57	10.01 \pm 1.96	6.37 \pm 1.39	0.329
Dead Forb	1.65 \pm 0.51	1.15 \pm 0.52	1.39 \pm 0.57	0.746
Bare Ground	32.70 \pm 2.61	32.38 \pm 1.55	27.06 \pm 4.54	0.218
Vegetation Height (cm)	9.48 \pm 0.80 ^a	33.59 \pm 3.29 ^b	25.22 \pm 5.50 ^{ab}	0.0008
Vegetation Density (cm)	2.49 \pm 0.17 ^a	6.41 \pm 1.32 ^b	5.40 \pm 1.22 ^{ab}	0.002

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0	0.01 ± 0.01	0	
Cactaceae				
<i>Opuntia macrorhiza</i> Engelm.	0.40 ± 0.30	0.29 ± 0.13	0.19 ± 0.12	0.359
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.02 ± 0.02	0	0	
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.04 ± 0.03	0	0	
<i>Kochia scoparia</i> (L.) Schrad.	3.14 ± 2.32	0.05 ± 0.04	0.13 ± 0.09	0.146
<i>Salsola</i> spp. ¹	0.05 ± 0.03	0.01 ± 0.01	0.09 ± 0.06	0.536
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.19 ± 0.19	0.06 ± 0.06	0	0.702
Malvaceae				
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	2.87 ± 0.48 ^a	1.67 ± 0.33 ^{ab}	1.11 ± 0.22 ^b	0.028
Brassicaceae				
<i>Erysimum asperum</i> (Nutt.) DC.	0.04 ± 0.03	0.04 ± 0.03	0	0.485
<i>Lepidium densiflorum</i> Schrad.	0.07 ± 0.04	0	0.14 ± 0.14	0.381

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Caesalpiniaceae				
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.04 \pm 0.04	0	0	
Fabaceae				
<i>Astragalus gracilis</i> Nutt.	0	0.05 \pm 0.04	0.08 \pm 0.08	0.209
<i>Astragalus missouriensis</i> Nutt.	0	0.08 \pm 0.08	0	
<i>Astragalus mollissimus</i> Torr.	0	0.06 \pm 0.06	0.02 \pm 0.02	0.373
<i>Astragalus plattensis</i> Nutt. ex T. & G.	0.09 \pm 0.08	0	0	
<i>Astragalus</i> spp. ³	0.01 \pm 0.01 ^a	0.10 \pm 0.04 ^b	0.03 \pm 0.03 ^{a,b}	0.022
<i>Dalea enneandra</i> Nutt.	0	0.11 \pm 0.07	0	
<i>Melilotus</i> spp. ⁴	0.08 \pm 0.06	3.05 \pm 2.56	0.22 \pm 0.19	0.344
<i>Oxytropis lambertii</i> Pursh	0.01 \pm 0.01	0	0	
<i>Psoralea tenuifolia</i> Pursh	0.05 \pm 0.05 ^a	1.20 \pm 0.64 ^b	0.11 \pm 0.08 ^{a,b}	0.029
<i>Sophora nuttalliana</i> B. L. Turner	0.19 \pm 0.12	0.91 \pm 0.42	0.96 \pm 0.58	0.057
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.15 \pm 0.05	0.15 \pm 0.05	0.08 \pm 0.03	0.452

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Euphorbiaceae				
<i>Euphorbia lata</i> Engelm.	0.14 \pm 0.08	0	0	
<i>Euphorbia marginata</i> Pursh	0.02 \pm 0.02	0	0	
<i>Euphorbia stictospora</i> Engelm.	0.08 \pm 0.05	0	0	
<i>Euphorbia</i> spp. ⁵	0.04 \pm 0.03	0	0.05 \pm 0.03	0.267
Linaceae				
<i>Linum pratense</i> (Norton) Small	0	0	0.02 \pm 0.02	
<i>Linum rigidum</i> Pursh.	0.02 \pm 0.02	0.11 \pm 0.08	0.25 \pm 0.25	0.571
Zygophyllaceae				
<i>Tribulus terrestris</i> L.	0	0.02 \pm 0.02	0	
Asclepiadaceae				
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.02 \pm 0.02	0	0	
Solanaceae				
<i>Physalis hederifolia</i> A. Gray	0.04 \pm 0.04	0	0	
<i>Quincula lobata</i> (Torr.) Raf.	0.02 \pm 0.02	0	0	
<i>Solanum elaeagnifolium</i> Cav.	0	0	0.03 \pm 0.03	

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Solanaceae				
<i>Solanum rostratum</i> Dun.	0.02 \pm 0.02	0	0	
Convulvulaceae				
<i>Convulvulus arvensis</i> L.	0	0.02 \pm 0.02	0	
<i>Convulvulus equitans</i> Benth.	0.02 \pm 0.02	0.04 \pm 0.03	0	0.345
<i>Evolvulus nuttalliana</i> R & S.	0.04 \pm 0.03	0	0	
<i>Ipomea leptophylla</i> Torr.	0.02 \pm 0.02	0	0	
Boraginaceae				
<i>Cryptantha minima</i> Rydb.	0.06 \pm 0.04	0	0	
<i>Lappula</i> spp. ⁶	0.02 \pm 0.02	0	0	
<i>Lithospermum incisum</i> Lehm.	0.12 \pm 0.07	0.02 \pm 0.02	0	0.387
Verbenaceae				
<i>Verbena bipinnatifida</i> Nutt.	0.56 \pm 0.28	0.42 \pm 0.42	0.75 \pm 0.45	0.425
<i>Verbena bracteata</i> Lag. & Rodr.	0.04 \pm 0.04	0.02 \pm 0.02	0	0.702
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.35 \pm 0.15	0.02 \pm 0.02	0.54 \pm 0.34	0.075

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Scrophulariaceae				
<i>Penstemon albidus</i> Nutt.	0	0.02 ± 0.02	0	
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.12 ± 0.07	0.05 ± 0.05	0.16 ± 0.02	0.648
<i>Ambrosia psilostachya</i> DC.	0.02 ± 0.02	0.09 ± 0.06	0	0.108
<i>Aster falcatus</i> Lindl.	0	0.02 ± 0.02	0	
Asteraceae ⁷	0	0.01 ± 0.01	0	
<i>Cirsium ochrocentrum</i> A. Gray	0.02 ± 0.02	0.05 ± 0.03	0.23 ± 0.17	0.244
<i>Conyza canadensis</i> (L.) Cronq.	0.21 ± 0.08	0.17 ± 0.07	0.84 ± 0.44	0.362
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.87 ± 0.39	0.03 ± 0.02	0.43 ± 0.22	0.189
<i>Erigeron divergens</i> T. & G.	0.02 ± 0.02	0.09 ± 0.06	0	0.269
<i>Evax prolifera</i> Nutt. ex DC.	0.02 ± 0.02	0	0	
<i>Gaillardia pulchella</i> Foug.	0.02 ± 0.02	0.02 ± 0.02	0.35 ± 0.35	0.812
<i>Grindelia squarrosa</i> (Pursh) Dun.	0.08 ± 0.08	0.02 ± 0.02	0	0.702
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.32 ± 0.27	0	0	
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.12 ± 0.07	0.03 ± 0.03	0.03 ± 0.03	0.728

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Asteraceae				
<i>Helianthus annuus</i> L.	0.06 ± 0.03	0.01 ± 0.01	0	0.386
<i>Hymenoxys odorata</i> DC.	0.04 ± 0.03	0	0	
<i>Kuhnia eupatorioides</i> L.	0.15 ± 0.07	0.06 ± 0.04	0.09 ± 0.09	0.801
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0.35 ± 0.12	0.62 ± 0.28	0.80 ± 0.24	0.172
<i>Ratibida tagetes</i> (James) Barnh.	0.05 ± 0.03	0.11 ± 0.11	0.04 ± 0.04	0.907
<i>Senecio riddellii</i> T. & G.	0.04 ± 0.04	0	0	
<i>Taraxacum officinale</i> Weber	0	0.02 ± 0.02	0	
<i>Thelesperma</i> spp. ^a	0.25 ± 0.25	0.14 ± 0.07	0	0.127
<i>Trapopogon dubius</i> Scop.	0	0.01 ± 0.01	0	
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.16 ± 0.12	0.78 ± 0.45	0.69 ± 0.44	0.112
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.27 ± 0.23	4.06 ± 4.06	0.75 ± 0.75	0.982
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	3.20 ± 1.95	1.24 ± 0.57	0.64 ± 0.52	0.798
<i>Aristida purpurea</i> Nutt.	15.60 ± 2.74 ^a	4.92 ± 1.30 ^{a,b}	4.12 ± 0.88 ^b	0.006
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.06 ± 0.06 ^a	17.85 ± 5.37 ^b	2.67 ± 1.39 ^{a,b}	0.001

Table 5. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Poaceae				
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	15.07 \pm 4.70 ^a	16.74 \pm 3.02 ^a	40.80 \pm 6.61 ^b	0.005
<i>Bromus japonicus</i> Thunb. ex Murr.	0	0.18 \pm 0.16	0.28 \pm 0.21	0.431
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	17.44 \pm 4.68	5.12 \pm 2.51	12.29 \pm 3.61	0.136
<i>Chloris verticillata</i> Nutt.	0.08 \pm 0.04	0.08 \pm 0.06	0.03 \pm 0.03	0.872
<i>Elymus canadensis</i> L.	0	0	0.08 \pm 0.08	
<i>Hilaria jamesii</i> (Torr.) Benth.	0	0	0.24 \pm 0.24	
<i>Hordeum pusillum</i> Nutt.	0.23 \pm 0.09 ^a	0.23 \pm 0.09 ^a	1.03 \pm 0.26 ^b	0.001
<i>Panicum hillmanii</i> Chase	0	0	0.03 \pm 0.03	
<i>Panicum capillare</i> L.	0	0.02 \pm 0.02	0	
<i>Panicum virgatum</i> L.	0	0	0.03 \pm 0.03	
<i>Schedonardus paniculatus</i> (Nutt.) Trel.	2.44 \pm 0.46 ^a	0.87 \pm 0.49 ^b	0.46 \pm 0.22 ^b	0.013
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L. Hitchc.	0.09 \pm 0.07	0.05 \pm 0.03	0.07 \pm 0.05	0.765
<i>Sporobolus asper</i> (Michx.) Kunth	0	0.17 \pm 0.17	0	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.24 \pm 0.13 ^a	1.97 \pm 0.66 ^b	0.75 \pm 0.29 ^{a,b}	0.033
<i>Tridens pilosus</i> (Buckl.) Hitchc.	0.15 \pm 0.09	0.11 \pm 0.07	0	0.435

Table 5. Continued

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau

² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

³ *Astragalus lotiflorus* Hook. and *A. nuttallianus* DC.

⁴ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.

⁵ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

⁶ *Lappula redowskii* (Hornem.) Greene. and *L. texana* (Scheele) Britt.

⁷ *Baccharis wrightii* A. Gray, *Lygodesmia juncea* (Pursh) Hook., and *Stephanomeria tenuifolia* (Torr.) Hall.

