



## **Presence of both Active and Inactive Colonies of Prairie Dogs Contributes to Higher Vegetation Heterogeneity at the Landscape Scale**

Authors: Aamand Gervin, Cæcilie, Bruun, Hans Henrik, Seipel, Tim, and Burgess, Neil D.

Source: The American Midland Naturalist, 181(2) : 183-194

Published By: University of Notre Dame

URL: <https://doi.org/10.1674/0003-0031-181.2.183>

---

BioOne Complete ([complete.BioOne.org](http://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Presence of both Active and Inactive Colonies of Prairie Dogs Contributes to Higher Vegetation Heterogeneity at the Landscape Scale

CÆCILIE AAMAND GERVIN<sup>1</sup> AND HANS HENRIK BRUUN

*Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark*

TIM SEIPEL

*Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717*

AND

NEIL D. BURGESS

*UN Environment World Conservation Monitoring Centre (UNEP WCMC), 219 Huntingdon Road, Cambridge, CB3 0DL, United Kingdom and Natural History, Museum of Denmark, Centre for Macroecology, Evolution & Climate, University of Copenhagen, Denmark*

**ABSTRACT.**—Black-tailed prairie dogs are herbivorous rodents known to have large effects on grassland landscapes in North America. They have considerable impacts on prairie plant communities as the result of repeated clipping of vegetation that can reduce preferred forage species and may indirectly result in increased abundance of disturbance-tolerant species. We investigated plant communities within three different habitat types: Active and inactive prairie dog colonies, and adjacent suitable, but unoccupied, control areas in the Northern Great Plains of Montana, U.S.A. Plant species richness did not vary markedly between the three habitat types. However, plant composition measured as cover of plant life forms (forbs, shrubs, and graminoids), which was further divided into native status (native or introduced), and plant species indicators (plant species associated with a specific habitat) did vary distinctly between the three habitat types. Differences in plant composition between the habitat types suggests black-tailed prairie dog activities result in greater diversity of plant microhabitats at a landscape scale, and prairie dogs are an important component of the overall ecosystem in the Northern Great Plains of North America.

## INTRODUCTION

Different ecological processes (*e.g.* grazing by prairie dogs and bison, wallowing by bison, and fire) are natural components of the prairie ecosystem that affect its species composition. Understanding the role of these different processes on plant communities is valuable for improved conservation management of the remaining natural grassland.

Black-tailed prairie dogs (*Cynomys ludovicianus*) – hereafter simply “prairie dogs” – are burrowing mammals known to impact grassland landscapes and are often considered as keystone species (Kotliar *et al.*, 1999; Kotliar *et al.*, 2000, Kotliar *et al.*, 2006; Miller *et al.*, 1994). Prairie dogs numbered about five billion individuals in the late nineteenth century and their colonies occupied millions of hectares in the U.S.A., Canada, and Mexico. However, range managers perceived prairie dogs as competing with domestic livestock and prairie dogs were often killed. Persecution, habitat destruction, and disease (*i.e.* sylvatic plague) are the main factors behind the reduction in prairie dog populations to less than two percent of their historic numbers about 200 years ago (Hoogland, 2006).

<sup>1</sup> Corresponding author: Telephone: (4500) 20768100; e-mail: caecilie.gervin@hotmail.com

Several animal species rely to some extent on the occurrence of prairie dogs (Augustine and Baker, 2012; Lomolino and Smith, 2003) and the loss of prairie dogs may be a threat to the overall diversity of the prairie ecosystem (Miller *et al.*, 1994; Sampson and Knopf, 1994). For example, prairie dogs are important to the burrowing owl (*Athene cunicularia*) that nests in prairie dogs' burrows (Restani *et al.*, 2001) and to the black-footed ferret (*Mustela nigripes*) that preys on the prairie dogs and depend on their burrows for shelter (Reading and Matchett, 1997). The burrowing and grazing activities of prairie dogs also influence the prairie vegetation (Archer *et al.*, 1987; Bonham and Lerwick, 1976; Coppock *et al.*, 1983; Johnson-Nistler *et al.*, 2004; Weltzin *et al.*, 1997a; Whicker and Detling, 1988). For example, Coppock *et al.* (1983) found grasses dominate areas recently colonized by prairie dogs and forbs increase over time following colonization. Late in the colonization process, they found both forbs and sub-shrubs (*Artemisia frigida*) dominated. Furthermore, Klatt and Hein (1978) studied the vegetation in one active prairie dog colony and three colonies that had been inactive for 1, 2, and 5 y, respectively. They found the cover of perennial grasses to be highest in the active colony and decreasing with time after abandonment. In addition, they found markedly more species of forbs in the area abandoned by prairie dogs for 1 y as compared to the other areas. However, studies of the vegetation within inactive prairie dog colonies are limited (Klatt and Hein, 1978; Osborn and Allan, 1949). The goal of our study was to assess the effect of black-tailed prairie dogs on plant species richness and plant composition within both active and inactive prairie dog colonies compared to control areas with no history of prairie dog presence. Because the presence of different "disturbance" levels creates greater vegetation heterogeneity in the landscape, we hypothesized that the presence of both active and inactive prairie dog colonies would influence vegetation heterogeneity more than the presence of active colonies alone.

