Effects of black-tailed prairie dogs on the mixed-grass prairie in Montana
by Carolyn Marie Johnson

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal and Range Sciences
Montana State University

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ABSTRACT

Forty paired sites were examined in northeastern Montana to compare the effects of prairie dog colonies on vegetation attributes. Thirty 0.025m^2 quadrats were placed in colonized and uncolonized locations and matched by environmental conditions. Cover and standing crop biomass of each plant species was estimated using a double sampling procedure where every third plot was clipped and estimated. A total of 2400 quadrats were estimated, while 720 were clipped over 2 growing seasons. Crude protein, digestibility, NDF and ADF were determined based on vegetative classes (cool-season grasses, warm-season grasses, standing dead grass, forbs and dwarf-shrubs). Standing crop biomass, plant species richness, litter, standing crop crude protein, sagebrush canopy cover and density was greater ($P<0.05$) on uncolonized areas. Bare ground and crude protein concentration was greater ($P<0.05$) on areas colonized by prairie dogs. Digestibility and fiber content of both areas was not different ($P>0.05$). Prairie dog activity reduced productivity of the mixed-grass prairie by reducing cool-season grasses and eliminating sagebrush.

CHAPTER 1

INTRODUCTION

Meriwether Lewis first documented the black-tailed prairie dog *(Cynomys ludovicianus)* in 1804 (Thwaites 1904). Occupation of grasslands prior to European settlement is uncertain, but estimates from the turn of the 20th century suggest that prairie dogs inhabited 100-200 million acres throughout the Great Plains (Merriam 1902). Prairie dogs rapidly colonized areas that had been overgrazed or converted to croplands. The prairie dog was seen as an agricultural pest, and widespread eradication programs began as early as the 1920's throughout the species' home range of the prairie dog (Barko 1997). Poisoning and shooting campaigns continued throughout most of the 20th century. The public's attitude toward the prairie dog has shifted in recent years, as preservation of the grassland ecosystem has gained importance. In 1998, the United States Fish and Wildlife Service (USFWS) received a petition requesting immediate consideration of the black-tailed prairie dog to be protected as a threatened species.

This recent petition to list prairie dogs heightened the controversy surrounding prairie dogs. The USFWS found that protection was warranted, but was precluded due to other species in more imminent need of protection. The black-tailed prairie dog is currently considered a "candidate" species, one that receives yearly review by the USFWS to determine whether protection is needed.

The petition to list the prairie dog suggested that prairie dogs have "beneficial or neutral effects on livestock forage" (Graber et al. 1998). Much of the literature supporting this idea suggest that the activities of prairie dogs do not affect standing crop biomass, increase plant species richness, and increase plant nutrient content on prairie dog colonies (Graber et al. 1998).

The research supporting these conclusions has been conducted on the mixed-grass prairie in South Dakota and the short-grass steppe in Colorado, but do not appear to address observed effects of prairie dogs on the mixed-grass prairie of Montana. The objectives of this study were to compare total plant biomass, plant species richness, cover, nutritional differences, and shrub dynamics between prairie dog colonies and adjacent uncolonized sites.

CHAPTER 2

LITERATURE REVIEW

Features of the Mixed-Grass Prairie

The mixed-grass prairie is the largest of North American range regions, occupying 30 million ha. (Holechek et al. 1998). Nearly 60% of agricultural lands in this region support native vegetation and are used for livestock grazing (Lauenroth et al. 1994). The mixed-grass prairie is one of the most productive types of rangeland for both livestock and wildlife.

Precipitation of the northern mixed grass prairie averages 28 cm annually. During a normal year, about 80% of the precipitation falls during the April-September growing season (USDA 1981). Winters are cold with a long-term January average of –10.4° C. Summers are warm with a long-term July average of 19.2° C (USDA 1981). The growing season lasts approximately 112 days and begins mid-May. High winds, blizzards, droughts and thunderstorms are common in this region (Goetz 1988)

Topography of the northern mixed-grass prairie varies from flat upland plains to gently sloping hills. Elevations range from 600 to 1060 meters. Soils have a thin soil surface underlain by hardpan. Permeability is slow. Soil taxonomic units which characterize this site include Absher, Elloam and Thoeny (USDA 1981).

Vegetation of the Mixed-Grass Prairie

In pristine condition, the mixed-grass prairie consists largely of a variety of cool and warm-season short and mid-grasses. These may include a dominance of cool-season grasses such as western wheatgrass (*Agropyron smithii* Rydb.) and needle-and thread (*Stipa comata* Trin & Rupr.). Relative composition of many ecological sites consists of approximately 75% cool-season (C_3) grass, 10% warm-season (C_4) grass, 10% forbs, and 5% shrubs (USDA 1981). Forbs occur seasonally throughout the mixed grass prairie, and become an important component at certain times of the year. Big sagebrush (*Artemisia tridentata Nutt.*) may be present in undisturbed rangelands. Sagebrush harbors tremendous value to the native rangeland in that it retains moisture in the soil (Lusby 1979), contributes nutrients to the soil (Hormay 1970), and allows associated grass species to grow (Daubenmire 1970).

Although of little or no value to livestock, sagebrush has important food and cover values for many wildlife species associated with rangelands at high seral stage such as sage grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Pediocetes phasianellus*), elk (*Cervus elephus*), mule deer (*Odocoileus hemionus*) and antelope (*Antilocapra americana*) (Peterson 1995). Efforts to remove sagebrush have been shown to reduce the seral stage of a vegetative community (Muegler 1980).

Heavy herbivory by cattle may also change plant communities. Long term grazing has produced and maintained early seral vegetation throughout much of the west

(Longhurst et al. 1982). In areas heavily grazed by livestock, productive perennial grasses that are usually associated with an ecosystem in a high seral stage are gradually replaced by plants of increasingly lower productivity generally associated with rangeland in a lower seral stage such as fringed sagewort (*Artemisia frigida* Willd.) and prickly pear cactus (*Opuntia spp.*) (Holochek et al. 1989).

