

NRB.6

FINAL REPORT

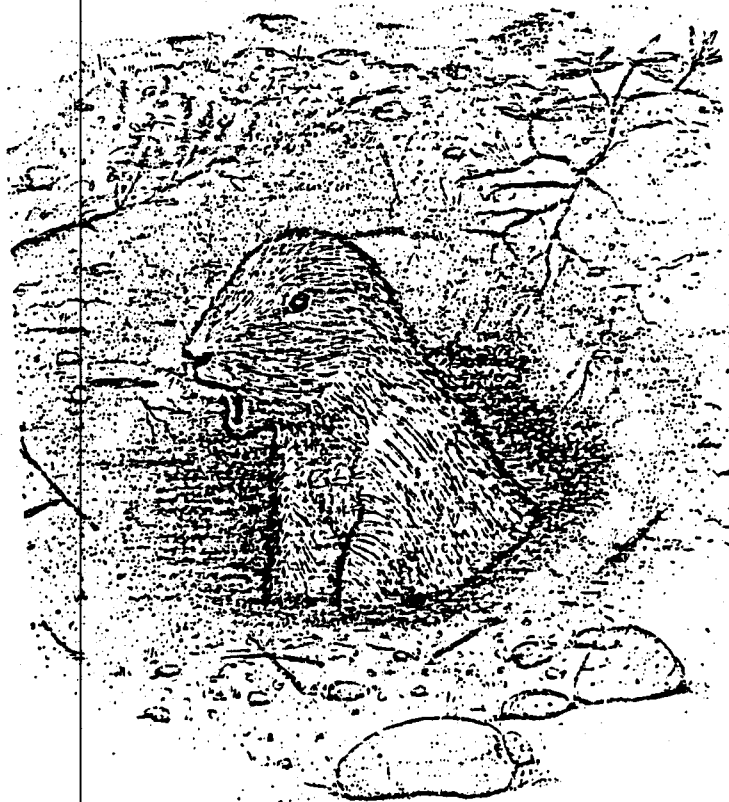
ECOLOGY OF THE BLACK-TAILED PRAIRIE DOG
IN THE BADLANDS NATIONAL PARK

Richard P. Cincotta, Daniel W. Uresk

bibkey:164330

and

Richard M. Hansen



Final report is a contribution from National Park Service, Rocky Mountain
Regional Office, Contract No. CX1200-1-B035.

FINAL REPORT

ECOLOGY OF THE BLACK-TAILED PRAIRIE DOG
IN THE BADLANDS NATIONAL PARK

Richard P. Cincotta, Daniel W. Uresk

and

Richard M. Hansen¹

¹Authors are Graduate Research Assistant at Colorado State University, now Assistant Professor, Range Science Department, Utah State University, Logan, Utah 84322; Research Biologist, USDA-Forest Service, Rocky Mountain Forest and Range Experiment Station, Rapid City, South Dakota 57701, and Professor, Range Science Department, Colorado State University, Ft. Collins, Colorado 80503. Final report is a contribution from National Park Service, Rocky Mountain Regional Office, Contract No. CX1200-1-B035.

EXECUTIVE SUMMARY

The ecology of the black tailed prairie dog (Cynomys ludovicianus) was examined on prairie dog towns in the Badlands National Park, southwestern South Dakota, over a 3 year period. This study was designed to: (1) examine characteristics of vegetation and soils in prairie dog towns, (2) estimate differences among population, age and sex structure on towns, (3) determine demographic differences in dispersed and resident populations, and (4) define a set of environmental variables that can be used to predict prairie dog town expansion.

Experiments in this study quantitatively defined 4 habitat zones (young town edge, interior, center, and old town center) that can exist in dog towns, concentrically arranged around the town center, which differed in environment and dog demography. Different conditions of quantity and quality of forage were associated with these zones. Peak standing crop biomass (g/m^2) was greater outside dog towns than inside towns that were grazed by large herbivores. Old town centers were zones that prairie dogs have inhabited for long periods of time (≥ 25 yrs.). Continuous burrowing and foraging by prairie dogs had significantly altered plant composition in the town centers. Forage in vitro dry matter digestibilities (IVDMD) were highest in the old town center. This difference was related to plant succession, prairie dog clipping activities, and phenological stage of plant growth within the 4 habitat zones. Soil organic matter, nitrogen, and phosphorus estimates differed among the 4 habitat zones within a town, which were related to activities of prairie dogs (soil movement, litter, and fecal matter).

Female reproductive success was lowest in the old town center and young town edge, zones that represent long-term and very short-term occupancy by prairie dogs, respectively. Reproductive success was highest in the young town interior because of better forage quality and closer proximity to better forage at the town edge. Reproductive success in the old town centers may have been influenced by density dependent social interactions. As black-tailed prairie dog towns increased in size, the habitat zone of highest quality (indicated by reproductive success) was shifted farther away from the town center. Thus, old towns, without expansion, were lower in habitat quality with reduced reproductive success.

Female prairie dogs that immigrated from other towns became established at town edges. Female immigrants were excluded from the interior of the prairie dog towns. Females that became established in the young town interior, center, and old town center, were progeny of territorial residents. Solitary coteries (family groups) were rare, and immigrants generally established themselves near existing towns.

Areas of potential prairie dog settlement could be recognized (if sufficient dispersers were available) based upon: (1) size of the prairie dog population at the closest point to the area in question, (2) distance of the area to the town edge, and (3) degree of vertical visibility (height and density of vegetation).

Intensive management of prairie dog towns is possible, since managers can manipulate vertical visibility and population concentrations along the town edge. Deferment of grazing prior to, and at the time of, immigration (May-June), and application of fertilizer (Snell and Hlavachick 1980, Uresk et al. 1981) may help to sustain thick, tall vegetation around edges of

dog towns and decrease town expansion. Judicious use of rodenticides may be required to decrease population concentrations at town edges and further reduce dog town expansion. Areas heavily impacted by prairie dogs and large herbivores may require rodenticide treatment and revegetation for successful management.

INTRODUCTION

The black-tailed prairie dog (Cynomys ludovicianus) is a herbivorous, social mammal native to the Great Plains of North America. Black-tailed prairie dogs live in large social aggregates known as prairie dog towns. Within these towns, prairie dogs dig burrows and alter the composition of the vegetation (Koford 1958, Coppock et al. 1983a). Large populations of black-tailed prairie dogs presently exist within the boundaries of Badlands National Park, South Dakota.

Prairie dog towns have, during the past 10 years, expanded on the Park and other Federal, state, and private rangeland and farmland (Schenbeck 1982). Managers have sought to reduce black-tailed prairie dog populations by the application of rodenticides. However, this practice is not always cost effective (Collins et al. 1984). An effective black-tailed prairie dog management program that strives to minimize the application of rodenticides, requires knowledge of the ecology of black-tailed prairie dogs.

The objectives of this study were to: (1) determine the characteristics of vegetation and soil that are present in a black-tailed prairie dog town, (2) estimate population, densities, age, and sex structure of prairie dogs in a town, (3) determine demographic differences in disperser and resident populations, and (4) define a set of environmental variables that can be used to predict prairie dog town expansion.

STUDY AREA AND METHODS

Study Sites

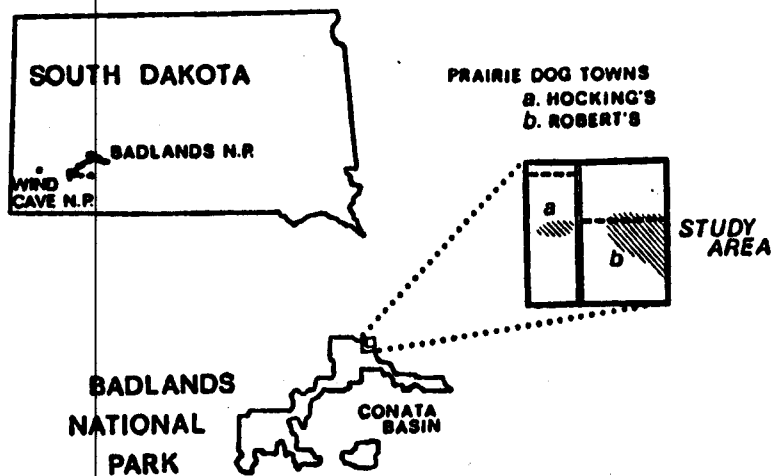
The study was conducted during three summer field seasons from 1981 to 1983 on 3 prairie dog towns in Badlands National Park, southwestern South Dakota (Fig. 1a). The area receives approximately 40 cm of precipitation annually, most of which falls between early April and mid-July during intense, patchy thunderstorms. The mean temperature was 10°C, ranging from -5°C in January to 26°C in July.

Soils in these study areas were deep sandy-loam sediments interspersed with thin layers of sand and gravel from former stream beds. Topography of the area was gently rolling mixed-grass prairie. Dominant plant species were western wheatgrass (Agropyron smithii), buffalograss (Buchloe dactyloides), needle-and-thread grass (Stipa comata), blue grama (Bouteloua gracilis), Patagonia Indianwheat (Plantago patagonica) and prostrate vervain (Verbena bracteata).

Hockings prairie dog town was totally enclosed by a fence and unavailable for grazing to both bison (Bison bison) within the National Park, and to domestic cattle from adjacent rangelands. This town was grazed by cattle and horses prior to 1979 and had been poisoned for prairie dogs in 1978. Roberts town was located within the park boundary and accessible to bison, antelope, and mule deer. Greatest use by bison was in August of each year. The 3rd prairie dog town in the park extended onto private land and was grazed by cattle.

At the beginning of the study (1981) in the Badlands National Park, the center of one prairie dog town had been occupied for about 8 years (Hockings), and was considered to be an example of a "young town" (Fig. 1).

a.



b.

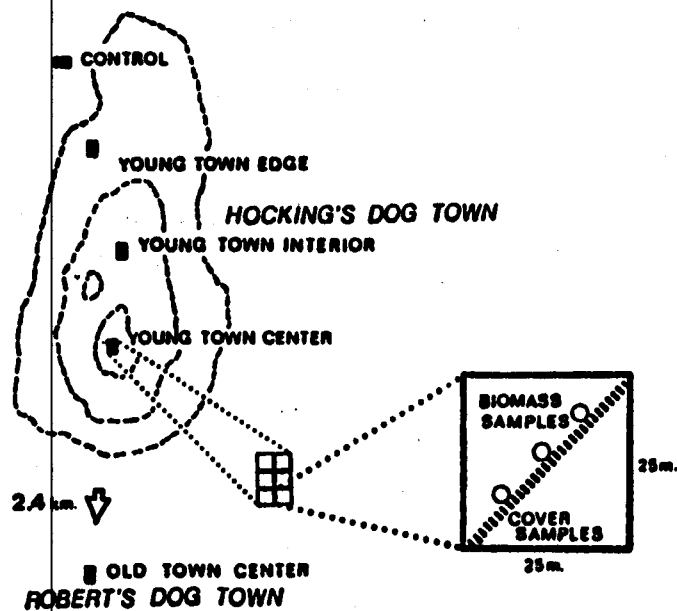


Figure 1. (a) Badlands National Park and study area location, and (b) location of sampling cells within habitat zones and sampling scheme for standing crop biomass and cover.

The prairie dog town located on private and national park lands had been occupied approximately 10 years and also considered to be a "young town". The center of Roberts town had been occupied by prairie dogs for approximately 25 years and was considered an "old town".

Prairie Dog Rodenticide Treatment

The 3rd prairie dog town (12 ha) located on private and national park land. Six ha on private land was treated with 2% zinc phosphide coated grain after pretreatment grain was applied. Rodenticide was placed on edges of all burrow mounds during the last week of August 1981 and 1982. The 6 ha on park lands was left undisturbed. All prairie dogs were trapped during the first week in June and third week in August of 1982 and 1983 on untreated and treated sites. The number of prairie dogs which remained on the rodenticide treated site were compared to the number of prairie dogs which repopulated the treated area.

Soils

Soil cores (10 cm depth) were collected during late December 1982, early June 1983, mid-July 1983, and late August 1983. Soil cores were collected in each of the 4 habitat zones and control on the 2 prairie dog towns without rodenticide treatment. Soil organic matter was determined in the laboratory. Available soil nitrogen was determined by chemically reducing NO_3 anions to NO_2 anions with cadmium and copper as reducing agents, and analyzing the reduced sample with a color-metric flow-injection autoanalyzer (FIA). Available soil phosphorous was determined with

NH_4HCO_3 -DTPA extract. Soil analyses were conducted at CSU Soil Testing Laboratory, Colorado State Univ., Fort Collins, CO 80523.

Vegetation

Four habitat zones on prairie dog towns (Hockings, Roberts) were subjectively defined which represented a cross section of plant succession from a relatively undisturbed condition, to a highly disturbed condition. These zones were (Fig. 1b):

1. Control - relatively undisturbed vegetation and no prairie dogs.
2. Young town edge - territories of prairie dogs bordered by undisturbed vegetation, forbs were less than 25% of total cover.
3. Young town interior - territories of prairie dogs bordered on all sides by young town edge and center, forbs were less than 25% of total cover.
4. Young town center - forbs were greater than 25% but less than 75% of total cover.
5. Old town center - forbs were greater than 75% of total cover.

All habitat zones consisted of 6 grid squares, 25 m by 25 m cells. Six cells were located outside the dog town perimeter, 50 m from areas grazed by prairie dogs, and were designated as experimental controls. These cells were sampled simultaneously in all habitat zones (Fig. 1b).

