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Plant Community and Forage Preferences of Cattle on Native Aspen Parkland Range

by

Ronald Lee Arthur

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Date April 26, 1984

ABSTRACT

The aspen parkland of east central Alberta offers a variety of grassland, shrubland and forest plant communities from which cattle can select their diets. This study was designed to determine the plant community and forage preferences of cattle during two seasons (June and October), under two grazing intensities (light and heavy) and in two years (1980 and 1981). Secondly, a study of the determinants of observed preferences was undertaken with particular focus on the relative quality, availability and dry matter intake rate (foraging efficiency) of forest and grassland forages. Finally, use and mortality of more than 200 aspen suckers were monitored each year in four treatments to assess the impact of cattle upon aspen invasion of grasslands.

Grassland plant communities were generally preferred by cattle over forests or shrublands. However, exceptions did occur in portions of some grazing periods. Under drought conditions and heavy grazing in June, 1981, cattle selectivity between grasslands and forest decreased sharply in an apparent response to forage availability. In October, 1981, an abnormally late killing frost delayed the senescence of palatable forbs and abscission of browse species until the second week of the grazing period. Prior to the frost, cattle utilized these forages heavily and in turn showed high preference for forest and shrubland communities. Normally, grasslands were more preferred and forest more avoided in October than in June due to the lack

of available leafy browse. Grasslands were more preferred under heavy grazing than light in both seasons.

Cattle were principally grazers. However, browsing was significant in all treatments, and ranged from 7 to 28% of total foraging time. This represented an increase of 40 to 400% over data in other reports in the literature. Time spent grazing was greater under a heavy grazing intensity, in October and in 1980, the non-drought year. Grassland herbage was the major source of forage ranging from 62 to 92% of the cattle diet. Important secondary diet components included forest and shrubland herbage, aspen, rose, western snowberry and saskatoon.

Cattle exhibited significantly higher bite rates (48 bites/minute), bite sizes (0.99 g dry matter/bite), and foraging efficiencies (52 g dry matter/minute) when selecting grassland forages relative to forest forages (22 bites/minute, 0.58 g dry matter/bite, 13 g dry matter/minute, respectively). Forest forages were more quickly depleted, especially under a heavy grazing intensity. Bite sizes were smaller and bite rates greater under a heavy grazing intensity. Bite rates were also higher in the year of drought (1981). The barrier effect of woody stems upon grazing was negatively correlated with bite rates, bite sizes and foraging efficiencies of cattle.

Diet selection by cattle was positively correlated with foraging efficiency (dry matter intake rate). Quality attributes showed no consistent relationship with forage or community preferences. Animal response at the community level was an integrated response largely dependent upon the dry matter intake rate for each forage and its relative availability.

Cattle use of aspen suckers on the forest margin of all treatments occurred prior to severe depletion of herbaceous forage supplies. The number of browsings per sucker was twice as great under heavy grazing as under light and four times greater in June than in October. As the number of browsings per sucker increased, mortality rates also increased. Mortality rates were greater under a heavy grazing intensity (37%) than under light (21%), and greater in June (47%) than in October (7%). Accordingly, heavy grazing in June resulted in the highest aspen sucker mortality (58%) among treatments.

Foraging efficiency (dry matter intake rate) was the primary factor determining cattle response to forages and communities. Quality was of secondary importance. However, food density or forage availability served to alter the relative importance of those two factors. As forage availability and cattle selectivity increased, quality became an increasingly important determinant of foraging behavior while dry matter intake became less important.

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1. INTRODUCTION

The aspen parkland covers much of central Alberta. It has been described as a large tension area or ecotone between the boreal forest and mixed prairie (Moss and Campbell 1947; Coupland and Brayshaw 1953). Most of the remaining native aspen parkland range occurs on strongly undulating topography developed on glacial moraine or till, known locally as knob and kettle terrain. The resultant variability in microclimate accounts for numerous vegetation types expressed along a catenary gradient. There are several kinds of grasslands on upper slopes, then shrubland, forest, willow and finally sedge wetland in swales (Wroe 1971). This rangeland provides a wide variety of plant communities and forage species from which cattle select their diet. Consequently, the preferences and avoidances of plant communities and forages must be known to be included in range management grazing strategies. However, at present stocking rates in the aspen parkland are determined on the basis of herbaceous production (Smoliak et al. 1976; Wroe et al. 1981). Consideration of cattle preferences for browse species as forage and the effects of environment and stocking rates on forage palatability, availability and animal selectivity is lacking. Adjustments for these factors might qualify present value estimates of various plant communities and forages.

Fundamental to the above problems is the need to determine the major factors governing foraging behavior.

Diet selection by cattle may be based on optimization of nutritional balance (Rapport 1971; Ellis et al. 1976). Cattle maintain a nutritionally wise feeding strategy by certain adaptive mechanisms. They select a diverse diet (Zahorik and Houpt 1977) and prefer leaves and new growth (Arnold 1964; Zahorik and Houpt 1977). This strategy usually makes the diet higher in quality components and limiting nutrients (Arnold 1964; Zahorik and Houpt 1977). However, while sensory responses are developed enough to provide adequate nutrition, universal relationships of herbivore preferences with nutritional fractions show numerous inconsistencies (Arnold and Hill, 1972). This is likely related to the fact that cattle are classified as one of the least selective ruminant herbivores due to their digestive anatomy, mouth morphology and food habits (Rice et al. 1971; Ellis and Travis 1975; Willms 1978). Accordingly, cattle have relatively high intake rates. Chacon and Stobbs (1976) estimated dry matter (DM) intake rates reaching 18 g/minute for cattle. This exceeds observed foraging rates for wapiti (13 g DM/minute) (Hudson and Nietfeld 1984) and smaller species such as reindeer (Trudell and White 1981), mule deer (Collins and Urness 1983), and domestic sheep (Allden and Whittacker 1970). However, Hudson and Nietfeld (1984) noted higher intake rates for bison (23 g DM/minute). Intake rates for cattle appear largely dependent on two positively related factors, bite size and leaf yield (Chacon and Stobbs 1976). Whatever the controlling factors, studies of foraging behavior have additional significance for aspen parkland range. Observation of cattle use of browse species, in particular aspen, could provide information needed to develop brush control strategies.

Settlement of the prairies and the consequent control of fire has favored aspen forest encroachment onto the *Festuca scabrella* grassland (Moss and Campbell 1947; Maini 1960). The average increase in aspen cover has ranged from 0.05% per year (Bailey and Wroe 1974) at the dry southern edge of the parkland to 0.75% per year at the University of Alberta ranch, Kinsella (Scheffler 1976) and in the Porcupine Hills of southwestern Alberta (Johnson and Smoliak 1968). Aspen invasion causes a decline in grass production (Bailey and Gupta 1973; Whysong and Bailey 1975). Hilton and Bailey (1974) noted annual herbage production of 2039 and 125 kg/ha in grassland and aspen forest, respectively. Bailey and Wroe (1974) found 1944 and 154 kg/ha, respectively, in the same two vegetation types. Obviously, forest invasion into grassland has negative effects on carrying capacity.

The literature reports wide variability in cattle use of aspen (Smith et al. 1972; Hilton and Bailey 1974). The major determining factors of aspen use are poorly understood and rarely documented. FitzGerald (1982) and Smith et al. (1972) found that cattle browsed aspen more readily in the second half of the growing season. Bailey et al. (1980) also noted a seasonal effect whereby aspen use in October (usually after leaf fall) was lower relative to June. In the same study, Bailey[1] also observed greater aspen use under heavier grazing intensities. Age of aspen suckers has been discussed as a determinant of aspen use by cattle. Smith et al. (1972) contended that aspen sprouts were most palatable at emergence but Sampson (1919) found no preference for younger suckers in the first 4 years of growth. FitzGerald (1982), noted suckers in the second year of growth after a forest burn were more preferred by cattle than new sprouts.

Research into the effects of season, grazing intensities and alternate available forages upon cattle response to aspen appear essential to define brush control strategies. Thus, a study of changes in foraging activities, community and species preferences under different seasons and grazing intensities is desirable. Such an approach may indicate methods of aspen control in concert with other shrubby species and provide strategies to obtain optimal use of various plant communities.

Therefore, this research project was designed with the following objectives in mind:

1. To determine patterns in community preferences displayed by cattle over two seasons, two grazing intensities and two years.
2. To determine foraging activities and forage preferences among communities, seasons, grazing intensities and years.
3. To determine differences in the foraging efficiency

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[1] Bailey, A.W. 1980. Personal communication.

(g DM intake/minute) or the profitability of grazing in forest and grassland.

4. To determine if cattle select plant communities and/or forages in direct response to herbaceous productivity and quality or in proportion to foraging efficiency.

5. To determine cattle use and mortality of aspen suckers in the grassland at the forest edge under different seasons, grazing intensities, and years; and secondly, to relate aspen use to herbage availability and aspen sucker parameters.

An in-depth literature review regarding these objectives was divided into introductory sections within respective chapters of this study. This was done to expedite publications from this manuscript.

2. STUDY AREA

2.1 Location

The study area was located on NW28-47-11-W4 of the University of Alberta Ranch at Kinsella, Alberta (approximate latitude 53 02 degrees North, longitude 111 33 degrees West) at an elevation of 700 to 900 m above sea level.

2.2 Geology and Soils

The soils in the Kinsella area developed from the heavy textured till of Viking moraine, deposited about 15,000 years ago by recession of the Kehewin ice sheet (Wyatt et al. 1944). The moraine overlies bedrock of the Pale beds division and is responsible for the strongly undulating surface expression known locally as knob and kettle topography. Soils are generally of medium loam texture with few to many stones and black topsoil averaging 7-10 cm in depth. Profile depth and texture vary from shallow and heavy on knolls to deep and friable in depressions. Soils are usually classified as thin black Chernozems although pockets of dark brown chernozems (knolls) and gleysolic soils (depressions) are often found (Scheffler 1976; Wheeler 1976).

2.3 Climate

The Kinsella area is generally classified as a "dry subhumid" climate with cold winters and mild dry summers (Wonders 1969). Approximately 75% of average annual precipitation falls in the growing season (April-September) (Environment Canada 1981). Average monthly precipitation and temperatures recorded at the University of Alberta Ranch from 1962 to 1981 are presented in Tables 2.1 and 2.2 along with data for 1980 and 1981, the two experimental years. There was above average rainfall during the growing season of 1980 while 1981 was an abnormally dry year. Rainfall and temperature were recorded about 9 km south of the study area at the summit of a large hill. Consequently, when killing frosts were noted at the study area, temperatures recorded on the hill were higher than those usually required for a killing frost. Evapotranspiration averages 120-180 mm per annum while the normal frost-free period between mid to late May and early September is 100 to 120 days (Wonders 1969). Prevailing winds are normally from the west and northwest (Wyatt et al. 1944).

2.4 History and Treatments

The study area became part of a homestead in 1916 and was heavily grazed from that time until about 1947[2]. From about 1947 to 1970 it had been cut for hay on an alternate year basis. By 1972, the area was typical aspen parkland in

---

[2] Bailey, A.W. 1980. Personal communication.

Table 2.1 Monthly precipitation (mm) at Kinsella for 1980, 1981, and the 20-year average.

Month	1980	1981	1962-81 Ave.
January	26.5	4.0	23.1
February	17.2	4.7	15.6
March	32.6	8.4	17.1
April	4.9	27.5	18.3
May	51.4	10.0	43.3
June	179.1	24.5	75.2
July	119.3	65.2	85.3
August	123.2	20.0	56.6
September	30.5	16.1	36.2
October	16.2	20.0	15.5
November	4.3	8.5	14.8
December	33.9	11.0	19.8
Total	639.1	219.9	420.8

Table 2.2 Mean monthly maximum and minimum temperatures (°C) for 1980, 1981, and the 20-year average.

Month	1980		1981		1962-81 Ave.	
	Min.	Max.	Min.	Max.	Min.	Max.
January	-20.6	-10.7	-10.8	-2.0	-20.3	-13.4
February	-15.0	-3.5	-13.5	-2.6	-15.5	-7.5
March	-12.6	-1.6	-5.6	5.2	-10.2	-1.4
April	2.1	16.0	-1.5	11.4	-0.3	8.2
May	5.4	20.6	5.4	19.5	6.6	16.3
June	9.7	20.6	6.9	20.8	10.6	19.9
July	10.0	23.2	11.5	23.1	12.7	22.0
August	7.9	18.9	12.1	27.1	11.2	21.9
September	4.0	16.8	6.0	19.8	6.2	15.5
October	1.3	13.8	-1.4	9.2	1.1	9.7
November	-4.7	5.1	-4.6	4.0	-8.7	-1.7
December	-19.7	-10.3	-15.0	-6.9	-15.7	-9.9

excellent range condition. The experimental site was grazed heavily in October, 1972, to uniformly remove the heavy litter accumulation on the ungrazed native grassland range. At that time, a grazing research project was designed to study differences over two seasons of growth (early summer and autumn) and two intensities of grazing (light and heavy, 8 animal unit months (AUM's)/field and 24 AUM's/field, respectively) (Bailey et al. 1980). Four fields ranging in size from 7 to 10 ha were then fenced to each include about 6 ha of rough fescue-western porcupine grass grassland. Then the four treatments described in Table 2.3 were applied each year beginning in 1973.

This study was conducted in 1980 and 1981, the 8th and 9th years of treatments. Yearling heifers were used in both experimental years. The methods used to achieve the objectives of this study are presented in each chapter.

2.5 Vegetation

Nine plant communities were defined in the study area (Table 2.4). Criteria were selected to highlight differences in species composition and habitat structure that might affect animal response.

The open phase grassland community exhibited the dominant grassland association of *Festuca scabrella - Stipa spartea var. curtiseta*, typical of the aspen parkland (Coupland and Brayshaw 1953). In that association, *Festuca scabrella* dominates on mesic, undisturbed sites while on

Table 2.3 Treatments applied to the experimental site, 1973 to 1981 (using one-month grazing periods).

Treatment	Grazing Intensity	Season
1†	light (8 AUM/field)	June
2†	heavy (24 AUM/field)	June
3	heavy (24 AUM/field)	October
4	light (8 AUM/field)	October

† Treatments 1 and 2 were stocked at 4 and 12 AUM/field, respectively, in 1973 and 1974.

Table 2.4 Definition of Plant Communities.

Community	Determining Criteria	References
Carex wetland	inundation for part of growing season; Carex spp. or Calamagrostis spp. dominant.	Walker and Coupland 1970; Wroe 1971; Scheffler 1976.
Salix wetland	composition similar to Carex wetland but with greater than 75% cover of Salix spp.	Wroe 1971; Scheffler 1976.
Aspen forest	nearly continuous overhead canopy of aspen trees; presence of low shrub layer, rich or sparse, and a lower strata of herbs.	Moss 1955; Wroe 1971; Scheffler 1976.
Shrubland	absence of aspen tree canopy; presence of shrub layer of Rose, Snowberry, or Saskatoon with cover greater than 75% and a herbaceous understory with less than 25% cover.	Wheeler 1976.
Open grassland	grassland with shrubby cover less than 25%.	Wroe 1971; Wheeler 1976.
Forest edge phase grassland	herbaceous cover greater than 90%; presence of aspen suckers in a 5 to 30 meter band from forest margins; less than 75% cover of Snowberry.	Scheffler 1976; Bailey 1978.
Snowberry phase grassland	herbaceous cover greater than 90%; Snowberry cover greater than 25% and less than 75%.	Wheeler 1976.
Silverberry phase grassland	herbaceous cover greater than 90%; Snowberry cover less than 25%; Silverberry cover greater than 25%.	Wheeler 1976.
Brushed fencelines	bulldozed in 1970	

more xeric sites it codominates with *Stipa spartea var. curtiseta*, *Agropyron spp.* and *Bouteloua gracilis*. Other subdominants include *Agropyron subsecundum*, *Agropyron dasystachyum*, *Solidago spp.*, *Cerastium spp.* and upland *Carex spp.* (Sinton 1980). Shrubs found on moister, lower slope positions of the grassland provided the distinction for three shrubby phase grassland communities, despite the same herbaceous species as open grassland (Wroe 1971; Wheeler 1976). The first of these was the forest edge phase grassland where aspen invasion was occurring. Presence of *Populus tremuloides* suckers on the forest margin distinguished it from other grassland communities (Scheffler 1976; Bailey 1978). The snowberry phase grassland community had a cover of *Symphoricarpos occidentalis* exceeding 25% but not greater than 75% (Wheeler 1976). Finally, the silverberry phase grassland had a cover of *Elaeagnus commutata* exceeding 25% with *Symphoricarpos occidentalis* cover less than 25% (Wheeler 1976). Excessive cover of shrubby species causing herbaceous cover to be less than 90% of that in open grassland resulted in non-classification as a grassland community. Over the eight year exposure to treatments, Bailey et al. (1980) noted a gradual decrease in grass production and an increase in forb production in the grassland communities under heavy June and October treatments. Increases in forb and grass production were noted in the light June treatment. Personal observations (1980) confirmed that the greatest changes in composition of grasslands occurred under heavy June grazing. *Festuca scabrella* had been largely replaced by *Agropyron subsecundum*, *Bouteloua gracilis*, and other grasses adapted to more xeric conditions as well as a variety of forbs. The major grassland forbs included *Thermopsis rhombifolia*, *Selaginella densa*, *Cirsium arvense*, *Achillea millefolium*, *Frageria virginiana*, *Artemisia ludoviciana*, *Artemisia frigida*, and *Galium boreale*. *Aster laevis* and *Solidago missouriensis* were the two most palatable forbs available. Under light June grazing, an excellent stand of *Festuca scabrella* still dominated throughout all grassland communities after eight years (Bailey et al. 1980). Increases in cover of the forb species noted above occurred only on small locally overgrazed areas such as hilltops or cattle resting sites. The light October treatment area was also largely unchanged in terms of the original species composition and productivity of grasslands (Bailey et al. 1980). However, the forest edge phase grassland was becoming progressively wider in area and structural diversity than in other treatments. The heavy October treatment showed increased forb cover throughout grasslands, particularly *Cirsium arvense*, *Thermopsis rhombifolia*, *Galium boreale*, *Achillea millefolium*, and *Artemesia ludoviciana*. Despite the low grass productivity noted by Bailey et al. (1980) in this treatment, grasses were still the major sward component of grassland communities.

The fifth community was the *Populus tremuloides* forest. It had an overhead canopy of aspen trees, a rich or sparse low layer of shrubs and a lower herb stratum (Moss 1955; Wroe 1971). The shrub layer was comprised of *Symphoricarpos occidentalis, Amelanchier alnifolia, Rosa woodsii, Rosa acicularis, Rubus strigosus* and *Salix spp.* (Hilton 1970). The herb layer consisted of *Rubus pubescens, Aster spp., Vicia americana, Lathyrus ochroleucus, Pyrola secunda, Frageria virginiana, Galium boreale, Epilobium angustifolium, Viola adunca, Smilacina stellata, Thalictrum venulosum, Calamagrostis spp., Anemone canadensis,* and *Agropyron trachycaulum.* Changes in composition and structure of the aspen forest after eight years of the heavy June treatment were apparent. That forest lacked a productive lower shrub layer of rose, aspen, saskatoon, or snowberry as well as the taller herbs normally found intertwining such shrubs. *Vicia americana, Lathyrus ochroleucus,* and *Smilacina stellata* were the herbs most notably lacking in abundance. A similar but much less pronounced difference was discernable in portions of the forest in the heavy October grazing treatment.

The sixth community was the shrubland. It lacked the aspen tree canopy but had a shrubby cover of *Rosa acicularis, Symphoricarpos occidentalis* or *Amelanchier alnifolia* exceeding 75% (Wheeler 1976). Furthermore, the rather continuous shrub cover had an obvious negative effect on herbaceous productivity. Thus, the herbaceous understory normally had a cover of less than 25%. Compositional and structural differences among treatments after eight years were minimal in the shrubland community.

Two wetland communities were present in the catenary sequence. Localized wet depressions or fresh water sloughs dominated by various *Carex spp.*, *Calamagrostis inexpansa*, *Calamagrostis canadensis*, *Glyceria grandis*, *Beckmannia syzigachne*, *Sium suave* and others represent the *Carex* wetland community (Walker and Coupland 1970; Wroe 1971). The margins of these wetlands are dominated by *Salix petiolaris* and *Salix discolor* in a shrubby community leading into aspen forest (Bird 1961). This *Salix* wetland community exhibited *Salix spp.* cover of 79 and 88% as determined by Wroe (1971) and Scheffler (1976), respectively. Differences in community structure and composition among treatments were not apparent in the two wetland communities. The final community was the disturbed area along fencelines of the study area. It consisted of any areas cleared of brush in 1970 to facilitate fencing. Herbaceous cover and production in this brushed fenceline community was relatively low and highly variable. Differences among treatments after eight years were apparent with regards to the cover and density of aspen suckers. In 1980, the two October treatments showed heavy aspen domination of fencelines. Aspen ranged in height from new suckers to 4-m trees that represented successful regeneration from the clearing operation. The two June treatments showed less dense aspen growth and lower aspen cover. The light June treatment exhibited varying degrees in aspen sucker height (0-3 m tall) while the heavy June treatment showed no brush species taller than 1-m and by far the lowest aspen cover of any treatment.

3. PLANT COMMUNITY PREFERENCES

3.1 Introduction

Grasslands are usually the major source of dietary components for cattle, while shrublands and forests are relatively minor (Smith et al. 1972; Miller et al. 1976; Hansen et al. 1977). In the aspen parkland, such preference patterns appear to be less consistent. In Colorado, Ellison and Houston (1958) and Paulsen (1969) observed that cattle did not use the aspen forest as much as the grassland. Similarly, Hilton and Bailey (1972) observed minimal use of the forest in central Alberta under late August - mid September grazing. However, the next year they noted preferential use of forest relative to grassland during a June drought. Bailey et al. (1980) also found significant use of aspen in June. FitzGerald et al. (1984) noted cattle preference for spring-burned grassland in early July but preference for spring-burned forest in August. This was associated with increased browsing in August.

The effect of grazing intensity upon community preferences appears largely unstudied. However, numerous reports indicate increased use of browse species and browse type communities as grazing intensity is increased (Sampson 1919; Vavra et al. 1977; Bailey et al. 1980).

The objective of this chapter was to determine the plant community preferences and avoidances of cattle under different seasons, grazing intensities and years.

3.2 Methods

A 1:990 scale aerial photograph with a 1-cm² grid overlay was used as a base map of the study area. In May, 1980, communities were mapped in the field on the gridded photograph using the criteria noted in Table 2.4 to identify plant communities. An electronic planimeter was used to determine actual proportions of communities available for cattle use within each of the four fields.

Grazing periods were about 4 weeks in length and the number of yearling heifers required to achieve stocking rates varied among treatments according to animal weight (Appendix A). Cattle use was monitored by observation of groups of grazing cattle, normally done every day with never more than a 3-day span between observation sessions. Most group observations were performed during the major grazing periods, early morning and evening (Dwyer 1961). A lesser number were conducted in late morning and early afternoon. Observation sessions normally lasted 2.5 to 3 hours, were recorded via portable tape recorder and later transcribed. Details of the number of cattle per group, the number grazing or browsing, the number foraging in respective plant communities and the spatial position of the group with regards to the grid map were recorded approximately every 10 minutes. Frequencies on use of the plant communities were determined as a proportion of the total number of group observations within treatments. Frequencies were weighted for the number of animals per group divided by the average number of animals per group in respective communities. Following Neu et al. (1974), observed frequencies of use were tested against the expected frequencies of use (proportions of plant communities in each field) to obtain a chi-square value. This chi-square value was called the index of cattle selectivity among communities. It measured the probability that cattle used plant communities in proportion to their available area. Continuing the procedure, goodness of fit comparisons of the observed and expected (the available proportion) use of individual communities were performed to indicate preference and avoidance responses via confidence intervals on chi-square values (Appendix B). In other words, a preference index (observed use/expected use) with confidence limits was calculated for each community in each treatment. When observed use exceeded expected use, the resultant index value was greater than 1. This was indicative of a preference response. Conversely, an index value less than 1 indicated an avoidance response. Patterns in response were then identified across seasons, grazing intensities, and years.

3.3 Results

Cattle exhibited significant plant community selectivity in both years of every treatment (Table 3.1). Selectivity among communities was consistently higher in October. Further insight into the relative use and preference of specific plant communities demands closer

Table 3.1 Indices of cattle selectivity among plant communities (X^2), and the probability that cattle use was proportional to community area (p) under various treatments, 1980 ar 1981.

	1980		1981	
Treatment	X^2	p	X^2	p
light June grazing	43	.00	29	.00
heavy June grazing	112	.00	39	.00
light October grazing	91	.00	120	.00
heavy October grazing	133	.00	75	.00

scrutiny of individual treatments.

3.3.1 Light Grazing in June

The two major communities utilized both years in the light June treatment were the aspen forest and the open grassland (Fig. 3.1). However, the aspen forest was highly avoided by cattle while open grassland use was proportional to it's available area. The snowberry phase grassland was also heavily used in 1980. Cattle grazed throughout grassland communities in 1980, and often circled or turned about when reaching a shrubland or forest perimeter in order to remain in the grassland. At the forest perimeter, animals would frequently graze the grassland along the forest edge rather than using open grassland or forest. Upon entrance into the forest, the animals foraged in a dominantly uni-directional manner until another community perimeter was reached. Then the cattle usually left the forest in

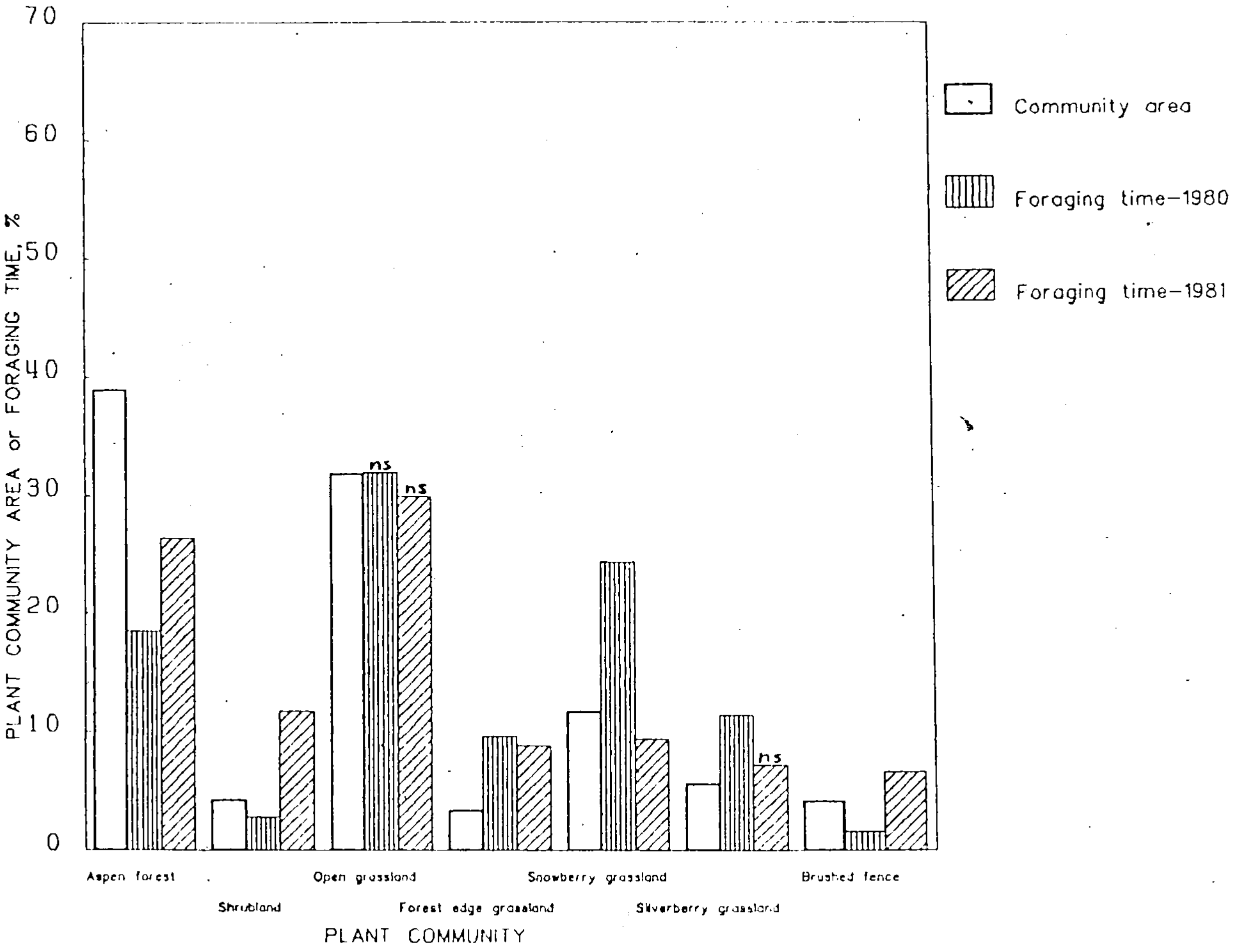

Figure 3.1 Area (%) in each plant community and proportion of total time (%) spent foraging in each under light June grazing, 1980 and 1981 (preferences or avoidances are significant at p≤.05 unless denoted by non-significance (ns)).

preference for a grassland community. The animals often camped for major rest periods at the water or salting areas. The watering area was separated from the main body of open grassland by a large shrubland area heavily interspersed with snowberry and silverberry phase grasslands. Thus, the cattle often grazed or trailed directly through this area after leaving the water site.