## METHODS

### STUDY SITE

Vegetation was sampled from May to July 2013 at Sun Prairie on the American Prairie Reserve (APR) (47°74'46"N, 107°77'59"W) just north of the Missouri River and the Charles M. Russell Wildlife Refuge in Phillips County, Montana (Fig. 1). Precipitation in Sun Prairie averages 280 mm annually. Winters are cold with a long-term January average of -13.3 C, whereas summers are warm with a long-term July average of 19.2 C. The frost-free growing season averages 112 d and begins mid-May. The study area is at the southern tip of the glaciated plains and topography varies from flat plains to gently sloping hills (Johnson-Nistler *et al.*, 2004).

The region is a top priority for grassland conservation due to its wildlife species and intact native vegetation (TNC, 1999). The APR was established in 2004 with the aim to promote the conservation of diverse prairie ecosystems, including establishing a wild bison herd and promoting the expansion of prairie dogs (APR, 2018). The vegetation of this area is classified as northern mixed-grass prairie, where grasses typical of a mixed-grass prairie, such as western wheatgrass (*Pascopyrum smithii*) and Sandberg bluegrass (*Poa secunda*), dominate the area (Johnson-Nistler *et al.*, 2004). However, big sagebrush (*Artemisia tridentata*) also covers large areas. The majority of land in the area is administered by the Bureau of Land Management (BLM), and the United States Fish and Wildlife Service (USFWS), for the purpose of conserving wildlife habitat and providing allotments for domestic livestock grazing.

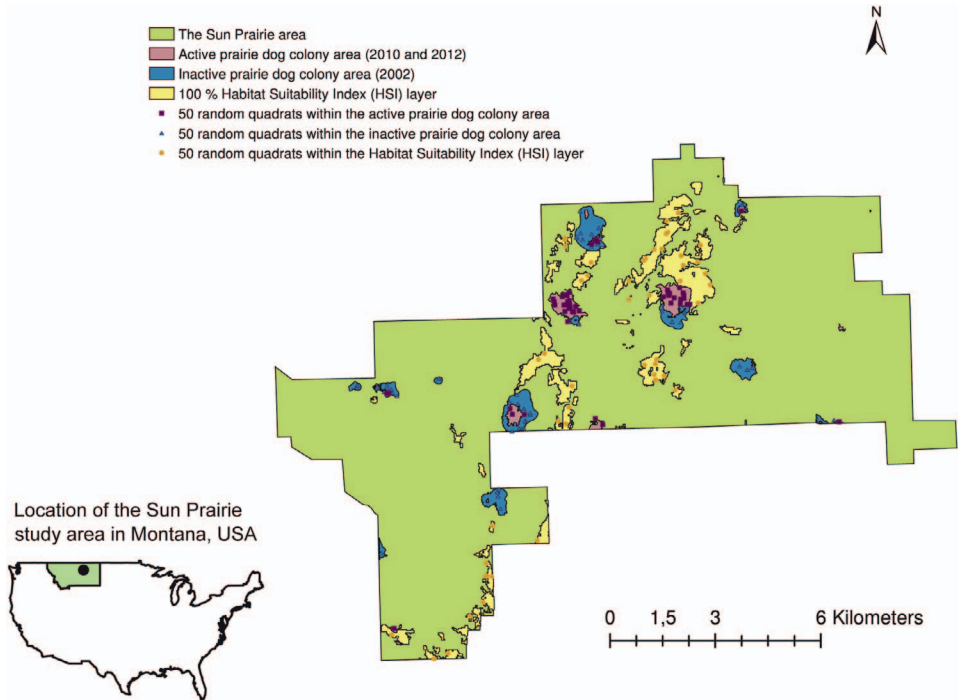


FIG. 1.—The study site at the Sun Prairie, American Prairie Reserve, Phillips County, Montana, with the placement of the 150 quadrats within the three habitat types: (1) Active prairie dog colony areas, (2) inactive prairie dog colony areas, and (3) control areas (the 100 % Habitat Suitability Index layer) (ArcGIS version 10.2)

Herbivorous mammals in the APR region include *e.g.* the black-tailed prairie dogs (*Cynomys ludovicianus*), American bison (*Bison bison*) together with other ungulates (APR, 2018). Prairie dogs have occupied the region continuously; however, some colonies have died out locally due to sylvatic plague.

#### SAMPLING DESIGN

Prairie dog colonies were mapped using Global Positioning System (GPS) across southern Phillips County, including the APR, in the years 2002, 2010, and 2012. Colony boundaries were determined using prairie dog burrows at the edge of the colony. Based on the mapping in 2010 and 2012, 16 colonies were selected for further study (Fig. 1). Mapping from 2002 was used to select 13 inactive colonies that had been abandoned between 2002 and 2012. We did not have information on the age of colonies, but it is likely that we sampled colonies of different ages. Control areas with no colonies present were identified as habitats suitable for prairie dogs using a habitat suitability Index (HSI) made in a Geographical Information System (GIS; Fig. 1). The HSI layer was based on the following variables: (I) four specific vegetative categories (low cover grasslands, salt-desert shrub, dry salt-flats, and mixed barren

sites); (II) slopes of 0–4% (approximately 0–2°); and (III) clay-loam soils (Proctor, 1990). The HSI layer is scored as a percentage, such that areas assessed as most suitable for prairie dogs score 100%. Areas of the HSI layer that overlapped with either inactive or active colonies were excluded so that the HSI layer could function as control area (Fig. 1). Only areas with a score of 100% were used as control areas in this study.

The vegetation survey used a stratified random design, where 50 quadrats were randomly placed within each of three different strata – hereafter referred to as habitat types - in the survey area: (1) active prairie dog colonies, (2) inactive colonies (abandoned more than 1 y previously), and (3) control areas with no recent or known history of prairie dog activity, but identified as habitats suitable for prairie dogs (using HSI layer). The 50 quadrats were distributed randomly within each of the three habitat types using GIS (ArcGIS version 10.2) (Fig. 1). Quadrats were located in the field using a GPS.