⁸ *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 6. Mean \pm SE frequency of all species detected within 0.10 m² plots for prairie dog colonies (n = 13), non-colonized random sites (n = 8), and non-colonized shortgrass sites (n = 6) in 1997. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0	0.01 \pm 0.01	0	
Cactaceae				
<i>Opuntia macrorhiza</i> Engelm.	0.03 \pm 0.02	0.03 \pm 0.01	0.02 \pm 0.01	0.329
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.01 \pm 0.01	0	0	
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.01 \pm 0.01	0	0	
<i>Kochia scoparia</i> (L.) Schrad.	0.09 \pm 0.04	0.01 \pm 0.01	0.02 \pm 0.01	0.081
<i>Salsola</i> spp. ¹	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.645
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.01 \pm 0.01	0.01 \pm 0.01	0	0.702

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Malvaceae				
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	0.35 ± 0.05 ^a	0.24 ± 0.04 ^a	0.14 ± 0.03 ^b	0.016
Brassicaceae				
<i>Erysimum asperum</i> (Nutt.) DC.	0.01 ± 0.01	0.01 ± 0.01	0	0.485
<i>Lepidium densiflorum</i> Schrad.	0.01 ± 0.01	0	0.02 ± 0.02	0.380
Caesalpiniaceae				
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.01 ± 0.01	0	0	
Fabaceae				
<i>Astragalus gracilis</i> Nutt.	0	0.01 ± 0.01	0.01 ± 0.01	0.204
<i>Astragalus missouriensis</i> Nutt.	0	0.01 ± 0.01	0	
<i>Astragalus mollisimus</i> Torr.	0	0.01 ± 0.01	0.01 ± 0.01	0.365
<i>Astragalus plattensis</i> Nutt. ex T. & G.	0.01 ± 0.01	0	0	
<i>Astragalus</i> spp. ³	0.01 ± 0.01 ^a	0.02 ± 0.01 ^b	0.01 ± 0.01 ^{a,b}	0.027
<i>Dalea enneandra</i> Nutt.	0	0.01 ± 0.01	0	
<i>Melilotus</i> spp. ⁴	0.01 ± 0.01	0.10 ± 0.07	0.02 ± 0.02	0.412
<i>Oxytropis lambertii</i> Pursh	0.01 ± 0.01	0	0	

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Fabaceae				
<i>Psoralea tenuifolia</i> Pursh	0.01 ± 0.01 ^a	0.09 ± 0.05 ^b	0.01 ± 0.01 ^{a,b}	0.024
<i>Sophora nuttalliana</i> B. L. Turner	0.02 ± 0.01	0.09 ± 0.04	0.09 ± 0.05	0.058
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.03 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	0.503
Euphorbiaceae				
<i>Euphorbia lata</i> Engelm.	0.01 ± 0.01	0	0	
<i>Euphorbia marginata</i> Pursh	0.01 ± 0.01	0	0	
<i>Euphorbia stictospora</i> Engelm.	0.01 ± 0.01	0	0	
<i>Euphorbia</i> spp. ⁵	0.01 ± 0.01	0	0.01 ± 0.01	0.267
Linaceae				
<i>Linum pratense</i> (Norton) Small	0	0	0.01 ± 0.01	
<i>Linum rigidum</i> Pursh.	0.01 ± 0.01	0.02 ± 0.01	0.03 ± 0.03	0.571
Zygophyllaceae				
<i>Tribulus terrestris</i> L.	0	0.01 ± 0.01	0	

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asclepiadaceae				
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.01 \pm 0.01	0	0	
Solanaceae				
<i>Physalis hederifolia</i> A. Gray	0.01 \pm 0.01	0	0	
<i>Quincula lobata</i> (Torr.) Raf.	0.01 \pm 0.01	0	0	
<i>Solanum elaeagnifolium</i> Cav.	0	0	0.01 \pm 0.01	
<i>Solanum rostratum</i> Dun.	0.01 \pm 0.01	0	0	
Convulvulaceae				
<i>Convulvulus arvensis</i> L.	0	0.01 \pm 0.01	0	
<i>Convulvulus equitans</i> Benth.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.345
<i>Evolvulus nuttalliana</i> R & S.	0.01 \pm 0.01	0	0	
<i>Ipomea leptophylla</i> Torr.	0.01 \pm 0.01	0	0	
Boraginaceae				
<i>Cryptantha minima</i> Rydb.	0.01 \pm 0.01	0	0	
<i>Lappula</i> spp. ⁶	0.01 \pm 0.01	0	0	
<i>Lithospermum incisum</i> Lehm.	0.02 \pm 0.01	0.01 \pm 0.01	0	0.387

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Verbenaceae				
<i>Verbena bipinnatifida</i> Nutt.	0.04 \pm 0.02	0.03 \pm 0.03	0.06 \pm 0.04	0.344
<i>Verbena bracteata</i> Lag. & Rodr.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.702
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.06 \pm 0.02	0.01 \pm 0.01	0.09 \pm 0.06	0.070
Scrophulariaceae				
<i>Penstemon albidus</i> Nutt.	0	0.01 \pm 0.01	0	
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.01	0.561
<i>Ambrosia psilostachya</i> DC.	0.01 \pm 0.01	0.02 \pm 0.01	0	0.108
<i>Aster falcatus</i> Lindl.	0	0.01 \pm 0.01	0	
Asteraceae ⁷	0	0.01 \pm 0.01	0	
<i>Cirsium ochrocentrum</i> A. Gray	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.292
<i>Conyza canadensis</i> (L.) Cronq.	0.04 \pm 0.01	0.03 \pm 0.01	0.12 \pm 0.06	0.357
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.11 \pm 0.05	0.01 \pm 0.01	0.06 \pm 0.04	0.201
<i>Erigeron divergens</i> T. & G.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.325

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Asteraceae				
<i>Evax prolifera</i> Nutt. ex DC.	0.01 ± 0.01	0	0	
<i>Gaillardia pulchella</i> Foug.	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.03	0.812
<i>Grindelia squarrosa</i> (Pursh) Dun.	0.01 ± 0.01	0.01 ± 0.01	0	0.702
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.02 ± 0.02	0	0	
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.722
<i>Helianthus annuus</i> L.	0.01 ± 0.01	0.01 ± 0.01	0	0.386
<i>Hymenoxys odorata</i> DC.	0.01 ± 0.01	0	0	
<i>Kuhnia eupatorioides</i> L.	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.768
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0.06 ± 0.02	0.07 ± 0.02	0.12 ± 0.04	0.250
<i>Ratibida tagetes</i> (James) Barnh.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.881
<i>Senecio riddellii</i> T. & G.	0.01 ± 0.01	0	0	
<i>Taraxacum officinale</i> Weber	0	0.01 ± 0.01	0	
<i>Thelesperma</i> spp. ⁸	0.04 ± 0.04	0.03 ± 0.01	0	0.127
<i>Trapotogon dubius</i> Scop.	0	0.01 ± 0.01	0	

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.02 ± 0.01	0.09 ± 0.05	0.03 ± 0.03	0.095
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.01 ± 0.01	0.09 ± 0.09	0.02 ± 0.02	0.982
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	0.08 ± 0.04	0.05 ± 0.02	0.03 ± 0.02	0.679
<i>Aristida purpurea</i> Nutt.	0.62 ± 0.07 ^a	0.24 ± 0.06 ^b	0.25 ± 0.04 ^b	0.004
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 ± 0.01 ^a	0.43 ± 0.12 ^b	0.10 ± 0.06 ^{a,b}	0.001
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.38 ± 0.09 ^a	0.42 ± 0.08 ^a	0.81 ± 0.07 ^b	0.012
<i>Bromus japonicus</i> Thunb. ex Murr.	0	0.03 ± 0.02	0.05 ± 0.04	0.430
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.44 ± 0.09	0.16 ± 0.08	0.37 ± 0.08	0.092
<i>Chloris verticillata</i> Nutt.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.889
<i>Elymus canadensis</i> L.	0	0	0.01 ± 0.01	
<i>Hilaria jamesii</i> (Torr.) Benth.	0	0	0.01 ± 0.01	
<i>Hordeum pusillum</i> Nutt.	0.05 ± 0.02 ^a	0.03 ± 0.01 ^a	0.16 ± 0.04 ^b	0.002
<i>Panicum hillmanii</i> Chase	0	0	0.01 ± 0.01	
<i>Panicum cappillare</i> L.	0	0.01 ± 0.01	0	
<i>Panicum virgatum</i> L.	0	0	0.01 ± 0.01	

Table 6. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Poaceae				
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.22 ± 0.04 ^a	0.08 ± 0.04 ^b	0.06 ± 0.03 ^b	0.012
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.842
Hitchc.				
<i>Sporobolus asper</i> (Michx.) Kunth	0	0.01 ± 0.01	0	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.03 ± 0.01 ^a	0.16 ± 0.05 ^b	0.08 ± 0.02 ^{a,b}	0.011
<i>Tridens pilosus</i> (Buckl.) Hitchc.	0.02 ± 0.01	0.01 ± 0.01	0	0.429

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau

² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

³ *Astragalus lotiflorus* Hook. and *A. nuttallianus* DC.

⁴ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.

⁵ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

⁶ *Lappula redowskii* (Hornem.) Greene. and *L. texana* (Scheele) Britt.

⁷ *Baccharis wrightii* A. Gray, *Lygodesmia juncea* (Pursh) Hook., and *Stephanomeria tenuifolia* (Torr.) Hall.

⁸ *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 7. Mean \pm SE frequency of all species detected within 10.0 m² plots for prairie dog colonies (n = 13), non-colonized random sites (n = 8), and non-colonized shortgrass sites (n = 6) in 1997. P-values are from F-tests and Kruskal-Wallis tests between treatments in which the mean \pm SE > 0. Different superscripts indicate significant differences from pair-wise comparisons. Significant P-values from pair-wise comparisons involving three treatments are provided in the text.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Ranunculaceae				
<i>Delphinium virescens</i> Nutt.	0	0.01 \pm 0.01	0	
Nyctaginaceae				
<i>Mirabilis linearis</i> (Pursh) Heimerl	0.05 \pm 0.01	0.07 \pm 0.02	0.01 \pm 0.01	0.090
Cactaceae				
<i>Coryphantha vivipara</i> (Nutt.) Britt. & Rose	0.03 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.01	0.827
<i>Opuntia macrorhiza</i> Engelm.	0.27 \pm 0.07	0.31 \pm 0.09	0.44 \pm 0.11	0.475
Chenopodiaceae				
<i>Chenopodium berlandieri</i> Moq.	0.02 \pm 0.01	0	0.01 \pm 0.01	0.945
<i>Chenopodium incanum</i> (S. Wats.) Heller.	0.04 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.292
<i>Chenopodium pratericola</i> Rydb.	0.02 \pm 0.01	0	0.01 \pm 0.01	0.623

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Chenopodiaceae				
<i>Kochia scoparia</i> (L.) Schrad.	0.23 ± 0.05 ^a	0.03 ± 0.01 ^b	0.09 ± 0.04 ^{a,b}	0.004
<i>Salsola</i> spp. ¹	0.11 ± 0.03 ^b	0.01 ± 0.01 ^a	0.02 ± 0.01 ^a	0.024
Amaranthaceae				
<i>Amaranthus</i> spp. ²	0.03 ± 0.01	0.01 ± 0.01	0	0.084
Portulacaceae				
<i>Portulaca oleracea</i> L.	0.01 ± 0.01	0	0	
Polygonaceae				
<i>Eriogonum annuum</i> (Nutt.)	0	0	0.01 ± 0.01	
Malvaceae				
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	0.72 ± 0.05	0.71 ± 0.06	0.53 ± 0.11	0.144
Violaceae				
<i>Hybanthus verticillatus</i> (Ort.) Baill.	0	0	0.02 ± 0.02	
Cucurbitaceae				
<i>Cucurbita foetidissima</i> H. B. K.	0.01 ± 0.01	0	0	

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Brassicaceae				
<i>Descurainia</i> spp. ³	0.01 \pm 0.01	0	0	
<i>Erysimum asperum</i> (Nutt.) DC.	0.09 \pm 0.03	0.09 \pm 0.03	0.07 \pm 0.04	0.806
<i>Lepidium densiflorum</i> Schrad.	0.09 \pm 0.03	0.04 \pm 0.02	0.15 \pm 0.08	0.445
Caesalpinaceae				
<i>Caesalpinia jamesii</i> (T. & G.) Fisher	0	0.01 \pm 0.01	0.01 \pm 0.01	0.751
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	0.01 \pm 0.01	0	0	
Fabaceae				
<i>Astragalus gracilis</i> Nutt.	0.01 \pm 0.01	0.05 \pm 0.03	0.03 \pm 0.02	0.177
<i>Astragalus missouriensis</i> Nutt.	0	0.06 \pm 0.06	0	
<i>Astragalus mollissimus</i> Torr.	0.02 \pm 0.01	0.05 \pm 0.05	0.02 \pm 0.01	0.689
<i>Astragalus plattensis</i> Nutt. ex T. & G.	0.06 \pm 0.03	0.15 \pm 0.05	0.11 \pm 0.03	0.063
<i>Astragalus</i> spp. ⁴	0.07 \pm 0.02	0.16 \pm 0.04	0.05 \pm 0.03	0.079
<i>Dalea enneandra</i> Nutt.	0	0.06 \pm 0.03	0.04 \pm 0.03	0.474
<i>Melilotus</i> spp. ⁵	0.05 \pm 0.04	0.18 \pm 0.10	0.09 \pm 0.05	0.181
<i>Oxytropis lambertii</i> Pursh	0.01 \pm 0.01	0	0	

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Fabaceae				
<i>Psoralea tenuifolia</i> Pursh	0.12 ± 0.04 ^a	0.44 ± 0.11 ^b	0.18 ± 0.08 ^a	0.014
<i>Sophora nuttalliana</i> B. L. Turner	0.09 ± 0.03	0.25 ± 0.09	0.22 ± 0.12	0.213
Onagraceae				
<i>Gaura coccinea</i> Pursh	0.11 ± 0.03 ^a	0.26 ± 0.05 ^b	0.07 ± 0.02 ^a	0.005
<i>Oenothera triloba</i> Nutt.	0.03 ± 0.02 ^a	0.02 ± 0.01 ^{a,b}	0.06 ± 0.01 ^b	0.015
Euphorbiaceae				
<i>Argythamnia humilis</i> (Engelm. & Gray) Muell. Arg.	0	0	0.01 ± 0.01	
<i>Croton texensis</i> (Kl.) Muell. Arg.	0	0.01 ± 0.01	0	
<i>Euphorbia lata</i> Engelm.	0.05 ± 0.03	0.02 ± 0.02	0.01 ± 0.01	0.728
<i>Euphorbia marginata</i> Pursh	0.05 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.079
<i>Euphorbia stictospora</i> Engelm.	0.09 ± 0.03 ^a	0.01 ± 0.01 ^b	0.03 ± 0.02 ^{a,b}	0.006
<i>Euphorbia</i> spp. ⁶	0.05 ± 0.01	0.01 ± 0.01	0.03 ± 0.02	0.103
Linaceae				
<i>Linum pratense</i> (Norton) Small	0	0.01 ± 0.01	0.03 ± 0.03	0.751
<i>Linum rigidum</i> Pursh.	0.04 ± 0.02	0.09 ± 0.07	0.07 ± 0.07	0.989