Standing crop biomass was sampled for 2 prairie dog towns (Roberts, Hocking) in circular one-eighth m^2 plots with 3 plots clipped per cell, 16 plots within each habitat zone. All plants were clipped at ground level and species pooled. Samples were oven-dried at 60°C for 48 hours and weighed. All sampling was done at estimated peak aboveground biomass which

occurred sometime from mid-July to early August during the study. Canopy cover and frequency of occurrence of forbs and grasses were sampled using 30 rectangular (50 cm by 20 cm) plots per grid cell in each habitat zone and control for 3 years. Cover was estimated using 6 visual cover classes (Daubenmire 1957). Mean canopy cover per grid cell was calculated for data analyses.

In vitro dry matter digestibility (IVDMD) was determined for 2 plant samples (combined species) per grid cell over a 3 year period (Tilley and Terry 1963). Fifty ml of an acid pepsin mixture (17.8 ml HCl and 24 g pepsin per liter of water) was added to 5 g samples. Samples were placed in a water bath for 48 hours at 39.5°C. All samples were stirred at 2, 6, 24, 36 and 48 hours after being placed in the bath. After 96 hours, samples were centrifuged with the supernatant discarded. Warm water was added (50 ml) to the centrifuged mixture and supernatant was discarded. Samples were oven dried overnight at 100°C and reweighed. The forage digestibility (%) per grid cell was the calculated mean value of the two samples.

Trapping

Prairie dogs were trapped in each zone from mid-May until the first week in September using 52 Tomahawk 32-inch live-traps (no. 206) baited with commercial sweet chop, a molasses-coated mixture of cracked corn, rolled barley and rolled oats. Each of the 3 towns were trapped for prairie dogs. All animals were toe-clipped for identification, sexed, and released. Total population estimates were used for statistical analyses.

Food Habits

Fresh fecal material was collected directly from 20 adult female prairie dogs trapped during July 1983. Five females were sampled per habitat zone. A minimum of 10 fecal pellets were collected from each animal and combined. Each female was regarded as a sample, and the fecal content was analyzed and recorded separately. Composition of plant material in the feces was estimated using the microhistological technique (Baumgartner and Martin, 1939; Sparks and Malacheck, 1968). A total of 100 microscope fields of identifiable material was observed per sample. Data were expressed and analyzed as percent relative density and percent relative frequency by habitat zones.

Reproductive Success

Reproductive success was estimated by the ratio of juveniles/potentially reproductive female (adult and yearling) captured. Only "resident" females were considered as potentially reproductive. Resident females were those that occupied in their present territory during the previous year as opposed to "immigrant" females which occupied other territories during the previous year.

Establishment of Prairie Dogs

Prairie dogs were assumed to be immigrants for all towns if they were adults captured in an area one year, but not captured there the previous year. Since immigrating black-tailed prairie dogs usually settle at distances less than 50 m from an established coterie (family group), this distance was considered for settlement. Four variables in each grid cell

within 50 m of the dog town edge were measured, and related to the establishment of a coterie in previously unoccupied areas, during 1981 and 1982. These variables were: (1) number of burrows in the nearest occupied grid cell, (2) vertical visibility (height and density) of vegetation, (3) the distance of expansion burrows from the town edge, and (4) canopy cover of forbs.

The number of burrows per grid cell were counted during the first week of July 1981, 1982, and 1983. The number of burrows per grid cell was used as an index of population density.

Vertical visibility of a grid cell was measured with a 1-m by 1-m fluorescent orange board covered with 50 (2 cm by 2 cm) white squares equally and alternately spaced on its surface (checkerboard pattern). The erect board was observed at a distance of 18 m. If all white squares were visible, visibility was 100%. When a white square was obscured, 2% was subtracted from 100%. During an observation, the board was placed at each corner of the grid cell and observed from the center (18 m). The average of 4 observations was recorded for each grid cell.

All grid squares within 50 m of the town edge were sampled in mid-August each year for vertebrate visibility, canopy cover of forbs, and number of burrows. All areas were sampled during mid-June for distance of newly established prairie dog burrows from previously established prairie dog burrows. Grid cells were then categorized as occupied or not occupied by prairie dogs.

Statistical Analysis

The effect of habitat zone, year, and zone by year interaction were determined with analysis of variance on soil chemistry standing crop biomass, ratio of forb cover to grass cover, and plant IVDMD, (Nie et al. 1975). Differences were considered significant at $\alpha = 0.05$.

The demography of female prairie dog dispersers, successful in establishing new territories, was analyzed with chi-square analysis of observed and expected establishment ($\alpha = 0.05$). Random settlement of dispersers, regardless of habitat zone within a town, was assumed and 2 null hypotheses generated: (1) dispersers randomly settled throughout the zone, and (2) dispersers randomly settled in the town and control.

Burrow density, vertical visibility, distance of burrows from town edge, and canopy cover of forbs were statistically tested using discriminant analysis to determine if these variables would classify grid areas as suitable for expansion (BMDP7M, University of California, Los Angeles, CA). Discriminant analysis determined whether each variable, or linear combinations of the variables, could be used to differentiate between cells with prairie dogs and cells without dogs. Variables were added to the discriminant function with a forward stepwise procedure (F-to-enter = 4.0, F-to-remove = 3.996). Based on jackknifing procedures (Lachenbruch and Micky 1968) error rates were estimated for classification.

Canopy cover of plants and prairie dog food habits were analyzed using stepwise discriminant analysis. These analysis determined which plant species discriminated among the 4 habitat zones. Discriminant classification functions were developed to estimate habitat changes within prairie dog towns.

Plant compositional changes between grid cells were tested using the multi-range permutation procedure (O'Reilly and Meilke 1980). This nonparametric permutation procedure calculates the probability of an "a priori" grouping being a strictly random collection of groups chosen from the total data set.

RESULTS AND DISCUSSION

Soils

Soil organic matter, available phosphorous, and available soil nitrogen were different between habitat zones (Table 1). Significant seasonal differences occurred in soil organic matter and available nitrogen. Season x zone interactions were significant with regard to organic matter, available nitrogen and available phosphorus. Soils of black-tailed prairie dog towns were chemically altered when compared to mixed grass prairie (control). Organic matter generally showed monthly changes for all zones including the control. The control was lowest in organic matter of the soil and young town edge zone was the highest in soil organic matter. Phosphorus content of the soil was greatest in the young town center and was the least in the old town center. Monthly changes in phosphorus content of the soil occurred for all zones and control. Available soil nitrogen was greatest in the young town interior and least in the control. Monthly differences in phosphorus content of the soil occurred among all zones and control.

Table 1. Soil organic matter, available phosphorus, and available nitrogen in 4 habitat zones of black-tailed prairie dog towns including a zone outside of the town(control). Values represent means $\pm$ 95% confidence intervals.

Date	Control	Young Town Edge	Young Town Interior	Young Town Center	Old Town Center
ORGANIC MATTER (%)					
Dec 30	1.8 $\pm$ 0.2	4.5 $\pm$ 0.7	3.5 $\pm$ 0.3	2.9 $\pm$ 0.3	3.1 $\pm$ 0.1
June 1	1.6 $\pm$ 0.3	4.1 $\pm$ 0.7	3.0 $\pm$ 0.7	3.7 $\pm$ 0.5	3.4 $\pm$ 0.4
July 15	4.1 $\pm$ 0.3	2.9 $\pm$ 0.4	4.2 $\pm$ 0.7	3.9 $\pm$ 0.4	3.2 $\pm$ 0.8
Aug 30	3.9 $\pm$ 0.3	3.6 $\pm$ 0.3	3.9 $\pm$ 0.2	4.0 $\pm$ 0.3	3.8 $\pm$ 0.2
PHOSPHORUS (ppm)					
Dec 30	1.0 $\pm$ 0	28.6 $\pm$ 5.3	4.2 $\pm$ 1.5	2.6 $\pm$ 1.1	3.6 $\pm$ 1.7
June 1	1.0 $\pm$ 0	19.8 $\pm$ 7.5	2.2 $\pm$ 0.8	6.8 $\pm$ 6.0	1.2 $\pm$ 0.4
July 15	8.4 $\pm$ 2.5	13.8 $\pm$ 5.5	4.6 $\pm$ 2.6	6.0 $\pm$ 7.3	2.2 $\pm$ 1.6
Aug 30	6.4 $\pm$ 1.3	15.4 $\pm$ 3.4	3.0 $\pm$ 1.0	3.0 $\pm$ 0.7	2.2 $\pm$ 1.3
NITROGEN (ppm)					
Dec 30	3.6 $\pm$ 2.1	10.6 $\pm$ 5.1	3.6 $\pm$ 1.8	1.6 $\pm$ 0.6	1.1 $\pm$ 0.6
June 1	1.8 $\pm$ 0.8	6.4 $\pm$ 7.4	7.8 $\pm$ 8.1	3.1 $\pm$ 1.4	2.0 $\pm$ 1.4
July 15	2.7 $\pm$ 0.4	2.8 $\pm$ 0.8	2.3 $\pm$ 2.6	6.4 $\pm$ 6.1	7.6 $\pm$ 11.4
Aug 30	1.0 $\pm$ 0	2.0 $\pm$ 1.2	1.0 $\pm$ 0	1.0 $\pm$ 0	1.0 $\pm$ 0

Soils in the center of the "old town" were lightly packed and eroded. This was also observed by Koford (1958), and Tileston and Lechleitner (1966). In this zone, prairie dog densities were low (12-16 animals/ha). Available soil nitrogen in the old town center was not different from the control (Table 1).

Rapid mineralization of soil nitrogen, phosphorus and organic matter may be related to increased microbial populations. Heavily grazed plants exude carbon from roots, and provide forage for microbial grazers (Bokari and Singh 1974). Black-tailed prairie dog towns support populations of nematodes greater than those populations outside dog towns (Ingham and Detling 1984). Since heavily grazed areas are more apt to support higher microbial populations, the zone x season interaction of available phosphorus, nitrogen, and organic matter indicates that differential populations of soil microbes are exerting an influence on soil fertility.

Black-tailed prairie dogs alter soil structure and chemical composition by burrowing, and adding excrement as well as plant material to the soil. Koford (1958) reported burrows of nearly 5 m in depth. Wilcomb (1954) excavated 12 burrows in Oklahoma and found that they had from 1 to 4 entrances, and averaged approximately 10 m in length. Prairie dog burrowing activity brought about 3.6 m of soil to the surface from 25 burrow entrances.

Black-tailed prairie dog towns exist on a wide range of soils, but are generally confined to deep loamy soils rather than the shallow soils characteristic of steep slopes and ridges (Reid 1954). Prairie dogs commonly excavate large rocks from their burrows, and dig through heavy clays (Koford 1958). They favor areas of softer materials, especially when

beginning a town. High densities of prairie dog burrows along old fence lines, in soils previously excavated by pocket gophers (Geomys sp.), and old fields from past farming practices were common in our study area. Black-tailed prairie dogs avoid excavating burrows on slopes greater than 15% in the Badlands National Park. Reid (1954) reported the upper limit of slope used by dogs to be 30% in North Dakota. Koford (1958) regarded the upper limit to be 22% from observations made in the Black Hills of South Dakota.

Vegetation

The 4 habitat zones and the mixed grass prairie zone (control) were significantly separated by discriminant analysis using canopy cover of 6 plant species (Table 2). Three perennial grasses [buffalograss, western wheatgrass, and tumblegrass (Schedonnardus paniculatus)], 1 annual grass, 6-week fescue (Vulpia octoflora), and 2 forbs [Patagonia Indianwheat, and prairie dogweed (Dyssodia papposa)] were most important in the discriminant functions ($P < .01$; error rate using jackknife classification = 10%). Error rates were greatest for the young town edge (33%) and in the control (17%). The method used for prairie dog habitat classification within a town involves collecting canopy cover data for each of the 6 plant species. The mean cover values obtained are multiplied by the coefficients with values of the constant included. These values are summed and the habitat with the highest score is the particular site assignment for the data collected (MacCracken et al. 1983). This information can be used to monitor changes in habitat zones over time within a prairie dog town. However, some caution should be used with this approach to classification

Table 2. Classification coefficients for canopy cover of plants associated with 4 prairie dog habitat zones on towns and mixed grass prairie (control).

COEFFICIENTS					
<u>Variable</u>	<u>Old Town Center</u>	<u>Young Town Center</u>	<u>Young Town Interior</u>	<u>Young Town Edge</u>	<u>Control</u>
<u>Plantago patagonica</u>	-1.12208	20.42869	13.53371	12.07238	12.63904
<u>Agropyron smithii</u>	- .23854	2.85443	1.44367	1.70882	2.83810
<u>Bachloe dactyloides</u>	- .19544	3.89478	5.14497	4.74508	4.75192
<u>Vulpia octaflora</u>	- .18045	2.01721	.68621	1.66920	4.01270
<u>Schedenardus paniculatus</u>	- .79725	17.81446	12.84127	11.16556	10.94678
<u>Dyssodia papposa</u>	6.56054	- 4.85253	- 3.05186	- 2.88169	- 3.41382
CONSTANT	-52.60401	-293.82901	-255.93638	-219.51019	-233.17598

of habitats (Rumble 1983), since, a small sample of prairie dog towns were used in this study. Other parameters may have to be measured in future studies depending upon the goals and objectives.