In 1981, a few minor behavioral changes were observed. Firstly, the animals spent more time browsing in the shrubland community near the water than grazing in the adjacent snowberry and silverberry phase grasslands. Similarly, the forest was more preferred by cattle in 1981 than in 1980. Although their behavior upon leaving the forest did not change, the cattle seemed less apt to turn away from the forest perimeter and regraze grasslands. To summarize, the cattle were less discriminative among communities in 1981.

Over both years, the forest edge grassland was the most consistently preferred community, reflecting the grazing behavior observed at forest perimeters. Preference for snowberry and silverberry phase grasslands was inversely related to shrubland preference in both years, one determinant being the close spatial proximity of these communities to the water source. All three shrubby phase grassland communities were preferred over open grassland in 1980 but only the forest edge grassland showed a similar response in 1981. However, total shrubby phase grassland (3 communities pooled) was still more preferred than open grassland in both years (Appendix B).

3.3.2 Heavy Grazing in June

Cattle consistently avoided the aspen forest in both years but because of its large area (52%) it was still used considerably (Fig. 3.2). The most heavily used communities were the various grasslands. Behavior appeared largely dependent upon species preferences and the quantities of alternate available forages. In 1980, the cattle exhibited consistent use of all grassland communities throughout the grazing period (Fig. 3.3). Initially, the animals concentrated on selection of palatable forbs and green grass, and usually grazed along the forest edge prior to entering forest or returning to open grassland. However, by the second week, animals would usually enter directly into the forest upon reaching its perimeter. Foraging within the forest varied between grazing and browsing, depending on the thickness of browse cover. Animals would often stop suddenly after a period of forest foraging and trail to the nearest grassland before resuming grazing. They would sometimes trail through the forest from one grassland to another and then resume grazing. These observations increased in frequency as the grazing period proceeded, accompanying the depletion of readily available forest herbage and browse. Conversely, in the grassland communities animals rarely quit grazing unless they were about to lie down or trail to water

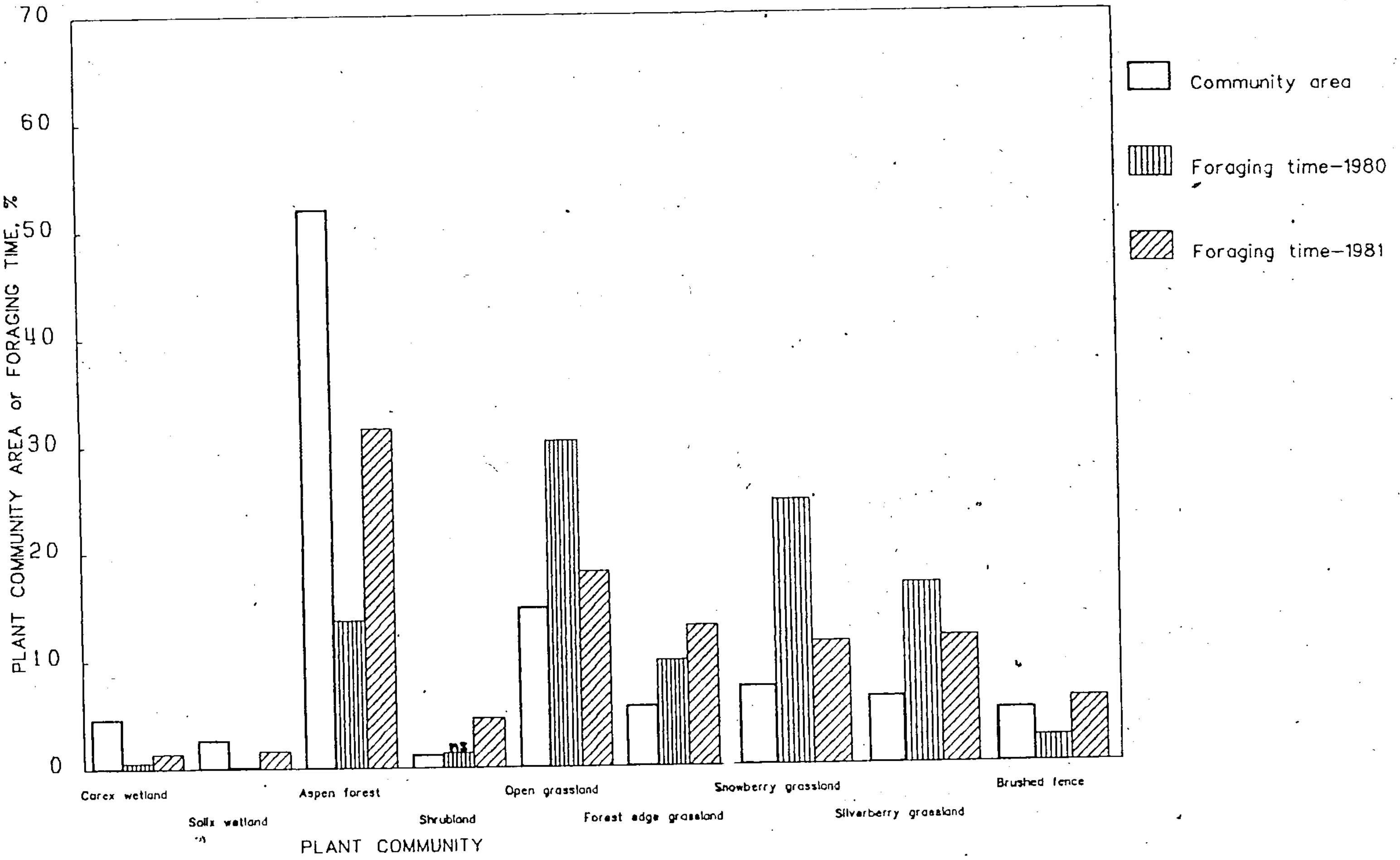

Figure 3.2 Area (%) in each plant community and proportion of total time (%) spent foraging in each under heavy June grazing, 1980 and 1981 (preferences or avoidances are significant at p≤.05 unless denoted by non-significance (ns)).

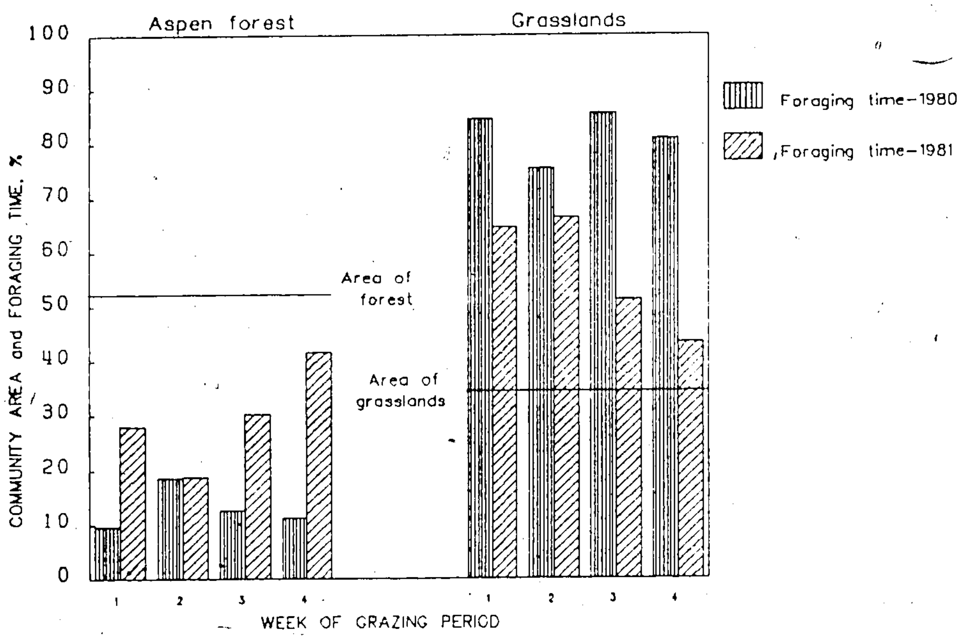

Figure 3.3 Availability and weekly use of aspen forest and all grasslands under heavy June grazing (preferences or avoidances are significant at $p \leq .05$).

or salt. The cattle avoided wetland communities although infrequent use was noted, especially in the *Salix* wetland where *Salix* leaves were highly preferred in comparison to adjacent sedges.

In 1981, a year dissimilar from 1980, there was a large decrease in selectivity among communities (Table 3.1). Grazing behavior was very similar to 1980 for the first two weeks. However, as the grazing period progressed, animals spent less time in the grassland and more time in the forest (Fig. 3.3). Unlike 1980 when green regrowth on grasslands maintained a source of readily available forage, the 1981 drought forced cattle into forest and shrubland communities. By the fourth week of June, 1981, animals were heavily utilizing unpalatable plants including Western snowberry, silverberry, yarrow and buffalo bean. Indeed, by the end of the fourth and final week the only observable selectivity was a reluctance to graze buffalo bean and older, woody portions of trees and shrubs. However, there was still a consistent avoidance of the forest and wetlands, and a preference for all grassland communities in both years.

Comparison of the selectivity indices for the light and heavy June treatments confirmed greater discrimination among communities under heavy grazing (Table 3.1). Preference for the grasslands as a whole was greater under heavy June grazing. In both treatments the total shrubby grassland was consistently preferred over the open grassland. Similarly, both treatments showed decreased forest avoidance and increased shrubland preference in 1981.

3.3.3 Light Grazing in October

The open grassland was obviously the most important community to foraging cattle (Fig. 3.4). Silverberry phase grassland and the shrubland in 1981 were the major secondary sources of forage. Cumulative use for all grassland communities was over 97 and 75% of the total in 1980 and 1981, respectively. Cattle showed a strict preference for the open grassland in 1980. They tended to congregate on hilltops and south-facing slopes within the grassland when grazing. This patchy distribution resulted in local areas of heavy utilization where grazing and regrazing occurred, thereby preventing the build-up of standing litter. When grazing in less well utilized areas, cattle were much more selective in attempting to avoid the litter. Locally over-utilized areas were also observed in the silverberry phase grassland community. The inability of animals to graze in this manner in the snowberry phase grassland because of the barrier effect of western snowberry stems and litter build-up may partially explain their indifference to that community in both years. Use of the forest, shrubland, and forest edge phase grassland communities was minimal in 1980. As noted in Chapter 2, the structure of inner portions of the forest edge in the light October treatment was similar to that of the forest. The only observed grazing in the forest edge phase grassland occurred in its extreme outer

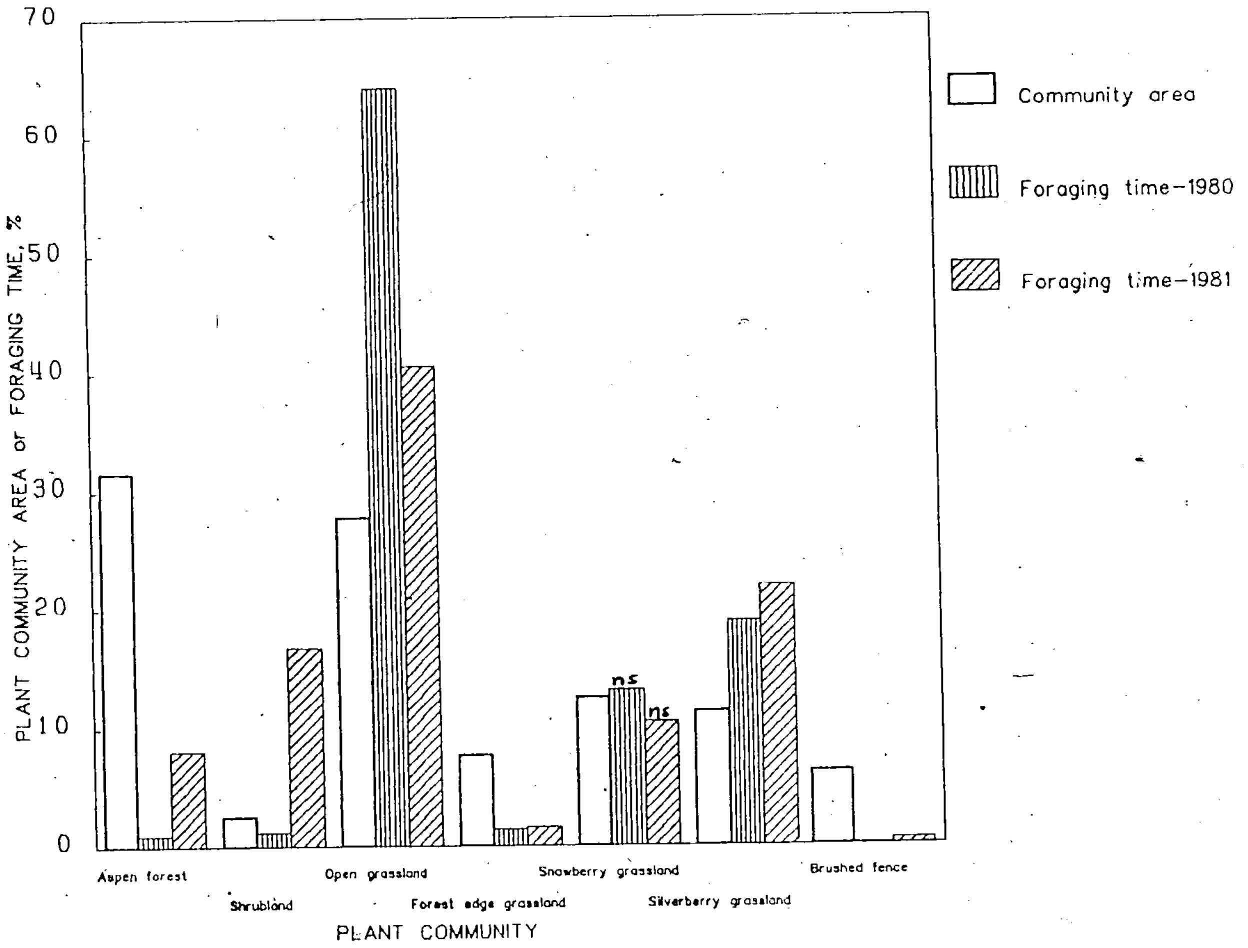

Figure 3.4 Area (%) in each plant community and proportion of total time (%) spent foraging in each under light October grazing, 1980 and 1981 (preferences or avoidances are significant at $p \leq .05$ unless denoted by non-significance (ns)).

limits where grassland structural characteristics predominated. Similar observations were made in the brushed fenceline community, structurally similar to forest and the inner limits of the forest edge.

In 1981, the summer drought resulted in relatively low available herbage supplies in grasslands in October. Then, a late killing frost nine days into the grazing period (0°C on Sept. 23 and -1.0°C on Sept. 25 at the hilltop recording station) resulted in abnormal availability of forbs in the forest and shrubland communities. Unlike 1980 when the killing frost preceded the grazing period (-2.5°C on Sept. 18), cattle highly preferred the forest during the first week of October, selecting leaves of woody plants and rapidly senescing forbs, primarily *Lathyrus ochroleucus* (Fig. 3.5). However, by the end of the first week, *Lathyrus* had senesced or had been largely depleted, making it difficult for animals to harvest. Subsequently, a dramatic return to the norm of forest avoidance and grassland preference was observed in week 2. The first three weeks of October, 1981 also featured heavy utilization of the shrubland community located near the water (Fig. 3.6). Unlike forest forb senescence, leaf abscission of woody plants was a much slower process following the killing frost. Thus, browse was available as a forage source well into the third and fourth weeks of grazing in the shrubland community. However, by the end of week 3, use of shrublands was considerably less extensive, perhaps due in part to

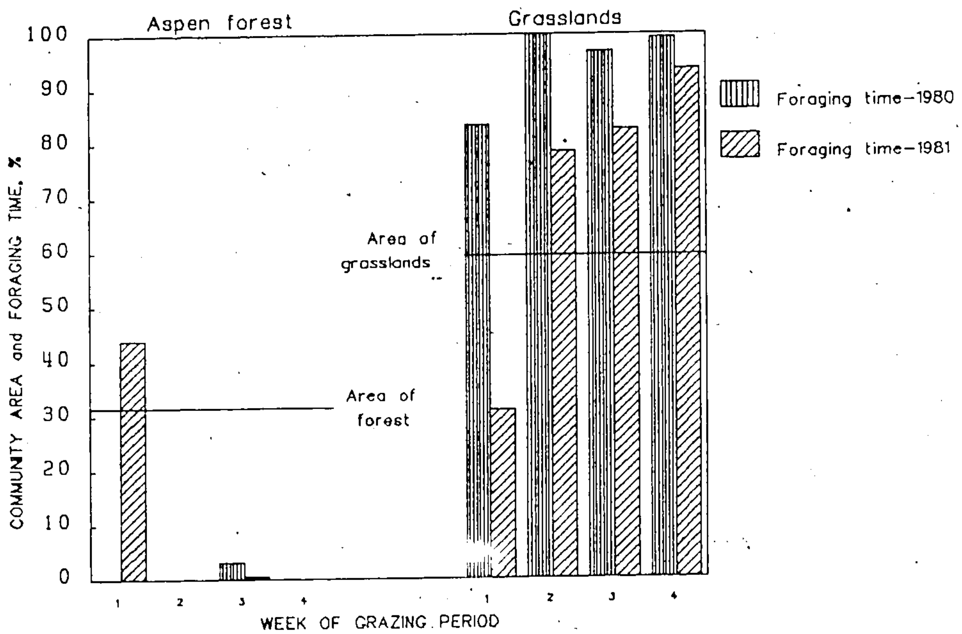

Figure 3.5 Availability and weekly use of aspen forest and all grasslands under light October grazing (preferences or avoidances are significant at $p \leq .05$).

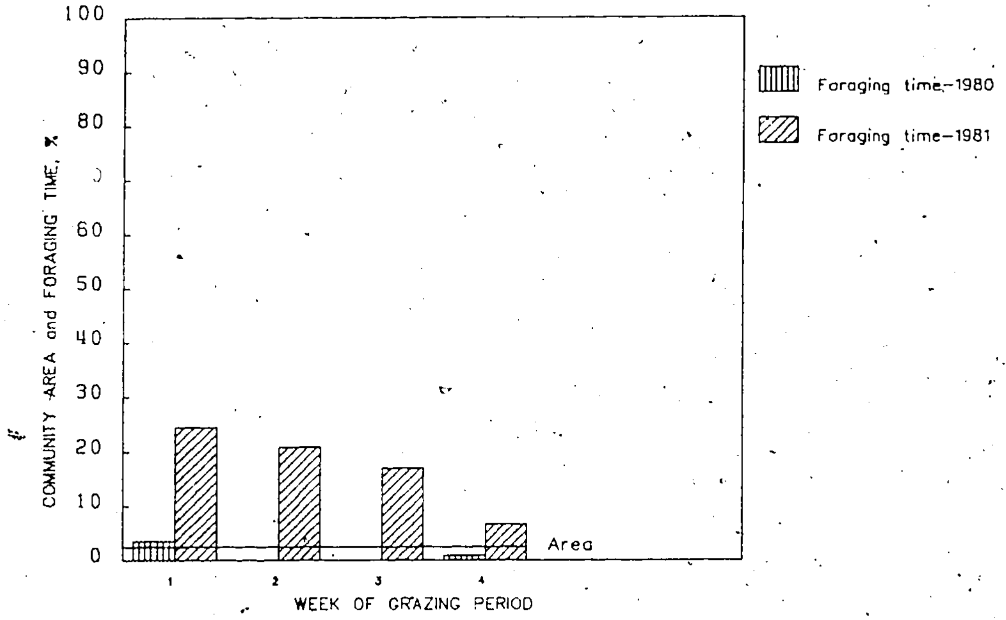

Figure 3.6 Availability and weekly use of shrubland under light October grazing (preferences or avoidances are significant at $p \leq .05$).

depletion of available browse as well as the effect of abscission. Nevertheless, selectivity among communities s greater in 1981 due to the environmental changes favoring browse availability and use (Table 3.1).

Overall, the aspen forest, forest edge phase grassland and brushed fenceline communities were consistently avoided while open grassland and silverberry phase grassland communities were preferred (Fig. 3.4). The shrubland was the most preferred in 1981, although only a secondary community in terms of use. Preference for open grassland was greater than for total shrubby phase grassland (pooled) in both years. Likewise, the most open of the shrubby phase grassland communities, the silverberry phase grassland, was more preferred than either the forest edge or snowberry phase grasslands.

Comparison of selectivity indices for the light June and light October treatments shows greater selectivity among communities in October (Table 3.1). In both years, a greater preference for open grassland and greater avoidance of forest and forest edge phase grassland was observed in October relative to June (Appendix B). Preference for total grassland (pooled) was greater in October than in June both years.

3.3.4 Heavy Grazing in October

The most heavily used community was the open grassland while the largest community, the aspen forest, was avoided both years (Fig. 3.7). The grasslands as a whole represented 92% and 74% of total use in 1980 and 1981, respectively. In 1980, the cattle grazed and regrazed the grassland several times. Cattle continued grazing throughout the various shrubby grassland communities, but the woody stems created an impediment to the grazing act and in turn, the intake rate. Thus, animals would sometimes quit grazing in a shrubby phase grassland community and trail to an open grassland, especially when the woody stem density and impediment to grazing were relatively high.

Cattle usually avoided the forest perimeter. However, use in the forest was sometimes noted where forage was available in quantity. The brushed fenceline and wetland communities were also generally avoided, although considerable use of a dry *Carex* wetland was noted during the final week of grazing when grassland forage supplies were largely depleted. This heavy use during the final week contributed to an insignificant avoidance index for *Carex* wetland in 1980.

Minor differences in behavior were observed in 1981. Cattle used the forest and shrublands more in an apparent response to the late growing season and late frost. The increased use was a function of the increased availability of forages, particularly woody leaves and current annual growth. An increase in use on the forest edge and snowberry phases was also noted, particularly during the first week of grazing when palatable browse was still available. However,

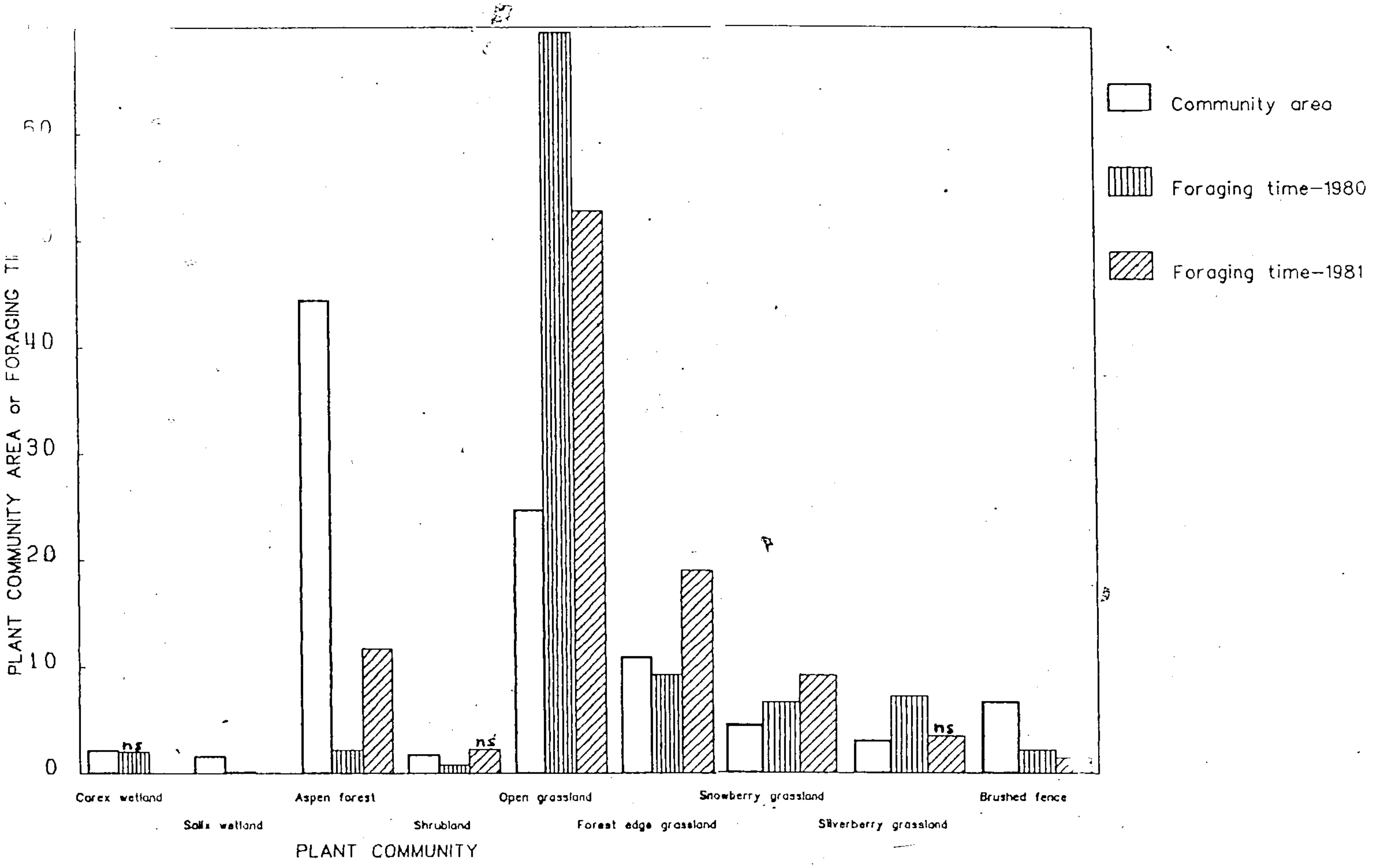

Figure 3.7 Area (%) in each plant community and proportion of total time (%) spent foraging in each under heavy October grazing, 1980 and 1981 (preferences or avoidances are significant at p≤.05 unless denoted by non-significance (ns)).

under heavy grazing, the more palatable sources of browse were largely depleted by the end of the first week and cattle returned to more available forage sources in the open grassland. In the third week of grazing an increase in use of western snowberry was noted. It was the only remaining source of browse with leaves and berries attached and, due to grassland herbage depletion under heavy grazing and summer drought, it had become a relatively preferred source of forage. Thus, an increase in use of shrubland, forest, forest edge grassland and snowberry phase grassland was evident. The fourth and final week of grazing showed another return to herbaceous foraging in grassland communities following snowberry depletion.