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Zygophyllaceae				
<i>Tribulus terrestris</i> L.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.382
Asclepiadaceae				
<i>Asclepias engelmanniana</i> Woods.	0	0	0.01 ± 0.01	
<i>Asclepias latifolia</i> (Torr.) Raf.	0.01 ± 0.01 ^a	0.03 ± 0.01 ^b	0.01 ± 0.01 ^{a,b}	0.021
<i>Asclepias pumila</i> (A. Gray) Vail	0.01 ± 0.01	0	0	
<i>Asclepias subverticillata</i> (A. Gray) Vail	0.02 ± 0.01	0	0	
Solanaceae				
<i>Physalis hederifolia</i> A. Gray	0.02 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.938
<i>Quincula lobata</i> (Torr.) Raf.	0.04 ± 0.02	0.01 ± 0.01	0.01 ± 0.01	0.232
<i>Solanum elaeagnifolium</i> Cav.	0.01 ± 0.01	0.03 ± 0.03	0.01 ± 0.01	0.862
<i>Solanum rostratum</i> Dun.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.514
Solanaceae ⁷	0.01 ± 0.01	0.01 ± 0.01	0	0.722
Convulvulaceae				
<i>Convulvulus arvensis</i> L.	0	0.01 ± 0.01	0	
<i>Convulvulus equitans</i> Benth.	0.01 ± 0.01 ^a	0.04 ± 0.01 ^b	0.01 ± 0.01 ^a	0.001

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Convulvulaceae				
<i>Evolvulus nuttalliana</i> R & S.	0.05 \pm 0.02	0	0	
<i>Ipomea leptophylla</i> Torr.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.341
Boraginaceae				
<i>Cryptantha minima</i> Rydb.	0.14 \pm 0.04	0	0	
<i>Lappula</i> spp. ⁸	0.02 \pm 0.02	0	0	
<i>Lithospermum incisum</i> Lehm.	0.07 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.050
Verbenaceae				
<i>Verbena bipinnatifida</i> Nutt.	0.16 \pm 0.06	0.10 \pm 0.09	0.22 \pm 0.13	0.277
<i>Verbena bracteata</i> Lag. & Rodr.	0.06 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.02	0.206
<i>Verbena stricta</i> Vent.	0	0	0.03 \pm 0.03	
Plantaginaceae				
<i>Plantago patagonica</i> Jacq.	0.19 \pm 0.05	0.03 \pm 0.01	0.21 \pm 0.11	0.051
Scrophulariaceae				
<i>Penstemon albidus</i> Nutt.	0	0.01 \pm 0.01	0	

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asteraceae				
<i>Ambrosia confertifolia</i> DC.	0.02 \pm 0.01	0.03 \pm 0.02	0.03 \pm 0.02	0.646
<i>Ambrosia grayii</i> (A. Nels.) Shinnery	0	0.01 \pm 0.01	0	
<i>Ambrosia psilostachya</i> DC.	0.03 \pm 0.02	0.04 \pm 0.01	0.01 \pm 0.01	0.105
<i>Artemisia filifolia</i> Torr.	0	0.01 \pm 0.01	0	
<i>Aster falcatus</i> Lindl.	0	0.07 \pm 0.05	0	
Asteraceae ⁹	0.07 \pm 0.03	0.04 \pm 0.01	0.02 \pm 0.01	0.611
<i>Chrysopsis villosa</i> (Pursh) Nutt.	0	0	0.01 \pm 0.01	
<i>Cirsium ochrocentrum</i> A. Gray	0.18 \pm 0.06	0.11 \pm 0.04	0.17 \pm 0.09	0.987
<i>Conyza canadensis</i> (L.) Cronq.	0.29 \pm 0.07	0.19 \pm 0.05	0.49 \pm 0.13	0.083
<i>Dyssodia papposa</i> (Vent.) Hitchc.	0.25 \pm 0.07	0.05 \pm 0.02	0.19 \pm 0.11	0.192
<i>Engelmannia pinnatifida</i> A. Gray ex Nutt.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.341
<i>Erigeron bellidiastrum</i> Nutt.	0.02 \pm 0.01	0.03 \pm 0.01	0.02 \pm 0.01	0.688
<i>Erigeron divergens</i> T. & G.	0.01 \pm 0.01	0.03 \pm 0.01	0	0.074
<i>Evax prolifera</i> Nutt. ex DC.	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.954
<i>Gaillardia pulchella</i> Foug.	0.16 \pm 0.05	0.07 \pm 0.05	0.16 \pm 0.12	0.378

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean \pm SE	mean \pm SE	mean \pm SE	
Asteraceae				
<i>Grindelia squarrosa</i> (Pursh) Dun.	0.02 \pm 0.01	0.02 \pm 0.02	0.01 \pm 0.01	0.352
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	0.12 \pm 0.06	0.02 \pm 0.01	0.04 \pm 0.01	0.247
<i>Haplopappus spinulosus</i> (Pursh) DC.	0.05 \pm 0.02	0.13 \pm 0.06	0.05 \pm 0.01	0.236
<i>Helianthus annuus</i> L.	0.14 \pm 0.04	0.09 \pm 0.03	0.13 \pm 0.05	0.656
<i>Hymenopappus tenuifolius</i> Pursh.	0.01 \pm 0.01	0.02 \pm 0.01	0.01 \pm 0.01	0.506
<i>Hymenoxys odorata</i> DC.	0.07 \pm 0.05	0	0.03 \pm 0.02	0.235
<i>Kuhnia eupatorioides</i> L.	0.09 \pm 0.03	0.15 \pm 0.04	0.09 \pm 0.04	0.581
<i>Lactuca serriola</i> L.	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.01	0.114
<i>Leucelene ericoides</i> (Torr.) Greene.	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.01	0.357
<i>Liatris punctata</i> Hook.	0.01 \pm 0.01	0.01 \pm 0.01	0	0.776
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	0.47 \pm 0.08	0.39 \pm 0.07	0.61 \pm 0.11	0.366
<i>Ratibida tagetes</i> (James) Barnh.	0.03 \pm 0.01	0.04 \pm 0.02	0.01 \pm 0.01	0.769
<i>Senecio douglassii</i> DC. Var. <i>longilobus</i> (Benth.) Benson	0.01 \pm 0.01	0.01 \pm 0.01	0	0.113
<i>Senecio riddellii</i> T. & G.	0.02 \pm 0.02	0.02 \pm 0.01	0.01 \pm 0.01	0.236
<i>Taraxacum officinale</i> Weber	0	0.01 \pm 0.01	0	

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Asteraceae				
<i>Thelesperma</i> spp. ¹⁰	0.07 ± 0.07 ^a	0.19 ± 0.09 ^b	0.04 ± 0.02 ^{a,b}	0.003
<i>Tratopogon dubius</i> Scop.	0.01 ± 0.01 ^a	0.07 ± 0.03 ^b	0.10 ± 0.04 ^b	0.001
Poaceae				
<i>Agropyron smithii</i> Rydb.	0.04 ± 0.02	0.16 ± 0.08	0.10 ± 0.06	0.214
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	0.02 ± 0.02	0.11 ± 0.11	0.03 ± 0.02	0.577
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	0.16 ± 0.08	0.20 ± 0.07	0.17 ± 0.07	0.303
<i>Aristida adscensionis</i> L.	0	0.01 ± 0.01	0	
<i>Aristida purpurea</i> Nutt.	0.87 ± 0.04 ^a	0.56 ± 0.09 ^b	0.72 ± 0.07 ^{a,b}	0.012
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.04 ± 0.03 ^a	0.58 ± 0.13 ^b	0.18 ± 0.10 ^{a,b}	0.0006
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.52 ± 0.11	0.62 ± 0.09	0.92 ± 0.04	0.054
<i>Bromus japonicus</i> Thunb. ex Murr.	0	0.16 ± 0.06	0.18 ± 0.14	0.437
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.65 ± 0.08 ^a	0.32 ± 0.12 ^b	0.74 ± 0.07 ^a	0.020
<i>Cenchrus longispinus</i> (Hack.) Fern.	0	0	0.01 ± 0.01	
<i>Chloris verticillata</i> Nutt.	0.07 ± 0.03	0.06 ± 0.02	0.05 ± 0.02	0.743
<i>Elymus canadensis</i> L.	0	0	0.01 ± 0.01	

Table 7. Continued

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
Poaceae				
<i>Hilaria jamesii</i> (Torr.) Benth.	0	0	0.02 ± 0.01	
<i>Hordeum pusillum</i> Nutt.	0.14 ± 0.04 ^{ab}	0.07 ± 0.03 ^a	0.45 ± 0.11 ^b	0.019
<i>Munroa squarrosa</i> (Nutt.) Torr.	0.01 ± 0.01	0.01 ± 0.01	0	0.776
<i>Panicum hillmanii</i> Chase	0	0.01 ± 0.01	0.02 ± 0.01	0.369
<i>Panicum cappillare</i> L.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.441
<i>Panicum virgatum</i> L.	0	0.01 ± 0.01	0.01 ± 0.01	0.916
<i>Schedonardus paniculatus</i> (Nutt.) Trel.	0.66 ± 0.06 ^a	0.22 ± 0.06 ^b	0.26 ± 0.06 ^b	0.0001
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L. Hitchc.	0.16 ± 0.05	0.23 ± 0.04	0.18 ± 0.06	0.194
<i>Sporobolus asper</i> (Michx.) Kunth	0	0.01 ± 0.01	0	
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.10 ± 0.04 ^a	0.38 ± 0.09 ^b	0.37 ± 0.11 ^b	0.010
<i>Tridens pilosus</i> (Buckl.) Hitchc.	0.08 ± 0.04	0.04 ± 0.02	0	0.908
Agavaceae				
<i>Yucca glauca</i> Nutt.	0.01 ± 0.01	0.02 ± 0.01	0	0.309

¹ *Salsola collina* Pall. and *S. iberica* Senn. & Pau² *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

Table 7. Continued

- ³ *Descurainia pinnata* (Walt.) Britt. and *D. sophia* (L.) Webb ex Prantl.
- ⁴ *Astragalus lotiflorus* Hook. and *Astragalus nuttallianus* DC.
- ⁵ *Melilotus alba* Medic. and *M. officinalis* (L.) Pall.
- ⁶ *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.
- ⁷ *Chamaesaracha coniodes* (Moric. ex Dun.) Britt. and *Solanum triflorum* Nutt.
- ⁸ *Lappula redowskii* (Hornem.) Greene. and *L. texana* (Scheele) Britt.
- ⁹ *Baccharis wrightii* A. Gray, *Lygodesmia juncea* (Pursh) Hook., and *Stephanomeria tenuifolia* (Torr.) Hall.
- ¹⁰ *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

Table 8. Species richness (S), Shannon's diversity index (H'), evenness (E'), the inverse of Simpson's diversity index (1/D), and P-values using data from 0.10 m² and 10.0 m² plots for prairie dog colonies (n = 13), non-colonized random sites (n = 8), and non-colonized shortgrass sites (n = 6) in 1997. P-values are from F-tests and Kruskal-Wallis tests. See text for details on the calculation of diversity indices using 1997 data.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites	P-value
	mean ± SE	mean ± SE	mean ± SE	
0.10 m ² plots				
S	11.31 ± 0.89	11.00 ± 0.77	11.25 ± 1.06	0.969
H'	2.05 ± 0.09	2.07 ± 0.09	2.09 ± 0.11	0.953
E	0.86 ± 0.01	0.88 ± 0.01	0.88 ± 0.01	0.557
1/D	8.11 ± 0.87	8.74 ± 0.87	8.88 ± 1.69	0.851
10.0 m ² plots				
S	29.21 ± 1.32	29.94 ± 1.53	28.06 ± 1.37	0.731
H'	3.05 ± 0.06	3.09 ± 0.06	3.01 ± 0.06	0.722
E	0.91 ± 0.01	0.91 ± 0.01	0.91 ± 0.01	0.583
1/D	21.15 ± 1.34	22.37 ± 1.44	20.16 ± 1.53	0.644

Table 9. Number of perennial grasses, annual grasses, perennial forbs, and annual forbs on prairie dog colonies and non-colonized random sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest. Data is from the 0.10 m² and 10.0 m² plots for both 1996 and 1997.