Changes in plant composition which separate the control from early stages of prairie dog invasion are related to reductions in tall grasses and increases in shortgrasses (Bonham and Lerwick 1976, Agnew et al. 1986). Further changes in vegetation on these prairie dog towns occurred as they become dominated by Patagonia Indianwheat which grows in the exposed soil surrounding crater mounds. However, Patagonia Indianwheat does not dominate all dog towns in western South Dakota. Vegetation at the young town center was characterized by increases in annual grasses and annual forbs. The old town center was dominated by forb species.

Standing crop biomass of plants differed among habitat zones and years (Fig. 2). A year x habitat interaction was also evident ($P < 0.05$). Plant composition differed ($P < 0.05$) among the habitat zones, as related to prairie dog activity (Fig. 3). The IVDMD of vegetation was different ($P < 0.05$) among habitat zones (Fig. 4). These differences among habitats in IVDMD were related to changes in phenological development of plants. Prairie dog use and activities suppressed phenological development and maintain the vegetation in a vegetative stage. Young vegetation being higher in nutritional qualities than older mature plants. Annual differences occurred in forb/grass ratios among habitat zones (Fig. 5), but not in IVDMD (Fig. 4).

Forbs and grasses which were present near town centers were clipped close to the ground by prairie dogs and maintained in a state of vegetative regrowth. Some species took on a prostrate form, e.g. western wheatgrass

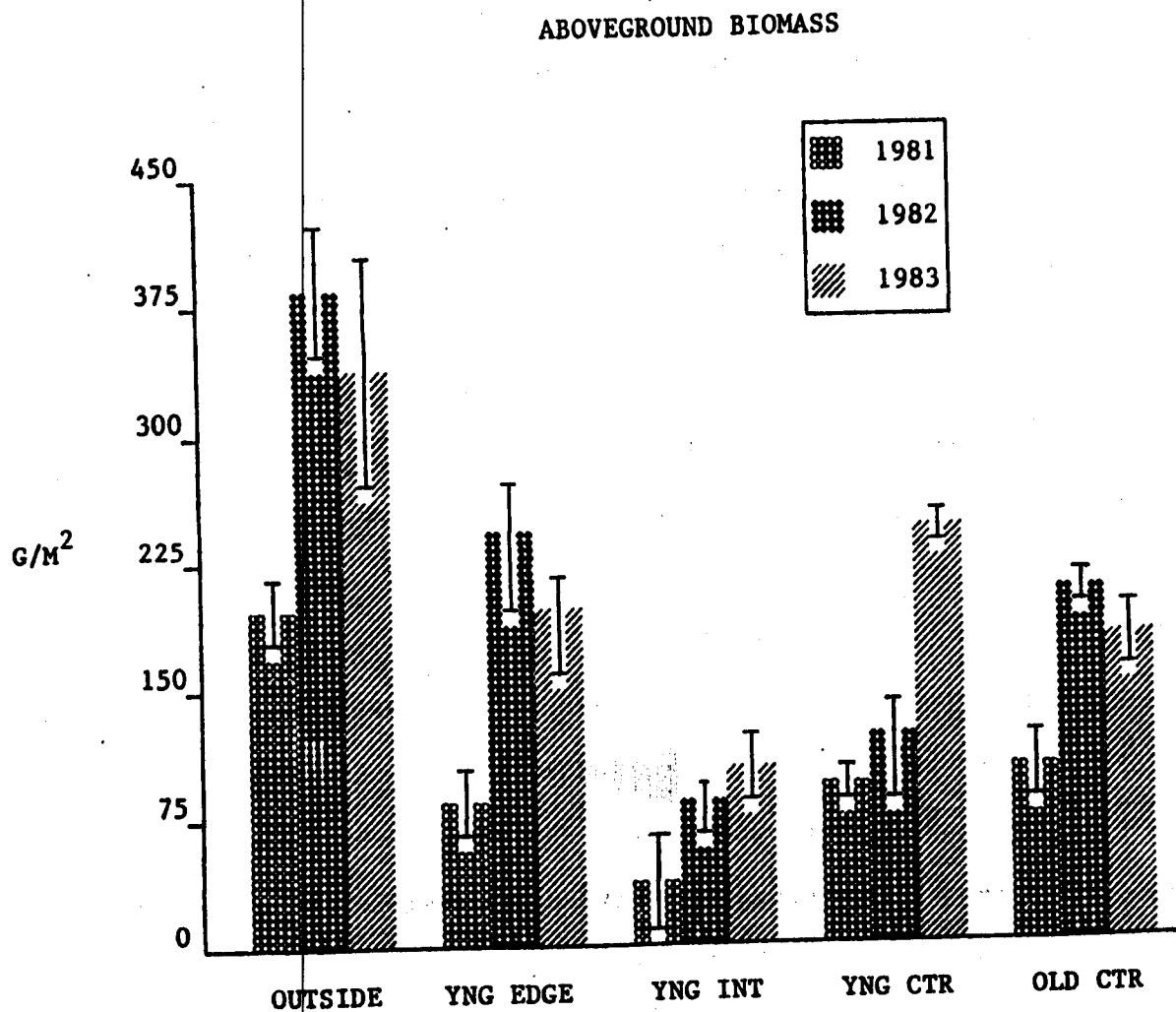


Figure 2. Total above ground biomass of plants on the outside of the prairie dog towns, young town edge (YNG EDGE), young town interior (INT), young town center (CTR) and old town center at peak during the period of maximum aboveground biomass. Bars are 95% confidence limits for the mean (n=6).

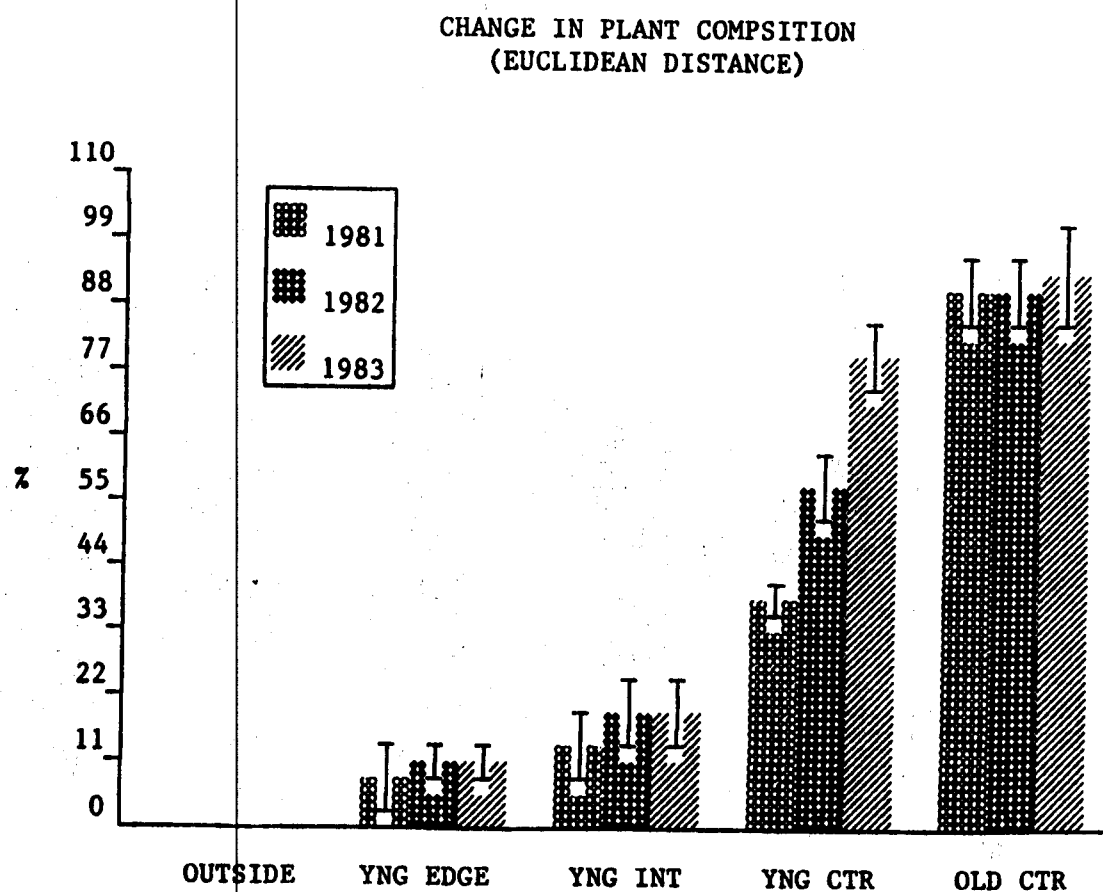


Figure 3. Change in plant composition among the 4 habitat zones within prairie dog towns and outside the towns during the period of maximum aboveground biomass. Prairie dog town zones include young town edge (YNG EDGE), interior (INT), center (CTR) and old town center. Bars are 95% confidence limits for the mean (n=6).

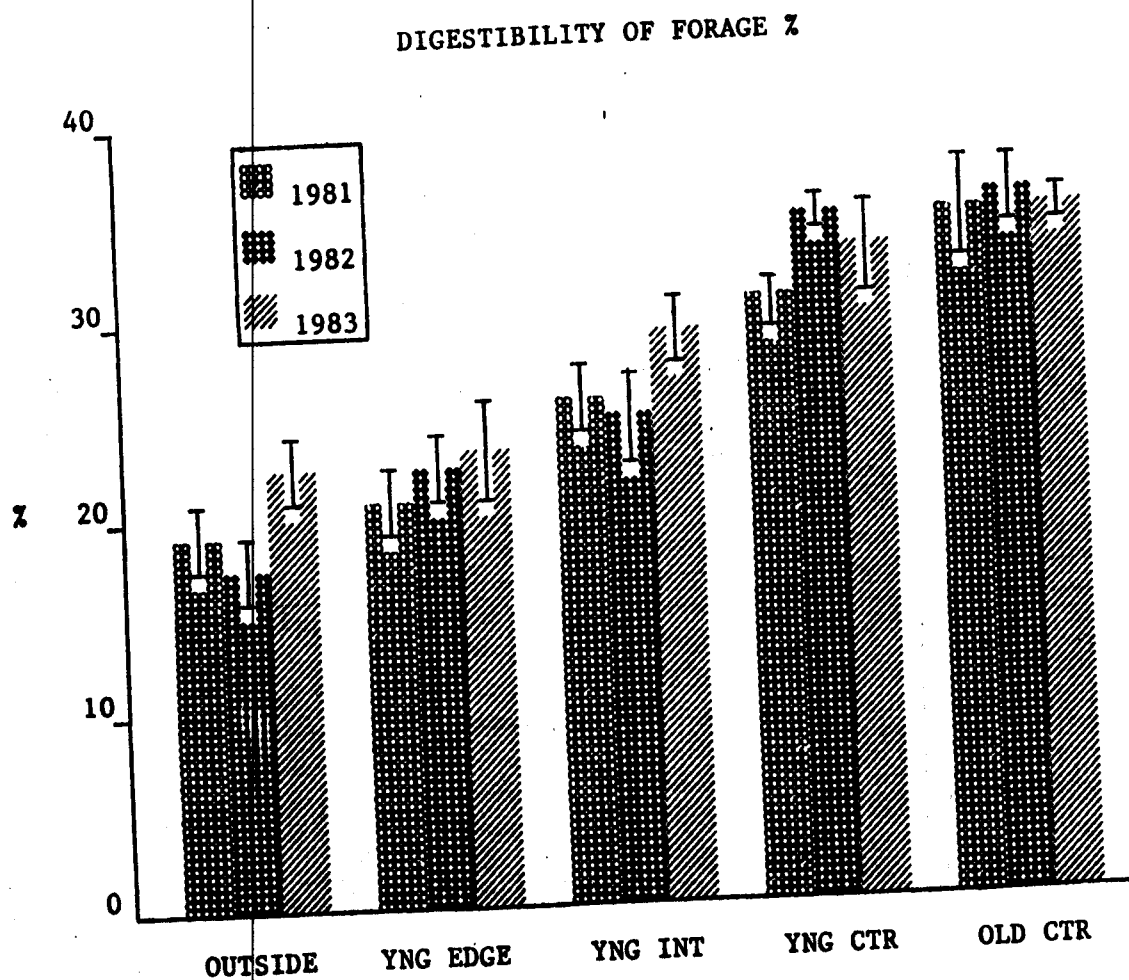


Figure 4. Digestibilities of forage among the 4 habitat zones within prairie dog towns and outside the towns during the period of maximum aboveground biomass. Prairie dog town zones include young town edge (YNG EDGE), interior (INT), center (CTR) and old town center. Bars are 95% confidence limits for the mean (n=6).

