

THESIS

**CATTLE USE OF PRAIRIE DOG TOWNS ON THE
SHORTGRASS STEPPE OF COLORADO**

Submitted by

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In partial fulfillment of the requirements

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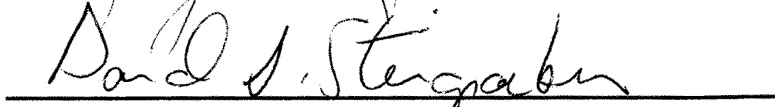
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR
SUPERVISION BY DEBRA GUENTHER ENTITLED CATTLE USE OF PRAIRIE
DOG TOWNS ON THE SHORTGRASS STEPPE OF COLORADO BE ACCEPTED
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ABSTRACT OF THESIS
CATTLE USE OF PRAIRIE DOG TOWNS ON THE
SHORTGRASS STEPPE OF COLORADO

Studies on the mixed-grass prairie have found that native large herbivores preferentially graze on prairie dog towns. I investigated the use of prairie dog towns by cattle (*Bos taurus*) in northeast Colorado by conducting surveys of cattle and vegetation on the Shortgrass Steppe Long Term Ecological Research Site from June-August, 1999. Twelve pastures containing 15 black-tailed prairie dog (*Cynomys ludovicianus*) towns were surveyed three times a week, and the number of cattle on the towns and their behavior were recorded. A subset of three pastures was intensively surveyed twice weekly wherein the habitat and activity of a randomly chosen focal animal was recorded every six minutes for 3.5 hours. Bite and step counts of other individuals were recorded for five-minute intervals. Vegetation height and cover data were collected monthly on each of the six habitat types.

Resource selection functions for driving survey data indicated no significant difference between prairie dog town use and availability. Regression analysis showed no correlation between rain events and prairie dog town use by cattle. The intensively surveyed pastures yielded similar results: i.e., cattle did not significantly prefer or avoid the prairie dog towns. Cattle spent 60% of their time grazing, 13% resting, and 15% traveling when present on prairie dog towns. These percentages were not significantly different from most other habitat types. There were no significant differences in the number of bites per step taken by cattle on towns compared to off town swales, *Atriplex*

canescens terraces, and crested wheatgrass (*Agropyron cristatum*) strips. Five plant species palatable to cattle occurred in relatively high frequencies (36-65%) on prairie dog towns. In general, bare ground, litter, and vegetation cover on prairie dog towns did not significantly differ from most other habitat types. Vegetation on prairie dog towns was however significantly shorter on (mean = 6.7cm) than that off (mean = 11.9cm) prairie dog towns. This research indicates that cattle on the shortgrass steppe use prairie dog towns randomly and do not avoid them despite the shorter vegetation on prairie dog towns. However, cattle do not prefer to graze on prairie dog towns as bison (*Bison bison*) do on the mixed-grass prairie.

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INTRODUCTION

Since the introduction of domestic cattle (*Bos taurus*) to the prairies of the western United States, prairie dogs have been viewed by many as vermin, depleting rangelands of forage and creating holes that cattle and horses step in, breaking their legs. Merriam (1901) estimated that, based on body size, 256 prairie dogs consume the same amount of forage as one cow. Taylor and Loftfield (1924) claimed that Zuni prairie dogs (*Cynomys gunnisoni zuniensis*) can destroy up to 80% of the total potential annual production of forage by their feeding and clipping. They concluded that “The prairie dog has not been shown to have a single beneficial food habit; nor is there any argument.....against its complete eradication on all grazing ranges.” As animosity towards prairie dogs grew, extermination programs were initiated and continue to this day.

There is no mistaking that prairie dog grazing has an effect on vegetation. On the shortgrass steppe, prairie dog activities increase the number of both annual and perennial species and, through selective grazing, exert selective pressure against blue grama (*Bouteloua gracilis*) and in favor of buffalograss (*Buchloe dactyloides*) (Bonham and Lerwick 1976). When prairie dogs colonize an area in mixed-grass prairie, canopy height decreases as taller grass species are removed and shortgrass species become relatively more abundant (Painter et al. 1993). As the colony ages, the older center areas become dominated by forbs and dwarf shrubs, while the more recently colonized edges are dominated by grasses (Whicker and Detling, 1988).

There is also an overlap in diets and preferred species between prairie dogs and cattle. On the Colorado shortgrass steppe of the Central Plains Experimental Range (CPER), Hansen and Gold (1977) reported a 64% annual similarity in diet, with the greatest overlap occurring in the spring (69%). Blue grama and sedges (*Carex* spp.) made up the largest percentage of the diet of both species along with scarlet globemallow (*Sphaeralcea coccinea*) to a lesser extent. In western Oklahoma, O'Meilia et al. (1982) observed less blue grama, sand dropseed (*Sporobolus cryptandrus*), and other grasses palatable to cattle on prairie dog towns than on control pastures, and speculated that there was a high degree of competition between cattle and prairie dogs.

Koford (1958) noted that since the relative value of different plants or plant parts can change with seasons, it might be better to judge competition between prairie dogs and livestock in terms of plant nutrition instead of forage yield. Indeed, some studies have shown that prairie dog grazing activities may actually positively affect large herbivores by influencing forage quality and species composition. Some species of plants, blue grama and buffalograss for example, are palatable to both cattle and prairie dogs and are also tolerant of grazing (Milchunas et al. 1989, Gould and Shaw 1983). On the shortgrass steppe, two species preferred by both cattle and prairie dogs, needleleaf sedge (*Carex eleocharis*) and scarlet globemallow, were shown to be tolerant of grazing by prairie dogs (Bonham and Lerwick 1976). On the mixed-grass prairie of South Dakota, at Wind Cave National Park (WCNP), Coppock et al. (1983a) analyzed nitrogen content in C₃ and C₄ grass species which occurred on the prairie dog towns. The highest crude protein concentrations were found in plants from the longest colonized areas on the town and lowest in plants from the uncolonized areas. Live:dead vegetation ratios and in vitro

digestible dry matter readings were all higher on the towns than off. Even though the prairie dog town had 40% less forage standing crop than surrounding uncolonized areas, bison (*Bison bison*) strongly selected for prairie dog colonies to graze and rest on whenever they were in the vicinity of one. Bison rested mostly on the older forb and dwarf shrub dominated part of the colony (>26 years occupied) and grazed in the younger, grass dominated areas of the colony (2-8 years occupied) (Coppock et al., 1983b).

Another study at WCNP concluded that rather than a competitive relationship, bison and prairie dogs have a mutually beneficial relationship (Krueger 1986). While the two herbivores have similar diets at species and forage class levels, they differed somewhat in plant parts eaten. Bite:step ratios were highest, foraging groups larger, and nearest neighbor distances lowest for pronghorn (*Antilocapra americana*) on forb and dwarf shrub-dominated town centers and for bison on grass-dominated town edges compared to uncolonized areas. Vanderhye (1985) quantified diet quality differences on and off prairie dog towns at WCNP and developed a model to simulate possible reproductive benefits to bison from feeding on prairie dog towns. Her model indicated that both adult and immature bison that selectively feed on towns in the summer could significantly increase body weight, thus increasing their inclusive fitness.

Cattle have replaced bison as the dominant herbivore on most of the Great Plains. While some studies have examined the effects of prairie dog grazing on forage preferable to cattle or diet overlap between the two herbivores (Hansen and Gold 1977, O'Meilia 1982, Uresk 1983, 1984, 1985), few quantitative data have been gathered regarding whether cattle actually prefer to graze on prairie dog towns (Stapp, Lindquist, SGS-

LTER, unpublished data). Also, most of the studies involving prairie dog interactions with large herbivores have been conducted on mixed-grass prairie, which is a very different ecosystem from the shortgrass steppe (Milchunas et al. 1998). However, there is reason to believe that cattle might respond to changes induced by prairie dogs on the shortgrass steppe. A study conducted on the CPER found that cattle were more likely to be found grazing in areas of high relative aboveground standing nitrogen (crude protein) than in areas of high aboveground biomass (Senft et al. 1985). If the plants on prairie dog towns on the shortgrass steppe do have higher concentrations of crude protein than surrounding uncolonized grassland, it is possible that cattle may prefer to graze on the towns.

The objectives of this study were to: (a) estimate the amount of time cattle spend on prairie dog towns compared to other habitats; (b) compare foraging rates of cattle on prairie dog towns with foraging rates on other habitats in the pasture; and (c) track changes in vegetation cover, height, and diversity on and off prairie dog towns over the summer. My null hypotheses were:

- 1) Cattle will use all habitats within a pasture randomly; i.e., in proportion to their availability, measured by the area of the pasture that habitat occupies.
- 2) Foraging rates of cattle do not differ on the prairie dog town compared to other habitat types.

STUDY AREA

This study was conducted at the Shortgrass Steppe Long Term Ecological Research Site (SGS-LTER) which is located in northeastern Colorado and includes the Pawnee National Grassland (PNG) and the CPER. The PNG covers 78,162 ha and the CPER, located on the northwestern side of the PNG, covers 5,926 ha (Hazlett, 1998).

The dominant plant species of this region are blue grama (*Bouteloua gracilis*) and prickly pear cactus (*Opuntia polyacantha*), with blue grama making up 90% of the basal plant cover (Lauenroth and Milchunas, 1991). Annual precipitation is low, ranging from 300-550mm. Seventy percent of the total annual precipitation occurs between May and September in the form of localized thunderstorms (Lauenroth and Milchunas, 1991). Most soils are well drained loams or sandy loams. The topography consists of rolling hills, with a range in elevation from 1,310m to 1,935m (Hazlett, 1988).

There are a few winter pastures; however, cattle are present on the SGS-LTER in the greatest numbers from mid-May until mid-October. Cattle herds in this area are made up of a mix of varieties including Angus, Hereford, Charolais, and Gelbvieh for beef production. Pasture sizes range from 120 to 2,400 ha. The black-tailed prairie dog (*Cynomys ludovicianus*) towns range in size from 1 to 60 ha and occupy 0.1 to 11% of the pastures.

Since there are not many persistent open water sources, most pastures contain a windmill and stock tank to supply cattle with water. On mixed-grass prairie in Montana, Knowles (1986) found cattle more frequently on quarter sections with prairie dog colonies than on quarter sections without. Knowles (1986) suggested that this might be due to cattle overgrazing areas near water tanks, creating suitable habitat for prairie dogs to establish a town. In situations such as these, it may not be clear whether the cattle are using these areas due to the presence of the prairie dog town or the water tank. Therefore I chose prairie dog towns for this study which were not adjacent to or surrounding water tanks. Pastures are grazed at similar “moderate” stocking rates (1.74 ha/cow/month, Bob Peterson, pers. comm.) on both the PNG and the CPER. When possible, the prairie dog

towns chosen were located on undisturbed vegetation rather than land that had been plowed in the past. Most of these prairie dog towns are less than 10 years old because of plague-induced die outs and subsequent prairie dog recolonizations (Mark Ball, pers. comm.).

METHODS

I conducted driving surveys to observe cattle use on a large number of prairie dog towns occupying varying percentages of each pasture (Table 1). A route covering 15 prairie dog towns located on 12 pastures was driven approximately three times a week from 28 May to 15 August, 1999. Because cattle are most active during the half hour before sunrise until mid-morning and from mid-evening until a half hour after sunset (Arnold and Dudzinski 1978), I restricted my cattle surveys to those time periods. Time (morning vs. evening), starting location, and order of visitation of the towns was changed with each survey. The number of cattle on each prairie dog town and their behavior (grazing, resting, or traveling) were recorded. Cattle were considered to be grazing if feeding while moving or standing still. Resting was defined as cattle lying down on the ground, and traveling was considered movement with the head up. Since pastures were often very large, behavior of cattle off of prairie dog towns was not recorded.

