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Prairie Dog Population Growth: Relationships to Population Density, Habitat, and Livestock Grazing Management

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PRAIRIE DOG POPULATION GROWTH: RELATIONSHIPS TO POPULATION DENSITY, HABITAT, AND LIVESTOCK GRAZING MANAGEMENT

by

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PRAIRIE DOG POPULATION GROWTH: RELATIONSHIPS TO POPULATION DENSITY, HABITAT, AND LIVESTOCK GRAZING MANAGEMENT

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Population growth of black-tailed prairie dogs (Cynomys ludovicianus) was studied in 1985 and 1986 in the short- and mixed-grass rangeland of western Nebraska. The purposes of the study were to determine the efficacy of 2 years of deferred (1 May - 1 Sept.) grazing in reducing reinfestation rates of prairie dogs following population reduction, and to examine potential relationships between population growth and population density and habitat vegetative characteristics.

In 1985, population growth measures did not differ significantly between treatments, perhaps due to dry conditions. In 1986, 2 of 3 measures of population growth were significantly lower on deferred sites than on grazed sites. Deferred sites studied both years showed reductions in 1986 active areas ($P>t=0.07$): 4 of 5 deferred sites decreased in size; 6 of 8 grazed sites increased in size ($P>t=0.04$).

Correlations between population growth and density suggest a positive relationship exists when density is low. Population growth was not positively related to density at higher densities.

Visual observations on deferred sites suggested that as town

size contracted, prairie dog activities became less generally distributed across colonies, and clumps of activity resulted. These clumps of prairie dogs appeared to be separated by relatively taller vegetation. Population growth:habitat relationships suggested that during a dry year, low levels of vegetation might be conducive to prairie dog population growth. Higher levels of foliar cover and standing biomass did not appear to encourage growth, and high foliar volume appeared to prohibit population growth.

A key factor in limiting colony expansion may lie in encouraging vegetation that has high peripheral vegetative structure relative to the structure present on the main colony area. The efficacy of deferred grazing in reducing population growth rates of prairie dogs in western Nebraska appears to be heavily dependent on rainfall. Below average rainfall appears to limit vegetative response, and result in population growth rates similar to those seen on grazed sites.

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INTRODUCTION

Once a significant component of North American grassland ecosystems, the black-tailed prairie dog (Cynomys ludovicianus) has long been regarded by ranchers and range managers as a rangeland pest. This view arises from the widespread belief that prairie dogs compete with domestic livestock for forage, and are responsible for severe range deterioration (Knowles 1982). Historically a target of control efforts, prairie dog populations have been increasing since the institution of restrictions on the use of principal rodenticides in 1972 (Fagerstone 1982; Knowles 1982) and the cessation of federal animal damage control (ADC) activities aimed at prairie dogs.

The physical appearance of prairie dog towns, and similarities in cattle and prairie dog diets (Bonham and Lerwick 1976; Hansen and Gold 1977; Summers and Linder 1978; Fagerstone 1982; Uresk 1984), contribute to the belief that prairie dogs and cattle compete for forage. Although the degree to which prairie dogs and cattle compete for the same food source is a matter of some debate, it is apparent that prairie dogs may exert a strong influence on rangeland habitat. The physical structure and species composition of vegetative communities may be profoundly influenced by prairie dog clipping, foraging, and mound-building activities (King 1955; Koford 1958; Bonham and Lerwick 1976; Uresk 1984).

Prairie dog activities may result in a decrease in herbage availability for cattle (O'Meilia et al. 1982). Prairie dog grazing can alter species composition of vegetative communities in such a way as to reduce rangeland productivity (Hansen and Gold 1977).

Prairie dog activities appear to alter vegetative communities directly and indirectly (Koford 1958). Direct effects are through the removal of a part of the crop each year. Indirect effects occur through long term influences on some species. Repeated defoliation of individual plants appears to result in a decrease in carbohydrate reserves, causing less rapid shoot growth (Coppock et al. 1983). Under frequent and heavy grazing, selection for shorter and less productive grass ecotypes may occur in 15 years or less (Coppock et al. 1983). Agnew et al. (1986) believed prairie dogs act as "ecosystem regulators" by maintaining shortgrass plant associations with less mulch cover and lower vegetative height than surrounding, prairie dog-free mixed-grass rangeland.

The influence of prairie dogs on rangeland has resulted in control efforts by ranchers and range managers. Legal control techniques typically employed to reduce prairie dog populations include poison bait application, fumigation, and shooting. Although these methods may result in immediate population reduction, they frequently do not produce a long term decrease in animal numbers for a particular site unless applied regularly. Repopulation of treated prairie dog colonies has been a recurring problem. On western U.S. Forest Service lands, retreatment of colonies appears to be necessary at least every 3 years (Schenbeck 1982). The necessity of frequent retreatment, and the cost of such control methods, have sparked interest in developing other methods of prairie dog population regulation or control.

Garrett and Franklin (1982, 1983) achieved some success in limiting prairie dog population expansion through the use of visual barriers and chemosterilants, although construction and maintenance of the barriers was time consuming. Material and labor costs of these control measures may dictate their use on a limited scale, or only in very specific situations (e.g., expansion of colonies across property boundaries).

In recent years, there has been increasing interest in potential ecological relationships between prairie dog population growth and large ungulate grazing. The establishment and growth of prairie dog towns appears to be favored by intensive cattle grazing (Knowles 1982). Apparently, prairie dogs thrive best in short-grass habitats, or mid- and tall-grass areas which receive heavy livestock use. Knowles (1982) suggested that prairie dogs probably cannot maintain towns in mixed-grass habitats without the influence of large ungulate grazing, except if sites had inherently low productivity, or if sites were not conducive to forb growth. Koford (1958) also suggested that prairie dogs without large ungulates cannot produce and maintain short-grass associations. It is theorized that the prairie dog's visual predator detection system is aided by the maintenance of short vegetation; additionally, it is possible that prairie dogs in taller vegetation may undergo some stress factor, or may have a reduction in natality brought about by nutritional shortages or social pressures (Snell and Hlavachick 1980).

The apparent dependence in certain habitats of prairie dogs on large ungulate grazing may have practical application in prairie dog control. Of particular interest in this study is the applicability of this apparent dependence in reducing prairie dog population growth in the short- and mixed-grass rangeland of western Nebraska.

Smith (1958) stated that "proper management of cattle is the keynote of success in reducing the numbers of prairie dogs on rangeland". Although this is a popular concept in the literature, there has been little direct evidence or experimentation regarding what the degree of this dependence might be, or the time scale and habitat type involved. Basic information regarding the relationship of prairie dog population growth to habitat vegetative characteristics is poorly understood, so it is difficult to predict population responses to specific management techniques. Without this basic information, specific recommendations to ranchers and range managers regarding livestock management practices effective in reducing prairie dog population growth cannot be made.

The initial work investigating prairie dog - livestock grazing relationships suggests that the removal of livestock grazing from prairie dog towns may allow enough of a release from grazing pressure to result in a response from the vegetation. The increased vegetative growth, or response, appears to have a negative impact on prairie dog populations. Several observations support this theory.

Osborn and Allan (1949) believed an abandoned prairie dog town found on the Wichita Mountains Wildlife Refuge, Oklahoma was a result of an inability of the prairie dogs to keep tall vegetation clipped when cattle grazing in the area ceased. Knowles (1982) observed that of 3 prairie dog towns (mixed-grass range) where cattle grazing had not occurred for 7 to 10 years, one town was inactive, and two were greatly reduced in size. Uresk and Bjugstad (1983) observed a reduction in active burrow densities when cattle were excluded from pastures with prairie dogs, which they attributed to the occurrence of taller vegetation. Uresk, et al. (1982) found that burrow densities in southwestern South Dakota on sites grazed by cattle increased at twice the rate of sites not grazed. An ungrazed exclosure on a town in mixed-grass appeared to contain a prairie dog population that was heavily dependent on immigrants to maintain animal numbers (Knowles 1982).

In an uncontrolled test, a 46 ha (110 a) prairie dog town in Barber County, Kansas (64 cm average annual rainfall) was reduced to 5 ha (12 a) in size following 4 successive seasons of deferred (June - August) livestock grazing (Snell and Hlavachick 1980). Located on a range site with the potential for mid-grasses, only short-grasses were observed prior to deferral, due to poor range condition. Snell and Hlavachick attributed vegetative recovery to dormant rootstock present. After 8 years, this town was 0.08 ha (0.2 a) in size (Anonymous 1984).

Although these observations are encouraging from a prairie dog control perspective, recent work in mixed-grass range of western South Dakota suggests that vegetative response to release in grazing pressure may occur at a very slow rate. Uresk (1985) found that controlling prairie dogs did not result in a positive increase in forage production after 4 years. Uresk and Bjugstad (1983) suggested that total exclusion from herbivores (cattle and prairie dogs) for 9 or more years may be required to increase forage production when range is in a low condition class. Because of the observed slow vegetative recovery, it was theorized that any potential vegetative response to deferred livestock grazing in western Nebraska might be aided by concurrently reducing prairie dog grazing pressure through population reduction. It is not known what effect the resulting reduced prairie dog densities would have upon population growth, i.e. documentation is lacking on relationships between population growth and density.

The objectives of this study were to:

1) Determine the efficacy of two years of deferred livestock grazing in reducing population growth rates of prairie dogs following population reduction (i.e. control).
2) Examine potential relationships between prairie dog

population growth and prairie dog population density.

3) Examine potential relationships between prairie dog population growth and habitat vegetative characteristics.

METHODS

Study Sites

Twenty and 18 prairie dog towns were used as study sites in 1985 and 1986, respectively. Due to the necessity of replacing some of these sites between the 2 years of the study, a total of 25 different prairie dog towns was studied. Three of these sites were on public lands; the remainder of the sites were under private ownership.

All of the study sites were located in the short- and mixed-grass rangeland of western Nebraska (see Table 1 for legal descriptions). Average annual rainfall in the Nebraska Panhandle is 36 to 43 cm (14 to 17 inches). Common grass species on the sites included western wheatgrass (*Agropyron smithii*), crested wheatgrass (*Agropyron cristatum*), slender wheatgrass (*Agropyron trachycaulum*), intermediate wheatgrass (*Agropyron intermedium*), needleandthread (*Stipa comata*), downy brome (*Bromus tectorum*), red three-awn (*Aristida longiseta*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), little bluestem (*Schizachyrium scoparium*), sixweeksgrass (*Vulpia octoflora*), and sideoats grama (*Bouteloua curtipendula*). Common forb and shrub species included woolly indianwheat (*Plantago patagonica*), small soapweed (*Yucca glauca*), scarlet globemallow (*Sphaeralcea coccinea*), desert princesplume (*Stanleya pinnata*), fringed sagebrush (*Artemesia frigida*), silver sagebrush (*Artemesia cana*), sand sagebrush (*Artemesia filifolia*), cudweed sagewort (*Artemesia ludoviciana*),

Table 1. Legal description, soil type, control method, and treatment of western Nebraska study sites.

Site no.	Location: County	Location: Description	Soil type	Treatment	Control type	Years of use
1	Morrill	S1/2, SE1/4, Sec 6, T21N, R51W	Epping - Keota silt loam	Deferred	Shooting	1985, 1986
2	Morrill	W1/2, NE1/4, Sec 12, T21N, R52W	Sarben very fine sandy loam	Deferred	Bait, shooting	1985
3	Cheyenne	N1/2, SE1/4, Sec 27, T13N, R49W	Rosebud loam	Deferred	Bait	1985, 1986
4	Morrill	W1/2, NE1/4, Sec 3, T20N, R51W	Dix loamy coarse sand	Deferred	Bait	1985, 1986
5	Scotts Bluff	SE1/4, Sec 34, T22N, R58W	Anselmo fine sandy loam	Deferred	Shooting	1985, 1986
6	Scotts Bluff	SE1/4, Sec 34, T22N, R58W	Mitchell silt loam	Deferred	Shooting	1985
7	Cheyenne	W1/2, SE1/4, Sec 34, T15N, R52W	Rough broken land	Deferred	Bait	1985
8	Morrill	S1/2, SW1/4, Sec 11, T18N, R47W	Otero very fine sandy loam	Deferred	Bait	1985, 1986
9	Scotts Bluff	SE1/4, Sec 34, T22N, R58W	Anselmo fine sandy loam	Deferred	Bait	1986
10	Sioux	W1/2, NW1/4, Sec 8, T32N, R55W	Epping silt loam	Deferred	Bait	1986
11	Sioux	W1/2, NW1/4, Sec 8, T32N, R55W	Epping silt loam	Deferred	Shooting	1986
12	Sioux	S1/2, SE1/4, Sec 6, and N1/2, NE1/4, Sec 7, T34N, R54W	Orman clay loam	Grazed	Bait	1985, 1986
13	Morrill	S1/2, SE1/4, Sec 11, T18N, R47W	Bankard loamy coarse sand	Grazed	Bait	1985
14	Morrill	S1/2, SW1/4, Sec 11, T18N, R47W	Otero very fine sandy laom	Grazed	Bait	1985, 1986
15	Morrill	S1/2, SW1/4, Sec 35, T21N, R52W	Minatare-Janise complex	Grazed	Bait, fumigant	1985
16	Morrill	SW1/4, Sec 19, T18N, R47W	Valent loamy fine sand	Grazed	Bait, fumigant	1985
17	Dawes	SE1/4, SW1/4, Sec 19, T33N, R48W	Keith silt loam	Grazed	Bait, shooting	1985,
18	Morrill	NE1/4, Sec 3, R20N, R52W	Janise loam	Grazed	Shooting	1985, 1986
19	Morrill	NE1/4, Sec 3, R20N, R52W	Janise loam	Grazed	Shooting	1985, 1986
20	Sioux	E1/2, NE1/4, Sec 7, T34N, R54W	Orman clay loam	Grazed	Bait	1985, 1986
21	Morrill	S1/2, SE1/4, Sec 29, T21N, R51W	Sarben very fine sandy loam	Grazed	Shooting	1985
22	Dawes	NW1/4, Sec 22, T33N, R49W	Bridget silt loam	Grazed	Bait	1985, 1986
23	Dawes	S1/2, NW1/4, Sec 36, T29N, R51W	Bankard loamy fine sand	Grazed	Bait	1985, 1986
24	Cheyenne	W1/2, SE1/4, Sec 34, T15N, R52W	Rough broken land	Grazed	Bait, fumigant	1986
25	Morrill	S1/2, SE1/4, Sec 11, T18N, R47W	Bankard loamy coarse sand	Deferred	Bait	1986

pricklypear (Opuntia spp.), broom snakeweed (Xanthocephalum sarothrae), tumble mustard (Sisymbrium altissimum), black greasewood (Sarcobatus vermiculatus), kochia (Kochia scoparia), threadleaf sedge (Carex filifolia), sunflower (Helianthus spp.), curlycup gumweed (Grindelia squarrosa), and fourwing saltbush (Atriplex canescens).