	Number of Species or Taxonomic Groups			
	Perennial Grasses	Annual Grasses	Perennial Forbs	Annual Forbs
<u>Significantly Different</u>				
Prairie Dog Colonies	3	0	0	4
Non-colonized Random Sites	2	0	7	0
<u>Differences Approached Significance</u>				
Prairie Dog Colonies	0	0	1	2
Non-colonized Random Sites	1	0	2	0
<u>Species of Interest</u>				
Prairie Dog Colonies	0	0	1	1
Non-colonized Random Sites	0	1	1	0
<u>Total</u>				
Prairie Dog Colonies	3	0	2	7
Non-colonized Random Sites	3	1	10	0

Table 10. Number of perennial grasses, annual grasses, perennial forbs, and annual forbs on prairie dog colonies and non-colonized shortgrass sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest. Data is from the 0.10 m² and 10.0 m² plots for both 1996 and 1997.

	Number of Species or Taxonomic Groups			
	Perennial Grasses	Annual Grasses	Perennial Forbs	Annual Forbs
<u>Significantly Different</u>				
Prairie Dog Colonies	2	0	1	0
Non-colonized Shortgrass Sites	2	1	0	1
<u>Differences Approached Significance</u>				
Prairie Dog Colonies	0	0	1	2
Non-colonized Shortgrass Sites	0	0	0	0
<u>Species of Interest</u>				
Prairie Dog Colonies	1	0	1	2
Non-colonized Shortgrass Sites	0	0	0	0
<u>Total</u>				
Prairie Dog Colonies	3	0	3	4
Non-colonized Shortgrass Sites	2	1	0	1

Table 11. Number of perennial grasses, annual grasses, perennial forbs, and annual forbs on non-colonized random sites and non-colonized shortgrass sites where higher frequencies of occurrence are statistically significant or approach statistical significance, and species of interest. Data is from the 0.10 m² and 10.0 m² plots for both 1996 and 1997.

	Number of Species or Taxonomic Groups			
	Perennial Grasses	Annual Grasses	Perennial Forbs	Annual Forbs
<u>Significantly Different</u>				
Non-colonized Random Sites	1	0	3	0
Non-colonized Shortgrass Sites	2	1	1	1
<u>Differences Approached Significance</u>				
Non-colonized Random Sites	0	0	0	0
Non-colonized Shortgrass Sites	0	0	1	2
<u>Species of Interest</u>				
Non-colonized Random Sites	1	0	0	0
Non-colonized Shortgrass Sites	0	0	0	0
<u>Total</u>				
Non-colonized Random Sites	2	0	3	0
Non-colonized Shortgrass Sites	2	1	2	3

CHAPTER 3

BREEDING BIRD COMMUNITIES OF BLACK-TAILED PRAIRIE DOG COLONIES AND NON-COLONIZED AREAS IN SOUTHWEST KANSAS AND SOUTHEAST COLORADO

ABSTRACT

This research sought to determine if there were differences in the bird communities on black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies and non-colonized areas in southwest Kansas and southeast Colorado. Species richness and relative abundances were quantified in 1996 during a period characterized by drought conditions, and in 1997 during a period characterized by above average precipitation amounts. Bird communities in 1996 were species poor relative to 1997, and prairie dog colonies were not characterized by higher species richness than non-colonized areas during either year. Burrowing owls appear highly dependent on prairie dog colonies in the area of this study but there were several species for which prairie dog colonies were sub-optimal habitat. Horned lark habitat preference alternated between prairie dog colonies and non-colonized sites, probably in response to the influence of climatic variation on vegetation conditions. The results of this study and an examination of results from other studies indicate that regional differences in climate and characteristic vegetation likely contribute to regional differences in the ability of prairie dogs to influence bird populations. These results also suggest that grassland birds utilize various

coping strategies that enable them to succeed in grassland environments which are characterized by dynamic habitat conditions.

INTRODUCTION

Prairie dogs (*Cynomys* spp.), through their burrowing activities and herbivory, have the ability to create localized communities of plants and animals that differ considerably from surrounding grassland landscapes (Whicker and Detling 1988). Several studies have generated lists of vertebrates and invertebrates that are associated with prairie dog colonies (Wilcomb 1954, Koford 1958, Campbell and Clark 1981, Clark et al. 1982, Reading et al. 1989, Sharps and Uresk 1990). While the descriptive data provided by these studies have been helpful in understanding prairie dog ecosystems and in formulating further research questions, comparative studies are necessary to quantify how prairie dog colonies differ from the non-colonized grasslands they are associated with. To date the results of only two studies, Agnew et al (1986) and Barko (1996), have compared the composition of vertebrate communities on prairie dog colonies to non-colonized grasslands.

Agnew et al (1986) reported higher species richness, higher total bird abundance and higher abundance of five bird species on prairie dog colonies than on non-colonized sites in South Dakota mixed grass prairie. Agnew et al. (1986) attributed the differences they found between colonized and non-colonized sites in part to the intensely grazed, low stature vegetation that is characteristic of prairie dog colonies, which resulted in high abundances of bird species that favor low vegetative structure. Barko (1996) reported

higher total bird abundance on prairie dog colonies than that found on non-colonized shortgrass prairie in Oklahoma during a sampling period characterized by high vegetative growth. However, when sampling was conducted pre-growing season and during a drought period, she found no significant differences in total bird abundances between prairie dog colonies and non-colonized sites (Barko 1996).

A substantial portion of the research on prairie dog ecosystems has been conducted in a limited area of the Great Plains, the northern mixed-grass prairie region (see Whicker and Detling 1988). However, the dynamics of prairie dog ecosystems in one region of the Great Plains may not be duplicated in other regions. It has been previously proposed that prairie dog ecosystems in shortgrass regions functioned differently than prairie dog ecosystems in mixed-grass regions because of differences in the characteristic climatic conditions and vegetation of the two regions (Winter et al. In Press *a* and *b*). This suggestion was based on a comparison of the results of Agnew et al. (1986) to preliminary results of this study and an interpretation of the Barko's (1996) results. The results reported in this chapter further illustrates regional differences in the ability of prairie dogs to influence bird populations, as well as potential similarities between-regions.

STUDY SITE AND METHODS

Study sites were located at the Cimarron National Grassland and adjacent private land in Morton County, southwest Kansas, and Baca County, southeast Colorado.

Cimarron National Grassland comprises more than 43,700 ha of land administered by the

U.S. Forest Service. Cimarron National Grassland is characterized by perennial grasses north of the Cimarron River and perennial grasses and sand sagebrush (*Artemisia filifolia* Torr.) south of the Cimarron River. The majority of this land is grazed by cattle (*Bos taurus* L.). Most of the surrounding private land is used for the production of annual crops, though some areas remain in perennial grass cover and are used for cattle grazing. Study sites were located north of the Cimarron River and occupied areas with silty loam soils and slopes of 0 to 6%. Mean precipitation (1901 - 1996) recorded at the Elkhart weather station in Morton County is 44.75 cm (National Weather Service Cooperative Observer Network, Personal Communication). Precipitation during the twelve months preceding the 1996 sampling period was 34.35 cm, 77 % of the long term mean. Precipitation during the twelve months preceding the 1997 sampling period was 67.97 cm, 150 % of the long term mean.

In 1996 eight of the largest prairie dog colonies and five non-colonized sites on Cimarron National Grassland were selected for study. The criterion used to select non-colonized sites was a visual determination that the short-statured perennial grasses *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths and *Buchloe dactyloides* (Nutt.) Engelm., alone or together, were the dominant species at the non-colonized site. Subsequent vegetation sampling confirmed the dominance of these two species at these sites (Chapter 2). Study sites in 1996 varied in size from 32.4 ha to 64.8 ha. One of the prairie dog colonies sampled in 1996 was not sampled in 1997, but all of the non-colonized shortgrass sites sampled in 1996 were sampled again in 1997. In 1997 thirteen prairie dog colonies and six shortgrass sites were selected for study on Cimarron National

Grassland and surrounding private land in Morton County Kansas and Baca County Colorado. Additionally, eight non-colonized sites on Cimarron National Grassland were randomly selected from a list of potential sites that had soil types and slopes that were identical to the soil types and slopes that characterized the prairie dog colonies. Non-colonized random sites were selected without a prior knowledge of what type of vegetation was growing at the sites. Subsequent vegetation sampling indicated that the mid-height perennial grass *Bouteloua curtipendula* (Michx.) Torr.) was a co-dominant with *Bouteloua gracilis* and *Buchloe dactyloides* (Chapter 2). Study sites in 1997 varied in size from 6 to 80 ha.

Data collection occurred between 27 May and 18 June during both years. Bird data were collected using line transects that varied in length from 0.40 to 1.60 km, depending on the size of a study site, and there were one to five parallel transects on each study site. In 1996 there were a total of 12.5 km of transects on prairie dog colonies and 8.5 km of transect at non-colonized shortgrass sites. In 1997 there were a total of 11.3 km of transects on prairie dog colonies, 9.5 km of transects on non-colonized shortgrass sites and 13.8 km of transects on non-colonized random sites. At study sites with more than one transect, transects were separated by 250 m.

Bird data were collected between sunrise and 10:30 a.m. when it was not raining and winds were estimated to be less than 30 km/hr. Birds detected by sight or sound on the ground or perched on vegetation within 100 m of a transect were recorded. Birds flying over the study site were not recorded and birds perched on or within 20 m of livestock watering facilities were not included in the analysis. In 1997 all hawks, owls

and shorebirds within the boundaries of each study site during the time of data collection were recorded regardless of their distance from the transect, and care was taken not to record individuals more than once. The expanded sampling effort was intended to provide more information about this group of species which were infrequently detected in 1996. Statistical analyses of species included within this group, however, utilized only the data representing individuals within 100 m of the transects. For these analyses all bird species were treated as equally detectable.

In 1997, vegetation structure was measured using a visual obstruction pole modified from Robel et al. (1970) at randomly located points along each transect used to collect bird data. The number of points sampled at each site varied from 35 to 120, in proportion to the area of the site. Observations were made one meter from the pole at a height of one meter. Vegetation height was determined by recording the highest point at which vegetation crossed between the observer and the pole. Vegetation density was determined by recording the lowest point at which the pole was visible.

Classical F-test analysis of variance computed by SAS v. 6.11 (1996) was used when the assumptions of the F-test were approximately satisfied. When the assumptions of the F-test were not satisfied, the Kruskal-Wallis non-parametric test computed by SAS v. 6.11 (1996) and a Tukey-type non-parametric multiple comparison (Zar 1996) were used. Two-tailed tests were used to test the null hypothesis that there was not a significant difference between the means of treatments. When the null hypothesis was rejected, the results are discussed in terms of higher or lower values of the variable being examined. The probability of type I error was accepted at $\alpha = 0.05$ for tests. A test

statistic value of $Q > 2.39$ generated by the Tukey-type test indicated significant differences. The tables that accompany the results section provide P-values from analysis of variance and Kruskal-Wallis tests. When data from three treatments were used in statistical tests, significant Q and P-values from pair-wise comparisons are provided in the text in the results section. In instances where individuals of a particular species were not detected at any study replicates of a treatment, that treatment was not included in statistical analyses. Mixed model repeated measures analysis of variance was computed using SAS v. 6.11 (1996) to test for differences between years and treatments (prairie dog and shortgrass), and year by treatment interactions for relative abundance of all birds combined and relative abundance of horned larks and western meadowlarks.

In cooperation with the Heritage Program administered by the Kansas Biological Survey, records were kept of the locations where long-billed curlews, burrowing owls, and mountain plovers were sighted in 1996. Data were collected at all times during the field season and at all places within Morton and Baca Counties that were traveled by the investigator. The date, number of individuals, legal description of the location, and the type of land use was recorded for each sighting. In 1997 this information was only collected for burrowing owls and mountain plovers. In instances where individuals of the same species were recorded at the same location multiple times in a field season, the results reported utilize the largest number of individuals seen at that location at one time. Nomenclature follows American Ornithologists' Union (1983), Great Plains Flora Association (1986), and Wilson and Reeder (1993). Scientific names and authorities of species encountered in this study are provided in the data tables.

