J. Range Manage.
55: 502-508 September 2002

# Vegetation of prairie dog colonies and non-colonized shortgrass prairie

STEPHEN L. WINTER, JACK F. CULLY, JR., AND JEFFREY S. PONTIUS

*Authors are Refuge Operations Specialist, USFWS, Santa Ana NWR, Rt. 2, Box 202A, Alamo, Tex. 78516; Assistant Unit Leader-Wildlife, USGS-BRD Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, Kans. 66506; and, Assistant Professor, Department of Statistics and Kansas State Research and Extension, Kansas State University, Manhattan, Kans. 66506. At the time of the research, the senior author was a Graduate Student, Division of Biology, Kansas State University.*

## Abstract

**Black-tailed prairie dogs have declined by 98% in the past century. Due to continued declines, the U. S. Fish and Wildlife Service designated the species as a candidate for listing in 2000. Prairie dogs foster both plant and animal diversity, and their continued presence is a concern in the Great Plains. We compared vegetation structure and composition of black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies in southwest Kansas and southeast Colorado to non-colonized grassland in 1996, and 1997. Dominant species on prairie dog colonies were *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths (14% cover in 1996, 15% in 1997), *Buchloe dactyloides* (Nutt.) Engelm. (7% cover in 1996, 17% in 1997) and *Aristida purpurea* Nutt. (9% cover in 1996, 16% in 1997). Dominant vegetation at randomly selected non-colonized sites were *Bouteloua curtipendula* (Michx.) Torr. (16% cover in 1996, 18% in 1997), *Bouteloua gracilis* (13% cover in 1996, 17% in 1997) and *Buchloe dactyloides* (5% cover in 1996, 5% in 1997). Non-colonized shortgrass sites were dominated by *Bouteloua gracilis* (23% cover in 1996, 41% in 1997) and *Buchloe dactyloides* (8% cover in 1996, 12% in 1997). Cover of grass was higher ($P < 0.01$) on random sites (44%) than on prairie dog colonies (31%) or shortgrass sites (33%) in 1996, whereas cover of forbs was higher ($P < 0.01$) on prairie dog colonies (18%) than on random sites (7%) or shortgrass sites (8%) that year. Vegetation height was greater ($Q = 3.66$) and visual obstruction was greater ($Q = 3.39$) on random sites (33.6 and 6.4 cm, respectively) than on prairie dog colonies (9.5 and 2.5 cm, respectively) in 1997, the only year these variables were measured. Percent bare ground did not differ ($P > 0.05$) among treatments either year. While components of the vegetation on prairie dog colonies differed from that found on non-colonized sites, the vegetation of prairie dog colonies was, nonetheless, characteristic of a shortgrass region. Prairie dogs undoubtably alter vegetation structure and composition in shortgrass prairie, and likely have a great influence on landscape heterogeneity, but our results suggest that shortgrass prairie is well adapted to the herbivory and soil disturbing activities of prairie dogs.**

## Resumen

**La población del perro de la pradera (cola negra) (*Cynomys ludovicianus* Ord) ha disminuido por 98% durante el siglo pasado. Debido a la reducción de su población, el perro de la pradera fuedesignado por el U.S. Fish and Wildlife Service (Servicio Estadounidense de Pesca y Vida Silvestre) con un estatus de candidato, en peligro de extinción. Los biologos se preocupan por la existencia continuada del perro de la pradera porque esta especie fomenta la biodiversidad en los ecosistemas donde habita. En la presente investigación, comparamos la estructura y composición del la vegetación de praderas colonizadas y no-colonizadas por perros de la pradera , en el suroeste de Kansas y el sureste de Colorado, en 1996 y 1997. Las especies dominantes en las colonias de perros de la pradera eran *Bouteloua gracilis* (H.B.K.) Lag ex Griffiths (14% y 15% cobertura en 1996 y 1997, respectivamente), *Buchlöe dactyloides* (Nutt.) Engelm. (7% y 17% cobertura en 1996 y 1997, respectivamente) y *Aristida purpurea* (9% y 16% cobertura en 1996 y 1997, respectivamente). La cobertura de vegetación dominante en sitios no-colonizados por perros de la pradera, seleccionados al azar, era *Bouteloua curtipendula* (Michx.) Torr. (16% y 18% en 1996 y 1997), *Bouteloua gracilis* (13% y 17% en 1996 y 1997) y *Buchlöe dactyloides* (5% en ambos años). En las praderas bajas no-colonizadas por perros de la pradera, las plantas predominantes eran *Bouteloua gracilis* (23% y 41% cobertura en 1996 y 1997) y *Buchlöe dactyloides* (8% y 12% cobertura en 1996 y 1997). La cobertura de gramíneas era mayor ($P < 0.01$) en los sitios seleccionados al azar (44%) que en las colonias de perros de la pradera (31%) o praderas bajas (33%) en 1996. Al contrario, la cobertura de plantas herbáceas era mayor ($P < 0.01$) en las colonias de perros de la pradera (18%) que en los sitios seleccionados al azar (7%) o en las praderas bajas (8%) durante el mismo año. La altura de vegetacion era mayor ($Q = 3.66$) y la obstrucción visual era mayor ($Q = 3.39$) en los sitios seleccionados al azar (33.6 y 6.4 cm, respectivamente) que en las colonias de perros de la pradera (9.5 y 2.5 cm, respectivamente) en 1997, el único año que estos datos eran mensurados. No existía diferencias ($P > 0.05$) en el porcentaje de suelo abierto entre los tratamientos durante ambos años. Aunque existen diferencias en algunos componentes de la vegetación de las colonias de perros de la pradera y los sitios no-colonizados, sin embargo la vegetacion de las colonias era característica de la region de praderas bajas. Los perros de la pradera ciertamente alteran la estructura y composición de la pradera baja, y probablemente tienen gran influencia sobre la heterogenidad del paisaje. No obstante, los resultados sugieren que la pradera baja está bien adaptada al herbívoro y los estorbos edáficos de los perros de la pradera.**

---

Funding for this project was provided by Kansas State University, Division of Biology, the U. S. Fish and Wildlife Service and the U. S. Forest Service. Access to private land in Morton County, Kans., and Baca County, Colo., was provided by the Addington, Cogburn, Eskew, Frownfelter, Jackson, Jones and Morrise families. Authors would like to acknowledge the help and support received from the following people: B. Gill and D. Mulhern, U. S. Fish and Wildlife Service; J. Hartman, J. Cline, N. Brewer, D. Simmons and K. Willimon, U. S. Forest Service; and J. Brite, Kansas Cooperative Fish and Wildlife Research Unit. E. Agner, A. Storey, J. Kretzer, J. Wertz and D. Winslow provided assistance in the field. C. Best provided the Spanish translation of the abstract. Anonymous reviewers provided numerous comments that greatly improved the manuscript.