Range sites in northeastern Montana that have sustained heavy grazing typically have higher proportions of warm-season vegetation, unpalatable shrubs and annual forbs, characteristic of rangeland in low seral stage (Holochek 1989 and Singh et al. 1983) when compared to ungrazed rangeland in higher seral stage. The relative composition by weight of vegetation at a low seral site is approximately 15% cool-season (C_3) grasses, 15% warm-season (C_4) grasses, 50% forbs and 20% shrubs for northeastern Montana (USDA 1981). Forbs and shrubs replace grass as the dominant plant type, and warm-season low-statured grasses such as blue grama replace many of the cool-season mid-grasses such as western and bluebunch wheatgrass.

The plant species composition shifts that occur due to overgrazing will facilitate a change in associated animal species as well. Areas characteristic of an intensely grazed lower seral stage, may attract fauna which require less herbaceous cover and more bare ground than areas in more pristine conditions such as mountain plovers (*Charadrius montanus*), burrowing owls (*Speotyto cunicularia*) and black-tailed prairie dogs (*Cynomys ludovicianus*) (Clark 1992).

Prairie Dog Colonies

Prairie dog towns are located on relatively level terrain. The slope of most prairie dog colonies ranges from 2-4%. In north-central Montana, there were more colonies and a higher percentage of colony area on land with 0-2% slope than there were on randomized polygons of the study area (Reading, 1997).

Agricultural producers and scientists have continued to question the impacts of prairie dogs on rangelands, especially since the petition to list prairie dogs as a threatened species was written. Previous research from various geographic locations has examined the effects of prairie dogs on vegetation of the mixed-grass prairie.

Effects of Prairie Dogs on Vegetation

Early literature documenting effects of prairie dogs on rangeland suggest that activities of prairie dogs greatly diminish forage production. King (1955) found activities of prairie dogs cause "destruction of grass." Koford (1958) stated that, "under certain conditions, prairie dogs may remove all of the forage crop." These findings lead early investigators to conclude that the presence of prairie dogs provided no benefit to man or livestock.

Literature published in the last thirty years suggests that prairie dogs may not be entirely detrimental to rangelands. Bonham and Lerwick (1976) quantified vegetation changes induced by prairie dogs and concluded that "prairie dogs are not always destructive to rangelands." Whicker and Detling (1988) suggest that large herbivores preferentially select for prairie dog colonies over other areas and therefore may improve grazing conditions for other ungulates.

Standing Crop Biomass and Plant Species Composition

Prairie dogs have been shown to have varying effects on plant production. Standing crop biomass on prairie dog colonies has been evaluated in relation to age of establishment, influences of cattle grazing, and production within and outside of grazing exclosures. Because potential plant communities vary due to range site, many different results have been reported.

Prairie dogs have significant impacts on the standing crop biomass of the southern mixed-grass prairie (Weltzin et al. 1997). Total live herbaceous standing crop biomass was reported as being three to four times greater off a prairie dog colony when compared to that found on the same colony. A major contributor to this difference was cool season midgrasses that were 6-15 times greater on the uncolonized rangeland. Shortgrasses did not differ between treatments (Weltzin et al. 1997).

Age of different zones within a prairie dog town has been found to affect plant biomass production (Coppock et al. 1983). On the mixed-grass prairie of South Dakota, plant production of three zones within a colony and one area adjacent to a prairie dog town were sampled. These categories were: uncolonized rangeland, an edge zone (occupied for less than two years), a moderately grazed zone (occupied for three to eight years), and a heavily utilized zone (occupied for greater than 26 years). Greatest peak live plant biomass was reported on the uncolonized rangeland (190g/m^2). The least amount of biomass was reported on the young portion of the prairie dog colony (95g/m^2). Peak live plant biomass of the oldest portion of the colony did not differ from the adjacent uncolonized rangeland (170g/m). Although total biomass production was not different, less than 3% of the available biomass on the oldest portion of the prairie dog town consisted of graminoids, whereas graminoids composed greater than 85% of the total available biomass on the adjacent uncolonized rangeland (Coppock et al.1983).

In an effort to evaluate prairie dog control in South Dakota, production data was collected on an ungrazed exclosure and an area grazed by prairie dogs only (Collins et al. 1984). Total production was not significantly different on a prairie dog grazed area (1199 kg/ha) when compared to an ungrazed exclosure (1170 kg/ha). However, production of needleleaf sedge, *Carex eleocharis* Bailey, was approximately two times greater within the grazing exclosure than within the prairie dog grazed area. Additionally, production of scarlet globemallow, *Sphaeralcea coccinea* Pursh Rydb., was more than two times as abundant within the prairie dog grazed area than within the grazing exclosure (Collins et al. 1984).

The activities of prairie dogs have been shown to alter plant communities. The grass:forb ratio usually decreases with increased prairie dog occupancy (Bonham and Lerwick 1976). Archer et al. (1987) reported a shift from perennial grasses to annual and perennial forbs, as well as a shift from taller to shorter morphs of the same plant species with increased prairie dog occupancy. As prairie dogs are controlled, mesquite increases in abundance (Miller at al. 1994). Weltzin et al. (1997) found that prairie dogs remove pods and seeds and strip bark from young mesquite (*Prosopis glandulosa*) plants, thereby preventing or reducing mesquite establishment on colonies.

Findings from Texas were inconsistent with those from South Dakota. This may be due to differences in range site, precipitation or age of colony sampling zone. Results indicate that effects of prairie dog colonies on native vegetation are not uniform throughout the home range of the prairie dog.

Species Richness

Activities of prairie dogs may influence plant species composition on native rangelands. One way to measure plant species composition is by simply counting the total number of plant species found at one site and comparing it to that at another site. This is known as plant species richness and may vary temporally and geographically.

Research has shown that time since colonization plays an important role in plant species composition within a prairie dog town (Archer et al. 1987). In the mixed grass prairie of South Dakota, species richness of grasses decreased while species richness of forbs increased with increasing age of a prairie dog town. Total species richness was reported as increasing up to six years after occupancy by prairie dogs (Archer et al. 1987). This is consistent with findings of research completed three years earlier in the same geographic region (Coppock et al. 1983). In the shortgrass steppe of Colorado, prairie dog activity increased both perennial and annual species, resulting in greater species richness within a prairie dog colony when compared to uncolonized rangeland (Bonham and Lerwick 1976).