RESULTS

In 1996, 136 individual birds of five species were recorded at prairie dog colonies and 136 individuals of seven species were recorded at the non-colonized shortgrass sites. Table 1 lists the relative abundances of all species and P-values from statistical tests. During 1996 horned larks were more abundant at non-colonized shortgrass sites than at prairie dog colonies. The relative abundance of all birds combined approached significance when prairie dog colonies were compared to non-colonized shortgrass sites. There was no difference in the relative abundances of killdeer, mourning doves, and western meadowlarks. Figure 1 shows cumulative species richness plotted on cumulative transect length for the prairie dog colonies and non-colonized shortgrass sites using 1996 data. New species were not encountered in prairie dog colonies or non-colonized shortgrass sites after approximately six cumulative kilometers of transect had been sampled.

In 1997, 241 individual birds of seven species were recorded on prairie dog colonies, 297 individuals of eight species were recorded on non-colonized shortgrass sites and 552 individuals of nine species were recorded on non-colonized random sites. Table 2 lists the relative abundances of all species and P-values from analysis of variance and Kruskal-Wallis tests. P- and Q-values from pair-wise comparisons that indicated significant differences between pairs of treatments are provided in the text that follows. Relative abundance of horned larks was higher on the prairie dog colonies than the non-colonized random sites ($P = 0.003$). Relative abundance of lark buntings ($P = 0.014$) was higher on non-colonized shortgrass sites than on prairie dog colonies. Relative

abundance of all birds combined ($P = 0.001$), western meadowlarks ($Q = 2.62$), lark buntings ($P = 0.0001$), and grasshopper sparrows ($Q = 4.19$) were higher on the non-colonized random sites than on the prairie dog colonies. Vegetation height ($Q = 3.66$) and density ($Q = 3.39$) were higher on the non-colonized random sites than on the prairie dog colonies.

Figure 2 shows cumulative species richness plotted on cumulative transect length for the prairie dog colonies, non-colonized shortgrass sites and non-colonized random sites using 1997 data. Individuals detected with the expanded sampling methodology (in excess of 100 m from the transect) were not used in constructing these curves. New species were not encountered after approximately eight cumulative kilometers of transect on the prairie dog colonies and the non-colonized shortgrass sites, whereas no new species were encountered after approximately twelve cumulative kilometers of transect on the non-colonized random sites.

When data from 1996 and 1997 were combined for the prairie dog colonies and non-colonized shortgrass sites, relative abundance of all birds combined was higher on non-colonized shortgrass sites than prairie dog colonies ($P = 0.028$), and was higher during 1997 than during 1996 ($P = 0.0002$). The effect of interaction of treatment and year on relative abundance of all birds combined was not significant ($P = 0.494$). Horned lark relative abundance was not significantly different between prairie dog colonies and non-colonized shortgrass sites ($P = 0.915$) or between years ($P = 0.185$). The effect of interaction of treatment and year on relative abundance of horned larks was significant ($P = 0.047$). Relative abundance of western meadowlarks was not significantly different

between prairie dog colonies and non-colonized shortgrass sites ($P = 0.827$) or between years ($P = 0.243$). The effect of interaction of treatment and year on the relative abundance of western meadowlarks approached significance ($P = 0.076$).

The results of the expanded sampling effort that are reported represent individuals detected in addition to the individuals reported in Table 2. Using the expanded sampling effort one Swainson's hawk was detected on a non-colonized shortgrass site, but this species was not encountered on prairie dog colonies or non-colonized random sites. One long-billed curlew was detected on a prairie dog colony, one additional long-billed curlew was detected on a non-colonized shortgrass site, and three additional long-billed curlews were detected on non-colonized random sites. Twenty-nine additional burrowing owls were detected on prairie dog colonies, but this species was not encountered on non-colonized shortgrass sites or non-colonized random sites.

During the extensive surveys conducted in 1996 long-billed curlews were sighted in 1 prairie dog colony ($n = 1$), 12 non-colonized rangeland locations ($n = 20$), 5 disced cropland locations ($n = 9$), 3 idled cropland locations ($n = 20$), 3 growing cropland locations ($n = 25$), and 1 road ditch ($n = 1$). Burrowing owls were sighted in 22 prairie dog colonies ($n = 58$), 2 non-colonized rangeland locations ($n = 2$), and 1 growing cropland location ($n = 1$). Mountain plovers were sighted at 1 non-colonized rangeland location ($n = 1$) and 3 disced cropland locations ($n = 4$). Long-billed curlews and burrowing owls were sighted throughout the field season from 22 May to 15 July. Mountain plovers were only sighted between 26 May and 16 June.

During the extensive surveys conducted in 1997, burrowing owls were sighted at

17 prairie dog colonies (n = 56) and 2 non-colonized rangeland locations (n = 4). A burrowing owl nest burrow (indicated by pellets, excrement and a freshly killed juvenile mouse at the entrance) was found in a non-colonized rangeland site. This is the only evidence found during two years of field work suggesting burrowing owls nest in non-colonized locations in Morton and Baca Counties. Mountain plovers were sighted at 4 prairie dog colonies (n = 6), 2 roadside/growing cropland locations (n = 2), 2 roadside/disc'd cropland locations (n = 5), 1 roadside/burned non-colonized rangeland location (n = 2), and 3 locations where birds were seen flying and could not be associated with a land-use type (n = 3). Burrowing owls were sighted throughout the 1997 field season from 27 April to June 30, but mountain plovers were only sighted from 26 April to 1 June.

DISCUSSION

In South Dakota mixed-grass prairie, bird communities on prairie dog colonies differed from those on non-colonized sites, presumably because prairie dogs altered the structure and composition of vegetative communities to the extent that birds perceived prairie dog colonies as a distinct habitat type (Agnew et al. 1986). Agnew et al. (1986) found significantly higher abundances of horned lark, mourning dove, killdeer, barn swallow (*Hirundo rustica* Linnaeus) and burrowing owl on prairie dog colonies, while non-colonized sites had significantly higher abundances of red-winged blackbird, upland sandpiper (*Bartramia longicauda* Bechstein) and lark bunting. In Oklahoma shortgrass prairie, Barko (1996) found that the combined abundance of all birds was significantly

higher on prairie dog colonies than on non-colonized sites during a non-drought period when vegetation was actively growing.

This study found higher abundances of horned larks on non-colonized shortgrass sites in 1996. In 1997 horned larks were more abundant on prairie dog colonies, while western meadowlarks, lark buntings and grasshopper sparrows were more abundant on non-colonized random sites. Burrowing owls were only detected on prairie dog colonies during sampling periods in 1996 and 1997. The difference in relative abundance of common nighthawks between non-colonized random sites and non-colonized shortgrass sites approached significance in 1997, their absence at prairie dog colonies suggests that this species prefers non-colonized random sites over prairie dog colonies. Considering the similarity in total length of transect sampled at the three types of sites, the absence of long-billed curlews at prairie dog colonies in 1997 suggests that this species may prefer non-colonized sites as well. This opinion is further supported by the results of the extensive surveys for long-billed curlews in 1996 in Morton and Baca Counties.

The 1996 field season occurred following twelve months of below average precipitation. Much of the vegetation in the region of this study, including the dominant grasses, had not resumed growth after winter dormancy at the time of sampling (May-June) in 1996. Vegetation height and density were not measured in 1996, and there seemed to be little if any difference in the height or density of the vegetation on the prairie dog colonies and the non-colonized sites. However, the higher abundances of horned larks on the non-colonized shortgrass sites in 1996 indicates that some factor relevant to the birds was different between the prairie dog colonies and the non-colonized

shortgrass sites.

In spite of the assumption that the vegetation structure was similar between prairie dog colonies and non-colonized shortgrass sites, it may have been dissimilar enough to cause horned larks to differentiate between the two areas. It is also possible that a difference in some other factor such as food supply caused the disparity in abundance of horned larks between the two treatments in 1996. Measurements of vegetation height and density in 1997 reveal that vegetation structure on prairie dog colonies was significantly different from the vegetation structure on non-colonized random sites during that field season. Most of the significant differences that this study found in bird abundances was between prairie dog colonies and non-colonized random sites. It seems likely that the differences in bird abundance that this study detected are a function of the differences in vegetation structure between the treatments. The results of this study indicate that there are many more differences in vegetation structure and bird community composition when prairie dog colonies are compared to non-colonized random sites than when prairie dog colonies are compared to non-colonized shortgrass sites. In 1997 the only significant difference between prairie dog colonies and non-colonized shortgrass sites was the abundance of lark buntings.

This study indicates that the presence of a prairie dog colony in the landscape of the study area precludes the occurrence of otherwise abundant species such as lark buntings and grasshopper sparrows in that particular location as well. However, these results also indicate the great importance of prairie dog colonies in the study area to burrowing owls. Statistical tests were not appropriate for burrowing owls. However, the

results of the extensive surveys in Morton and Baca Counties, and the high numbers of burrowing owls detected on prairie dog colonies in 1997 as a result of the expanded sampling efforts, demonstrates that burrowing owls are highly dependent on the prairie dog burrows for shelter and nest sites in this study area.

Western burrowing owls are reported to be capable of excavating burrows on their own, but rarely do so, and are typically dependent on the burrowing activities of various mammals (Haug et al. 1993). During the two field seasons in Morton and Baca Counties, evidence of burrowing by badgers (*Taxidea taxus* Schreber) was never seen, nor were badgers ever sighted. Coyotes (*Canis latrans* Say) were frequently sighted but only two coyote dens were found, and swift fox (*Vulpes velox* Say) are rarely encountered in the area (C. Roy, Kansas Department of Wildlife & Parks, Personal Communication). Two Lagomorphs (*Sylvilagus audubonii* Baird and *Lepus californicus* Gray) were present at the study sites, but neither is considered a burrowing animal (Bee et al. 1981). The other burrowing Sciurids that occur in Morton and Baca Counties (*Spermophilus tridecemlineatus* Mitchill and *S. spilosoma* Bennett) excavate burrows that are too small for use by burrowing owls. In this study area burrows suitable for use by burrowing owls appear to occur almost exclusively on prairie dog colonies.

This study and the results of Barko (1986) demonstrate that prairie dog ecosystems in shortgrass steppe influence bird populations differently than has been reported from northern mixed-grass prairie (Agnew et al. 1986). The results of this study identify numerous bird species that prefer non-colonized grasslands but only two species (horned larks and burrowing owls) that exhibited a preference for prairie dog colonies.

Agnew et al. (1986) reported numerous species that preferred prairie dog colonies over non-colonized areas in northern mixed-grass prairie. This study did not find evidence of higher bird species richness on prairie dog colonies (see figures 1 and 2), as was reported by Agnew et al (1986). Further contrasting with the results of Agnew et al (1986), which found higher abundances of all birds combined on prairie dog colonies, this study found significantly higher abundances of all birds combined on non-colonized random sites in 1997, and the higher abundances of all birds combined on the non-colonized shortgrass sites approached significance in 1996.

When Barko (1996) conducted sampling during pre-growing season and drought periods in Oklahoma shortgrass prairie, there were no significant differences in the bird communities of prairie dog colonies and non-colonized sites. Barko (1996) believed that the lack of a difference during the pre-growing season and drought periods was explained by an apparent similarity in the vegetation structure of prairie dog colonies and non-colonized sites during those times. Similarly, this study found relatively few differences in the bird communities of prairie dog colonies and non-colonized sites during a field season (1996) that occurred at the end of a drought. Two species (grasshopper sparrows and lark buntings) that preferred non-colonized sites in 1997 apparently found non-colonized sites and prairie dog colonies equally unsuitable in 1996. This suggests that in the semiarid shortgrass steppe the ability of prairie dogs to influence bird communities is heavily influenced by climatic conditions.

It has previously been proposed that severe climatic conditions (drought) in semi-arid regions can suppress vegetative productivity to the point that birds do not perceive

prairie dog colonies to be habitats that are markedly distinct from non-colonized grasslands (Winter et al. In Press). Zimmerman (1992) reported a similar influence of climate on the abundances of tallgrass prairie birds in Kansas via the influence of climate on vegetation productivity. The abundances of most tallgrass prairie birds did not differ between burned and unburned watersheds during normal and wet years, but when drought conditions depressed the vegetative productivity of tallgrass prairie, bird abundances were lower on the burned watersheds (Zimmerman 1992). Zimmerman (1992) described fire interacting with drought to produce vegetation structure that is below an acceptable threshold for breeding birds. In shortgrass prairie, it appears that drought suppresses vegetation productivity to a point that is below a threshold for breeding birds that prefer non-colonized sites during non-drought years, causing them to judge non-colonized sites to be as unsuitable as prairie dog colonies.