Several criteria were used as the basis for selection of prairie dog towns as study sites: town size, location, recency of control, and landowner cooperation. Sixteen ha (40 a) was the maximum acceptable size for prairie dog towns at the onset of the study, to facilitate vegetative data collection and visual population censuses. Location was a criterion because of the large number of towns studied. It was not possible to arrange all 20 study sites in 1 or 2 counties, so an attempt was made to clump sites, i.e. locate sites so that a minimum of 2 sites occurred within driving distance of each other, approximately 33 km (20 mi). The clumped distribution facilitated population censuses by making it possible to census more than 1 town per census period.

Landowner cooperation was a major factor in study site selection. It was necessary to seek cooperators who either had decided on livestock grazing plans for the 2 years of the study, or were amenable to a requested livestock use. Additionally, sites were required on which no control was planned during the study period. It was also necessary that cooperators be able to supply information regarding previous control efforts on the sites, i.e. recency and type of control.

Table 1 contains descriptive information on each prairie dog town used in the study. Legal description, soil type, treatment, and method of population reduction are listed for each site.

In 1986, it was necessary to replace some of the study sites used in 1985. Site replacement was necessary due to landowner prairie dog control efforts prior to the completion of the study, change in livestock grazing management, sale of property, or change in site use (i.e. one landowner constructed dikes on a study site). A total of 5 replacement sites was selected; 1 grazed and 4 deferred. Statistical comparisons made between 1985 and 1986 were conducted only on those sites used in both years of the study.

Treatment

Two treatments were applied on a whole-town basis for 2 years: grazed by livestock, and deferred. All of the deferred sites except one had livestock excluded from the entire pasture. One site ("Lenzen Town") had livestock excluded only from the prairie dog town by an electric fence; the rest of the pasture was grazed. Assignment of treatments to sites was based on landowner livestock grazing plans, or willingness of landowner to follow recommended livestock usage.

Deferral of livestock grazing was during the period of May 1 to September 1 of 1985 and 1986. Landowners were permitted to winter pasture livestock or hay deferred pastures September -

April.

In 1985 there were 12 grazed and 8 deferred sites; 1986 there were 9 grazed and 9 deferred sites. No attempt was made to exclude wild herbivores from study sites, e.g., rabbits, deer, pronghorn, and grasshoppers, although relative densities of grasshoppers were quantified. Landowners were requested to estimate livestock stocking rate on grazed pastures; a range of 1.6 to 6.1 ha (4 - 15 a) per animal unit month (AUM) was reported.

All of the sites had reduced prairie dog populations. Population reduction occurred within 2 years of the onset of the study by one or a combination of 3 methods: shooting, poison bait application, or fumigation. Initial prairie dog densities estimated from the early 1985 census ranged from 1.5 to 10.9 adults per hectare. Hoogland (1979a) reported densities of prairie dogs as high as 32.7 adults and yearlings per hectare. Adult and pup densities have been reported as high as 148 animals per hectare (Boddicker 1983).

Prairie Dog Population Estimation

Population growth measures were based on visual population censuses. Two census periods were used in each year of the study: early and late. The early census was conducted May 14 - June 24 1985, and May 23 - June 23 1986. The timing of this period was based on several goals. An estimate of natality was desired, so it was necessary to count young of the year after they began above-ground activities, but before extensive above-ground predation could occur. Emergence of pups in North and South Dakota occurs in late May (King 1955; Stockrahm 1979); Colorado pups emerge about May 7 (Tileston and Lechleitner 1966); Oklahoma pups emerge mid-April (Anthony and Foreman 1951; Tyler 1968). Pups in western Nebraska were observed to begin above-ground activities by mid-May. The early census period is also an estimator of overwintering adult prairie dogs. Peak intercolony dispersal of adult prairie dogs appears to occur in early June, and is apparently triggered by the high prairie dog densities resulting from pup emergence (Garrett 1982). Thus, the timing of the early census period was an attempt to count late enough to get a complete census on pups, yet early enough to not reflect a large influx of immigrant adults.

The late census was conducted 5 - 20 August 1985 and July 28 - August 22 1986. This census period was timed so as to be as late as possible in the field season.

Each census period consisted of 4 separate count sequences of each town, with count sequences conducted a minimum of 2 different days. Each sequence consisted of 4 counts, for a total of 16 counts per town per census. The maximum number of prairie dogs observed above ground at one time from the 16 counts was used as the population estimate from each census. Knowles (1982) tested visual population censuses for prairie dogs and found that the maximum count was highly correlated with actual population size (r^2=0.942). Fagerstone (1983), comparing visual counts of

Richardson's ground squirrel (Spermophilus richardsonii) with mark-recapture population estimates, indicated visual estimates may be reliable indices of populations.

Counts were conducted during 2 activity periods: morning and afternoon. Morning count sequences commenced 2 hours after sunrise, with the last sequence starting 4 hours after sunrise. Afternoon count sequences commenced 4 hours before sunset, with the last count sequence starting 2 hours before sunset. Counts were conducted at 15-minute intervals, with the first count commencing upon arrival at the town. A maximum of 1 count sequence was conducted/town/activity period/day. Counts were not made in seasonally adverse weather conditions, i.e. extreme heat or cold, rain, fog, mist, or strong winds.

Counts were conducted from inside or on top of a stationary pickup truck, depending on proximity to active burrows, reaction of nearby prairie dogs, and topography of the prairie dog town. Counts on towns with greater topographic relief, or larger area, were aided by the increased observer height gained from the top of the truck.

Generally, counts were made from a single census point. An optimal point would have the characteristics of an unobstructed view of the entire town and no active burrows in the vicinity of the truck. Some towns were too large to census from a single point, due to visual obstruction by topography or vegetation, or large town size. These towns were censused from multiple points, chosen to allow complete observation of entire town area, without overlap of census areas. Where potential overlap existed, surveyor's flags were used to discriminate between census areas.

Counts were made using 7x35 binoculars and a 15-60 X zoom spotting scope mounted on a tripod or window mount. Pups were differentiated from adults in the early census period primarily on the basis of size, although coat color and texture, and behavioral characteristics were of some aid. Pups could not be reliably differentiated at a distance in the late census period.

Three potential measures of population growth were utilized in the statistical analysis:

1. Increase in animal density (number of prairie dogs per hectare).
2. Percent increase in animals
3. Pup:adult ratio

The first 2 population growth measures are based on growth in terms of the difference between the number of adult prairie dogs present on sites during the early census period, and the total number of prairie dogs present during the late census period. These 2 population growth measures incorporate but do not discriminate between natality, immigration, emigration, and survivorship during that period. The third measure of population growth is treated as an indication of natality, and is based on the early census.

Population density estimates consisted of 2 components:

population estimate and area estimate. Area of each town was measured in June of each year by mapping the outermost active prairie dog burrows. These peripheral burrows were marked with surveyor's flags. Angle and distance between the flags were determined with a compass and rolatape (Rolatape Corp., Los Angeles, CA); a polar planimeter was used to convert the mapped periphery into an area estimate. Surveyor's flags left at the peripheral burrows after mapping indicated little area expansion between June and August.

The differentiation between active and inactive burrows was based on whether the burrow entrance was closed by dirt, heavy vegetation growth, or heavy spider webbing. Other evidence of activity included fresh digging, fresh droppings (Stockrahm 1979), presence of clipped vegetation on the mound, and observations of use during census periods.

A measure of prairie dog town expansion was based on the difference between active area of prairie dog towns in 1985 and 1986. Town maps and areas were compared for the 2 years of the study to determine whether towns were expanding, contracting, or remaining the same size.

Trapping

In spring of 1985 and fall of 1986 prairie dogs were live-trapped for the purpose of obtaining body weight data, a potential indication of the general condition of the animals. Fourteen prairie dog towns (8 deferred; 6 grazed) were trapped in 1985; 10

towns (7 deferred; 3 grazed) were trapped in 1985. Capture dates were May 17 - July 1, 1985 and Sept. 16 - Oct. 8, 1986.

Prairie dogs were trapped in burrow entrance traps and Tomahawk squirrel traps. Burrow entrance traps (Wobeser and Leighton 1979), were inserted directly into mound entrances. Only active mounds were selected for trapping. Traps measured 10 x 10 x 50 cm long, and were constructed from 2.5 cm (1 in.) wire mesh. Several small areas of each town (e.g., 0.4 ha or less) were trapped intensively, rather than scattering traps over the entire town.

Tomahawk squirrel traps, baited with whole oats and staked in place with surveyor's flags, were also concentrated in small areas of each town. One to 3 traps per active mound were used, located 1 - 2 meters from burrow entrances. Three trap sizes were used: 12 x 12 x 40 cm single door, 17 x 17 x 48 cm single door, and 15 x 15 x 60 cm double door. Traps were held open with clothespins for 3 to 5 days prior to commencement of capture in order to habituate prairie dogs to trap presence and increase trapping success and efficiency.

Trapping success varied with trap type. In general, burrow entrance traps used in 1985 were not successful in capturing prairie dogs, except for very young pups just beginning above-ground activities. These naive animals apparently were less adverse to entering the traps, and several pups could be caught in 1 trap. Occasionally, older pups or adults were captured; the latter tended to be adult females, perhaps following pups into the traps. Frequently, burrow entrance traps were filled with waste dirt from tunnelling activities, sometimes completely filled over. Construction of new tunnels around the traps was a frequent occurrence. Due to the lack of trapping success with burrow entrance traps, 1986 trapping was conducted with only the Tomahawk squirrel traps.

Captured prairie dogs were transferred from traps to a wire mesh handling cone to facilitate handling and data collection. Prairie dogs were sexed, weighed, aged as pup or adult, and permanently identified with ear tags (#1 monel tag, National Band and Tag Co., Newport, KY). Aging was based on size and coat criteria.

Habitat Vegetative Measurements

Habitat vegetative characteristics quantified included basal and foliar cover, foliar volume (vegetation height and density), and standing biomass. All habitat vegetative data were collected in 2 zones present on each town: "peripheral" and "main". The peripheral zone was defined as the rangeland area extending outwards 15 meters from the outermost active prairie dog mounds. The main zone was defined as the area contained within the peripheral zone. All of the study sites used in 1986 had each zone present; all but 2 of the 1985 study sites had each zone. Two of the prairie dog towns studied in 1985 were bordered by roads, marsh, and/or ditches, and did not have rangeland contiguous to the outermost active prairie dog burrows, so vegetative sampling was not obtained from the peripheral zone for these 2 sites.

The justification for this dual zone sampling scheme was the speculation that any potential vegetative response to a decrease in livestock grazing pressure would probably occur most measureably in the peripheral zone, the area of vegetation typically least modified by prairie dog activities. However, it was suspected that if peripheral and main data were combined together, the vegetative response may not have been statistically detectable. Additionally, recent research suggests that the function of the 2 zones to prairie dogs may differ, i.e. a relatively unmodified peripheral area may serve as an important food source and can be thought of as available unused habitat (Garrett et al. 1982). Garrett et al. suggest a peripheral area extending outwards 5 meters may serve as a feeding area; observations in western Nebraska suggest the animals may feed farther out, at least at some of the prairie dog towns studied.

Number of samples collected for each vegetative measurement was determined from pilot studies using the following formula (Steel and Torrie 1980):

$$N = (t^2 s^2)/d^2$$

where

N = number of samples predicted

t = tabulated t-value for the desired confidence level of 0.90 and degrees of freedom of initial sample

s = standard deviation of initial sample

d = initial sample mean x designated accuracy level of 0.25

Initial sample size for pilot studies was 9. Pilot studies were conducted in July for standing biomass and basal cover, and August for foliar volume and foliar cover measurements. All samples were randomly located by the use of a random numbers table.

Basal cover was measured during July using a 10-point frame (Stoddart and Smith 1955). Percent basal cover, forbs, grasses, litter, and bare ground were quantified.

Foliar cover was measured in August by the focal-point technique, using a modified surveyor's transit (Burzlaff 1966). This method facilitates the use of a circular line-transect at each sample point to determine % foliar cover, forbs, grasses, litter, and bare ground. Ten readings were taken at each sample point.

Foliar volume (visual obstruction measurements) was measured in August using a Robel pole (Robel et al. 1970). The pole was modified to include 0.25 decimeter readings, in order to detect finer differences in vegetation. The average of 4 pole readings (90 degrees apart) per sample point was used as sample measurement. Readings were taken at a distance of 4 meters from the pole at 1 meter height.