Prairie dog activity has also been shown to have detrimental effects on plant species richness (Agnew et al. 1986, Weltzin et al. 1997). In a two-year study conducted in South Dakota, plant species richness was found to be greater both years on ungrazed rangeland than land occupied by prairie dogs (Agnew et al. 1986). On the mixed-grass prairie of Texas, prairie dogs altered relative distribution, abundance and composition of vegetation, resulting in a dominance of warm season shortgrasses and lower species richness on a prairie dog colony when compared to uncolonized rangeland. (Weltzin et al. 1997).

Cover

Ground cover may have important implications for wildlife species and overall plant production, serving as an indicator of a site (Wilde and Leaf 1955). Litter and increased organic matter are inputs to soil and may provide micro-habitats useful to birds and invertebrates. Increased amounts of bare ground tend to increase soil erosion and water runoff (Dyksterhuis 1947). Ground cover as well as percent cover of individual plant species may be impacted by the activities of prairie dogs.

Prairie dog colonization on native rangeland may have varying effects on percent cover. Vegetative cover has been shown to be greater off a prairie dog colony at certain times of the year when compared to colonized areas (Agnew et al. 1986). Percent cover of grass and litter tend to decrease due to prairie dog colonization, while forb percent cover tended to increase (Agnew et al. 1986, Archer et al. 1987).

Colonization by prairie dogs may have an impact on plant species cover as well. In the short-grass steppe of Colorado, it has been shown that percent cover of blue grama (*Bouteloua gracilis* H.B.K. Lag ex Steud), and buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.) is higher on uncolonized rangeland, while percent cover of sixweeks fescue (*Vulpia octoflora* (Walt.) Rydb.) is higher in an area colonized by prairie dogs (Bonham and Lerwick 1976).

Associated Fauna

Presence of prairie dog colonies may have a substantial impact on associated animal species. The effect of prairie dog colonies on birds and small rodent populations may vary from beneficial for some species to detrimental to others (Agnew et al. 1986).

Clark et al. (1982) reported 107 vertebrate species and subspecies associated with colonies of prairie dogs. These species include: the black-footed ferret (*Mustela nigripes*), swift fox (*Vulpes velox*), golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*), mountain plover (*Charadrius montanus*), and burrowing owl (*Speotyto cunicularia*).

Although there are a number of animal species associated with prairie dog towns, the black-footed ferret is the only species which relies solely on prairie dog colonies for survival. The black-footed ferret, currently an endangered species, relies on prairie dogs as a primary food source and makes its home in prairie dog burrows (Campbell 1987).

Presence of prairie dog colonies tend to increase the presence of fauna such as black-footed ferrets and burrowing owls which thrive on the habitat created by prairie dogs (Clark 1992). This alteration of habitat may decrease the presence of other species such as western harvest mice and 13-lined ground squirrels (Agnew et al. 1986).

Prairie Dog Colonies and Ungulate Grazing

Prairie dog colony effects on livestock grazing have been questioned almost as long as domestic livestock have been present on the Great Plains. In the past, lands inhabited by prairie dogs were considered practically worthless for livestock grazing (King 1955, Koford 1958). More recently, it has been suggested that prairie dogs may enhance ungulate grazing by increasing the nutritive content of forages located on a prairie dog colony and therefore increasing grazing use (Coppock et al. 1983).

Research on the mixed-grass prairie of South Dakota found that shoot nitrogen concentration and in vitro dry matter digestibility (IVDMD) was lowest in plants collected from a site uncolonized by prairie dogs and increased as a function of time since colonization by prairie dogs on the mixed-grass prairie of South Dakota (Coppock et al. 1983a). These authors concluded that prairie dogs facilitate bison *(Bison bison)* habitat selection by causing a structural change in the vegetation in these areas and that bison prefer to graze on prairie dog towns (Coppock et al. 1983b). It has been suggested that the increase in crude protein content on prairie dog towns may be beneficial to cattle as well (Long 1998).

The effect of herbivory, regardless of the grazing animal, has been shown to increase nutrient concentration availability on rangelands. Heitschmidt et al. (1989) reported higher crude protein content and higher digestibility from forage in an area that had been heavily grazed by cattle versus one that had been moderately grazed. This phenomenon occurs because plants that are constantly being grazed have comparatively low proportions of structural carbohydrates and are less mature, thereby increasing the protein value, compared to areas that are grazed little (Houston and Pinchak 1991). While it is true that ungulates usually prefer greener, more succulent material associated with grazed areas, other studies suggest large ungulate selection of grazing areas is not based solely on crude protein concentration.

Within a landscape, ungulates choose individual plants to graze based on factors including leaf:stem ratio, live vs. dead material, and succulence (Stuth 1991). Succulance is highly correlated with crude protein concentration, digestibility, and fiber content. Plant material crude protein concentration and digestibility decreases as a function of increased fiber contained within the cell wall. Fiber content is often determined by the nuetral detergent fiber (NDF) and acid detergent fiber (ADF) analyses. NDF includes cellulose, hemicellulose, and lignin fractions within a cell wall and is generally an indicator of animal intake (Van Soest 1982). The ADF analysis includes cellulose and lignin fractions within a cell wall and is generally an indicator of digestibility (Van Soest 1981).

While cattle may select foraging areas based on nutrient quality within a landscape, a number of variables will dictate which landscape cattle are grazing. These include abiotic factors such as slope, aspect and distance to water (Bailey 1996). Cattle also select for total quantity of forage available within a given area. Areas cattle choose to forage upon has been most highly correlated to total standing crude protein and not just crude protein concentration (Senft et al. 1985).

Therefore, it appears that it is unlikely that increasing crude protein concentration alone would facilitate large ungulate grazing on prairie dog colonies. This explanation does not account for any loss of total standing crude protein biomass associated with prairie dog colonies. The increase in crude protein concentration reported on prairie dog towns may be offset by a decrease in total quantity of forage available. Previous studies have not attempted to quantify standing crop crude protein associated with forages on and off prairie dog colonies.