Because of differences in the characteristic vegetation of shortgrass prairie and mixed-grass prairie, climate may not normally moderate the effect of prairie dogs on bird populations in northern mixed-grass prairie. Both Agnew et al. (1986) and Archer et al. (1987) report that vegetation height is shorter on prairie dog colonies than non-colonized northern mixed-grass prairie. But non-colonized mixed-grass prairie is characterized by the dominance of numerous mid-height grasses (Coupland 1992), and the characteristic effect of prairie dogs on mixed-grass prairie vegetation involves the displacement of mid-height grasses by short grasses (Coppock et al. 1983, Archer et al. 1987). The ability of prairie dogs to create patches of short-statured vegetation within shortgrass prairie is tempered by the fact that semi-arid Great Plains grasslands are characterized by dominant

grasses that are short-statured to begin with (Lauenroth and Milchunas 1992). Climatic conditions that suppress vegetation productivity in shortgrass prairie would further diminish the ability of prairie dogs to modify vegetation structure, because adjacent non-colonized vegetation should exhibit reduced stature as well.

Detritus accumulation from previous growing seasons has been reported to be an important structural feature for some grassland breeding birds (Zimmerman 1988, 1997). Detritus could moderate the effect of drought on grassland bird habitat if detritus functions as a structural feature that is important to birds in the absence of a current years growth of vegetation. The research of Agnew et al (1986) utilized non-colonized sites that were not grazed by large herbivores, so presumably there would have been substantial accumulated detritus at these sites. Even if drought suppressed the vegetation productivity of mixed-grass prairie, residue from previous growing seasons may provide habitat structure on non-colonized sites that would be different from the structure found on prairie dog colonies, where detritus would not accumulate because of the clipping activities of prairie dogs.

Grazing by large herbivores reduces the amount of detritus accumulation in North American grasslands in general (Sims et al. 1978) and in mixed-grass prairie specifically (Brand and Goetz 1986, Coupland 1992). Fire can also eliminate vegetation detritus in mixed-grass prairie (Dix 1960). Grazing by large herbivores also causes compositional shifts in mixed-grass prairie vegetation so that short stature grasses such as *Bouteloua* and *Buchloe* increase or even predominate (Sims et al 1978, Coupland 1992). Heavily grazed pastures in mixed-grass regions can in fact be characterized by bird communities that are

dominated by species associated with shortgrass habitats (Kantrud 1981). Both large ungulate herbivory and fire have the potential to negate differences between the vegetation structure of prairie dog colonies and non-colonized mixed-grass sites. Coppock and Detling (1986) reported that a prescribed fire on non-colonized mixed-grass prairie adjacent to a prairie dog colony induced bison to switch their preference for grazing on the prairie dog colony to grazing on the burned non-colonized area, illustrating the potential for herbivory and fire to interact and influence avian habitat conditions on and adjacent to prairie dog colonies.

Horizontal and vertical habitat structure of grasslands is altered by climate, fire and herbivory (Vinton and Collins 1996). Drought, fire and large herbivore grazing, acting alone or concurrently, may affect non-colonized mixed-grass prairie sites so that their associated bird communities would be very similar to those found on prairie dog colonies. The findings of Agnew et al (1986) probably represent only one of many possible situations when a comparison of prairie dog colonies is made with non-colonized sites in mixed-grass prairie, the outcome of the comparison depending on the dynamics of the various factors influencing the study sites at the time of the study. Drought, fire and large herbivore grazing in shortgrass steppe would surely have an influence that varies in time and space as well, which implies that the findings of Barko (1996) and this study also provide only a partial understanding of the role of prairie dogs in altering vertebrate distribution and abundance in shortgrass landscapes.

The shortgrass steppe is characterized by extreme variability in inter and intra-annual precipitation (Lauenroth and Milchunas 1992). Weins (1974) proposed that the

extremes of climatic variability in grassland environments act as "bottlenecks" that limit the number of species that are capable of successfully tolerating these extremes. Climatic extremes can also be responsible for extreme variability in annual populations of grassland birds (Krause 1968, Weins 1974, George et al. 1992). Weins (1974) and Cody (1985) discussed how a likely strategy for coping with habitat conditions that frequently change in response to climatic conditions would be a lack of philopatry, or site tenacity. Individual birds that are able to opportunistically "track" optimum resources as they shift in time and space should have higher fitness than individuals which faithfully return to breed, regardless of resource conditions, to the location where they were hatched (Weins 1974, Cody 1985).

Natal philopatry (return to area of hatching) has been shown to be low or non-existent for McCown's longspur (*Calcarius mccownii* Lawrence), chestnut-collared longspur (*Calcarius ornatus* Townsend), western meadowlark and eastern meadowlark (*Sturnella magna* Linnaeus) (Lanyon 1994, With 1994, Lanyon 1995, Hill and Gould 1997). In contrast to the low incidence of natal philopatry among these species, philopatry of adults to previous breeding areas in these species does occur and can be common (Lanyon 1994, Ryder 1972 in With 1994, Lanyon 1995, Hill and Gould 1997). Beason (1995) and Lowther (1996) report that data for natal philopatry in horned lark and Le Conte's sparrow (*Ammodramus leconteii* Audubon), respectively, are not available. Limited data on philopatry of adult Le Conte's sparrow for previous breeding areas indicate that it occurs (Murray 1969), while philopatry of adult horned larks to previous breeding areas can be common (Boyd 1976, Beason 1970 in Beason 1995).

Historically, herbivory and soil disturbance by bison (*Bison bison* L.), antelope (*Antilocapra americana* Ord) and prairie dogs likely influenced the vegetation of the shortgrass steppe in a manner that varied greatly in space and time (Knopf 1996b). It seems intuitive that birds of the shortgrass steppe should have strategies for coping with environments that are highly variable independent of climatic variability, such as the capability to utilize newly created habitats (Owens and Myres 1973). Populations of chestnut-collared longspurs, a species that prefers grazed grasslands (Hill and Gould 1997), have been shown to fluctuate as they opportunistically use areas that have been recently mowed (Owens and Myres 1973), a land use which in part mimics shifting herbivory pressures. Numerous grassland bird species are also reported to respond favorably to the low stature, but temporary, vegetative conditions created by grassland fires (Krause 1968, Oberholser 1974, Knopf 1996a). Large changes in the abundance and habitat use by several bird species in this study suggest that birds in the shortgrass steppe are highly adapted to the temporal variability in habitat structure that may be caused by climatic variability, fire and the activities of other organisms.

Throughout their range horned larks inhabit open areas characterized by short vegetation (Beason 1995), and horned lark populations have been reported to respond favorably to high levels of herbivory (Weins 1973, Kantrud 1981, Bock and Webb 1984). The positive response of horned lark populations to herbivory may be further exemplified by the findings of Agnew et al (1986) in South Dakota if it is accepted that prairie dog colonies represent areas of greater herbivory relative to non-colonized mixed-grass prairie. Higher abundances of horned larks on non-colonized sites in this study during

1996 suggests that in semi-arid regions the interaction of prairie dog herbivory and drought can alter vegetation structure to a point that horned larks perceive prairie dog colonies as inferior habitats relative to non-colonized sites during a drought year.

Barko's (1996) results from Oklahoma shortgrass prairie for this species allude to this as well. Although she did not report the results of statistical tests for horned larks, they were detected more often on prairie dog colonies during a non-drought sampling period, and more often on non-colonized sites during two of three sampling periods that occurred pre-growing season or during a drought (Barko 1996). In this study, horned lark abundance on non-colonized short-grass sites in 1996 was very similar to their abundance on prairie dog colonies in 1997. Habitat switching is supported by the significant effect of the interaction of treatment and year on relative abundance of horned larks using the data pooled from both years. Horned larks at the study sites appear to cope with climatic extremes by opportunistically using different habitats within a landscape, i.e. tracking resources over a local scale. There is a suggestion that western meadowlarks may also use this strategy, as indicated by the effect of the interaction of treatment and year on relative abundance which approached significance. The ability to switch habitat preferences within a landscape may moderate the effect that climatic variability would have on annual population levels in that landscape.

In contrast to the strategy of horned larks, the complete absence of lark buntings in 1996 followed by their high numbers in 1997 implies that this species opportunistically tracks resources over a much larger scale. This species was seen only a couple of times in Morton and Baca Counties during the 1996 field season, and there was no evidence to

indicate that it was a breeding species in the areas monitored during that year. The high populations present in 1997 could not have been comprised of individuals that bred or were hatched there the previous year. Grasshopper sparrows were not detected on the study sites when sampling occurred in 1996. Singing male grasshopper sparrows were occasionally sighted in Morton and Baca Counties that year, and though rare, it can be presumed that this species was breeding. The high abundances of grasshopper sparrows present in 1997 surely consisted primarily of individuals hatched in other areas and individuals that had bred in other areas the previous year which were opportunistically utilizing the optimum conditions present in Morton and Baca Counties that year. Thus, grasshopper sparrows also appear to utilize a strategy of opportunistically tracking resources at large scales, but not to the extreme degree suggested by the population fluctuations of lark buntings in the study area.

Other researchers have reported similar fluctuations in grassland bird populations which were associated with extreme fluctuations in climatic condition. In North Dakota mixed-grass prairie George et al. (1992) reported that densities of vesper sparrows (*Pooecetes gramineus* Gmelin), grasshopper sparrows, Baird's sparrows (*Ammodramus bairdii* Audubon), and Sprague's pipit (*Anthus spragueii* Audubon) were significantly lower during and/or after a severe drought than pre-drought densities. In a multi-state region of the northern Great Plains Igl and Johnson (1995) reported dramatic increases in the densities of Le Conte's sparrows in planted grasslands when increased precipitation followed multiple years of drought. In Texas shortgrass prairie Weins (1974) reported that densities of lark buntings and grasshopper sparrows declined to zero at the end of

two years of drought. During the third year of research, which was characterized by increased precipitation and increased vegetative productivity, grasshopper sparrows re-invaded the region and were present in high densities, suggesting to Weins that this species can opportunistically track resources (Weins 1974).

Herbivory and burrowing activities of prairie dogs alters the distribution and abundance of numerous bird species, both in shortgrass and mixed-grass prairie landscapes. Even though numerous species were identified that prefer non-colonized grasslands over prairie dog colonies, the bird communities of Morton and Baca Counties are enriched by the existence of prairie dog colonies in the landscape. One species (burrowing owl) appears highly dependent on the existence of prairie dog colonies in the study area, while the preference of horned larks and perhaps western meadowlarks for prairie dog colonies or non-colonized sites appears to be determined by climatic conditions and their presumed effects on vegetation structure.

The extent to which prairie dogs influence the bird community of a region is probably in large part a function of the difference in the vegetative structure of prairie dog colonies and non-colonized sites. Vegetation sampling in this study demonstrated that there were far greater differences between the vegetation structure of prairie dog colonies and non-colonized random sites than when prairie dog colonies are compared to non-colonized shortgrass sites (Chapter 2). These differences in vegetation structure are reflected in differences in the composition of bird communities as well. The potential for a difference in the vegetation structure of a prairie dog colony and adjacent non-colonized grassland is much greater in mixed-grass prairie than in shortgrass steppe where lower

precipitation amounts constrain primary productivity. Abiotic and biotic processes such as drought, fire and large herbivore grazing all have the potential, acting alone or together, to magnify or negate the contrast in vegetative structure of prairie dog colonies and non-colonized areas.

Grassland ecosystems are characterized by dynamic abiotic and biotic conditions. Four key factors are evident that would influence bird communities at differing scales within grasslands: climate, fire, large mammal herbivory and prairie dog colonization. Prairie dog colonies represent localized areas of intense herbivory and soil disturbance within grassland landscapes, contributing to landscape heterogeneity. The heterogeneity of grassland landscapes containing prairie dog colonies is further influenced by the variable effects of fire and large mammal herbivory operating at larger scales. Finally, these landscapes exist within a context imposed by regional climatic variability. The interaction of these factors creates habitat conditions that can change greatly in space and time. Birds in this study area appear to utilize contrasting coping strategies that enables them to succeed in grassland environments that are characterized by dynamic habitat conditions.