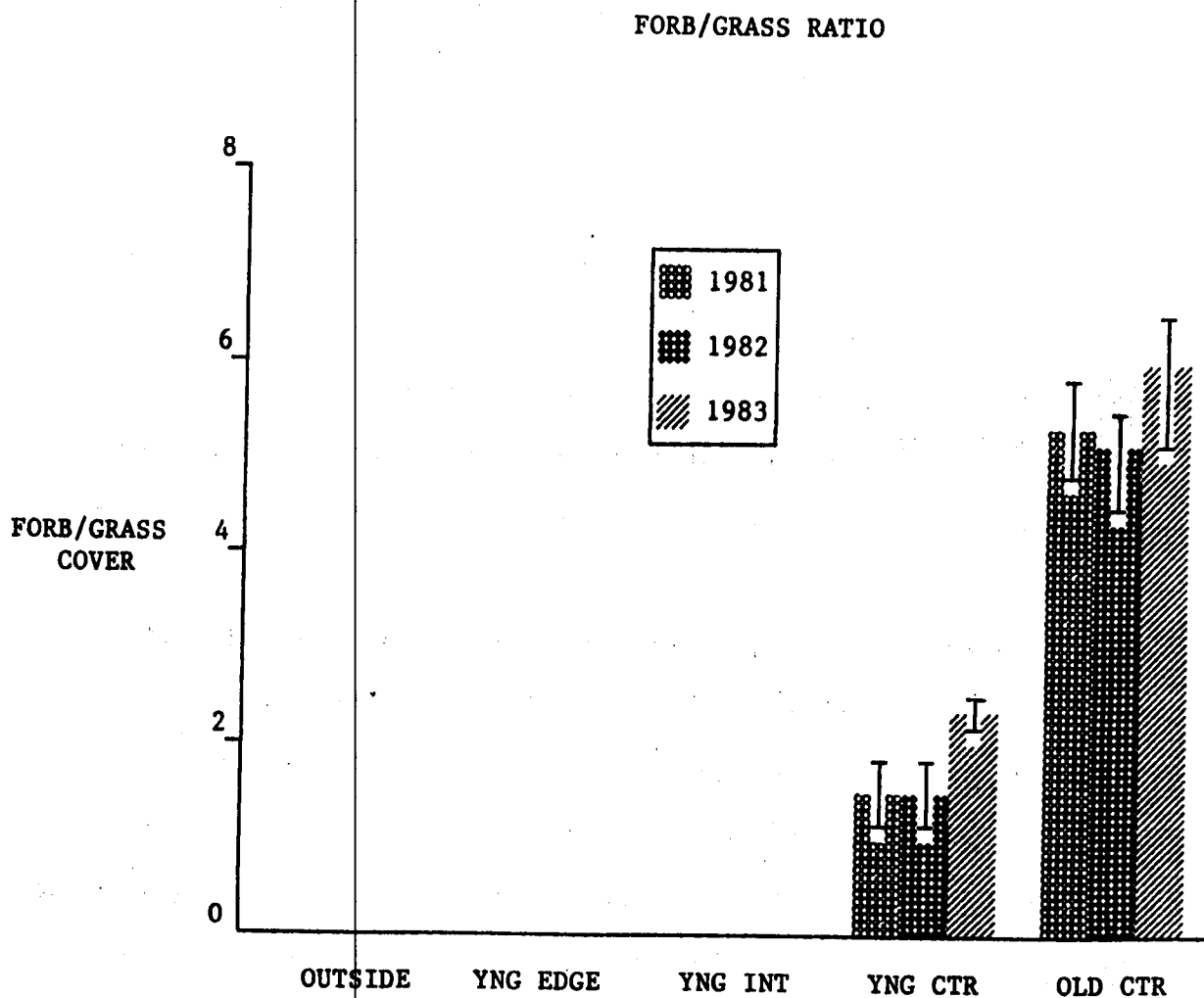


Figure 5. Forb/grass ratios based on % canopy cover during June among the 4 habitat zones within prairie dog towns and outside the towns. Prairie dog town zones include young town edge (YNG EDGE), interior (INT), center (CTR) and old town center. Bars are 95% confidence limits for the mean (n=6).

(Detling and Painter 1983). Plants farther away from the center of the dog town were utilized less. Forage conditions near town centers contrasted sharply with forage conditions along town edges. Prairie dogs and other herbivores eliminated standing dead plant material (Coppock et al. 1983a). Vegetation in earlier phenological stages, e.g. tillering (Everson 1966, Painter and Detling 1981), accounted for the greater IVDMD of forage as shown in this study. Coppock et al. (1983a) found increases in the IVDMD as time of prairie dog inhabitation on towns increased. He also reported an increase in shoot nitrogen content of vegetation in black-tailed prairie dog towns with long histories of inhabitation by prairie dogs.

Black-tailed prairie dogs influence plant composition through grazing and burrowing. Prairie dogs forage by clipping plants at the base of the stem (Koford 1958), and by occasionally digging roots. Root digging in our study occurred only during winter and early spring. Prairie dogs create areas of bare soil which increases plant seedling establishment. Dome mounds (King 1955), which are made of excavated mineral soil from burrow interiors, were dominated by forbs, including prostrate vervain, prairie tomato (Solanum triflorum), Russian thistle (Salsola kali), scarlet gaura (Gaura coccinea), scarlet globemallow (Spharalcea coccinea), and pigweed Amaranthus spp. Crater mounds, built of packed top soil and organic material were vacant of plants. The immediate area surrounding crater mounds, which was scraped bare of top soil for the mound's construction, was usually dominated by Patagonia Indianwheat. The cumulative effect of prairie dog activity on plant composition was a change from a mixed-grass prairie dominated by perennial grasses, to dominance of annual forbs and fringed sage (Artemisia frigida).

Food Habits

Diet composition varied greatly ($P < 0.05$) among the 4 habitat zones. Average forb/grass ratios in fecal samples were greatest in the old town center (6.3) and decreased in the young town center (1.1), young town interior (0.9) and young town edge (0.1). These changes in forb to grass ratios corresponded to changes which occurred in relative frequency of the vegetation (Fig. 6).

Stepwise discriminant analysis discriminated among diets of prairie dogs in habitat zones based on 4 plant species ($P < .01$), out of 17 variables (14 plant species, grass seeds and glumes, forb seeds, and forb flower parts). These 4 species were western wheatgrass, prairie dogweed, summercypress (Kochia scoparium), and Patagonia Indianwheat. Diets of prairie dogs in the young town interior were similar to prairie dog diets of the young town edge. These analyses indicate that prairie dog diets differ among some habitat zones of a prairie dog town.

Western wheatgrass was the only grass in prairie dog feces from the old town center, and made up a major portion of the diet (Fig. 7). Western wheatgrass was less abundant ($P < 0.05$) in prairie dog diets from other zones in the young town, while buffalograss and grass seeds were more abundant.

Both grass and forb seeds were abundant in prairie dog feces (Fig. 8). Grass seeds were a major food item (63%) at the town edge. Prairie dogs foraged among grasses which were not heavily grazed and high in seed production at the towns edge. Forb seeds were heavily used (28%) by prairie dogs located in the young town center. Most of these seeds were

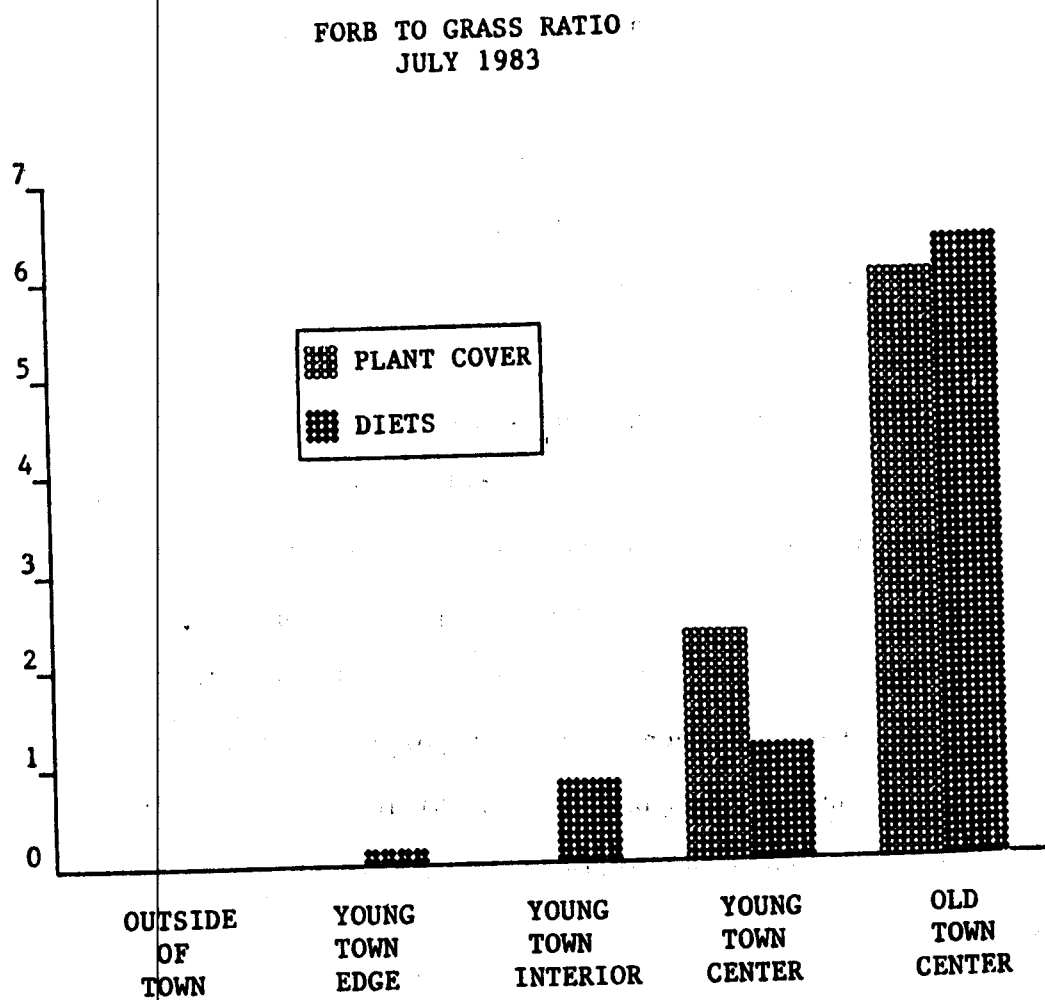


Figure 6. Average forb to grass ratio of prairie dog diets and plant canopy cover during July.

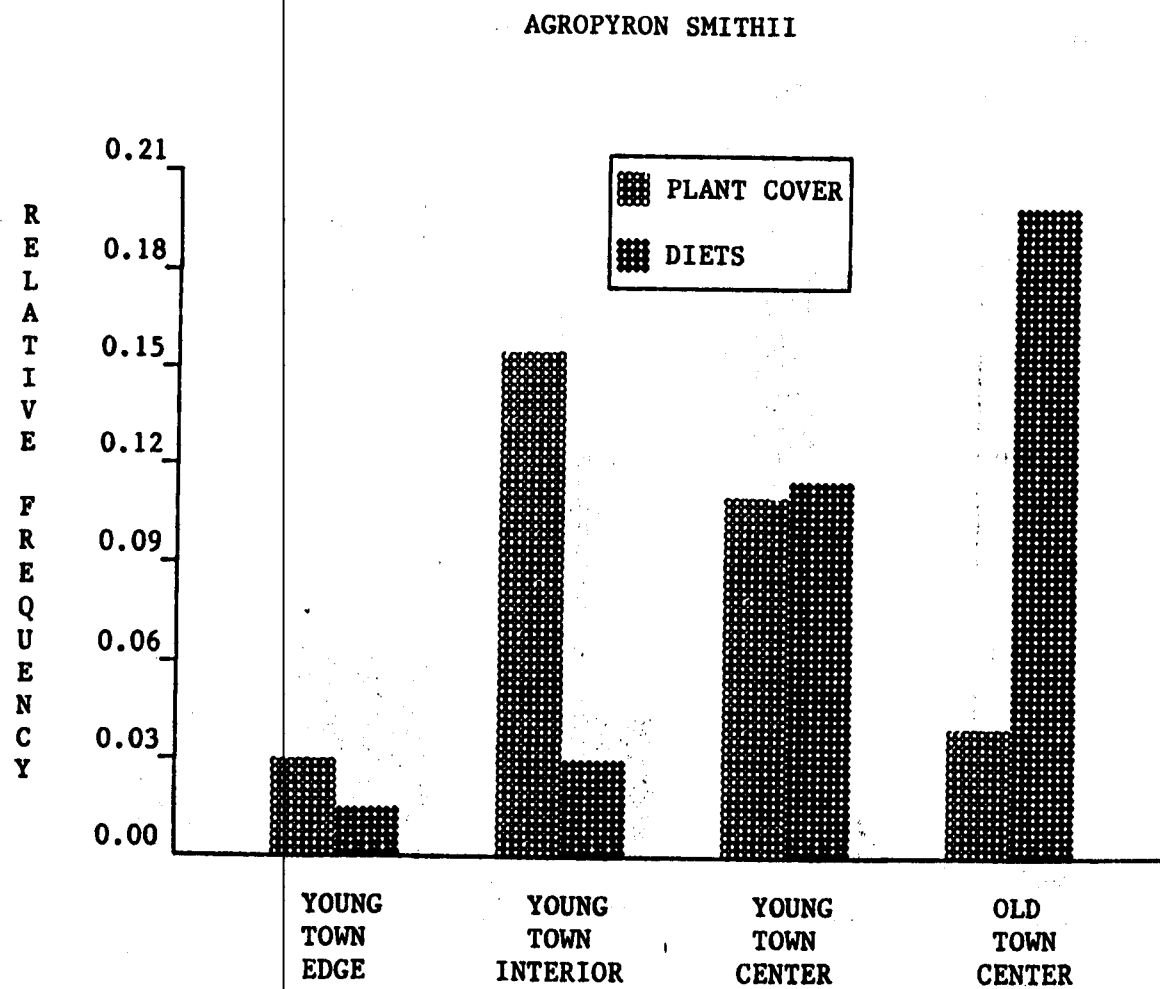


Figure 7. Relative frequency of western wheatgrass on the prairie dog town and in prairie dog diets from 4 zones within prairie dog towns.