Manuscript accepted 27 Dec. 01.

**Key Words: black-tailed prairie dog, *Cynomys ludovicianus*, cover, bare ground, frequency, shortgrass prairie, herbivory, soil disturbance**

Black-tailed prairie dogs (*Cynomys ludovicianus* Ord) alter vegetation structure, 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. 1983, Krueger 1986), Texas mixed-grass prairie (Weltzin et al. 1997b), Texas mesquite (*Prosopis glandulosa* Torr.) savanna (Weltzin et al. 1997a), and Colorado shortgrass prairie (Bonham and Lerwick 1976). The importance of prairie dog ecosystems to numerous vertebrates in the Great Plains has been demonstrated (Kotliar et al. 1999), and increased awareness of this role has prompted appeals for heightened protection of prairie dogs and changes to the management of public and private rangelands (Miller et al. 1994, Davitt et al. 1996). Black-tailed prairie dogs have declined by 98% in the past century, and due to continued recent declines, the U.S. Fish and Wildlife Service designated the species as a candidate for listing in 2000 (U.S.D.I. 2000).

The states across the range of black-tailed prairie dogs are developing an interstate conservation strategy for the species, so prairie dog conservation efforts will increasingly influence future management of western rangelands (Van Pelt 2000). Accurate information on the effects of prairie dogs on vegetation in different areas of their range will contribute significantly to rangeland management. Our purpose was to quantify differences in vegetation among prairie dog colonies and non-colonized sites in the shortgrass prairie of southwest Kansas and southeast Colorado. These findings will enhance prairie dog conservation as well as cooperation of land managers, livestock producers, conservationists, and policy makers in ensuring the maintenance of biotic integrity and economic vitality of western rangelands.

## Study Sites and Methods

Study sites were located at Cimarron National Grassland in Morton County, southwest Kansas, and adjacent private lands in Baca County, southeast Colorado (lat 37° 07'N, Long. 102° 00'W). Cimarron National Grassland comprises > 43,700 ha of predominantly grazed land administered by the U.S. Forest Service. Most of the surrounding private land is cropped, but some areas remain in perennial grass cover and are grazed by cattle (*Bos taurus* L.). A substantial portion of Cimarron National Grassland is abandoned farmland that was reclaimed between 1930 and 1950 in the Morton County Land Utilization Project (Schumacher and Atkins 1965), and it is unlikely that any of our study sites represent undisturbed relict vegetation (T. Watson, USDA-NRCS, pers. comm.).

Many areas at Cimarron National Grassland are characterized by mid-height vegetation, which may reflect the composition of seed mixes used to reclaim abandoned farmland in the 1930's to 1950's (Schumacher and Atkins 1965). Other areas are characterized by shorter vegetation which may reflect past grazing history. We chose to compare the vegetation on prairie dog colonies to 2 types of non-colonized grassland: 1) areas of short vegetation that are presumably characteristic of a shortgrass region (shortgrass sites), and 2) randomly selected areas (random sites). The criterion used to select shortgrass sites was a visual determination of dominance by the perennial shortgrasses *Buchloe dactyloides* (Nutt.) Engelm. and *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths. Conversely, random sites were selected from a list of potential sites that had soil types and slopes identical to those characterizing the prairie dog colonies. Selection of random sites occurred without knowledge of the vegetation present at those sites.

All study sites occupied 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). Even though soil type was not considered in the selection of shortgrass sites, soil type and slope of these sites were identical to those of prairie dog colonies. Mean precipitation (1901–1996) at the Elkhart weather station in Morton County is 44.8 cm (National Weather Service Cooperative Observer Network, Pers. Comm.). Precipitation during the 12 months prior to sampling in 1996 (1 July 1995, to 30 June 1996) was 34.3 cm, 76 % of the long term mean. Precipitation during the 12 months prior to sampling in 1997 (1 July 1996, to 30 June 1997) was 68.0 cm, 152% of the long term mean.

In 1996 we selected 8 of the largest prairie dog colonies on Cimarron National Grassland ($\bar{x}$ = 41.49 ha, range = 20–64 ha, total approximately 332 ha) for sampling. For comparison we selected 8 random sites ($\bar{x}$ = 56.68 ha, range = 32–64 ha, total approximately 454 ha) and 5 non-colonized shortgrass sites on Cimarron National Grassland ($\bar{x}$ = 42.10 ha, range = 32–64 ha, total approximately 210 ha). Between the 1996 and 1997 field seasons, one of the prairie dog colonies had been destroyed by plague (Cully et al. 2000) and the boundaries of another changed sufficiently to make it unsuitable for sampling, so these sites were not sampled in 1997. Completion of the 1996 field season indicated that it would be logistically possible to sample more sites, so 7 additional prairie dog colonies on Cimarron National Grassland and adjacent private lands were sampled in 1997 (n = 13, $\bar{x}$ = 39.25 ha, range = 8–125 ha, total approximately 555 ha) as well as 1 additional shortgrass site on private land (n = 6, $\bar{x}$ = 43.18 ha, range = 32 -64 ha, total approximately 260 ha). The 8 random sites evaluated in 1996 were sampled again in 1997. The exact age of prairie dog colonies sampled in this study is unknown, but at least 6 of the colonies were present in 1989 (Behan 1989).

Cattle grazing occurred at all sites prior to the study, with periods of use being variable. Season-long, rotational grazing, and fall and winter grazing were all practiced on Cimarron National Grassland and adjacent private lands. Three prairie dog colonies and 2 shortgrass sites were not grazed by cattle in 1996 and 1997. Due to drought conditions in 1996, cattle turnout did not occur until 17 June. In 1997, cattle turnout occurred 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 permittees did not rigorously adhere to grazing plans. Also, such data would have questionable value because stock were not uniformly distributed about the area.