Overall, the aspen forest was avoided and open grassland preferred (Fig. 3.7). Forest and shrubland were avoided less and the forest edge and snowberry phase grasslands more preferred in 1981. Conversely, the two most open communities, the silverberry phase and open grasslands, showed lower preference responses in 1981. However, open grassland was still more preferred than total shrubby phase grassland (pooled) in both years.

Comparison of selectivity indices with the light October treatment showed greater selectivity among communities under heavy October grazing in 1980 only (Table 3.1). Consistently greater preference for grassland as a whole (pooled) was observed under heavy grazing, in agreement with June results (Appendix B).

Comparison of the selectivity indices for the heavy October and heavy June treatments showed greater discrimination among communities in October, consistent with results of the two light grazing treatments (Table 3.1). Actual preferences showed consistently greater avoidance of forest and shrubland and greater preference of open grassland in October (Appendix B). The open grassland was more preferred than shrubby grassland (pooled) in October and the opposite was observed in June, a result consistent with the light grazing comparisons.

3.4 Discussion

3.4.1 Seasonal Patterns

Cattle were more selective among communities in October than in June. This difference was reflected by greater avoidance of closed communities (forest) and greater preference for more open communities (open grassland). The most obvious determinant of this behavior was a decrease in available forest forage from June to October. This was demonstrated in 1981 when a late killing frost delayed abscission of leafy browse and senescence of succulent forbs in forest and shrubland communities in late September. Subsequent use of those two communities in both light and heavy treatments was greater than in 1980, especially in the first week. These observations support FitzGerald (1982) who observed the apparent readiness of cattle to graze within the forest rather than the adjacent grassland in late August. Hilton and Bailey (1972) observed similar preferences for aspen forest during August. In both reports it was suggested that the August shift towards forest preference was due to grassland forage maturation and the relatively high moisture content of forest forage species. Indeed, Gesshe and Walton (1981) noted a strong positive correlation between moisture content and selection of mature forages. From the observed behavior in autumn, it appears that this shift in preference may last until leaf fall for browse species, or until killing frost or depletion of forest forbs occurs. Fall grassland regrowth under favorable growth conditions may further modify preference. In June, cattle also showed greater use of closed communities in 1981 than in 1980. This was largely due to the lack of palatable herbaceous regrowth on grasslands under drought conditions in June, 1981. The lack of green regrowth contributed to a rapid decline in herbaceous quality and availability. These results support the studies cited above. Cattle exhibited a shift towards forest and shrubland preference under summer drought conditions (Hilton and Bailey 1972; FitzGerald 1982). This shift was a function of forage quality as well as availability.

In addition to quality and availability, other factors were involved in seasonal differences in community preference. The negative effects of standing litter and woody stems upon the selection process and intake rate were observed in both seasons. Yet, cattle showed consistently greater preference for shrubby phase grasslands over open grassland in June, and vice versa in October. In the light June treatment, the shrubby phase grassland communities contained higher amounts of palatable forbs, native grasses and available browse relative to the open grassland. The tall forbs and long tillers of grasses tended to grow through or were spatially above the true litter layer. Cattle were quite adept at selecting grass or forbs above the litter layer with their mouths and then uprooting it with a quick jerk of the head. Under heavy June grazing, the shrubby phase grasslands provided higher levels of dead herbage biomass and browse than the open grassland. These alternate supplies of forage were more important under heavy grazing because live herbage was often depleted. In October, forbs and grasses were often mature and/or intertwined with the accumulating litter layer while most browse species were less preferred due to leaf abscission. Cattle in October were observed in long and often unsuccessful attempts to separate green forage from litter using their tongues and muzzles. The autumn leaf fall of shrubs also contributed to litter biomass in shrubby grassland communities. Thus, in addition to a direct barrier effect on the grazing process (Bailey 1970), woody stems contributed to the litter accumulation which in turn inhibited selection of palatable herbage. These factors made preferred herbage more accessible and available in the open grassland.

3.4.2 Patterns across Grazing Intensities

The major pattern discerned was greater discrimination between communities under heavy grazing. It was consistent throughout except for October, 1981, when relatively large sustainable sources of browse under light grazing caused an increase in selectivity for forest and shrubland. Nevertheless, consistently greater preference for grassland was observed under heavy grazing. This is in agreement with Royama (1970) and others who noted that consumers spend most of their foraging time in places where food acquisition is most profitable, and that they may select less preferred or lower quality food if it is more abundant than preferred food. Thus, cattle apparently found the grasslands more profitable as sources of forage. However, the effects of June drought in 1981 caused increased forest use, perhaps due to eventual depletion of grassland forage and a lack of green regrowth. Hilton and Bailey (1972) noted similar decreases in grassland use under June drought conditions in the aspen parkland. The effect of drought upon grassland forage regrowth vigor, quality, and availability appears to cause a lowering of the "profitability" threshold for cattle grazing the forest.

The foraging behavior of cattle in plant communities has been demonstrated in this chapter. However, the preferences and avoidances of communities are mostly a function of cattle response to plant species or species groups. This will be considered next.

4. FORAGING ACTIVITIES AND DIET COMPONENTS

4.1 Introduction

The preference of cattle for open habitats is a manifestation of their foraging strategy. Therefore, differences in activities and diet proportions of specific forages should help clarify the community preferences and avoidances observed in Chapter 3. Moreover, diet proportions of forages will enable relation of animal response to quality, availability and foraging efficiency for specific forages.

Most diet composition studies have used fecal, esophageal or plant utilization estimates (Table 4.1). They indicate that browse species generally contribute less than 5% of forage consumed (or of total foraging time) by cattle foraging in summer on native rangelands. In aspen parkland, utilization estimates show that use of herbage generally exceeds that of browse (Smith et al. 1972; Hilton and Bailey 1974). However, FitzGerald and Bailey (1984) observed extensive browsing by cattle in regenerating aspen forest. They also noted a seasonal ffect whereby cattle deferred browsing in June and early July until herbage was depleted to 750 kg/ha, but would initiate browsing in mid to late August when herbage levels still exceeded 2000 kg/ha. In spite of these implications of greater browse use, the proportion of time spent grazing or browsing on native aspen parkland range remains essentially unstudied.

Table 4.1 The proportion of browse in cattle diets (%) as estimated by various experimental methods.

Method	% Browse in diet	Range type (location)	Reference
Plant utilization estimate	4	Ponderosa pine-Blue bunch wheatgrass-Orchardgrass (Foothills-NE Oregon)	Miller and Krueger 1976.
Fecal analysis	≤5	Sagebrush-Pinyon pine-Needlegrass-Wheatgrass (Douglas Mtn., Colorado)	Hansen et al. 1977.
Fecal analysis	≤5	Southern pine-Bluestem (Louisiana)	Pearson 1976.
Esophageal fistulae	5	Blue grama shortgrass range (NE Colorado)	Vavra et al. 1977.
Fecal analysis	≤5	Mesquite-Side oats grama-Texas wintergrass (North central Texas)	Sanders et al. 1973.
Plant utilization estimate	≤5	Aspen-Spruce-Wheatgrass-Bluegrass (Subalpine range in Utah)	Smith et al. 1972.
Direct animal observation	≤5	Blue grama shortgrass range (Eastern Colorado)	Reppert 1959.

The objective of the work described in this chapter was to determine the major forage sources in the diet of cattle and the relative time spent utilizing each forage.

4.2 Methods

The group observations of cattle described in Chapter 3 were used to determine activity frequencies. These frequencies represented the proportion of animals grazing and browsing in each group observed. Thus, the two frequencies were inversely related. Mean browsing and grazing frequencies across communities, treatments and years were weighted for the number of animals in each group observed. To maintain proper degrees of freedom, each observation was also weighted for the average number of animals per group in respective communities, treatments and years. Analysis of variance tests were performed to determine if there were significant effects of community, season, grazing intensity and year on foraging activity. Sample means were tested for differences according to Steel and Torrie's (1980) method of testing unequally replicated means with the Studentized multiple-range test. Although sample means were not least squares means, the test can be considered valid in that the differences were between pairs of means in logical groupings (Winer 1971). Furthermore, the number of observations obtained for each cell was certainly large enough to produce acceptable sample means [3].

Behaviour of randomly selected individual animals was observed and recorded during the intervals between group observations. These individual observations normally lasted 3 to 5 minutes. Subsequently, thousands of bites of various forages selected by cattle were observed (Appendix C). Recorded behavior included the length of time observed, the plant community, the forages selected and the number of bites of each forage. Forages or forage sources were defined

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[3] Hardin, R.T. 1980. Personal communication.

according to species for browse plants while herbaceous species were pooled into one forage source called herbage. It was not possible to consistently recognize individual herbaceous species without disturbing the animal. Time spent by animals that lifted their heads to trail to another locale or break from feeding for more than 5 seconds was subtracted from the total time observed. The proportion of each forage source in the diet was determined by dividing the selec[illegible]r of bites by the total number of bites taken in e[illegible]ervation. The length of each observation, adjust[illegible] average length of observations in respective communities, treatments and years, was used as a weighting factor when mean diet proportions were calculated across treatments and years. Then, analysis of variance in the proportion of each major forage source in the diet was performed to determine the effect of seasons, grazing intensities and years.

Finally, an analysis of variance in diet diversity or breadth was performed. Diet breadth was defined as the number of different forage sources selected by an animal during an individual observation.

4.3 Results

Browsing represented a significant portion of total foraging time in all treatment-by-year combinations (Fig. 4.1). The proportion of foraging time spent browsing rather than grazing was greater in the drought year of 1981 than in

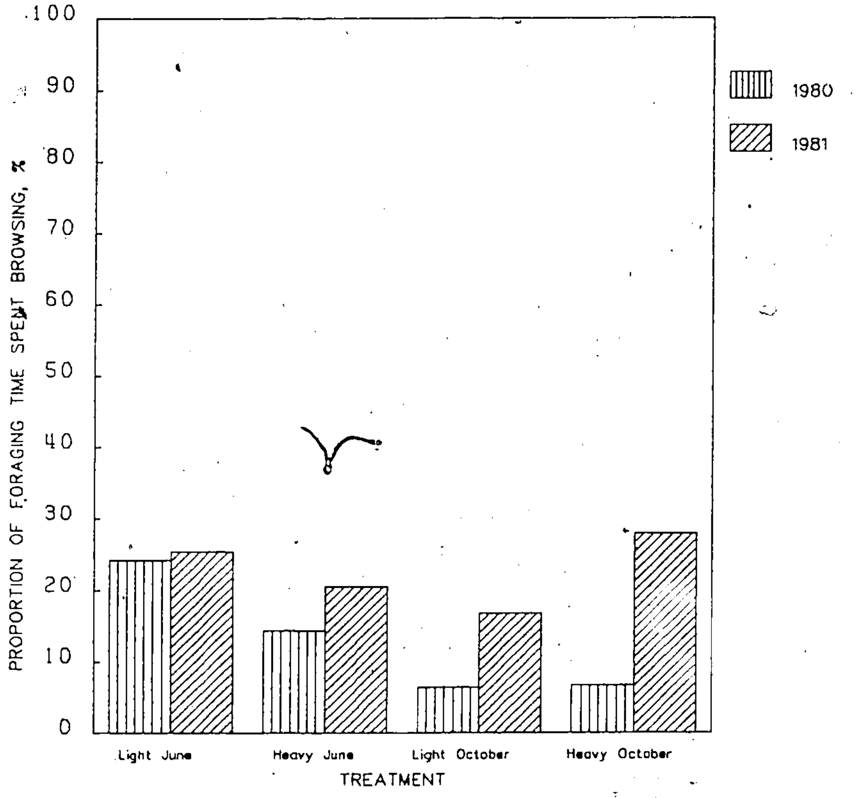

Figure 4.1 Proportion of foraging time spent browsing rather than grazing in four treatments during 1980 and 1981.

1980. Differences in the time spent grazing by cattle were noted among communities (Table 4.2). Shrubland and forest communities showed the lowest grazing frequency while the *Carex* wetland, silverberry phase grassland, and open grassland communities were essentially free of browsing activity. The time spent grazing in forest and shrubland communities was less in October than in June (Table 4.3).

Grassland herbage was the major forage source and ranged from 62 to 92% of the cattle diet (Table 4.4). Important secondary diet components were forest and shrubland herbage, aspen, rose, western snowberry and saskatoon. Grassland herbage represented a greater portion of the diet in 1980 than in 1981 (Table 4.5). Accordingly, forest and shrubland herbage use was less in 1980 and greater in 1981. A similar inverse relationship was observed for the effect of season. Grassland herbage in the diet was greater while forest and shrubland herbage was lower in October than in June. Other seasonal effects showed lower and higher diet proportions of aspen and western snowberry, respectively, in October. Diets in the two heavy grazing treatments had greater proportions of grassland herbage.

Diet diversity was greater in June than in October (Table 4.6). The forest and *Salix* wetland communities showed greatest diet diversity with shrubland, forest edge and snowberry phase grassland communities intermediate (Table 4.7). Lowest diversity was exhibited in *Carex* wetland, silverberry phase and open grassland communities. Diet

Table 4.2 Proportion of foraging time (%) spent grazing rather than browsing in nine plant communities.

Plant community	proportion of time grazing (%)
Shrubland	29 e
Aspen forest	40 d
Salix wetland	40 de
Brushed fenceline	58 d
Snowberry phase grassland	84 c
Forest edge phase grassland	88 bc
Silverberry phase grassland	100 a
Open grassland	100 a
Carex wetland	100 ab

Means followed by the same letter are not significantly different (p≤.05).

Table 4.3 Effect of season of use on the proportion of foraging time (%) spent grazing rather than browsing in nine plant communities.

	Season		
Plant community	June		October
Shrubland	38	**	4
Aspen forest	44	**	21
Salix wetland	18	**	71
Brushed fenceline	67	**	25
Snowberry phase grassland	83	ns	84
Forest edge phase grassland	89	ns	86
Silverberry phase grassland	100	ns	100
Open grassland	100	ns	100
Carex wetland	100	ns	100

** means are significantly different (p≤.05).

Table 4.4 Major forages in cattle diets (% of total bites).

	Treatment							
	light June		heavy June		light October		heavy October	
Forage source	1980	1981	1980	1981	1980	1981	1980	1981
Grassland herbage	68	62	77	71	85	72	92	79
Shrubland or forest herbage	7	12	6	11	2	6	+	2
Aspen	4	6	5	3	0	0	+	+
Rose	18	6	8	8	3	12	+	[illegible]
Western snowberry	0	0	+	3	9	7	7	12
Saskatoon	2	7	2	3	2	4	0	2
Total herbaceous forage	74	74	83	82	87	77	92	81
Total browse	26	26	17	18	13	23	8	19

Table 4.5 Effect of year, grazing intensity, and season on the proportions of major forages in cattle diets (%).

	Year			Intensity			Season		
Forage source	1980		1981	light		heavy	June		Oct.
Grassland herbage	78	**	71	69	**	77	71	**	83
Shrubland or forest herbage	5	**	9	8		6	9	**	2
Aspen	4		3	3		3	4	**	+
Rose	8		7	11		6	9		4
Western snowberry	2		5	2		4	1	**	9
Saskatoon	2		4	4		2	3		1
Total herbaceous forage	83		80	76	*	84	80		85
Total browse	17		20	24	*	16	20		15

** denotes significant difference between means (p≤.05).
* denotes significant difference between means (p≤.10).

Table 4.6 Effect of year, grazing intensity and season of use on the number of forage sources selected during an observation.

	Year			Intensity			Season		
	1980		1981	light		heavy	June		Oct.
number of forage sources	1.79	ns	1.67	1.84	ns	1.68	1.91	**	1.28

** denotes significant difference between means (p≤.05).

Table 4.7 The number of forage sources selected during an observation in nine plant communities.

Plant community	number of forage sources
Carex wetland	1.00 de
Open grassland	1.10 e
Silverberry phase grassland	1.15 e
Snowberry phase grassland	1.78 d
Forest edge phase grassland	1.87 cd
Shrubland	2.11 c
Brushed fenceline	2.46 bc
Salix wetland	2.89 b
Aspen forest	3.66 a

Means followed by the same letter are not significantly different (p≤.05).

diversity was greater in the forest, forest edge phase grassland and snowberry phase grassland communities in June than in October (Table 4.8). There was a consistent trend of greater diet diversity in June than in October in five of the six other plant communities.

4.4 Discussion

Grazing was the major foraging activity of cattle but browsing was significant in all treatments and in most plant communities at levels usually exceeding those documented in the literature.

The summer-long drought of 1981 resulted in less foraging time spent grazing and more browsing than in 1980. Drought inhibited regrowth of grasses and forbs following grazing in June. This had negative effects on availability of green herbage and the overall quality of herbaceous forage. The effect on quality was more important under light June grazing where forage availability and selectivity were relatively high. The ample grassland forage remaining after initial grazing was predominantly poor quality dead herbage. This dead herbage included carryover from previous growing seasons as well as standing drought-killed herbage from the current growing season. Thus, animals increased use of palatable browse and forest forbs. Conversely, the lack of regrowth under heavy June grazing caused animals to deplete dead herbage supplies as well as browse supplies. In this treatment, the increase in use of browse species was largely

Table 4.8 Effect of season of use on the number of forage sources selected during an observation in nine plant communities.

Plant community	number of forage sources selected in: June		October
Carex wetland	1.00	ns	1.00
Open grassland	1.14	ns	1.03
Silverberry phase grassland	1.22	ns	1.00
Snowberry phase grassland	1.88	**	1.57
Forest edge phase grassland	1.95	**	1.35
Shrubland	2.18	ns	1.98
Brushed fenceline	2.53	ns	1.40
Salix wetland	3.00	ns	1.00
Aspen forest	3.80	**	2.50

** denotes significant difference between means ($p \leq .05$).

a function of declining food availability and selectivity (Emlen 1966; Menge 1972). The drought also resulted in lower supplies of grassland forage in October. In addition, leaf abscission in browse species was delayed due to the late killing frost. Thus, an increase in browsing occurred in October, 1981, as cattle heavily utilized leafy browse and forbs in shrubland and forest communities. However, forest forbs were generally depleted or senesced by the middle of the second week of grazing (Fig. 3.5), while an abundance of western snowberry, rose and saskatoon leaves remained available in the shrubland until the final week of grazing (Fig. 3.6). Accordingly, use of these browse species was greater than in October, 1980.

Proportion of time spent grazing was greater in October than in June due to the lower availability of browse leaves as alternate forage. As documented in Chapter 3, cattle spent considerably more time in grassland communities in October than in June. Similarly, more time was spent grazing under a heavy intensity because cattle were forced back onto grasslands following shrubland and forest forage depletion. This rapid depletion of shrubland and forest forages was partially due to the low productivity and vigor of shrub layers after 8 years exposure to the heavy grazing treatments (Chapter 2).

The most significant determinant of foraging activity was the plant community and its interaction with season. The *Carex* wetland, open grassland and silverberry phase grassland communities had essentially no palatable cattle browse. Cattle browsed aspen, rose, and western snowberry in the forest edge and snowberry phase grasslands in both June and October. The cattle preferred aspen and rose over western snowberry in June. The opposite was true in October because western snowberry was the only browse species to normally retain leaves and berries throughout October. Indeed, foraging activities in the brushed fenceline, similar in composition but lacking the herbaceous productivity of these two grasslands, illustrate the use of western snowberry in autumn. This community exhibited browsing for 33 versus 79% of foraging time in June versus October, respectively. The *Salix* wetland was mainly browsed in June and grazed in October. This was due to the heifers' preference for *Salix* leaves in June and their relative unavailability in October following abscission. The forest and shrubland communities showed the greatest changes in activities between seasons. Cattle spent considerable time grazing succulent forbs in June while in October these communities were predominantly browse sources; this due to the quick senescence of palatable forbs following the first killing frost of autumn.

At the forage source level, the results confirmed the dominant foraging activities and community preferences discussed in Chapter 3. Herbaceous forages dominated cattle diets in both June and October, in agreement with major published works (Pearson 1976; Hansen et al. 1977; Miller et al. 1976; Vavra et al. 1977; Reppert 1959; Ellis and Travis 1975). However, total browse as forage ranged from 7 to 26% of the diet in various treatments. This ranges from about 40 to 400% higher than previously reported.

With the exception of western snowberry, cattle used less browse (especially aspen) in autumn than in June. Western snowberry showed a dramatic increase in use in autumn because it retained leaves and palatable berries long after leaf abscission had occurred in other browse species. However, use of western snowberry under light October grazing in 1981 was less than the previous autumn because the prolonged growing season had delayed abscission of other browse species. This caused an increase in use of other browse species, specifically rose and saskatoon, and abnormally available forest and shrubland forbs. Similar behavior occurred in the heavy October treatment, but increases in use of forbs, rose and saskatoon were limited by the relatively low productivity of those strata in that treatment (as noted in Chapter 2). Accordingly, grassland herbage use was substantially less in October, 1981. This effect of year upon grassland and forest herbage use was apparent throughout 1981. The drought in June of 1981 inhibited grassland regrowth and caused increased use of forest and shrubland herbage. Hilton and Bailey (1974) and FitzGerald (1982) observed greater use of sprayed and burned aspen forest, respectively, during extended periods of dry weather. In both studies it was suggested that quality factors, particularly moisture, played an important role in determining the shift in preference. This study's results support those suggestions. In 1981, unlike the previous year, a rapid decline in moisture and crude protein content of grassland forages occurred during the second half of both June treatment grazing periods (Appendix E). These changes accompanied the shift towards increased shrubland and forest use. The differences in quality of herbage between grassland communities and forest or shrubland communities was also obvious (Appendix E). Furthermore, the quality of certain available browse species also favored use of closed communities under drought conditions. Greater use of grassland herbage under heavy grazing was due mainly to the rapid depletion of forest and shrubland forage sources forcing animals to return to grasslands for forage. The low productivity of herb and low shrub strata under heavily grazed treatments contributed to the rapid depletion of forest and shrubland forages.

Diet breadth or diversity was greater in June than in October. The greater availability of green and leafy browse species in June was the main cause of this behavior. Similarly, the browse species composition of the forest community made it the most diverse in terms of diet composition. The largest decreases in diet diversity across seasons occurred in the forest and forest edge grassland communities. In the forest, senescence of forbs and abscission of browse species like aspen, dogwood, rose and saskatoon contributed to the large decrease in diversity. In the forest edge phase grassland, the main reason for the decrease in diet diversity in October was cattle avoidance of aspen suckers and other browse species on the forest fringe, excepting western snowberry. Similarly, diets for all other communities showed decreased diversity; largely associated with changes in browse species morphology.

Grazing was the major foraging activity of cattle and was closely linked to domination of the diet by grassland herbage. However, the greater browse use by cattle in 1981 under drought indicates that forage and community preferences are related to the quality, abundance and availability of various forage sources.

5. FORAGING RATES AND EFFICIENCIES

5.1 Introduction

Forage and community preferences indicate that grasslands likely contain the most profitable sources of forage. The apparent differences in DM intake rates among forages and communities represent the effects of forage abundance, composition and structure upon animal response.

Cattle are generally considered relatively non-selective ruminant herbivores due to their rate of food passage, rumen and mouth morphology (Rice et al. 1971; Ellis and Travis 1975; Willms 1978). Ellis and Travis (1975) classify them as non-selective bulk and roughage eaters that pack their large rumens with coarse fibrous foods during lengthy and intensive bouts of grazing. Nevertheless, they are known to prefer leaves and new growth (Arnold 1964; Chacon and Stobbs 1976). As the leafy component is removed from the sward, cattle are forced to take small bites in efforts to harvest remaining leaves. Cattle cannot fully compensate for reduced bite size and available herbage by increasing foraging rates and grazing time (Chacon and Stobbs 1976), unlike wapiti and other smaller ruminants (Hudson and Nietfeld 1984). Therefore, bite size and leaf yield are major factors determining intake rates for cattle. Indeed, their large incisor row width (Clutton-Brock and Harvey 1983), enables them to increase intake rates at biomass levels exceeding 3000 kg/ha (Chacon and Stobbs

1976). In comparison, caribou and wapiti are unable to increase intake rates at biomass levels greater than 1000 and 2500 kg/ha, respectively (White et al. 1975; Hudson and Nietfeld 1984).

The major objective of this part of the study was to determine differences in bite size, bite rate, and DM intake rate among major grassland and forest forages. These comparisons should indicate whether foraging behavior is largely dependent on food abundance and the relative profitability of intake amongst forages. At the same time, the measures will provide the data base necessary to formally test the relationship. They will also assist in interpretation of forage and community preferences.

5.2 Methods

Observations of individual heifers (Chapter 4) provided the measures needed to determine bite rates for the various communities, seasons, grazing intensities and years. The total number of bites taken in each individual observation was divided by the length of the observation (in minutes) to determine the bite rate. Overall bite rates were weighted for the length of observations and the average length of observations in respective communities, treatments and years. An analysis of variance was performed on bite rates and sample means tested for least significant differences according to Steel and Torrie's (1980) method for comparing unequally replicated means (Chapter 4).

In June, 1981, bite size estimates were collected by mimicking actual bites of heifers during the individual observations. Each bite estimate was hand picked to duplicate as closely as possible the amount and species composition ingested, then retained in a separate bag for weighing. Three randomly selected bites of not less than five animals were estimated for eight forage types on each of six days in both June treatments. These estimates were obtained during days 5, 6, 7, 20, 21, and 22 of the four-week grazing period. This gave a minimum total of 45 bite estimates per forage type for days 5-7 and 20-22, respectively, in each treatment. Forage types were defined as certain forage sources obtained from certain plant communities. The forage types sampled included aspen, rose, saskatoon, and herbage from the forest community, and herbage from the four grassland communities. An analysis of variance of bite size (g) across forage types, day of grazing period and grazing intensity was performed and sample means were tested for least significant differences according to Steel and Torrie (1980). Similar procedures were then applied to the estimated DM intake rate, the product of bite size and bite rate.

Measures of herbaceous biomass (kg/ha) for the major communities were obtained from 0.5 m² plots clipped before and after grazing periods (Appendix D). These plots were placed in the four grassland communities, the aspen forest and shrubland communities at ten randomly chosen points per community in each treatment-by-year combination. Plots were harvested prior to and after grazing and biomass was separated into live and dead herbage in each of the ten clip points per community. Samples were placed in paper bags in the field, then dried at 64°C for 24 hours and weighed. In addition, combined samples made up of small portions from the ten live and dead samples were collected for each community and retained in a plastic bag in the field. Moisture was determined by weighing the sample prior to and after oven drying for 24 hours. Dried samples were then ground with a 10 cm diameter Wiley mill (1 mm screen size) and subjected to chemical composition analysis for acid detergent fiber, phosphorus and nitrogen (crude protein) levels. The herbaceous biomass levels (kg/ha) determined for the communities were regressed with bite rates (bites/minute) and bite sizes (g/bite). The crude protein quality attribute (%) was tested for any additive effect to DM intake (g DM/minute) as the best indicator of foraging behavior by regressing crude protein intake (grams crude protein/minute) with the same attributes.

Finally, plant communities were ranked according to the degree of barrier imposed by brush upon grazing animals (Table 5.1). Rankings were subjective assessments of the physical barrier to grazing based on % cover, shrub density, and growth habit. For example, western snowberry usually represented a greater impediment to grazing than silverberry due to its low, wide growth habit, high cover and stem

Table 5.1 Definition of rankings for the barrier effect of brush on grazing.