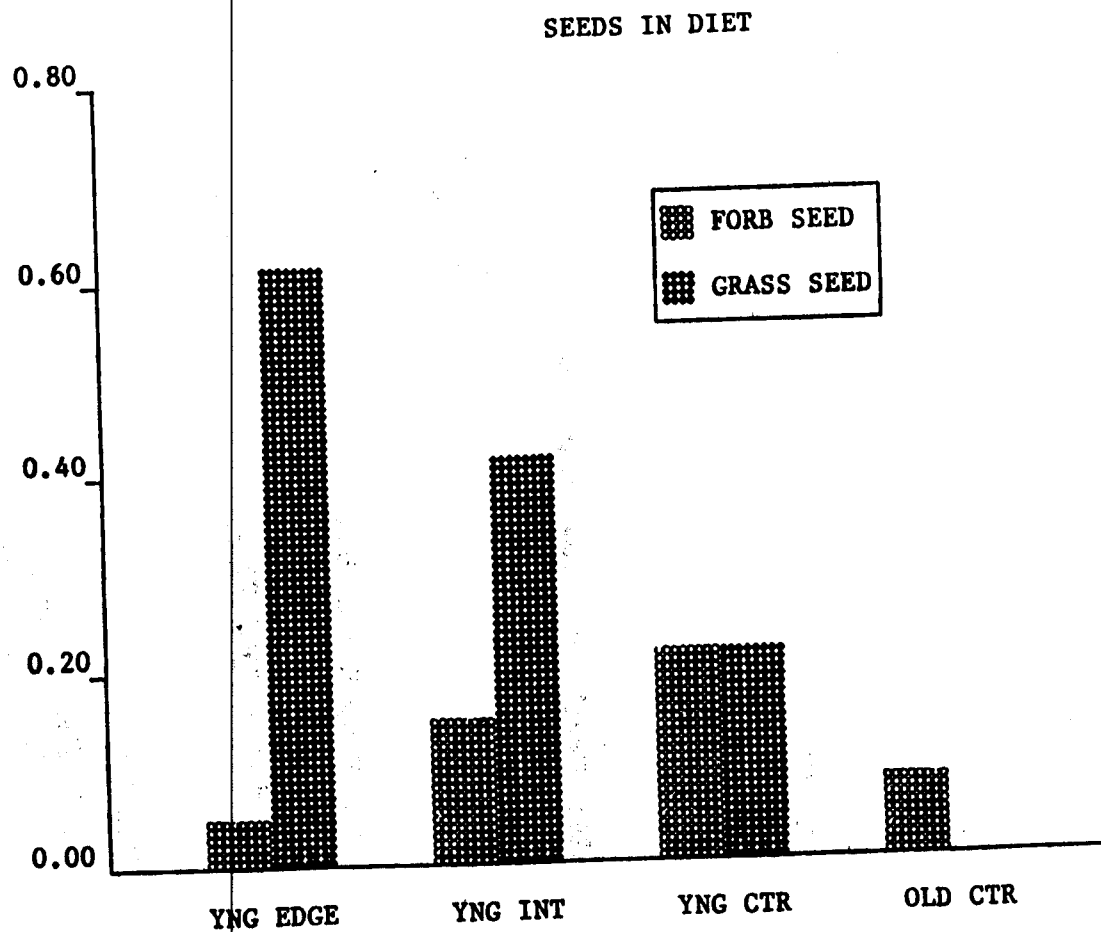


Figure 8. Relative frequency of forb and grass seeds in prairie dog diets from the young town edge (YNG), interior (INT), center (CTR) and old town center.

Patagonia Indianwheat and summercypress. Other forb seeds were buckwheat (Polygonum convolvulus), and an unidentified legume.

Forbs, especially species of pigweed, euphorbia (Euphorbia spp., prickly lettuce (Lactuca serriola), cutleaf nightshade (Solanum triflorum), and buffalo burr (S. rostratum) were abundant on the loose soil of dome mounds. Where mineral soil was scraped bare of topsoil adjacent to crater mounds, summercypress and Patagonia Indianwheat quickly became established. Summercypress and Patagonia Indianwheat, when available, were both heavily grazed by prairie dogs (Fig. 9). Summercypress was most abundant in prairie dog feces from the old town center. Indianwheat was found mainly in diets of prairie dogs from the young town interior and center (Fig. 10).

Prairie dogweed was available only in the old town center, and was present in diets of prairie dogs located in this habitat zone. This habitat was characterized by bare ground and sparse plant cover, similar to results reported by Coppock et al. (1980). Prairie dogweed was highly aromatic and one of a very few species available to prairie dogs. The presence of prairie dogweed on dog towns was indicative of long-term prairie dog inhabitation generally over 15 years. Black-tailed prairie dogs appear capable of foraging upon a wide range of grasses and forbs. When available, seeds and flower parts make up a large part of their diets. Plant changes which prairie dogs induce upon an area was related to feeding activities. Differential digestion of plant species by prairie dogs is not known to occur at this time.

Black-tailed prairie dogs were generally limited to foraging within their coterie territory. Only individuals which inhabit territories at the town edge were able to forage freely in the relatively undisturbed prairie.

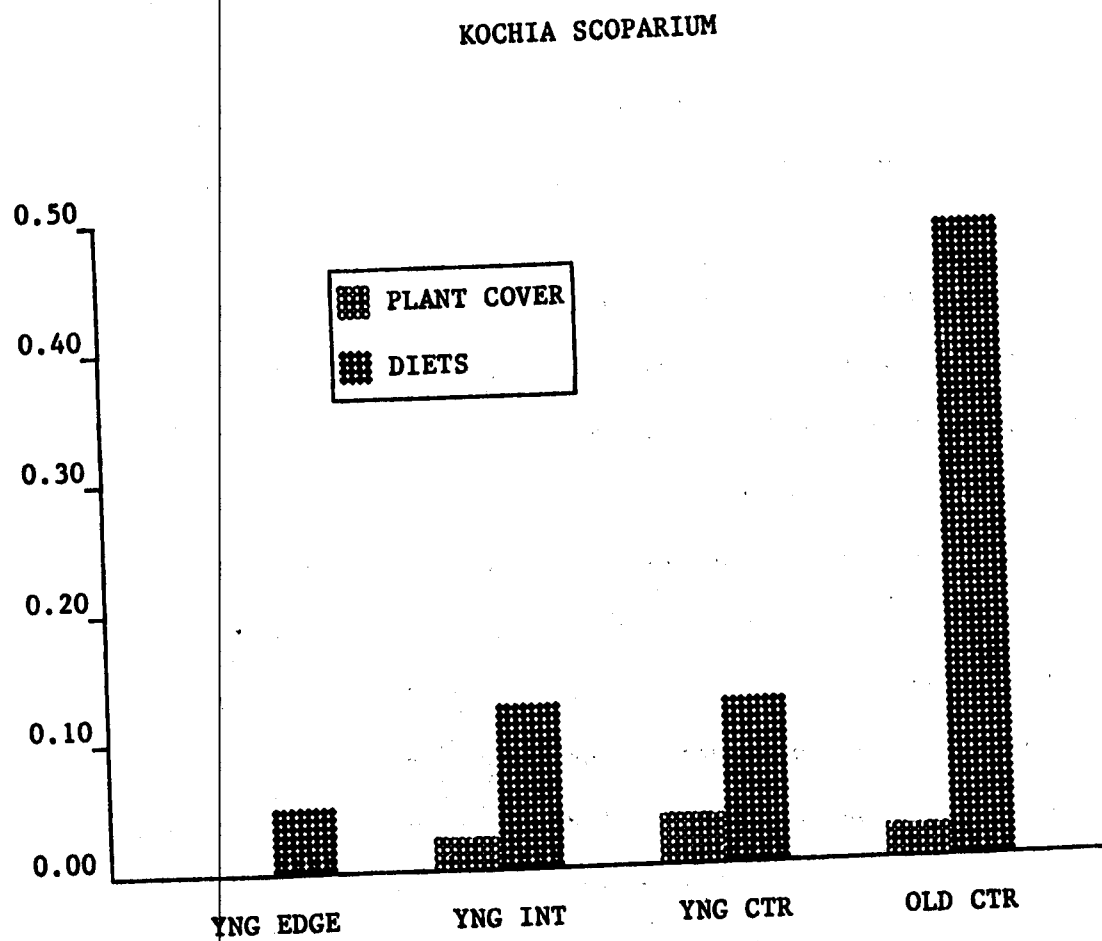


Figure 9. Relative frequency of *summercypress* on prairie dog towns and in prairie dog diets within zones of a young prairie dog town edge, (YNG), interior (INT), center (CTR) and old town center.

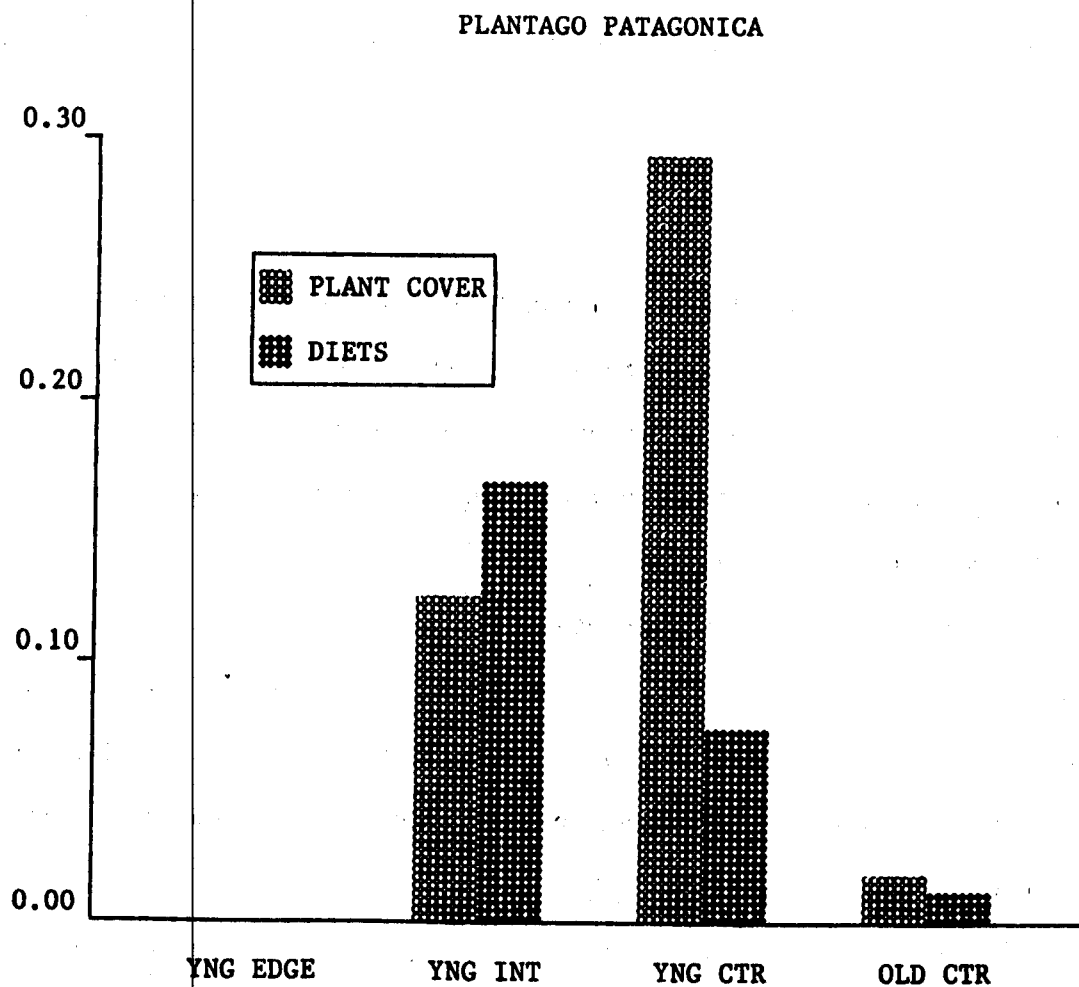


Figure 10. Relative frequency of indianwheat on prairie dog towns and in prairie dog diets within zones of a young town edge (YNG), interior (INT), center (CTR), and old town center.

With changes in plant composition within a prairie dog town, prairie dogs were able to adjust their diets accordingly as shown in our study and by Fagerstone et al. (1977). Prairie dogs have been found to consume a wide variety of plant species and seeds, but generally show a preference for grasses (Fagerstone et al. 1981, Fagerstone 1982, Uresk 1984, Summers and Linder 1978).

Vegetation

Plant composition of the young town center was different from interior, edge and control areas (Fig. 11). In the central town area, annual forbs dominated over grasses. Forbs such as prostrate vervain, Patagonia Indianwheat and monolepis (Monolepis nuttalliana) were abundant and perennial grasses decreased.

Areas outside the town center also showed plant compositional changes. Concentrated grazing and excavation by prairie dogs were not uniform within a town (Fig 12). Small secondary concentrations of prairie dog activity were common within the general town structure and accompanied associated changes in plant composition.

Changes from perennial grasses to annual forbs were clearly evident on prairie dog towns, however, exact plant species composition of town centers varied among dog towns. Plant species diversity increased after the initial invasion of prairie dogs, with introduction of forbs on disturbed areas and around dome mounds in this study and also reported by King (1955). On old town sites, plant species diversity was low (Coppock et al. 1983a). Agnew et al. (1986) found that fewer plant species occurred on prairie dog towns, compared to relatively undisturbed mixed grass prairie sites.