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-$m^2$ circular plot centered on one corner of a 0.10-$m^2$ rectangular plot. Canopy cover of grass, forbs, canopy cover of individual species, and percent bare ground were estimated within the 0.10-$m^2$ plot. Frequency of occurrence of each species was quantified using both the 0.10-$m^2$ and the 10.0-$m^2$ plot. The appropriate plot size for detecting statistical differences in the frequency of a species is influenced by the density and dispersion of that species within a community (Hyder et al. 1963, 1965, 1975). Previous research in shortgrass prairie has shown that small plots sample the dominant grass, *Bouteloua gracilis*, at optimal frequencies, but fail to detect less common species (Hyder et al. 1965, 1975). We used 2 different plot sizes because concurrent use of small and large plots insures adequate sampling of species which are common and abundant, as well as species which are less commonly encountered (Hyder et al. 1965, 1975).

Congeneric species that were difficult to differentiate in the field, such as *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats. and *A. retroflexus* L., were grouped into single taxonomic groups for data analysis (e.g. *Amaranthus* spp). Nomenclature follows Great Plains Flora Association (1986). 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. Again, number of points sampled at each site varied from 35 to 120 in proportion to the area of the site. The visual obstruction pole was marked in 1 cm increments, and observations were made 1 meter from the pole at a height of 1 meter. One observation was made from each of the 4 cardinal directions at each point, and a mean calculated for each point. Vegetation height was determined by recording the highest point at which vegetation crossed between the observer and the pole. Visual obstruction 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-m$^2$ and the 10.0-m$^2$ plots. Diversity index equations were obtained from Magurran (1988). Lower values for H', E and 1/D indicate lower diversity, or a less equitable distribution of abundances among species in a sample, whereas higher values indicate more species or that abundances among species are more equitably distributed (Magurran 1988). Extreme dominance by 1 or a few species in a sample can reduce values of H', E, and 1/D, whereas maximum values are obtained when all species have equal abundances (Magurran 1988). Species richness and diversity indices for 1996 were calculated by determining the total number of species encountered at each study site (40 plots sampled per site). Because the number of points sampled at each site was variable in 1997, richness and diversity values generated using all plots at each site would not be comparable among treatments. Richness and diversity indices for 1997 were calculated by determining the number of species encountered on a 10-plot basis at each study site. Plots within each study replicate were assigned to 10 plot groups on a random basis without replacement. Richness and diversity indices for each study site were then obtained by calculating the mean of the 10-plot groups within each site.

Two-tailed tests were used to test the null hypothesis that there was not a significant difference among the means of the 3 treatments (prairie dog colonies, random sites, and shortgrass sites). The experimental units were each site within a treatment (i.e. 8 prairie dog colonies in 1996, 13 in 1997). Response variables were % cover, % bare ground, vegetation height, visual obstruction, and frequency. Data from the 2 years were not combined for analysis because of the different sampling times in each year and the addition and deletion of study sites between the 2 years. For statistical analysis we used one-factor ANOVA with 3 treatments, using SAS v. 6.11 proc glm (1996), when the assumptions of the F-test were satisfied. When the assumptions of the F-test were not satisfied, we used the Kruskal-Wallis nonparametric test (SAS v. 6.11 proc nparlway 1996) and a Tukey-type nonparametric multiple comparison method (Zar 1996). We set $\alpha = 0.05$ for hypothesis tests. A test statistic value of $Q > 2.39$ generated by the Tukey-type test indicated significant differences. When a species was detected at only 1 site it was not included in statistical evaluations.

## Results

In 1996 and 1997, respectively, we detected a total of 84 and 92 plant species or taxonomic groups on prairie dog colonies, 91and 96 on random sites, and 75 and 87 on shortgrass sites. During the 2 years, 6 species and 2 taxonomic groups were restricted to prairie dog colonies and 23 species were restricted to non-colonized sites. Nine of the 23 were encountered only on random sites, while 7 were encountered only on shortgrass sites. When frequency data from both the 0.10-m$^2$ and 10.0-m$^2$ plots were used to calculate species richness and diversity indices in 1996 and 1997, there were no significant differences ($P > 0.05$) among any of the treatments (Table 1).

In 1996, more grass cover ($P < 0.01$) occurred on random sites than on prairie dog colonies or shortgrass sites, while grass cover was similar among treatments

**Table 1. Mean (± SE) 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) of vegetation sampled in prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites during 1996 (n = 8, 8, and 5, respectively), and 1997 (n = 13, 8, and 6, respectively), in Kansas and Colorado.**

| | Prairie Dog Colonies | Random Sites | Shortgrass Sites |
|---|---|---|---|
| 0.10-m$^2$ plots - 1996 | | | |
| richness | 20.25 ± 1.05 | 18.13 ± 1.83 | 18.60 ± 2.52 |
| H' | 2.36 ± 0.05 | 2.20 ± 0.13 | 2.20 ± 0.17 |
| E | 0.79 ± 0.02 | 0.77 ± 0.02 | 0.76 ± 0.02 |
| 1/D | 8.06 ± 0.50 | 7.21 ± 1.04 | 7.14 ± 1.41 |
| 10.0-m$^2$ plots - 1996 | | | |
| richness | 41.38 ± 2.28 | 44.63 ± 1.99 | 41.2 ± 2.08 |
| H' | 3.18 ± 0.05 | 3.21 ± 0.07 | 3.12 ± 0.04 |
| E | 0.86 ± 0.01 | 0.85 ± 0.01 | 0.84 ± 0.01 |
| 1/D | 19.91 ± 0.81 | 19.68 ± 1.75 | 18.37 ± 1.06 |
| 0.10-m$^2$ plots - 1997 | | | |
| richness | 11.31 ± 0.89 | 11.00 ± 0.77 | 11.25 ± 1.06 |
| H' | 2.05 ± 0.09 | 2.07 ± 0.09 | 2.09 ± 0.11 |
| E | 0.86 ± 0.01 | 0.88 ± 0.01 | 0.88 ± 0.01 |
| 1/D | 8.11 ± 0.87 | 8.74 ± 0.87 | 8.88 ± 1.69 |
| 10.0-m$^2$ plots - 1997 | | | |
| richness | 29.21 ± 1.32 | 29.94 ± 1.53 | 28.06 ± 1.37 |
| H' | 3.05 ± 0.06 | 3.09 ± 0.06 | 3.01 ± 0.06 |
| E | 0.91 ± 0.01 | 0.91 ± 0.01 | 0.91 ± 0.01 |
| 1/D | 21.15 ± 1.34 | 22.37 ± 1.44 | 20.16 ± 1.53 |