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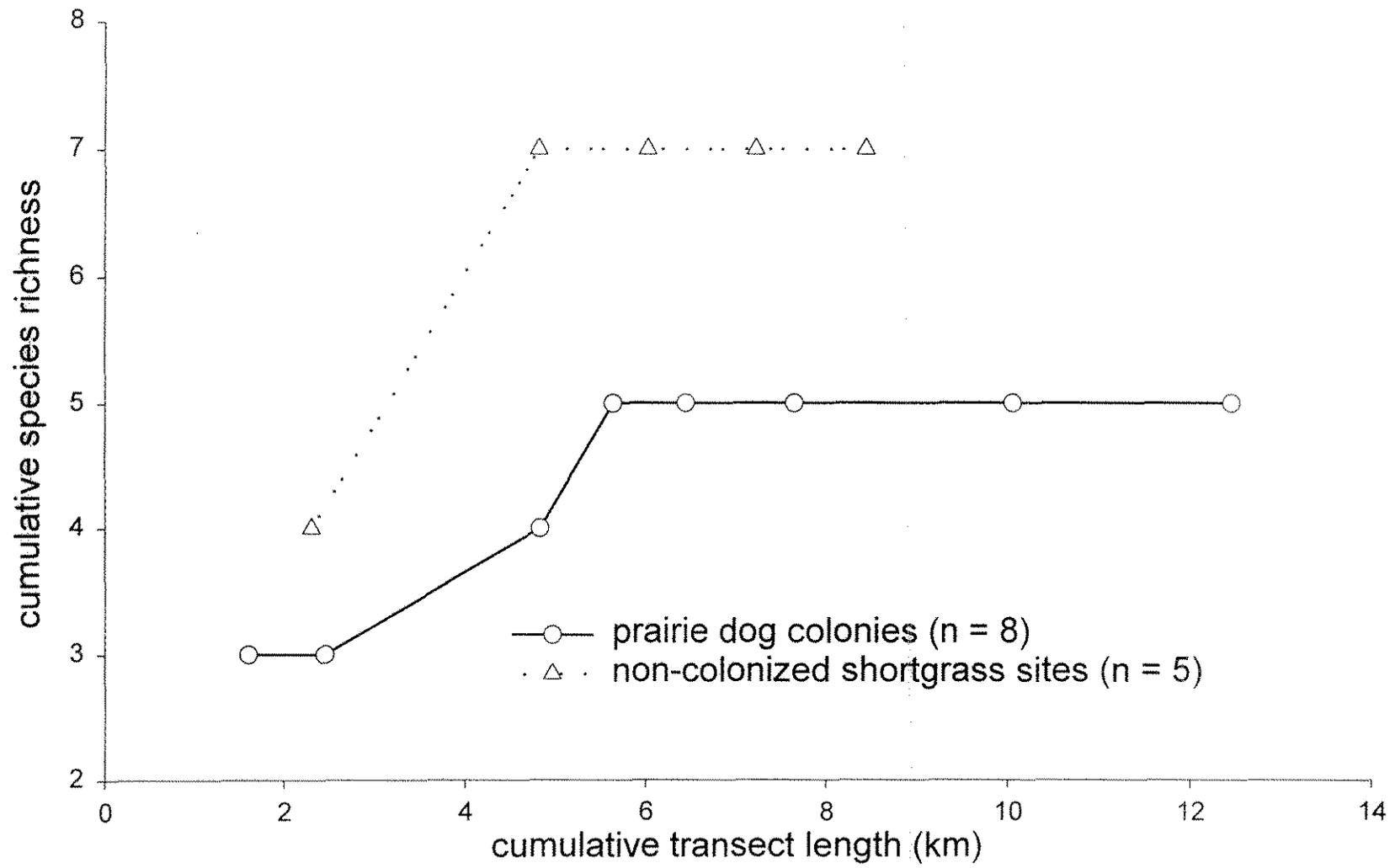
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FIGURE LEGENDS

Figure 1. Cumulative species richness plotted on cumulative transect length (km) for eight prairie dog colonies and five non-colonized shortgrass sites in 1996.

Figure 2. Cumulative species richness plotted on cumulative transect length (km) for thirteen prairie dog colonies, six non-colonized shortgrass sites and eight non-colonized random sites in 1997.



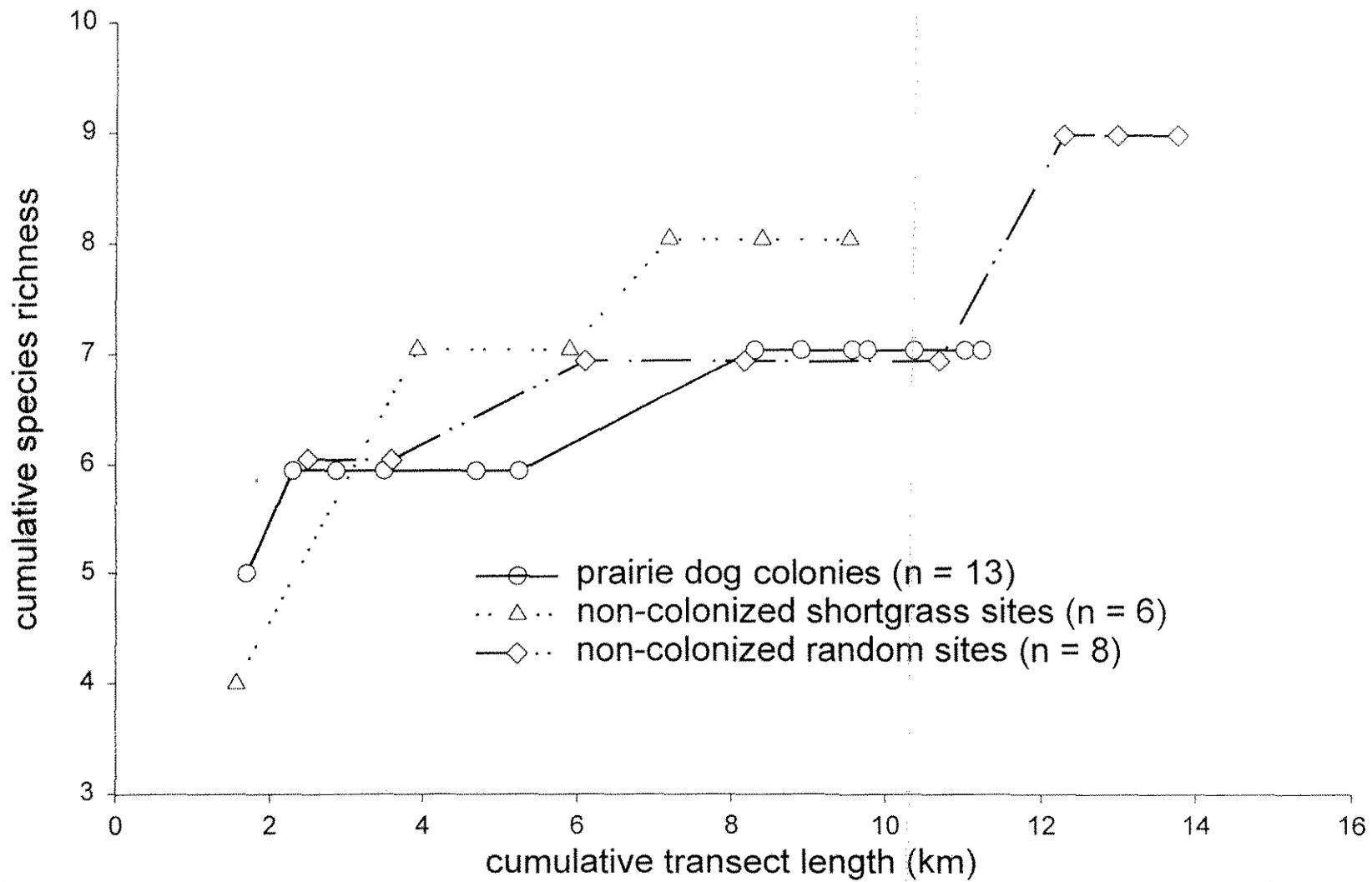


Table 1. Mean \pm SE relative abundance (individuals/km of transect) and total number detected (#) on prairie dog colonies (n = 8) and non-colonized shortgrass sites (n = 5) in 1996. P-values are from F-tests and Kruskal-Wallis tests. Treatments in which no individuals were detected were not included in statistical tests.

	Prairie Dog Colonies		Shortgrass Sites		P-value
	mean \pm SE	#	mean \pm SE	#	
All Birds	11.11 \pm 1.82	136	16.07 \pm 1.13	136	0.072
Killdeer	0.16 \pm 0.16	3	0.08 \pm 0.08	1	0.523
<i>Charadrius vociferus</i> L.					
Mountain Plover	0	0	0.08 \pm 0.08	1	
<i>Charadrius montanus</i> Townsend					
Mourning Dove	0.23 \pm 0.16	4	0.08 \pm 0.08	1	0.692
<i>Zenaida macroura</i> L.					
Burrowing Owl	0.98 \pm 0.76	7	0	0	
<i>Athene cunicularia</i> Molina					
Common Nighthawk	0	0	0.17 \pm 0.17	2	
<i>Chordeiles minor</i> Forster					

Table 1. Continued.

	Prairie Dog Colonies		Shortgrass Sites		P-value
	mean \pm SE	#	mean \pm SE	#	
Western Kingbird	0	0	0.08 \pm 0.08	1	
<i>Tyrannus verticalis</i> Say					
Horned Lark	7.46 \pm 1.45	91	14.91 \pm 1.26	123	0.005
<i>Eremophila alpestris</i> L.					
Western Meadowlark	2.28 \pm 0.7	31	0.66 \pm 0.38	7	0.158
<i>Sturnella neglecta</i> Audubon					

Table 2. Mean \pm SE relative abundance (individuals/km of transect), total number detected (#), and vegetation height and density on prairie dog colonies (n = 13), non-colonized shortgrass sites (n = 6) and non-colonized random sites (n = 8) in 1997. P-values are from F-tests and Kruskal Wallace tests. Different superscripts indicate significant differences from pair-wise comparisons. P-values for significantly different pair-wise comparisons are provided in the text. Treatments in which no individuals were detected were not included in statistical tests.

	Prairie Dog Colonies		Shortgrass Sites		Random Sites		P-value
	mean \pm SE	#	mean \pm SE	#	mean \pm SE	#	
All Birds	22.59 \pm 1.88 ^a	241	30.88 \pm 4.20 ^{a,b}	297	40.19 \pm 4.65 ^b	552	0.002
Mountain Plover	0.02 \pm 0.02	1	0	0	0	0	
<i>Charadrius montanus</i>							
Long-billed Curlew	0	0	0.53 \pm 0.31	5	0.38 \pm 0.25	5	0.452
<i>Numenius americanus</i> Bechstein							
Mourning Dove	1.11 \pm 0.51	9	0.23 \pm 0.16	3	0.83 \pm 0.45	10	0.717
<i>Zenaida macroura</i>							
Burrowing Owl	0.54 \pm 0.24	7	0	0	0	0	
<i>Athene cunicularia</i>							

Table 2. Continued.

	Prairie Dog Colonies		Shortgrass Sites		Random Sites		P-value
	mean \pm SE	#	mean \pm SE	#	mean \pm SE	#	
Common Nighthawk	0	0	0.07 \pm 0.07	1	0.58 \pm 0.19	7	0.054
<i>Chordeiles minor</i>							
Horned Lark	16.48 \pm 1.64 ^a	172	10.51 \pm 4.07 ^{a,b}	101	6.78 \pm 1.13 ^b	89	0.008
<i>Eremophila alpestris</i>							
Dickcissel	0	0	0	0	0.39 \pm 0.39	5	
<i>Spiza americana</i> Gmelin							
Lark Bunting	2.18 \pm 0.97 ^a	32	11.92 \pm 3.43 ^b	115	18.31 \pm 3.81 ^b	254	0.0002
<i>Calamospiza melanocorys</i> Stejneger							
Grasshopper Sparrow	0.27 \pm 0.18 ^a	4	4.34 \pm 1.49 ^{a,b}	44	8.22 \pm 1.28 ^b	126	0.0001
<i>Ammodramus savannarum</i> Gmelin							
Red-winged Blackbird	0	0	0	0	0.23 \pm 0.23	3	
<i>Agelaius phoeniceus</i> Linnaeus							
Western Meadowlark	1.84 \pm 0.89 ^a	16	2.91 \pm 0.85 ^{a,b}	26	4.19 \pm 0.72 ^b	51	0.028
<i>Sturnella neglecta</i>							

Table 2. Continued.

	Prairie Dog Colonies		Shortgrass Sites		Random Sites		P-value
	mean \pm SE	#	mean \pm SE	#	mean \pm SE	#	
Brown-headed Cowbird	0	0	0.28 \pm 0.28	2	0	0	
<i>Molothrus ater</i> Wagler							
Unidentified Species	0	0	0	0	0.26 \pm 0.17	2	
Vegetation Height (cm)	9.48 \pm 0.80 ^a		25.22 \pm 5.50 ^{a,b}		33.59 \pm 3.29 ^b		0.0008
Vegetation Density (cm)	2.49 \pm 0.17 ^a		5.40 \pm 1.22 ^{a,b}		6.41 \pm 1.32 ^b		0.002

APPENDIX

Appendix Table 1. Plant specimens collected in Morton County, Kansas, and Baca County, Colorado, in 1996 and 1997. Includes specimens not detected during sampling. All specimens are deposited in the Division of Biology Herbarium, Kansas State University.