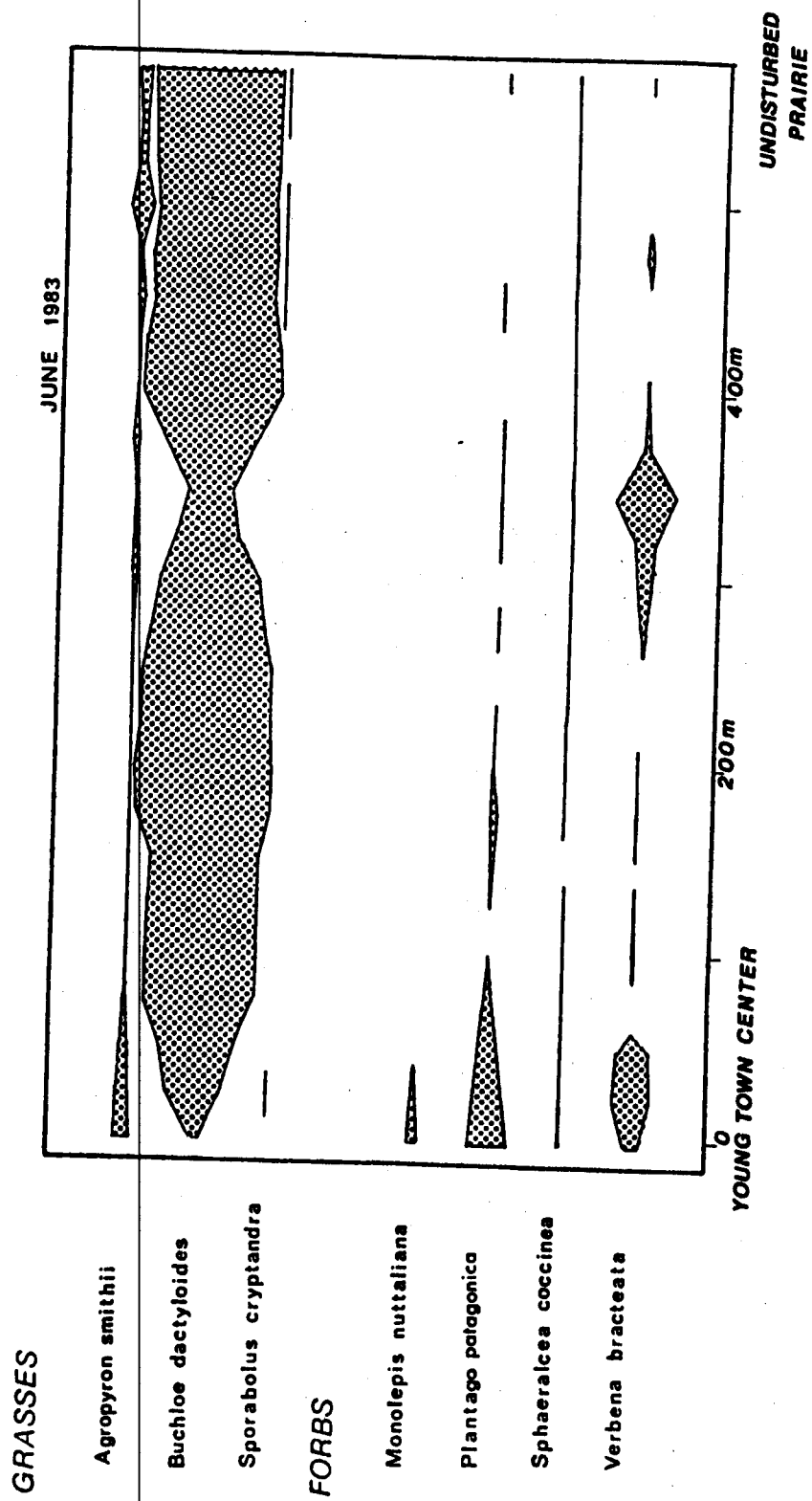


Figure 11. Relative plant composition of grasses and forbs from the young prairie dog town center to undisturbed mixed grass prairie. Values determined by canopy cover during June.

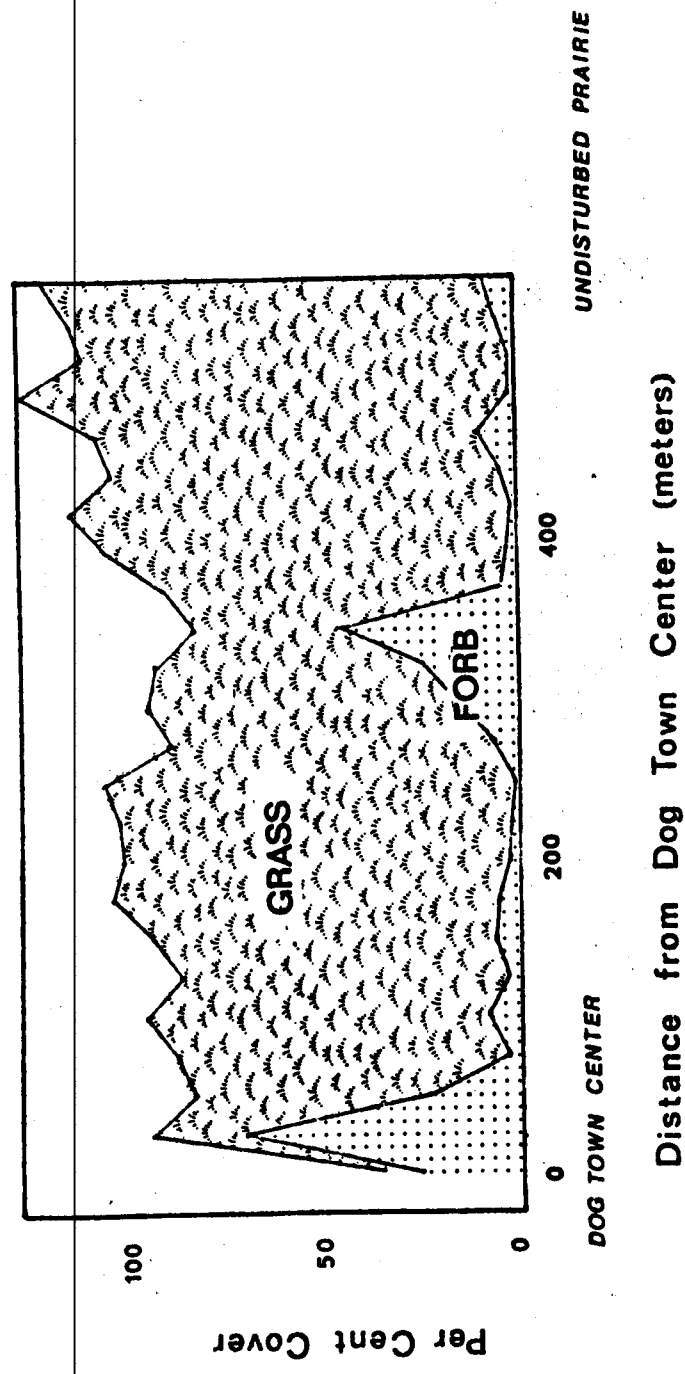


Figure 12. Canopy cover of grasses and forbs from the young prairie dog town center to undisturbed mixed grass prairie during June.

Although plant species composition differed grossly from one town to the next, the overall trend was a change from perennial grasses to forbs (Koford 1958, King 1955, Garrett et al. 1982). The general pattern in our study areas was concentric vegetation zones surrounding a central core where the town originated. The dog town center was sparsely vegetated with forbs, and accompanied by a low density of prairie dogs. Near the town edge, the soil surface was less disturbed and grasses dominated.

Reproductive Success

The habitat by zones within a prairie dog town were found to have an effect ($P < .01$) upon number of juveniles per female produced (Fig. 13). Reproduction was greatest ($P < 0.01$) for individual females whose territories were situated well inside the town edge, but in areas with no major changes in plant composition from grasses to forbs.

Prairie dogs within the young town interior had the greatest ($P < 0.01$) reproductive success averaging approximately 5 juveniles/adult female. Reproductive success was lowest ($P < 0.01$) for prairie dogs in the old town center, 2/female. Abundant perennial plant biomass, and low frequency of density limiting behavioral interactions at the town edge may have contributed to a greater reproductive success of adults and greater survival of juveniles. The effect of these factors may be offset by predation (King 1955, Hoogland 1981a). Though less likely to be victims of predation, prairie dogs at the town interior are dependent on annual forbs as food which do not persist during the winter (black-tailed prairie dogs are active all winter). Exclusion from surrounding territories further limited forage supplies for individuals in town interiors.

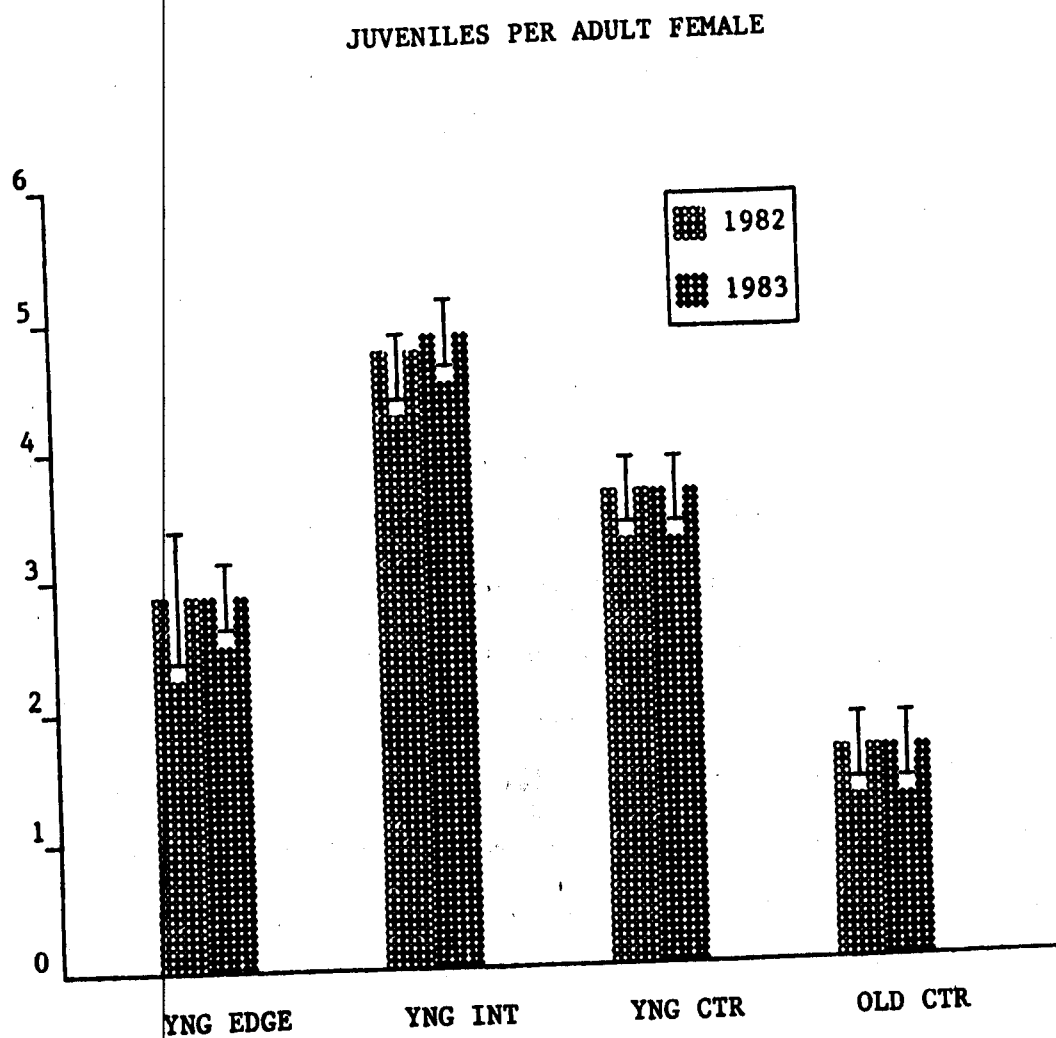


Figure 13. Number of prairie dog juveniles produced per adult female within the 4 habitat zones of prairie dog towns. The town zones are young town edge (YNG), interior (INT), center (CTR) and old town center. Bars represent 95% confidence intervals.

Garrett et al. (1982) reported lower prairie dog densities and lower reproductive rates in a 25 year old town when compared to one less than 5 years old. Long-term inhabitation by prairie dogs results in reduced reproductive success due to poor forage supplies and density limiting social interactions.

Reproductive potential of black-tailed prairie dogs, which bear a single litter annually, has been determined by counting corpora lutea, placental scars, and embryos. Theisen (1981) reported that the annual reproductive rate per female ranged from 2 to 7 based upon corpora lutea counts, from 2 to 5 from counts of placental scars, and between 4 and 5 based on embryo counts. Theisen also reported litters of yearling females as large as those of adults. Stockrahm (1979) reported placental scar counts ranging from 1 to 11 with an average of 5 (± 2 , 95% CI) per female. Pfeiffer (1972) reported a mean embryo count of 5, while Koford (1956) and Tileston (1961) reported 4 and 5, respectively.