Ranking	Barrier to grazing	Plant communities typified
1	none	Open grassland, Carex wetl
2	light	Salix wetland, Silverberry phase grassland, Forest edge grassland having Snowberry cover ≤ 25%.
3	moderate	Snowberry phase grassland, Forest edge grassland having Snowberry cover ≥ 25%, Aspen forest.
4	heavy	Shrubland.

density. These arbitrary rankings were used for nonparametric correlation with bite rates, bite sizes and DM intake rates.

5.3 Results

The bite rates of cattle varied significantly by year, grazing intensity and community. Interaction of community with grazing intensity was also a significant source of variation. Bite rates were greater in 1981 and under heavy grazing treatments (Table 5.2). Wide variations in bite rates among communities were also noted. Bite rates were lowest in shrubland and forested communities and became progressively higher on more open communities, the highest rate occurring in the open grassland (Table 5.3). Greater bite rates were apparent under heavy grazing for all

Table 5.2 Effect of year, grazing intensity and season of use on the bite rates of cattle (bites/minute).

	Year			Intensity			Season		
	1980		1981	light		heavy	June		Oct
Bite rate (n/min.)	42	**	49	40	**	47	44	ns	47

** denotes significant difference between means (p≤.05).

Table 5.3 Bite rates of cattle (bites/minute) in nine plant communities.

Plant community	bite rate (n/min.)
Salix wetland	19.2 [illegible]
Shrubland	19.4 [illegible]
Aspen forest	21.9 f
Brushed fenceline	29.6 e
Snowberry phase grassland	37.9 d
Carex wetland	42.3 bcde
Forest edge phase grassland	42.9 c
Silverberry phase grassland	52.4 b
Open grassland	59.2 a

Means followed by the same letter are not significantly different (p≤.05).

grassland communities while forest and shrubland communities showed no differences in bite rates between grazing intensities (Table 5.4). In grassland communities, a significant negative relationship of bite rate to total herbaceous biomass prior to grazing was apparent (Fig. 5.1). No consistent relationship was established in the forest and shrubland communities.

Bite size varied significantly by forage type and grazing intensity in June, 1981. The interaction of the number of days of grazing (in the 28 day grazing period) and grazing intensity also had a significant effect on bite size. Overall, bite size was greatest under light grazing (Table 5.5). However, this difference between treatments was apparent only on the second sampling date (Table 5.6). The difference was due to the apparent unlimiting supply of available forage on the grasslands of the light June treatment, as evidenced by the positive relation of bite size with days of grazing for that treatment (Table 5.7). In contrast, the grassland under heavy grazing showed a negative but insignificant relationship of bite size with days of grazing. Both forest communities exhibited a decreasing bite size also, significant under light grazing and indicative of some degree of forage depletion.

Bite sizes were, on average, higher for grassland forages than for forest forages (Table 5.8). However, differences in bite size amongst individual forages were less dramatic than for bite rates. Bite sizes for rose,

Table 5.4 Effect of grazing intensity on the bite rates of cattle (bites/minute) in nine plant communities.

Plant community	Intensity light		Intensity heavy
Salix wetland	19	ns	28
Shrubland	20	ns	19
Aspen forest	23	ns	21
Brushed fenceline	24	ns	31
Snowberry phase grassland	32	**	40
Carex wetland	42	ns	42
Forest edge phase grassland	40	*	44
Silverberry phase grassland	48	**	54
Open grassland	54	**	62

** means are significantly different ($p \leq .05$).
* means are significantly different ($p \leq .10$).

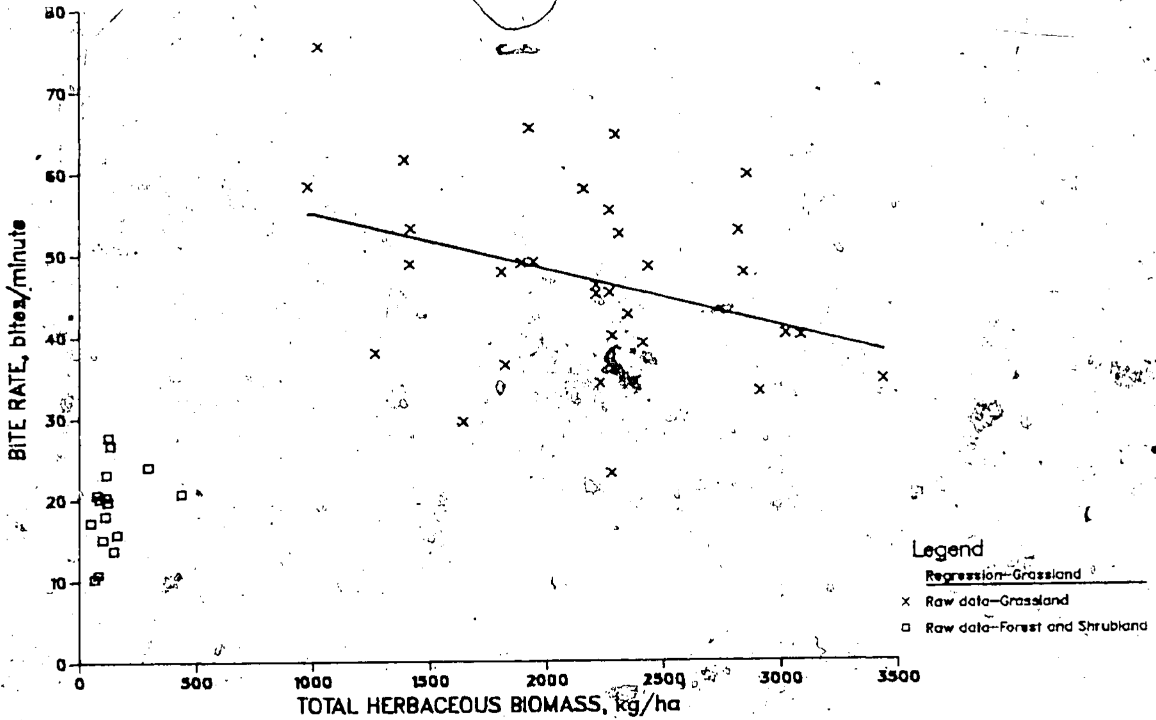

Figure 5.1 Regression of bite rates with total herbaceous biomass prior to grazing for grasslands, forests and shrublands in all treatments and both years (Regression equations: for grasslands $Y=-.007X+61.9$ at $p \leq .02$, $R^2=.13$; for forest and shrublands not significant at $p \leq .05$).

Table 5.5 Effect of grazing intensity and number of days of grazing (during a 28-day grazing period) on bite size (g DM/bite).

	Intensity			Day of grazing		
	light		heavy	6th		21st
bite size (g DM/bite)	0.97	**	0.69	0.81	ns	0.84

** denotes significant difference between means (p≤.05).

Table 5.6 Effect of day of grazing on bite size (g DM/bite) under light and heavy June grazing, 1981.

	Treatment and day of estimates			
	light June 6th day	heavy June 6th day	light June 21st day	[illegible] June [illegible] day
bite size (g DM/bite)	0.81 b	0.81 b	1.17 a	0.58 b

Means followed by the same letter are not significantly different (p≤.05).

Table 5.7 Effect of number of days of grazing on bite size in forest and grassland communities under light and heavy June grazing, 1981, as expressed by the simple correlation coefficient (r) and its significance level (p).

Correlating bite size with day of grazing for:	forest		grassland	
	r	p	r	p
light June grazing	-.60	.057	.81	.007
heavy June grazing	-.39	ns	-.45	ns

ns-not significant at p≤.10.

Table 5.8 Effect of forage type on bite size (g DM/bite).

Forage type (plant community)	bite weight (g DM)
Herbage (forest)	0.42 c
Rose (forest)	0.49 bc
Saskatoon (forest)	0.56 bc
Herbage (Snowberry phase grassland)	0.83 abc
Aspen (forest)	0.85 abc
Herbage (Forest edge phase grassland)	0.89 ab
Herbage (Silverberry phase grassland)	1.03 ab
Herbage (Open grassland)	1.22 a
Mean of the four forest forages	0.58 b
Mean of the four grassland forages	0.99 a

Means followed by the same letter are not significantly different (p≤.05).

saskatoon and aspen in the forest and the forage in the three shrubby phase grassland communities were not significantly different. The only two extremes in bite size were the herbage in the forest and open grassland communities. The former had a smaller bite size than three grassland forages while the latter had a bite size greater than three forest forages. However, by day 21 of the grazing period, bite sizes of all forest forage types were significantly lower than any of the grassland forages in both treatments. Thus forest forage depletion from Day 6 to Day 21 was apparent under both grazing intensities.

The interaction of grazing intensity and forage type showed that bites of forest edge and open grassland forages were smaller under heavy grazing; indicative of repeated grassland use following forest and shrubland depletion in that treatment.

Bite size showed no relationship with total herbaceous biomass levels in the forest community but there was a positive relationship in grassland communities (Fig. 5.2). In grasslands, bite rates were lower and bite sizes greater in areas with higher herbaceous biomass.

The DM intake rate was the product of bite rate and bite size. It represented a measure of the foraging efficiency of cattle. The foraging efficiency of cattle varied significantly among forage types. Forest forages had the lowest foraging efficiencies while forages from shrubby phase grasslands were intermediate (Table 5.9). Dry matter

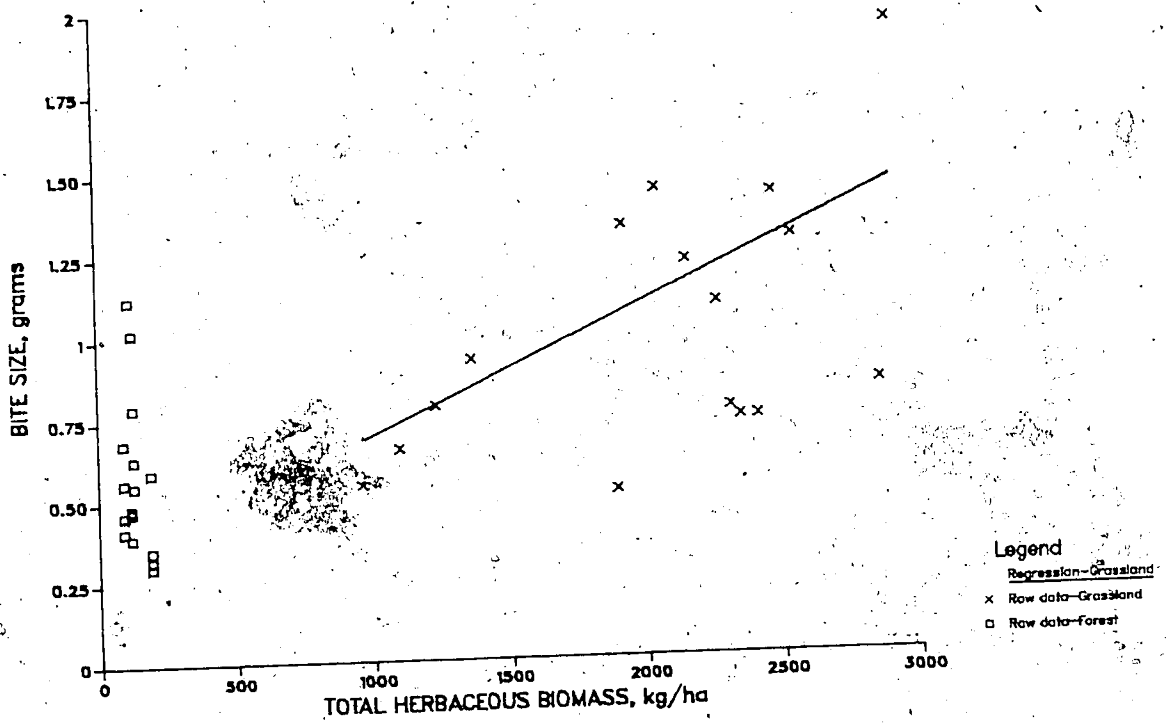

Figure 5.2 Regression of bite size with total herbaceous biomass prior to grazing, June, 1981 (Regression equations: for grasslands $Y=.0004X+.29$ at $p \leq .01$, $R^2=.30$; for forests not significant at $p \leq .05$).

Table 5.9 Foraging efficiency (g DM Intake/minute) of various forages in June, 1981.

Forage type (plant community)	g DM Intake/minute
Rose (forest)	11.2 c
Saskatoon (forest)	12.9 c
Herbage (forest)	14.2 c
Aspen (forest)	14.3 c
Herbage (Snowberry phase grassland)	33.6 bc
Herbage (Forest edge phase grassland)	38.9 bc
Herbage (Silverberry phase grassland)	59.3 ab
Herbage (Open grassland)	74.1 a
Mean of the four forest forages	13.2 b
Mean of the four grassland forages	51.5 a

Means followed by the same letter are not significantly different (p≤.05).

intake was highest in the open grassland, five times more than the greatest intake rate for a forest forage. Intake was positively related to bite rates and bite sizes in grassland and forest, forest forages being associated with the lowest intake rates (Figs. 5.3, 5.4). Dry matter intake showed no significant relationships with total herbaceous biomass levels for forest or grassland forage types over the whole grazing period (Fig. 5.5). However, a positive relationship between foraging efficiency and herbaceous biomass was apparent in grassland at the second sampling date. By that date, herbaceous biomass levels in all grassland communities had been depleted to less than 1500 kg/ha under heavy grazing. Accordingly, foraging efficiency was also lower in that treatment, indicating the importance of bite size in determining intake rates. The multiplication of a forage quality factor (crude protein) with DM intake rates produced measures of quality intake rates for cattle (g of crude protein/minute). However, they did not improve clarity of the relationships noted above.

Finally, the barrier effect of brush showed a consistent negative effect upon bite rates, bite sizes and foraging efficiency over all communities and amongst grasslands alone (Table 5.10).

To summarize, cattle exhibited higher bite rates, bite sizes and foraging efficiencies in more open grassland communities. Forest forages were more quickly depleted than grassland forages. Crude protein, a quality indicator,

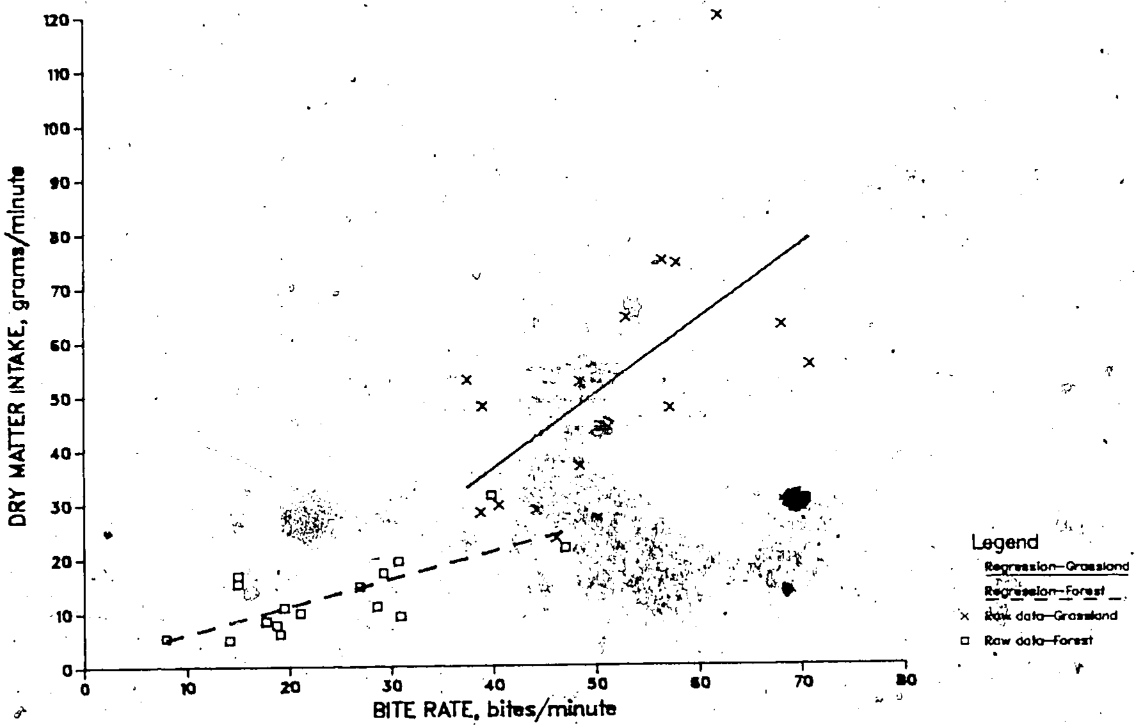

Figure 5.3 Regression of foraging efficiency (DM intake rate) with bite rates, June, 1981 (Regression equations: for grasslands $Y=1.37X-18.3$ at $p\leq.01$, $R^2=.33$; for forests $Y=.50X+1.27$ at $p\leq.00$, $R^2=.52$).

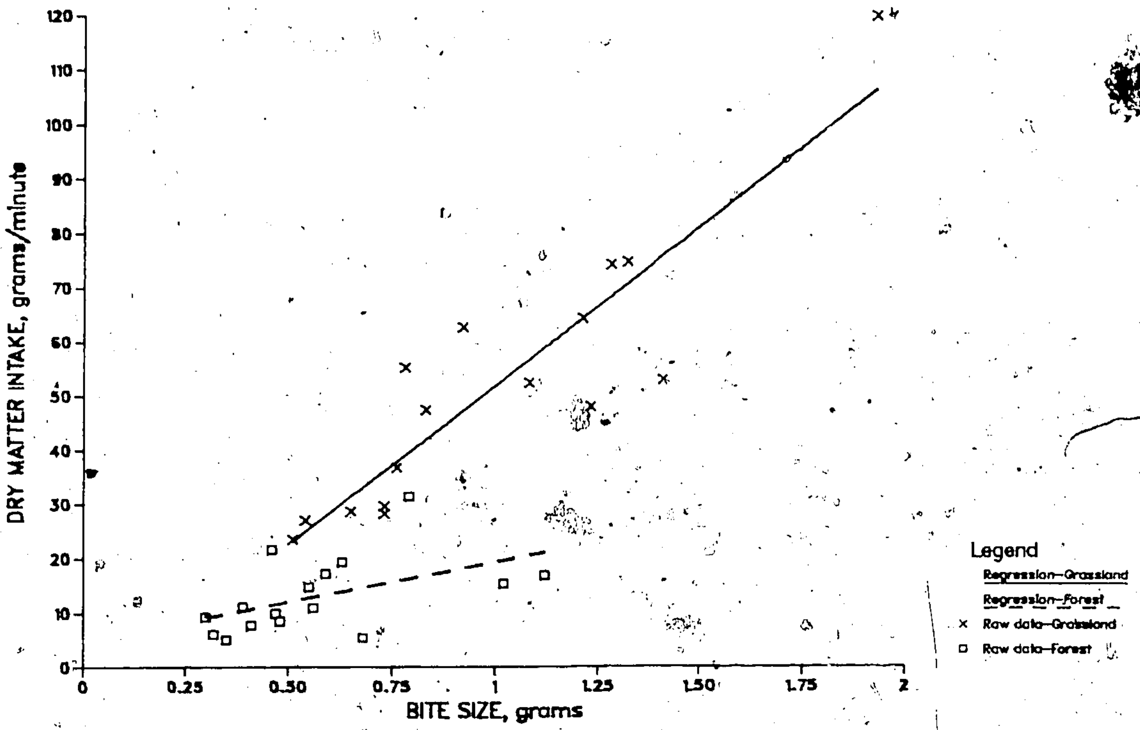

Figure 5.4 Regression of foraging efficiency (DM intake rate) with bite size, June, 1981 (Regression equations: for grasslands $Y=58.26X-6.45$ at $p \leq .00$, $R^2=.81$; for forests $Y=14.54X+4.87$ at $p \leq .03$, $R^2=.24$).

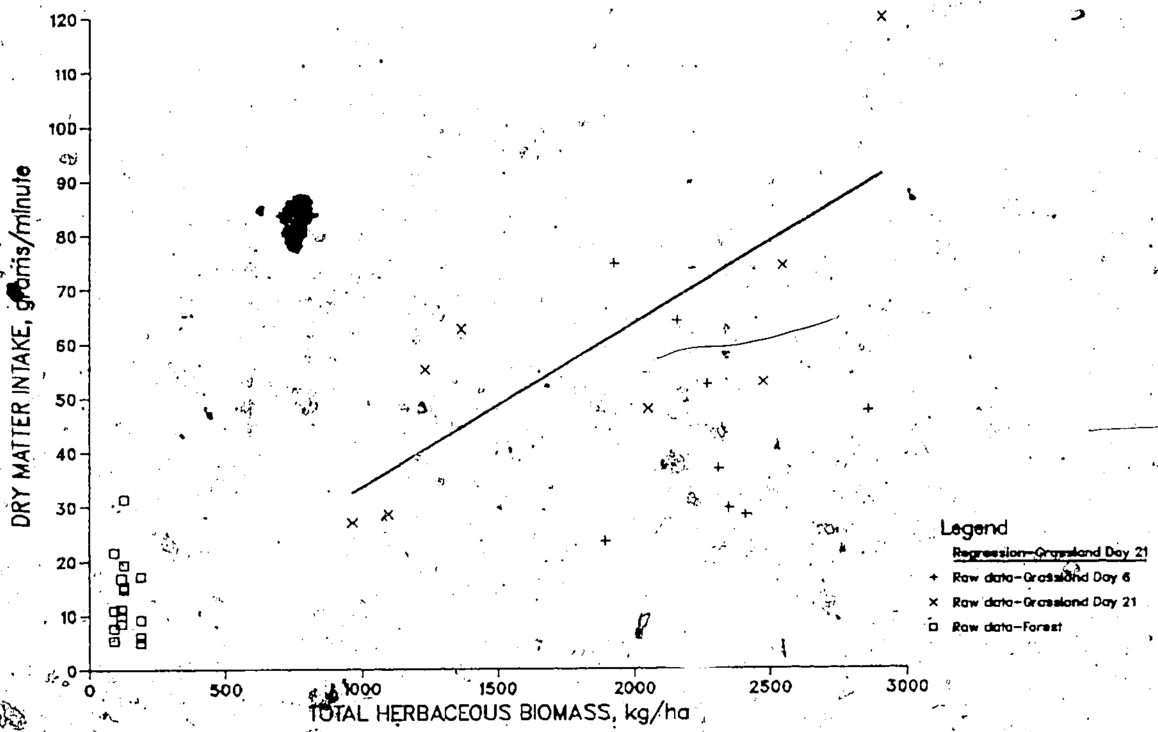

Figure 5.5 Regression of foraging efficiency (DM intake rate) with total herbaceous biomass during June, 1981 (Regression equations: for grasslands on day 6 not significant at $p \leq .05$; for grasslands on day 21 $Y = .03X + 3.62$ at $p \leq .01$, $R^2 = .60$; for forests not significant at $p \leq .05$).

Table 5.10 Barrier effect of brush on bite rate, bite size and foraging efficiency (DM intake rate) in June, 1981, as expressed by the Spearman's correlation coefficient (r) and significance level (p).

Correlating the barrier effect with:	bite rate		bite size		DM intake	
	r	p	r	p	r	p
for all forage types	-.85	.000	-.58	.001	-.78	.001
for grassland forage types only	-.74	.001	-.45	.040	-.67	.002

showed no additional predictive effect to DM intake as the measure of foraging efficiency for cattle.

5.4 Discussion

Yearly effects upon the foraging rates of cattle were observed. These yearly differences were largely due to the pronounced drought in 1981 that affected forage availability. Unlike 1980, the drought inhibited grassland herbaceous regrowth after the first grazing by cattle in June, 1981. Cattle responded by increasing their bite rates in attempts to increase intake (Chacon and Stobbs 1976). This decreased selectivity under situations of lowered food density or availability has been confirmed in other studies (Emlen 1966; Menge 1972). These observations are further qualified by the effect of intensity whereby bite rates were greater under heavy grazing. The cattle exhibited a foraging strategy based on maximizing intake. Conversely, cattle under light grazing were more selective amongst numerous abundant food types and utilized palatable forbs and browse species longer without depletion. This supports work by Ellis et al. (1976) who stated that "when the choice of available foods is limited by food availability, preferences play a less important role in determining diet composition". Furthermore, grasslands in the light grazing intensity treatments often contained large amounts of litter that inhibited selection of palatable herbaceous species. Finally, the simple effect of forage abundance upon bite size could be expected to result in lower bite rates under light grazing treatments (Chacon and Stobbs 1976). Thus, bite rates in grassland communities were negatively correlated to total herbaceous biomass levels prior to grazing. However, these differences in bite rates with respect to grazing intensity were restricted to grassland communities only. Forest and shrubland bite rates were consistently low for both intensities and showed no relationship to total herbaceous biomass, in part a function of the limited range in herbaceous biomass levels among the forests of respective treatments. It was also likely due to the highly selective response to the diverse diet available as well as the absence of litter as an effect on selection in the forest. Furthermore, animals were unable to harvest browse and forb species as quickly as herbaceous material in grasslands due to differences in species morphology and the spatial proximity of plants.

The open grassland community exhibited the highest bite rate. Bite rates in grassland communities were similar to those determined by Chacon and Stobbs (1976) on tame pasture. However, rates in that study were based on a 24 hour period while in this study they were determined during major feeding periods. Therefore, foraging rates in this study were likely lower when averaged over a 24 hour period. Such a method would have accounted for periods of less intensive grazing (Dwyer 1961). A strong negative relationship of bite rate with the woody stem barrier to grazing was established amongst the grassland communities. This supports research by Bailey (1970) who observed the barrier effect of silverberry upon grazing. Silverberry and aspen growth habits were notably less inhibitive to grazing than rose, saskatoon or western snowberry. Bite rates in the shrubby phase grasslands indicated as much. The snowberry phase grassland, which contained the highest cover of western snowberry and rose, had the lowest bite rate. The forest edge phase grassland, having aspen and some western snowberry as the dominant shrubs, had an intermediate bite rate. Finally, the silverberry phase grassland, having only silverberry as the dominant shrub, exhibited the highest bite rate of the three communities. The barrier effect of woody stems contributed to litter build-up as well (Bailey 1970), which in turn had additional negative effects upon bite rates in shrubby phase grasslands, especially under light grazing.

Bite rates within communities were generally not different between seasons. An exception was the forest edge grassland which showed greater bite rates in October. This was likely due to the relatively greater grazing pressure in grasslands associated with the non-use of forest in October (Chapter 3) and the lower use of aspen suckers as forage.

Bite sizes of cattle in this study ranged from about 0.25 to 2.0 g/bite. This is significantly more than estimates by Chacon and Stobbs (1976) ranging from 0.07 to 0.35 g/bite on tame pasture in Australia. Hudson and Nietfeld (1984) found bite sizes for wapiti ranged from 0.11 to 0.36 g/bite in grass openings of an aspen-boreal forest. The similarity of that habitat to the study area and the documented difference in mouth size between wapiti and cattle indicates the bite size estimates in this study were reasonably realistic.

Over the complete grazing period of June, 1981, bite sizes were larger under light grazing. However, this difference was not apparent at day 6 of the grazing period. Cattle were selecting palatable herbaceous species and green grass at this time. This preference for live and leafy biomass has been confirmed by Chacon and Stobbs (1976) and others. Then, by day 21, bite size increased under light grazing. This happened because grassland regrowth on locally overgrazed areas had been inhibited by drought thereby forcing cattle to utilize less palatable herbage in areas containing considerable amounts of herbaceous litter. Unlike grassland forages, bite sizes for forest forages actually decreased from day 6 to day 21 under light grazing. In essence then, forest forages were largely depleted by Day 21 relative to the grasslands. On the basis of herbaceous biomass levels within the forest, depletion could be expected in spite of the light grazing intensity. However, use of the forest forages was not due to severe limitations on grassland forage availability since similar levels of browse use were observed in June, 1980 (Chapter 4). Under the heavy grazing intensity, bite sizes in both forest and grassland forages decreased (insignificantly) from day 6 to day 21. Due to the lack of grassland regrowth under drought, cattle used the forest and shrublands heavily as emergency sources of forage. Thus, both grasslands and forest were largely depleted of forage supplies by the end of the grazing period, selectivity was almost nil and use was governed predominantly by availability (Chapter 3).