**Table 2. Mean cover (± SE) of grasses, forbs, bare ground and the 4 dominant grasses on prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites in 1996 (n = 8, 8 and 5, respectively) and 1997 (n = 13, 8, and 6, respectively), and mean (± SE) vegetation height and visual obstruction in 1997, in Kansas and Colorado. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.**

| | Prairie Dog Colonies | Random Sites | Shortgrass Sites |
|---|---|---|---|
| 1996 | | | |
| grass | $30.71 \pm 1.79^{a}$ | $44.29 \pm 2.19^{b}$ | $32.84 \pm 1.23^{a}$ |
| forb | $18.31 \pm 2.96^{a}$ | $7.11 \pm 1.73^{b}$ | $7.63 \pm 1.47^{b}$ |
| bare ground | $30.11 \pm 3.17^{a}$ | $32.10 \pm 3.08^{a}$ | $28.25 \pm 1.95^{a}$ |
| *Aristida purpurea* Nutt. | $8.53 \pm 1.86^{a}$ | $4.29 \pm 1.62^{ab}$ | $1.67 \pm 0.47^{b}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.13 \pm 0.12^{a}$ | $16.38 \pm 4.64^{b}$ | $0.09 \pm 0.07^{a}$ |
| *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths | $14.28 \pm 4.60^{a}$ | $13.18 \pm 2.69^{a}$ | $22.99 \pm 3.08^{a}$ |
| *Buchloe dactyloides* (Nutt.) Engelm. | $7.16 \pm 1.53^{a}$ | $5.08 \pm 2.98^{a}$ | $7.62 \pm 1.74^{a}$ |
| 1997 | | | |
| grass | $51.85 \pm 3.10^{a}$ | $51.41 \pm 0.68^{a}$ | $60.01 \pm 2.90^{a}$ |
| forb | $10.56 \pm 2.57^{a}$ | $10.01 \pm 1.96^{a}$ | $6.37 \pm 1.39^{a}$ |
| bare ground | $32.70 \pm 2.61^{a}$ | $32.38 \pm 1.55^{a}$ | $27.06 \pm 4.54^{a}$ |
| *Aristida purpurea* Nutt. | $15.60 \pm 2.74^{a}$ | $4.92 \pm 1.30^{ab}$ | $4.12 \pm 0.88^{b}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.06 \pm 0.06^{a}$ | $17.85 \pm 5.37^{b}$ | $2.67 \pm 1.39^{ab}$ |
| *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths | $15.07 \pm 4.70^{a}$ | $16.74 \pm 3.02^{a}$ | $40.80 \pm 6.61^{b}$ |
| *Buchloe dactyloides* (Nutt.) Engelm. | $17.44 \pm 4.68^{a}$ | $5.12 \pm 2.51^{a}$ | $12.29 \pm 3.61^{a}$ |
| vegetation height | $9.48 \pm 0.80^{a}$ | $33.59 \pm 3.29^{b}$ | $25.22 \pm 5.50^{ab}$ |
| visual obstruction | $2.49 \pm 0.17^{a}$ | $6.41 \pm 1.32^{b}$ | $5.40 \pm 1.22^{ab}$ |

in 1997 (Table 2). In 1996, more forb cover ($P < 0.01$) occurred on prairie dog colonies than on random or shortgrass sites, but was similar ($P > 0.05$) among treatments in 1997. The amount of bare ground was similar ($P > 0.05$) among treatments in 1996 and 1997. In 1997, vegetation height was greater ($Q = 3.66$) and visual obstruction was greater ($Q = 3.39$) on random sites than on prairie dog colonies.

Based on cover, the 4 most dominant grasses were *Aristida purpurea* Nutt., *Bouteloua curtipendula* (Michx.) Torr., *Bouteloua gracilis* and *Buchloe dactyloides*. In 1996, there was more cover of *Bouteloua curtipendula* on random sites than on prairie dog colonies ($Q = 3.11$) or shortgrass sites ($Q = 2.47$), and there was more ($P = 0.01$) cover of *Aristida purpurea* on prairie dog colonies than on shortgrass sites (Table 2). In 1997, there was more cover of *Bouteloua gracilis* on shortgrass sites than on the prairie dog colonies ($P < 0.01$) or the random sites ($P < 0.01$), more ($Q = 3.84$) cover of *Bouteloua curtipendula* on the random sites than on the prairie dog colonies, and more ($Q = 2.92$) cover of *Aristida purpurea* on the prairie dog colonies than on the shortgrass sites.

Across years and plot sizes, 7 species or taxonomic groups of perennial forbs were more frequent on random sites than on prairie dog colonies during at least 1 year (Tables 3 and 4). Using the 0.10-m$^2$ plot, this difference was detected for *Psoralia tenuifolia* Pursh in 1997 ($P < 0.01$). Using the 10.0-m$^2$ plot, this difference was detected for *Astragalus lotiflorus* Hook. in 1996 ($P = 0.04$), *Gaura coccinea* Pursh in 1997 ($P < 0.01$), *Asclepias latifolia* (Torr.) Raf. in 1997 ($Q = 2.78$), *Convulvulus equitans* Benth. in 1997 ($Q = 3.49$), *Thelesperma* spp. in 1997 ($Q = 3.32$) and *Trapopogon dubius* Scop. in 1997 ($Q = 3.07$). There were no perennial forbs more frequent on prairie dog colonies than random sites.

Across years and plot sizes, 5 species or taxonomic groups of annual forbs were more frequent on prairie dog colonies than on random sites (Tables 3 and 4). Using the 0.10-m$^2$ plot, this difference was detected for *Amaranthus* spp. ($P = 0.01$) and *Euphorbia* spp. ($P < 0.01$) in 1996. Using the 10.0-m$^2$ plot, this difference was detected for *Kochia scoparia* (L.) Schrad. ($Q = 3.33$), *Salsola* spp. in 1997 ($P < 0.01$), *Euphorbia strictospora* Engelm. in 1997 ($Q = 3.15$), and for *Euphorbia* spp. in 1996 ($P < 0.01$). In both years, the annual forb, *Cryptantha minima* Rydb., was only detected on prairie dog colonies. There were no annual forbs more frequent on random sites than prairie dog colonies.