Examination of the Coppock et al. (1983b) data suggest there are certain periods of the year when prairie dog colonies are not preferred grazing locations. On the short-grass steppe of Colorado, for instance, cattle were observed using prairie dog colonies in proportion to their availability within a pasture, and did not "prefer" to graze on these sites (Guenther 2000). These findings suggest that ascribing on an increase of crude protein concentration to explain grazing facilitation by bison or cattle is questionable.

Summary of the Literature

Examination of research conducted on prairie dog colonies demonstrates that effects of prairie dogs on rangelands are not uniform. A number of factors including age of colony, location and climate may influence impacts of prairie dog colonies on the mixed-grass prairie. Prairie dogs alter their habitat by shifting plant species composition and creating niches for some species (both floral and faunal) and removing niches for others. It appears prairie dogs increase nutrient quality of plants located on colonies, yet it remains unclear what effect this has on total nutrient standing crop.

Although research of effects of prairie dogs on vegetation has been completed throughout much of the Great Plains region, little information has come from the mixed-grass prairie in Montana, where cool-season wheatgrasses are dominant. Prairie dog research has examined vegetative differences between zones of different ages. I am primarily interested in comparing the most representative areas within a prairie dog colony to the uncolonized rangeland. In addition, because I was interested in making county-wide inferences in my study area, I wanted to examine many prairie dog colonies, whereas past research had been limited to a few (1-3) colonies per study. Finally, because many areas in eastern Montana are co-dominated by big sagebrush, I was interested in any impacts caused by prairie dog colonies on the native sagebrush communities. My study quantifies the differences between standing crop biomass, plant species richness, cover, crude protein concentration, total standing crop crude protein, digestibility and fiber content of vegetation located on prairie dog colonies and uncolonized rangeland. I also assessed big sagebrush canopy cover and density.

CHAPTER 3

METHODS

Study Sites

This study was conducted in South Phillips County, located in north-central Montana on the northern mixed-grass prairie. The study area was approximately 24-85 km south of Malta, Montana. Land ownership was a mixture of federal, private, and state lands.

Topography varied from flat upland plains to gently sloping hills. Slopes ranged from 0 to 5% and occurred on all exposures. Elevations ranged from 610 to 1070 meters. Soils have a thin soil surface underlain by hardpan. Permeability is slow. Soils were derived from glacial till and were of the order Aridosol. Soil series which characterize this site include Absher, Elloam and Thoeny (USDA 1981).

Precipitation averages 28 cm annually (USDA 1981). Precipitation for 2000 and 2001 was 32% and 22% below average, respectively. During a normal year, about 80% of precipitation falls during the April-September growing season. Winters are cold with a long-term January average of 13.3° F. Summers are warm with a long-term July average of 66.5° F (USDA 1981). The frost free growing season averages 112 days and begins mid-May. High winds, blizzards, droughts and thunderstorms are common in this region (Goetz 1988).

Grasses typical of a mixed-grass prairie dominated the area, but Wyoming big sagebrush (*Artemisia tridentata* Nutt *ssp. wyomingensis.*) was often common throughout the region. Major grasses included western wheatgrass (*Agropyron smithii* Rydb.), blue grama (*Bouteloa gracilis* H.B.K. Lag *ex* Steud), needle-and-thread (*Stipa comata* Trin. & Rupr.), and Sandberg's bluegrass (*Poa secunda* Presl). Cattle ranching represented the major land use.

Nineteen prairie dog colonies and adjacent uncolonized sites were sampled during the summer of 2000 and an additional 21 paired sites were sampled during the summer of 2001 for a total of 40 sites. Both on and off colony sites were grazed by cattle at some time during the year, although sites grazed by cattle prior to sampling for that year were avoided when possible. Less than 25% of sites sampled were grazed by cattle prior to sampling. Study sites were chosen to represent the majority of the interior of a prairie dog colony, and were typical of mixed-grass prairie grassland communities in South Phillips County, Montana. On and off prairie dog colony sites were matched by topography, slope, soil and elevation to avoid any confounding effects. Because soil is an important factor influencing plant production in our study area, a soil scientist visited approximately 75% of my sites, to ensure the study was not confounded due to differences in soil.

Thirty of the 40 paired sites were co-dominated by Wyoming big sagebrush at the uncolonized site. Colonized sites varied in age from less than 10 years to greater than 50 years of colonization by prairie dogs. Average time since colonization was greater than

20 years. Legal descriptions of each site, along with soil series, burrow density, and date sampled are contained in Appendix 1.

Sampling Methods

Comparisons consisted of colonized and uncolonized sites. Areas representative of the majority of the prairie dog colony and adjacent uncolonized rangeland were chosen for sampling locations. From a random point within this area, a 30m north/south line was established using a compass. This became the center line of the plot. Two additional 30m lines were established 10m east and west of the center line. Thirty 0.25m^2 quadrats, one every 3m, were used to estimate cover and biomass of individual plant species. A total of 1200 quadrats at both on and off prairie dog colonies (2400 total quadrats) were estimated for cover and biomass, while 360 quadrats both on and off prairie dog colonies (720 total) were clipped and estimated for all herbaceous plant species.

Standing crop biomass estimates for each plant species were corrected using a double-sampling method (Wilm et al. 1944) based on 10 clipped plots per site. Every third quadrat was estimated and clipped to ground level, and plants were bagged by species to obtain dry weights. In order to ensure estimator accuracy, I estimated and clipped plots on a weekly basis for the major plant species. I did not estimate plants unless the R^2 values for estimated and actual wet weights exceeded 0.90. Linear regressions to convert estimated weights to “corrected” weights for each plant species were constructed using the GLM procedure of SAS. For each individual plant species, weekly regression equations were tested against the seasonal equation. The overall seasonal regression equation was used for 95% of the plant species since they were not different ($P>0.10$). Equations were compiled for similar morphological species when the plant was rare and an inadequate number of estimated and clipped plots were available. Collected plants were dried at 60°C for 48 hours prior to weighing. Dry weight was recorded, and vegetation samples were composited based on vegetative classes. Each plant sample was assigned to one of the following groups: cool-season (C_3) grasses, warm-season (C_4) grasses, standing dead grasses, forbs, or dwarf-shrubs.