#### VEGETATION SAMPLING PROCEDURE

We recorded the cover of each plant species within 1 m<sup>2</sup> quadrats, as recommended for grasslands (Kent, 2012). A pinpoint frame (Jonasson, 1988; Kent, 2012) consisting of a grid of 100 intersecting grid points made up each quadrat. A pin was inserted vertically through each of the 100 grid points and the number of plant species that were touched by the pin was recorded. Plant cover was determined as a percentage. In addition, we recorded whether the same plant species (either as the same individual or as another individual) was touched more than once by a pin at each grid point. Plant species that were not touched by a pin, but were located within the quadrat, were allocated a cover value of 0.1%. All vascular plants in each quadrat were identified to species level in each habitat type. Nomenclature follows the *Manual of Montana Vascular Plants* (Lesica, 2012) and the United States Department of Agriculture (USDA) plants database (USDA, 2018). A complete plant species list is in Appendix 1.

#### PLANT DIVERSITY METRICS AND DATA ANALYSIS

All analyses were conducted in the R statistical environment (R Core Team, 2016). Plant species richness was determined as the number of plant species within a quadrat. Differences in plant species richness among the three habitat types were assessed using one-way ANOVA and post-hoc Tukey test (R Core Team, 2016).

The cover by different plant life forms (forbs, shrubs, or graminoids) was determined by summing covers of plant species belonging to each category within the quadrats and then calculating the mean value for each habitat type. Plant life form categories were taken from the USDA plants database (USDA, 2018). For plant life form category individually, we assessed differences in mean cover between habitat types using Kruskal-Wallis H-test and post-hoc Mann-Whitney U-test (R Core Team, 2016). In addition, the cover of the different plant life forms within each habitat type were further divided according to native status (native or introduced). Native status was taken from the USDA plants database (USDA, 2018).

To assess whether plant species were associated with either active colonies, inactive colonies, or control areas, we used Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997; R Core Team, 2016). The probability that a species was indicative of the habitat type in question was calculated based on a permutation test (De Cáceres and Legendre, 2009).

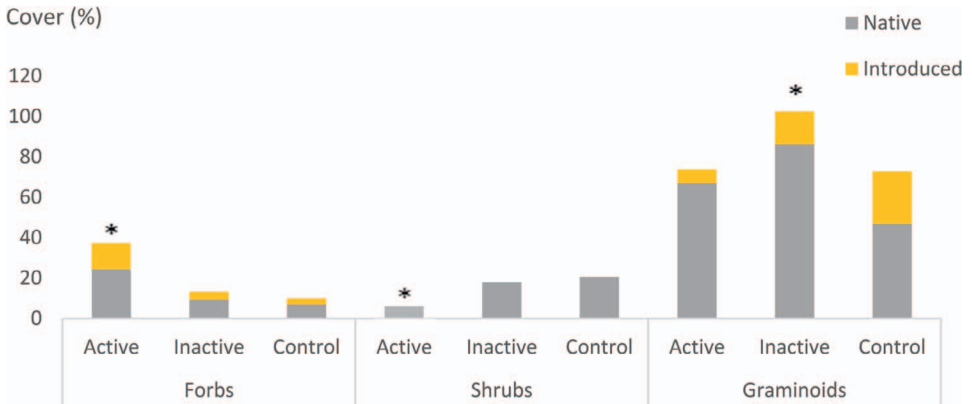


FIG. 2.—Mean values of life form cover in percentage: Forbs, shrubs, and graminoids were found from a total of 50 quadrats in each habitat type: Active prairie dog colonies (active), inactive prairie dog colonies (inactive), and control areas (control). An asterisk indicates if medians were significantly different (Mann-Whitney U-test,  $P < 0.05$ ). In addition, the distribution of cover of native and introduced plant species within each life form for each habitat type has been added to the figure, where color indicates cover values by native status

## RESULTS

### PLANT SPECIES RICHNESS

Variation in plant species richness between habitat types was generally small, compared to variation within habitat types. However, plant species richness was slightly higher in inactive colonies ( $10.4 \pm 3.9$  SD) than control areas ( $9.7 \pm 3.3$  SD) or active colonies ( $8.0 \pm 3.9$  SD), with the difference between active and inactive colonies being significant ( $df = 147$ ,  $F = 5.54$ ,  $P < 0.01$ ).

### PLANT LIFE FORM COMPOSITION AND NATIVE STATUS

All three habitat types were dominated by graminoids with mean covers between 72.9–102.5 % (Fig. 2). The cover of forbs ( $df = 2$ ,  $H = 10.44$ ,  $P < 0.01$ ), shrubs ( $df = 2$ ,  $H = 20.17$ ,  $P < 0.01$ ), and graminoids ( $df = 2$ ,  $H = 10.11$ ,  $P < 0.01$ ) varied between each habitat type. The cover of forbs was significantly higher in active colonies ( $37.3 \pm 58.0$  SD) compared to both inactive colonies ( $13.1 \pm 14.7$  SD) and control areas ( $9.8 \pm 12.0$  SD). The cover of graminoids was significantly higher in the inactive colonies ( $102.5 \pm 57.6$  SD) compared to both active colonies ( $73.7 \pm 72.7$  SD) and control areas ( $72.9 \pm 57.8$  SD). The cover of shrubs was significantly lower in the active colonies ( $5.8 \pm 16.8$  SD) compared to both inactive colonies ( $17.8 \pm 30.7$  SD) and control areas ( $20.5 \pm 24.5$  SD).