Driving survey data were analyzed using resource selection functions (Manly et al. 1993). The ratio of the proportion of the cattle population occupying a habitat (α_i) to the proportion of pasture area the habitat occupies (π_i) gives a selection ratio (\hat{w}_i), where i = habitat type (in this case, on or off prairie dog towns):

$$\hat{w}_i = \alpha_i / \pi_i \quad (\text{Eq. 1})$$

Table 1. Characteristics of pastures and prairie dog towns surveyed during summer 1999, on the Shortgrass Steppe LTER.

allotment	ha	town #	area of town (ha)	% pasture occupied by town	type of cattle	# of cattle	age of town (yrs.)	side of grass- lands
Pawnee National Grasslands								
Roe	1468	79	5.6	0.37	cow/calf	175	6	W
Coal	1535	51	8.7	0.56	cow/calf	144	6	W
Keota	2378	17	14.3	0.60	cow/calf	168	2	E
Simmons	1948	13	5.1	0.26	cow/calf	252	18	E
Fiscus	534	30	3.3	0.60	cow/calf	64	5	E
Box	1536	35	40.5	2.64	cow/calf	144	6	E
Stoneham	1173	5	81.6	8.13 (total)	cow/calf	147	6	E
		8	13.8				6	E
Central Plains Experimental Range								
5W*	130	5	13.9	10.7	steer	20	3	W
29-30*	324	29	7.9	3.2 (total)	yr ling breeder	65	2	W
		30	2.4				3	W
22W*	130	22	4.4	3.3	steer	17	2	W
27-34	332	27	3.0	1.4 (total)	stock heifers	62	3	W
		28NE	1.7				3	W
28N	130	28N	3.5	2.7	steer	14	3	W

*Pastures used for more intensive surveys.

These selection ratios are standardized (B_i) to values between 0 and 1 wherein:

$$B_i = \hat{w}_i / (\sum_{i=1}^1 \hat{w}_i) \quad (\text{Eq. 2})$$

Standardized selection ratios can be interpreted as probabilities, for example, the probability of selecting habitat type i next if all of the habitat types could somehow be made equally available. When only two habitat types are considered, (on and off towns in this case) values above 0.5 indicate preference for a habitat, values of 0.5 indicate random use, and values below 0.5 indicate avoidance of a habitat. Standard errors and Chi-square values can be calculated for the selection ratios to determine significant differences from 0.5. Sign tests (Lehner 1996) were also used to determine significance levels of preference or avoidance using values above 0.5 as positive and values below 0.5 as negative.

Surveyed pastures were divided into east and west groups to evaluate a possible correlation of use of prairie dog towns by cattle and recent rain events. Due to the sporadic rain events on the Shortgrass Steppe LTER, towns on the west side were correlated with data from a weather station near the LTER headquarters, and towns on the east side were correlated with data from a National Climatic Data Center weather station in New Raymer, Colorado. Cattle use of prairie dog towns was compared with precipitation by regressing the average precipitation for the five days previous to the survey against the resource selection function for all pastures (on that side) for that survey day. I also used sign tests to determine significant avoidance or use for each side over the summer.

A subset of three smaller pastures (two of 130 ha, one of 324 ha) from the driving surveys, located on the CPER, were chosen for more intensive surveys conducted from

4 June to 20 August, 1999 (Figure 1). Plant communities on these pastures were divided into six habitat types: prairie dog towns, swales, rocky ridgetops, uplands, crested wheatgrass (*Agropyron cristatum*) strips, and *Atriplex canescens* terraces (Table 2).

During a 3.5 hour feeding bout (morning or evening), a randomly chosen focal animal (Altmann 1974) was observed every six minutes. To minimize disturbance, cattle were observed from a vehicle at a distance of at least 1km, using 7x35 binoculars or a 15 to 60 x zoom spotting scope. Habitat type, behavior (grazing, resting, traveling, or other), and number of conspecifics within a 50m radius were recorded. Frequency of behaviors were analyzed using tests of two percentages (Lehner 1996). In between the focal animal observations, I conducted foraging surveys. The number of bites and steps in a five-minute period was recorded for randomly chosen individuals. Each jaw movement when the head was touching vegetation constituted a bite and each movement of a front leg was considered a step. Comparison of foraging data between habitat types was conducted using an ANOVA and t-tests. The three pastures were mapped in September with a hand-held Global Positioning System (GPS) unit (Trimble Navigation Ltd., Sunnyvale, CA 94086) and areas of each habitat type were determined using PC ARC/INFO 3.5.1 and ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, CA 92373).

Log-ratio compositional analysis (Aebischer et al. 1993) was used to analyze the focal animal survey data. This method examines the proportional habitat use by animals in comparison to habitat availability. Instead of the number of locations, it uses the number of animals as the sample size; therefore, it does not require independence of sequentially collected locations. This method also accounts for the unit-sum constraint, a common problem when using compositional data, wherein habitat proportions are non-

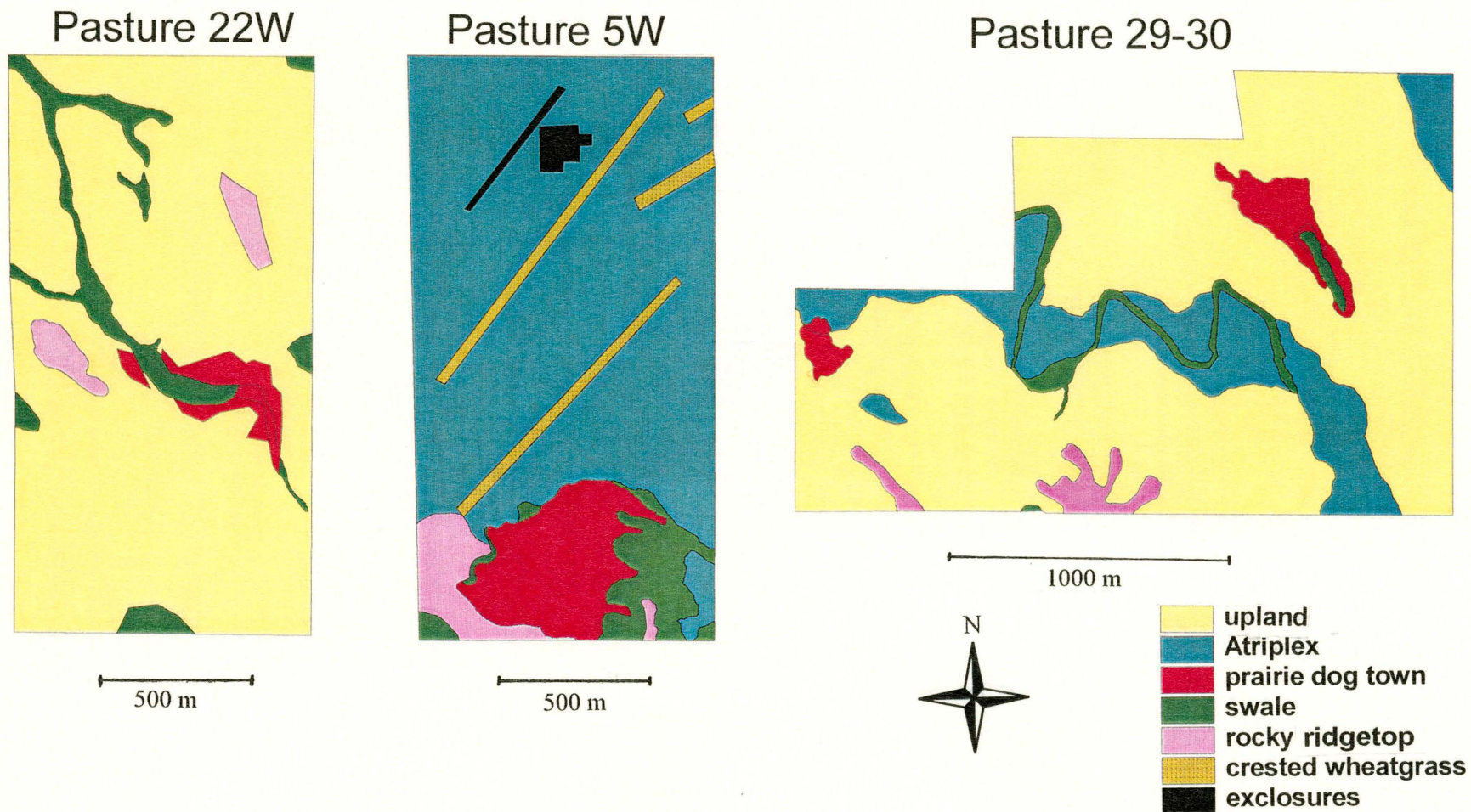


Figure 1. Habitat maps of the three pastures intensively surveyed during summer, 1999, on the Central Plains Experimental Range in northeastern Colorado. Exclosures were not sampled. Note different scale for pasture 29-30.

Table 2. Description of habitat types of the three intensively surveyed pastures on the Central Plains Experimental Range and relative composition of the types within each pasture.

Pasture	Habitat type	Description	Percent of pasture
29-30	upland	Rolling hills usually dominated by <i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i> , <i>Stipa comata</i> and <i>Aristida longiseta</i> . Sandy loam soils.	75.4
	Atriplex	Flat terraces dominated by <i>Atriplex canescens</i> , and <i>Bouteloua gracilis</i> . Usually bordering lowland intermittent ponds/streams. Loam soils.	16.1
	town	Two separate prairie dog towns on this pasture, one surrounding a swale and one on a hillside	3.4
	swale	Lowland areas with intermittent ponds. Dominated by <i>Carex</i> spp., <i>Pascopyrum smithii</i> , and <i>Buchloe dactyloides</i> . Fine sandy loam soils.	3
	rocky	Rocky ridgetops dotted with <i>Yucca glauca</i> and dominated by forbs, considerable bare ground. Sandy loam soils.	2.1
5W	cw	Crested wheatgrass strips (<i>Agropyron cristatum</i>) planted in the 1970's. Some native species encroaching on edges.	4.9
	Atriplex	See above.	73.7
	swale	No intermittent pond in this swale. Otherwise same as above.	6.3
	town	One large growing town on this pasture. Located primarily in the swale.	10.7
	rocky	No yucca in this patch, otherwise same as above.	4.4
22W	swale	See above.	7.9
	rocky	See above.	2.8
	upland	See above.	86
	town	This town occurs on the upland along both sides of the swale and partly in the swale.	3.3

independent and must sum to 1. For example, if an animal avoids one habitat, it must spend time in another, leading to an apparent preference for that habitat type. Finally, compositional analysis accounts for the arbitrary definition of habitat preference by allowing habitats to be ranked according to relative use.

Log-ratio compositional analysis (Aebischer et al. 1993) first tests whether habitat use differs significantly from random simultaneously across all habitats. The three pastures used in this study were analyzed separately due to differing habitat types among them. First, the log-ratios of habitat use (y) are calculated:

$$y = \ln(U_{i,n}/U_{x,n}) \quad (\text{Eq. 3})$$

where $U_{i,n}$ is the proportion of habitat i used by animal n , and $U_{x,n}$ is the proportion of habitat x used by animal n . The choice of habitat denominator depended on which type had no zero use proportions (upland for pastures 22W and 29-30, *Atriplex* for pasture 5W). In the case of zeros in the numerator, the value 0.01 (an order of magnitude lower than the lowest use value) was inserted. Next, y_o is calculated:

$$y_o = \ln(A_{i,n}/A_{x,n}) \quad (\text{Eq. 4})$$

where $A_{i,n}$ is the proportion of habitat i available to animal n , and $A_{x,n}$ is the proportion of habitat x available to animal n . Then the equation:

$$d = y - y_o \quad (\text{Eq. 5})$$

is used to form a residual matrix (R_2) calculated from the raw sums of squares and cross-products of d , and another matrix (R_1) is developed from the mean-corrected sums of squares and cross-products calculated from d . A Chi-square value (X^2) is calculated using the formula:

$$X^2 = -n \ln \Lambda \quad (\text{Eq. 6})$$

where $\Lambda = |R_1| / |R_2|$. Using a Chi-square table, with $k - 1$ degrees of freedom, (k = number of habitat types), the null hypothesis $d = 0$ is tested. If H_0 is rejected, the animals were not using the habitat randomly.

The next step is to rank the habitats in order of use using the formula:

$$d_{ij} = \ln (X_{Uj}/X_{Ui}) - \ln (X_{Aj}/X_{Ai}) \quad (\text{Eq. 7})$$

where X_{Ui} and X_{Uj} are the use proportions for habitats i and j respectively, X_{Ai} and X_{Aj} are the availability proportions for habitats i and j respectively, and d_{ij} is the pairwise difference between habitats i and j . When d_{ij} is positive, it implies that habitat j is used more than expected relative to habitat i . The values of d_{ij} are averaged over n individuals and an antisymmetrical matrix of habitats can be developed of all possible combinations of habitat types. In the resulting “summary” matrix, the number of positive d_{ij} ’s in each row is summed and can be used to rank habitats from first ($k-1$) to last (0) for use. A ratio of the mean d_{ij} to standard error gives a t -value allowing determination of significant differences between habitats after the ranking has been completed. The data for the three pastures were divided into two periods (Period I = May 28 to July 9, Period II = July 12 to August 15) and analyzed for changes in seasonal use and as well as combined to examine habitat use over the entire season.