As with bite rates, bite sizes were greatest in the open grassland community where the impediment to grazing by brush was minimal. Woody stems, particularly western snowberry, impeded bite selection in the forest edge and snowberry phase grasslands.

Foraging efficiency estimates averaged 52 g/minute in grassland communities in this study. That exceeds previously documented maximum intake rates of 18 g/minute for both cattle (Chacon and Stobbs 1976) and wapiti (Hudson and

Nietfeld 1984). The estimates from this study may be overly large in that foraging rates and bite sizes were determined during major feeding periods when maxima are most likely attained (Dwyer 1961). Nevertheless, based on their larger mouth size and ability to increase intake rates at higher biomass levels than wapiti, larger estimates than 18 g/minute could be expected for cattle. Indeed, larger estimates than 18 g/minute are especially likely when considering that the estimates from this study and the wapiti estimates (Hudson and Nietfeld 1984) were obtained in very similar habitat types.

Foraging efficiency, dependent on bite rates and sizes, was more profitable in grassland communities than in forest or shrublands. In the forest, low productivity and irregular spatial proximity of morphologically variable forage species contributed to low bite rates and sizes. Conversely, in the grasslands, foods had relatively uniform growth habits, were spatially close, densely populated and easily accessible with a minimal barrier effect by shrubs. Accordingly, amongst the grassland communities, the open grassland had the highest bite rates, bite sizes and DM intake rates. Differences in foraging efficiency due to grazing intensity were not apparent in grassland communities at day 6 of the grazing period. However, by day 21, herbaceous biomass depletion of grasslands under heavy grazing caused lower foraging efficiencies than under light grazing. This concurs with Chacon and Stobbs (1976) who noted a close relationship of foraging efficiency with bite size and leaf availability.

The foraging efficiency of cattle appears to be a major determinant of their foraging behavior. Therefore, a formal test of this relationship is desirable. However, direct effects of specific qualitative and quantitative attributes of forages upon animal response must also be considered.

6. DETERMINANTS OF RESOURCE USE BEHAVIOUR

6.1 Introduction

Grasslands are generally preferred by cattle over than shrubland or forest communities. Furthermore, higher bite rates, bite sizes and foraging efficiencies were exhibited in grassland communities. This implies that cattle favor plant communities where there is a high relative efficiency of forage intake. The alternative hypothesis is that cattle respond to specific forage attributes like moisture and chemical composition. Formal tests of these hypotheses are needed.

Many studies have been conducted regarding the determinants of cattle response. Most have focused on the direct effects of specific forage quality components on forage preference (Table 6.1). However, while many workers have found significant positive or negative relationships, the reports are often conflicting. This may be due to the confounding effects of environmental or animal variables, forage palatability and availability (Heady 1964; Ellis et al. 1976; Willms 1978). Work by Emlen (1966,1968) and others has demonstrated that consumers may select less preferred or lower quality foods when those foods are more available than preferred foods. Conversely, consumers will become more selective when food density or availability is high (Emlen 1966; Rapport 1971; Menge 1972). Palatability has been noted as an important determinant of forage preference (Heady

Table 6.1 Relationship of selected quality attributes to forage preference.

Attribute	Relationship	References
Protein or Nitrogen	None	Archibald et al. 1943; Reid and Jung 1965; Reid et al. 1966; Reid et al. 1967; O'Donovan et al. 1967; Buckner et al. 1969.
	Positive	Hardison et al. 1954; Cook 1959; Blaser et al. 1960; Burton et al. 1964; Gangstad 1964; Heady 1964; Fontenot and Blaser 1965.
Crude fiber, ADF or cell walls	None	Leigh 1961; Reid et al. 1966 and 1967;
	Negative	Archibald et al. 1943; Hardison et al. 1954; Buckner 1955; Blaser et al. 1960; Gangstad 1964; Arnold 1964; Heady 1964; Fontenot and Blaser 1965.
Ether extract or fat	Positive	Hardison et al. 1954; Blaser et al. 1960; Gangstad 1964; Fontenot and Blaser 1965; Louw et al. 1967.
Minerals or total ash	None	Marten and Donker 1964; Reid and Jung 1965.
	Positive	Beaumont et al. 1933; Hardison et al. 1954; Ivins 1955; Cook 1959; Cowlishaw and Alder 1960; Leigh 1961; Gangstad 1964.
Cellulose	None	Brown 1961.
	Negative	Cook 1959.
Carotene	None	Buckner 1955.
	Positive	Archibald et al. 1943.
Vitamins	None	Hardison et al. 1954; Reid and Jung 1965.
Organic acids	Positive	Allen and Porter 1954; Jones and Barnes 1967.
% Moisture	Positive	Hilton and Bailey 1972; Gesshe and Walton 1981.
Digestibility	Positive	Beaty and Engel 1980; Gesshe and Walton 1981.

Sugars	Positive	Bland and Dent 1964; Gangstad 1964; Marten and Donker 1964; Reid et al. 1966; Reid et al. 1967; Hironaka and Bailey 1968.
Tannins	Negative	Wilkins et al. 1953; Donnelly 1954; Burns 1966.
Coumarins	Negative	Ashton and Jones 1959.
Isoflavones	None	Arnold and Hill 1972.
Alkaloids	Negative	Gordon and Henderson 1951; Roe and Mottershead 1962; Yates and Tookey 1965; Bush et al. 1970; Gladstones 1970; Kennedy and Holgate 1971.

1964; Arnold and Hill 1972; Zahorik and Houpt 1977). Chacon and Stobbs (1976) noted the availability or yield of leaves and the leaf to stem ratio as major factors determining forage preference. Animal factors such as individual animal variation, previous experiences and physiological condition are known to have effects on forage preferences (Arnold and Hill 1972; Zahorik and Houpt 1977; Ellis et al. 1976). Environmental variables such as climate, soil, and topography are also recognized as important factors (Heady 1964; Arnold and Hill 1972; Willms 1978). Less direct determinants have also been noted. The dead components of available DM may influence preference indirectly by affecting digestibility and palatability (Beaty and Engel 1980). Woody shrubs may influence preference by creating a physical barrier against selection of available forage (Bailey 1970).

Recognition of this multitude of determinants provides the basis for the integrated response hypothesis. That is, cattle may have the ability to assess changes in numerous environmental and food variables and adjust their foraging strategy accordingly (Ellis et al. 1976). The objective of this chapter is to relate observed community preferences and diet proportions of forages to foraging efficiency and to specific attributes representing community and forage productivity, availability, quality and structure.

6.2 Methods

Preference indices for plant communities determined from group observations (Chapter 3) were correlated with specific community attributes for various treatments and years. Measurements of the community attributes were obtained from the herbage biomass clip plots described in Chapter 5. Dry matter weights of live and dead herbage were measured before and after grazing periods in the six major communities (Appendix D). In addition, one combined sample of live herbage from the ten randomly located clip plots within each community by treatment cell was collected before and after grazing for chemical analyses. The herbage was analyzed for DM, acid detergent fiber, phosphorus, nitrogen and crude protein (Appendix E). The above attributes were then correlated with community preference indices for the first and second halves of grazing periods to obtain Pearson correlation coefficients and significance levels. These coefficients were averaged to obtain a mean coefficient for the entire grazing period. One additional plant community attribute was measured. The barrier effect of brush, as defined in Chapter 5, was nonparametrically correlated with the rank order of community preference indices to obtain Spearman's correlation coefficients.

Diet proportions of eight forage sources, as determined from individual observations of foraging cattle (Chapter 4), were correlated with specific attributes of forages. Forage sources measured for attributes included five herbaceous forages and three browse species (Chapter 5). Attributes used for these correlations were the same as those used for the community correlations described above. However, these correlations only used attributes measured prior to grazing. Measures of attributes for herbaceous forages were derived from the herbaceous biomass clip plots described in Chapter 5 (Appendices D and E). Measures of biomass were not obtained for the three browse species. However, chemical analyses were performed on samples of leaves and current annual growth clipped according to the same sampling methods used for herbaceous forages (Appendix F). Samples for the October grazing treatments were collected prior to leaf abscission. Then, diet proportions of the eight forage sources were correlated with the corresponding attribute measures obtained in various treatments and years.

Finally, diet proportions of the same eight forage sources were regressed with their corresponding DM and protein intake rates (Chapter 5) for June, 1981. As in Chapter 5, crude protein intake provided no additional clarity to any relationships. Thus, DM intake was assumed to be the best measure to relate to animal response.

Community preferences during June, 1981, were then related to animal response at the forage source level. Community preference indices (proportion of time spent foraging/proportion of total area available) determined in Chapter 3 were regressed with preference indices for major forage sources (proportion of total bites/proportion of total area available) found in each community. The indices were determined for the first and second halves of the grazing period. Each grassland community had one major forage source (herbage) while the forest community had four (aspen, rose, saskatoon and herbage). The use of indices adjusted for the effects of area on community use and diet proportions of forages. This clarified the relationship and allowed an indirect relation of community preference to foraging efficiency.

6.3 Results

No consistent relationship was established with any specific community or forage attribute but cattle preferences were, in general, positively correlated with communities containing lower quality forages and higher biomass levels. However, preference for forest and shrubland forages was sometimes apparent. Cattle diets were highly dependent on foraging efficiencies among forages and communities.

6.3.1 Light June Grazing

Plant communities with greater herbaceous biomass and lower quality herbage were preferred in 1980 (Table 6.2). In 1981, no community preferences were apparent from these correlations. Forage sources with attributes typical of grassland herbage were positively correlated with diet proportions in both years (Table 6.3). The discrepancy between the correlations for community preferences and diet proportions of forages in 1981 was likely due to differences between the group and individual observations. Diet proportions of forage sources were determined from the number of bites of individuals (Chapter 4) while community preferences were determined from the relative time spent foraging by groups of cattle (Chapter 3). Thus, when cattle exhibited higher bite rates utilizing grassland forages, the resultant diet proportions were also weighted for that effect. A notable difference in preference for live and dead components of forage sources was also apparent (Table 6.3). Cattle disliked dead herbage in spite of their general preference for communities containing low quality herbaceous biomass (Table 6.2).

Table 6.2 Relationship of various community attributes to cattle preference indices for six plant communities under light June grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Community attribute	r	p	r	p
Live herbage biomass	.80	.029	.21	ns
Dead herbage biomass	.91	.009	-.03	ns
Total herbaceous biomass	.87	.014	-.16	ns
% Dry matter of live herbage	.64	.089	-.16	ns
% Acid detergent fiber of live herbage	.72	.057	-.53	ns
% Phosphorus of live herbage	-.71	.060	-.13	ns
% Crude Protein of live herbage	-.58	ns	.11	ns
Barrier effect of brush†	-.52	ns	.05	ns

ns-not significant at $p \leq .10$.
† Correlation coefficients are Spearman's r values.

Table 6.3 Relationship of various forage attributes to diet proportions of eight forage sources under light June grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Forage attribute	r	p	r	p
Live biomass	.82	.023	.68	.067
Dead biomass	.51	ns	.19	ns
Total biomass	.74	.048	.58	ns
% Dry matter of live biomass	.59	.036	.66	.019
% Acid detergent fiber of live biomass	.58	.041	.49	.077
% Phosphorus of live biomass	-.47	.087	-.51	.068
% Crude Protein of live biomass	-.54	.052	-.72	.009

ns-not significant at p≤.10.

6.3.2 Heavy June Grazing

Diet proportions of forages were positively correlated with some attributes of grassland forages in both years, consistent with the light June treatment results (Table 6.4). Correlations of community preferences with attributes also showed similar results to those under light June grazing. Cattle preferred communities with lower quality, high biomass herbage in 1980 while no preferences were apparent in 1981 (Table 6.5). However, differences in response to communities were observed within the grazing period under heavy grazing (Table 6.6). In 1981, animals

Table 6.4 Relationship of various forage attributes to diet proportions of eight forage sources under heavy June grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Forage attribute	r	p	r	p
Live biomass	.56	ns	.69	.066
Dead biomass	.23	ns	.39	ns
Total biomass	.43	ns	.64	.084
% Dry matter of live biomass	.40	ns	.79	.003
% Acid detergent fiber of live biomass	.69	.013	.55	.051
% Phosphorus of live biomass	-.64	.023	-.89	.000
% Crude Protein of live biomass	-.51	.068	-.83	.001

ns-not significant at p≤.10.

Table 6.5 Relationship of various community attributes to cattle preference indices for six plant communities under heavy June grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Community attribute	r	p	r	p
Live herbage biomass	.75	.046	-.14	ns
Dead herbage biomass	.54	ns	.43	ns
Total herbaceous biomass	.70	.064	.05	ns
% Dry matter of live herbage	.57	ns	-.42	ns
% Acid detergent fiber of live herbage	.59	ns	.46	ns
% Phosphorus of live herbage	-.78	.049	-.43	ns
% Crude Protein of live herbage	-.65	.099	.28	ns
Barrier effect of brush†	-.63	.094	.17	ns

ns-not significant at p≤.10.

† Correlation coefficients are Spearman's r values.

Table 6.6 Relationship of live and dead herbage biomass to cattle preference indices for six plant communities in the first and second halves of the heavy June grazing period, as expressed by the simple correlation coefficient (r) and significance level (p).

	1st half				2nd half			
	1980		1981		1980		1981	
Attribute	r	p	r	p	r	p	r	p
Live herbage biomass	.77	.038	.07	ns	.72	.054	-.35	ns
Dead herbage biomass	.53	ns	.91	.006	.55	ns	-.06	ns

ns-not significant at $p \leq .10$.

preferred communities with high levels of dead herbage during the first half of the grazing period. Then, during the second half of grazing, animals showed no preferences for live or dead herbage levels among communities. The drought during that month forced cattle to use live and dead herbage supplies in grasslands during the first half of the grazing period. Then, with no live herbage regrowth or remaining supplies of dead herbage, animals exhibited non-selectivity among communities during the second half of the grazing period. This was reflected in the correlations of community preferences with attributes in 1981 (Table 6.5). Conversely, animals preferred communities with high levels of live herbage and low levels of dead herbage throughout 1980. Obviously, the above average rainfall of that month allowed animals to utilize live herbage regrowth instead of dead herbage supplies.

6.3.3 Light October Grazing

No significant correlation of an attribute with community preference was apparent in 1980 or 1981 (Table 6.7). A trend indicating preference for communities with poorer quality herbage was apparent in both years. In 1981 a trend indicating preference for communities with low herbaceous biomass levels occurred. This was due to the late killing frost which resulted in abnormally high use of forest and shrubland communities. The diet was comprised of forages with relatively high levels of % DM in both years (Table 6.8). This supported the trend of preference for communities with low quality forages. However, no relationships were established with biomass levels of herbaceous forages. This indicates that while forage preference was based largely on dry matter intake, forage sources with the highest levels of biomass were not necessarily preferred. This relates to the large dead component of herbaceous forage sources in this treatment. There was a definite trend for preference of communities with high levels of live herbage but that effect was confounded with the variation in levels of dead herbage.

Table 6.7 Relationship of various community attributes to cattle preference indices for six plant communities under light October grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Community attribute	r	p	r	p
Live herbage biomass	.32	ns	-.42	ns
Dead herbage biomass	.02	ns	-.37	ns
Total herbaceous biomass	.18	ns	-.40	ns
% Dry matter of live herbage	.30	ns	.07	ns
% Acid detergent fiber of live herbage	-.33	ns	.19	ns
% Phosphorus of live herbage	-.29	ns	-.52	ns
% Crude Protein of live herbage	-.31	ns	-.17	ns
Barrier effect of brush†	-.55	ns	.03	ns

ns-not significant at p≤.10.
† Correlation coefficients are Spearman's r values.

Table 6.8 Relationship of various forage attributes to diet proportions of eight forage sources under light October grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Forage attribute	r	p	r	p
Live biomass	.41	ns	.52	ns
Dead biomass	-.07	ns	.17	ns
Total biomass	.23	ns	.42	ns
% Dry matter	.49	.077	.63	.025
% Acid detergent fiber	.16	ns	.20	ns
% Phosphorus	-.26	ns	-.14	ns
% Crude Protein	-.30	ns	-.31	ns

ns-not significant at p≤.10.

6.3.4 Heavy October Grazing

In 1980, community preference was positively correlated with many attributes of grassland communities (Table 6.9). Similar but fewer significant correlations were observed in 1981. Cattle preferred communities with high levels of live herbage in both years. However, differences in response to communities were apparent within the grazing periods of 1980 and 1981 (Table 6.10). In 1980, an above average year for rainfall, cattle showed preference for communities with high levels of live herbage throughout the grazing period. In 1981, cattle preferred communities with high levels of live

Table 6.9 Relationship of various community attributes to cattle preference indices for six plant communities under heavy October grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Community attribute	r	p	r	p
Live herbage biomass	.73	.050	.66	.095
Dead herbage biomass	.41	ns	.51	ns
Total herbaceous biomass	.59	ns	.61	ns
% Dry matter of live herbage	.79	.034	.78	.056
% Acid detergent fiber of live herbage	-.76	.042	.54	ns
% Phosphorus of live herbage	-.84	.019	-.60	ns
% Crude Protein of live herbage	.14	ns	-.34	ns
Barrier effect of brush†	-.86	.015	-.60	ns

ns-not significant at p≤.10.

† Correlation coefficients are Spearman's r values.

Table 6.10 Relationship of live and dead herbage biomass to cattle preference indices for six plant communities in the first and second halves of the heavy October grazing period, as expressed by the simple correlation coefficient (r) and significance level (p).

	1st half				2nd half			
	1980		1981		1980		1981	
Attribute	r	p	r	p	r	p	r	p
Live herbage biomass	.77	.036	.85	.016	.69	.065	.47	ns
Dead herbage biomass	.50	ns	.79	.031	.31	ns	.22	ns

ns-not significant at p≤.10.

and dead herbage during the first half of the grazing period. During the second half of grazing, no preferences were apparent. Correlation of diet proportions of forages with attributes indicated that grassland forages were the main dietary components for cattle (Table 6.11). In 1980, forages with low amounts of phosphorus were preferred. A trend indicating higher diet proportions of forages with higher herbaceous biomass levels was also observed. In 1981, biomass levels and % DM of forages were the most important attributes affecting forage use. These results support the aforementioned severe depletion of herbaceous biomass in October, 1981. Diet selection could be expected to be highly dependent on DM intake rates and biomass under those conditions.

Table 6.11 . Relationship of various forage attributes to diet proportions of eight forage sources under heavy October grazing, as expressed by the simple correlation coefficient (r) and significance level (p).

	1980		1981	
Forage attribute	r	p	r	p
Live biomass	.51	ns	.63	.090
Dead biomass	.24	ns	.50	ns
Total biomass	.42	ns	.62	.096
% Dry matter	-.01	ns	.84	.001
% Acid detergent fiber	.23	ns	.27	ns
% Phosphorus	-.52	.060	-.35	ns
% Crude Protein	.13	ns	-.37	ns

ns-not significant at p≤.10.

To summarize, the lower quality foods found in grasslands were the major food source in all treatments. Percent dry matter was the single most important forage attribute determining diet proportion in the October grazing treatments. Biomass levels were of greater importance under heavy grazing than under light grazing in October, especially in 1981. Other attributes were of little importance. In June, the preference for live herbage relative to dead herbage in grassland communities had the most prominent effect on animal response. Various quality attributes were significantly correlated with community preferences and diet proportions of forages. Biomass levels were most important under a heavy grazing intensity. Community preferences of cattle in the two heavy grazing treatments showed more changes within grazing periods than those of cattle in the light grazing treatments, especially in 1981.

Diet proportions of major forage sources showed a positive relationship with DM intake rate or foraging efficiency (Fig. 6.1). Lower diet proportions were associated with forest forages that exhibited smaller intake rates. Despite the lack of DM intake rates at the community level, an indirect positive relationship of foraging efficiency with community preference was apparent in the positive relationship of community preference to forage preference (Fig. 6.2). Obviously, response to major food sources was an important determinant of response at the community level.

6.4 Discussion

There were no attributes to which cattle response was consistently significant. Indeed, Arnold and Hill (1972) qualify such attempts at universal relations with the statement, "Insignificance of a correlation of one attribute with preference indicates only that it is not of great importance, while significance is not proof that it is the main determinant unless all factors are adjusted for." Furthermore, correlations with preferences must be related

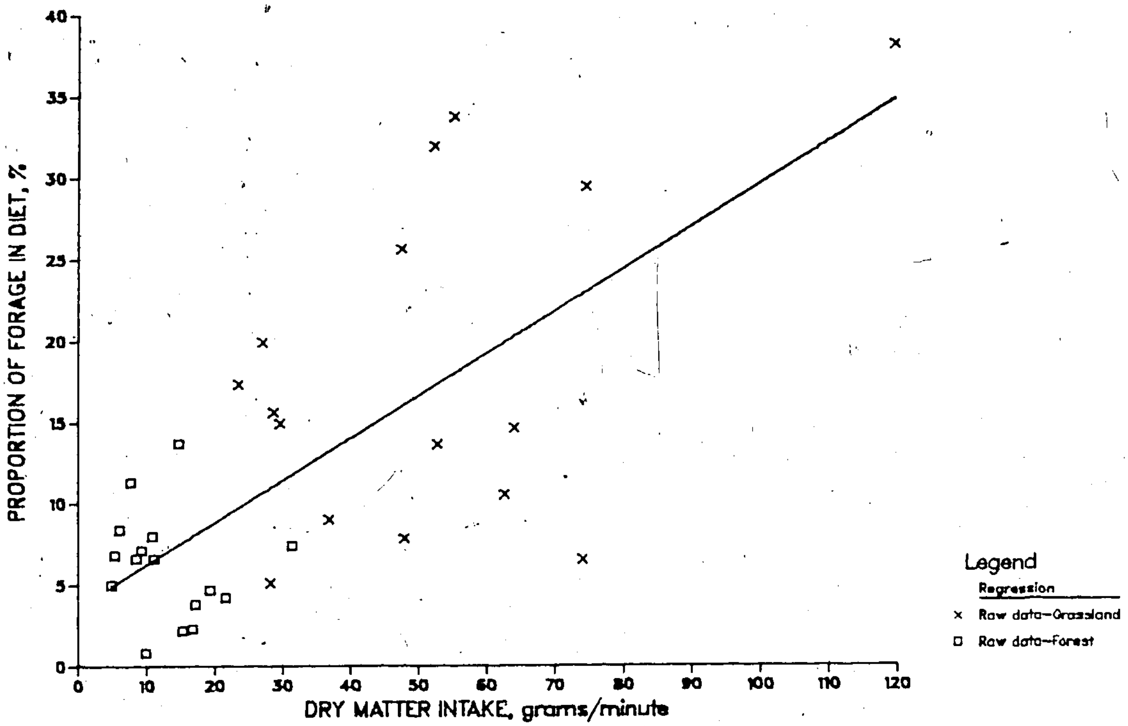

Figure 6.1 Regression of diet proportions of eight forages with foraging efficiency (DM intake rate), June, 1981 (Regression equation: Y=.26X+3.64 at p≤.00, R^2=.47).

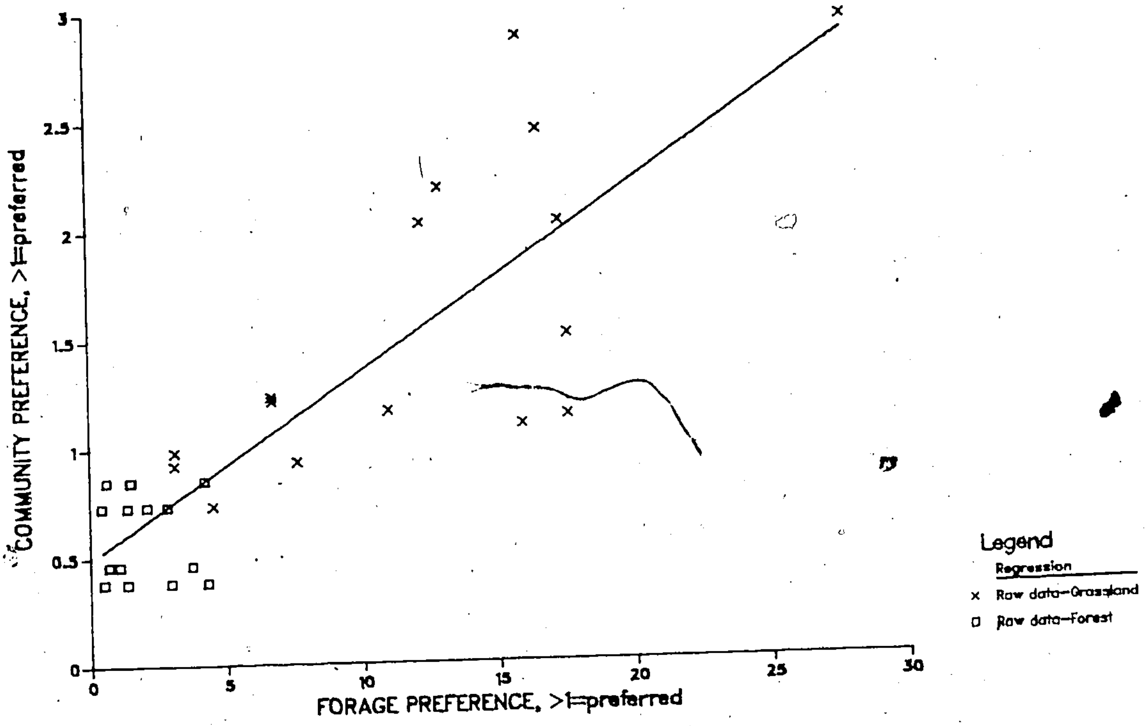

Figure 6.2 Regression of community preference indices (proportion of time spent foraging/proportion of total area available) with forage preference indices (proportion of total bites/proportion of total area available) for the major forages in each community, June, 1981 (Regression equation: $Y=.086X+.489$ at $p \leq .00$, $R^2=.71$).

to specific compounds or physical properties of plants since animals cannot select food simply because it is high in "protein" or "energy" (Arnold and Hill 1972; Zahorik and Houpt 1977). The differences in attribute correlations indicated that the selection process was a multidimensional response. The wide variation in environmental conditions in 1980 and 1981 served to emphasize this. However, the correlations did relate community and forage preferences to forage quality and quantity in a general sense. Cattle showed a general preference for lower quality forages available in large quantities in grassland communities. This concurs with Emlen (1966,1968) and Menge (1972) who noted that consumers may select lower quality foods when they are available in greater abundance than higher quality foods. However, animals utilizing the "low quality" forage referred to in the grasslands of this study were far from the point of suffering nutritional deficiencies (Appendix E). The grassland forages were of lower quality only in a relative sense when compared to forest and shrubland forages. Within grassland communities, cattle exhibited preference for the live component of total herbaceous biomass. This supports research showing cattle prefer new growth over old and leaves over stems and dead material (Heady 1964; Chacon and Stobbs 1976; Zahorik and Houpt 1977). It also indicates that while response was largely governed by DM intake, forage quality was important in situations of ample forage availability. That is, cattle were more selective in situations of high food density (Emlen 1966; Menge 1972; Ellis et al. 1976). The drought conditions of June, 1981, enhanced the effects of availability on animal response. Increased use of high quality forages in forests and shrublands in the second half of the grazing period occurred under both light and heavy grazing. This was a response to the lack of herbaceous regrowth on grasslands and the preference for green forest forages over the dead grassland herbage that remained after the initial grazing. Under light grazing, forest forages were less quickly depleted resulting in insignificant correlations of grassland attributes with community preferences. Still, when forest depletion did occur, the grasslands provided unlimited supplies of forage. Under heavy June grazing, cattle depleted live and dead herbage supplies in grasslands during the first half of the grazing period. Then, forest forages were quickly depleted and cattle had to return to grasslands for forage. Thus, in spite of a non-selectiveness among plant communities in the second half of grazing, cattle diets were still dominated by grassland forages. Again, the low productivity and poor vigor of forest forbs and browse after long-term exposure to heavy grazing was a prime contributor to grassland over-use. In October, 1981, the late killing frost resulted in abnormally available forage sources in the forest and shrubland communities. This promoted short term increases in high quality forage use. It also indicated that forage quality was of greater importance when food availability was relatively high. When leaf abscission and forb senescence occurred, obvious negative effects on foraging efficiency and quality caused use of forest forages to decrease dramatically. This supports Chacon and Stobbs (1976) who noted that intake rates for cattle were largely dependent on a high leaf yield and leaf to stem ratio. The effects of frost on foraging efficiency were obviously most important because after leaf abscission browse species were still higher quality forages than dead herbage. Thus, due to the relatively high abundance and availability of grassland forage sources, overall preferences in the light October treatment were still pre-dominantly governed by DM intake.