All three habitat types were dominated by native plant species in terms of cover (Fig. 2). However, native plant species had higher relative cover in active and inactive colonies than in control areas.

### INDICATOR PLANT SPECIES

For each habitat type, five to seven plant species were indicators, meaning that these species occurred more often than expected by chance within the three different habitat

TABLE 1.—The Indicator Species Analysis was based on a total of 50 quadrats in each habitat type: Active prairie dog colonies, inactive prairie dog colonies, and control areas. Abbreviations for the life form categories: AF: Annual forbs, PF: Perennial forbs, AG: Annual graminoids, PG: Perennial graminoids and PS: Perennial shrubs. Abbreviations for native status: N: Native and I: Introduced

| Plant species                  | Life form and native status | Indicator value (%) | P value |
|--------------------------------|-----------------------------|---------------------|---------|
| Active                         |                             |                     |         |
| <i>Monolepis nuttalliana</i>   | AF, N                       | 48.03               | 0.001   |
| <i>Plantago elongata</i>       | AF, N                       | 36.70               | 0.014   |
| <i>Kochia scoparia</i>         | AF, I                       | 35.51               | 0.004   |
| <i>Euphorbia serpyllifolia</i> | AF, N                       | 33.52               | 0.001   |
| <i>Plantago patagonica</i>     | AF, N                       | 21.44               | 0.038   |
| <i>Lappula redowski</i>        | AF, N                       | 19.24               | 0.011   |
| <i>Rumex crispus</i>           | PF, I                       | 8.00                | 0.032   |
| Inactive                       |                             |                     |         |
| <i>Pascopyrum smithii</i>      | PG, N                       | 42.13               | 0.003   |
| <i>Bouteloua gracilis</i>      | PG, N                       | 19.89               | 0.035   |
| <i>Filago arvensis</i>         | AF, I                       | 19.62               | 0.002   |
| <i>Hedeoma hispida</i>         | AF, N                       | 13.48               | 0.039   |
| <i>Koeleria macrantha</i>      | PG, N                       | 13.14               | 0.014   |
| Control                        |                             |                     |         |
| <i>Bromus japonicus</i>        | AG, I                       | 32.86               | 0.048   |
| <i>Opuntia polyacantha</i>     | PS, N                       | 29.39               | 0.001   |
| <i>Agropyron cristatum</i>     | PG, I                       | 27.20               | 0.001   |
| <i>Artemisia tridentata</i>    | PS, N                       | 25.03               | 0.028   |
| <i>Thlaspi arvense</i>         | AF, I                       | 13.28               | 0.021   |
| <i>Elymus elymoides</i>        | PG, N                       | 12.74               | 0.023   |
| <i>Lepidium perfoliatum</i>    | AF, I                       | 10.00               | 0.019   |

types. Indicators of active colonies were mainly forbs, where two indicator species out of seven were introduced plant species. Indicators of inactive colonies were a mix of forbs and graminoids, where one indicator species out of five was an introduced species. Indicators of control areas were a mix of forbs, shrubs, and graminoids, where four indicator species out of seven were introduced species (Table 1).

#### DISCUSSION

We have shown that plant species richness was slightly lower in active prairie dog colonies than in either inactive colonies or the surrounding matrix, and there were significant differences in plant species richness between active and inactive colonies; however, the difference was small (2.4 plant species on average). Despite little variation in species richness, we found distinct differences in plant community composition between active and inactive colonies and areas not occupied by prairie dogs.

The higher cover of forbs in the active colonies compared to the other two habitat types could be due to most forb species in the active colonies being annuals (Appendix 1), which can serve as pioneer species as they are often more adapted to colonize disturbed sites compared to perennials (Braidek *et al.*, 1984). Adding to this, is the fact that prairie dogs, in general, select against forbs and prefer graminoids for forage (Hansen and Gold, 1977; Uresk, 1984). In addition, indicator species of the active colonies were all short-lived, disturbance-adapted forbs. This result is also in agreement with the study by Coppock *et al.*

(1983), which found that forbs can dominate as a result of prairie dog disturbance. In contrast, Klatt and Hein (1978) found a higher cover of forbs in colonies abandoned for 1 y. This is likely a transient effect of terminated disturbance, in which the pioneer-adapted forbs have a greater chance to colonize the area before competition from other perennial plant species begins. The inactive colonies in our study were likely abandoned for more than 1 y, which may help explain the differences we found. The cover of shrubs was significantly lower in the active colonies than in the other two habitat types. Previous studies have found similar patterns. For example, Nistler *et al.* (2004) found the cover of the shrub *Artemisia tridentata* was greater in uncolonized sites than colonized sites, which were on average older than 20 y, and suggested prairie dogs actively eliminate *Artemisia tridentata* during their colonization process. A similar study showed the woody species, Honey mosquito (*Prosopis glandulosa*), was suppressed by prairie dogs (Weltzin *et al.*, 1997b). In our study, the cover of *Artemisia tridentata* in particular was much lower in the active colonies than in the other two habitat types (Appendix 1). Prairie dogs actively cut down *Artemisia tridentata* to create a better view of potential predators or for communication purposes (Archer *et al.*, 1987).