Vegetation data were collected in June, July, and August on the subset of three pastures. Twenty 0.1 m^2 Daubenmire frames (Daubenmire 1959) were placed randomly in each habitat type to determine plant species composition, canopy cover, and average height of the vegetation. Vegetation heights, and canopy cover were analyzed using an ANOVA and Tukey’s HSD procedure. Diversity was plotted using species-area curves.

RESULTS

Driving Surveys

Thirty-one driving surveys were conducted from the end of May through August. Standardized resource selection ratios for each survey day across the season for all pastures displayed no clear trend in the use of prairie dog towns by cattle (Figure 2). No significant difference was found between prairie dog town habitat use and availability using a sign test; however, a Chi-square test (Appendix A) indicated a slight preference ($B_i = 0.527$) for the use of prairie dog towns by cattle over the entire sampling period.

Standardized resource selection ratios were also calculated for each pasture over the entire season (Table 3). Some prairie dog towns were used by cattle almost four times more than expected (eg. pastures 29-30 and 28N) while others were almost completely or totally avoided (eg. pastures 5W and Keota). The proportion of a pasture that a prairie dog town occupied did not seem to affect selection or avoidance by cattle. Dividing the driving survey data for pastures into two time periods (early summer and late summer) (Table 4) did not affect the selection index patterns for most individual pastures. When all pastures were combined for each period, no significant differences were revealed by sign tests between prairie dog town use and avoidance; however, a significant selection ($B_i = 0.587$) for prairie dog towns was seen in the first period, and a slight but significant avoidance ($B_i = 0.471$) in the second period was seen using Chi-square analysis (Appendix B). When survey data were divided into morning and evening surveys for all pastures over the season, Chi-square values using resource selection ratios showed cattle to significantly avoid prairie dog towns in the morning ($B_i = 0.419$) and significantly select prairie dog towns to graze on in the evening ($B_i = 0.595$).

Figure 2. Standardized resource selection ratios (B_i) for cattle occurring on prairie dog towns from driving survey data ($n=31$) for all pastures from May 28 to August 15, 1999. Values above 0.5 represent selection for prairie dog towns, values below 0.5 represent avoidance of prairie dog towns, and 0.5 represents random use of prairie dog towns.

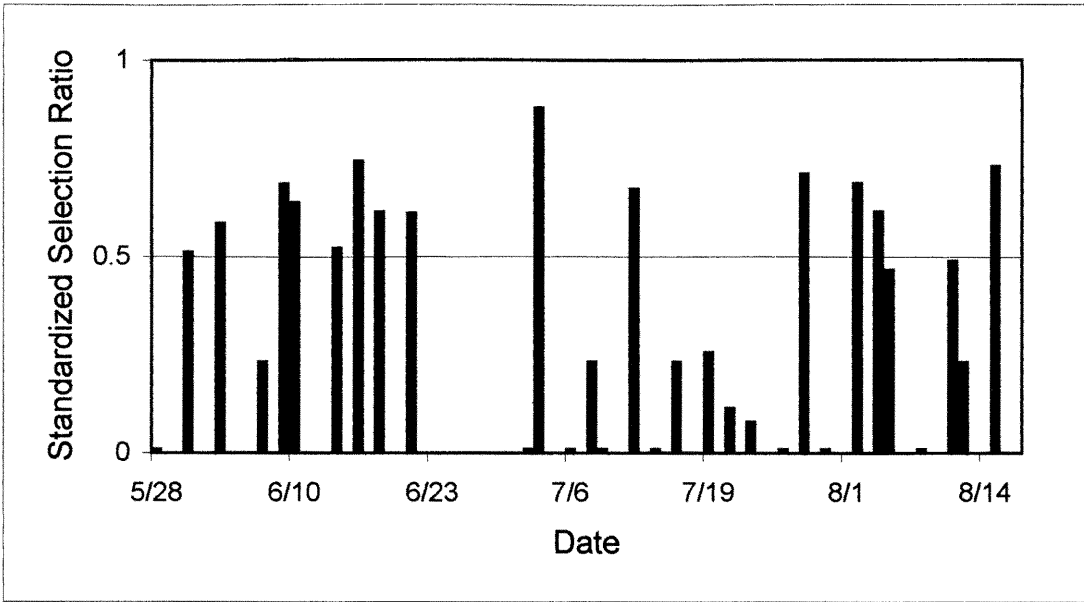


Table 3. Standardized resource selection ratios (B_i) from driving survey ($n=31$) data for cattle use of prairie dog towns for each pasture and averaged across all pastures. Pastures are ordered according to the proportion of pasture the town occupies from highest to lowest.

Pasture		availability	use	B_i
5W		0.107	0.037	0.243
Stoneham		0.081	0.039	0.315
29-30		0.034	0.116	0.788
22W		0.033	0.021	0.384
28N		0.027	0.104	0.807
Box		0.026	0.014	0.338
27-34		0.014	0.053	0.795
Fiscus		0.006	0.016	0.731
Keota		0.006	0.000	0.000
Coal		0.006	0.013	0.693
Roe		0.004	0.004	0.486
Simmons		0.003	0.004	0.597
29-30 town	town 29	0.767	0.438	0.191
comparison ¹	town 30	0.233	0.462	0.809
A.M. surveys		0.018	0.013	0.419
P.M. surveys		0.018	0.026	0.597
All pastures		0.018	0.020	0.527

¹ This analysis compared the use of the lowland town (29) to the use of the smaller upland town (30) taking into account the areas of only those two towns.

Table 4. Standardized resource selection ratios (B_i) from driving survey data divided into two seasonal periods (I = May 28 to July 9, 1999; II = July 12 to August 15, 1999) for cattle use of prairie dog towns for each pasture and averaged across all pastures.

Pasture	Period	availability	use	B_i
5W	I	0.107	0.020	0.145
	II	0.107	0.053	0.319
Stoneham	I	0.0813	0.069	0.455
	II	0.0813	0.011	0.112
29-30	I	0.034	0.114	0.785
	II	0.034	0.117	0.791
22W	I	0.033	0.000	0.000
	II	0.033	0.040	0.553
28N	I	0.027	0.081	0.761
	II	0.027	0.125	0.838
Box	I	0.0264	0.028	0.517
	II	0.0264	0.000	0.000
27-34	I	0.0141	0.029	0.676
	II	0.0141	0.065	0.832
Fiscus	I	0.006	0.026	0.816
	II	0.006	0.039	0.871
Keota	I	0.006	0.000	0.000
	II	0.006	0.000	0.000
Coal	I	0.0056	0.026	0.825
	II	0.0056	0.000	0.000
Roe	I	0.0037	0.000	0.000
	II	0.0037	0.007	0.648
Simmons	I	0.0026	0.008	0.754
	II	0.0026	0.000	0.000
29-30 comparison ¹	29-I	0.767	0.297	0.114
	30-I	0.233	0.703	0.886
	29-II	0.767	0.565	0.283
	30-II	0.233	0.434	0.716
All pastures	I	0.018	0.025	0.587
	II	0.018	0.016	0.471

¹ This analysis compared the use of the lowland town (29) to the use of the smaller upland town (30) taking into account the areas of only those two towns.

Pasture 29-30 was unusual in that it contained two prairie dog towns, one large (7.9 ha) town surrounding a swale which often had standing water, and one smaller (2.4 ha) upland town not near a water source. Cattle used the smaller upland prairie dog town four times more ($B_i = 0.809$) than the lowland town ($B_i = 0.191$), and this difference was significant using Chi-square analysis.

A regression on precipitation events and cattle use of prairie dog towns did not reveal a correlation on either the east side ($p = 0.977$) (Figure 3) or the west side ($p = 0.390$) (Figure 4) of the survey route (Appendix C). A sign test for the east side resource selection data showed cattle to be significantly avoiding the prairie dog towns, while on the west side, use of prairie dog towns did not differ from random. Of 789 cattle observed on prairie dog towns over the season, 91.4% were grazing, 5.7% were resting, and 2.9% were standing still.

Focal Animal Surveys

Sixteen focal animal surveys were conducted on each of the three pastures over the season. During the 3.5 hour time period, cattle traveled an average of 1.5 km, 2.2 km, and 2.1 km on pastures 22W, 5W, and 29-30 respectively. Cattle were observed in an average of 2.6 habitats/survey on pasture 22W ($n = 4$ habitats), 3.0 habitats/survey on pasture 5W ($n = 5$ habitats), and 3.4 habitats/survey on pasture 29-30 ($n = 5$ habitats). Focal animals appeared to be representative of a substantial portion of the herd. The focal animal was within a 50 m radius of 50% of the herd 56.6, 74.0, and 30.4% of the time for pastures 22W, 5W, and 29-30 respectively. On pasture 29-30, the focal animal was within 50m of 30% of the herd 64.6% of the time.

Figure 3. Standardized resource selection ratios (B_i) from driving survey data and precipitation data for the east side of the Pawnee National Grasslands from May 28 to August 15, 1999. Values above 0.5 represent selection for prairie dog towns, values below 0.5 represent avoidance of prairie dog towns, and 0.5 represents random use of prairie dog towns.