Use of the 0.10-m$^2$ plot indicated the annual grass *Hordeum pusilum* Nutt. was more frequent ($P < 0.01$) on shortgrass sites than prairie dog colonies in 1997 (Table 4). Another annual grass, *Bromus japonicus* Thunb. ex Murr., was not detected on prairie dog colonies during either year, but occurred on random and shortgrass sites in 1997. Frequencies of all other annual grasses were similar ($P > 0.05$) when prairie dog colonies were compared to shortgrass sites and random sites.

Higher frequencies ($P \leq 0.02$ in 1996, $Q \geq 2.68$ in 1997) of the perennial grass *Aristida purpurea* on prairie dog colonies than random and shortgrass sites were detected when the 0.10-m$^2$ plot was used, while both plot sizes indicated the perennial grass *Schedonnardus paniculatus* was more frequent ($P \leq 0.01$) on prairie dog colonies than random and shortgrass sites in 1997. Use of the 10.0-m$^2$ plot in 1997 indicated the perennial grass *Buchloe dactyloides* was more frequent ($P = 0.01$) on prairie dog colonies than random sites that year.

Across years and plot sizes, the perennial grass *Bouteloua curtipendula* was more frequent ($Q \geq 2.44$) on random sites than prairie dog colonies, while the perennial grass *Bouteloua gracilis* was more frequent ($P \leq 0.03$) on shortgrass sites than

**Table 3. Mean frequencies (± SE) of species that differed significantly among treatments during sampling of prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites (n = 8, 8, and 5, respectively) in Kansas and Colorado during 1996. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.**

| | Prairie Dog Colonies | Random Sites | Shortgrass Sites |
|---|---|---|---|
| 0.10-m$^2$ plots | | | |
| *Amaranthus* spp.[1] | $0.09 \pm 0.04^{a}$ | $0.01 \pm 0.01^{b}$ | 0 |
| *Euphorbia* spp.[2] | $0.72 \pm 0.07^{a}$ | $0.23 \pm 0.09^{b}$ | $0.56 \pm 0.09^{a}$ |
| *Aristida purpurea* Nutt. | $0.55 \pm 0.09^{a}$ | $0.28 \pm 0.08^{b}$ | $0.16 \pm 0.04^{b}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.01 \pm 0.01^{a}$ | $0.46 \pm 0.12^{b}$ | $0.01 \pm 0.01^{a}$ |
| *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths | $0.54 \pm 0.12^{a}$ | $0.41 \pm 0.08^{a}$ | $0.89 \pm 0.05^{b}$ |
| 10.0-m$^2$ plots | | | |
| *Astragalus lotiflorus* Hook. | $0.02 \pm 0.01^{a}$ | $0.11 \pm 0.04^{b}$ | 0 |
| *Euphorbia* spp.[2] | $0.93 \pm 0.03^{a}$ | $0.50 \pm 0.12^{b}$ | $0.93 \pm 0.05^{ab}$ |
| *Cryptantha minima* Rydb. | $0.01 \pm 0.01$ | 0 | 0 |
| *Ambrosia confertifolia* DC. | $0.05 \pm 0.03^{ab}$ | $0.01 \pm 0.01^{a}$ | $0.11 \pm 0.06^{b}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.01 \pm 0.01^{a}$ | $0.62 \pm 0.14^{b}$ | $0.04 \pm 0.02^{ab}$ |
| *Buchloe dactyloides* (Nutt.) Engelm. | $0.68 \pm 0.07^{ab}$ | $0.39 \pm 0.14^{a}$ | $0.88 \pm 0.05^{b}$ |

[1] *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.
[2] *Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

**Table 4. Mean frequencies (± SE) of species that differed significantly among treatments during sampling of prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites (n = 13, 8 and 6, respectively) in Kansas and Colorado during 1997, as well as notable species which could not be statistically analyzed. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.**