Taxon	Collection Number
Ranunculaceae	
<i>Delphinium virescens</i> Nutt.	137, 521
Papaveraceae	
<i>Argemone squarrosa</i> Greene	140
Nyctaginaceae	
<i>Abronia fragans</i> Nutt. ex Hook.	155
<i>Mirabilis linearis</i> (Pursh) Heimerl	184, 215, 329
<i>Mirabilis nyctaginea</i> (Michx.) MacM.	143
Cactaceae	
<i>Coryphantha vivipara</i> (Nutt.) Britt. & Rose	428
<i>Echinocereus viridiflorus</i> Engelm.	150, 388
<i>Opuntia macrorhiza</i> Engelm.	148
<i>Opuntia polyacantha</i> Haw.	386
Chenopodiaceae	
<i>Chenopodium berlandieri</i> Moq.	236
<i>Chenopodium incanum</i> (S. Wats.) Heller.	192, 239
<i>Chenopodium pratericola</i> Rydb.	235
<i>Kochia scoparia</i> (L.) Schrad.	202
Amaranthaceae	
<i>Amaranthus albus</i> L.	222, 254, 255, 290, 365, 377, 572
<i>Amaranthus graecizans</i> L.	266, 375, 513, 571
<i>Amaranthus palmeri</i> S. Wats.	328, 344
<i>Amaranthus retroflexus</i> L.	169, 214, 237, 271, 293, 317, 356, 364, 374, 394, 570
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	267
Portulacaceae	
<i>Portulaca oleracea</i> L.	230

Table 1. Continued

Taxon	Collection Number
Polygonaceae	
<i>Eriogonum annuum</i> (Nutt.)	555
<i>Polygonum ramosissimum</i> Michx.	173
<i>Rumex stenophyllus</i> Ledeb.	170
Malvaceae	
<i>Callirhoe involucrata</i> (T. & G.) A. Gray	142
<i>Hibiscus trionum</i> L.	308, 319
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	111
Violaceae	
<i>Hybanthus verticillatus</i> (Ort.) Baill.	252, 330, 560, 561, 562
Brassicaceae	
<i>Descurainia pinnata</i> (Watt.) Britt.	247, 346, 499
<i>Descurainia sophia</i> (L.) Webb.	241, 497
<i>Erysimum asperum</i> (Nutt.) DC.	131, 229, 414
<i>Lepidium densiflorum</i> Schrad.	246, 487, 493
Caesalpinaceae	
<i>Caesalpinia jamesii</i> (T. & G.) Fisher	145
<i>Hoffmanseggia glauca</i> (Ort.) Eifert	134
Fabaceae	
<i>Astragalus gracilis</i> Nutt.	421, 457, 503, 522
<i>Astragalus lotiflorus</i> Hook.	218, 307, 333, 455, 482, 491
<i>Astragalus missouriensis</i> Nutt.	424, 452, 453, 519
<i>Astragalus mollissimus</i> Torr.	233, 361, 410
<i>Astragalus nuttalianus</i> DC. var. <i>austrinus</i> (Small) Barneby	256, 454
<i>Astragalus nuttalianus</i> var. <i>nuttalianus</i> DC.	469, 500
<i>Astragalus pectinatus</i> Dougl. Ex. G. Don.	392, 464
<i>Astragalus plattensis</i> Nutt. ex T. & G.	451, 511, 530, 544
<i>Dalea enneandra</i> Nutt.	183, 261, 283, 302
<i>Dalea jamesii</i> (Torr.) T. & G.	463
<i>Dalea tenuifolia</i> (A. Gray) Shinnars	125, 181
<i>Melilotus</i> spp. ³	273

Table I. Continued

Taxon	Collection Number
Fabaceae	
<i>Oxytropis lambertii</i> Pursh	456
<i>Psoralea tenuifolia</i> Pursh	117, 146
<i>Sophora nuttalliana</i> B. L. Turner	113, 191, 251, 282, 306, 379
Onagraceae	
<i>Calylophus hartwegii</i> (Benth.) Raven	179
<i>Calylophus lavandulifolius</i> (T. & G.) Raven	397, 401
<i>Gaura coccinea</i> Pursh	112, 204, 303, 425, 520, 524, 548
<i>Gaura villosa</i> Torr.	154
<i>Oenothera triloba</i> Nutt.	200, 370, 566
Euphorbiaceae	
<i>Argythamnia humilis</i> (Engelm. & Gray) Muell. Arg.	198, 558
<i>Croton texensis</i> (Kl.) Muell. Arg.	243, 405
<i>Euphorbia dentata</i> Michx.	234, 245, 248, 257, 258, 270, 288, 310, 311, 314, 326, 340
<i>Euphorbia geyeri</i> Engelm.	296
<i>Euphorbia glyptosperma</i> Engelm.	186, 301, 334
<i>Euphorbia lata</i> Engelm.	136, 217
<i>Euphorbia marginata</i> Pursh	199
<i>Euphorbia missurica</i> Raf.	206, 207, 297
<i>Euphorbia serpyllifolia</i> Pers.	393
<i>Euphorbia stictospora</i> Engelm.	187, 208, 299
Linaceae	
<i>Linum pratense</i> (Norton) Small	391, 462, 546
<i>Linum rigidum</i> Pursh.	176, 400, 492, 506
Polygalaceae	
<i>Polygala alba</i> Nutt.	158, 180
Zygophyllaceae	
<i>Kallstromia parviflora</i> Norton.	350, 373
<i>Tribulus terrestris</i> L.	185, 269
Apiaceae	
<i>Lomatium orientale</i> Coult. & Rose	466

Table 1. Continued

Taxon	Collection Number
Asclepiadaceae	
<i>Asclepias arenaria</i> Torr.	151
<i>Asclepias engelmanniana</i> Woods.	116, 263, 540, 567
<i>Asclepias latifolia</i> (Torr.) Raf.	159
<i>Asclepias pumila</i> (A. Gray) Vail	409, 564
<i>Asclepias subverticillata</i> (A. Gray) Vail	172, 205, 426, 468
Solanaceae	
<i>Chamaesaracha conoides</i> (Moric. ex Dun.) Britt.	228, 249, 300, 371
<i>Physalis hederifolia</i> A. Gray	141, 250, 359, 282, 490, 512
<i>Quincula lobata</i> (Torr.) Raf.	124, 406, 470
<i>Solanum elaeagnifolium</i> Cav.	119
<i>Solanum rostratum</i> Dun.	
<i>Solanum trifolium</i> Nutt.	232, 367, 569
Convulvulaceae	
<i>Convulvulus arvensis</i> L.	128
<i>Convulvulus equitans</i> Benth.	284, 331, 476
<i>Evolvulus nuttalliana</i> R & S.	182, 193, 203, 274, 389, 396, 484, 526, 552
Boraginaceae	
<i>Cryptantha minima</i> Rydb.	278, 420, 460
<i>Lappula redowski</i> (Hornem.) Greene	281, 395, 419
<i>Lappula texana</i> (Scheele) Britt.	366, 459, 495
<i>Lithospermum incisum</i> Lehm.	226, 358, 472, 485, 528
Verbenaceae	
<i>Lippea cuneifolia</i> (Torr.) Steud.	298, 413
<i>Verbena bipinnatifida</i> Nutt.	133, 135, 197, 279
<i>Verbena bracteata</i> Lag. & Rodr.	132, 166, 280, 335
<i>Verbena stricta</i> Vent.	556
Plantaginaceae	
<i>Plantago patagonica</i> Jacq.	347
Scrophulariaceae	
<i>Penstemon albidus</i> Nutt.	305, 398, 450, 461, 550

Table 1. Continued

Taxon	Collection Number
Asteraceae	
<i>Achillea millefolium</i> L.	121
<i>Ambrosia confertifolia</i> DC.	167, 194, 195
<i>Ambrosia grayii</i> (A. Nels.) Shinnars	412, 508
<i>Ambrosia psilostachya</i> DC.	289, 295, 354, 471, 483
<i>Artemisia filifolia</i> Torr.	157
<i>Aster falcatus</i> Lindl.	309, 332, 422a, 517, 533, 545
<i>Bacharis wrightii</i> A. Gray	189, 231, 322, 376, 390, 422b, 477, 480, 504, 538, 553, 573
<i>Chrysopsis villosa</i> (Pursh) Nutt.	380, 381, 543
<i>Chrysothamnus pulchellus</i> A. Gray	387
<i>Cirsium ochrocentrum</i> A. Gray	139, 324, 325, 378, 473, 474, 475
<i>Conyza canadensis</i> (L.) Cronq.	486
<i>Dyssodia papposa</i> (Vent.) Hitchc.	196
<i>Engelmannia pinnatifida</i> A. Gray ex Nutt.	120, 127
<i>Erigeron bellidiastrum</i> Nutt.	153, 175
<i>Erigeron divergens</i> T. & G.	353, 362
<i>Evax prolifera</i> Nutt. ex DC.	507
<i>Gaillardia pinnatifida</i> Torr.	465
<i>Gaillardia pulchella</i> Foug.	129, 318, 368
<i>Grindelia squarrosa</i> (Pursh) Dun.	168
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	165
<i>Haplopappus spinulosus</i> (Pursh) DC.	126
<i>Helianthus ciliaris</i> DC.	259
<i>Hymenopappus flavescens</i> A. Gray	122
<i>Hymenopappus tenuifolius</i> Pursh.	123, 211, 363
<i>Hymenoxys odorata</i> DC.	149, 276, 385, 554
<i>Kuhnia eupatorioides</i> L.	162, 209, 216, 220, 323, 327, 383, 384
<i>Lactuca serriola</i> L.	502, 559
<i>Leucelene ericoides</i> (Torr.) Greene.	357, 416
<i>Liatris punctata</i> Hook.	539, 549

Table 1. Continued

Taxon	Collection Number
Asteraceae	
<i>Lygodesmia junca</i> (Pursh) Hook.	411
<i>Machaeranthera tanacetifolia</i> (H. B. K.) Nees	147
<i>Melampodium luecanthum</i> T. & G.	147, 177, 178
<i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb.	341, 547, 551
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	130
<i>Ratibida tagetes</i> (James) Barnh.	160, 369, 488
<i>Senecio douglassii</i> DC. Var. <i>longilobus</i> (Benth.) Benson	138, 277
<i>Senecio riddellii</i> T. & G.	213, 221, 294, 505
<i>Senecio tridenticulatus</i> Rydb.	568
<i>Solidago mollis</i> Bartl.	403
<i>Stephanomeria pauciflora</i> (Torr.) A. Nels.	161, 201, 478, 479, 523, 537, 563, 565
<i>Taraxacum officinale</i> Weber	316
<i>Thelesperma filifolium</i> (Hook.) A. Gray	360, 515
<i>Thelesperma megapotamicum</i> (Spreng.) O. Ktze	118, 262, 518
<i>Trapopogon dubius</i> Scop.	268
<i>Vernonia marginata</i> (Torr.) Raf.	355
Commelineaceae	
<i>Commelina erecta</i> L.	156
<i>Tradescantia occidentalis</i> (Britt.) Smyth.	152
Cyperaceae	
	372
Poaceae	
<i>Agropyron smithii</i> Rydb.	174
<i>Andropogon ischaemum</i> L. var. <i>songaricus</i> Rupr. ex Fisch. & Mey.	242, 253, 286, 336, 348, 423, 496, 498, 525, 531, 534
<i>Andropogon saccharoides</i> Sw. var. <i>torreyanus</i> (Stued.) Hack.	171, 188, 467
<i>Aristida adscensionis</i> L.	272, 291, 535
<i>Aristida purpurea</i> Nutt.	287
<i>Bouteloua curtipendula</i> (Michx.) Torr.	224
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	320, 321
<i>Bromus japonicus</i> Thunb. ex Murr.	509
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	164

Table 1. Continued

Taxon	Collection Number
Poaceae	
<i>Chloris verticillata</i> Nutt.	219, 260, 313
<i>Elymus canadensis</i> L.	557
<i>Eragrostis cilianensis</i> (All.) E. Mosher	343a, 343b, 404, 415, 418
<i>Hilaria jamesii</i> (Torr.) Benth.	265, 489, 501, 591
<i>Hordeum pusillum</i> Nutt.	115, 417
<i>Muhlenbergia arenicola</i> Buck.	339, 399, 402, 407
<i>Munroa squarrosa</i> (Nutt.) Torr.	227, 349, 499
<i>Panicum hillmanii</i> Chase	292, 536
<i>Panicum capillare</i> L.	212, 244, 338, 532
<i>Panicum obtusum</i> H. B. K.	342
<i>Panicum virgatum</i> L.	304, 529, 542
<i>Panicum</i> sp.	510
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	225, 275, 285, 315, 352
<i>Setaria viridis</i> (L.) Beauv.	337
<i>Sitanion hystrix</i> (Nutt.) J. G. Sm. var. <i>brevifolium</i> (J. G. Sm.) C. L. Hitchc.	114, 223, 312, 345, 514
<i>Sporobolus asper</i> (Michx.) Kunth	238, 516
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	210, 240, 269, 312b, 351
<i>Tridens pilosus</i> (Buckl.) Hitchc.	190
Liliaceae	
<i>Allium drummondii</i> Regal	458