Standing biomass was measured as the weight of above-ground herbage from 0.1 m^2 plots. Meaurements were taken in August. Vegetation was clipped at ground level and wet weight determined in the field. Samples were oven dried at 38 degrees C until they reached a constant weight, i.e. approximately 48 hours. Wet and dry weights of forbs and grasses, and % moisture on a wet weight basis were determined. No estimate of prickly pear yield was attempted, although presence or absence of the species in standing biomass plots was noted.

Habitat Nonvegetative Measurements

Two uncontrolled variables which may exhibit a strong influence over habitat vegetative characteristics were measured: grasshopper density and rainfall. Estimation of grasshopper density was based on a visual technique used by Onsager (1977), which requires an observer to visualize an area, e.g., 1 ft^2 or 1 yd^2, approximately 12 - 20 feet distant. The observer slowly approaches and counts the grasshoppers present in the visualized plot. Advantages suggested for this methodology include speed and ease of use. Disadvantages suggested are personal bias and potential differences between individuals in the actual size of visualized subsample plots. Onsager's technique was modified by the use of a 0.1 m^2 frame thrown foward approximately 6 meters from the observer, so that bias and size variation between plots could be minimized. Sample points were randomly located within the main and peripheral zones. Number of sample points was determined by pilot studies conducted at each prairie dog town.

Rain gauges were used to measure precipitation on sites in 1985 and 1986. Rain gauges were in place early May through late August. Rainfall was measured to the nearest 0.25 cm (0.1 inch). Due to evaporation and disruption by cattle, 1985 rain gauge data were disregarded and nearest reporting station data (NOAA 1985) were used.

Statistical Analysis

Statistical analysis systems (SAS, Cary, North Carolina) computer packages were utilized in statistical analysis of data. The CORR and TTEST procedures were used to conduct simple univariate correlation analyses and independent t-tests. SAS MEANS procedure was used to perform paired t-tests. SAS GLM and LSD procedures were used to perform analysis of variance and Fisher's Protected Least Significant Difference test for mean comparisons, respectively.

RESULTS AND DISCUSSION

Independent t-tests indicated no significant differences in rainfall between treatments for either year of the study, although rainfall differed between years (Table 2). 1985 was a dry year in the Nebraska Panhandle, with some study sites receiving as little as 55% of the normal rainfall during May through August (NOAA 1985). 1986 was a much wetter year, with many study sites receiving normal or slightly above average rainfall. A paired t-test conducted on those sites used for both years of the study indicated 1985 rainfall was less than 1986 rainfall ($P>|t|=0.001$).

Population Growth

Three measures of population growth used in both years of the study were: increase in animal density, % increase in animals, and pup:adult ratio. Although increase in animal density and % increase in animals may appear to be redundant population growth measures, each measure has different weaknesses associated with it. Increase in animal density will be directly related to initial animal density if natality is density-independent, prairie dogs exhibit high survivorship between the early and late censuses, and emigration is negligible. No similar numerical dependence on initial density is expected for % increase in animals. The measure "% increase in animals" can be derived using prairie dog densities, or independently of prairie dog densities, with the same numeric result. However, validity of this measure may be questionable. For instance, a 100% increase in animals may

Table 2. Precipitation (cm) at prairie dog towns (May - August), western Nebraska, 1985 - 1986.

Year	Trt.	$\bar{X}$	s	Range
1985	D[1]	14.7	4.6	8.4 - 22.1
1985	G[2]	15.2	2.0	12.4 - 18.0
1986	D	20.8	5.1	15.0 - 28.2
1986	G	21.1	4.1	15.5 - 28.4

[1]D = deferred
[2]G = grazed

result from either an increase from 1 animal per ha to 2 animals per ha, or from 5 animals per ha to 10 animals per ha, although the second growth involves five times as many animals per ha. This measure may give heavy weightings to towns with lower prairie dog densities. If the use of this population growth measure introduced bias into the study results, the bias should act against rejecting the null hypothesis of no difference in population growth between treatments, because grazed sites tended to have lower population densities than deferred sites (Table 6). In the absence of a strong biological reason to select one measure over the other, both population growth measures were used in the analysis.

Table 3 contains results of the 3 measures of population growth. Independent t-tests were conducted to determine whether population growth measures differed between treatments, within each year of the study (Table 4). In 1985, no differences were found between treatments for any of the population growth measures. In 1986, 2 of the 3 population growth measures were lower for the deferred treatment than for the grazed treatment. Pup:adult ratio and % increase in animals were lower on deferred sites than on sites grazed by cattle ($P>t=0.06$ and $P>t=0.02$, respectively). Statistical comparisons of population growth measures between years of the study are probably not valid, because environmental conditions affecting prairie dog populations varied considerably. However, examination of $\overline{X}$ growth values

Table 3. Population growth values on prairie dog towns in western Nebraska, 1985 - 1986.

Population growth measure	Year	N	Trt.	$\bar{X}$	s	Range
Increase in animal density	1985	8	D[1]	9.9	9.7	0.0 - 26.9
Increase in animal density	1986	8	D	6.6	6.6	0.0 - 17.2
Increase in animal density	1985	12	G[2]	5.7	4.6	1.6 - 13.8
Increase in animal density	1986	9	G	8.9	4.5	3.3 - 17.0
% Increase in animals	1985	8	D	148.8	88.4	0.0 - 259.0
% Increase in animals	1986	8	D	87.0	80.9	0.0 - 242.0
% Increase in animals	1985	12	G	152.6	97.3	82.0 - 416.0
% Increase in animals	1986	9	G	179.6	88.3	67.0 - 363.0
Pup:Adult ratio	1985	8	D	2.2	1.0	1.0 - 3.7
Pup:Adult ratio	1986	8	D	1.4	0.9	0.1 - 2.4
Pup:Adult ratio	1985	12	G	1.8	1.1	0.0 - 4.2
Pup:Adult ratio	1986	9	G	2.1	0.9	0.7 - 3.8

[1]D = deferred
[2]G = grazed

Table 4. Treatment differences for population growth measures on prairie dog towns in western Nebraska, 1985 - 1986.

	1985			1986		
	Treatment $\bar{X}$			Treatment $\bar{X}$		
Population growth measure	D	G	P>t	D	G	P>t
Increase in animal density	9.9	5.7	*	6.6	8.9	*
% Increase in animals	148.8	152.6	*	87.0	179.6	0.02
Pup:Adult ratio	2.2	1.8	*	1.4	2.1	0.06

*P>0.10

(Table 3) reveals that all 3 population growth measures increased from 1985 to 1986 on grazed sites, whereas all growth measures decreased on deferred sites.

Change in town size is a growth measure of interest to landowners, who may equate extent of damage with extent of colony area. However, change in town size does not necessarily reflect degree of damage to rangeland vegetation, which may vary with prairie dog density, and does not necessarily reflect other measures of population growth. Active areas of study sites ranged from 0.4 to 20.3 ha (Table 5). Town sizes differed by treatment in 1985 ($P>|t|=0.01$) and 1986 ($P>|t|=0.04$), with deferred treatment towns covering less area than grazed treatment towns. Number of adult prairie dogs present on sites in the early census was positively correlated to town size on 1985 grazed sites ($r=0.78$, $P>|R|=0.003$), 1986 deferred sites ($r=0.66$, $P>|R|=0.08$), and 1986 grazed sites ($r=0.86$, $P>|R|=0.003$). Number of 1985 early census adults differed by treatment ($P>|t|=0.04$), with deferred sites having fewer adults than grazed sites (Table 6). 1986 deferred sites also appeared to have fewer adults than grazed sites, although a statistically significant difference was not detected.

No correlation was found between town size and early census adult density. Although deferred sites appeared to have higher early census densities than grazed sites (Table 6), no difference was detected between treatments in 1985 ($P>|t|=0.31$) or 1986 ($P>|t|=0.11$). Behavioral observations suggest ward size (i.e.

Table 5. Active area estimates (ha) of prairie dog towns in western Nebraska, 1985 - 1986.

Year	Trt.	N	$\bar{X}$	Range	s
1985	D[1]	8	2.4	0.9 - 7.2	2.1
1985	G[2]	12	7.2	0.4 - 18.0	5.3
1986	D	8	2.1	0.5 - 6.0	1.9
1986	G	9	7.8	0.5 - 20.3	6.9

[1]D = deferred
[2]G = grazed

Table 6. Prairie dog densities and number of adults present at western Nebraska prairie dog towns in early census, 1985 - 1986.

Variable	Trt.	Year	$\bar{X}$	s	Range
Adults/ha	D[1]	1985	5.1	3.4	1.5 - 10.4
Adults/ha	D	1986	9.4	6.2	5.0 - 23.6
Adults/ha	G[2]	1985	3.6	2.6	1.6 - 10.9
Adults/ha	G	1986	5.3	2.3	2.4 - 8.8
No. of adults	D	1985	8.9	4.7	2.0 - 15.0
No. of adults	D	1986	18.1	12.2	3.0 - 35.0
No. of adults	G	1985	22.4	20.0	1.0 - 63.0
No. of adults	G	1986	40.3	40.3	3.0 - 109.0

[1]D = deferred
[2]G = grazed

number of adult residents, or estimate of number of adult residents based on ward area) contributes to differences in alertness of individual prairie dogs and predator detection. Hoogland (1981) recorded alarm signals elicited in response to stuffed badger and weasel specimens, in order to compare antipredator defenses in relation to ward sizes. Hoogland found that the first alarm call occurred earlier with larger wards, and suggested reduced predation may result. Hoogland (1979b) also found that individuals of large wards are less watchful than those of smaller wards, and may be able to devote more time to such activities as feeding, but was unable to directly examine the effect of decreased individual alertness on reproductive success. However, no correlations were detected between the 3 measures of population growth and town size (ha) in western Nebraska. No correlations were detected between population growth measures and number of adults present in the early census for either deferred or grazed sites, except 1985 increase in animal density was positively correlated with number of early census adults on deferred sites ($r=0.62$, $P>|R|=0.10$). Since 1985 deferred sites tended to have fewer adults in the early census than other sites (Table 6), failure to detect similar correlations for other sites may be due to higher populations. Thus, although town sizes differed significantly between treatments, this difference probably had little influence over study results.

A ratio of perimeter:area (m/ha) was calculated for each study site (Table 7). This ratio may give some indication of the relative availability of the peripheral zone for feeding activities. Perimeter:area ratio did not differ significantly between treatments. Perimeter:area ratio is influenced by 2 physical factors: town size and shape. Perimeter:area ratio was negatively correlated with town size on 1985 deferred ($r=-0.84$, $P>|R|=0.01$) and grazed ($r=-0.72$, $P>|R|=0.01$) sites, and 1986 deferred ($r=-0.67$, $P>|R|=0.07$) and grazed ($r=-0.71$, $P>|R|=0.03$) sites. Perimeter:area ratio was not correlated with population growth on 1985 and 1986 grazed, or 1986 deferred sites. Perimeter:area ratio was positively correlated with increase in animal density ($r=0.67$, $P>|R|=0.07$) and pup:adult ratio ($r=0.73$, $P>|R|=0.07$) on 1985 deferred sites. This positive correlation may suggest that the availability of a peripheral zone for feeding activities is conducive to growth during dry periods, when vegetation would tend to exhibit relatively low productivity. In years with greater rainfall and more productivity, the importance of this zone may be reduced. The absence of a relationship between peripheral zone availability and population growth on grazed sites may be reflective of reduced vegetation present in peripheral zones on grazed sites due to forage consumption by livestock.

Active areas of the 5 deferred and 8 grazed sites changed between years of the study (Table 8). Active areas for deferred treatment sites decreased from 1985 to 1986 ($P>t=0.07$). Four of the 5 deferred treatment sites decreased in area inhabited by

Table 7. Perimeter:area (m/ha) ratio of prairie dog towns in western Nebraska, 1985 - 1986.

Year	Trt.	N	$\bar{X}$	Range	s
1985	D[1]	8	363.3	186 - 511	96.5
1985	G[2]	12	305.3	112 - 950	244.4
1986	D	8	422.7	208 - 823	213.7
1986	G	9	268.0	93 - 744	196.3

[1]D = deferred
[2]G = grazed

Table 8. Change in area (%) inhabited by prairie dogs at western Nebraska study sites, 1985 - 1986.

Trt.	1985 ha	1986 ha	% Increase/decrease in active area
D[1]	2.6	2.1	- 19[a]
D	1.3	1.4	+ 8[b]
D	7.2	3.5	- 51
D	1.1	0.5	- 55
D	2.2	0.7	- 68
G[2]	7.6	12.3	+ 62
G	2.7	3.8	+ 42
G	0.6	1.2	+100
G	0.4	0.5	+ 25
G	7.0	3.2	- 52
G	14.6	14.6	0
G	17.8	20.3	+ 14
G	3.6	4.0	+ 11

[1]D = deferred
[2]G = grazed
[a]Negative sign indicates decrease
[b]Positive sign indicates increase

prairie dogs, with a mean decrease on the 4 declining towns of 49%, and mean overall change in size of the deferred treatment towns of -37%. Conversely, 6 out of 8 grazed sites increased in active areas (P>t=0.04), with a mean increase on the 6 expanding towns of 42%, and mean overall change in size of grazed treatment towns of +25%.

A decrease in area inhabited by prairie dogs does not necessarily imply a decrease in prairie dog numbers or density: town contraction may result in a net increase in density. One study site decreased 51% in active area from 7.2 ha in 1985 to 3.5 ha in 1986. However, number of adults present in the early census increased from 12 (1.7 adults/ha) in 1985 to 21 (6.0 adults/ha) in 1986, a net increase in animals of 43% and a net increase in density of 253%. Knowles (1982) observed a 47% increase in area over a 2 year period, with a concurrent decline in density of 30.6 to 19.6 prairie dogs/ha. Knowles noted the change in density appeared to be correlated (r^2=0.85) with precipitation: two dry years occurred with low vegetative production, and the prairie dogs expanded into adjacent, abandoned areas. Rainfall would not appear to be the single controlling factor in western Nebraska, because precipitation did not differ between expanding and nonexpanding towns (Table 9). However, the combined influence of rainfall and livestock grazing on vegetation may have contributed to changes in town area. Low 1985 precipitation and livestock grazing would tend to result in low height and density

Table 9. Precipitation (cm) received on expanding and nonexpanding prairie dog towns at study sites in western Nebraska, 1985 - 1986.