| | Prairie Dog Colonies | Random Sites | Shortgrass Sites |
|---|---|---|---|
| 0.10-m$^2$ plots | | | |
| *Euphorbia* spp.[2] | $0.72 \pm 0.07^{a}$ | $0.23 \pm 0.09^{b}$ | $0.56 \pm 0.09^{a}$ |
| *Sphaeralcea coccinea* (Pursh) Rydb. | $0.35 \pm 0.05^{a}$ | $0.24 \pm 0.04^{a}$ | $0.14 \pm 0.03^{b}$ |
| *Astragalus* spp.[1] | $0.01 \pm 0.01^{a}$ | $0.02 \pm 0.01^{b}$ | $0.01 \pm 0.01^{ab}$ |
| *Psoralea tenuifolia* Pursh | $0.01 \pm 0.01^{a}$ | $0.09 \pm 0.05^{b}$ | $0.01 \pm 0.01^{ab}$ |
| *Aristida purpurea* Nutt. | $0.62 \pm 0.07^{a}$ | $0.24 \pm 0.06^{b}$ | $0.25 \pm 0.04^{b}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.01 \pm 0.01^{a}$ | $0.43 \pm 0.12^{b}$ | $0.10 \pm 0.06^{ab}$ |
| *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths | $0.38 \pm 0.09^{a}$ | $0.42 \pm 0.08^{a}$ | $0.81 \pm 0.07^{b}$ |
| *Hordeum pusilum* Nutt. | $0.05 \pm 0.02^{a}$ | $0.03 \pm 0.01^{a}$ | $0.16 \pm 0.04^{b}$ |
| *Schedonnardus paniculatus* (Nutt.) Trel. | $0.22 \pm 0.04^{a}$ | $0.08 \pm 0.04^{b}$ | $0.06 \pm 0.03^{b}$ |
| *Sporobolus cryptandrus* (Torr.) A. Gray | $0.03 \pm 0.01^{a}$ | $0.16 \pm 0.05^{b}$ | $0.08 \pm 0.02^{ab}$ |
| 10.0-m$^2$ plots | | | |
| *Kochia scoparia* (L.) Schrad. | $0.23 \pm 0.05^{a}$ | $0.03 \pm 0.01^{b}$ | $0.09 \pm 0.04^{ab}$ |
| *Salsola* spp.[2] | $0.11 \pm 0.03^{a}$ | $0.01 \pm 0.01^{b}$ | $0.02 \pm 0.01^{b}$ |
| *Dalea enneandra* Nutt. | 0 | $0.06 \pm 0.03^{a}$ | $0.04 \pm 0.03^{a}$ |
| *Psoralea tenuifolia* Pursh | $0.12 \pm 0.04^{a}$ | $0.44 \pm 0.11^{b}$ | $0.18 \pm 0.08^{a}$ |
| *Gaura coccinea* Pursh | $0.11 \pm 0.03^{a}$ | $0.26 \pm 0.05^{b}$ | $0.07 \pm 0.02^{a}$ |
| *Oenothera triloba* Nutt. | $0.03 \pm 0.02^{a}$ | $0.02 \pm 0.01^{ab}$ | $0.06 \pm 0.01^{b}$ |
| *Euphorbia stictospora* Engelm. | $0.09 \pm 0.03^{a}$ | $0.01 \pm 0.01^{b}$ | $0.03 \pm 0.02^{ab}$ |
| *Asclepias latifolia* (Torr.) Raf. | $0.01 \pm 0.01^{a}$ | $0.03 \pm 0.01^{b}$ | $0.01 \pm 0.01^{ab}$ |
| *Convulvulus equitans* Benth. | $0.01 \pm 0.01^{a}$ | $0.04 \pm 0.01^{b}$ | $0.01 \pm 0.01^{a}$ |
| *Cryptantha minima* Rydb. | $0.14 \pm 0.04$ | 0 | 0 |
| *Thelesperma* spp.[3] | $0.07 \pm 0.07^{a}$ | $0.19 \pm 0.09^{b}$ | $0.04 \pm 0.02^{ab}$ |
| *Trapopogon dubius* Scop. | $0.01 \pm 0.01^{a}$ | $0.07 \pm 0.03^{b}$ | $0.10 \pm 0.04^{b}$ |
| *Aristida purpurea* Nutt. | $0.87 \pm 0.04^{a}$ | $0.56 \pm 0.09^{b}$ | $0.72 \pm 0.07^{ab}$ |
| *Bouteloua curtipendula* (Michx.) Torr. | $0.04 \pm 0.03^{a}$ | $0.58 \pm 0.13^{b}$ | $0.18 \pm 0.10^{ab}$ |
| *Bromus japonicus* Thunb. ex Murr. | 0 | $0.16 \pm 0.06^{a}$ | $0.18 \pm 0.14^{a}$ |
| *Buchloe dactyloides* (Nutt.) Engelm. | $0.65 \pm 0.08^{a}$ | $0.32 \pm 0.12^{b}$ | $0.74 \pm 0.07^{a}$ |
| *Hordeum pusilum* Nutt. | $0.14 \pm 0.04^{ab}$ | $0.07 \pm 0.03^{a}$ | $0.45 \pm 0.11^{b}$ |
| *Schedonnardus paniculatus* (Nutt.) Trel. | $0.66 \pm 0.06^{a}$ | $0.22 \pm 0.06^{b}$ | $0.26 \pm 0.06^{b}$ |
| *Sporobolus cryptandrus* (Torr.) A. Gray | $0.10 \pm 0.04^{a}$ | $0.38 \pm 0.09^{b}$ | $0.37 \pm 0.11^{b}$ |

[1] *Astragalus lotiflorus* Hook. and *A. nuttallianus* DC.
[2] *Salsola collina* Pall. and *S. iberica* Senn. & Pau
[3] *Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

prairie dog colonies when the 0.10-m$^2$ plot was used both years. Use of both plot sizes indicated the perennial grass *Sporobolus cryptandrus* (Torr.) A. Gray was more frequent ($P < 0.01$) on random sites than prairie dog colonies in 1997.

## Discussion

Numerous species were detected only on prairie dog colonies, or on only 1 of the non-colonized treatments, and statistical analyses was not possible for these and many others. Because the majority of these species were encountered so rarely, their presence or absence from any of the treatments is likely of no biological significance. However, some of these species deserve mention because when they did occur on 1 of the treatments, they were present in relatively high frequencies. This includes the annual forb *Cryptantha minima*, found solely on prairie dog colonies. Notable species found solely on non-colonized sites include the perennial forb *Dalea enneandra* Nutt., and the annual grass *Bromus japonicus*.

For many of the species examined in this study, differences in frequency among treatments were detected 1 year and not the other. This is likely explained by the great difference in precipitation amounts preceding each field season. Also, statistical analyses detected significant differences for some species using results from one plot size, but not the other. This is to be expected because density and dispersion characteristics of each species greatly influences the effectiveness of different sized plots used for statistical sampling (Hyder et al. 1963, 1965), and we used 2 plot sizes to account for these differences.

While analyses of the diversity indices indicated no significant differences among the treatments, analyses of the cover and frequency data revealed numerous differences, and definite trends in the data are evident. Prairie dog colonies tended to be characterized by higher cover and frequencies of perennial shortgrasses and annual forbs, whereas non-colonized random sites were characterized by higher cover and frequencies of perennial mid-height grasses and perennial forbs. Other studies have reported comparable results. Research in South Dakota (Coppock et al. 1983, Agnew et al. 1986, Archer et al. 1987) and Texas (Weltzin et al. 1997b) has consistently reported higher cover values, frequencies and biomass of mid-height grasses on non-colonized mixed-grass prairie relative to prairie dog colonies. In Colorado, Bonham and Lerwick (1976) reported higher cover of annual forbs on prairie dog colonies than in non-colonized shortgrass prairie. Likewise, in South Dakota, Archer et al. (1987) reported higher frequencies of annual forbs on prairie dog colonies than in non-colonized mixed-grass prairie. Finally, Weltzin et al. (1997b) reported that prairie dog colonies were characterized by significantly lower biomass of perennial forbs and annual grasses than non-colonized mixed-grass prairie in Texas.