The plant life form composition in the inactive colonies may be the product of ceased grazing pressure making the habitat less disturbed but with the former presence of prairie dogs continuing to have legacy effects. The significantly higher cover of graminoids in inactive colonies may be attributed to release from grazing but where the larger shrubs has not yet started to outcompete the grasses as seen in the control areas (Fig. 2). In addition, three graminoids, *Pascopyrum smithii*, *Bouteloua gracilis*, and *Koeleria macrantha*, were indicator species of the inactive colonies. Other studies have found the cover of perennial grasses to peak in active colonies (Klatt and Hein 1978). However, at the species level, our findings agree with Klatt and Hein (1978), who found that the dominant perennial grass *Pascopyrum smithii* to have its lowest cover in active colonies. Detling and Painter (1983) found *Pascopyrum smithii* to produce more tillers in a prairie dog colony compared to a grazing enclosure, corroborating our observation of a release effect.

Both active and inactive colonies contained more native plant species than the control areas. Moreover, Larson *et al.* (2003) and Beals *et al.* (2014) also found a higher number of native plants within prairie dog colonies compared to undisturbed areas. A reason could be that prairie dogs are long-standing inhabitants of the northern Great Plains (Goodwin, 1995) and their effects on soil and vegetation create a disturbance regime under which native plants have had the opportunity to adapt (Koford, 1958). Beals *et al.* (2014) found prairie dogs actually increase not only the number of native forbs but also the number of introduced forbs. They attributed this to ample propagules of introduced plants within the surrounding urban landscape. Consistent with Beals *et al.* (2014), we found that the cover of introduced forbs was higher in active colonies compared with control areas. This can be attributed to *Kochia scoparia*, an introduced agricultural weed common in surrounding crop fields and highly disturbed areas. In addition, *Kochia scoparia* was an indicator species of active colonies. In contrast, the cover of introduced graminoids was highest in the control areas compared to the other two habitat types, which could partly be due to the relatively high number of introduced *Agropyron cristatum* (Appendix 1). An opposite pattern is found for the widespread native rhizomatous *Pascopyrum smithii*, which seems to have adapted to the prairie dog grazing by producing tillers.

To summarize, this study suggests prairie dogs do not contribute to higher within-colony plant species richness. However, plant community composition, specifically the distribution in cover of different plant life forms, the distribution of native and introduced plant species, and plant species indicators varied among active and inactive colonies, and control areas.



The plant community patterns we found confirm our hypothesis that prairie dogs create vegetation heterogeneity, and the resulting vegetation within active colonies can be regarded as highly disturbed by prairie dogs, inactive colonies can be regarded as moderately affected by the former disturbance by prairie dogs, and the control areas without any colonization history can be regarded as undisturbed or mostly undisturbed.

*Acknowledgments.*—We thank the American Prairie Reserve for access to sites and information on the distribution of prairie dogs. We thank Dennis Jorgensen, Kristy Bly, and Sarah Olimb from the World Wildlife Fund (WWF) for logistical help. Also a special thanks to Steve Bless for all his support in the beginning of the fieldwork. Thanks to Ryan L. Rauscher, wildlife Biologist from the Montana Fish, Wildlife and Parks for giving information about the habitat suitability index (HSI) used as control areas in this study. Thanks to Christian Nyrop Albers and Ingelise Nørgaard from the Geological Survey of Denmark and Greenland (GEUS) for their help with the soil analyses. Thanks to Ida Theilade, professor, and Henrik Meilby, professor from the University of Copenhagen for inspiration and help.

#### LITERATURE CITED

- APR. 2018. American Prairie Reserve, <http://www.americanprairie.org/>.
- 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
- AUGUSTINE, D. J. AND B. W. BAKER. 2012. Associations of grassland bird communities with black-tailed prairie dogs in the North American Great Plains, *Conserv Biol.*, **27**:324–334
- BEALS, S. C., L. M. HARTLEY, J. S. PREVÉY, AND T. R. SEASTEDT. 2014. The effects of black-tailed prairie dogs on plant communities within a complex urban landscape: An ecological surprise?, *Ecology*, **95**:1349–1359
- BONHAM, C. D., AND A. LERWICK. 1976. Vegetation changes induced by prairie dogs on shortgrass range, *J Range Manage*, **29**:221–225
- BRAIDEK, J. T., P. FEDEC, AND D. JONES. 1984. Field survey of halophytic plants of disturbed sites on the Canadian prairies, *Can J Plant Sci*, **64**:745–751
- 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
- DE CÁCERES, M. D., AND P. LEGENDRE. 2009. Associations between species and groups of sites: indices and statistical inference, *Ecology*, **90**:3566–3574
- DETLING, J. K., AND E. L., PAINTER. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing, *Oecologia*, **57**:65–71
- DUFRENE, M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach, *Ecol Monogr*, **67**:345–366
- GOODWIN, H. T. 1995. Pliocene-pleistocene biogeographic history of prairie dogs, genus *Cynomys* (Sciuridae), *J Mammal*, **76**:100–122
- HANSEN, R. M., AND I. K. GOLD. 1977. Blacktail prairie dogs, desert cottontails and cattle trophic relations on shortgrass range, *J Range Manage*, **30**:210–214
- HOOGLAND, J. L. 2006. Conservation of the black-tailed prairie dog, saving North America's western grasslands. 1st edition. Island Press. 342 pages
- JOHNSON-NISTLER, C. M., B. F. SOWELL, H. W., SHERWOOD, AND C. L. WAMBOLT. 2004. Black-tailed prairie dog effects on Montana's mixed-grass prairie, *J Range Manage*, **57**:641–648
- JONASSON, S. 1988. Evaluation of the point intercept method for the estimation of plant biomass, *Oikos*, **52**:101–106
- KENT, M. 2012. Vegetation description and data analysis, a practical approach, Second edition. Wiley-Blackwell. 428 pages
- KLATT, L. E., AND D., HEIN. 1978. Vegetative differences among active and abandoned towns of black-tailed prairie dogs (*Cynomys ludovicianus*), *J Range Manage*, **31**:315–317

- KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama, *Wildlife Monogr*, **3**:3–78
- 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
- KOTLIAR, N. B. 2000. Application of the new keystone-concept to prairie dogs: How well does it work? *Conserv Biol*, **14**:1715–1721
- KOTLIAR, N. B., B. J., MILLER, R. P., READING, AND T. W. CLARK. 2006. The Prairie Dog as a Keystone Species, p. 70–81. In HOOGLAND, J. L. (ed.). Conservation of the black-tailed prairie dog, saving North America's western grasslands. 1st edition. Island Press
- LARSON, D. L. 2003. Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie, *Plant Ecol*, **169**:317–333
- LESICA, P. 2012. Manual of Montana vascular plants, Brit Press
- LOMOLINO, M. V., AND G. A. SMITH. 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns, *Biol Conserv*, **115**:89–100
- MILLER, B., G. CEBALLOS, AND R. READING. 1994. The prairie dog and biotic diversity, *Conserv Biol*, **8**:677–681
- OSBORN, B., AND P. F. ALLAN. 1949. Vegetation of an abandoned prairie-dog town in tall grass prairie, *Ecology*, **30**:322–332
- PROCTOR, J. 1990. A GIS model for identifying potential black-tailed prairie dog habitat in the Northern Great Plains shortgrass prairie. M.S. Thesis, University of Montana, Montana, 56 pages
- R CORE TEAM. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- READING, R. P., AND R. MATCHETT. 1997. Attributes of black-tailed prairie dog colonies in Northcentral Montana, *J Wildlife Manage*, **61**:664–673
- RESTANI, M., L. R. RAU, AND D. L., FLATH. 2001. Nesting ecology of burrowing owls occupying black-tailed prairie dog towns in Southeastern Montana, *J Raptor Res*, **35**:296–303
- SAMPSON, F., AND F., KNOPF. 1994. Prairie conservation in North America, *BioScience*, **44**:418–421
- TNC, THE NATURE CONSERVANCY, 1999. Ecoregional Planning in the Northern Great Plains Steppe, [https://www.conservationgateway.org/ConservationPlanning/SettingPriorities/EcoregionalReports/Documents/ngps\\_final\\_feb99.pdf](https://www.conservationgateway.org/ConservationPlanning/SettingPriorities/EcoregionalReports/Documents/ngps_final_feb99.pdf).
- URESK, D. W. 1984. Black-tailed Prairie Dog Food Habits and Forage Relationships in Western South Dakota, *J Range Manage*, **37**:325–329
- USDA, NRCS. 2018. The PLANTS Database National Plant Data Team, Greensboro, NC 27401-4901 USA, <http://plants.usda.gov>
- WELTZIN, J. F., S. L. DOWHOWER, AND R. K. HEITSCHMIDT. 1997a. Prairie dog effects on plant community structure in southern mixed-grass prairie, *Southwest Nat*, **42**:251–258
- WELTZIN, J. F., S. ARCHER, AND R. K. HEITSCHMIDT. 1997b. Small-mammal regulation of vegetation structure in a temperate savanna, *Ecology*, **78**:751–763
- WHICKER, A. D., AND J. K. DETLING. 1988. Ecological consequences of prairie dog disturbances, *Bioscience*, **38**:778–785

SUBMITTED 15 JULY 2018

ACCEPTED 11 SEPTEMBER 2018

APPENDIX 1.—Plant species list with mean cover values of quadrats (in %) for each habitat type