Herbaceous understory cover within each quadrat was divided into the following categories: bare ground, live vegetation, litter, rock, lichen and club moss (*Selaginella densa* Rydb.). Quadrats that were located on prairie dog mounds, generally void of vegetation, were included in the sample since it was representative of the vegetation in the area but generally less than 6% of the total quadrats located on a prairie dog colony were located on mounds. Wyoming big sagebrush was sampled using three 2x29.4m belt transects per site. Within these belt transects, average sagebrush percent canopy cover was measured by the line intersection method (Canfield 1941). Density (plants/m^2) within these belt transects was measured as well. Sagebrush available winter biomass was determined from measurements taken from 30 plants at each site according to Wambolt et al. (1994). This conversion represents a conservative estimate of sagebrush biomass since it was used to estimate winter biomass.

Nutritional content of plants was determined using 10 clipped plots per site. These analyses included: percent crude protein concentration, percent IVDMD (AOAC

1995), percent NDF and percent ADF (Van Soest 1981.), and were determined based on the 5 vegetative classes presented above. These results were combined with biomass data to estimate total standing crude protein for both treatments.

Statistical Analyses

Comparisons were made between on and off prairie dog colonized areas within the same site for standing crop biomass, species richness, herbaceous understory canopy coverage, total standing crude protein, sagebrush biomass, sagebrush canopy cover, and sagebrush density using paired t-tests (Steele and Torre 1980) (n=40). Differences between sites in crude protein concentration, IVDMD, NDF and ADF were tested using unpaired t-tests based on small sample sizes.

The experimental unit was individual site. Traditional analysis of variance was not possible as treatments were nested within years and therefore year x treatment interactions could not be tested. Nineteen on and off sites were paired and sampled in 2000 and 21 on and off sites were paired in 2001 for a total sample size of forty. Differences were declared significant when P-value < 0.05.

CHAPTER 4

RESULTS AND DISCUSSION

Standing Crop Biomass

Total standing crop biomass was more than 2 times greater (P=0.001) on uncolonized rangeland than on the interior portion of a prairie dog colony (Table 1).

Table 1. Standing crop biomass (kg/ha) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	47	134	7.5	0.001
C_4 Grass	45	75	6.2	0.010
Standing Dead Grass	15	102	5.7	0.001
Forbs	17	12	2.5	0.100
Dwarf Shrub	109	53	12.5	0.010
Sagebrush[1]	1	210	2.2	0.001
Total	234	586	37.7	0.001

n=40

[1] available sagebrush winter biomass (Wambolt et al. 1994)

Aboveground standing crop biomass for cool-season (C_3) grasses, dominated by western wheatgrass, needle-and-thread and Sandberg's bluegrass, was nearly 3 times greater off the prairie dog colony. Warm-season (C_4) grasses, consisting primarily of blue grama, were also greater (P=0.01) off the prairie dog colony.

Nearly seven times (P=0.001) the amount of standing dead grass was present off the prairie town when compared to the interior of the prairie dog town. The increased amount of standing dead biomass which was located on the uncolonized rangeland was due to the fact that prairie dogs constantly clip vegetation on their colonies to increase visibility and facilitate movement, thereby greatly decreasing the amount of grasses that reach maturity.

The ratio of C_3 to C_4 grasses was approximately 1:1 on prairie dog colonies. On the adjacent uncolonized rangeland, the ratio was approximately 2:1. This suggests prairie dog activity results in a replacement of cool-season grasses with warm-season grasses, similar to the effects of heavy grazing by cattle. Areas historically grazed by cattle have greater proportions of warm-season grasses, shrubs and forbs which may be indicative of retrogression, a reduction in seral stage, and may affect the long term production of a site (Fleischner 1994).

Forb standing crop biomass was not different (P=0.1) between the interior of a prairie dog colony when compared to the adjacent uncolonized rangeland. There was no difference (P=0.10) in total forb biomass between on and off colony sites, although there was an increase in the proportion of forb biomass with the presence of prairie dogs. Forbs accounted for 7% of the total biomass on a prairie dog town, and only 2% of the total biomass on uncolonized rangeland. This increase in forb biomass is consistent with research completed in other areas (Collins et al. 1984). Forb presence is generally a direct result of rainfall. Forb biomass may have been relatively low due to the low amount of precipitation in south Phillips County during the summers of 2000 and 2001.

More than twice the amount of dwarf shrub standing crop biomass, dominated by fringed sagewort (*Artemisia frigida* Willd.), was present on rangeland colonized by prairie dogs throughout the sampling seasons. The increase in dwarf shrub biomass agrees with the findings of Coppock et al. (1983) who reported over 55% of the total biomass on an area occupied by prairie dogs consisted of fringed sagewort. Areas with a large percentage of fringed sagewort biomass are associated with rangelands which have been heavily grazed (Spang 1954).

Sagebrush standing crop biomass was much greater (P=0.001) on uncolonized rangeland when compared to the interior of a prairie dog colony. There was virtually no live sagebrush within the interior of any colony sampled. Prairie dogs actively remove sagebrush until entire stands have been destroyed. Removal of sagebrush tends to create a more xeric site, making it extremely difficult for sagebrush to re-establish (Lusby 1979). This may lower the overall productivity of a site, changing the plant community.

My study did not agree with the findings by Coppock et al. (1983) or by Whicker and Detling (1988), who found no difference in standing crop biomass on prairie dog colonies when compared to uncolonized areas. The primary reason that my work differed from that conducted in South Dakota was that I sampled areas which represented at least 70% of the prairie dog colony, while other researchers focused on different zones or age classes within a colony, including younger portions of the prairie dog town and an edge zone. Recently colonized areas may not have the same vegetation characteristics that would be present on older portions of the colony.