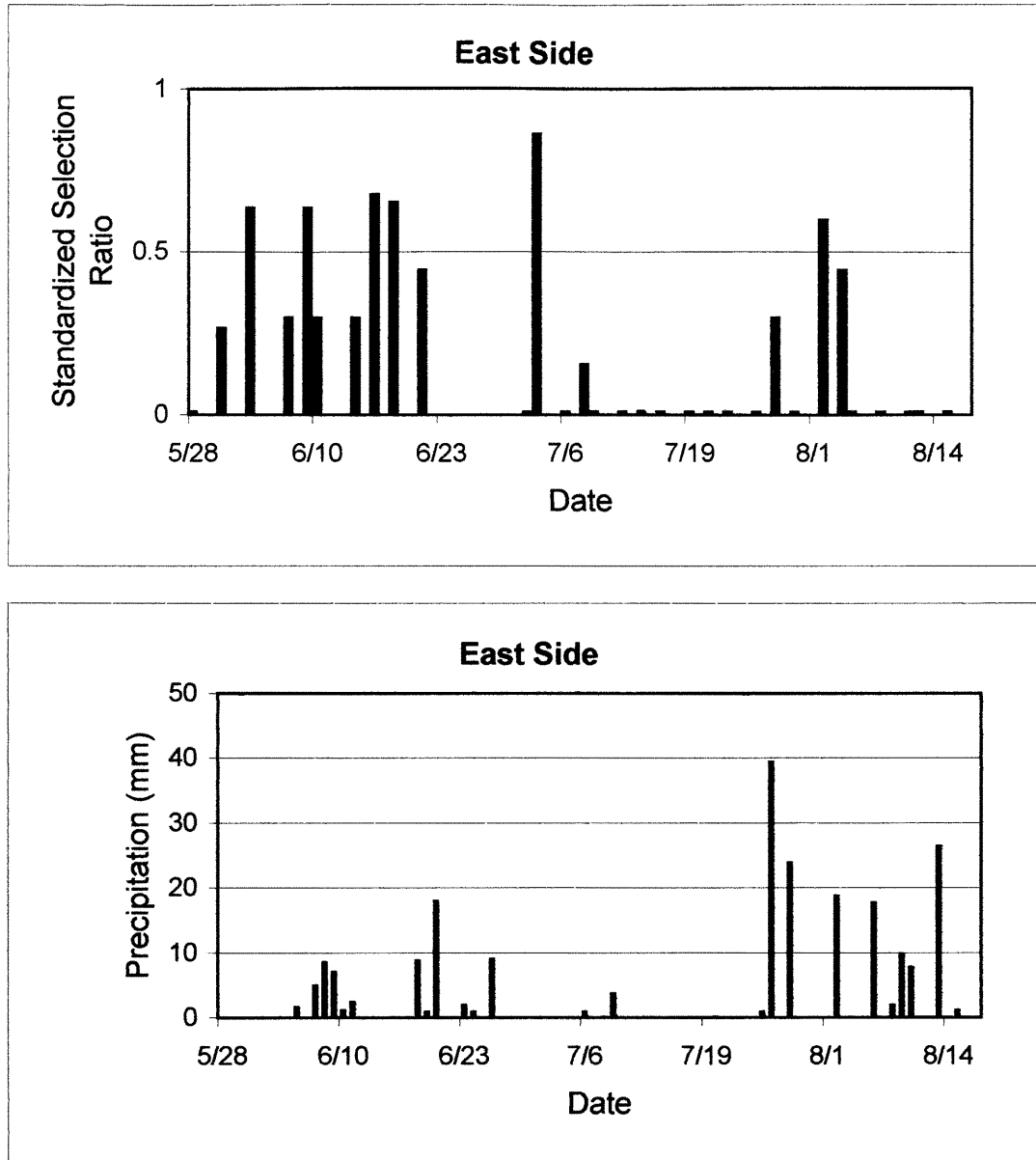
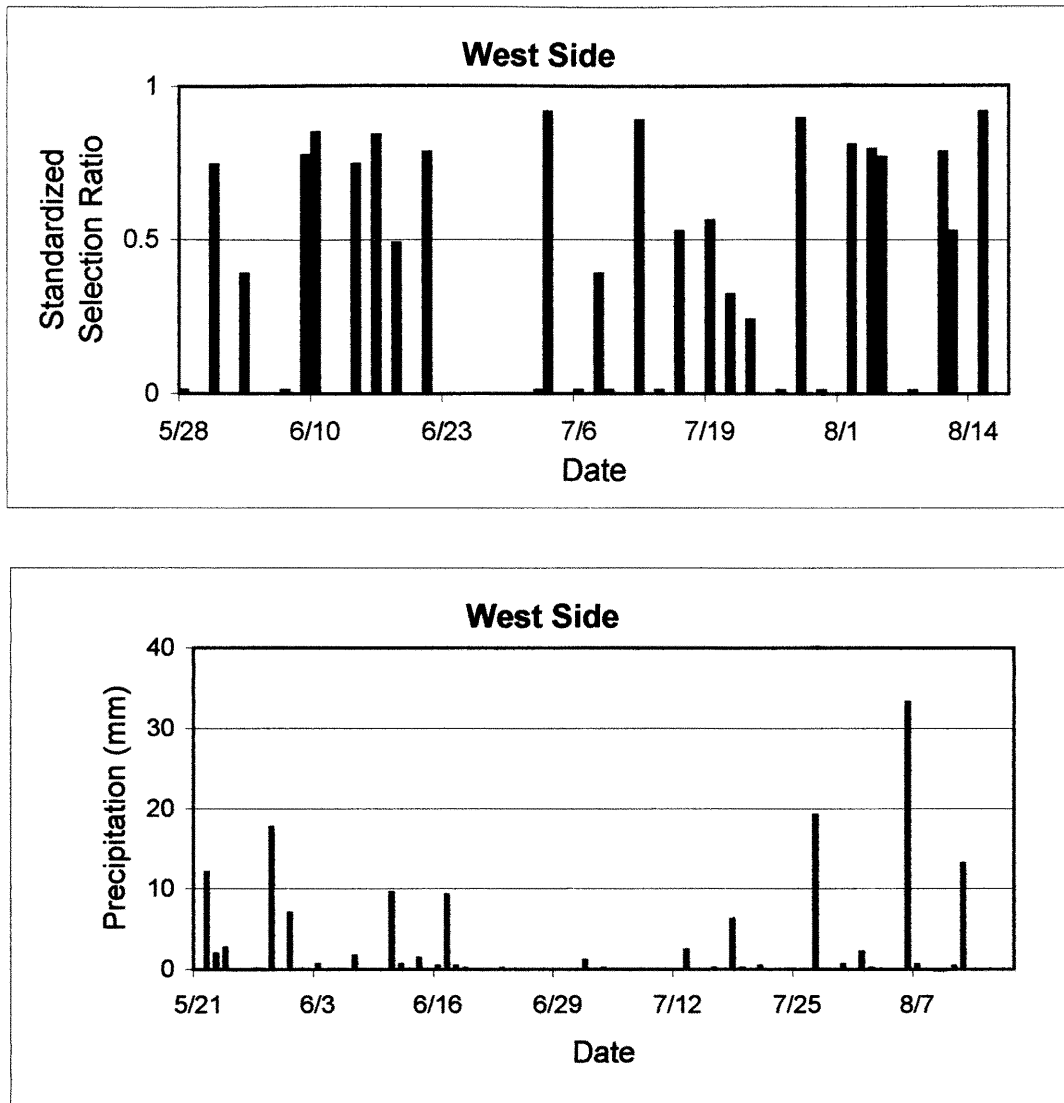


Figure 4. Standardized resource selection ratios (B_i) from driving survey data and precipitation data for the west side of the Pawnee National Grasslands from May 28 to August 15, 1999. Values above 0.5 represent selection for prairie dog towns, values below 0.5 represent avoidance of prairie dog towns, and 0.5 represents random use of prairie dog towns.



Cattle were not using habitat types randomly on any of the three intensively surveyed pastures based on log-ratio compositional analysis (Table 5). For all pastures, the swale was among the most preferred habitats and rocky ridgetops among the most avoided. The prairie dog town was consistently ranked last on pasture 22W for both Periods I, II, and I and II combined, but was not used significantly different from the rocky ridgetops. On pasture 5W, cattle used habitats almost in the direct order of availability, with the exception of the swale being ranked higher than the town. Again, there were no significant seasonal differences, with the town consistently ranked in the middle. Pasture 29-30 revealed the only significant seasonal difference regarding the prairie dog towns. The town was ranked last in Period I (early summer) and first in Period II (late summer), whereas the swale switched from the first rank in Period I to second to last in Period II. Combined data over the season for pasture 29-30 ranked the town as second to last.

In comparison to the log-ratio compositional analysis, somewhat different results for the focal animal data were obtained when selection was estimated simply by calculating the difference in proportional use to proportional availability (Figure 5). Analysis of habitat type for each pasture over the entire season show that upland areas on pastures 22W and 29-30 were significantly avoided whereas log-ratio analysis ranked these habitats among the most preferred (Appendix D). Behavior observations ($n = 1,720$) of the focal animals (Figure 6) indicated that cattle spent the majority of their time grazing during the 3.5 hour observation period. While on the prairie dog towns, cattle spent 60% of their time grazing, 13% resting, 15% traveling, and 12% doing other activities such as interacting with other cattle or drinking

Table 5. Results of the log-ratio compositional analysis for the three intensively surveyed pastures including the Chi-square test for random use and habitat rankings with significant differences at $p < 0.05$.

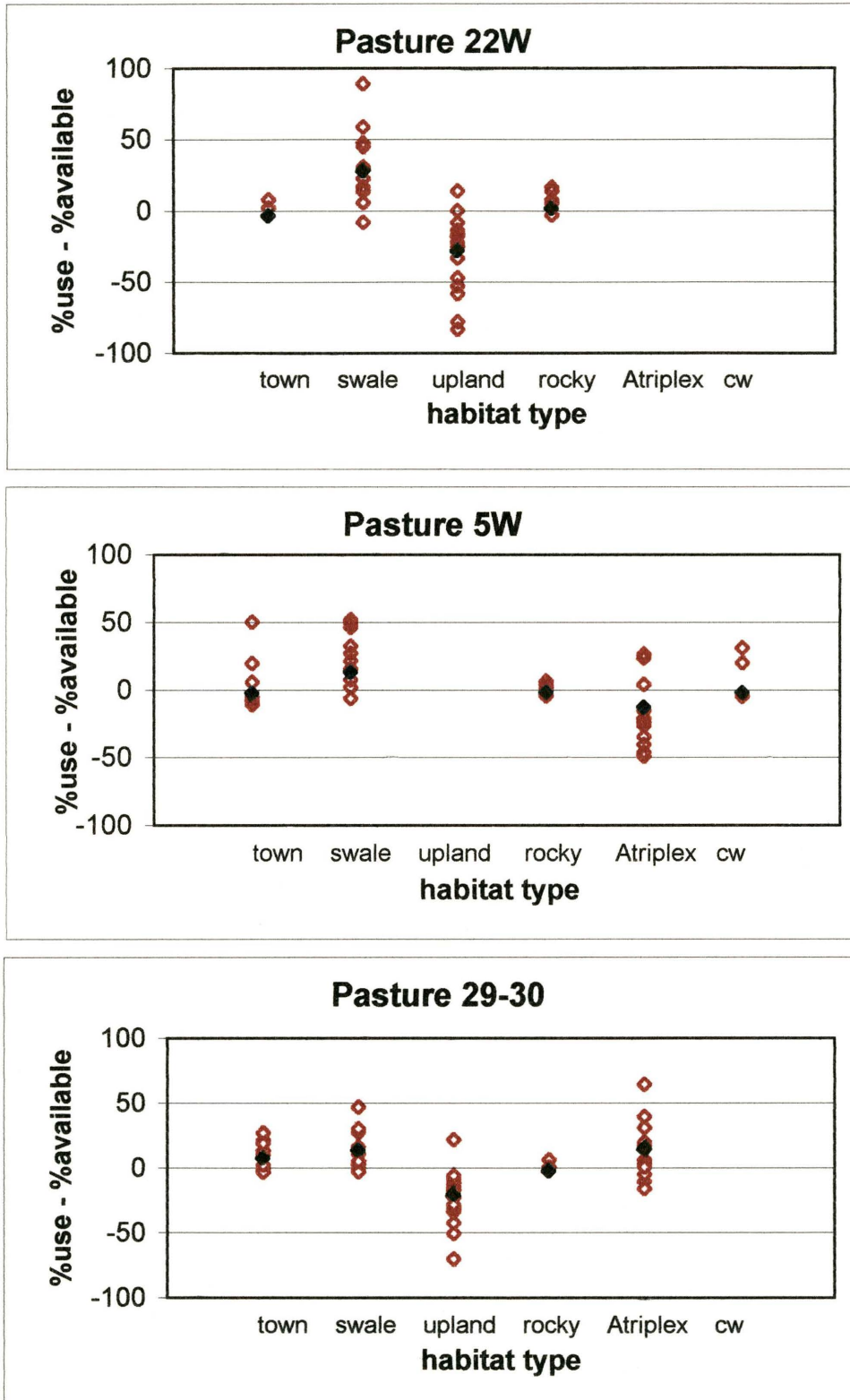
Chi-square				habitat rankings according to availability ¹	habitat rankings according to use
pasture	value	p-value	df		
22W				upland > swale > town > rocky	<div>swale > upland > rocky > town</div> <div>swale > upland > rocky > town</div> <div>swale > upland > rocky > town</div>
Period I ²	16.36	p<0.001	3		
Period II ³	18.33	p<0.001	3		
Combined	25.72	p<0.001	3		
5W				Atriplex > town > swale > cw > rocky	<div>swale > Atriplex > town > cw > rocky</div> <div>Atriplex > swale > town > cw > rocky</div> <div>Atriplex > swale > town > cw > rocky</div>
Period I	9.75	p<0.05	4		
Period II	22.09	p<0.001	4		
Combined	26.64	p<0.001	4		
29-30				upland > Atriplex > town > swale > rocky	<div>swale > upland > Atriplex > rocky > town</div> <div>town > Atriplex > upland > swale > rocky</div> <div>Atriplex > upland > swale > town > rocky</div>
Period I	18.88	p<0.001	4		
Period II	57.58	p<0.001	4		
Combined	23.22	p<0.001	4		

¹ "cw" represents crested wheatgrass (*Agropyron cristatum*) habitat

² Period I refers to surveys conducted from June 3 to July 8, 1999.

³ Period II refers to surveys conducted from July 13 to August 21, 1999.

Figure 5. Selection variability for sixteen individual animals for each pasture and each habitat type over the entire growing season ("cw" refers to the crested wheatgrass (*Agropyron cristatum*) habitat). Mean values are represented by the black diamonds.