Under heavy October grazing, forage availability was of greater importance. In 1980, herbaceous production provided a supply of live herbage sufficient for the entire grazing period. However, animals were forced to utilize live and dead herbage supplies in the first half of the grazing period in October, 1981. Then, live and dead herbage supplies were largely depleted during the second half of grazing. Non-selectivity among communities was the result. Thus, the summer-long drought and late killing frost of 1981 affected forage availability such that the relative "profitability" of feeding in forest and shrubland communities increased over the short term. The drought limited herbaceous forage production while the frost delayed leaf abscission of shrubs and senescence of forest forbs. Thus, both quality and availability of forages were factors contributing to increased use of forest forages. Cattle exhibited the ability to assess the profitability among forages and communities and adjust their foraging strategy accordingly (Royama 1970; Smith and Dawkins 1971; Simons and Alcock 1971). Under average environmental conditions, cattle indicated grasslands provided the most profitable forage sources, as indicated by the high foraging efficiencies. But under heavy grazing intensities, drought, or in late summer prior to the killing frost, this profitability may favor shrubland and forest use.

To summarize, animal response at the community level was related primarily to foraging efficiency at the species level. In other words, community preferences depended on diet selection of forages. Diet selection was an integrated response largely dependent on the relative foraging efficiency, quality, and availability of major food sources. Forage quality became a more important factor as food availability increased due to the increase in cattle selectivity. Under average range conditions in the aspen parkland, the effect of availability is such that cattle find the highest foraging efficiency amongst grassland forages. However, the effects of environment (drought) and management (grazing intensity) may alter this behavior.

7. CATTLE USE OF ASPEN SUCKERS IN THE FOREST EDGE GRASSLAND

7.1 Introduction

In view of the negative effects of aspen invasion on the productivity of grassland forages (as noted in Chapter 1), an in-depth analysis of cattle response to aspen in the forest edge grassland community is desirable. The forage preferences and dominant foraging activities of cattle within the community have been elucidated. Further study of the impact of cattle grazing on aspen invasion is desirable. Patterns of cattle use and the extent of aspen mortality may be useful in developing control strategies to curb aspen invasion.

There is little published research concerning strategic brush control using cattle, despite the early recognition of aspen in their diet by Sampson (1919). Moss (1932) hypothesized that cattle could prevent aspen invasion while Johnson et al. (1971) recognized cattle browsing and trampling as inhibitory factors to brush invasion. Hilton and Bailey (1974) found utilization levels by cattle on 3-year old aspen regrowth ranging from about 15 to 25%. Smith et al. (1972) attributed aspen injury rates of 23, 8, and 9% respectively in the first three years following a clearcut in Utah to the effects of cattle browsing and trampling. However, mean utilization of aspen in that study did not exceed 10% in any of the three years. Greatest use (53% of suckers) was observed in the shortest height class of suckers (≤60 cm) while use of suckers taller than 150 cm was minimal. Smith et al. (1972) also noted that cattle browsed aspen more readily as the summer season advanced. This agrees with observations by FitzGerald and Bailey (1984) and Hilton and Bailey (1972) who found greater aspen use in August than in early spring or summer. Results from this study generally support such observations within the summer season but also indicate a dramatic decrease in aspen use after leaf fall. FitzGerald and Bailey (1984) also demonstrated successful control of aspen regrowth using heavy grazing in August. However, they noted an inability to control succession of other shrub species, particularly western snowberry, without additional application of seasonally timed grazing periods, or other control measures.

Thus, this part of the study was designed to determine the levels of aspen use and subsequent mortality attributable to cattle across seasons, grazing intensities and years. Secondly, it was desirable to relate cattle use and the mortality of aspen to specific plant parameters and community attributes.

7.2 Methods

Use and mortality measurements of aspen suckers during grazing treatments were obtained from 20 to 25 mapped suckers in ten randomly chosen transects or areas in the forest edge grassland community of each treatment. New transects were selected each year. Within each area, suckers were mapped relating their distance and order of coincidence to a string stretched between two markers aligned perpendicular to the forest margin. The markers extended from the inner to outer limits of the forest edge phase grassland community and mapped suckers were within 1 m of the string (on either side). When more than 25 suckers were available within a transect area, suckers were selected randomly. Individual suckers were monitored approximately every 3 days during the grazing period. Measurements included height, number of main branches, age, the number of times browsed, and any changes in the above measures due to browsing. Mortality and reason for mortality were also noted during and following the grazing period, and during the following spring.

One portable 2-m² exclosure was set up near each transect before grazing and randomly relocated approximately every week of the grazing period. Before the weekly relocation, herbaceous biomass was harvested in two 0.5-m² quadrats, one inside and one outside each exclosure. Biomass was separated into live and dead herbage fractions for inside and outside quadrats, bagged, and later weighed. Weights of inside and outside quadrats for weekly exclosures within transect areas were used to determine live, dead and total herbaceous biomass levels throughout the grazing period. Biomass levels in each area were based on two quadrats. For example, live herbage from the outside quadrat harvested before grazing was averaged with the live herbage harvested from the inside quadrat 1 week later. Similarly, the outside quadrat harvested after 1 week was paired with the inside quadrat after 2 weeks of grazing and so on Thus, the weekly herbaceous biomass estimates for various treatments (Appendix G) were means based on 20 quadrats (2 quadrats for each of 10 transect areas). Measures of the aspen density (number/m^2) and canopy cover estimate (%) of western snowberry were also made for each quadrat harvested.

Cumulative use of marked aspen suckers and the relative depletion of herbaceous biomass over the grazing period were plotted for each treatment. Analysis of variance tests were performed on the number of browsings per sucker and mortality rates across seasons, grazing intensities and years. The number of browsings per sucker was calculated by dividing the total number of observed browsings by the average number of live aspen suckers available each day of the grazing period. Mortality rates were calculated using only marked suckers that could be accounted for. Suckers used by rabbits or other rodents or for which no remains could be found the following spring were not included in mortality rate calculations. Sample means were tested for least significant differences according to Steel and Torrie's (1980) method for unequally replicated means (Chapter 3). Finally, multiple regression analyses were performed to determine the relative effects of aspen density, snowberry cover, sucker height, number of branches, age, initial live, dead and total herbaceous biomass

(Appendix H) on aspen sucker mortality rate and number of browsings per sucker.

7.3 Results

Cumulative use of aspen suckers under light June grazing showed that fewer trees were browsed twice in 1980 than in 1981 (Fig. 7.1, 7.2). There were 41 and 23% live unbrowsed suckers at the end of the grazing periods in 1980 and 1981, respectively. Conversely, no live suckers remained unbrowsed under heavy June grazing (Fig. 7.3, 7.4). Over 29% of the suckers were browsed two or more times in this treatment. Immediate death of suckers during the grazing period was higher under heavy June grazing in 1980. Two major factors that contributed to immediate death during the grazing period in June were trampling and uprooting by browsing cattle. The average age of suckers was lower in 1980, especially in June (Appendix H). Thus, more young suckers were uprooted by cattle during June, 1980. In October, hare browsing was the most significant cause of sucker death during the grazing period. However, sucker deaths were fewer than in June. Immediate death due to hare browsing was more extensive in 1980 when there were more young suckers. The light October grazing treatment showed a relatively low number of browsed suckers (15 and 18% in 1980 and 1981, respectively) and a large number of live unbrowsed suckers following grazing, despite the severest effect of mortality due to hares (Fig. 7.5, 7.6). The heavy October

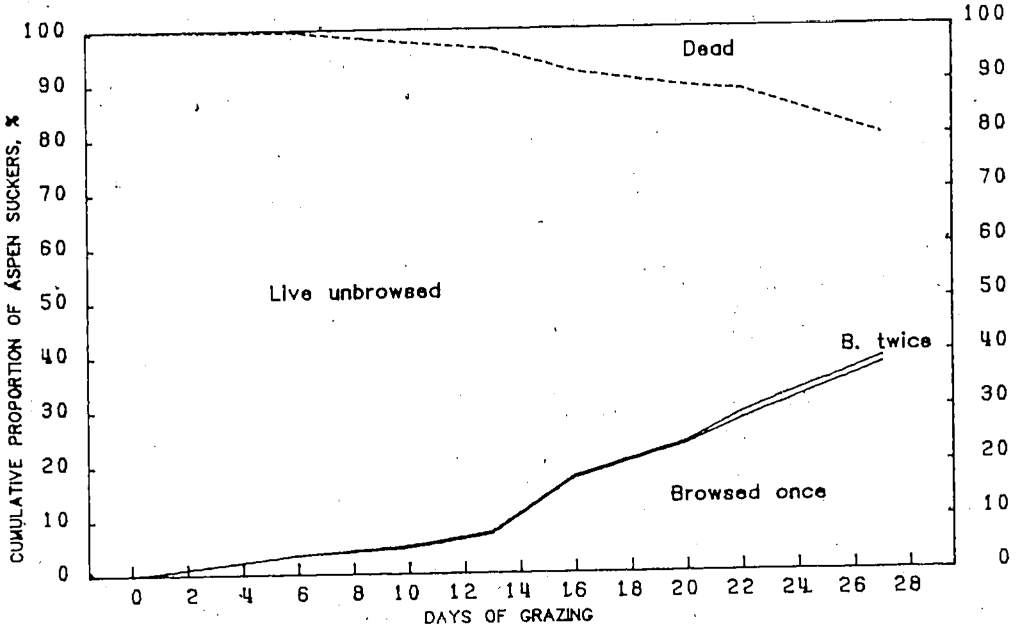

Figure 7.1 Cumulative use of aspen suckers by cattle under light June grazing, 1980.

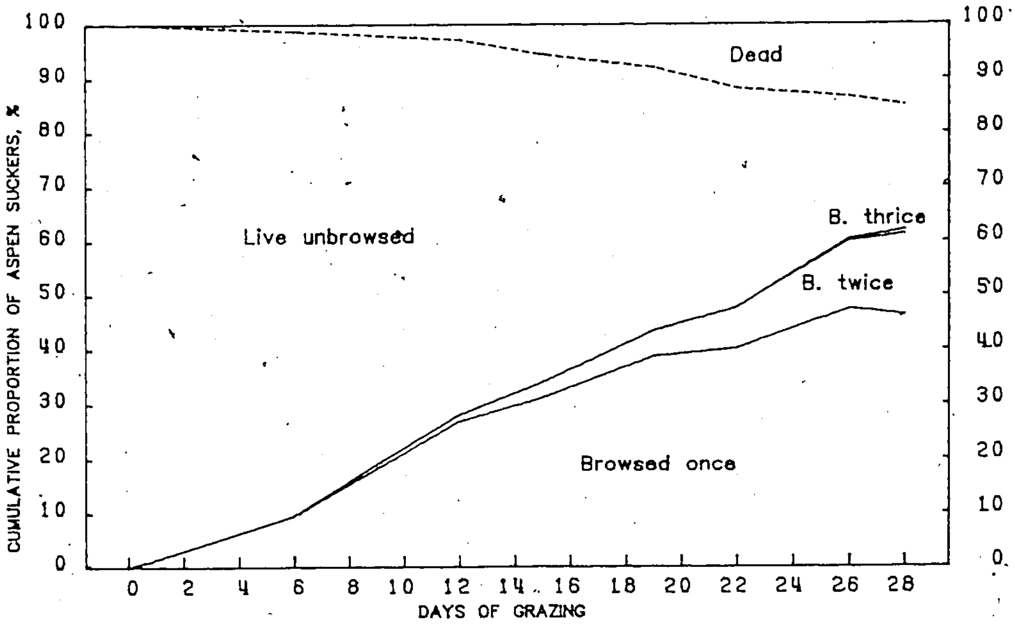

Figure 7.2 Cumulative use of aspen suckers by cattle under light June grazing, 1981.

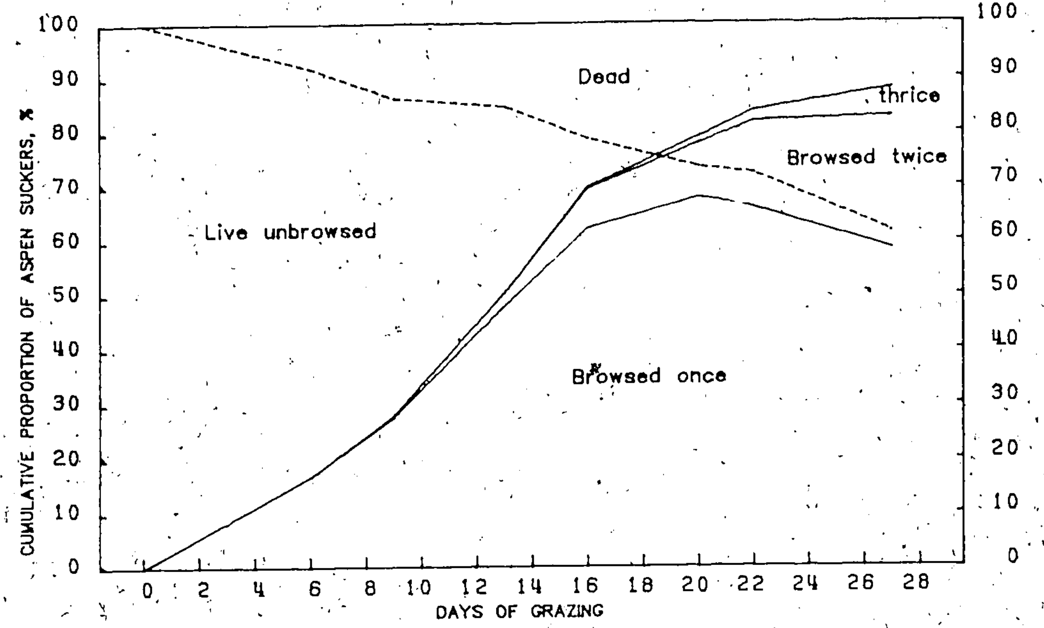

Figure 7.3 Cumulative use of aspen suckers by cattle under heavy June grazing, 1980.

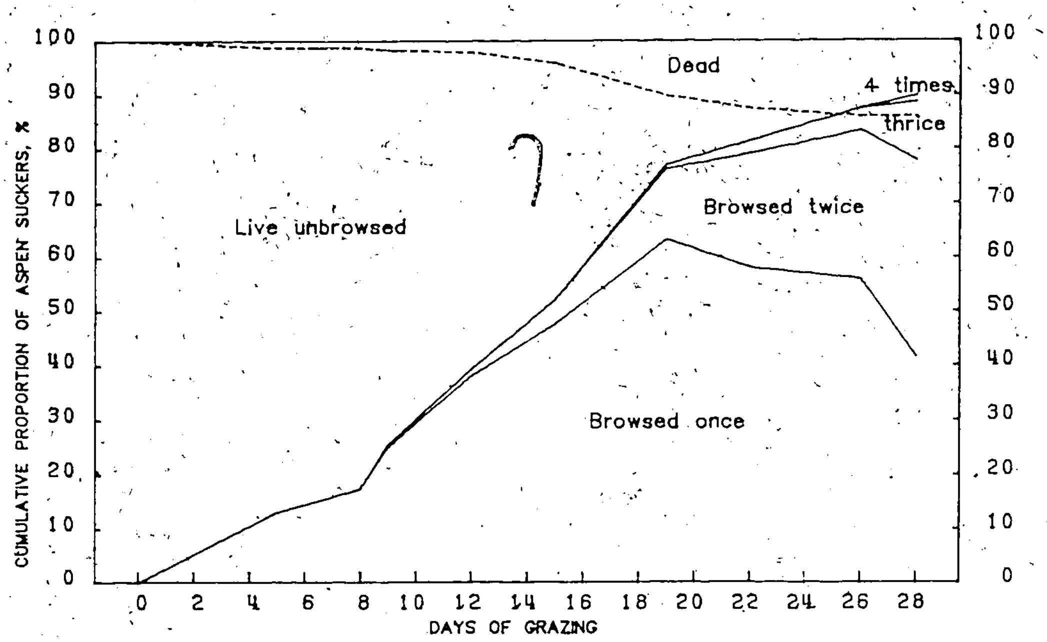

Figure 7.4 Cumulative use of aspen suckers by cattle under heavy June grazing, 1981.

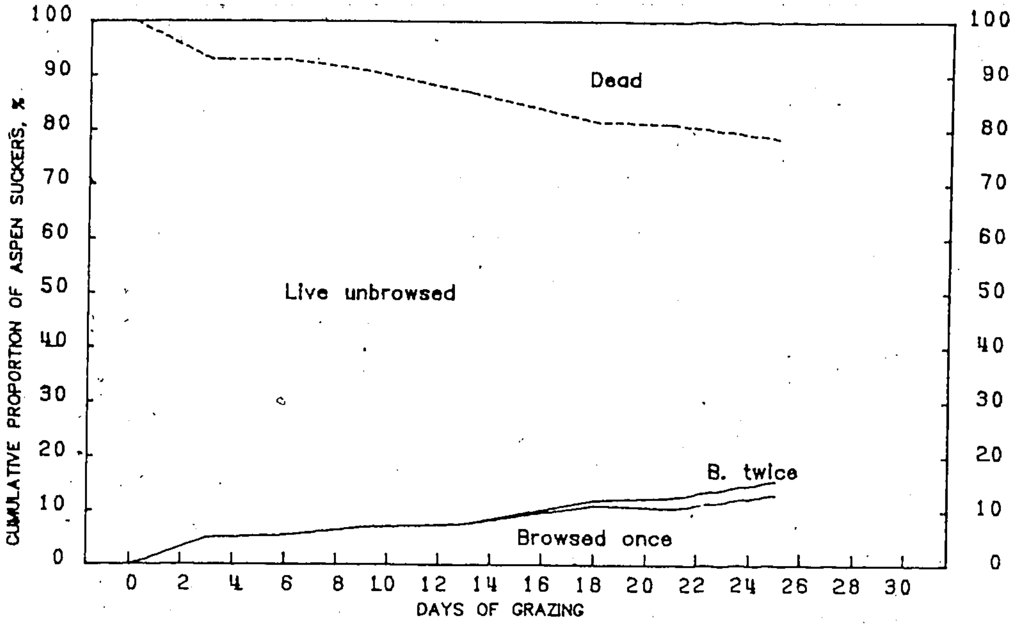

Figure 7.5 Cumulative use of aspen suckers by cattle under light October grazing, 1980.

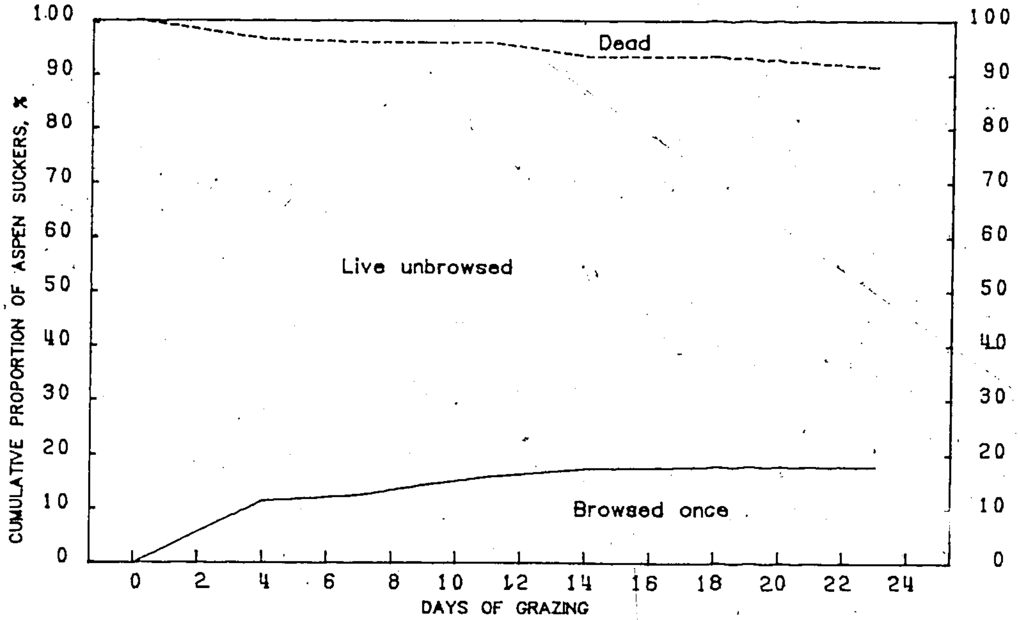

Figure 7.6 Cumulative use of aspen suckers by cattle under light October grazing, 1981.

treatment showed similarly large numbers of live unbrowsed suckers following grazing in both years, although aspen use in 1981 was greater (Fig. 7.7, 7.8). The majority of aspen use in October, 1981, came in the first ten days of grazing prior to widespread abscission of leaves.

Live, dead and total herbaceous biomass levels were not severely depleted by cattle under light June grazing in either year (Figures 7.9, 7.10). Depletion of live and total herbage was greater in 1980 but levels after grazing were still 1300 and 1900 kg/ha, respectively. Initial levels of live and total herbage were greater in 1981 because of an earlier start to the growing season than in 1980. In April, 1981, precipitation had been above the long-term average. Then, in May, although precipitation was below average, it occurred at regular intervals throughout the month (Environment Canada, 1980). Rainfall was recorded in 11 days of May while the longest interval between rains was 5 days. Thus, combined with snowmelt and April rainfall, the May precipitation was sufficient to maintain growth until June. Conversely, in 1980, a slow start to the growing season resulted in relatively low initial levels of herbaceous biomass in June. This was because precipitation had been far below average in April and most of the rainfall in May occurred in the last 5 days of the month. Dead herbage levels increased during the final week of grazing in June, 1981. This was associated with a decrease in live herbage, probably partially due to plant death caused by drought.

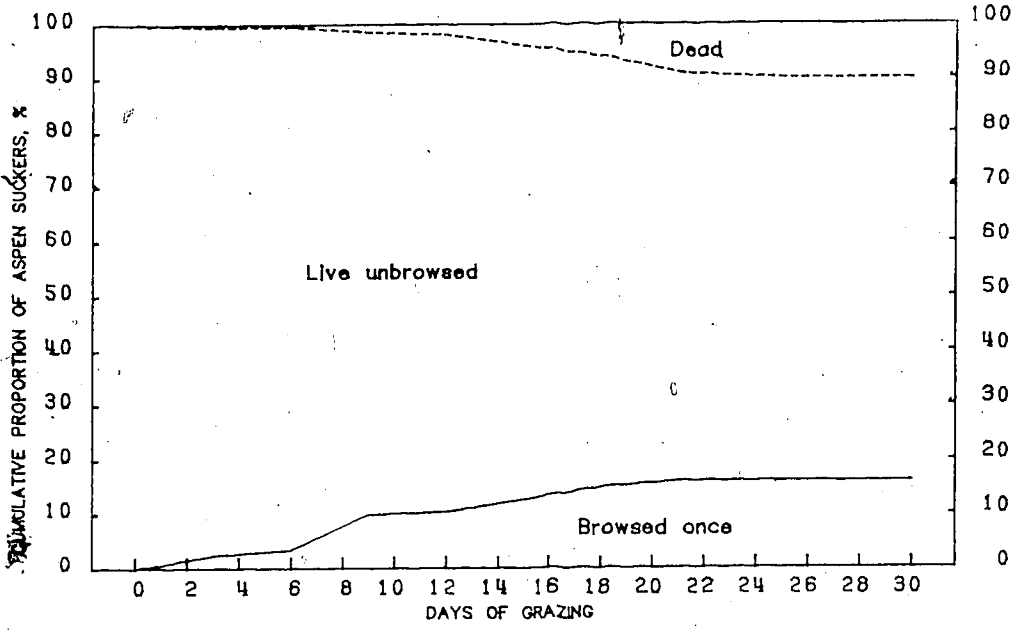

Figure 7.7 Cumulative use of aspen suckers by cattle under heavy October grazing, 1980.

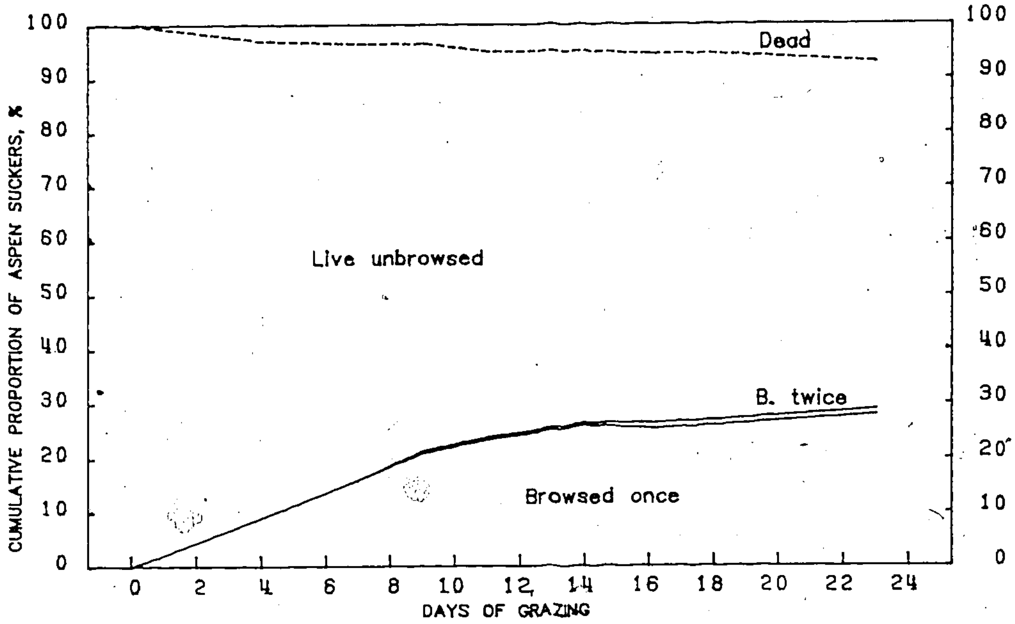

Figure 7.8 Cumulative use of aspen suckers by cattle under heavy October grazing, 1981.