An initial spike in plant primary productivity has generally been associated with moderate grazing, regardless of the grazer. This phenomenon is probably no different on prairie dog colonies, where vegetation is constantly being clipped. Recently colonized areas (occupied less than 10 years) may exhibit little difference in aboveground plant biomass, if not slightly higher. Repeated heavy grazing, on the other hand, often results in lower overall plant productivity and a change in seral stage. Areas grazed by prairie dogs for greater than 20 years may produce quite different vegetation than young prairie dog towns, or “edge” zones. In South Dakota, on a portion of a prairie dog town occupied for more than 26 years, grasses were “virtually eliminated” (Coppock et al 1983a).

My findings were in agreement with Weltzin et al. (1997), who concluded that standing crop biomass was greater off a colony when compared to the interior of a prairie dog colony. This is most closely related to the fact that sampling procedures were quite similar between these studies.

Total standing crop biomass was much higher (P=0.001) on uncolonized land when compared to areas colonized by prairie dogs. Warm and cool-season grass biomass both decreased, while dwarf shrub and forb biomass increased with grazing by prairie dogs and cattle. The replacement of C_3 grasses and sagebrush with C_4 grasses, forbs, and unpalatable dwarf shrubs suggest that prairie dogs activity combined with cattle grazing alters the plant community seral stage.

The northern mixed-grass prairie has a relatively low precipitation/evaporation (P/E) ratio (0.2-0.6). The low P/E ratio, combined with the short growing season suggests slow recovery to the pre-disturbance productivity level and successional stage.

Plant Species Richness

I found less total plant species (P=0.001) on a prairie dog colony when compared to the adjacent uncolonized rangeland in Montana (Table 2).

Table 2: Plant species richness on and off prairie dog colonies on the mixed-grass prairie in Montana in 2000, 2001.

	ON colony	OFF colony	SE	P
number of species	13	16	0.66	0.001

n=40

Colonization by prairie dogs has been documented as both increasing plant species richness (Archer et al. 1987, Coppock et al. 1983) and decreasing plant species richness (Agnew et al. 1986, Weltzin et al. 1997). My findings indicate that colonization of rangelands by prairie dogs in the mixed-grass prairie of Montana decreases the number of plant species found at a site. One factor contributing to these differences might be time since colonization, since plant species richness changes with increased time since prairie dog occupancy (Coppock et al. 1983). The prairie dog colonies which were sampled in South Dakota were younger than most of the prairie dog colonies I sampled in Montana. Repeated grazing may have similar effects on plant species richness as plant standing crop biomass. Plant species richness may increase initially following immediate grazing pressure, but may decrease in response to long-term grazing pressure.

Cover

Live herbaceous vegetative cover was similar (P=0.21) between paired on and off colony sites (Table 3). Bare ground cover was greater (P=0.01) within the interior of a prairie dog colony when compared to the adjacent uncolonized rangeland. Percent litter cover was greater (P=0.01) on the uncolonized rangeland when compared to the interior of a prairie dog colony. Rock, lichen and club moss cover was similar (P>0.05) between paired on and off colony sites.

Table 3. Percent understory cover on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
Live Herbaceous Vegetation	17	18	1.54	0.21
Bare Ground	27	17	1.64	0.01
Litter	23	27	1.81	0.01
Rock	15	13	2.09	0.35
Lichen	3	4	0.61	0.07
Club Moss	15	19	2.77	0.19

n=40

These findings are in contrast to those of Agnew et al. (1986) which found less vegetative cover on a prairie dog town at all times of the year when compared to the adjacent uncolonized site. Differences were probably most attributed to the presence of buffalograss (*Buchloe dactyloides* Nutt. Engelm.), which contributed greatly to the percent herbaceous cover at the study site of Agnew et al. (1986) and was not present on any of my sites.

The increase of percent bare ground on a prairie dog colony is a direct function of the decrease in percent litter cover at the same site. The increase in percent litter cover on a prairie dog town is directly related to the loss of standing dead and organic matter on a prairie dog colony. Percent rock, lichen and club moss are primarily a function of site, and would not be expected to change between treatments as range site was matched as closely as possible for all paired on/off sites.

The decrease in litter and increase in bare soil may result in a warmer, drier micro-environment (Archer et al.1987). Reductions in live and dead plant biomass and litter could result in a decrease in the interception of precipitation by vegetation. This increase in bare soil may also lead to an increase in evaporative losses. Therefore, water availability in the first few centimeters of soil will tend to be lower on heavily grazed sites, even after a precipitation event (Whicker and Detling 1988).

Big Sagebrush

Big sagebrush canopy cover and density was greater ($P<0.001$) on uncolonized rangeland compared to colonized areas (Table 4).

Table 4. Big sagebrush canopy cover and density on and off prairie dog colonies on the mixed-grass prairie in Montana in 2000, 2001

	ON colony	OFF colony	SE	P
canopy cover (%)	0.1	7	1.7	0.001
Density (plants/m^2)	0.03	1.4	2.2	0.001

n=40

It has been suggested that prairie dogs may actively destroy shrubs (Miller 1991) as part of their colony expansion process. My findings indicate that this statement is true. I observed 30 sites where prairie dogs were actively clipping sagebrush. Effects of prairie dogs on sagebrush colonies had not previously been quantified in the scientific literature, although prairie dogs have been documented as a control agent for mesquite (*Prosopis glandulosa* Torr.) in the southern mixed-grass prairie (Miller 1991).

Sagebrush may take up to 50 years to recover after stand removal due to fire. The removal of sagebrush by prairie dogs, however, is quite different than that from fire. Immediately after a fire has swept through an area, organic matter is deposited directly back into the soil. The seedstock and rootstock persist belowground. After removal due to the activities from prairie dogs, the seed and rootstock have been depleted, which may make sagebrush recovery difficult. For example, in an area in Phillips County where prairie dogs were poisoned nearly 50 years ago, there are still very little signs of sagebrush recovery. The full extent of the impact of prairie dogs on sagebrush requires further examination, although it appears that areas colonized for long periods of time will take even longer to fully recover, if full recovery is possible.