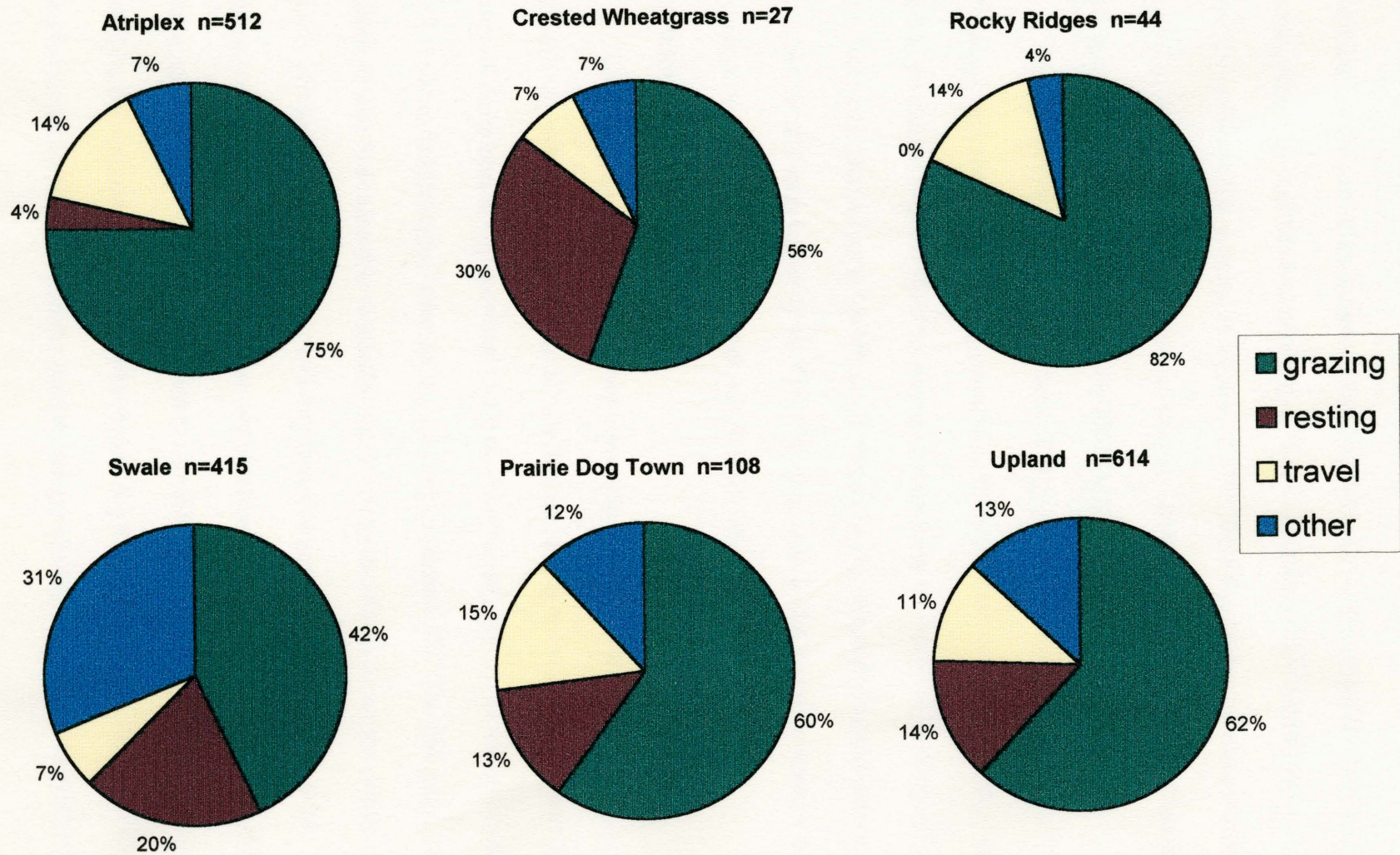


Figure 6. The proportion of behaviors of focal animals averaged over all three intensively surveyed pastures on the CPER, summer, 1999.

water. Behavior of cattle on prairie dog towns did not usually significantly differ from their behavior in most other habitat types (Appendix E). Cattle spent an equal proportion of time grazing on uplands and prairie dog towns but spent a significantly lower proportion of their time grazing in swales. Proportional time spent traveling across prairie dog towns was similar to that in *Atriplex*, rocky ridgetops, and upland habitats and cattle spent equal time resting on prairie dog towns, swales, and uplands.

Foraging observations of numbers of bites per step (Table 6) revealed few differences between cattle foraging on prairie dog towns (mean = 6.3 bites/step) and other habitats with the exception of rocky and upland habitats in which they had significantly fewer bites per step (4.7, and 4.8 bites/step respectively). Averaged across habitat types, cattle had significantly higher ($p < 0.0001$) foraging rates in the morning (mean = 6.9 bites/step) than in the evening (mean = 5.36 bites/step).

Vegetation Characterization

I compared vegetation cover and frequency measurements for five plant species palatable to cattle and two nonpalatable species, as well as cover of bare ground and litter across all three intensively surveyed pastures. Significant differences for cover ($\alpha = 0.05$) between habitat types were determined (Appendices F,G). The five palatable plant species (Table 7) occurred in relatively high frequencies (36-65%) on the prairie dog towns. Of the palatable plants, prairie dog towns in general had higher cover of *Pascopyrum smithii*, but this was often not significantly different from that in other habitat types. Prairie dog towns contained significantly less *Bouteloua gracilis* cover than *Atriplex* and upland habitats. The prairie dog towns and swales had significantly more cover of *Buchloe dactyloides* than the other habitats, occurring with 54-61%

Table 6. Least squares means of number of bites per step of foraging cattle by habitat type and significant differences between types at $\alpha = 0.05$.

habitat	# obs.	lsmean	std error	significant differences
swale	118	7	0.941	A
town	91	6.3	0.953	A
Atriplex	211	6.4	0.895	A
crested wheat	20	7.1	1.362	A
rocky	24	4.7	1.284	B
upland	200	4.8	0.895	B

Table 7. Average cover (%) and frequency (percent of total Daubenmire frames occupied) for five plant species palatable to cattle on each habitat type for June, July, and August of 1999, averaged across the three intensively surveyed pastures on the CPER.

		<u><i>Pascopyrum smithii</i></u>		<u><i>Bouteloua gracilis</i></u>		<u><i>Buchloe dactyloides</i></u>		<u><i>Carex eleocharis</i></u>		<u><i>Spharalcea coccinea</i></u>	
		%cover	frequency	%cover	frequency	%cover	frequency	%cover	frequency	%cover	frequency
June	Atriplex	4.81	35	35.81	87.5	3.75	17.5	2.63	30	5.06	52.5
	cw ¹	2.00	30	0.00	0	0.00	0	0.25	10	6.00	65
	rocky	1.25	25	12.67	76.7	8.79	46.7	1.75	28.3	2.00	38.3
	swale	8.42	83	8.46	33.3	20.83	66.7	4.21	55	1.41	23.3
	town	4.75	50	14.19	56.2	20.41	53.8	2.66	38	4.93	50
	upland	1.06	17.5	23.31	85	5.88	40	4.94	50	3.13	62.5
July	Atriplex	3.75	50	32.25	90	1.13	10	5.31	32.5	3.80	50
	cw	0.38	15	0.00	0	0.12	5	0.12	5	3.50	65
	rocky	1.83	31.7	8.67	63.3	10.67	58.3	3.08	41.7	2.00	46.7
	swale	6.41	75	3.08	20	27.8	70	4.42	53.3	0.88	18.3
	town	4.13	43.8	13.47	52.5	18.34	61.3	3.25	48.8	3.60	51.3
	upland	1.40	32.5	15.19	77.5	5.63	32.5	5.56	50	3.60	55
August	Atriplex	2.63	42.5	38.88	95	2.94	10	2.06	32.5	2.13	47.5
	cw	0.25	10	0.75	5	3.12	5	0.00	0	1.63	65
	rocky	1.54	28.3	12.54	83.3	7.75	31.67	2.33	43.3	1.50	43.3
	swale	9.00	78.3	5.67	35	25.00	58.3	3.16	51.7	0.50	11.7
	town	3.00	38.8	12.93	52.5	20.53	65	3.10	48.8	1.53	36.3
	upland	2.25	27.5	20.13	92.5	3.38	27.5	3.50	52.5	2.13	60

¹"cw" represents crested wheatgrass (*Agropyron cristatum*) habitat

frequency on prairie dog towns. Cover of *Carex eleocharis* and *Spharalcea coccinea* was low across all habitat types, but they both occurred in relatively high frequencies on the towns (38-49% and 36-50% respectively). Of the two prairie dog towns on pasture 29-30, the upland town (30) had significantly higher cover of *Bouteloua gracilis*, and the lowland town (29) had significantly higher cover of *Buchloe dactyloides* (Appendix H).

Of the non-palatable plants (Table 8), *Aristida longiseta* had a low frequency of occurrence (8-16%) on the prairie dog towns, and this was lower than on either the rocky ridgetops or upland habitats. *Vulpia octoflora* had low (0-2%) cover across habitats and few significant differences between habitats. However, *Vulpia octoflora* did have a high frequency (45%) on prairie dog towns. Of the two prairie dog towns on pasture 29-30, the lowland town (29) had significantly higher cover of *Aristida longiseta* (Appendix H). Crested wheatgrass and rocky ridgetops had significantly higher percentages of bare ground cover than all other habitat types including the prairie dog towns (Table 8). In general, bare ground, litter, and vegetation cover on prairie dog towns were not usually significantly different from most other habitats.

Vegetation heights were compared among habitat types and averaged over all three pastures in July and August (Figure 7). In both months, the vegetation on prairie dog towns (mean = 6.7cm) was significantly shorter than that in all other habitat types (mean = 11.9cm). Species-area curves (Figure 8) for each habitat type over the season indicate that prairie dog towns are not the most species rich habitats; however, there were eight species of plants which were unique only to the prairie dog towns. The swale had the most unique species (27) and the remaining habitat types had between three and ten unique species each (Appendix I).

Table 8. Average cover (%) and frequency (percent of total Daubenmire frames occupied) by plant species not palatable to cattle and mean cover (%) for bare ground and litter for each habitat type for June, July, and August, 1999, averaged across all three intensively surveyed pastures on the CPER.

		<u><i>Aristida longiseta</i></u>		<u><i>Vulpia octoflora</i>¹</u>		<u>Bare ground</u>	<u>Litter</u>
		%cover	frequency	%cover	frequency	%cover	% cover
June	Atriplex	0.00	0	1.12	20	28.20	35.60
	cw ²	0.00	0	0.00	0	73.80	6.25
	rocky	5.90	41	0.29	11.7	52.04	16.00
	swale	0.00	0	1.25	25	29.63	19.92
	town	0.34	7.5	1.28	45	29.62	28.06
	upland	5.70	35	2.00	55	29.38	27.19
July	Atriplex	0.00	0			30.12	30.40
	cw	0.00	0			66.50	7.40
	rocky	6.29	36.7			51.00	15.71
	swale	0.54	5			35.42	20.88
	town	0.88	16.3			39.22	19.90
	upland	6.81	45			35.69	26.80
August	Atriplex	0.62	2.5			36.00	22.94
	cw	0.00	0			72.07	6.25
	rocky	5.83	41.7			51.04	12.25
	swale	0.00	0			34.80	19.67
	town	2.34	16.3			37.10	17.94
	upland	8.12	55			32.80	21.63

¹ *Vulpia octoflora* only recorded in June.

² "cw" represents crested wheatgrass (*Agropyron cristatum*) habitat

Figure 7. Mean height (cm) of vegetation for all habitat types for July and August ("cw" represents the crested wheatgrass (*Agropyron cristatum*) habitat type). Columns headed by the same letter were not significantly different at $p < 0.05$.