Embryo counts from prairie dog populations have suggested an average litter size (at birth) of 5 juveniles. However, Garrett et al. (1982) reported 5 juveniles/female at birth but the number of juveniles emerging from the burrows was less. Our study showed a high of 5 juveniles/female emerged in a young prairie dog town. Garrett et al. (1982) reported a mean litter size of 3 in a newly established town, and 3 from a dog town over 25 years of age. Other reports of mean litter size, as determined by counting juveniles at burrow entrances after emergence in mid-spring, ranged from 3 (Kerwin 1972) to 5 (King 1955).

Establishment and immigration

A total population of 164 prairie dogs was estimated in the study area (Hockings, Roberts) during 1961, 206 in 1982, and 223 during 1983.

Immigrants of both sexes accounted for 15.5% (32) and 16.1% (36) of the population in 1982 and 1983. Nineteen female immigrants were captured on the study area during 1982, and 16 during 1983. These females made up 8.3% and 6.1% of the total population in 1982 and 1983 respectively.

Establishment by female immigrants was greatest ($P < 0.01$) at the edges of prairie dog towns (Fig. 14). Fewer immigrants become established within the interior of towns than expected by chance ($P < 0.01$).

The density of prairie dogs was not uniform ($P < 0.01$) over the 4 habitat zones (Fig. 15). Highest densities of animals were observed in the interior of the young town during 1982 (44.0 animals/ha., 3.8 burrow entrances/animal). The lowest densities of animals were observed in the old town center (13.9 animals/ha, 4.2 burrow entrances/animal).

Female immigrants established along the edge of the dog town, which resulted in the expansion of the town area. The choice open to dispersing females for colonization was the town edge or open prairie, as town interiors and centers were fully occupied. However, establishment of new prairie dog towns was rare on the open prairie (Garrett 1982). Female immigrants were restricted from settling within territories in the town interior. Recruitment in interior territories, which were bordered by other prairie dog territories, was restricted to progeny of females of a territory. Coterries of black-tailed prairie dogs were antagonistic toward individuals outside their own group (King 1955, Garrett 1982). The territorial system of this polygynous social herbivore was matrilineal,

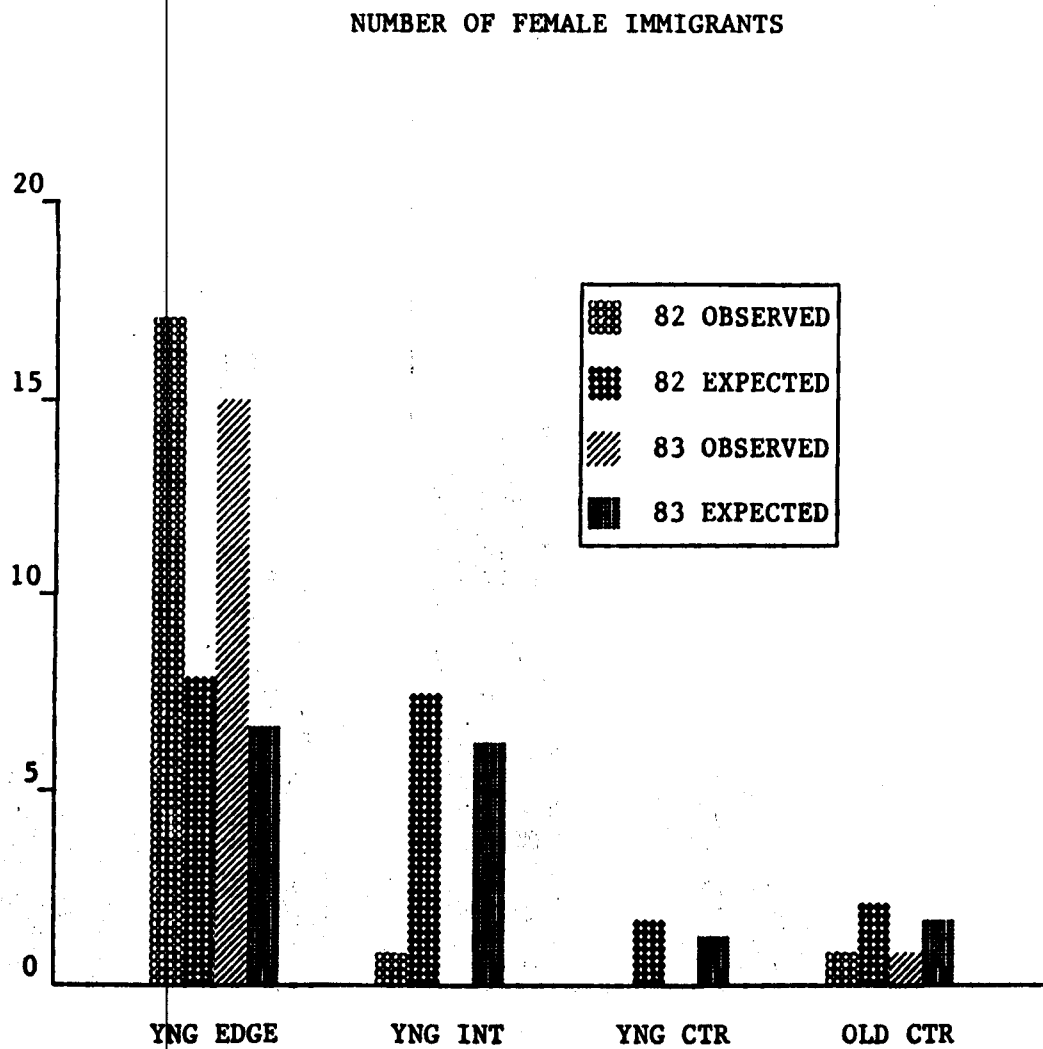


Figure 14. Number of female immigrants observed and expected with Chi square analysis on 4 habitat zones, young town edge (YNG), interior (INT), center (CTR) and old town center during 2 years.

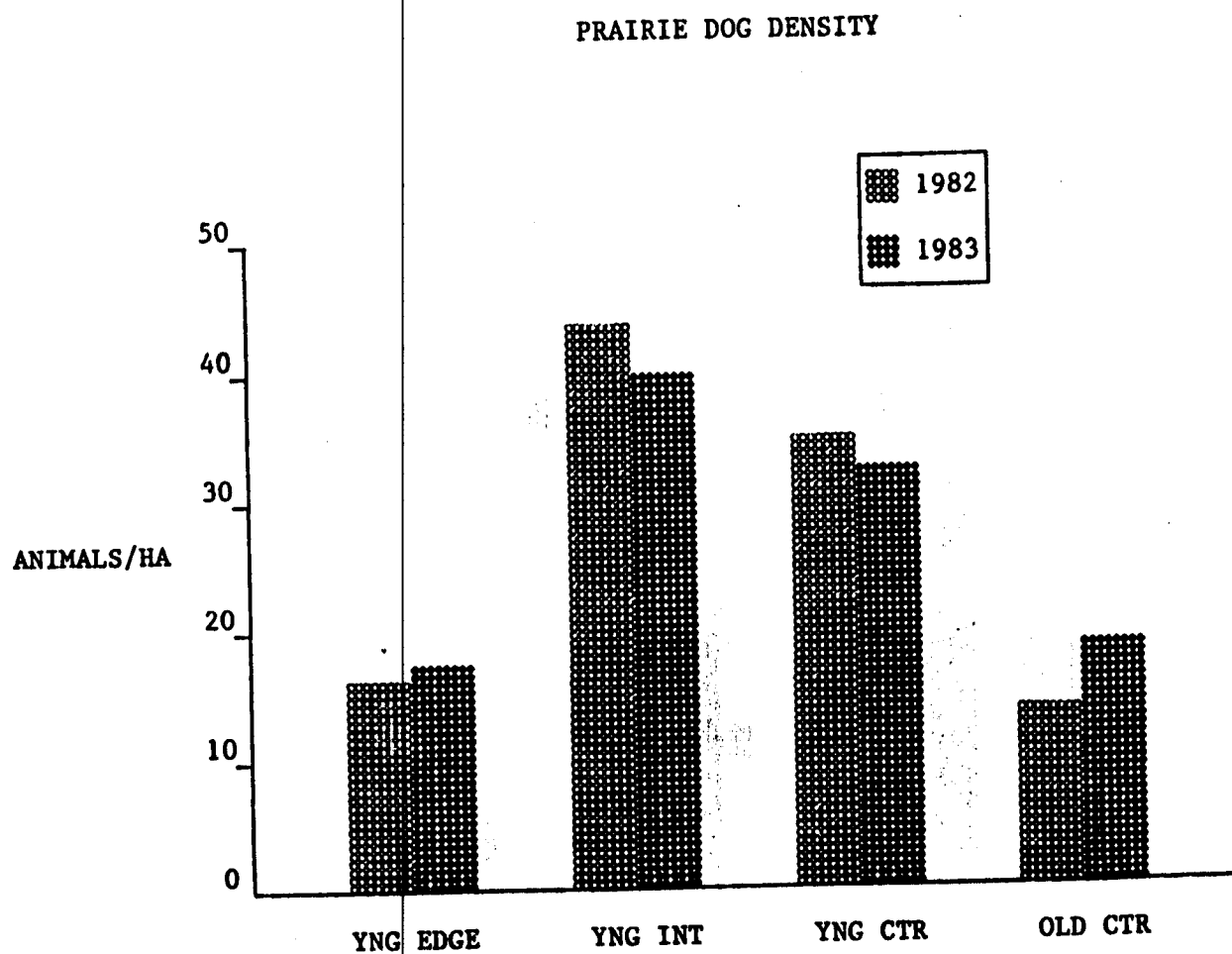


Figure 15. Density of black-tailed prairie dogs located within 4 zones of the town during 2 years. The zones are young town edge (YNG), interior (INT), center (CTR) and old town center.

i.e. territory remained under the occupancy of the coterie's female progeny. Though acceptance of female immigrants into territories within the town interior was rare, occasionally newly organized coterie's along the town edge incorporated immigrants of both sexes. Groups of prairie dogs with no opportunity to expand their territory limit their acceptance of new members to progeny. In this study, prairie dog immigrants preferred to settle at the edges of established dog towns. Similar results were reported by Garrett and Franklin (1982).

Response to Rodenticide Treatment

A total of 76 individuals were captured on the 6 ha rodenticide treated site in 1981 before zinc phosphide was applied (Table 3). During the 1982 season, after zinc phosphide treatment, 26 individuals were captured in the treated site, and 59 in the control (Table 4). After the second application of zinc phosphide in 1982, 19 individuals were captured in the treated site, and 68 in the control.

Numbers of males and females of the control population were not different ($P < 0.05$) from expected numbers (chi-square, 1 d.f.) during 1982 and 1983 (Table 3). Immigrant yearling numbers were greater than expected on treated sites when compared with immigrant adults ($P < 0.01$, chi-square, 1 d.f.). Non-lactating females made up 100% (13/13) of the female population of immigrants on treated sites in 1982 and 75% (6/8) in 1983. Numbers of non-lactating females were greater than expected among immigrants than among resident females in the control site ($P < 0.01$, chi-square, 1 d.f.). Non-lactating females on the control site made up 3% (1/30) of the potentially reproductive population in 1982, and 8% (3/38) in 1983.

Table 3. Black-tailed prairie dog densities (6 ha) on the edge of Roberts dog town with original pre-poison population, reinviation after 1st poisoning and reinviation after 2nd poisoning during 1981-1983.

Age Class	Pre-Poison				Reinviation after 1st Poisoning				Reinviation after 2nd Poisoning			
	Males		Females		Males		Females		Males		Females	
	-----1981-----		-----1982-----		-----1983-----		-----1983-----		-----1983-----		-----1983-----	
	June		August		June		August		June		August	
Adults	9	11	4	1	4	4	1	2	2	3	2	2
Yearlings	3	3	5	9	6	6	6	5	6	6	4	4
Juveniles	31	19	0	0	0	0	0	0	0	0	0	0
Total	43	23	9	10	10	10	7	7	8	9	6	6

¹ Zinc phosphide treatment in mid-August 1981.

² Zinc phosphide treatment in late-August 1982.

Table 4. Comparison of reinvading black-tailed prairie dogs that immigrated to a zinc phosphide treated and an adjacent untreated study area.

	Treated		Untreated	
	June	August	June	August
	-----1982 ¹ -----			
Adults	5	2	6	11
Yearlings	8	11	3	4
Juveniles	<u>0</u>	<u>0</u>	<u>20</u>	<u>30</u>
Total	13	13	29	30
	-----1983 ² -----			
Adults	3	2	5	13
Yearlings	8	6	3	5
Juveniles	<u>0</u>	<u>0</u>	<u>22</u>	<u>20</u>
Total	11	8	30	38

¹Reinvasion after zinc phosphide treatment in mid-August 1981.

²Reinvasion after zinc phosphide treatment in late-August 1982.

Application of zinc phosphide eliminated 98.7% of the prairie dogs in 1981, and 100% in 1982. There was no reproduction during either 1982 or 1983 among newly established prairie dogs on the treated site. This suggests that black-tailed prairie dogs disperse after the mating season, and do not give birth during the first year in a newly established territory.

Two yearling females, captured as juveniles in the same territory during August 1981 within the untreated site, were recaptured in the treated site in June 1982. Both travelled nearly 500 meters to their newly acquired territories. Both females showed no signs of lactation. By August 1982, one female had returned to her natal coterie. A similar instance of a returning immigrant was observed by Garrett (1982). In our study, this same female again immigrated into the treated area in 1983. At the time of her second immigration, she showed signs of lactation.