Crude Protein

Crude protein concentration of all vegetative classes was greater ($P<0.05$) on colonies when compared to off colony sites, with the exception of forbs, which contained similar concentrations of crude protein ($P=0.33$) for both treatments (Table 5). Forb production increased immediately following a precipitation event in approximately equal proportions on all sites. These forbs usually contained similar amounts of crude protein, and were affected equally by precipitation both on and off prairie dog colonies.

Table 5. Average crude protein (%) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	11.5	9.4	0.5	0.01
C_4 Grass	10.1	8.6	0.3	0.01
Standing Dead Grass	7.1	5.1	0.4	0.01
Forbs	14.0	12.9	0.8	0.33
Dwarf Shrub	11.9	10.6	0.3	0.01

These findings are consistent with those of Heitschmidt et al. (1989) who found a higher crude protein concentration in areas heavily grazed by cattle when compared to areas moderately grazed. This is also consistent with Coppock et al. (1983) who found higher crude protein concentrations within the interior of a prairie dog colony in the mixed-grass prairie of South Dakota. Results were not expected to differ, because regardless of study area, plants that are constantly grazed have comparatively low proportions of structural carbohydrates and are less mature, thereby increasing the protein value, compared to areas that are grazed lightly (Houston and Pinchak 1991).

Standing Crude Protein

Total standing crude protein (kg/ha) was determined by multiplying crude protein concentrations by the standing crop of each vegetative class (crude protein (kg/ha) = standing crop biomass (kg/ha) x crude protein (%)) (Table 6). Total standing crude protein yield was 17% greater ($P<0.05$) on uncolonized rangeland when compared to the interior of a prairie dog town. These results do not include any contribution of sagebrush to total standing crop protein. Had sagebrush been included, total standing crude protein off prairie dog colonies would increase greatly, while that on prairie dog colonies would not change substantially.

Table 6. Standing crude protein (kg/ha) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	5.5	12.7	0.80	0.001
C_4 Grass	4.8	6.1	0.61	0.136
Standing Dead Grass	1.1	5.1	0.32	0.001
Forbs	2.4	1.5	0.37	0.062
Dwarf Shrub	12.8	5.8	1.49	0.001
Total	26.6	31.2	1.86	0.007

n=40

Cool-season (C_3) grasses accounted for 41% of the total standing crude protein available off a prairie dog colony, while making up only 21% of the total standing crude protein located on a prairie dog colony. This represents a 130% decrease in the total amount of crude protein available (kg/ha) from cool-season grasses on a prairie dog town when compared to uncolonized rangeland. This decrease in standing crop crude protein of cool-season grasses may be detrimental to cattle, which have been shown to preferentially select for cool-season grasses where available (Uresk 1986).

Warm-season (C_4) grasses on prairie dog colonies showed no difference ($P=.14$) in total crude protein when compared to off colony areas. This indicates that the activities of prairie dogs, when grazed with cattle, may not have significant impacts on the total amount of standing crop protein available from warm-season grasses.

Nearly five times the amount ($P<0.05$) of total standing crude protein from standing dead grass was located off the prairie dog colony when compared to the interior of the prairie dog town. Although standing dead grass comprised only 4% of the total standing crude protein available on a prairie dog colony, it accounted for 16% of the total standing crude protein located off a prairie dog colony. For cattle, this may have some interesting effects. Cattle have been shown to prefer plants with lower fiber content, which would indicate that they may avoid areas with high amounts of standing dead grass. However, cattle may utilize areas with higher total amounts of standing crude protein (kg/ha) (Senft 1985). If this is correct, the high amounts of crude protein contributed by standing dead grass to the total amount of crude protein may have some benefits to livestock grazing.

There was no difference ($P=0.062$) between available standing crude protein from forbs in either treatment. However, nearly twice the amount of total standing crude protein on a percent basis was available from the forb component on a prairie dog town when compared to the adjacent uncolonized rangeland. Whereas forbs accounted for 5% of the total amount of standing crude protein on uncolonized rangeland, the forb component comprised 9% of the total standing crude protein on a prairie dog town.

Dwarf shrubs accounted for 120% more standing crude protein on colonized areas than uncolonized rangeland, and composed nearly 50% of the total available crude protein on prairie dog colonies. The dwarf shrub component made up approximately 20% of the total available nitrogen off prairie dog colonies. Fringed sagewort was the dominant dwarf shrub at all sites. Fringed sagewort is a highly unpalatable and undesirable forage for many ungulates, including cattle (Spang 1954).

There was a greater amount of total standing crude protein available off prairie dog colonies when compared to colonized areas. Because the majority (50%) of total nitrogen on a prairie dog town comes from fringed sagewort, which cattle tend to avoid, and the majority (40%) of total nitrogen off a prairie dog town comes from cool-season grasses, which cattle tend to prefer, cattle would be just as likely to graze off a prairie dog colony as on a colony. For example, based on opportunistic sightings during the summers of 2000 and 2001, of 604 cattle observed grazing on allotments which contained prairie dog colonies, nearly 75% were grazing uncolonized areas.

It has been suggested that the activities of prairie dogs increase plant crude protein concentrations on prairie dog colonies, and this may be the mechanism that facilitates bison grazing on these areas (Coppock et al. 1983) however, this theory has not been tested directly in the field. This idea has been applied to cattle as well (Long 1998).

However, this explanation does not agree with other findings that suggest cattle selection of grazing areas is not based solely on crude protein concentration (Bailey 1996, Senft et al. 1985). Because cattle choose grazing areas based on a number of other variables, including patch and landscape dynamics (Stuth 1991), abiotic factors including slope and distance to water and total quantity of forage available (Bailey 1996), it is unlikely that changing crude protein concentration alone would facilitate large ungulate grazing on prairie dog colonies. This explanation does not account for the total loss of standing crude protein associated with prairie dog colonies.