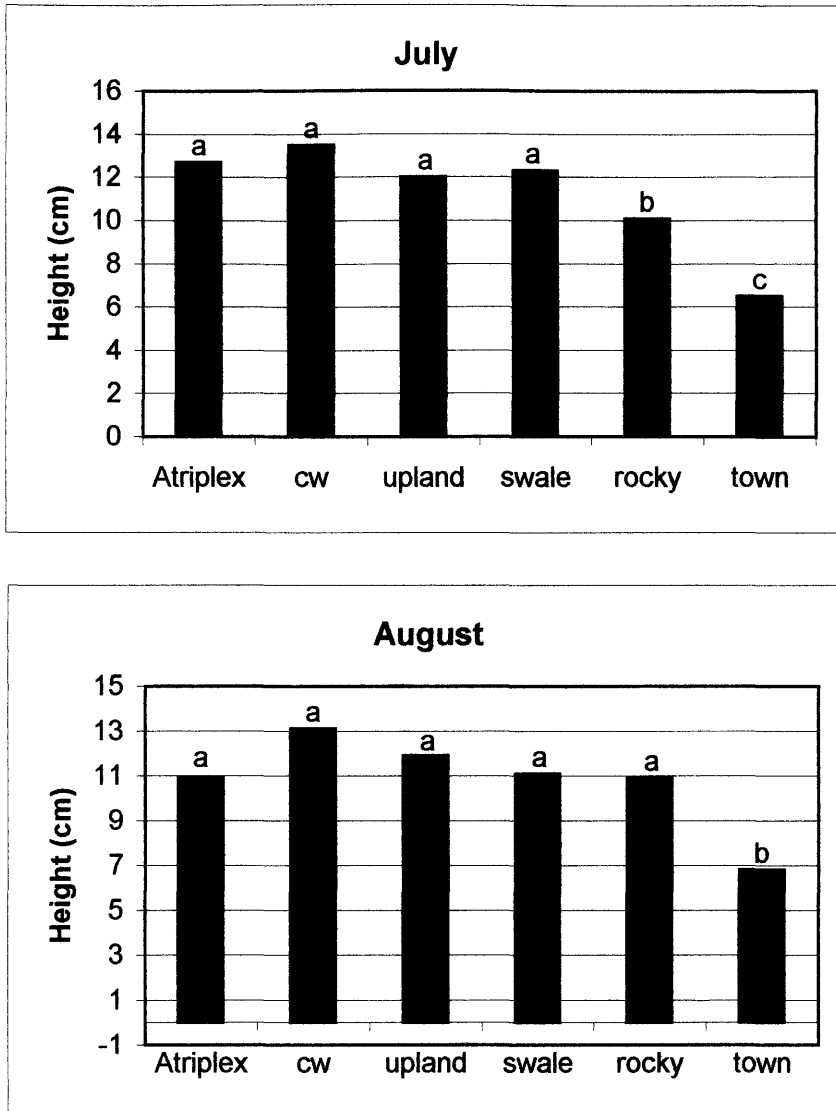
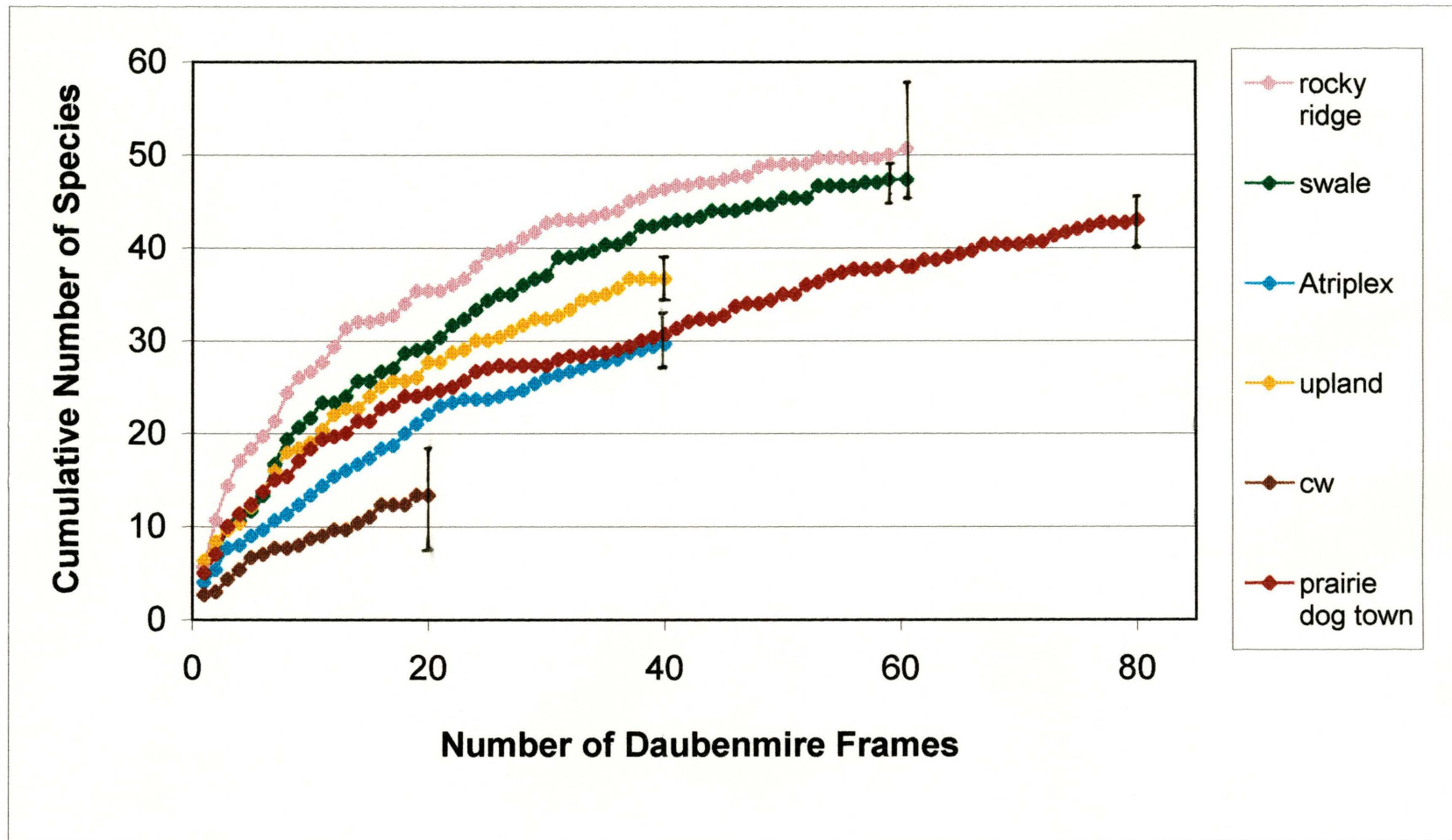


Figure 8. Species-area curves for each habitat type on the intensively surveyed pastures on the CPER, averaged over June, July, and August, 1999 ("cw" represents the crested wheatgrass [*Agropyron cristatum*] habitat). The bars indicate the maximum and minimum values for the season.



DISCUSSION

Based on summarized results from the driving surveys, despite a slight selection indicated by the Chi-square result, it appears that overall cattle use of prairie dog towns is random on the shortgrass steppe of Colorado (Table 9). However, some prairie dog towns were selected for as much as four times more than expected while others were almost completely ignored. One reason for this variability may be the wide range of pasture sizes which can affect cattle grazing behavior (Hart et al. 1993). Roath and Krueger (1982) observed home range behavior of cattle in pastures greater than 1000 ha. Several pastures used in the driving surveys were at least this large, sometimes with towns that made up a small proportion of the pasture area (<1%). In the case of Keota, where no cattle were seen on the prairie dog town over the entire season, it was possible that their home range may not have included the town. However, the proportion of the area of a pasture that a town made up did not appear to be a good predictor of cattle avoidance or preference for towns. Another reason for variability could be that some towns may have been closer or farther away from mesic plant communities or water sources which are strong predictors of cattle distribution (Senft et al. 1985).

Cattle have spatial memory and can remember quantity and quality of forage patches as well as their location (Bailey et al. 1989, Rittenhouse 1991). Cattle will remember a low quality patch and will avoid it for up to 21 days (Bailey 1995). Therefore, movements of cattle are not independent from day to day, and if vegetation on prairie dog towns is remembered as low quality, cattle may not return to the prairie dog town until their memory decays or there are changes in the vegetation. Despite the variability in individual towns, and although the Chi-square tests indicated a slight

Table 9. Summary of results from driving surveys indicating cattle use of prairie dog towns, summer, 1999, on the Shortgrass Steppe LTER.

Analysis	Sign test result	Chi-square result
entire season, all pastures combined	random use	slight selection
individual pastures	N/A	some selected, some avoided
split - early summer	random use	slight selection
split - late summer	random use	slight avoidance
split - morning	random use	avoidance
split - evening	random use	selection
lowland town 29	N/A	avoiding
upland town 30	N/A	selection
east side	avoidance	N/A
west side	random use	N/A

selection in the early summer, slight avoidance during the late summer, and slight selection over the entire summer, cattle did not have a strong preference for prairie dog towns as bison do on the mixed-grass prairie (Krueger 1986, Coppock 1983b).

During the driving surveys, cattle were observed more often on prairie dog towns in the evening than in the morning. Studies (Arnold and Dudzinski 1978) indicate that cattle diets contain higher nitrogen concentrations in the evening. It is believed that in the morning, cattle are hungrier and eat quickly, consuming more grass than later in the evening when cattle tend to selectively graze for higher nitrogen containing forbs. The foraging data from this study did indeed show higher foraging rates in the morning than in the evening. Cattle may be selecting prairie dog towns to graze on in the evening because compared to off town areas of the pasture, plants on prairie dog towns would have higher leaf to stem ratios and lower leaf age, consequently containing higher concentrations of nitrogen than plants off of prairie dog towns (Detling 1987).

Based on an examination of the data, I had hypothesized that precipitation might be a factor limiting an increase in new tissue growth or a nitrogen response in plants on prairie dog towns on the shortgrass steppe, and that rain events might cause an increase in the use of prairie dog towns by cattle. However, driving survey data revealed no correlation between rain events and cattle use on either the west or east side of the grasslands. Cattle significantly avoided prairie dog towns on the east side of the survey route despite receiving 247mm of rain over the season compared to the west side total of 152mm. However, most prairie dog town use on the east side occurred early in the season, whereas most of the precipitation was received later in the summer. Cattle on the west side of the survey route showed no significant difference between town use and

availability. The precipitation on the west side of the grasslands appears to have been more evenly distributed. Milchunas et al. (1995) found that due to dilution effects from plant growth, water supplements added to grazed plants on the shortgrass steppe actually caused decreases in nitrogen concentrations and digestibilities. Therefore, additional moisture may not significantly enhance nitrogen concentrations compared to usual levels.

Comparison of the two prairie dog towns on pasture 29-30 yielded surprising results. The smaller upland town was used four times more than the larger lowland town. The upland town did have significantly higher cover of the palatable grass *Bouteloua gracilis*, and the lowland town had significantly higher cover of the non-palatable *Aristida longiseta*. However, it may be more likely that this selection for the upland town can be explained by its proximity to a fence and corner which cattle are often attracted to when grazing (Dean 1974, Senft et al. 1983).

On the more intensively surveyed pastures, focal animals represented herd movements well. Preference rankings derived from log-ratio compositional analysis indicated that over the season, swales and *Atriplex* habitats were usually ranked highest in use and rocky ridgetops were often ranked lowest. In general, prairie dog towns were ranked near the middle or end but significance tests did not indicate differences between the prairie dog towns and anywhere from one to four other habitat types. An interesting seasonal difference occurred on pasture 29-30. Swales were ranked first at the beginning of the summer and shifted to second to last at the end of the summer, whereas the prairie dog town changed from being ranked last to first over the season. This is consistent with Senft's (1983) findings that swales are preferred during the growing season. Senft et al. (1985) also contend that cattle prefer to graze on areas with high standing crops of

nitrogen. It is possible that after the nitrogen resource was depleted in the swale, the next best choice for nitrogen concentration levels was on the prairie dog towns where cattle began grazing more frequently.

Focal animal survey data were analyzed in two different ways. I estimated cattle use of prairie dog towns by calculating the difference in proportion of use to proportion of availability, and the results indicated significant avoidance of upland habitats on pastures 22W and 29-30. In contrast, log-ratio compositional analysis resulted in high rankings for the upland habitats on those pastures. This example illustrates why it is important to use log-ratio analysis for compositional data. The upland habitats are by far the largest habitat components of those pastures. Since availability measurements are based on areas, a difference in use calculated, for example, by subtracting 40% observed use from 80% expected use (i.e., available area) will appear to be considerably larger than for a smaller habitat type with 8% expected use minus 4% observed use even though the relative difference in availability and use is the same for either example. The prairie dog towns used in this study made up relatively small proportions of the pastures, so results from either method may have sufficed for that one habitat type of interest. However, if the prairie dog towns had occupied a much larger percentage of the pasture, the results may have been skewed.