|   | Native status | Habitat type |          |         |
|---|---------------|--------------|----------|---------|
|   |               | Active       | Inactive | Control |
| <b>Annual forbs</b>                                       |               |              |          |         |
| <i>Alyssum desertorum</i> Stapf                           | I             | 0.022        | 0.122    | 0.04    |
| <i>Androsace occidentalis</i> Pursh                       | N             | 0.002        | 0        | 0       |
| <i>Atriplex suckleyi</i> (Torr.) Rydb.                    | N             | 0            | 0.08     | 0.004   |
| <i>Camelina microcarpa</i> Andr. ex DC.                   | I             | 0.35         | 0.85     | 1.1     |
| <i>Chenopodium berlandieri</i> Moq.                       | N             | 0.004        | 0        | 0       |
| <i>Chenopodium leptophyllum</i> (Moq.) Nutt. ex S. Watson | N             | 0.002        | 0.02     | 0.002   |
| <i>Chorispora tenella</i> (Pall.) DC.                     | I             | 0.022        | 0.04     | 0       |
| <i>Collomia linearis</i> Nutt.                            | N             | 0            | 0        | 0.042   |
| <i>Draba verna</i> L.                                     | I             | 0.2          | 0.068    | 0       |
| <i>Euphorbia serpyllifolia</i> Pers.                      | N             | 1.94         | 0        | 0.028   |
| <i>Filago arvensis</i> L.                                 | I             | 0.002        | 0.412    | 0.006   |
| <i>Hedeoma hispida</i> Pursh                              | N             | 0.026        | 0.15     | 0.002   |
| <i>Helianthus annuus</i> L.                               | N             | 0            | 0.002    | 0.042   |
| <i>Kochia scoparia</i> (L.) Schrad                        | I             | 9.796        | 1.116    | 0.122   |
| <i>Lactuca serriola</i> L.                                | I             | 0.022        | 0.08     | 0.028   |
| <i>Lappula redowski</i> (Hornem. Greene)                  | N             | 0.256        | 0.086    | 0.004   |
| <i>Lepidium densiflorum</i> Schrad.                       | N             | 0.41         | 0.286    | 0.154   |
| <i>Lepidium perfoliatum</i> L.                            | I             | 0.1          | 0.02     | 0.6     |
| <i>Monolepis nuttalliana</i> (Schult.) Greene             | N             | 10.034       | 0.348    | 0.898   |
| <i>Myosurus minimus</i> L.                                | N             | 0.04         | 0.02     | 0.002   |
| <i>Plagiobothrys leptocladus</i> (Greene) I. M. Johnst.   | N             | 1.262        | 0.022    | 0       |
| <i>Plantago elongata</i> Pursh                            | N             | 4.77         | 0.622    | 0.328   |
| <i>Plantago patagonica</i> Jacq.                          | N             | 0.57         | 0.062    | 0.006   |
| <i>Ranunculus testiculatus</i> Crantz                     | I             | 0.082        | 0.002    | 0.002   |
| <i>Solanum triflorum</i> Nutt.                            | N             | 0.006        | 0        | 0       |
| <i>Thlaspi arvense</i> L.                                 | I             | 0            | 0.006    | 0.11    |
| <i>Tragopogon dubius</i> Scop.                            | I             | 0.122        | 0.182    | 0.226   |
| <i>Veronica peregrina</i> L.                              | N             | 0.022        | 0        | 0.02    |
| <b>Perennial forbs</b>                                    |               |              |          |         |
| <i>Achillea millefolium</i> L.                            | N             | 0            | 0.02     | 0.002   |
| <i>Allium textile</i> A. Nelson & J. F. Macbr.            | N             | 0.048        | 0.486    | 0.452   |
| <i>Astragalus adsurgens</i> Pall.                         | N             | 0            | 0        | 0.06    |
| <i>Astragalus agrestis</i> Douglas ex G. Don              | N             | 0.202        | 0.4      | 0       |
| <i>Astragalus purshii</i> Douglas ex Hook.                | N             | 0            | 0        | 0.002   |
| <i>Atriplex argentea</i> Nutt.                            | N             | 0.962        | 0.006    | 0.144   |
| <i>Boechea retrofracta</i> (Graham) A. Löve & D. Löve     | N             | 0.02         | 0        | 0       |
| <i>Cirsium arvense</i> (L.) Scop.                         | I             | 0            | 0.04     | 0       |
| <i>Cymopterus acaulis</i> (Pursh) Raf.                    | N             | 0            | 0        | 0.002   |
| <i>Descurainia pinnata</i> (Walter) Britton               | N             | 0            | 0.046    | 0.06    |
| <i>Erigeron ochroleucus</i> Nutt.                         | N             | 0            | 0.082    | 0.004   |
| <i>Euphorbia spathulata</i> Lam.                          | N             | 0.002        | 0        | 0       |
| <i>Glycyrrhiza lepidota</i> Nutt. ex Pursh                | N             | 0            | 0.002    | 0       |
| <i>Grindelia squarrosa</i> (Pursh) Dunal                  | N             | 0            | 0        | 0.08    |
| <i>Lactuca pulchella</i> (Pursh) DC.                      | N             | 0            | 0.04     | 0       |
| <i>Liatris punctata</i> Hook.                             | N             | 0            | 0        | 0.002   |
| <i>Limosella aquatica</i> L.                              | N             | 0.402        | 0        | 0       |