Total prairie dog numbers in the treated area remained relatively constant, although many of the individuals changed. During 1982, 72% of the immigrants on the treated area were the same individuals captured in June and recaptured in August. During 1983, 68% of the prairie dogs were common to both trapping sessions. Newly established dog town edges supported populations of transient prairie dogs. Females switched burrows regularly between trapping sessions, perhaps searching for suitable winter burrows and to bear young in the spring.

The large percentage of non-lactating females that immigrated from their original territories indicates that reproductive failure stimulates immigration. Non-lactating females immigrated following an unsuccessful breeding season. Older females that immigrated after reproduction may have

lost their young. Some non-reproductive yearlings remained in their natal territories. Barren females possibly served as helpers and protected the young. All non-reproductive yearling females that remained in natal territories successfully reproduced the following year.

Black-tailed prairie dog towns treated with rodenticide were soon reoccupied by prairie dogs. Since the majority of immigration occurred from early May to mid-June, rodenticide treatment after this period would be most effective. Garrett and Franklin (1982) also reported that immigration occurred during this same time period. Knowles (1982) used zinc phosphide to eradicate prairie dog populations by treating prairie dogs at town edge and centers. He found that prairie dog populations recovered to their original numbers within 2 years. Treatment of town centers was more successful. Eradication of entire towns were totally recolonized after 4 years.

The demography of prairie dog immigrants is not well known. King (1955) reported that females immigrated after weaning juveniles, leaving territories to their young. King also reported that newly established territories were occupied by highly unstable populations where many different adults were trapped over a short period of time. Garrett and Franklin (1982) reported that the sex ratio for dispersers was skewed toward males. Though females outnumbered males in black-tailed prairie dog towns (Koford 1958, King 1955), males were more likely to disperse as a result of coterie structure. Juvenile females often remained as members of their natal territory and bore young in that territory. Males immigrated as yearlings (Hoogland 1981a). Yearling males which remained in the coterie roamed the town, searching for unoccupied territories, or territories with

few members (Knowles 1982, this study). In this study, all yearling males left before their second spring in the coterie. Hoogland (1982) reported that adult males tend to leave a territory after about 2 years, then establish residence in a nearby territory.

Expansion of Prairie Dog Towns

Newly established areas were discriminated from vacant areas based on burrow densities, distance of burrows from town edge, and vertical visibility (height and density of vegetation) ($P < .01$, Table 5). Prairie dog burrow densities, distance of burrows from town edge, and vertical visibility were positively related to establishment of prairie dogs. With these variables, 76% of the sites examined could be correctly classified as to suitability for prairie dog occupancy. On areas not suitable for establishment, 80% of the sites could be correctly classified. Vertical visibility was the most influencing variable for prairie dog establishment. Prairie dogs were not attracted to areas with low visibility. Prairie dogs became established in areas near territories of large numbers of coterie, with high burrow densities. Immigrating prairie dogs selected areas where buffalograss and blue grama were abundant. Shortgrasses provided greater vertical visibility as opposed to other vegetation. The presence of large numbers of coterie and high-visibility habitat were components necessary for prairie dog establishment, a distance 40 m from the town edge. The abundance of forbs had no influence on establishment of prairie dogs.

Dispersing black-tailed prairie dogs become established near an existing town edge. Newly established prairie dogs, at great distances from the town edge, increased the town perimeter and indicated rapid town growth.

Table 5. Classification coefficients for established and unestablished black-tailed prairie dogs on and off prairie dog towns as related to burrow densities/ha distance away from burrows at town edge (m) and percent vertical visibility (height and density of vegetation).

<u>Variable</u>	<u>COEFFICIENTS</u>	
	<u>Established</u>	<u>Unestablished</u>
Burrows	0.017	- 0.359
Distance	0.014	0.100
Visibility	14.227	15.888
Constant	-27.855	-34.147

Topography (Knowles 1982, Koford 1958) and soils (Koford 1958, Smith 1958) have also been suggested as affecting the rate of expansion. In this study, the number of prairie dog immigrants was an important regulator in the establishment of new coterries, and therefore had an effect on town growth. Availability of vacant burrows, often created by application of rodenticides to prairie dog towns, encouraged prairie dog establishment.

Intense livestock grazing on grasslands has been implicated in influencing settlement and expansion of black-tailed prairie dog towns (Koford 1958, Snell and Hlavachick 1980, Uresk et al. 1981, Snell 1985) because of increased vertical visibility. High visibility (low, sparse vegetation) was a natural feature of the vegetation found growing on particular soil types in this study. Sandy, well drained areas in the Badlands were vegetated by sparse blue grama and buffalograss mixtures. Disturbed areas such as oldfields, fallows, trampled ground around cattle watering tanks and gates along fence lines have high visibility. High visibility due to reduced height of vegetation during drought also contributes to the expansion of prairie dog towns.

In this study, the proximity of other prairie dog towns was a factor in the growth of young towns (also reported by Knowles, 1982). Migration was common between prairie dog towns, and occurred over relatively great distances. Prairie dogs have been reported to travel approximately 7 km before establishment at the edge of a dog town (Garrett 1982).

Prairie dog towns provide habitat for the endangered black-footed ferret (Fortenbery 1972, Sheets et al. 1972) and are regularly used by terrestrial predators (Cahalane 1950, Smith 1958, Garrett 1982) and provide habitat for many birds (Agnew et al. 1986). They are preferred areas for

bison in Badlands and Wind Cave National park (Coppock et al. 1983b). In order to efficiently manage black-tailed prairie dog populations, range and wildlife managers will need to manipulate the height and density of vegetation, and population densities at the town edge. Management of the vegetation by grazing reductions, revegetation to tall plant species, and fertilization of rangeland may help limit expansion of black-tailed prairie dog towns. In some cases, rodenticide use at the town edge may be required to control expansion of prairie dog towns.

LITERATURE CITED

- Agnew, W., D. W. Uresk and R. M. Hansen. 1986. Flora and Fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *J. Range Manage.* 39:135-139.
- Baumgartner, L. L., and A. C. Martin. 1939. Plant histology as an aid in squirrel food habitat studies. *J. Wildl. Manage.* 3:266-268.
- Bokhari, U. G., and J. S. Singh. 1974. Effects of temperature and clipping on growth, carbohydrate reserves, and root exudation of western wheatgrass in hydroponic culture. *Crop Sci.* 14:790-794.
- Bonham, C. D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. *J. Range Manage.* 29:221-225.
- Cahalane, V. H. 1950. Badger-coyote "partnerships". *J. Mammal.* 31:354-355.
- Collins, A. R., J. P. Workman, and D. W. Uresk. 1984. An economic analysis of black-tailed prairie dog (Cynomys ludovicianus) control. *J. Range Manage.* 37:358-361.
- Coppock, D. L., J. K. Detling, and M. I. Dyer. 1980. Interactions among bison, prairie dogs and vegetation in Wind Cave National Park. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, USA.
- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. 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 (Berl)* 56:1-9.

- Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983b.
 Plant-herbivore interactions in a North American mixed-grass prairie,
 II. responses of bison to modification of vegetation by prairie dogs.
Oecologia (Berl) 56:10-15.
- Daubenmire, R. 1959. A canopy coverage method of vegetational analysis.
Northwest Science 35(1): 43-64.
- Everson, A. C. 1966. Effects of frequent clipping at different stubble
 heights on western wheatgrass (Agropyron smithii, Rydb.). *Agron. J.*
 58:33-35.
- Fagerstone, K. S., H. P. Tietjen, and G. K. Lavoie. 1977. Effects of
 range treatment with 2,4-D on prairie dog diet. *J. Range Manage.*
 30:57-60.
- Fagerstone, K. A., H. P. Tietjen, and O. Williams. 1981. Seasonal
 variation in the diet of black-tailed prairie dogs. *J. Mamm.*
 62:820-824.
- Fagerstone, K. A. 1982. A review of prairie dog diet and its variability
 among animals and colonies. Pages 178-184 In R. M. Timm and R. J.
 Johnson, editors. *Proceedings: Fifth Great Plains Wildlife Damage
 Control Workshop. Institute of Agriculture and Natural Resources,
 University of Nebraska, Lincoln, Nebraska, USA.*
- Fortenbery, D. K. 1972. Characteristics of the black-footed ferret. U.S.
 Govt. Print. Office, Washington, D.C., USA.
- Garrett, M. G. 1982. Prairie dog dispersal in Wind Cave National Park.
 MS Thesis. Iowa State University, Ames, Iowa, USA.
- Garrett, M. G., and W. L. Franklin. 1982. Prairie dog dispersal in Wind
 Cave National Park: possibilities for control. Pages 185-198 In R. M.

- Timm and R. J. Johnson, editors. Proceedings: Fifth Great Plains Wildlife Damage Control Workshop. University of Nebraska, Lincoln, Nebraska, USA.
- Hoogland, J. L. 1981a. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: Cynomys leucurus and C. ludovicianus). Ecology 62:252-272.
- Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. Science 215:1639-1641.
- Ingham R. E., and J. K. Detling. 1984. Plant-herbivore interactions in a North American mixed-grass prairie: III. soil nematode populations and root biomass on Cynomys ludovicianus colonies and adjacent colonies and adjacent uncolonized areas. Oecologia (Berlin) 63:307-313.
- Kerwin, L. 1972. Population size and productivity of the black-tailed prairie dog in Saskatchewan. Blue Jay 30:107-109.
- King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie-dog town in the Black Hills of South Dakota. Contributions from the Lab. of Vert. Biol., No. 67, University of Michigan, Ann Arbor, Michigan, USA.
- Knowles, C. J. 1982. Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge. Ph. D. Dissertation. University of Montana, Missoula, Montana, USA.
- Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildl. Monogr. No. 3.

- Lachenbruch, P., and R. M. Mickey. 1968. Estimation of error rates in discriminant analysis. *Technometrics* 10:1-11.
- MacCracken, J. G., D. W. Uresk, and R. M. Hansen. 1983. Plant community variability on a small area in southeastern Montana. *Great Basin Natur.* 43:660-668.
- O'Reilly, F. J., and P. W. Mielke. 1980. Asymptotic normality of MRPP statistics from invariance principles of U-statistics. *Comm. Stat. Theor. Meth.* A9:629-637.
- Painter, E. L., and J. K. Detling. 1980. Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. *J. Range Manage.* 34:68-71.
- Pfeiffer, D. G. 1972. Effects of diethistibestrol on reproduction in the black-tailed prairie dog. MS thesis, South Dakota State University, Brookings, South Dakota, USA.
- Reid, N. J. 1954. The distribution of the black-tailed prairie dog in the badlands of southwestern North Dakota. M. S. Thesis. Iowa State Univ., Iowa City. 30 pp.
- Rumble, M. A. 1983. Classification of aquatic resources: A quantitative approach. Pages 89-99. In Proceedings of Third Plains Aquatic Research Conference, August 24-25, 1983, Bozeman, MT.
- Schenbeck, G. L. 1982. Management of black-tailed prairie dogs on the national grasslands. Pages 207-213 In R. M. Timm and R. J. Johnson, editors. Proceedings: Fifth Great Plains Wildlife Damage Control Workshop, University of Nebraska, Lincoln, Nebraska, USA.

- Sheets, R. G., R. L. Linder, and R. B. Dahlgren. 1972. Food habits of two litters of black-footed ferrets in South Dakota. *Am. Midl. Nat.* 87:249-251.
- Smith, R. E. 1958. Natural history of the prairie dog in Kansas. University of Kansas, Museum of Nat. Hist. and State Biol. Surv., Lawrence, Kansas, USA.
- Snell, G. P., and B. D. Hlavachick. 1980. Control of prairie dogs--the easy way. *Rangelands* 2:239-240.
- Snell, G. P. 1985. Results of control of prairie dogs. *Rangelands* 7(1):30.
- Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. *J. Range Manage.* 21:264-265.
- Stockrahm, D. M. R. B. 1979. Comparison of population structures of black-tailed prairie dog, (Cynomys ludovicianus Ord), towns in southwestern North Dakota. MS Thesis, University of North Dakota, Grand Forks, North Dakota, USA.
- Summers, C. A., and R. L. Linder. 1978. Food habits of the black-tailed prairie dog in western South Dakota. *J. Range Manage.* 31:134-136.
- Theisen, P. W. 1981. Age-specific reproduction in the black-tailed prairie dog (Cynomys l. ludovicianus). MS Thesis, University of North Dakota, Grand Forks, North Dakota, USA.
- Tileston, J. V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. *Amer. Midl. Nat.* 75:292-316.
- Tilley, J. M. A., and R. A. Terry. 1963. A two stage technique for the in vitro digestion of forage crops. *J. Brit. Grassl. Soc.* 18:104-111.

- Uresk, D. W., J. G. MacCracken, and A. J. Bjugstad. 1981. Prairie dog density and cattle grazing relationships. p. 199-201. In Robert M. Timm and Ron J. Johnson (eds.), Fifth Great Plains Wildl. Damage Control Workshop. Proc. Oct. 13-15, 1981. Univ. Nebraska, Lincoln.
- Uresk, D. W. 1984. Black-tailed prairie dog food habits and forage relationships in western South Dakota. J. Range Manage. 37:325-329.
- Wilcomb, M. J. 1954. A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. Ph. D. Thesis. Univ. Okla., Norman. 158 pp.