Town type	Year	$\bar{X}$	s	Range
Expanding	1985	14.5	1.2	8.4 - 18.0
Nonexpanding	1985	15.0	1.0	12.4 - 18.0
Expanding	1986	19.3	1.4	15.5 - 23.1
Nonexpanding	1986	21.6	2.1	15.0 - 28.4

of grazed-site vegetation, and encourage expansion by prairie dogs into adjacent areas. Absence of livestock grazing on deferred sites, in combination with high 1986 precipitation, may result in greater vegetation height and density on deferred sites, and discouragement of prairie dog expansion.

Independent t-tests were performed to determine whether prairie dog towns that expanded from 1985 to 1986 differed from towns that did not expand on the basis of 1985 population growth measures (Table 10). Expanding towns had higher increase in animal density ($P>|t|=0.04$) and % increase in animals ($P>|t|=0.08$) than nonexpanding towns. Thus, area expansion appeared to reflect population growth.

Town size and perimeter:area ratio did not appear to contribute to differences in area expansion. Expanding (increasing area) and nonexpanding (area not increasing) towns did not differ significantly in town size in 1985 (expanding $\bar{X}$ = 4.9 ha, s = 6.2; nonexpanding $\bar{X}$ = 5.8 ha, s = 5.0) or 1986 (expanding $\bar{X}$ = 6.2 ha, s = 7.4; nonexpanding $\bar{X}$ = 4.1 ha, s = 5.3). Expanding and nonexpanding towns did not differ significantly in number of adults present in the early census in 1985 (expanding $\bar{X}$ = 16.0, s = 19.1; nonexpanding $\bar{X}$ = 11.0, s = 7.3) or 1986 (expanding $\bar{X}$ = 35.0, s = 37.1; nonexpanding $\bar{X}$ = 16.2, s = 13.9). Expanding and nonexpanding towns did not differ significantly in perimeter:area ratio in 1985 (expanding $\bar{X}$ = 405.7, s = 289.4; nonexpanding $\bar{X}$ = 252.5, s = 99.8) or 1986 (expanding $\bar{X}$ = 301.1, s = 81.8;

Table 10. Population growth measures of expanding and nonexpanding prairie dog towns in western Nebraska, 1985.

1985 population growth measure	Town type	$\bar{X}$	s	Range
Increase in animal density	E[1]	7.7	6.0	1.5 - 17.0
Increase in animal density	N[2]	1.8	1.2	0.0 - 3.8
% Increase in animals	E	175.4	117.7	100.0 - 416.0
% Increase in animals	N	78.7	40.0	0.0 - 112.0
Pup:Adult ratio	E	2.1	1.4	0.0 - 4.2
Pup:Adult ratio	N	1.4	0.8	0.8 - 3.0

[1]E=expanding
[2]N=nonexpanding

nonexpanding $\overline{X}$ = 351.0, s = 186.4). Expanding towns appeared to have higher initial 1985 adult density ($\overline{X}$ = 4.5, s = 3.3) than nonexpanding towns ($\overline{X}$ = 2.2, s = 0.7), although the difference was not statistically significant ($P>|t|=0.12$). Initial 1986 adult density did not differ significantly between expanding ($\overline{X}$ = 7.9, s = 7.2) and nonexpanding ($\overline{X}$ = 5.4, s = 1.5) towns. Although area expansion may be triggered by animal density, the initial 1985 adult densities encountered in this study were considerably lower than typical prairie dog densities, due to control efforts prior to commencement of the study. This may suggest that expanding towns differed from nonexpanding towns in respect to characteristics that would tend to encourage or discourage expansion, such as food supply or vegetative structure.

Independent t-tests were performed to determine whether expanding towns differed from nonexpanding towns on the basis of habitat characteristics. Expansion of towns in 1985 and 1986 may be attributed to 2 periods of colony growth: growth in summer 1985, and growth in spring 1986. Therefore, both the 1985 and 1986 vegetative characteristics were examined, although how the measurements potentially relate to town expansion may differ. 1985 vegetative measurements may be viewed as quantifying foliar biomass and vegetative structure of study sites during the period of town expansion, whereas 1986 measurements were a less direct indicator because measurements were taken in July and August, and expansion was quantified in June. Thus, although the 1986 measurements were taken after expansion occurred, it was possible the measurements served as an index of the vegetative conditions to which the prairie dogs may have responded in spring of 1986.

No significant differences were detected in 1985 basal cover between expanding and nonexpanding towns (Table 11). Expanding towns had less 1986 basal cover than nonexpanding towns in the main ($P>|t|=0.01$) and peripheral ($P>|t|=0.06$) zones. Expanding towns had higher 1985 % foliar cover ($P>|t|=0.04$) and % grass foliar cover ($P>|t|=0.05$) in the peripheral zones than did nonexpanding towns (Table 12). No significant differences were detected in 1986 foliar cover. Expanding towns had higher 1985 peripheral zone foliar volume ($P>|t|=0.07$) than did nonexpanding towns (Table 13). Nonexpanding towns had higher 1986 main zone foliar volume ($P>|t|=0.05$) than expanding towns. Expanding towns had higher 1985 peripheral zone grass dry weight standing biomass ($P>|t|=0.05$), grass wet weight standing biomass ($P>|t|=0.07$), total wet weight standing biomass ($P>|t|=0.08$), and total dry weight standing biomass $P>|t|=0.05$) than nonexpanding towns (Table 14). Expanding towns had significantly lower 1986 peripheral zone forb dry weight ($P>|t|=0.04$) and forb wet weight ($P>|t|=0.02$) than nonexpanding towns. Differences in forb wet weight probably reflected more recent inhabitation by prairie dogs, as prairie dog feeding and clipping activities frequently resulted in a higher proportion of forbs than grasses.

Behavioral observations in 1985 may suggested a limited food supply during this study year. Prairie dogs on several sites

Table 11. Basal cover (%) measurements of expanding and nonexpanding prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Zone	Town type	1985 $\bar{X}$	1985 s	1985 Range	1986 $\bar{X}$	1986 s	1986 Range
Basal cover	M[1]	E[2]	11.4	6.2	2.5 - 19.1	10.1	2.2	7.2 - 13.4
Basal cover	M	N[3]	11.4	4.0	5.9 - 16.9	14.3	2.7	11.8 - 18.3
Basal cover	P[4]	E	14.2	7.4	6.9 - 30.0	11.5	1.3	9.0 - 12.9
Basal cover	P	N	12.4	3.1	9.7 - 16.8	14.2	2.7	10.0 - 17.0
forbs	M	E	0.5	0.6	0.0 - 1.6	1.5	1.5	0.0 - 3.6
forbs	M	N	0.4	0.4	0.0 - 1.0	2.2	3.3	0.0 - 8.3
forbs	P	E	1.0	1.5	0.0 - 4.4	0.5	0.7	0.0 - 1.5
forbs	P	N	0.6	0.7	0.0 - 1.9	1.3	1.3	0.0 - 3.1
grasses	M	E	10.9	6.7	0.9 - 19.1	8.7	3.4	4.3 - 12.1
grasses	M	N	11.0	4.1	5.4 - 16.7	12.2	5.3	4.2 - 18.3
grasses	P	E	13.2	6.0	6.7 - 25.6	11.0	1.5	8.0 - 12.9
grasses	P	N	11.8	3.4	8.3 - 16.3	12.9	3.0	8.8 - 17.0
Litter	M	E	44.2	19.4	6.9 - 66.4	32.0	16.1	9.1 - 56.9
Litter	M	N	49.2	19.7	29.8 - 76.2	33.6	25.3	14.5 - 79.2
Litter	P	E	56.1	21.4	11.9 - 73.3	48.5	10.2	35.4 - 60.0
Litter	P	N	52.6	14.8	37.0 - 73.8	32.7	24.1	18.6 - 81.0
Bare ground	M	E	44.0	25.1	19.7 - 90.6	57.8	17.7	31.9 - 82.7
Bare ground	M	N	39.4	20.9	9.1 - 61.6	52.0	27.2	2.5 - 73.6
Bare ground	P	E	29.7	15.4	11.1 - 58.1	40.0	10.9	27.8 - 53.8
Bare ground	P	N	34.7	16.4	8.5 - 48.1	53.1	25.3	2.0 - 68.8

[1]M = main
[2]E = expanding
[3]N = nonexpanding
[4]P = peripheral

Table 12. Foliar cover (%) measurements of expanding and nonexpanding prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Zone	Town type	1985 $\bar{X}$	1985 s	1985 Range	1986 $\bar{X}$	1986 s	1986 Range
Foliar cover	M[1]	E[2]	35.3	11.9	11.9 - 46.0	45.5	13.6	16.5 - 55.0
Foliar cover	M	N[3]	33.2	8.0	17.8 - 40.0	57.0	10.5	44.0 - 71.0
Foliar cover	P[4]	E	46.4	7.9	38.0 - 60.0	63.0	9.2	54.4 - 80.0
Foliar cover	P	N	36.4	6.5	26.0 - 42.0	61.3	5.5	54.0 - 69.0
forbs	M	E	2.8	2.9	0.0 - 7.0	6.8	5.4	0.0 - 15.6
forbs	M	N	1.3	1.5	0.0 - 4.0	12.2	8.6	1.0 - 23.0
forbs	P	E	2.3	3.3	0.0 - 9.0	2.6	2.7	0.0 - 6.7
forbs	P	N	1.7	2.0	0.0 - 5.0	13.8	15.1	2.0 - 41.0
grasses	M	E	32.5	14.1	7.5 - 46.0	38.7	17.2	6.5 - 55.0
grasses	M	N	31.9	8.5	16.4 - 39.0	44.8	17.1	21.0 - 70.0
grasses	P	E	44.1	6.6	34.0 - 51.0	60.4	10.3	50.0 - 80.0
grasses	P	N	34.7	8.2	21.0 - 41.2	47.5	16.5	21.0 - 62.0
Litter	M	E	36.2	16.1	7.5 - 54.0	25.9	13.5	2.6 - 41.0
Litter	M	N	40.1	9.8	25.0 - 51.0	23.3	4.0	17.0 - 27.0
Litter	P	E	41.9	10.4	25.0 - 54.0	23.9	12.2	5.0 - 39.0
Litter	P	N	42.8	8.1	30.2 - 52.0	23.7	6.1	17.0 - 33.0
Bare ground	M	E	28.5	27.0	3.0 - 80.6	28.6	26.5	6.0 - 80.9
Bare ground	M	N	26.7	13.4	9.0 - 41.4	19.7	10.8	3.0 - 33.0
Bare ground	P	E	11.7	9.9	2.0 - 27.0	13.0	8.8	4.0 - 24.0
Bare ground	P	N	20.8	9.3	6.0 - 29.0	15.0	8.0	1.0 - 23.0

[1] M = main
[2] E = expanding
[3] N = nonexpanding
[4] P = peripheral

Table 13. Foliar volume (dm) measurements of expanding and nonexpanding prairie dog towns in western Nebraska, 1985 - 1986.

Town type	Zone	1985			1986		
		$\bar{X}$	s	Range	$\bar{X}$	s	Range
E[1]	M[2]	0.2	0.1	0.1 - 0.3	0.3	0.1	0.2 - 0.4
N[3]	M	0.1	0.1	0.1 - 0.2	0.6	0.3	0.4 - 1.2
E	P[4]	0.5	0.3	0.2 - 1.2	1.1	1.0	0.3 - 3.3
N	P	0.3	0.1	0.1 - 0.3	0.9	0.3	0.5 - 1.4

[1]E = expanding
[2]M = main
[3]N = nonexpanding
[4]P = peripheral

Table 14. Standing biomass measurements (gm/0.1 m^2) of expanding and nonexpanding prairie dog towns in western Nebraska, 1985 - 1986.