Log-ratios normalize the data to prevent this problem from occurring. All habitat types are considered simultaneously and a common habitat type is used in the denominator for the log ratios to allow the habitat types to be considered independent, thus accounting for the unit-sum constraint (Aebischer et al. 1993). For these reasons,

the log-ratio compositional analysis technique is preferable for analyzing habitat use and availability data when information on individual animals is available.

Cattle behavior data revealed few significant differences on and off prairie dog towns. Cattle spent a significantly higher proportion of their time grazing on prairie dog towns and uplands than on swales. This may be due to the high proportion of “other” activities on swales such as drinking water, interacting with other cattle, or standing still. Cattle spent equal proportions of time resting on towns, swales, and uplands. Proportion of time spent traveling across prairie dog towns was equal to that in all other habitat types except swales and crested wheatgrass strips.

Foraging rates (i.e. bite/step ratios) on prairie dog towns were also not significantly different from most other habitats with the exception of rocky ridgetops and uplands which had lower numbers of bites per step. Bison on mixed-grass prairie were found to have significantly higher bite/step ratios on prairie dog towns compared to uncolonized areas in all months of the year except for November (Krueger 1986). An experimental study using cattle on the shortgrass steppe found that forage velocities (rates of walking in steps/minute) only changed if the differences in forage quantity were great (Bailey 1988, Bailey et al. 1996). It may well be that the differences in magnitude of forage quantity or quality on and off prairie dog towns on the shortgrass steppe are not sufficiently large for cattle to change their foraging rates.

Vegetation characterization of the pastures in this study demonstrates that plant species palatable to cattle (Vavra et al. 1977) appear to be quite common on prairie dog towns. Percent cover of *Buchloe dactyloides* is relatively high on prairie dog towns and the percent frequencies of *Bouteloua gracilis*, *Carex eleocharis*, and *Spharacelcea*

coccinea are also relatively high on the towns. Bare ground cover on prairie dog towns did not significantly differ from swales, uplands, or *Atriplex* habitat types. Significantly higher cover percentages and the highest frequencies of *Pascopyrum smithii* occur on swales in these pastures. Senft et al. (1985) indicated that the percent frequency of this species is an important predictor of cattle distributions, and this was consistent with the results of this study. One important difference found in vegetation on and off prairie dog towns was that the plants growing on prairie dog towns were significantly shorter than all of the other habitat types. While cattle did not appear to be selecting prairie dog towns to graze on, they also did not significantly avoid them, even though the vegetation was shorter there.

One other unpublished study has been conducted on the CPER examining cattle activity on prairie dog towns (Paul Stapp, Mark Lindquist, unpublished data). My results are consistent with fecal pat counts conducted during the summers of 1997 and 1998. Fecal pat densities are indicative of the amount of time cattle spend in an area (Senft 1980, Milchunas et al. 1989). Fecal pat densities were estimated on five prairie dog colonies and five control plots and no significant differences were found.

In contrast to bison on the mixed-grass prairie, cattle do not appear to prefer prairie dog towns on the shortgrass steppe to graze or rest on. Cattle and bison are similar in that they are both generalist herbivores, but they differ somewhat in their diet selection. Cattle are more selective feeders than bison, foraging on plants that are more digestible than those that bison feed on (Peden et al. 1974). Cattle tend to prefer cool season grasses (C₃) and forbs, whereas bison prefer to graze on warm season grasses (C₄) (Schwartz and Ellis 1981, Plumb and Dodd 1993). Prairie dog towns on the shortgrass

steppe tend to be dominated by warm season grasses (*Bouteloua gracilis* and *Buchloe dactyloides*) (Bonham and Lerwick 1976). The data from this study have shown that vegetation on and off prairie dog towns is relatively similar with the exception that cool season grasses such as *Pascopyrum smithii* is more abundant in the swales. This would indicate that except for the swales, cattle may not have much reason to select one habitat type more than another. It is also possible that bison might prefer to graze on prairie dog towns, more so than cattle, due to the long evolutionary relationship that bison have with the shortgrass steppe (Larson 1940).

However, the major difference in this situation might be the ecosystem and not the large herbivore. The shortgrass steppe is a very different system from the mixed grass prairie. On the mixed-grass prairie, vegetation on prairie dog towns has higher levels of nitrogen, less standing dead, and higher digestibilities than areas off towns (Coppock et al 1983a). Defoliation of vegetation on the shortgrass steppe by prairie dogs may not have as large an effect on the nitrogen concentrations in the plants on the towns because increases in nitrogen levels depend on several factors including interspecific competition, soil nutrition, and frequency of grazing (Milchunas 1995). Atsedu (1995) found differences in nitrogen content increases of plants growing on the shortgrass steppe to be dependent on grazing histories and intensities. *Pascopyrum smithii* plants which had been protected from grazing had higher nitrogen concentration increases after defoliation compared to plants that had grazing histories. In a field study, previously grazed *Bouteloua gracilis* had significant increases in nitrogen concentration only after severe defoliation (Atsedu 1995). Cattle may not be preferentially grazing on prairie dog towns even though nitrogen concentrations may be higher on the towns because the

magnitude of the difference on and off towns may not be large enough to cause actual selection for the towns.

Plants growing on a prairie dog town are significantly shorter than surrounding uncolonized areas and can even differentiate into prostrate or dwarf ecotypes (Painter et al. 1993). Vegetation on prairie dog towns on the shortgrass steppe may be so short that even if the leaf to stem ratio is higher or the magnitude of difference in nitrogen content is large enough on and off towns, the amount of biomass cattle would gain by grazing on the prairie dog town may not make it worth their while. However, it is interesting to note again, that in this study, while perhaps not preferring to graze on the towns, cattle also did not significantly avoid the towns, even though the vegetation was shorter.

Year to year weather differences might have an effect on cattle selection of prairie dog towns on the shortgrass steppe. The field work for this study was conducted over only one growing season, and the summer of 1999 was unusually wet. Green (1998) reported that during wet years on the mixed-grass prairie, bison grazed on prairie dog towns preferentially. He attributed this to the additional moisture causing grasses on surrounding ungrazed habitat to grow taller and seed out, whereas the grazed grasses on prairie dog towns were not seeding out and had high leaf:stem ratios. During dry years bison did not graze preferentially on the towns. On the shortgrass steppe, Lerwick (1974) found that prairie dogs and cattle switched diets during drought years with prairie dogs consuming more grass and cattle consuming more forbs than in non-drought periods. Variation in year to year weather definitely has an effect on plant-herbivore and herbivore-herbivore relationships, and surveys conducted on the shortgrass steppe during a drought year might show very different results.

Climate constrains forage quality, bite size, and the capacity for cattle to regrazed on the shortgrass steppe. Coppock et al. (1983*b*) hypothesized that a response by large ungulates to prairie dog towns would likely only be seen in highly productive systems where the difference in habitat on and off towns is greatest. The examination of cattle use of prairie dog towns on mixed-grass prairie or of bison use of prairie dog towns on shortgrass prairie would provide insights as to whether it is cattle or the shortgrass system that is causing the selection or avoidance of the prairie dog towns. The issue of carrying capacity is important as well (Hobbs and Hanley 1990). Future studies should inspect how the presence of prairie dog colonies affects cattle carrying capacity.

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APPENDIX

Appendix A. Chi-square values used to calculate significant differences from standardized resource selection ratios of 0.5 are given for each pasture over the entire season, for the comparison between prairie dog towns #'s 29 and 30, morning and evening surveys, and for all pastures over the entire season (w_i = non-standardized resource selection ratio).

Pasture	on/off town	w_i	se (w_i)	Chi-square value	significance at 0.5 level
5W	on town	0.347	0.116	31.68	significant
	off town	1.078	0.014	31.48	significant
Stoneham	on town	0.480	0.050	109.04	significant
	off town	1.046	0.004	108.96	significant
29-30	on town	3.400	0.119	408.51	significant
	off town	0.915	0.004	413.63	significant
22W	on town	0.632	0.236	2.44	non-significant
	off town	1.010	0.008	1.54	non-significant
28N	on town	3.850	0.288	97.82	significant
	off town	0.921	0.008	97.98	significant
Box	on town	0.518	0.091	28.12	significant
	off town	1.013	0.002	27.82	significant
27-34	on town	3.727	0.191	204.41	significant
	off town	0.961	0.003	204.41	significant
Fiscus	on town	2.688	0.289	34.12	significant
	off town	0.999	0.002	0.33	non-significant
Keota	on town	0.000	0.178	31.44	significant
	off town	1.000	0.001	0.00	non-significant
Coal	on town	2.240	0.199	38.65	significant
	off town	0.993	0.001	38.84	significant
Roe	on town	0.947	0.223	0.06	non-significant
	off town	1.004	0.001	23.37	non-significant
Simmons	on town	1.477	0.222	4.63	barely sig.
	off town	0.999	0.001	4.32	barely sig.
29-30 comp comparison	town 29	0.571	0.036	141.16	significant
	town 30	2.410	0.119	140.72	significant
AM surveys	on town	0.725	0.052	81.50	significant
PM surveys	on town	1.469	0.054	26.07	significant
all pastures combined	on town	1.110	0.037	8.75	significant
	off town	0.998	0.001	8.60	significant

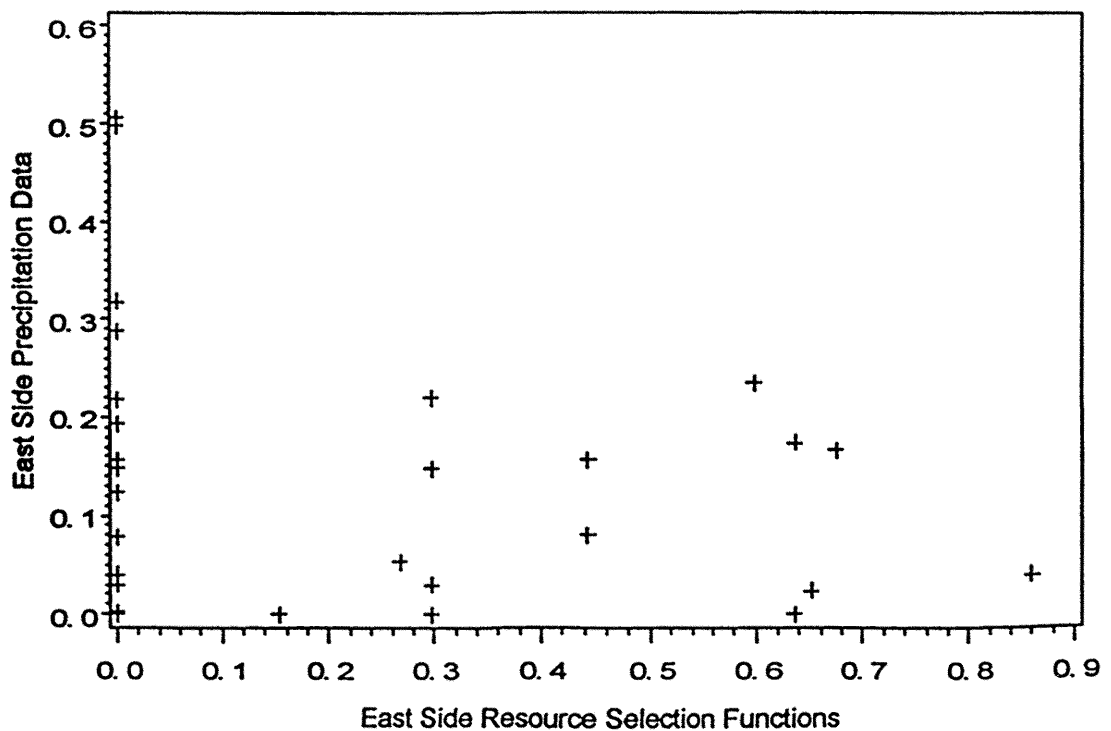
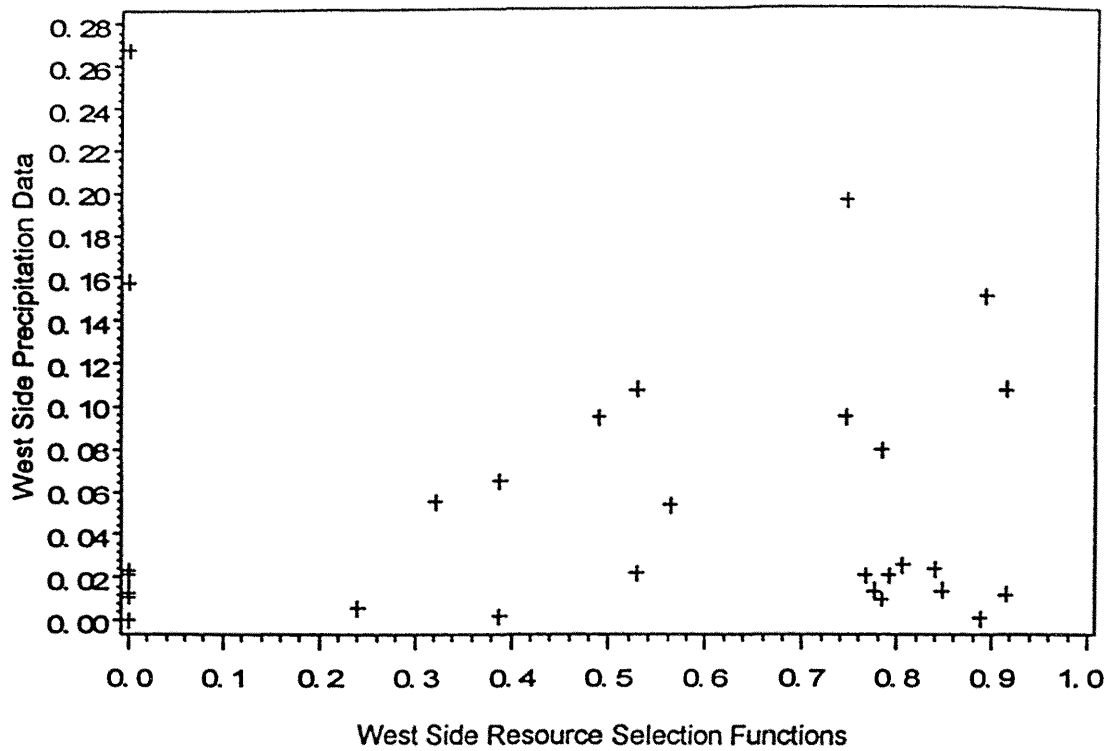
Appendix B. Chi-square values used to calculate significant differences from standardized resource selection ratios of 0.5 are given for Period I (May 28 to July 9, 1999) and Period II (July 12 to August 15, 1999). Significance values are given for each pasture, for the comparison between prairie dog towns #'s 29 and 30, and for all pastures over the two time periods (w_i = non-standardized resource selection ratio).