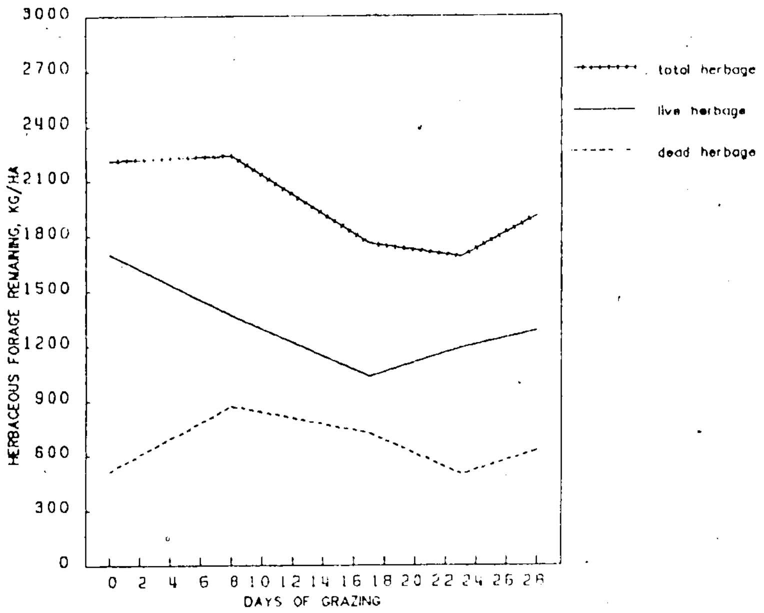

Figure 7.9 Live, dead and total herbaceous biomass levels (kg/ha) under light June grazing, 1980.

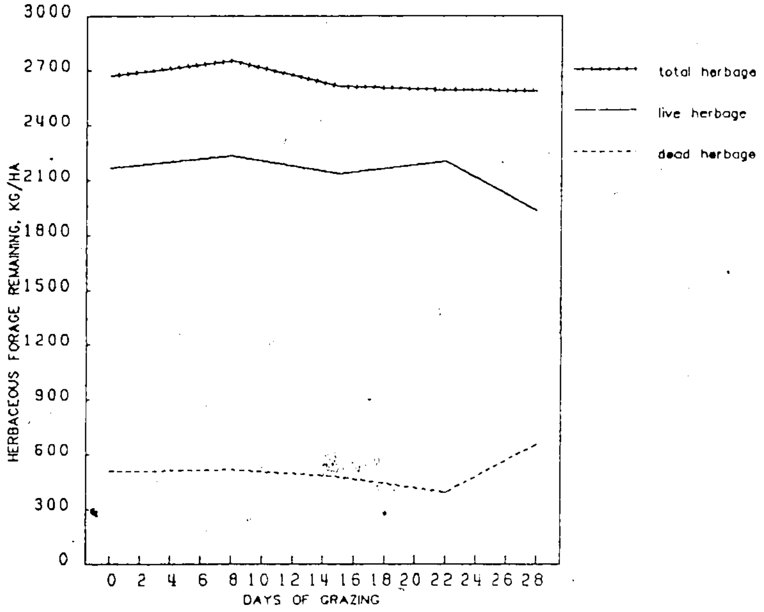

Figure 7.10 Live, dead and total herbaceous biomass levels (kg/ha) under light June grazing, 1981.

Under heavy June grazing, depletion of live and total herbage did not approach critical levels until the last week of grazing (Figures 7.11, 7.12). However, total herbaceous biomass remaining after grazing was consistently less than half that remaining in other treatments. As in the light June treatment, initial levels of dead and live herbage were lesser and greater, respectively, in 1981 than in 1980. Under light October grazing, live and total herbage were not depleted below 1000 and 2900 kg/ha (Figures 7.13, 7.14). In addition to cattle use, depletion of live herbage was enhanced by senescence of green herbage after the first killing frost. This effect was more pronounced in 1981 when the initial herbaceous biomass quadrats were harvested prior to the first killing frost. Accordingly, dead herbage levels showed more dramatic increases during the 1981 grazing period after the frost occurred. Total herbaceous biomass levels were generally higher in 1981, perhaps unexpected considering the summer-long drought in that year. However, these levels were partially related to dead herbage carryover from the previous year. The year 1980 was preceded by a dry year (1979 had only 335 mm of precipitation) while 1981 was preceded by an above average year for rainfall. Thus, more carryover likely occurred into 1981 than into 1980. The timing of quadrat harvesting was also an important factor. Peak biomass levels occurred just before the killing frost. Therefore, the 1981 grazing period coincided with peak biomass levels while the 1980 grazing period occurred

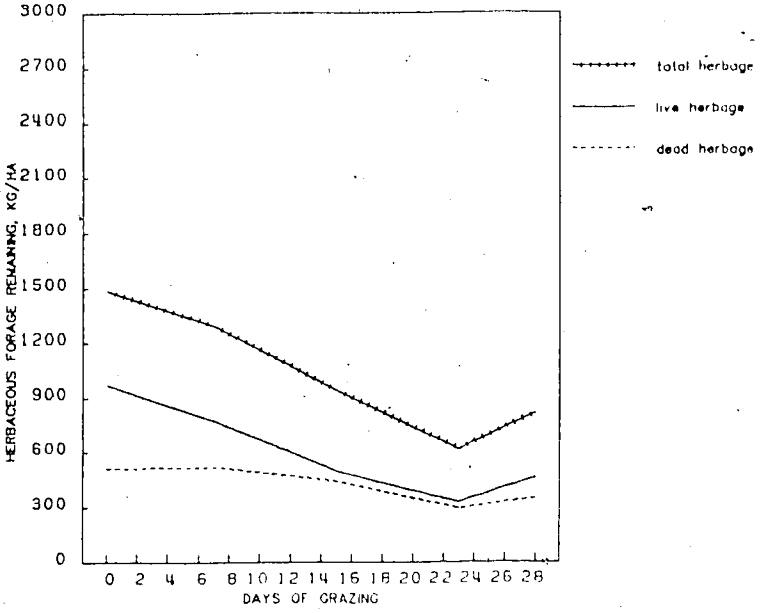

Figure 7.11 Live, dead and total herbaceous biomass levels (kg/ha) under heavy June grazing, 1980.

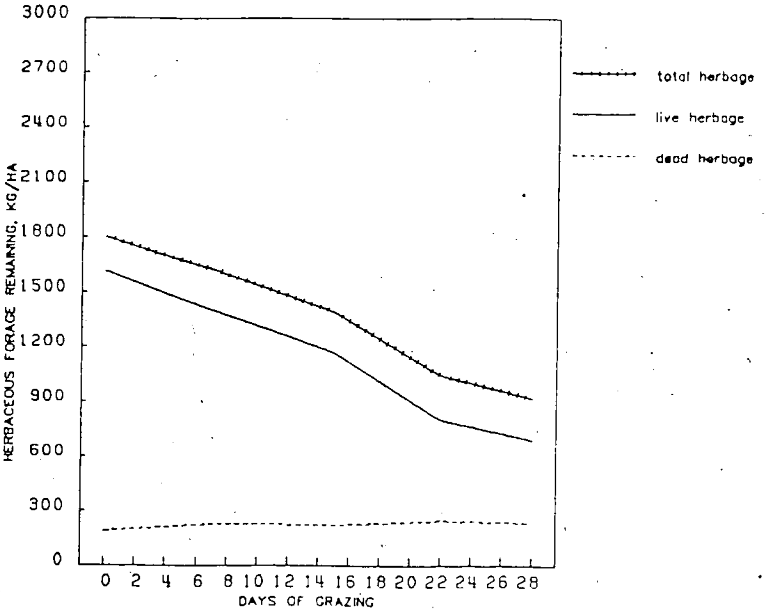

Figure 7.12 Live, dead and total herbaceous biomass levels (kg/ha) under heavy June grazing, 1981.

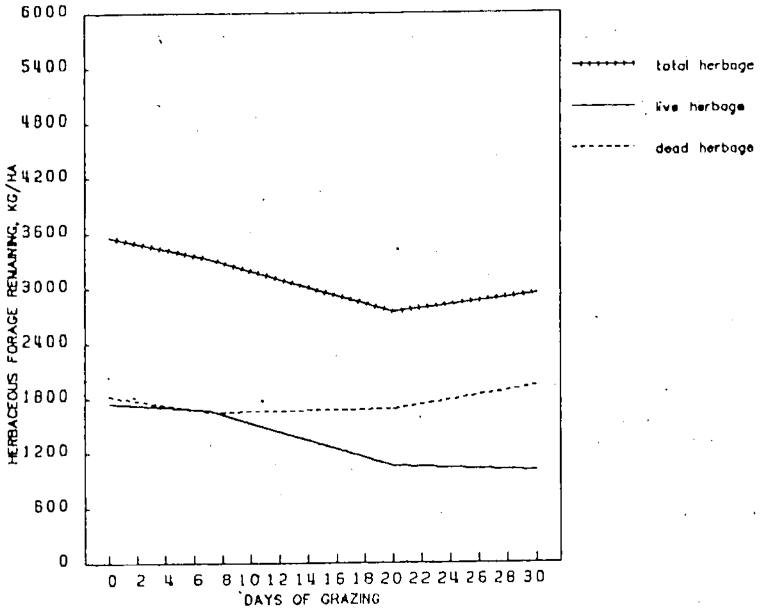

Figure 7.13 Live, dead and total herbaceous biomass levels (kg/ha) under light October grazing, 1980.

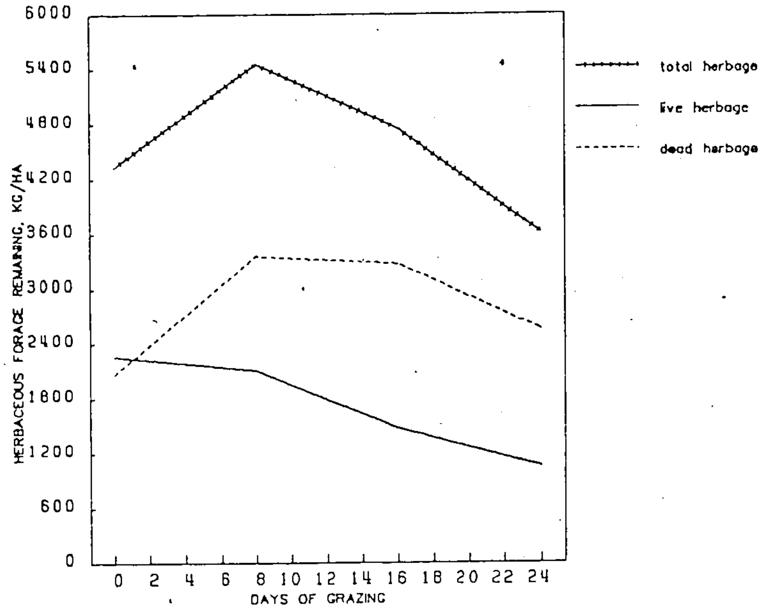

Figure 7.14 Live, dead and total herbaceous biomass levels (kg/ha) under light October grazing, 1981.

after this peak. Finally, in spite of the initial differences, levels of herbaceous biomass remaining after grazing were very similar between years, especially when considering that the grazing period was 6 days shorter in 1981. Under heavy October grazing, live and total herbage were depleted to similar levels in both years (Figures 7.15, 7.16). The delay of the killing frost in 1981 resulted in lower initial levels of dead herbage than in 1980, but levels remaining after grazing were similar. The summer-long drought had a greater effect on levels of total herbage under heavy October grazing. Unlike the light October treatment, initial levels were less in 1981 than in 1980. Levels of total herbage remaining after heavy grazing were higher in October than in June by 600 and 325 kg/ha in 1980 and 1981, respectively.

Grazing intensity and season had the greatest effect on the number of browsings per aspen sucker. The number of browsings per sucker was two times greater under heavy grazing and nearly five times higher under June grazing (Table 7.1). Accordingly, the greatest use of aspen occurred in the heavy June treatment (Table 7.2).

Under light June grazing, cattle preferred shorter suckers having fewer terminal branches (Table 7.3). Areas with high amounts of initial herbaceous litter showed a lower number of browsings per sucker. Aspen density and snowberry cover had little effect on aspen use in the light June treatment. Under heavy June grazing, sucker height was

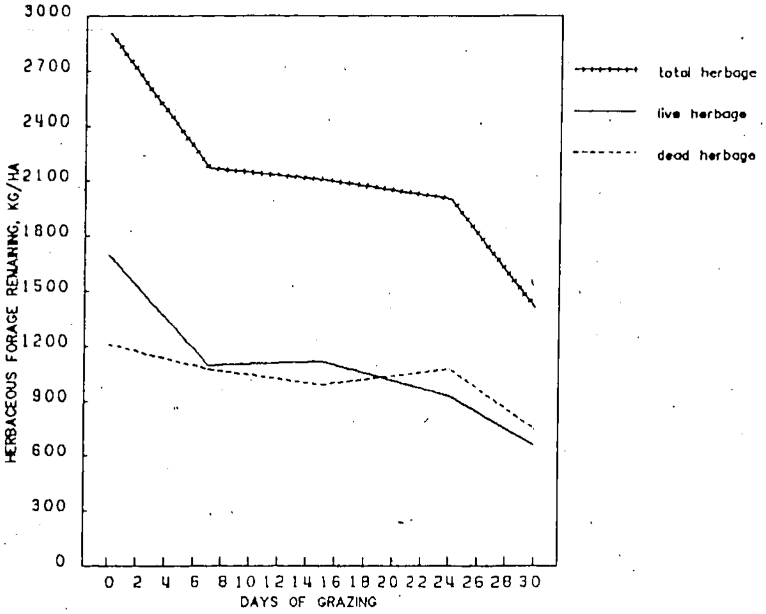

Figure 7.15 Live, dead and total herbaceous biomass levels (kg/ha) under heavy October grazing, 1980.

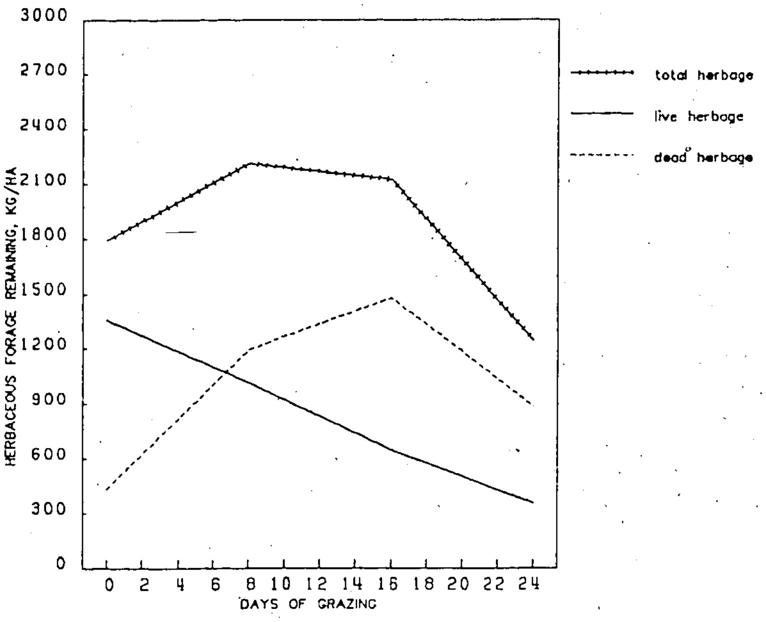

Figure 7.16 Live, dead and total herbaceous biomass levels (kg/ha) under heavy October grazing, 1981.

Table 7.1 Effect of year, grazing intensity and season of use on the number of browsings per aspen sucker.

	Year			Intensity			Season		
	1980		1981	light		heavy	June		Oct.
Average number of browsings	0.57	**	0.75	0.44	**	0.88	1.02	**	0.22

** denotes significant difference between means ($p \leq .05$).

Table 7.2 Effect of grazing intensity on the number of browsings per aspen sucker in June and October.

	Treatment			
	light June	heavy June	light October	heavy October
Average number of browsings	0.63 b	1.43 a	0.20 b	0.24 b

Means followed by the same letter are not significantly different ($p \leq .05$).

Table 7.3 Effect of various attributes on the number of browsings per sucker, as expressed by the simple correlation coefficient (r) and the total variation accounted for (R^2).

	Treatment							
	light June		heavy June		light October		heavy October	
Attribute	R^2	r	R^2	r	R^2	r	R^2	r
Height of sucker	.07	-.43	.19	.43	.16	-.51	.07	-.35
Age of sucker	.15	ns	.03	ns	.06	-.43	.05	ns
Number of main branches	.30	-.55	.06	ns	.32	-.57	.00	ns
Aspen density in area	.05	ns	.05	ns	.00	ns	.19	-.44
Snowberry cover in area	.02	ns	.09	ns	.04	ns	.08	ns
Initial total herbage biomass	.05	ns	.03	ns	.00	ns	.00	-.31
Initial live herbage biomass	.00	ns	.00	ns	.06	-.44	.00	ns
Initial dead herbage biomass	.00	-.47	.00	ns	.02	ns	.16	-.36

ns-correlation coefficient not significant ($p \leq .05$).

the only attribute significantly correlated with aspen use. Taller suckers were browsed more often while the number of branches and age showed no relationship. Under light October grazing, the number of browsings were greater on younger, shorter suckers with fewer main branches. Transect areas with high initial levels of live herbaceous biomass showed fewer browsings per sucker. Under heavy October grazing, taller suckers were browsed less often. Areas having a high aspen density or high initial levels of total and dead herbaceous biomass exhibited fewer browsings per sucker.

Grazing intensity and season had the greatest effect on aspen mortality. Mortality was nearly two times greater under heavy grazing and over six times greater in June than in October (Table 7.4). Thus, the greatest mortality was observed under heavy June grazing (Table 7.5).

The number of browsings per sucker accounted for most of the variation in aspen mortality under light June grazing (Table 7.6). Mortality was higher for suckers that were browsed more often. However, taller suckers with more main branches showed lower mortality rates. Similarly, suckers found in areas having high western snowberry cover or high initial levels of dead herbage were also more likely to survive. Under heavy June grazing, sucker height was the major determinant of aspen mortality. Shorter, younger suckers with fewer main branches had higher mortality rates. Suckers in areas with a high aspen density also showed lower mortality. This related directly to the number of browsings

Table 7.4 Effect of year, grazing intensity and season of use on the mortality rate (%) of aspen suckers.

	Year			Intensity			Season		
	1980		1981	light		heavy	June		Oct.
Mortality rate (%) of aspen suckers	26.1	**	32.3	21.3	**	37.0	46.7	**	7.4

** denotes significant difference between means (p≤.05).

Table 7.5 Effect of grazing intensity on the mortality rate (%) of aspen suckers in June and October.

	Treatment			
	light June	heavy June	light October	heavy October
Mortality rate (%) of aspen suckers	35.1 b	57.9 a	3.9 b	10.7 b

Means followed by the same letter are not significantly different (p≤.10).

Table 7.6 Effect of various attributes on the mortality rate of aspen suckers, as expressed by the simple correlation coefficient (r) and the total variation accounted for (R^2).

	Treatment							
	light June		heavy June		light October		heavy October	
Attribute	R^2	r	R^2	r	R^2	r	R^2	r
Number of times browsed	.36	.60	.11	ns	.52	.72	.30	.55
Height of sucker	.06	-.49	.24	-.49	.02	-.50	.04	ns
Age of sucker	.06	ns	.02	-.39	.01	-.30	.00	ns
Number of main branches	.08	-.52	.00	-.44	.01	-.34	.00	ns
Aspen density in area	.08	ns	.02	-.30	.02	ns	.00	ns
Snowberry cover in area	.07	-.34	.01	ns	.00	ns	.13	ns
Initial total herbage biomass	.04	ns	.00	ns	.00	ns	.00	ns
Initial live herbage biomass	.01	ns	.07	.33	.08	ns	.00	ns
Initial dead herbage biomass	.00	-.40	.00	ns	.09	ns	.02	-.33

ns-correlation coefficient not significant ($p \leq .05$).

per sucker whereby areas of higher aspen density had fewer browsings per sucker (simple $r=-.39$ at $p\leq .05$). Finally, areas with high initial levels of live herbaceous biomass showed higher mortality of aspen under heavy June grazing. In the light October treatment, the number of browsings per sucker was the major positive determinant of mortality. Taller, older, multibranched suckers had lower mortality rates. Initial levels of dead herbaceous biomass had an indirect relationship with mortality. Dead herbage levels were positively correlated (simple $r=.39$ at $p\leq .05$) with the number of main branches per sucker. Thus, areas with higher initial levels of dead herbage were often areas where suckers had many branches and were less susceptible to mortality. The number of browsings per sucker was the major determinant of aspen mortality under heavy October grazing. It was positively correlated with mortality rates. Areas with higher initial levels of dead herbage showed lower aspen mortality. Dead herbage levels were also positively correlated (simple $r=.49$ at $p\leq .05$) with western snowberry cover, an indirect indication of lower aspen mortality in areas of high snowberry cover.

7.4 Discussion

Season of grazing was the most important factor affecting aspen sucker mortality. Cattle preferred aspen as a browse species in June when current annual growth was green and leafy. In October, after abscission of leaves, aspen was less preferred than saskatoon, rose, and western snowberry. The leaves of western snowberry remained attached longer than aspen after the first killing frost making it particularly attractive browse. In October, 1981, the extended green season resulted in an increase in aspen use, notably in the first two weeks of grazing prior to the killing frost and leaf abscission. In all grazing treatments, browsing of aspen occurred prior to any severe depletion of live herbage or total herbaceous biomass. This supports a "diverse diet" foraging strategy where cattle continuously sample various forages in search of the most efficient food source (Royama 1970; Smith and Dawkins 1971; Simons and Alcock 1971; Zahorik and Houpt 1977).

Under light June grazing, herbaceous biomass levels were never limiting in either year. However, the June drought of 1981 inhibited herbaceous regrowth in small, locally overgrazed areas of the forest edge phase grassland. These areas had supplied cattle with green herbaceous regrowth void of dead herbage throughout the grazing period in 1980. But, under drought, animals were forced to utilize areas where live and dead herbage were mixed (as the bite sizes indicated from day 6 to day 21 in Chapter 5). Animals responded negatively to the forced use of dead herbage by increasing use of aspen and other browse species in 1981. This concurs with work by Hilton and Bailey (1972) who noted that cattle use of aspen forest increased under a June drought despite ample available herbage in grasslands. It indicates that cattle may consider aspen and other browse as more profitable alternate forage than dead herbage over the short term. The dislike for dead herbage by cattle also had negative effects on aspen use. Areas with high initial levels of dead herbage showed fewer browsings and lower mortality of aspen. This is likely related to the direct avoidance of dead herbage by cattle. However, the dead herbage layer also protected younger, shorter suckers from browsing, particularly those in the first year of growth having one terminal branch. This effect has been confirmed by Sampson (1919). The protection of new suckers, combined with avoidance of older, taller, woodier suckers resulted in insignificant correlations of age with browsings per sucker and mortality rates. Preferred plants were suckers in the second or third year of growth that had extended one or two terminal branches above the litter layer. This was confirmed by negative correlations of sucker height and number of main branches with browsings per sucker and mortality rates. The greater use of shorter suckers and avoidance of older, taller suckers was consistent with research by Smith et al. (1972). Western snowberry had additional negative effects on aspen mortality. It promoted dead herbage build-up and impeded forage selection by acting as barrier to grazing animals (Bailey 1970). Herbaceous biomass depletion was greatest under heavy June grazing. Levels of herbage reached critical levels by the final week of grazing in both years. However, in 1980, cattle were able to utilize green herbaceous regrowth throughout the grazing period due to above average rainfall. Conversely, in 1981, the severe drought inhibited herbaceous regrowth. Accordingly, cattle use of aspen and other browse species was greater in 1981, consistent with results for the light June treatment. However, aspen use was much higher under heavy grazing given that depletion of live and dead herbage supplies were equally extensive. This increasd browse use indicates a dietary adjustment by cattle in response to low availability of preferred foods (Emlen 1966; Menge 1972; Ellis et al. 1976). Since no live unbrowsed suckers remained after grazing in either year, more suckers were browsed twice, three and four times in 1981. Due to the high number of browsings, older multibranched suckers had a shorter growth habit than those in the light June treatment. The taller suckers were often in the second or third year of growth and had only two or three long terminal branches. Therefore, these suckers had considerable current annual growth available after the initial browsing. In contrast, young suckers in the first year of growth were often totally depleted of leaves or uprooted by one bite. They were not protected by a heavy litter layer as in the light June treatment. Thus, taller suckers were browsed more often. However, multibranched suckers, usually older than 4 years, were less preferred because they had many short terminals that were less efficiently harvested by cattle. This was due to the proximity of the woody attachment to current annual growth on twigs. Animals had trouble severing woody tissue when their bites extended onto the woody portion of twigs. In contrast, animals easily severed the current annual growth of twigs having long terminals. These responses to older, multibranched suckers resulted in insignificant correlations of age and number of branches with browsings per sucker. Aspen mortality was higher for younger, shorter suckers with fewer main branches. Obviously, young suckers totally depleted by one bite could be expected to have higher mortality than older, less easily depleted suckers. Since the number of browsings per sucker was consistently high under heavy June grazing, its predictive effect on mortality was largely a function of age, height and number of branches per sucker. Nevertheless, the number of browsings per sucker was greater in areas with a low aspen density. These areas also showed higher mortality. Cattle were less selective and used aspen more heavily in situations where aspen density was low, consistent with research by Emlen (1966) and Menge (1972). Aspen mortality was also higher in areas where initial levels of live herbage were greater. Obviously, cattle used these areas more often for forage acquisition. Therefore, use and mortality of aspen was also greater on the basis of the continual sampling of forages by cattle (Royama 1970; Smith and Dawkins 1971; Zahorik and Houpt 1977). By the same theory, the high levels of aspen use and mortality observed in this [illegible]nt indicated that cattle recognized aspen as a profitable alternate forage source for much of the grazing period. This was in part due to the low availability of herbage. Under light October grazing, herbaceous biomass levels were the highest among treatments before and after grazing. Cattle preferred to graze in locally overgrazed areas where, following initial use, they could regraze any fall regrowth without the hindrance of high dead herbage biomass or woody stems. Areas with high initial levels of live herbage showed lower aspen use. When cattle could obtain preferred live herbage, aspen became an unprofitable alternate forage in October due to its lack of leaves following abscission. Western snowberry was a more acceptable alternate forage for cattle because it retained leaves and berries long after the killing frost. The late frost in 1981 emphasized the effect of abscission on cattle response to aspen in October. Leaf abscission of aspen did not occur until the second week of the grazing period that year. Accordingly, aspen use was abnormally high during the first half of the grazing period. Then, after leaf abscission, use plummeted in the second half of grazing in a return to the norm of aspen avoidance in October. This behavior supports research by FitzGerald and Bailey (1984) who noted the readiness of cattle to browse aspen during August in the prescence of ample herbaceous biomass. FitzGerald (1982) and Hilton and Bailey (1972) suggested that the quality of herbage in late summer was such that aspen and other browse became more acceptable forages.

Certainly, cattle exhibited a similar foraging strategy prior to leaf abscission in this study. This study also indicated that a lower range in forage quality exists between browse and herbaceous forages in October than in June (Chapter 6). Cattle preferred leafy suckers in the first or second year of growth with one or two terminal branches. Unlike the light June treatment, new suckers had completed a full growing season. Therefore, most were well established and extended above the dead herbage layer. However, while more available, a single browsing was less likely to totally deplete or uproot suckers as in June. Numerous suckers in the second year of growth having two terminal branches were observed, a direct observation of lower mortality in October. Obviously, light use when plants are entering the dormant state results in a multibranched growth habit less easily depleted by browsing (FitzGerald 1982). Sucker mortality was highly dependent on the number of browsings per sucker. This indicates that while suckers were more resistant to mortality in October, they were not immune to the stress inflicted by browsing.