Composition differences in the vegetation of prairie dog colonies and non-colonized sites are likely explained by differences in the frequency and intensity of herbivory and soil disturbance. Although graminoids tend to comprise the bulk of prairie dog diets (Hansen and Gold 1977, Summers and Linder 1978, Fagerstone et al. 1981, Wydeven and Dahlgren 1982, Uresk 1984), herbivory pressure on all vegetation within colonies should be intense, relative to non-colonized grassland. Prairie dogs can defoliate plants at the ground surface and they will dig into the soil to expose plant tissue after aboveground parts have been removed (King 1955, Koford 1958, Smith 1967). Additionally, prairie dogs forage within the confines of the colony throughout the year, so plants may be defoliated season-long, year after year. We do not know the exact ages of the colonies we sampled. However, others have demonstrated that longer periods of occupancy by prairie dogs results in greater compositional and structural contrasts between prairie dog colonies and non-colonized areas (Coppock et al 1983, Archer et al. 1987).

The perennial grasses that dominated prairie dog colonies in this study were characterized by traits that should be beneficial in environments characterized by high rates of herbivory. These include a short stature (*Bouteloua gracilis* and

*Buchloe dactyloides*), a sprawling habit (*Schedonnardus paniculatus*), and sharp-tipped awns (*Aristida purpurea*). *Buchloe dactyloides* has also been shown to be very tolerant of high rates of cattle herbivory (Klipple and Costello 1960, Launchbaugh 1967, Hart and Ashby 1998). The non-colonized random sites were characterized by taller grasses such as *Bouteloua curtipendula* and *Sporobolus cryptandrus*. The extreme herbivory pressures on prairie dog colonies likely reduces the competitive influence of many species within a colony (e.g. *Bouteloua curtipendula*), allowing species which are less palatable, or exceptionally adept at avoiding or tolerating herbivory, to experience competitive release (e.g. *Buchloe dactyloides* and *Aristida purpurea*). Differences that we detected in graminoid composition, vegetation height and visual obstruction suggest there may be less forage available for cattle on prairie dog colonies relative to non-colonized areas. However, others have argued that because a large proportion of the forage within a colony is high quality regrowth, reductions in forage quantity on colonies is compensated by an increase in forage quality (O'Meilia et al. 1982, Coppock et al. 1983, Krueger 1986).

The burrowing, digging and scratching of soil by prairie dogs may also benefit species which compete poorly with dominating perennial vegetation. Small-scale soil disturbances in shortgrass prairie have been described as "safe sites" where the overwhelming competitive effects of perennial grasses are greatly reduced (Milchunas et al. 1992, Aguilera and Lauenroth 1995). Bare and disturbed soils within prairie dog colonies may provide "safe sites" for ruderal species that can avoid or tolerate prairie dog herbivory (e.g. *Amaranthus* spp., *Euphorbia* spp., *Salsola* spp., *Kochia scoparia* and *Cryptantha minima*). While our methods were not suitable for identifying whether ruderal species were actually growing in areas of disturbed soil within a prairie dog colony, as opposed to growing within undisturbed sod, our results demonstrate that prairie dog colonies provided superior environments, relative to non-colonized areas, for many of these species.

Shortgrass prairie vegetation is considered well adapted to the herbivory of large ungulates (Mack and Thompson 1982, Milchunas et al. 1988, 1998, Hart and Ashby 1998). In shortgrass prairie, cattle grazing can homogenize vegetation, in part because the already dominant shortgrasses increase their dominance in response to herbivory (Milchunas et al. 1988, 1992, 1998, Milchunas and Lauenroth 1989). The effects of intense grazing and soil disturbance by prairie dogs on shortgrass prairie may counter the homogenizing effects of cattle grazing. The importance of prairie dogs in promoting heterogeneity in shortgrass landscapes has been asserted by others (Knopf and Sampson 1997), in part because colonies occur at a much larger scale than other disturbances in shortgrass prairie, such as cattle fecal pats, harvester ant nest sites, gopher mounds, small mammal diggings, and areas infested with root feeding beetle larvae (Coffin and Lauentroth 1988, Martinsen et al. 1990, Milchunas et al. 1992).

We found numerous differences among the vegetation of prairie dog colonies and non-colonized areas, especially when prairie dog colonies were compared to random sites. We conclude that prairie dogs influence shortgrass prairie in a manner which causes the vegetation of colonies to be distinct from that of adjacent non-colonized areas. However, in spite of these differences, our results also lead us to conclude that prairie dogs do not substantially alter the essential character of shortgrass vegetation. While frequencies of various plant components were altered on prairie dog colonies, and some lesser components were missing, all of the components typical of the region's vegetation were present. Colonies were dominated by perennial warm-season grasses characteristic of a shortgrass region, and colonies had similar amounts of bare ground when compared to non-colonized sites.

Shortgrass prairie is considered well adapted to the herbivory of large ungulates. We suggest shortgrass prairie is also well adapted to the levels of prairie dog herbivory and soil disturbance that were present at our study sites. While prairie dogs undoubtably alter shortgrass prairie, they are one of many forces and disturbances that have shaped and defined the vegetation of this region, and prairie dog colonies represent one point along a gradient which depicts the range of variability for shortgrass vegetation.

## Literature Cited

**Agnew, W., D. W. Uresk, and R. M. Hansen. 1986.** Flora and Fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. J. Range Manage. 39:135–139.

**Aguilera, M. O. and W. K. Lauenroth. 1995.** Influence of gap disturbance and type of microsites on seedling establishment in *Bouteloua gracilis*. J. Ecol. 83:87–97.

**Archer, S., M. G. Garrett and J. K. Detling. 1987.** Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159–166.

**Behan, B. 1989.** Management of black-tailed prairie dogs on the Cimarron National Grassland. Unpublished Rep., Cimarron Nat. Grassl., USDA Forest Service.

**Bonham, C. D. and A. Lerwick. 1976.** Vegetation changes induced by prairie dogs on shortgrass ranges. J. Range Manage. 29:221–225.

**Cid, M. S., J. K. Detling, A. D. Whicker and M. A. Brizuela. 1991.** Vegetational response of a mixed prairie site following exclusion of prairie dogs and bison. J. Range Manage. 44:100–105.

**Coffin, D. P. and W. K. Lauenroth. 1988.** The effects of disturbance size and frequency on a shortgrass plant community. Ecol. 69:1609–1617.