Measurement	Zone	Town type	1985 $\bar{X}$	1985 s	1985 Range	1986 $\bar{X}$	1986 s	1986 Range
Total dry weight	M[1]	E[2]	3.9	2.0	2.2 - 6.6	8.9	3.1	4.7 - 13.6
Total dry weight	M	N[3]	2.7	1.2	1.5 - 4.4	14.7	8.1	8.6 - 30.1
Total dry weight	P[4]	E	7.9	3.7	3.4 - 13.2	15.3	7.3	6.4 - 29.1
Total dry weight	P	N	4.3	1.4	2.4 - 5.5	17.7	5.4	12.9 - 25.8
grass dry weight	M	E	3.1	2.3	0.5 - 6.5	6.9	3.9	3.3 - 13.4
grass dry weight	M	N	2.2	1.1	1.1 - 3.9	11.9	8.3	4.8 - 27.6
grass dry weight	P	E	7.3	3.8	3.4 - 12.5	14.4	7.6	6.3 - 29.1
grass dry weight	P	N	3.6	1.6	1.4 - 5.0	14.5	6.0	6.6 - 23.6
forb dry weight	M	E	0.7	0.7	0.0 - 1.7	2.1	2.4	0.1 - 6.4
forb dry weight	M	N	0.4	0.3	0.1 - 0.8	2.9	2.5	0.5 - 7.4
forb dry weight	P	E	0.5	0.5	0.0 - 1.3	0.9	1.3	0.0 - 3.1
forb dry weight	P	N	0.7	0.6	0.0 - 1.7	3.2	2.1	0.7 - 6.6
Total wet weight	M	E	5.7	3.2	2.7 - 11.5	17.8	5.2	8.5 - 24.3
Total wet weight	M	N	3.6	1.5	1.5 - 5.1	27.8	16.1	14.9 - 56.6
Total wet weight	P	E	11.8	7.8	3.4 - 26.6	27.7	13.4	11.3 - 52.2
Total wet weight	P	N	5.5	1.9	3.4 - 8.0	31.8	9.6	21.8 - 43.3
grass wet weight	M	E	4.5	3.8	0.5 - 11.4	12.8	6.6	6.2 - 23.8
grass wet weight	M	N	2.9	1.2	1.1 - 4.3	20.6	15.1	7.6 - 47.6
grass wet weight	P	E	10.8	7.6	3.2 - 24.7	25.8	14.3	10.6 - 52.2
grass wet weight	P	N	4.5	2.3	1.3 - 7.1	24.1	9.5	10.5 - 37.2
forb wet weight	M	E	1.2	1.0	0.1 - 2.6	5.0	5.0	0.5 - 13.2
forb wet weight	M	N	0.7	0.6	0.1 - 1.6	7.1	5.1	1.5 - 15.8
forb wet weight	P	E	1.0	0.9	0.1 - 2.3	1.8	2.4	0.0 - 5.7
forb wet weight	P	N	1.0	1.0	0.1 - 2.7	7.7	4.6	2.6 - 14.2
% Moisture	M	E	31.0	9.0	18.0 - 42.7	48.7	7.3	42.9 - 63.0
% Moisture	M	N	24.3	15.6	3.3 - 49.5	45.4	6.4	36.0 - 54.2
% Moisture	P	E	26.4	15.6	0.0 - 50.3	43.7	5.2	33.1 - 49.8
% Moisture	P	N	21.5	9.8	6.4 - 32.4	43.7	6.4	36.7 - 54.9

[1]M = main
[2]E = expanding
[3]N = nonexpanding
[4]P = peripheral

were observed consuming prickly pear and digging to obtain plant roots. Both of these activities usually occur in periods of low food availability, e.g. winter or early spring. Expanding towns appeared to have higher 1985 peripheral zone measurements of foliar biomass than nonexpanding towns, as indicated by higher standing biomass, foliar volume, and foliar cover. During a dry year with low vegetative production, the peripheral zone may have served as an important source of food. This food source may have had particular importance on grazed sites, which would support not only the feeding activities of prairie dogs, but those of livestock, as well. If foliar biomass was insufficient to meet the foraging requirements of prairie dogs on grazed sites, expansion may have been a response to low food supply. 1986 foliar volume may indicate a lower height and density of vegetation on expanding towns than nonexpanding towns. In a year with more rainfall and higher production, vegetative structure may have negatively influenced population expansion.

Visually, the overall vegetative structure of deferred and grazed treatment sites appeared to differ, particularly in 1986. Deferred sites appeared to have higher vegetation height, although the taller plants were frequently rather sparsely located, and Robel readings were not necessarily correspondingly high. Prairie dog populations on contracting deferred sites appeared to be less contiguous than populations on grazed sites. As populations contracted, prairie dogs appeared to occur in a more clumped distribution, with areas of higher vegetation and little prairie dog activity interspersed between areas of prairie dog concentrations and low vegetative structure. The overall result was an apparent fragmentation of several of the deferred treatment colonies.

Grasshopper densities were lower on expanding towns in the 1985 main zone ($P>|t|=0.08$), which may have contributed to higher vegetation present. Grasshopper densities in 1986 were lower on expanding towns in the main zone ($P>|t|=0.10$), and peripheral zone ($P>|t|=0.04$) than on nonexpanding towns (Table 15). Low grasshopper densities in 1986 may be a reflection of less vegetation present on expanding sites.

Animal Condition

Body weight may be an indication of physical condition of prairie dogs (Garrett 1982), and can affect overwinter survivorship (Koford 1958) and success of immigration. Garrett (1982) determined that surviving immigrants into a colony lost or maintained body weight, while residents were gaining weight. Weight may be a crucial factor in determining breeding of yearling females, and may be influenced by climatic factors, intraspecific factors, and productivity (Knowles 1982). Stockrahm (1976) found that many yearling females in frequently disturbed (i.e. hunted) towns failed to ovulate, while nearly all females in undisturbed towns ovulated and had placental scars. She suggested that hunting pressure in disturbed towns possibly adversely affected physical growth by allowing less time to forage. Physical

Table 15. Grasshopper densities (No./0.1 m^2) of expanding and nonexpanding prairie dog towns in western Nebraska, 1985 - 1986.

Zone	Town type	1985 $\bar{X}$	1985 s	1985 Range	1986 $\bar{X}$	1986 s	1986 Range
M[1]	E[2]	0.5	0.4	0.0 - 1.0	0.9	1.1	0.0 - 3.0
M	N[3]	1.0	0.6	0.3 - 1.7	2.1	1.2	0.9 - 3.8
P[4]	E	0.7	0.3	0.4 - 1.2	0.9	1.0	0.0 - 2.5
P	N	1.3	0.7	0.4 - 1.9	2.3	1.2	0.7 - 4.0

[1]M = main
[2]E = expanding
[3]N = nonexpanding
[4]P = peripheral

immaturity of nonovulating females was suggested by lower $\overline{X}$ body weight than ovulating females. Stockrahm hypothesized that food availability was probably not limited, but less time spent foraging by pups in disturbed towns led to poor body condition during the first winter and failure to reproduce as yearlings in the spring. Koford (1958) stated that "differences between prairie dog towns in food supply or competition are not clearly revealed in the weights of adult prairie dogs, but these differences are strikingly shown in the weights of young in fall". He suggested reduction of population results in improved nutrition and growth of survivors, which may contribute to lowered mortality and rapid increase in animal numbers.

Body weight data were obtained from live-captured prairie dogs (Table 16). Independent t-tests indicated no significant differences in body weight between treatments for adult males and females captured in 1985 and 1986, and pups captured in 1986. However, pups captured on 1985 deferred sites weighed less ($P>t=0.07$) than those captured on grazed sites. Reasons for lower body weight may include less time spent foraging due to frequent disturbance or small town size requiring more individual alertness. However, 1985 deferred sites pup weight was negatively correlated with town size ($r=-0.82$, $P>|R|=0.09$). Less food availability due to intraspecific competition, low productivity, or lack of available peripheral quality forage may also contribute to low body weight. Garrett et al. (1982) compared demographic

Table 16. Body weight (gm) of prairie dogs live-captured spring 1985 and fall 1986 in western Nebraska.

Age & sex	Year	No. towns trapped	Trt.	$\bar{X}$	s	Range
Adult male	1985	8	D[1]	1003	121	800 - 1120
Adult male	1986	7	D	1050	97	900 - 1180
Adult male	1985	6	G[2]	967	81	840 - 1067
Adult male	1986	3	G	1114	64	1076 - 1187
Adult female	1985	8	D	804	75	693 - 900
Adult female	1986	7	D	988	50	940 - 1060
Adult female	1985	6	G	835	85	700 - 940
Adult female	1985	3	G	944	14	928 - 955
Pup	1985	8	D	362	103	202 - 487
Pup	1986	7	D	758	64	673 - 835
Pup	1985	6	G	460	97	280 - 543
Pup	1986	3	G	699	56	647 - 758

[1]D = deferred
[2]G = grazed

differences between a young and old town and found that animals at the young town had a greater proportion of successful pregnancies, larger litters, and juveniles that grew faster and weighed more in fall (young town $\overline{X}$ = 852.6 g; old town $\overline{X}$ = 595.0 g), although spring weights were similar. Yearlings at the young town were more likely to reproduce, survivorship of juveniles and adults was greater, and density was twice that of the other colony. Garrett et al. (1982) suggested that availability of unused habitat, i.e. a peripheral zone with relatively unmodified vegetation, may be responsible for these observed differences. However, vegetative measurements and perimeter:area ratio do not suggest lower food availability on 1985 deferred sites than on grazed sites. Deferred sites pup weight was not significantly correlated to animal density, so competition was not suggested.

Low forage quality may potentially contribute to low body weight. O'Melia et al. (1982) suggested that the foraging and clipping activities of prairie dogs may maintain herbage in an early phenological stage. Forage quality diminishes with plant tissue age, and higher quality herbage gives higher nutritional yield. Krueger (1986) compared prairie dog town centers, edges, and uncolonized areas grazed and ungrazed by ungulates and found that forage under the least foraging pressure had the lowest nitrogen content, as indicated by western wheatgrass nitrogen content. Vegetation under the highest foraging pressure, i.e. grazed by large ungulates and prairie dogs, had the highest nitrogen content. If prairie dog body weight and forage quality nitrogen content. If prairie dog body weight and forage quality are related, low quality forage may be suggested on 1985 deferred sites. Higher prairie dog densities associated with contracting deferred site active areas (Table 6) may have resulted in higher 1986 forage quality, which may have contributed to 1986 prairie dog body weight.

No significant differences in 1985 adult male body weights were detected between expanding ($\bar{X}$ = 989.0 g, s = 68.3) and nonexpanding ($\bar{X}$ = 1016.7 g, s = 105.0) towns, or in 1985 pup body weights between expanding ($\bar{X}$ = 445.3 g, s = 59.9) and nonexpanding ($\bar{X}$ = 363.3 g, s = 163.0) towns. 1985 adult females weighed significantly more ($P>|t|=0.01$) on expanding ($\bar{X}$ = 874.0 g, s = 56.4) than nonexpanding ($\bar{X}$ = 723.3 g, s = 51.3) towns. 1985 prairie dog density appeared to be greater on expanding than nonexpanding towns, and may have positively influenced forage quality and animal body weight.

Body weight was examined for correlations with population density and growth rate. In 1985, pup weight was positively correlated with pup:adult ratio on deferred sites ($r=0.80$, $P>|R|=0.10$). In 1986, pup weight was positively correlated with pup:adult ratio on deferred sites ($r=0.86$, $P>|R|=0.03$) and adult female weight was negatively correlated with pup:adult ratio ($r=-0.83$, $P>|R|=0.08$). 1986 grazed site correlations are suspect, as only 3 towns were trapped, but they may suggest relationships. Pup weight was positively correlated with increase in animal density ($r=1.00$, $P>|R|=0.05$) and pup:adult ratio ($r=0.99$, P>|R|=0.09), and adult female weight was positively correlated with early census adult density (r=0.98, P>|R|=0.11).

Population Growth: Density Relationships

Correlation analyses were conducted to investigate potential relationships between the 3 measures of population growth and initial population density as estimated by the number of adult prairie dogs present during the early census (Table 17). Strong positive correlations were detected in 1985 between prairie dog density and the population growth measures of increase in animal density (r=0.98, P>|R|=0.0001) and % increase in animals (r=0.89, P>|R|=0.003) on deferred sites; a weak positive correlation with increase in animal density (r=0.64, P>|R|=0.02) was detected on grazed sites. Deferred site correlations were not detected in 1986, although a weak grazed sites correlation was detected between density and increase in animal density (r=0.71, P>|R|=0.03). Although no significant correlations were detected between population density and pup:adult ratio of the corresponding year, 1986 grazed site pup:adult ratio was negatively correlated to density of the previous year (r=-0.71, P>|R|=0.07). No similar relationship was detected on deferred sites.

Knowles (1982) found that prairie dog towns on the Charles M. Russell National Wildlife Refuge in Montana grew at a very rapid rate soon after termination of poisoning efforts, with an annual expansion rate (r = 0.279) approaching his estimation of r_m

Table 17. Correlations between population growth and population density (adults/ha) at western Nebraska prairie dog towns, 1985 - 1986.

Population growth measure	Year	Trt.	r	P>|R|
Increase in animal density	1985	D[1]	0.98	0.0001
Increase in animal density	1985	G[2]	0.64	0.02
Increase in animal density	1986	D	*	*
Increase in animal density	1986	G	0.71	0.03
% Increase in animals	1985	D	0.89	0.003
% Increase in animals	1985	G	*	*
% Increase in animals	1986	D	*	*
% Increase in animals	1986	G	*	*
Pup:Adult ratio	1985	D	*	*
Pup:Adult ratio	1985	G	*	*
Pup:Adult ratio	1986	D	*	*
Pup:Adult ratio	1986	G	*	*

[1]D = deferred
[2]G = grazed
*P>0.10

(0.412). He speculated that early high growth rates were a result of much available habitat, especially poisoned sections of existing towns. He noted that as that habitat filled, growth rates fell ($r = 0.015$), and concluded that growth rates of prairie dog towns on the refuge were regulated in a density-dependent manner. In western Nebraska, where significant correlations were detected between density and the population growth measures of increase in animal density and % increase in animals, the relationships were positive. These positive relationships may be a result of the initial colony expansion that occurs following control efforts, when remaining prairie dog densities are low; positive correlations were not detected for 1986 deferred sites, which had higher population densities (Table 6). The negative relationship between 1986 grazed site pup:adult ratio and 1985 population density may be an indication that as prairie dog densities recovered from control efforts, population growth was limited. Deferred grazing may act to further limit growth through colony contraction, which can result in higher prairie dog densities.

Habitat Vegetative Measurements

Basal cover measurements are presented in Table 18. Paired t-tests indicated some differences in basal cover measurements between zones (Table 19). Main zones had higher amounts of bare ground and less litter than peripheral zones, perhaps reflecting a higher degree of use of the vegetation by prairie dogs. Coppock

Table 18. Basal cover (%) measurements on prairie dog towns in western Nebraska, 1985 - 1986.