Pasture	on/off town	period	w_i	se (w_i)	Chi-square value	significance at 0.5 level
5W	on town	1	0.187	0.167	23.76	significant
	off town	1	1.097	0.020	23.56	significant
	on town	2	0.496	0.161	9.74	significant
	off town	2	1.060	0.019	9.61	significant
Stoneham	on town	1	0.848	0.072	4.51	significant
	off town	1	1.013	0.006	4.21	significant
	on town	2	0.136	0.069	155.38	significant
	off town	2	1.076	0.006	153.51	significant
29-30	on town	1	3.348	0.171	189.19	significant
	off town	1	0.917	0.006	190.83	significant
	on town	2	3.450	0.165	219.72	significant
	off town	2	0.914	0.006	218.54	significant
22W	on town	1	0.000	0.339	8.70	significant
	off town	1	1.003	0.011	0.07	non-significant
	on town	2	1.225	0.328	0.47	non-significant
	off town	2	0.992	0.011	0.51	non-significant
28N	on town	1	3.009	0.414	23.52	significant
	off town	1	0.944	0.011	23.82	significant
	on town	2	4.647	0.401	82.67	significant
	off town	2	0.899	0.011	82.66	significant
Box	on town	1	1.070	0.131	0.29	non-significant
	off town	1	0.998	0.004	0.32	non-significant
	on town	2	0.000	0.126	62.47	significant
	off town	2	1.003	0.003	0.76	non-significant
27-34	on town	1	2.059	0.274	14.92	significant
	off town	1	0.984	0.004	16.65	significant
	on town	2	4.576	0.265	181.42	significant
	off town	2	0.923	0.004	411.25	significant
Fiscus	on town	1	4.340	0.415	64.64	significant
	off town	1	0.980	0.003	63.61	significant
	on town	2	6.510	0.402	187.66	significant
	off town	2	0.967	0.002	184.74	significant

Appendix B. Continued.

Pasture	on/off town	period	w_i	se (w_i)	Chi-square value	significance at 0.5 level
Keota	on town	1	0.000	0.256	15.21	significant
	off town	1	1.003	0.002	3.76	non-significant
	on town	2	0.000	0.248	16.23	significant
	off town	2	1.003	0.002	4.01	barely sig.
Coal	on town	1	4.630	0.287	160.30	significant
	off town	1	0.980	0.002	153.40	significant
	on town	2	0.000	0.278	12.97	significant
	off town	2	1.003	0.002	3.68	non-significant
Roe	on town	1	0.000	0.320	9.75	significant
	off town	1	1.003	0.001	6.36	significant
	on town	2	1.834	0.310	7.23	significant
	off town	2	0.997	0.001	6.79	significant
Simmons	on town	1	3.052	0.319	41.49	significant
	off town	1	0.995	0.001	36.25	significant
	on town	2	0.000	0.308	10.51	significant
	off town	2	1.003	0.001	19.92	significant
29-30 comparison	on town	1	0.388	0.052	136.86	significant
	off town	1	3.016	0.172	137.05	significant
	on town	2	0.737	0.050	27.78	significant
	off town	2	1.860	0.164	27.41	significant
all pastures combined	on town	1	1.412	0.053	59.36	significant
	off town	1	0.992	0.001	66.62	significant
	on town	2	0.893	0.052	4.27	barely sig.
	off town	2	1.002	0.001	4.44	barely sig.

Appendix C. Regression plots of cattle use of prairie dog towns (resource selection functions) against precipitation data for the east and west sides of the Shortgrass Steppe - LTER.



Appendix D. P-values associated with focal survey data for each pasture, indicating significant differences from the mean of %habitat use minus %availability measurements from zero.

Pasture	habitat	mean	p-value
22W	prairie dog town	-1.56	0.083
	swale	28.68	0.0004
	upland	-29.33	0.0008
	rocky ridgetop	2.16	0.268
5W	prairie dog town	-1.67	0.685
	swale	16.96	0.004
	rocky ridgetop	-2.66	0.008
	Atriplex	-12.41	0.075
	crested wheatgrass	-0.21	0.936
29-30	prairie dog town	4.59	0.101
	swale	9.50	0.021
	upland	-24.53	0.0003
	rocky ridgetop	-1.06	0.080
	Atriplex	11.50	0.038

Appendix E. Significant differences for focal animal behavior at alpha = 0.05.

activity	Significant differences
grazing	rocky > Atriplex > upland > town > cw ¹ > swale
resting	cw > swale > upland > town > Atriplex > rocky
traveling	town > Atriplex > rocky > upland > swale > cw

¹ "cw" refers to crested wheatgrass (*Agropyron cristatum*) strips

Appendix F. Monthly significant differences at $p < 0.05$ level for palatable species cover between habitat types, averaged over the three intensively surveyed pastures. ("cw" represents the crested wheatgrass [*Agropyron cristatum*] habitat)

Species	Month	Significant differences ($p < 0.05$)
<i>Pascopyrum smithii</i>	June	swale > town > Atriplex > upland > rocky > cw
	July	swale > town > Atriplex > upland > rocky > cw
	August	swale > upland > town > Atriplex > rocky > cw
<i>Bouteloua gracilis</i>	June	Atriplex > upland > town > rocky > swale > cw
	July	Atriplex > upland > rocky > town > swale > cw
	August	Atriplex > upland > rocky > town > swale > cw
<i>Buchloe dactyloides</i>	June	swale > town > rocky > upland > Atriplex > cw
	July	swale > town > rocky > upland > Atriplex > cw
	August	swale > town > rocky > upland > Atriplex > cw
<i>Carex eleocharis</i>	June	upland > swale > Atriplex > town > rocky > cw
	July	Atriplex > upland > swale > rocky > town > cw
	August	upland > swale > town > rocky > Atriplex > cw
<i>Sphaeralcea coccinea</i>	June	cw > Atriplex > town > upland > rocky > swale
	July	Atriplex > town > upland > cw > rocky > swale
	August	Atriplex > upland > cw > town > rocky > swale

Appendix G. Monthly significant differences at the $p < 0.05$ level for nonpalatable plant species cover and for litter and bare ground cover between habitat types, averaged over the three intensively surveyed pastures. ("cw" represents the crested wheatgrass [*Agropyron cristatum*] habitat)

Month		Significant differences ($p < 0.05$)
<u>Nonpalatable species</u>		
<i>Aristida longiseta</i>	June	rocky > upland > cw > Atriplex > town > swale
	July	rocky > upland > cw > town > Atriplex > swale
	August	upland > rocky > town > cw > Atriplex > swale
<i>Vulpia octoflora</i>	June	upland > swale > Atriplex > town > cw > rocky
<u>Bare ground and litter</u>		
Bare ground	June	cw > rocky > swale > upland > town > Atriplex
	July	cw > rocky > town > upland > swale > Atriplex
	August	cw > rocky > town > swale > Atriplex > upland
Litter	June	Atriplex > upland > town > swale > rocky > cw
	July	upland > Atriplex > swale > town > rocky > cw
	August	Atriplex > upland > swale > town > rocky > cw

Appendix H. P-values for vegetation comparisons between the lowland town (29) and the upland town (30) from pasture 29-30, averaged over the season, summer, 1999, on the CPER.

Species	mean % cover		p-value
	town 29	town 30	
<i>Pascopyrum smithii</i>	2.17	2.08	0.919
<i>Bouteloua gracilis</i>	14.58	30.92	<.001
<i>Buchloe dactyloides</i>	14.75	0.29	<.001
<i>Carex eleocharis</i>	3.50	2.87	0.518
<i>Sphaeralcea coccinea</i>	3.50	4.96	0.240
<i>Aristida longiseta</i>	4.08	0.04	0.003
<i>Vulpia octoflora</i>	1.87	2.50	0.407
bare ground	39.00	39.95	0.635
litter	23.70	27.40	0.290

Appendix I. Plant species unique to each habitat type for the three intensively surveyed pasture on the CPER over the entire season.

habitat type	unique species
Atriplex	<i>Descurania sophia</i> <i>Helianthus annuus</i> <i>Townsendia grandiflora</i> 1 unidentified forb
crested wheatgrass	<i>Agropyron cristatum</i> (planted) <i>Artemesia tridentada</i> (planted) <i>Medicago sativa</i> (planted)
rocky ridgetop	<i>Eriogonum pumilus</i> <i>Lupinus pusillus</i> <i>Penstemon albidua</i> <i>Phlox</i> (sp. Unknown) <i>Thelmasperma filifolium</i> <i>Tradescantia occidentalis</i> <i>Viola nuttallii</i> <i>Yucca glauca</i> 3 unidentified forbs
prairie dog town	<i>Bromus tectorum</i> <i>Chenopodium incanum</i> <i>Cirsium undulatum</i> <i>Cryptantha jamesii</i> <i>Cryptantha minima</i> <i>Ipomopsis laxiflora</i> 2 unidentified forbs
upland	<i>Orobanche fasciculata</i> 2 unidentified forbs
swale	<i>Ambrosia psilostachya</i> <i>Carex nebraskensis</i> <i>Carex</i> (species unknown) <i>Conyza canadensis</i> <i>Descurania pinnata</i> <i>Dyssodia papposa</i> <i>Equisetum</i> sp. <i>Grindelia squarrosa</i> <i>Juncus</i> sp. 1 <i>Juncus</i> sp. 2 <i>Kochia scoparia</i> <i>Lupinus argenteus</i> <i>Polygonum aviculare</i> <i>Poa pratensis</i> <i>Psoralea lanceolata</i> <i>Rosa arkansana</i> <i>Rumex crispus</i> <i>Thermopsis rhombifolia</i> 8 unidentified forbs 1 unidentified grass