**Coppock, D. L., J. K. Detling, J. E. Ellis and M. I. Dyer. 1983.** Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1–9.

**Cully, J. F. Jr., L. G. Carter, and K. L. Gage. 2000.** New records of sylvatic plague in Kansas. J. of Wildl. Diseases. 36:389–392.

**Davitt, K., R. Grandi, C. Neasel, and T. Skeele. 1996.** Conserving prairie dog ecosystems on the Northern Plains: learning from the past to insure the prairie dogs future. Predator Project, Bozeman, Mont.

**Dickey, H. P., W. R. Swafford, and Q. L. Markley. 1963.** Soil survey of Morton county, Kansas. USDA Soil Conserv. Service, U.S. Government Printing Office, Washington D.C.

**Fagerstone, K. A., H. P. Tietjen and O. Williams. 1981.** Seasonal variation in the diet of black-tailed prairie dogs. J. Mammal. 62:820–824.

**Great Plains Flora Association. 1986.** Flora of the Great Plains. University Press of Kansas. Lawrence, Kan.

**Hansen, R. M. and I. K. Gold. 1977.** Black-tailed prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. J. Range Manage. 30:210–214.

**Hart, R. H. and M. M. Ashby. 1998.** Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. J. Range Manage. 51:392–398.

**Hyder, D. N., C. E. Conrad, P. T. Tueller, L. D. Calvin, C. E. Poulton and F. A. Sneva. 1963**. Frequency sampling in sagebrush-bunchgrass vegetation. Ecol. 44:740–746.

**Hyder, D. N., R. E. Bement, E. E. Remmenga and C. Terwilliger, Jr. 1965.** Frequency sampling of blue grama range. J. Range Manage. 18:90–94.

**Hyder, D. N., R. E. Bement, E. E. Remmenga and D. F. Harvey. 1975.** Ecological responses of native plants and guidelines for management of shortgrass prairie. USDA-ARS Tech. Bull. No. 1503, U.S. Gov. Printing Office, Washington, D.C.

**King, J. A. 1955.** Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vertebr. Biol., Univ. Michigan. No. 67.

**Klipple, G. E., and D. F. Costello. 1960.** Vegetation and cattle responses to different intensities of grazing on shortgrass ranges of the central Great Plains. USDA Tech. Bull. 1216.

**Knopf, F. L. and F. B. Sampson. 1997.** Conservation of grassland vertebrates. P. 273–289. *In:* F. L. Knopf and F. B. Sampson (eds), Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York.

**Koford, C. B. 1958.** Prairie dogs, whitefaces, and blue grama. Wildl. Monogr. No. 3.

**Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999.** A critical review of assumptions about the prairie dog as a keystone species. Environ. Manage. 24:177–192.

**Krueger, K. 1986.** Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecol. 67:760–770.

**Launchbaugh, J. L. 1967.** Vegetation relationships associated with intensity of summer grazing on a clay upland range site in the Kansas 20- to 24-inch precipitation zone. Kansas Agr. Exp. Sta. Tech. Bull. 154.

**Mack, R. N. and J. N. Thompson. 1982.** Evolution in steppe with few large, hooved mammals. Amer. Natur. 119:757-773.

**Magurran, A. E. 1988.** Ecological Diversity and its Measurement. Princeton University Press, Princeton, N.J.

**Martinson, G. D., J. H. Cushman, and T. G. Whitham. 1990.** Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie. Oecologia 83:132–138.

**Milchunas, G. D. and W. K. Lauenroth. 1989.** Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82–86.

**Milchunas, D. G., W. K. Lauerenroth, and I. C. Burke. 1998.** Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos 83:65–74.

**Milchunas, D. G., W. K. Lauenroth, and P.L. Chapman. 1992.** Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. Oecologia 92:520–531.

**Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988.** A generalized model of the effects of grazing by large herbivores on grassland community structure. Amer. Natur. 132:87–106.

**Miller, B., G. Ceballos, and R. Reading. 1994.** The prairie dog and biotic diversity. Conserv. Biol. 8:677–681.

**O'Meilia, M. E., F. L. Knopf and J. C. Lewis. 1982.** Some consequences of competition between prairie dogs (*Cynomys ludovicianus*) and beef cattle. J. Range Manage. 35:580–585.

**Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970.** Relationships between visual obstruction measurements and weight of grassland vegetation. J. Range Manage. 23:295–297.

**SAS Institute. 1996.** SAS/STAT user's guide, version 6.11. SAS Institute, Cary, N.C.

**Schumacher, C. M. and M. D. Atkins. 1965.** Reestablishment and use of grass in the Morton County, Kansas, land utilization project. U.S. Dept. Agr., Soil Cons. Serv., SCS-TP-146.

**Smith, R. E. 1967.** Natural history of the prairie dog in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Pub. No 49.

**Summers, C. A. and R. L. Linder. 1978.** Food habits of the black-tailed prairie dog in western South Dakota. J. Range Manage. 31:134–136.

**Uresk, D. W. 1984.** Black-tailed prairie dog food habits and forage relationships in western South Dakota. J. Range Manage. 22:322–328.

**U.S.D. I. 2000.** Endangered and threatened wildlife and plants; 12-month finding for a petition to list the black-tailed prairie dog as Threatened. Federal Register 65:5476–5488.

**Van Pelt, W. E. 2000.** The black-tailed prairie dog conservation assessment and strategy-fifth draft. Arizona Game and Fish Dept, Phoenix, Ariz. http://www.r6.fws.gov/btprairiedog/conassstrat.htm

**Weltzin, J. F., S. Archer, and R. K. Heitschmidt. 1997a.** Small mammal regulation of vegetation structure in a temperate savanna. Ecol. 78:751–763.

**Weltzin, J. F., S. L. Dowhower, and R. K. Heitschmidt. 1997b.** Prairie dog effects on plant community structure in southern mixed-grass prairie. SW Natur. 42:251–258.

**Wydeven, P. R. and R. B. Dahlgren. 1982.** A comparison of prairie dog stomach contents and feces using a microhistological technique. J. Wildl. Manage. 46:1104–1108.

**Zar, J. H. 1996.** Biostatistical Analysis. Prentice-Hall, Inc. Upper Saddle River, N.J.