			1985			1986		
Percent	Trt.	Zone	$\bar{X}$	s	Range	$\bar{X}$	s	Range
basal cover	D[1]	M[2]	10.6	5.5	2.5 - 19.1	12.7	2.9	8.1 - 17.0
basal cover	D	P[3]	16.0	7.6	6.7 - 30.8	12.4	2.7	9.0 - 15.5
basal cover	G[4]	M	9.8	4.3	4.1 - 15.6	11.4	3.6	7.2 - 18.3
basal cover	G	P	9.8	3.7	4.2 - 16.8	12.6	2.8	8.3 - 17.0
forbs	D	M	1.0	0.6	0.0 - 1.6	2.2	2.7	0.0 - 8.3
forbs	D	P	0.9	1.6	0.0 - 4.4	0.8	1.0	0.0 - 3.1
forbs	G	M	0.5	0.5	0.0 - 1.5	0.9	1.1	0.0 - 2.9
forbs	G	P	0.8	0.8	0.0 - 2.5	0.7	1.0	0.0 - 2.7
grasses	D	M	9.6	6.1	0.9 - 19.1	10.5	4.7	4.2 - 17.0
grasses	D	P	15.1	6.6	5.5 - 25.6	11.6	2.6	8.0 - 14.4
grasses	G	M	9.3	4.6	3.5 - 15.6	10.4	4.4	4.3 - 18.3
grasses	G	P	9.1	3.8	3.8 - 16.3	12.0	2.5	8.3 - 17.0
litter	D	M	43.0	23.7	6.9 - 75.0	31.9	19.9	9.1 - 63.3
litter	D	P	50.2	23.2	11.9 - 75.6	37.6	14.3	19.4 - 58.9
litter	G	M	53.3	16.4	30.4 - 76.2	36.1	22.2	16.7 - 79.2
litter	G	P	59.3	11.5	42.6 - 73.8	46.0	20.7	18.6 - 81.0
bare ground	D	M	46.3	24.0	14.3 - 90.6	55.4	21.9	22.5 - 82.7
bare ground	D	P	33.7	21.7	10.1 - 58.1	49.9	14.6	26.1 - 68.8
bare ground	G	M	36.6	19.3	9.1 - 64.5	52.3	24.6	2.5 - 73.6
bare ground	G	P	30.9	12.0	8.5 - 50.3	41.4	21.9	2.0 - 65.9

[1] D = deferred
[2] M = main
[3] P = peripheral
[4] G = grazed

Table 19. Basal cover paired t-tests for zone differences on prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Year	Trt.	P>|t|
basal cover	1985	D[1]	*
basal cover	1985	G[2]	*
basal cover	1986	D	*
basal cover	1986	G	0.10
forbs	1985	D	*
forbs	1985	G	*
forbs	1986	D	0.10
forbs	1986	G	*
grasses	1985	D	*
grasses	1985	G	*
grasses	1986	D	*
grasses	1986	G	*
bare ground	1985	D	0.07
bare ground	1985	G	0.07
bare ground	1986	D	*
bare ground	1986	G	0.01
litter	1985	D	0.06
litter	1985	G	0.07
litter	1986	D	*
litter	1986	G	0.08

[1]D = deferred
[2]G = grazed
*P>0.10

et al. (1983) found that litter decreased as time since colonization increased. A progression from uncolonized areas to edge (short time since colonization) to young to old colony areas corresponded to a decrease in litter. 1986 grazed treatment peripheral zones had greater basal cover than main zones ($P>|t|=0.10$). Independent t-tests conducted to test whether basal cover measurements differed between treatments failed to detect differences in 1986 (Table 20). In 1985, deferred site periperhal zones had higher % basal cover ($P>t=0.04$) and % grasses ($P>t=0.01$) than grazed sites; deferred site main zones had higher % forbs ($P>t=0.03$) than grazed sites.

Table 21 contains results of foliar cover measurements. Table 22 indicates significant differences in foliar cover between zones. Higher amounts of bare ground were present on 1985 main zones than peripheral zones, perhaps reflecting a higher degree of use of main zone vegetation by prairie dogs. Both study years appeared to have higher amounts of foliar cover on peripheral zones than main zones. Table 23 indicates significant differences in foliar cover measurements. In 1985, deferred site peripheral zones had higher % foliar cover ($P>t=0.03$) and % grasses ($P>t=0.01$) than grazed sites. Bare ground was higher on 1986 deferred site peripheral zones than grazed sites ($P>t=0.06$). Litter results appear to conflict: 1985 and 1986 main zone litter measurements for deferred sites were greater than for grazed sites, but 1985 peripheral zone grazed sites had higher litter than deferred sites.

Table 20. Basal cover independent t-tests for treatment differences on prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Year	Zone	P>t
basal cover	1985	M[1]	*
basal cover	1985	P[2]	0.04
basal cover	1986	M	*
basal cover	1986	P	*
forbs	1985	M	0.03
forbs	1985	P	*
forbs	1986	M	*
forbs	1986	P	*
grasses	1985	M	*
grasses	1985	P	0.01
grasses	1986	M	*
grasses	1986	P	*
bare ground	1985	M	*
bare ground	1985	P	*
bare ground	1986	M	*
bare ground	1986	P	*
litter	1985	M	*
litter	1985	P	*
litter	1986	M	*
litter	1986	P	*

[1]M = main
[2]P = peripheral
*P>0.10

Table 21. Foliar cover (%) measurements on prairie dog towns in western Nebraska, 1985 - 1986.

			1985			1986		
Percent	Trt.	Zone	$\bar{X}$	s	Range	$\bar{X}$	s	Range
foliar cover	D[1]	M[2]	36.3	11.2	11.9 - 46.0	48.8	13.6	16.5 - 61.1
foliar cover	D	P[3]	49.4	9.6	37.0 - 64.0	62.1	9.0	53.0 - 80.0
foliar cover	G[4]	M	35.5	9.4	17.8 - 49.0	54.3	9.7	43.4 - 71.0
foliar cover	G	P	38.8	11.1	17.8 - 57.0	60.7	4.8	54.4 - 69.0
forbs	D	M	5.9	10.7	0.0 - 32.0	8.4	7.1	1.0 - 23.0
forbs	D	P	2.1	3.2	0.0 - 9.0	10.2	13.2	0.0 - 41.0
forbs	G	M	2.4	2.2	0.0 - 7.0	6.7	7.4	0.0 - 20.0
forbs	G	P	3.7	7.6	0.0 - 26.0	4.3	3.9	0.0 - 12.0
grasses	D	M	30.3	13.2	7.5 - 46.0	40.5	17.4	6.5 - 57.8
grasses	D	P	47.3	9.1	35.0 - 64.0	51.9	17.7	21.0 - 80.0
grasses	G	M	33.1	10.4	16.0 - 47.0	47.6	12.8	27.8 - 70.0
grasses	G	P	35.0	9.9	16.7 - 50.0	56.3	4.5	50.0 - 62.0
litter	D	M	33.8	13.4	7.5 - 49.0	23.5	9.9	2.6 - 35.0
litter	D	P	36.7	10.6	25.0 - 51.0	19.8	8.0	5.0 - 29.0
litter	G	M	42.3	8.8	28.0 - 54.0	26.8	9.1	17.0 - 41.0
litter	G	P	44.0	8.3	27.0 - 54.0	28.0	7.6	18.0 - 39.0
bare ground	D	M	30.0	22.9	7.0 - 81.0	27.6	22.5	8.0 - 80.9
bare ground	D	P	13.9	11.5	1.0 - 28.0	18.1	8.4	7.0 - 33.0
bare ground	G	M	22.2	15.3	3.0 - 14.4	18.9	13.9	3.0 - 38.9
bare ground	G	P	17.2	11.0	2.0 - 36.7	11.4	8.0	1.0 - 23.3

[1]D = deferred
[2]M = main
[3]P = peripheral
[4]G = grazed

Table 22. Foliar cover paired t-tests for zone differences on prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Year	Trt.	P>|t|
foliar cover	1985	D[1]	*
foliar cover	1985	G[2]	0.09
foliar cover	1986	D	0.06
foliar cover	1986	G	0.02
forbs	1985	D	*
forbs	1985	G	*
forbs	1986	D	*
forbs	1986	G	*
grasses	1985	D	0.04
grasses	1985	G	*
grasses	1986	D	*
grasses	1986	G	0.03
litter	1985	D	*
litter	1985	G	*
litter	1986	D	*
litter	1986	G	*
bare ground	1985	D	0.10
bare ground	1985	G	0.01
bare ground	1986	D	*
bare ground	1986	G	*

[1]D = deferred
[2]G = grazed
*P>0.10

Table 23. Foliar cover independent t-tests for treatment differences on prairie dog towns in western Nebraska, 1985 - 1986.

Percent	Year	Zone	P>t
foliar cover	1985	M[1]	*
foliar cover	1985	P[2]	0.03
foliar cover	1986	M	*
foliar cover	1986	P	*
forbs	1985	M	*
forbs	1985	P	*
forbs	1986	M	*
forbs	1986	P	*
grasses	1985	M	*
grasses	1985	P	0.01
grasses	1986	M	*
grasses	1986	P	*
bare ground	1985	M	*
bare ground	1985	P	*
bare ground	1986	M	*
bare ground	1986	P	0.06
litter	1985	M	0.05
litter	1985	P	0.06
litter	1986	M	*
litter	1986	P	0.02

[1]M = main
[2]P = peripheral
*P>0.10

Paired t-tests indicate higher Robel readings on peripheral zones than on main zones for the deferred treatment in 1985 (P>|t|=0.06) and 1986 (P>|t|=0.05), and the grazed treatment in 1985 (P>|t|=0.01) and 1986 (P>|t|=0.01) (Table 24). No statistically significant differences between treatments in foliar volume were found at the P=0.10 level, although potential differences may be indicated (P>t=0.11), suggesting higher Robel readings on peripheral zones for deferred treatment sites than for grazed sites for both years of the study.

Table 25 presents standing biomass measurements. Table 26 indicates differences between zones for total dry weight and wet weight standing biomass, and dry weight and wet weight of grass, for both treatments in 1985, and deferred treatment in 1986. Where differences were detected, peripheral zone standing biomass measurements were greater than main zone standing biomass measurements. Significant differences in standing biomass between treatments are indicated in Table 27. Statistically greater standing biomass for deferred treatment was detected in 1985 peripheral zone measurements of total dry weight (P>t=0.04), grass dry weight (P>t= 0.06), total wet weight (P>t = 0.02), and grass wet weight (P>t = 0.03). Although no statistically greater standing biomass measurements were detected in 1986 at the p=0.10 level, potential differences may be indicated, suggesting higher deferred treatment standing biomass measurements in the peripheral zone for total dry weight (P>t=0.14) and total wet weight

Table 24. Foliar volume (dm) measurements on prairie dog towns in western Nebraska, 1985 - 1986.

Year	Trt.	Zone	$\bar{X}$	s	Range
1985	D[1]	M[2]	0.19	0.09	0.06 - 0.32
1985	D	P[3]	0.55	0.36	0.26 - 1.17
1985	G[4]	M	0.16	0.08	0.05 - 0.28
1985	G	P	0.36	0.24	0.10 - 0.86
1986	D	M	0.46	0.20	0.18 - 0.80
1986	D	P	1.19	0.84	0.50 - 3.29
1986	G	M	0.49	0.30	0.25 - 1.16
1986	G	P	0.79	0.36	0.32 - 1.41

[1]D = deferred
[2]M = main
[3]P = peripheral
[4]G = grazed

Table 25. Standing biomass measurements (gm/0.1 m^2) on prairie dog towns in western Nebraska, 1985 - 1986.

Measurement	Trt.	Zone	1985 $\bar{X}$	1985 s	1985 Range	1986 $\bar{X}$	1986 s	1986 Range
total dry weight	D[1]	M[2]	3.8	1.9	1.7 - 6.5	11.0	3.1	6.3 - 17.2
total dry weight	D	P[3]	8.7	4.5	5.1 - 16.8	18.0	5.3	12.9 - 29.1
total dry weight	G[4]	M	3.9	3.0	1.3 - 11.6	13.0	7.8	4.7 - 30.1
total dry weight	G	P	5.4	3.1	2.4 - 12.6	14.9	5.8	6.4 - 25.8
grass dry weight	D	M	2.6	1.7	0.5 - 5.9	8.3	3.8	3.3 - 15.0
grass dry weight	D	P	7.8	4.9	3.7 - 16.6	15.6	6.5	6.6 - 29.1
grass dry weight	G	M	3.3	3.2	0.6 - 11.5	11.1	7.6	4.2 - 27.6
grass dry weight	G	P	4.5	3.3	1.4 - 12.5	13.3	5.2	6.3 - 23.6
forb dry weight	D	M	1.3	1.6	0.0 - 4.9	2.7	2.5	0.5 - 7.4
forb dry weight	D	P	0.9	1.2	0.2 - 3.5	2.4	2.0	0.0 - 6.6
forb dry weight	G	M	0.6	0.5	0.1 - 1.7	1.9	1.5	0.1 - 3.7
forb dry weight	G	P	0.8	0.8	0.0 - 2.7	1.6	1.7	0.0 - 4.7
total wet weight	D	M	6.3	4.1	2.5 - 14.5	19.8	4.9	13.5 - 29.6
total wet weight	D	P	13.8	7.8	5.4 - 26.6	32.4	10.0	21.8 - 52.2
total wet weight	G	M	5.8	4.4	1.5 - 16.3	25.4	14.8	8.5 - 56.6
total wet weight	G	P	7.3	4.1	3.4 - 16.1	26.5	10.5	11.3 - 43.3
grass wet weight	D	M	3.8	2.6	0.5 - 9.5	13.6	6.0	6.2 - 24.8
grass wet weight	D	P	11.7	7.9	4.9 - 24.7	26.7	12.3	10.5 - 52.2
grass wet weight	G	M	4.8	4.7	1.1 - 16.2	20.4	13.1	8.0 - 47.6
grass wet weight	G	P	5.9	4.5	1.3 - 16.1	22.9	8.4	10.6 - 37.2
forb wet weight	D	M	2.5	3.7	0.2 - 11.3	6.2	4.9	1.5 - 15.8
forb wet weight	D	P	2.1	3.4	0.3 - 9.8	5.7	4.4	0.0 - 14.2
forb wet weight	G	M	1.0	0.9	0.1 - 2.6	4.9	3.9	0.5 - 9.3
forb wet weight	G	P	1.4	1.1	0.1 - 3.3	3.7	4.1	0.0 - 11.7
% moisture	D	M	33.9	14.6	13.6 - 56.9	44.6	5.4	36.0 - 53.0
% moisture	D	P	32.9	16.6	6.4 - 54.7	43.1	4.6	36.0 - 49.8
% moisture	G	M	30.4	15.2	3.3 - 68.6	46.4	8.7	33.7 - 63.0
% moisture	G	P	25.3	15.3	0.0 - 58.6	42.7	6.8	33.1 - 54.9

[1]D = deferred
[2]M = main
[3]P = peripheral
[4]G = grazed

Table 26. Standing biomass paired t-tests for zone differences on prairie dog towns in western Nebraska, 1985 - 1986.