On the short-grass steppe of Colorado cattle were observed using prairie dog colonies in proportion to their availability within a pasture, rather than selecting for them (Guenther 2000). Further examination of the Coppock et al. (1983) data suggest there are times during the year when prairie dog colonies are not preferred grazing locations. These findings, coupled with my research may indicate prairie dogs may not facilitate grazing by cattle, although this hypothesis was never fully tested.

Digestibility

In Vitro Dry Matter Digestibility (IVDMD) was determined for all vegetative classes. Average IVDMD was not different ($P>0.05$) for any vegetative classes with the exception of dwarf shrubs which were higher ($P<0.05$) on colonized rangeland when compared to off colony rangelands (Table 7).

Table 7. IVDMD (%) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	41.2	39.6	2.2	0.629
C_4 Grass	29.2	28.0	1.7	0.640
Standing Dead Grass	29.7	24.6	2.2	0.203
Forbs	46.6	42.7	3.3	0.434
Dwarf Shrub	31.2	25.8	2.0	0.044

Findings were in accordance with research conducted in South Dakota. Coppock et al. (1983) found slightly higher percent digestibility in areas recently colonized by prairie dogs. Their study also reported higher percent digestibility of cool-season (C_3) grasses over warm-season grasses (C_4) in all areas, which was similar to my findings.

Areas heavily grazed by cattle have also been shown to have slightly higher digestibility than areas that have been moderately grazed. Heitschmidt et al. (1989) reported 46.7% IVDMD in an area that had been moderately grazed by cattle, while an area heavily grazed had a reported IVDMD of 49.3%. Plants that are constantly being grazed, regardless of the herbivore, usually exhibit less lignification. This results in greater digestibility.

Fiber

Neutral detergent fiber was not different for any vegetative classes between colonized areas and adjacent uncolonized areas (Table 8). It appears that activities of prairie dogs are not reducing hemicellulose, cellulose and lignin fractions within plant communities. The ADF concentrations were similar (P>0.05) across all vegetative classes with the exception of standing dead grass, which was higher (P<0.05) on uncolonized rangeland when compared to the interior of a prairie dog town (Table 9).

Table 8. NDF (%) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	63.4	63.3	0.74	0.867
C_4 Grass	67.6	67.5	0.58	0.892
Standing Dead Grass	65.1	68.0	0.90	0.069
Forbs	44.0	41.1	2.55	0.454
Dwarf Shrub	48.0	46.7	0.83	0.267

Table 9. ADF (%) on and off prairie dog colonies on the mixed-grass prairie in Montana during 2000 and 2001.

	ON colony	OFF colony	SE	P
C_3 Grass	31.7	33.1	0.67	0.173
C_4 Grass	32.7	32.2	0.54	0.551
Standing Dead Grass	35.7	40.6	0.84	0.004
Forbs	27.8	26.2	2.26	0.642
Dwarf Shrub	34.3	32.2	0.84	0.084

With the exception of standing dead grass, there were no differences (P>0.05) in the amounts of fiber contained in vegetative classes between vegetation located on prairie dog colonies and vegetation located off colonies. My findings indicate that presence of prairie dogs does not impact fiber concentrations in vegetation associated with these areas.

Summary and Conclusions

I compared the vegetation attributes on and off forty prairie dog colonies, which were occupied for at least 20 years, in north central Montana in 2000 and 2001. Comparisons were made between environmentally paired sites. Colonization by prairie dogs decreased total standing crop biomass, plant species richness, percent litter cover, percent sagebrush canopy cover and density, and total standing crude protein when compared to uncolonized rangeland. Colonization by prairie dogs increased percent bare ground cover, and percent crude protein of vegetation when compared to uncolonized areas.

Prairie dog colonies were characterized by an increased presence of warm-season grasses, forbs and dwarf shrubs, whereas off colony sites were characterized by a dominance of cool-season grasses. This replacement of cool-season perennial grasses by warm season grasses, forbs and dwarf shrubs on a colonized area indicate the activities of prairie dogs, when grazed with cattle, alter the plant species composition of the areas they occupy.

As grazing pressure increases, the site changes to a lower seral stage. When this grazing pressure is reduced or removed, the rate of succession to a higher seral stage depends on the extent to which soils, seedbank, and vegetative regeneration potential of the vegetation has been modified. When one group of plants has been displaced by another as a result of heavy disturbance, the new assemblage may be long-lived and persistant (Archer and Smeins 1991).

Prairie dogs actively eliminate and destroy sagebrush during their colonization process and long-term productivity of these sites may be diminished. Sagebrush creates a microclimate, which allows other plants to grow, and retains moisture in the soil, which can be taken up by other plants (Peters 1995). Removal of sagebrush may create more xeric conditions, thereby decreasing productivity. The changes associated with the removal of sagebrush indicate that these rangelands have crossed a threshold that may be difficult to overcome with out external inputs. Recovery of these sites to pre-disturbance conditions may be slow due to the low amounts of precipitation Phillips County receives annually.

The decrease in total standing crop biomass may have varying effects on different animal species. This may have a detrimental effect on species needing herbaceous cover, such as sage grouse (*Centrocercus minimus*) or mule deer (*Odocoileus hemionus*). The increase of bare ground that is found on prairie dog colonies may have a positive effect on animal species that require open spaces with less cover, such as the mountain plover (*Charadrius montanus*), or burrowing owl (*Speotyto cunicularia*).

Older prairie dog colonies located in the mixed-grass prairie of eastern Montana reduce total standing crop biomass, plant species richness, and total crude protein biomass when grazed by cattle. These findings are contradictory to those stated in the petition to list the prairie dog as a threatened species. The impacts of these effects will depend on the goals of land managers. My findings suggest that prairie dog colonies may not be ideal for grazing cattle due to a decrease in total standing crude protein. Unlike other findings that suggest prairie dogs may have beneficial or neutral effects to native rangeland, my study indicates that prairie dogs may have detrimental effects for some species. The unique area created by the presence of prairie dog colonies may have beneficial effects on prairie dogs, mountain plovers, and burrowing owls while having detrimental effects on cattle and sagebrush obligates such as sage grouse.

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APPENDICES

APPENDIX A

LOCATION OF COLONIES