## APPENDIX 1.—Continued

|   | Native status | Habitat type |          |         |
|---|---------------|--------------|----------|---------|
|   |               | Active       | Inactive | Control |
| <i>Linum rigidum</i> Pursh                                    | N             | 0            | 0        | 0.02    |
| <i>Lithospermum ruderale</i> Douglas ex Lehm.                 | N             | 0            | 0        | 0.002   |
| <i>Lomatium foeniculaceum</i> (Nutt.) J. M. Coult. & Rose     | N             | 0.08         | 0.226    | 0.224   |
| <i>Machaeranthera canescens</i> (Pursh) A. Gray               | N             | 0            | 0        | 0.006   |
| <i>Medicago lupulina</i> L.                                   | I             | 0            | 0.006    | 0       |
| <i>Medicago sativa</i> L.                                     | I             | 0            | 0        | 0.042   |
| <i>Melilotus officinalis</i> (L.) Pall.                       | I             | 0.04         | 0        | 0       |
| <i>Musineon divaricatum</i> (Pursh) Raf.                      | N             | 0.002        | 0.022    | 0.002   |
| <i>Pediomelum argophyllum</i> (Pursh) J. W. Grimes            | N             | 0            | 0.12     | 0       |
| <i>Phlox hoodii</i> Richardson                                | N             | 0            | 0.226    | 0.122   |
| <i>Polygonum aviculare</i> L.                                 | I             | 1.594        | 0.966    | 0.648   |
| <i>Rumex crispus</i> L.                                       | I             | 0.586        | 0        | 0       |
| <i>Selaginella densa</i> Rydb.                                | N             | 0.36         | 2.422    | 2.28    |
| <i>Symphotrichum falcatum</i> (Lindl.) G. L. Nesom            | N             | 0            | 0.04     | 0       |
| <i>Taraxacum officinale</i> F. H. Wigg                        | N             | 1.416        | 1.224    | 1.544   |
| <i>Verbena bracteata</i> Lag. & Rodr.                         | N             | 0.02         | 0.062    | 0       |
| <i>Vicia americana</i> Muhl. ex Willd.                        | N             | 0.882        | 2.1      | 0.382   |
| <i>Viola nuttallii</i> Pursh                                  | N             | 0.62         | 0        | 0       |
| <b>Annual graminoids</b>                                      |               |              |          |         |
| <i>Bromus japonicus</i> Thunb.                                | I             | 5.23         | 16.252   | 17.154  |
| <i>Hordeum pusillum</i> Nutt.                                 | N             | 0            | 0.2      | 0.144   |
| <i>Munroa squarrosa</i> (Nutt.) Torr.                         | N             | 0.004        | 0        | 0.002   |
| <i>Setaria viridis</i> (L.) P. Beauv.                         | I             | 0.02         | 0        | 0       |
| <i>Vulpia octoflora</i> (Walter) Rydb.                        | N             | 0.084        | 0.13     | 0.164   |
| <b>Perennial graminoids</b>                                   |               |              |          |         |
| <i>Agropyron cristatum</i> (L.) Gaertn.                       | I             | 1.4          | 0.202    | 9.08    |
| <i>Pascopyrum smithii</i> (Rydb.) Á. Löve                     | N             | 42.204       | 54.462   | 19.682  |
| <i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths | N             | 2.642        | 8.46     | 5.062   |
| <i>Carex filifolia</i> Nutt.                                  | N             | 0.002        | 0        | 0.24    |
| <i>Distichlis spicata</i> (L.) Greene                         | N             | 0.88         | 1.022    | 0.182   |
| <i>Eleocharis acicularis</i> (L.) Roem. & Schult              | N             | 0            | 0.02     | 0       |
| <i>Eleocharis palustris</i> (L.) Roem. & Schult.              | N             | 7.86         | 0        | 0       |
| <i>Elymus elymoides</i> (Raf.) Swezey                         | N             | 0            | 0.342    | 0.6     |
| <i>Hordeum jubatum</i> L.                                     | N             | 0.04         | 0        | 0.04    |
| <i>Koeleria macrantha</i> (Ledeb.) Schult.                    | N             | 0.26         | 2.204    | 0.22    |
| <i>Poa arida</i> Vasey  | N             | 0            | 0        | 0.82    |
| <i>Poa pratensis</i> L.                                       | N             | 0.34         | 2.124    | 0.942   |
| <i>Poa secunda</i> J. Presl                                   | N             | 12.59        | 16.25    | 16.648  |
| <i>Schedonnardus paniculatus</i> (Nutt.) Trel.                | N             | 0.112        | 0.148    | 0.068   |
| <i>Stipa comata</i> Trin. & Rupr.                             | N             | 0            | 0.68     | 1.7     |
| <i>Stipa viridula</i> Trin.                                   | N             | 0            | 0        | 0.16    |
| <b>Perennial shrubs</b>                                       |               |              |          |         |
| <i>Artemisia frigida</i> Willd.                               | N             | 0.418        | 0.39     | 0.086   |
| <i>Artemisia tridentata</i> Nutt.                             | N             | 2.84         | 14.226   | 14.866  |
| <i>Atriplex gardneri</i> (Moq.) D. Dietr.                     | N             | 0            | 0.104    | 0.44    |
| <i>Comandra umbellata</i> (L.) Nutt                           | N             | 0            | 0.04     | 0.002   |
| <i>Coryphantha missouriensis</i> (Sweet) Britton & Rose       | N             | 0.002        | 0.002    | 0       |

## APPENDIX 1.—Continued

|  | Native status | Habitat type |          |         |
|--|---------------|--------------|----------|---------|
|  |               | Active       | Inactive | Control |
| <i>Eriogonum pauciflorum</i> Pursh                               | N             | 0            | 0.24     | 0       |
| <i>Gaura coccinea</i> Pursh                                      | N             | 0            | 0.002    | 0       |
| <i>Gutierrezia sarothrae</i> (Pursh) Britton & Rusby             | N             | 0            | 0.462    | 0.002   |
| <i>Iva axillaris</i> Pursh                                       | N             | 0.002        | 0        | 0.062   |
| <i>Krascheninnikovia lanata</i> (Pursh) A. Meeuse & A. Smit      | N             | 0            | 0.002    | 0       |
| <i>Opuntia polyacantha</i> Haw.                                  | N             | 0.002        | 0.244    | 1.57    |
| <i>Picradeniopsis oppositifolia</i> (Nutt.) Rydb.                | N             | 0.002        | 0        | 0       |
| <i>Sarcobatus vermiculatus</i> (Hook.) Torr.                     | N             | 1.944        | 1.682    | 3.204   |
| <i>Sphaeralcea coccinea</i> (Nutt.) Rydb.                        | N             | 0.55         | 0.45     | 0.26    |
| <i>Suaeda nigra</i> (Raf.) J. F. Macbride                        | N             | 0.002        | 0        | 0       |
| <i>Suaeda occidentalis</i> (S. Watson) S. Watson                 | N             | 0            | 0        | 0.002   |
| <i>Xanthisma spinulosum</i> (Pursh) D. R. Morgan & R. L. Hartman | N             | 0.08         | 0        | 0       |

The cover of plant species in each habitat type (Active = active prairie dog colony, Inactive = inactive prairie dog colony and Control = control area) was measured provided with data about native status (N = Native species and I = Introduced species). The information about the plant species life forms and native status is from the Plants Database by the United States Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS) (USDA, 2018). Some of the plant species were categorized into more than one life form in the database. In these situations a subjective judgement of the most appropriate life form category was chosen for the plant species in question.