Measurement	Year	Trt.	P>|t|
total dry weight	1985	D[1]	0.05
total dry weight	1985	G[2]	0.001
total dry weight	1986	D	0.02
total dry weight	1986	G	*
grass dry weight	1985	D	0.05
grass dry weight	1985	G	0.003
grass dry weight	1986	D	0.03
grass dry weight	1986	G	*
forb dry weight	1985	D	*
forb dry weight	1985	G	*
forb dry weight	1986	D	*
forb dry weight	1986	G	*
total wet weight	1985	D	0.07
total wet weight	1985	G	0.002
total wet weight	1986	D	0.02
total wet weight	1986	G	*
grass wet weight	1985	D	0.07
grass wet weight	1985	G	0.01
grass wet weight	1986	D	0.03
grass wet weight	1986	G	*
forb wet weight	1985	D	*
forb wet weight	1985	G	*
forb wet weight	1986	D	*
forb wet weight	1986	G	*
% moisture	1985	D	*
% moisture	1985	G	*
% moisture	1986	D	*
% moisture	1986	G	*

[1]D = deferred
[2]G = grazed
*P>0.10

Table 27. Standing biomass independent t-tests for treatment differences on prairie dog towns in western Nebraska, 1985 - 1986.

Measurement	Year	Zone	P>t
total dry weight	1985	M[1]	*
total dry weight	1985	P[2]	0.04
total dry weight	1986	M	*
total dry weight	1986	P	0.14
grass dry weight	1985	M	*
grass dry weight	1985	P	0.06
grass dry weight	1986	M	*
grass dry weight	1986	P	*
forb dry weight	1985	M	*
forb dry weight	1985	P	*
forb dry weight	1986	M	*
forb dry weight	1986	P	*
total wet weight	1985	M	*
total wet weight	1985	P	0.02
total wet weight	1986	M	*
total wet weight	1986	P	0.13
grass wet weight	1985	M	*
grass wet weight	1985	P	0.03
grass wet weight	1986	M	*
grass wet weight	1986	P	*
forb wet weight	1985	M	*
forb wet weight	1985	P	*
forb wet weight	1986	M	*
forb wet weight	1986	P	*
% moisture	1985	M	*
% moisture	1985	P	*
% moisture	1986	M	*
% moisture	1986	P	*

[1]M = main
[2]P = peripheral
*P>0.10

(P>t=0.13).

Grasshopper density was measured because of its potentially strong influence on rangeland vegetation. Table 28 presents grasshopper densities at study sites. No differences were detected in 1986 grasshopper densities between zones; 1985 densities differed between zones for the deferred treatment only (P>|t|=0.04), with peripheral zone densities exceeding main zone densities. 1985 deferred treatment grasshopper densities were not significantly greater than grazed treatment densities, however, 1986 deferred site densities were higher than grazed site densities for both the main (P>t=0.09) and peripheral (P>t=0.02) zones.

Population Growth: Habitat Relationships

Correlation analyses were conducted to investigate potential relationships between the 3 measures of population growth and habitat vegetative characteristics. Examination of significant correlations (Tables 29, 30 and 31) reveals a lack of high correlation coefficients, i.e. r-values range from 0.50 to 0.74, indicating relationships between population growth measures and individual habitat measurements were not particularly strong. The lack of strong correlations may indicate measurements of biologically invalid habitat variables, or it may indicate complex relationships between prairie dogs and habitat that are not detectable through simple correlation analysis of individual habitat variables. If this is true, weak correlations may be indicators of potential relationships.

Table 28. Grasshopper densities (No./0.1 sq. m) at prairie dog towns in western Nebraska, 1985 - 1986.

Year	Trt.	Zone	$\bar{X}$ density	s	Range
1985	D[1]	M[2]	0.7	0.6	0.0 - 1.7
1985	D	P[3]	1.0	0.8	0.1 - 1.9
1985	G[4]	M	0.7	0.6	0.0 - 2.0
1985	G	P	0.9	0.6	0.0 - 1.9
1986	D	M	1.9	1.3	0.0 - 3.8
1986	D	P	1.9	1.3	0.0 - 4.0
1986	G	M	0.7	0.6	0.1 - 1.6
1986	G	P	0.7	0.7	0.0 - 1.7

[1]D = deferred
[2]M = main
[3]P = peripheral
[4]G = grazed

Table 29. Significant correlations between increase in animal density and habitat vegetative measurements on prairie dog towns in western Nebraska, 1985 - 1986.

Variable	Trt.	Zone	Year	r	P>|R|
% forb basal cover	D[1]	M[2]	1985	0.70	0.06
% foliar cover	G[3]	P[4]	1985	0.60	0.05
% grass foliar cover	G	P	1985	0.50	0.01
% litter foliar cover	G	P	1985	-0.55	0.08
foliar volume	G	P	1986	0.60	0.09
dry weight biomass	G	M	1985	0.57	0.05
grass dry weight	G	M	1985	0.55	0.06
wet weight biomass	G	M	1985	0.61	0.04

[1]D = deferred
[2]M = main
[3]G = grazed
[4]P = peripheral

Table 30. Significant correlations between % increase in animals and habitat vegetative measurements on prairie dog towns in western Nebraska, 1985 - 1986.

Variable	Trt.	Zone	Year	r	P>|R|
% litter basal cover	D[1]	P[2]	1986	-0.68	0.06
% bare ground basal cover	D	P	1986	0.63	0.10
% forb foliar cover	G[3]	M[4]	1985	0.66	0.02
% litter foliar cover	G	M	1985	-0.53	0.08

[1]D = deferred
[2]P = peripheral
[3]G = grazed
[4]M = main

Table 31. Significant correlations between pup:adult ratio and habitat vegetative measurements on prairie dog towns in western Nebraska, 1985 - 1986.

Variable	Trt.	Zone	Year	r	P>|R|
% basal cover	D[1]	M[2]	1985	-0.62	0.10
% forb basal cover	D	M	1985	0.75	0.03
% grass basal cover	D	M	1985	-0.64	0.09
% litter basal cover	D	M	1986	-0.74	0.04
% bare ground basal cover	D	P[3]	1986	0.73	0.04
% forb foliar cover	G[4]	M	1985	0.70	0.01
% litter foliar cover	G	M	1985	-0.59	0.04
% litter foliar cover	G	P	1985	-0.53	0.09
foliar volume	D	P	1985	0.73	0.06
dry weight biomass	D	P	1985	0.72	0.07
grass dry weight biomass	D	P	1985	0.71	0.08
wet weight biomass	D	P	1985	0.76	0.05
% moisture biomass	D	M	1985	-0.65	0.08

[1]D = deferred
[2]M = main
[3]P = peripheral
[4]G = grazed

Where statistically significant correlations were detected, foliar volume was positively related to population growth. These correlations were detected only in the peripheral zone of 1985 deferred sites and 1986 grazed sites. Although not statistically significant, a potential negative relationship with % increase in animal density may be indicated in the peripheral zone in 1986 for the deferred treatment ($r=-0.56$, $P>|R|=0.15$). Since the 1986 deferred treatment peripheral zone Robel readings were considerably higher than other Robel readings (Table 24), a possible interpretation of this discrepency is that certain levels of foliar volume appear to be conducive to population growth, perhaps representing a food source, but higher levels appear to be prohibitive to growth.

Where statistically significant correlations were detected, standing biomass was positively related to population growth. However, these correlations were detected only in 1985. Since 1985 standing biomass levels were considerably lower than 1986 standing biomass levels (Table 25), the failure to detect correlations between 1986 population growth and standing biomass may indicate that higher levels of standing biomass are not conducive to prairie dog population growth. Where statistically significant correlations were detected, standing biomass moisture was negatively correlated with population growth, perhaps indicating that dry conditions favor prairie dog population growth.

Where statistically significant correlations were detected, bare ground was positively correlated with population growth, and litter was negatively correlated with growth. These relationships may reflect a degree of use of vegetation by prairie dogs. That is, where growth is greater, vegetation may be more fully utilized, resulting in less litter and more bare ground.

Relationships between vegetative cover and population growth were complex. Most of the positive correlations with population growth were foliar cover measurements; all of the negative correlations were basal cover measurements. However, % forbs measured by basal cover was positively correlated with population growth. Positive correlations were only detected in 1985, when foliar cover was somewhat lower than in 1986 (Table 21). Apparently, either higher amounts of foliar cover were not conducive to population growth, or population growth was not conducive to foliar cover.

Correlation analyses were conducted to test for relationships between population growth and precipitation, grasshopper density, and perimeter:area ratio. The only statistically significant correlation detected with precipitation was a negative correlation between pup:adult ratio and 1986 precipitation ($r=-0.75$, $P>|R|=0.03$) on deferred sites. Two significant correlations were detected with perimeter:area ratio. Pup:adult ratio was positively correlated with 1986 perimeter:area ratio ($r=0.73$, $P>|R|=0.04$) on deferred sites, and increase in animal density was positively correlated with 1986 perimeter:area ratio ($r=0.67$, $P>|R|=0.07$) on deferred sites. Deferred site 1985 grasshopper densities were significantly negatively correlated with increase in animal density ($r=-0.70$, $P>|R|=0.05$) and % increase in animals ($r=-0.71$, $P>|R|=0.07$) on the main zone, and increase in animal density ($r=-0.77$, $P>|R|=0.03$) and % increase in animals ($r=-0.67$, $P>|R|=0.10$) on the peripheral zone. Since 1985 was a drought year, and vegetative production was low, negative correlations between growth and grasshopper densities may indicate competition for food. Grazed site 1986 grasshopper density was positively correlated with pup:adult ratio ($r=0.65$, $P>|R|=0.06$) on the peripheral zone. A positive correlation on the main zone ($r=0.57$, $P>|R|=0.11$) may also be indicated.

Lenzen Town

One 1986 deferred treatment site, "Lenzen town", was excluded from the overall statistical analyses due to lack of total exclusion of livestock grazing from the town. Cattle were excluded from the prairie dog town by an electric fence, but grazing of the rest of the pasture was permitted. The fence was erected May 1985, prior to the onset of 1985 livestock grazing. The fence was positioned several meters outwards from the outermost active prairie dog burrows, completely enclosing the 1.3 ha town. Town expansion occurred by fall 1985, but all of the outermost burrows were contained within the fence. The fence was moved outwards several meters April 1986 prior to onset of 1986 grazing, in order to compensate for 1985 expansion. At this time the town measured 2.1 ha. By June 1986, Lenzen town had expanded beyond the fenceline, and measured 4.7 ha. Expansion continued until August, and the town was measured at 9.5 ha in mid-August, an increase of 352% over the April area and 102% over the June area.

The 1986 town expansion resulted in 3 town areas, or locations: an inner, deferred treatment area inhabited by prairie dogs; an outer, grazed area inhabited by prairie dogs; and a peripheral, grazed area not inhabited by prairie dogs. Since the main zone received both the deferred and grazed treatments, Lenzen town was excluded from the 1986 statistical analyses, and the data are presented separately.

I. Population Growth

The 1986 early census indicated 38 adults and 70 pups present, resulting in a density estimate of 8.1 adults/ha and a pup:adult ratio of 1.8. Both figures fall within the range of observed values for other deferred treatment sites. The majority of observed prairie dog activities were contained within the fenceline, although 1 family unit was observed using burrows exterior to the fenced area. Total density of animals (adults and pups) within the fenced area was 51.4 animals/ha in the early census. August census indicated 106 prairie dogs, of which a maximum of 79 animals were observed outside and 27 animals inside the fence at any one time, although movements across the fenceline of some individuals were apparent. Total density of animals observed inside the fenced area in the August census was 12.9 animals/ha. If calculated in the same manner as used for other study sites, i.e. using June area estimate, August density was 16.8 animals/ha, resulting in an increase in animal density of 8.7 animals/ha. However, other study sites did not exhibit marked increases in inhabited area from June to August. If calculated using the August area estimate, August density was 11.1 animals/ha, resulting in an increase in animal density of 3.0. The propriety of density estimates as a measure of Lenzen town population growth is questionable, because of the large change in inhabited area, and subsequent lack of ability to compare Lenzen town with other study sites. Regardless of which density estimate is used, increase in animal density of Lenzen town is within the range of other deferred site values. Use of % increase in animals as the population growth measure alleviates the difficulty of comparisons with other study sites because it does not require the incorporation of an area estimate: it can be calculated on the basis of change in animal numbers, regardless of inhabited area. Lenzen town % increase in animals was 179%, which was within the range of other deferred site values.

II. Animal Condition

Table 32 presents body weights of prairie dogs live-captured from inside and outside of the fence. Pups taken from both locations did not differ in weight, although adult males differed by location ($P>|t|=0.03$), with males captured from inside the fence weighing more than those captured outside the fence.

Table 32. Body weight (gm) of Lenzen town prairie dogs live-captured fall 1986, western Nebraska.

Age and sex	Location	$\bar{X}$	s	Range
Adult male	I[1]	1290	127	1200 - 1380
Adult male	O[2]	967	64	920 - 1040
Adult female	I	850	42	820 - 880
Adult female	O	917	32	880 - 940
Pup	I	742	90	596 - 860
Pup	O	770	48	740 - 840

[1] I = inside of fence
[2] O = outside of fence

Although not statistically significant ($P>0.10$), adult female weights appeared to differ by location ($P>|t|=0.13$), with females captured outside the fence weighing more than those captured inside the fence. These results were contradictory, and failed to provide any strong evidence relating animal condition to livestock grazing. In comparison to 1986 body weights of prairie dogs from other sites, adult males inside the fence weighed more, males outside the fence weighed less, adult females inside and outside the fence tended to weigh less, and pups had similar weights.

III. Habitat Vegetative Measurements

Tables 33, 34, 35 and 36 contain habitat vegetative measurements and grasshopper densities from Lenzen town. In comparison to other study sites, Lenzen town basal cover measurements appeared to be similar. Foliar cover appeared to be somewhat higher, and grasshopper density somewhat lower, than other study sites. Foliar volume in the ungrazed main area appeared to be higher than foliar volume for other deferred site main zones.

Measurements were taken for 3 locations: main zone - grazed treatment, main zone - deferred treatment, and peripheral zone - grazed treatment. Analysis of variance indicated significant differences among locations for foliar volume ($P>F=0.001$), wet weight standing biomass ($P>F=0.09$), and foliar cover measurements of % litter ($P>F=0.08$), % bare ground ($P>F=0.05$), and % forbs ($P>F=0.03$). Fisher's Protected Least Significant Difference (LSD) test for mean comparisons was used if significant F-tests

Table 33. Lenzen prairie dog town basal cover (%), western Nebraska, 1986.

Percent	Location	$\bar{X}$	s	Range
basal cover	1[a]	13.3	6.5	0.0 - 20.0
basal cover	2[b]	13.8	7.2	0.0 - 30.0
basal cover	3[c]	13.6	6.3	0.0 - 20.0
% grasses	1	11.7	7.2	0.0 - 20.0
% grasses	2	13.1	7.9	0.0 - 30.0
% grasses	3	12.1	7.0	0.0 - 20.0
% forbs	1	1.7	3.9	0.0 - 10.0
% forbs	2	1.8	5.3	0.0 - 20.0
% forbs	3	1.4	5.3	0.0 - 20.0
bare ground	1	33.3	25.0	0.0 - 70.0
bare ground	2	25.6	24.0	0.0 - 70.0
bare ground	3	28.6	24.4	0.0 - 70.0
litter	1	53.3	23.9	20.0 - 90.0
litter	2	60.0	23.4	20.0 - 90.0
litter	3	57.9	24.2	20.0 - 90.0

[a]1 = main zone, deferred treatment
[b]2 = main zone, grazed treatment
[c]3 = peripheral zone, grazed treatment

Table 34. Lenzen prairie dog town foliar cover (%), western Nebraska, 1986.

Percent	Location	$\bar{X}$	s	Range
foliar cover	A[1]	74.4	10.1	60.0 - 90.0
foliar cover	B[2]	70.0	7.7	60.0 - 80.0
foliar cover	C[3]	73.0	8.2	60.0 - 80.0
grasses	A	64.4	10.1	50.0 - 80.0
grasses	B	67.3	11.0	50.0 - 80.0
grasses	C	71.0	9.9	50.0 - 80.0
forbs	A	10.0[a]	10.0	0.0 - 30.0
forbs	B	2.7[b]	4.7	0.0 - 10.0
forbs	C	2.0[b]	4.2	0.0 - 10.0
bare ground	A	5.6[a]	5.3	0.0 - 10.0
bare ground	B	0.9[b]	3.0	0.0 - 10.0
bare ground	C	2.0[ab]	4.2	0.0 - 10.0
litter	A	20.0[a]	8.7	10.0 - 30.0
litter	B	29.1[b]	8.3	20.0 - 40.0
litter	C	25.0[ab]	8.5	10.0 - 40.0

Means followed by the same letter are not significantly different (P>0.05) as indicated by Fisher's Protected Least Significant Difference test for mean comparisons.

[1]A = main zone, deferred treatment
[2]B = main zone, grazed treatment
[3]C = peripheral zone, grazed treatment

Table 35. Lenzen prairie dog town foliar volume (dm) and grasshopper densities (No./0.1 sq. m), western Nebraska, 1986.

Variable	Location	$\bar{X}$	s	Range
Robel reading	A[1]	1.1^a	0.3	0.8 - 1.6
Robel reading	B[2]	0.4^b	0.1	0.3 - 0.7
Robel reading	C[3]	0.4^b	0.1	0.3 - 0.5
grasshopper density	A	0.2	0.4	0.0 - 1.0
grasshopper density	B	0.1	0.3	0.0 - 1.0
grasshopper density	C	0.0	0.0	0.0 - 0.0

Means followed by the same letter are not significantly different (P>0.05) as indicated by Fisher's Protected Least Significant Difference test for means comparisons.

[1]A = main zone, deferred treatment
[2]B = main zone, grazed treatment
[3]C = peripheral zone, grazed treatment

Table 36. Lenzen prairie dog town standing biomass measurements ($gm/0.1\ m^2$), western Nebraska, 1986.

Variable	Location	$\bar{X}$	s	Range
total dry weight	A[1]	18.2	7.1	8.0 - 28.0
total dry weight	B[2]	14.1	9.0	5.0 - 35.0
total dry weight	C[3]	15.5	11.3	5.0 - 39.0
grass dry weight	A	15.8	8.9	2.0 - 28.0
grass dry weight	B	13.1	9.1	3.0 - 33.0
grass dry weight	C	12.3	7.1	5.0 - 26.0
forb dry weight	A	2.4	2.3	0.0 - 8.0
forb dry weight	B	1.1	1.2	0.0 - 3.0
forb dry weight	C	1.3	1.8	0.0 - 5.0
total wet weight	A	26.4[a]	6.9	12.0 - 35.0
total wet weight	B	19.0[ab]	9.9	9.0 - 42.0
total wet weight	C	17.5[b]	10.5	7.0 - 34.0
grass wet weight	A	21.4	8.2	7.0 - 35.0
grass wet weight	B	15.9	9.2	5.0 - 35.0
grass wet weight	C	15.2	8.6	7.0 - 29.0
forb wet weight	A	5.0	2.9	0.0 - 9.0
forb wet weight	B	2.9	2.8	0.0 - 7.0
forb wet weight	C	2.4	3.2	0.0 - 7.0
% moisture	A	34.0	18.3	0.0 - 67.0
% moisture	B	29.5	18.8	0.0 - 63.0
% moisture	C	19.5	16.9	0.0 - 44.0

Means followed by the same letter are not significantly different ($P>0.05$) as indicated by Fisher's Protected Least Significant Difference test for mean comparisons.

[1]A = main zone, deferred treatment
[2]B = main zone, grazed treatment
[3]C = peripheral zone, grazed treatment

indicated at least 1 location mean value differed from the rest (Tables 33 - 36). Main - deferred treatment location appeared to have higher foliar volume measurements, forb foliar cover, and wet weight standing biomass levels than other locations. Main - grazed treatment location appeared to have lower % bare ground and higher % litter than the other locations.

In the absence of a difference in prairie dog density or population growth measures between Lenzen town and other study sites, the outward movement of Lenzen town prairie dogs from the ungrazed main zone to adjacent grazed areas may indicate a habitat preference of the animals. Habitat selection appeared to be for vegetation with lower foliar volume, i.e. less vegetative height and density.

SUMMARY AND MANAGEMENT IMPLICATIONS

Three population growth measures (increase in animal density, % increase in animals, and pup:adult ratio) were used to evaluate the efficacy of deferred grazing in reducing the population growth rates of prairie dogs following population reduction. Two of the 3 measures of growth (% increase in animals and pup:adult ratio) were significantly lower on deferred sites than grazed sites for the second year of the study. Population growth measures did not differ significantly between treatments in 1985.

Correlations between population growth and density suggested a positive relationship when density was low. Population growth was not positively related to higher population densities. If deferred grazing tends to concentrate prairie dogs on contracting colony areas, it may act to slow the initial high rates of population growth that occur following control, through earlier arrival at limiting densities.

The efficacy of deferred grazing in reducing population growth rates of prairie dogs in the mixed- and short-grass rangeland of western Nebraska appeared to be heavily dependent on rainfall. Below average rainfall apparently limited vegetative response to a release from grazing pressure, and resulted in prairie dog population growth rates similar to those seen on sites with higher grazing pressure. The efficacy of deferred grazing would also be expected to vary with the natural productivity capacity of specific sites.

Vegetative characteristics that differed between treatments included basal cover, foliar cover, foliar volume, and standing biomass. Population growth:habitat relationships suggested that low levels of foliar cover, standing biomass, and foliar volume may be conducive to population growth, especially during a year of low vegetative production. Higher levels of foliar cover and standing biomass did not appear to be conducive to growth, and high foliar volume may have prohibited population growth.

Area expansion of prairie dog towns appeared to reflect other measures of population growth used in this study. Expanding towns differed from nonexpanding towns on the basis of habitat vegetative characteristics. In 1985, a year with below average rainfall, expanding towns had higher peripheral zone foliar biomass measurements than nonexpanding towns, which may have served as an important food source, especially on sites which also supported the feeding activities of livestock. In 1986, a year with average rainfall, nonexpanding towns had higher foliar height and density than expanding towns, suggesting vegetative structure may have negatively influenced area expansion.

On reduced-density colonies, livestock grazing would appear to permit or encourage expansion during either dry or normal rainfall years. In wet years, livestock presence may allow expansion by depressing vegetative structure through grazing and trampling of tall plants. In dry years, the consumption of food plants by livestock may encourage outward expansion of prairie dogs in search of food. Grazing deferral appears to discourage expansion in drought or normal rainfall years, although other population growth measures on deferred sites are similar to those for grazed sites in dry periods. In dry years, deferral may be less conducive to outward expansion of colony area than grazing, due to the presence of greater food supplies. In wet years, vegetative structure is probably prohibitive to growth of colonies.

Within the constraints of the study (i.e. town size 0.4 - 20.3 ha; 1.5 - 23.6 adults/ha), colony size and initial animal density would not appear to reduce the efficacy of deferred grazing in reducing population growth rates of prairie dogs. However, large towns and prairie dog densities more typical of uncontrolled towns were not studied. The ability of high prairie dog densities to limit potential vegetative response to removal of livestock grazing pressure may exist. If so, the application of deferred grazing is probably most efficacious as a method of reducing population growth when applied soon after population reduction.

Visual observations on deferred treatment sites suggest that as town area contracts, prairie dog activities become less generally distributed across colonies, and clumps, or centers of activity, result. These clumps of prairie dogs appear to be separated by relatively taller vegetation.

All but 1 deferred study site had livestock grazing excluded from the entire pasture within the deferral period. The remaining site had grazing excluded from the colony by means of an electric fence, and cattle were permitted to graze nearby. Although this site had population density, growth, and vegetative characteristcs within the range of those observed on other sites, it exhibited an uncharacteristic outwards movement of animals into adjacent grazed areas. This rapid colony expansion was not observed on any of the other study sites, and may indicate a habitat preference of the prairie dogs for vegetation with lower foliar volume.

The outward movement of prairie dogs on Lenzen Town suggests that a key factor in limiting expansion may lie in encouraging vegetation that has high peripheral vegetative structure relative to the structure present on the main colony area. Therefore, vegetative structure and anticipated land use of adjacent areas should be considered prior to adoption of deferred grazing. Deferred grazing is not a suitable control measure if it simply serves to shift colonies onto adjacent areas. Conversely, it may serve as a method of preventing growth onto neighboring areas if used as a border or vegetative "fence" to discourage prairie dog activities.

FURTHER NEEDED RESEARCH

Results from this study suggest deferred grazing may be an effective management decision in reducing prairie dog population growth rates. However, variability and predictability of response remain unanswered questions which may affect practical application of the technique. Weather and site-specific productivity would seem to greatly influence response, and should be further evaluated. The fate of individual animals might also be an important consideration. Grazing deferral appears to reduce natality, as measured by pup:adult ratio. However, survivorship and emigration on study colonies were not evaluated. The possibility of increased emigration resulting from grazing deferral may be an important practical consideration in application, if suitable areas exist nearby which could be colonized or reinvaded.

Another dimension, time, received little consideration in this study because of practical limitations. In some sense, the immediate question is whether deferred grazing is effective in the short-term; if not, deferral would probably receive little consideration as a management tool by ranchers and range managers. Another aspect is how deferred grazing varies with time, e.g. whether prairie dog populations under deferred grazing expand and contract as densities and weather change, and whether a stable, smaller colony size is eventually achieved.

Other practical considerations which should receive attention are cost-effectiveness and grazing intensity. The decision to incorporate deferred grazing into a prairie dog control plan could involve such factors as relative costs of various control techniques and the necessary frequency of application, costs of damage, and potential influence on non-target wildlife species. This study examined only the possiblity of complete deferral May 1 - September 1; population growth on grazed sites was not evaluated in respect to intensity of grazing pressure. It may be possible that some sites could support low intensity grazing or short-duration grazing systems. Additional flexiblity in the use of site production may increase the cost-effectiveness of this control method. The identification of threshold levels of vegetation at which population growth is negatively impacted could be an important step. If a range of values of vegetative structure is identified as being unsuitable for prairie dogs, environmental influences, site-specific productivity, and grazing intensity can be considered regarding their influence on the desired structure.

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