Sucker mortality under heavy October grazing was also highly dependent upon the number of browsings per sucker. As in the light October treatment, the vast majority of aspen use occurred prior to leaf abscission. This treatment showed greater depletion of herbaceous biomass than the light October treatment. Yet, unlike the heavy June treatment, cattle were able to utilize dead herbage supplies produced over a full growing season. Thus, because live herbage supplies were quickly depleted under heavy grazing and fall regrowth was minimal relative to that in June, cattle preferred areas with high levels of dead and total herbage. Use and mortality of aspen was lower in these areas because preferred forage was more available and aspen was a less profitable alternate forage after abscission. A second reason relates to the positive correlation of dead herbage levels with number of main branches per sucker. Since cattle were continuously sampling all forages, areas used more due to high herbage levels also attained a light use of aspen. The resultant growth habit of these lightly used suckers made them less susceptible to depletion by browsing. FitzGerald (1982) noted this effect on the growth habit of aspen browsed late in the growing season. The absence of a heavy dead herbage layer in this treatment resulted in less protection of young suckers. Animals were selecting forage largely on the basis of abundance and availability. Thus, shorter suckers within close range of the herbaceous and low shrub layers suffered higher use and mortality. Autumn preference for western snowberry resulted in greater use of older suckers than in the light October treatment. This was because older, multibranched suckers were about the same height as the western snowberry shrub layer under heavy grazing. Conversely, older suckers in the light treatment had much taller growth habits due to fewer browsings over the years. Furthermore, the western snowberry shrub layer was used more under heavy grazing due to the lack of abundant herbaceous biomass. These factors resulted in insignificant correlations of age and number of branches with aspen use and mortality under heavy October grazing. Aspen use was also greater in areas with a low aspen density. Again, this demonstrates the decrease in selectivity noted when food density is lower (Emlen 1966; Menge 1972; Ellis et al. 1976), consistent with behavior in the heavy June treatment. However, the wide differences in aspen use and mortality between the two heavy grazing treatments indicated that aspen was not considered a profitable alternate forage source in October. Animals preferred dead herbage supplies and western snowberry leaves and berries more than leafless aspen when depletion of live herbage occurred in October. However, significant use of aspen as an alternate forage source was observed prior to leaf abscission and in June.

Both light grazing treatments indicated that cattle preferred specific types of suckers based on height, age and number of main branches. Thus, under high food density, cattle were more selective regarding specific plant attributes (Emlen 1966; Menge 1972). The response to morphological attributes of suckers implied a possible relationship to differences in quality. One would suspect that the younger, preferred suckers were of higher quality than older suckers. They likely contained less fiber, more moisture, more protein and were more digestible. However, the direct relationship of animal selectivity to such nutritional fractions can be considered unpredictable and inconsistent based on the conclusions of Chapter 6 and other studies (Arnold and Hill 1972; Zahorik and Houpt 1977). Rather, response is more likely related to some specific chemical compound influencing response at the sensory level (Arnold and Hill 1972). Such compounds may or may not be a chemical derivative of quality fractions. The morphological attributes measured may also relate to physical factors affecting animal response. For example, ease of harvesting might be the factor determining preference for younger suckers, perhaps related to fiber and lignin content or simply the stem diameter. Cattle had notably more trouble severing woody stems than current annual growth. These factors certainly affected the intake rates for browse forages. The interaction of quality and physical factors with environmental variables further confounds explanations of animal response. Considering the integrated response theory confirmed in Chapter 6, all of these factors play some role in determining response. But, a limit to the separation of effects exists due to confounding by the interaction of variables.

The animal response to aspen suckers is largely governed by certain morphological attributes of aspen and the relative density and availability of all food types, especially live and dead herbage. Conversely, aspen sucker mortality is dependent on the number of browsings, its morphological and physiological state, and the indirect effects of the environment upon animal response.

8. CONCLUSIONS

Grassland communities were generally preferred over forests or shrublands. This was directly related to the relatively high foraging efficiency cattle achieved using grassland forages. Bite rates, bite sizes and DM intake rates for grassland forages were greater than for forest forages. Nevertheless, browsing was a significant foraging activity in all treatments at levels exceeding previous reports in the literature. Browse species represented higher proportions of cattle diets under a light grazing intensity, especially in June when browse leaves were available.

Supplies of forest forages were more quickly depleted than grassland forages. This depletion was more pronounced under a heavy grazing intensity, thereby imposing additional grazing pressure on grassland communities. Accordingly, grassland forages contributed a greater proportion to cattle diets under a heavy grazing intensity.

Cattle were normally more selective among plant communities in October than in June. They showed greater avoidance of forests and shrublands and greater preference for grasslands in October. However, abnormally high use of forest and shrubland communities occurred in October, 1981, when leaf abscission of shrubs and senescence of palatable forest forbs were delayed by a late frost. Animals utilized these unusually available forages as profitable alternatives to grassland herbage over the short term. Once depletion of these forages occurred, cattle diets were again dominated by grassland forages. Thus, cattle were able to determine the relative profitability of food acquisition among communities. They did this by continual sampling of forages and selection of a diverse diet. Their response was an integrated response largely dependent on the relative foraging efficiency, quality and availability of forages. Forage quality had its biggest effect under situations of high food availability. Cattle preferred live herbage over dead herbage, especially in June and under a light grazing intensity. Similarly, leafy browse was preferred over dead herbage when ample supplies of live herbage were available. However, browse species were avoided after leaf abscission, largely a response to the negative effects on foraging efficiency. This demonstrated the dominating influence of foraging efficiency on forage preference, considering that dead herbage was a lower quality forage than abscised browse.

The diverse diet strategy employed by cattle contributed to significant use and mortality of aspen in all treatments. Aspen mortality was two times greater under heavy grazing than under light grazing and five times greater in June than in October. Aspen was avoided in October because it was one of the first browse species to undergo leaf abscission. Browse that retained leaves and fruit longer was preferred, especially western snowberry. In June, aspen suckers were a preferred alternate source of forage, especially under heavy grazing where depletion of grassland herbage was most severe. Aspen mortality was highly dependent on sucker height and the number of browsings per sucker. Shorter suckers and suckers browsed more often had the highest mortality rates in all treatments.

This study has elucidated some of the effects that grazing intensity and season of use have on cattle response and, in [illegible] the range resource. The results have certain [illegible]ons to management. Firstly, greater use of grassland [illegible] observed under heavy grazing intensities. Repeated application of heavy grazing treatments for eight years has had negative effects on range condition and productivity in this study, especially in June (Bailey 1980). In addition, the summer-long drought during 1981 caused greater overuse of grasslands. Obviously, stocking rates should be adjusted for environmental conditions that affect forage production. Repeated application of light grazing treatments for eight years has resulted in unnecessarily high levels of dead herbage. Locally overused patches of rangeland that are grazed and regrazed in attempts to avoid the unpalatable litter have also developed. Obviously, stocking rates and season of use should be varied to avoid these problems. Cattle would utilize dead herbage more readily under a heavy grazing intensity applied in October when live herbage regrowth and palatable browse species are less available. Likewise, forage species suffering from repeated overuse and competition with unpalatables under heavy June grazing would benefit from a change in season of use. Grazing in the dormant state in October when carbohydrate reserves are most plentiful is less stressful on herbaceous species. Shorter grazing periods using higher stocking rates would also help reduce preferential grazing of preferred forages while at the same time forcing greater use of competitors.

On the basis of this study, cattle are a potentially inexpensive method of controlling aspen invasion onto grasslands. However, their effectiveness is highly dependent on the grazing intensity, season of use and morphology of suckers. Grazing strategies geared to achieve high aspen mortality should use a heavy grazing intensity in June, based on these results. However, high levels of aspen use prior to leaf abscission were noted in October, 1981. This supports other research indicating a high cattle preference for aspen and other browse in late summer (Smith et al. 1972; Hilton and Bailey 1972; FitzGerald and Bailey 1984). Further study of aspen mortality rates in response to browsing during late summer are desirable. Results of such research could be compared with the aspen mortality rates achieved in this study.

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10. APPENDICES.

10.1 Appendix A. Treatment periods, cattle numbers and group observations, 1980 and 1981.

Treatment	Year	Number of cattle	Day in	Day out	Grazing period in days	Number of days observed	Number of groups observed	Total animals observed
Light June	1980	11	June 4	July 1	28	14	323	1338
	1981	12	June 4	July 1	28	15	358	1625
Heavy June	1980	33	June 4	July 1	28	17	714	4567
	1981	34	June 4	July 1	28	17	1302	7131
Light October	1980	9	Sep. 22	Oct. 22	30	13	221	1185
	1981	8	Sep. 14	Oct. 7	24	9	296	1093
Heavy October	1980	28	Sep. 22	Oct. 22	30	13	529	5017
	1981	25	Sep. 14	Oct. 7	24	11	627	3306

10.2 Appendix B. Availability and use of plant communities.

Treatment	Community	%Available	1980			1981		
			%Use	Pref. Index	Confidence interval	%Use	Pref. Index	Confidence interval
Light June	Carex wetland	NR	-	-	-	-	-	-
	Salix wetland	NR	-	-	-	-	-	-
	Aspen forest	38.9	18.5	.48	.08	26.3	.68	.08
	Shrubland	4.3	2.8	.66	.29	11.7	2.71	.50
	Open grassland	31.8	31.9	1.01	.11	29.9	.94	.09
	Forest edge phase grassland	3.4	9.6	2.81	.73	8.8	2.60	.57
	Snowberry phase grassland	11.7	24.3	2.08	.28	9.4	.81	.17
	Silverberry phase grassland	5.7	11.4	1.99	.41	7.2	1.27	.31
	Brushed fenceline	4.2	1.6	.37	.20	6.6	1.57	.40
	Shrubby phase grasslands	20.8	45.2	2.17	.62	25.5	1.23	.53
	All grasslands	52.6	77.1	1.47	.20	55.4	1.05	.2[illegible]

NR-community not represented (≤0.2% of treatment area).

Appendix B (continued)

Treatment	Community	%Available	1980			1981		
			%Use	Pref. Index	Confidence interval	%Use	Pref. Index	Confidence interval
Heavy June	Carex wetland	4.7	0.6	.13	.07	1.4	.29	.08
	Salix wetland	2.7	0.2	.06	.06	1.6	.59	.15
	Aspen forest	52.0	13.7	.26	.02	31.6	.61	.03
	Shrubland	1.2	1.4	1.20	.37	4.6	3.84	.59
	Open grassland	14.9	30.4	2.04	.13	18.2	1.22	.09
	Forest edge phase grassland	5.7	9.9	1.73	.22	13.1	2.30	.19
	Snowberry phase grassland	7.4	24.6	3.33	.24	11.5	1.55	.14
	Silverberry phase grassland	6.3	16.8	2.67	.24	11.9	1.89	6
	Brushed fenceline	5.1	2.4	.48	.13	6.1	1.20	.16
	Shrubby phase grasslands	1[illegible].4	51.3	2.64	.69	36.5	1.88	.67
	All grasslands	34.3	81.7	2.38	.20	54.7	1.59	.39

Appendix B (continued).

Treatment	Community	%Available	1980			1981		
			%Use	Pref. Index	Confidence interval	%Use	Pref. Index	Confidence interval
Light October	Carex wetland	NR	-	-	-	-	-	-
	Salix wetland	NR	-	-	-	-	-	-
	Aspen forest	31.6	1.0	.03	.02	8.1	.26	.07
	Shrubland	2.6	1.2	.47	.35	16.8	6.47	1.16
	Open grassland	27.8	64.1	2.32	.15	40.5	1.47	.16
	Forest edge phase grassland	7.8	1.5	.19	.13	1.6	.20	.14
	Snowberry phase grassland	12.6	13.2	1.06	.23	10.5	.84	.21
	Silverberry phase grassland	11.4	19.0	1.68	.29	22.0	1.94	.31
	Brushed fenceline	6.3	0.1	.01	.04	0.5	.07	.09
	Shrubby phase grasslands	31.8	33.6	1.06	.39	34.0	1.07	.38
	All grasslands	59.6	97.7	[illegible]	[illegible]	74.6	1.25	.18

NR-community not represented (≤0.2% of treatment area).

Appendix B (continued).

Treatment	Community	%Available	1980			1981		
			%Use	Pref. Index	Confidence interval	%Use	Pref. Index	Confidence interval
Heavy October	Carex wetland	2.2	2.0	.89	.25	0.0	.00	[illegible]
	Salix wetland	1.6	0.2	.12	.12	0.0	.00	.00
	Aspen forest	44.4	2.2	.05	.01	11.7	.26	.03
	Shrubland	1.8	0.8	.45	.23	2.3	1.28	.39
	Open grassland	24.7	69.5	2.81	.07	52.7	2.13	.09
	Forest edge phase grassland	11.0	9.3	.85	.10	19.1	1.74	.18
	Snowberry phase grassland	4.5	6.6	1.47	.23	9.2	2.05	.32
	Silverberry phase grassland	3.1	7.3	2.35	.32	3.5	1.13	.29
	Brushed fenceline	6.7	2.2	.33	.09	1.5	.22	.09
	Shrubby phase grasslands	18.6	23.2	1.25	.62	31.9	1.72	.67
	All grasslands	43.3	92.7	2.14	.16	84.5	1.95	.22

10.3 Appendix C. Summary of individual observations of animals conducted among treatments in 1980 and 1981.

Treatment	Year	Number of individuals observed	Total time observed in minutes	Total number of bites observed
Light June	1980	186	657	22994
	1981	152	447	19774
Heavy June	1980	334	1196	48517
	1981	321	1002	46718
Light October	1980	77	238	9911
	1981	103	358	17218
Heavy October	1980	147	393	13301
	1981	127	447	26574

10.4 Appendix D. Herbaceous biomass levels in plant communities (10 quadrats per community per sample).

Treatment	Sample-	Community	Herbaceous biomass (kg/ha) Live	std. dev.	Dead	std. dev.	Total
Light June, 1980.	before grazing	Aspen forest	114	85	3	8	117
		Shrubland	56	49	0	0	56
		Open grassland	1402	467	405	195	1807
		Forest edge phase grassland	1627	359	599	227	2226
		Snowberry phase grassland	1040	322	603	307	1643
		Silverberry phase grassland	1376	412	832	370	2208
	after grazing	Aspen forest	185	120	25	23	210
		Shrubland	100	92	10	15	110
		Open grassland	1402	538	355	317	1757
		Forest edge phase grassland	1563	670	762	343	2325
		Snowberry phase grassland	1278	671	864	620	2142
		Silverberry phase grassland	1360	513	974	426	2334

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha)				
			Live	std. dev.	Dead	std. dev.	Total
Light June, 1981.	before grazing	Aspen forest	119	69	8	26	127
		Shrubland	174	120	123	89	297
		Open grassland	2317	504	538	295	2855
		Forest edge phase grassland	1767	282	500	344	2267
		Snowberry phase grassland	1551	805	859	561	2410
		Silverberry phase grassland	1696	506	613	270	2309
	after grazing	Aspen forest	93	60	0	0	93
		Shrubland	147	104	96	89	243
		Open grassland	2386	643	518	169	2904
		Forest edge phase grassland	1697	391	777	339	2474
		Snowberry phase grassland	1521	550	528	246	2049
		Silverberry phase grassland	1906	604	636	226	2542

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha)				
			Live	std. dev.	Dead	std. dev.	Total
Heavy June, 1980.	before grazing	Aspen forest	125	44	0	0	125
		Shrubland	113	[illegible]	0	0	113
		Open grassland	799	403	185	131	984
		Forest edge phase grassland	958	229	309	246	1267
		Snowberry phase grassland	1112	388	711	386	1822
		Silverberry phase grassland	1181	569	762	530	1943
	after grazing	Aspen forest	85	70	100	145	185
		Shrubland	80	50	200	185	280
		Open grassland	508	180	98	82	606
		Forest edge phase grassland	622	195	473	320	1095
		Snowberry phase grassland	554	303	385	302	939
		Silverberry phase grassland	659	363	456	321	1115

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha)				
			Live	std. dev.	Dead	std. dev.	Total
Heavy June, 1981.	before grazing	Aspen forest	118	107	0	0	118
		Shrubland	343	270	895	873	1238
		Open grassland	1667	436	258	263	1925
		Forest edge phase grassland	1656	387	237	297	1893
		Snowberry phase grassland	1933	735	414	250	2347
		Silverberry phase grassland	1706	312	451	689	2157
	after grazing	Aspen forest	68	56	122	316	190
		Shrubland	173	105	264	248	437
		Open grassland	921	336	308	426	1229
		Forest edge phase grassland	752	122	211	129	963
		Snowberry phase grassland	715	274	384	232	1099
		Silverberry phase grassland	1001	329	361	288	1362

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha)				
			Live	std. dev.	Dead	std. dev.	Total
Light October, 1980.	before grazing	Aspen forest	14	44	70	50	84
		Shrubland	35	110	100	105	135
		Open grassland	1673	[illegible]	535	545	2208
		Forest edge phase grassland	1663	767	1245	518	2908
		Snowberry phase grassland	1398	754	877	573	2275
		Silverberry phase grassland	1747	561	1337	520	3084
	after grazing	Aspen forest	0	0	100	120	100
		Shrubland	0	0	200	305	200
		Open grassland	774	689	477	432	1251
		Forest edge phase grassland	1204	635	2039	584	3242
		Snowberry phase grassland	529	372	1015	736	1544
		Silverberry phase grassland	638	337	1462	843	2100

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha) Live	std. dev.	Dead	std. dev.	Total
Light October 1981.	before grazing	Aspen forest	54	72	34	47	88
		Shrubland	79	97	70	104	149
		Open grassland	1780	532	513	482	2293
		Forest edge phase grassland	1876	536	963	610	2839
		Snowberry phase grassland	1330	473	949	641	2279
		Silverberry phase grassland	1993	486	826	620	2819
	after grazing	Aspen forest	0	0	74	83	74
		Shrubland	0	0	149	163	149
		Open grassland	958	511	766	432	1724
		Forest edge phase grassland	1081	482	1666	517	2747
		Snowberry phase grassland	911	470	948	514	1859
		Silverberry phase grassland	874	301	1375	933	2249

Appendix D (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha) Live	std. dev.	Dead	std. dev.	Total
Heavy October, 1980.	before grazing	Aspen forest	0	0	70	60	70
		Shrubland	1	1	100	125	101
		Open grassland	1618	399	649	376	2267
		Forest edge phase grassland	1890	512	1129	517	3019
		Snowberry phase grassland	1806	913	1629	862	3435
		Silverberry phase grassland	1612	367	821	472	2433
	after grazing	Aspen forest	0	0	110	135	110
		Shrubland	0	0	200	290	200
		Open grassland	736	259	658	340	1394
		Forest edge phase grassland	601	481	520	435	1121
		Snowberry phase grassland	559	284	1648	784	2207
		Silverberry phase grassland	308	110	317	287	625

Appendix D' (continued).

Treatment	Sample	Community	Herbaceous biomass (kg/ha)				
			Live	std. dev.	Dead	std. dev.	Total
Heavy October 1981.	before grazing	Aspen forest	47	67	32	41	79
		Shrubland	94	107	69	69	163
		Open grassland	906	271	119	97	1025
		Forest edge phase grassland	1248	313	169	147	1417
		Snowberry phase grassland	1226	421	187	148	1413
		Silverberry phase grassland	1203	348	188	166	1391
	after grazing	Aspen forest	0	0	40	52	40
		Shrubland	0	0	98	78	98
		Open grassland	202	114	86	51	288
		Forest edge phase grassland	298	141	221	158	519
		Snowberry phase grassland	286	182	290	192	576
		Silverberry phase grassland	261	119	310	201	571

10.5 Appendix E. Quality attributes of live herbage (10 quadrats per community per sample).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Light June, 1980.	before grazing	Aspen forest	18.0	30.0	.460	16.9	2.70
		Shrubland	20.0	32.0	.340	15.8	2.50
		Open grassland	50.4	39.4	.158	10.0	1.59
		Forest edge phase grassland	43.9	40.6	.179	11.1	1.78
		Snowberry phase grassland	41.4	37.0	.174	11.7	1.87
		Silverberry phase grassland	37.1	35.9	.156	12.9	2.07
	after grazing	Aspen forest	22.0	31.0	.420	16.0	2.65
		Shrubland	24.0	34.0	.300	15.0	2.45
		Open grassland	54.0	41.0	.130	9.9	1.50
		Forest edge phase grassland	47.1	42.6	.180	11.2	1.79
		Snowberry phase grassland	45.0	39.0	.165	10.8	1.80
		Silverberry phase grassland	41.0	37.0	.140	12.1	2.00

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Light June, 1981	before grazing	Aspen forest	18.5	31.8	.440	17.9	2.86
		Shrubland	19.7	34.7	.328	16.3	2.61
		Open grassland	57.0	40.6	.143	8.8	1.42
		Forest edge phase grassland	52.2	43.3	.172	9.9	1.58
		Snowberry phase grassland	43.9	42.7	.220	12.5	2.00
		Silverberry phase grassland	47.5	43.4	.158	12.0	1.93
	after grazing	Aspen forest	35.1	39.0	.289	12.8	2.04
		Shrubland	30.4	35.2	.193	13.5	2.16
		Open grassland	68.7	42.6	.099	7.0	1.11
		Forest edge phase grassland	58.4	41.3	.146	8.6	1.37
		Snowberry phase grassland	57.8	42.4	.144	9.0	1.44
		Silverberry phase grassland	58.7	40.5	.129	9.8	1.57

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Heavy June, 1980.	before grazing	Aspen forest	18.0	31.0	.390	19.0	3.00
		Shrubland	17.0	29.0	.300	15.0	2.40
		Open grassland	40.0	38.0	.200	10.2	1.60
		Forest edge phase grassland	29.5	36.6	.223	12.6	2.01
		Snowberry phase grassland	28.0	38.0	.230	12.2	1.95
		Silverberry phase grassland	26.0	35.0	.225	14.3	2.30
	after grazing	Aspen forest	23.0	34.0	.235	15.0	2.50
		Shrubland	20.0	31.0	.230	14.5	2.35
		Open grassland	55.0	43.0	.170	9.9	1.55
		Forest edge phase grassland	41.4	42.5	.186	12.3	1.97
		Snowberry phase grassland	38.0	41.0	.190	11.9	1.90
		Silverberry phase grassland	36.0	38.0	.195	14.0	2.25

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Heavy June, 1981.	before grazing	Aspen forest	22.9	33.7	.361	18.2	2.91
		Shrubland	19.9	30.7	.269	14.4	2.31
		Open grassland	56.3	40.6	.160	9.5	1.52
		Forest edge phase grassland	41.3	39.6	.192	11.9	1.90
		Snowberry phase grassland	38.3	40.0	.202	11.5	1.85
		Silverberry phase grassland	37.2	37.7	.195	13.7	2.18
	after grazing	Aspen forest	44.9	37.4	.209	10.6	1.70
		Shrubland	32.1	34.9	.213	14.6	2.34
		Open grassland	83.1	42.2	.132	9.3	1.49
		Forest edge phase grassland	69.8	42.3	.150	9.1	1.46
		Snowberry phase grassland	72.1	47.7	.129	7.9	1.26
		Silverberry phase grassland	67.9	40.9	.130	11.2	1.79

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Light October, 1980.	before grazing	Aspen forest	27.0	46.1	.162	8.4	1.35
		Shrubland	43.7	49.3	.114	6.5	1.04
		Open grassland	54.3	45.1	.114	6.7	1.08
		Forest edge phase grassland	45.6	48.6	.129	7.8	1.25
		Snowberry phase grassland	40.8	46.9	.147	7.5	1.20
		Silverberry phase grassland	45.1	44.1	.130	9.1	1.45
	after grazing	Aspen forest	60.0	47.0	.110	7.0	1.10
		Shrubland	70.0	50.0	.080	5.5	.85
		Open grassland	68.8	46.9	.089	5.6	.90
		Forest edge phase grassland	80.9	49.6	.085	4.5	.73
		Snowberry phase grassland	83.5	48.9	.088	6.1	.97
		Silverberry phase grassland	77.8	47.9	.085	6.0	.97

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Light October, 1981.	before grazing	Aspen forest	46.0	37.9	.176	8.6	1.38
		Shrubland	56.9	42.2	.079	7.3	1.17
		Open grassland	65.9	42.9	.127	7.4	1.18
		Forest edge phase grassland	52.9	41.6	.137	7.3	1.17
		Snowberry phase grassland	62.0	42.6	.116	7.3	1.17
		Silverberry phase grassland	60.6	42.6	.110	7.4	1.19
	after grazing	Aspen forest	56.0	40.0	.120	7.1	1.12
		Shrubland	67.0	44.0	.080	5.9	.97
		Open grassland	73.8	44.5	.094	5.7	.92
		Forest edge phase grassland	75.2	44.8	.074	7.2	1.15
		Snowberry phase grassland	74.4	45.8	.077	5.9	.94
		Silverberry phase grassland	69.9	43.3	.087	6.1	.98

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Heavy October, 1980.	before grazing	Aspen forest	18.3	48.8	.191	10.0	1.60
		Shrubland	24.0	49.0	.150	7.9	1.20
		Open grassland	37.9	45.6	.108	7.9	1.26
		Forest edge phase grassland	39.1	45.6	.142	8.5	1.35
		Snowberry phase grassland	38.3	49.0	.122	8.0	1.28
		Silverberry phase grassland	41.1	45.1	.114	8.7	1.39
	after grazing	Aspen forest	48.0	53.0	.180	8.0	1.30
		Shrubland	57.0	54.0	.140	7.4	1.10
		Open grassland	72.5	48.0	.098	7.4	1.19
		Forest edge phase grassland	66.4	50.6	.119	7.9	1.26
		Snowberry phase grassland	73.5	53.6	.105	6.5	1.04
		Silverberry phase grassland	62.9	47.9	.116	8.6	1.37

Appendix E (continued).

Treatment	Sample	Community	%DM	%ADF	%P	%CP	%N
Heavy October, 1981.	before grazing	Aspen forest	44.1	38.6	.151	9.9	1.58
		Shrubland	50.0	39.0	.159	8.0	1.27
		Open grassland	67.3	41.6	.147	8.2	1.30
		Forest edge phase grassland	61.3	42.7	.136	9.0	1.43
		Snowberry phase grassland	59.6	39.7	.155	8.8	1.41
		Silverberry phase grassland	62.4	41.0	.125	10.0	1.60
	after grazing	Aspen forest	60.0	44.0	.130	7.0	1.20
		Shrubland	66.0	45.0	.130	6.2	.98
		Open grassland	83.3	46.9	.087	6.3	1.01
		Forest edge phase grassland	77.7	48.3	.093	6.4	1.02
		Snowberry phase grassland	75.5	46.6	.105	6.9	1.11
		Silverberry phase grassland	78.1	48.7	.141	6.7	1.07

10.6 Appendix F. Quality attributes of four browse species (10 quadrats per browse species per sample).

Treatment	Sample	Browse species	%DM	%ADF	%P	%CP	%N
Light June, 1980.	before grazing	Aspen	38.5	22.5	.199	13.6	2.17
		Rose	36.0	20.0	.305	14.2	2.30
		Saskatoon	42.0	24.0	.300	14.0	2.22
		Western snowberry	36.0	21.7	.245	11.1	1.78
Light June, 1981.	before grazing	Aspen	37.0	40.0	.285	15.6	2.50
		Rose	34.4	19.1	.331	15.7	2.51
		Saskatoon	40.0	29.9	.320	15.6	2.50
		Western snowberry	36.0	22.0	.240	13.5	2.11

Appendix F (continued).

Treatment	Sample	Browse species	%DM	%ADF	%P	%CP	%N
Heavy June, 1980.	before grazing	Aspen	34.1	27.9	.251	13.4	2.14
		Rose	35.0	20.0	.270	14.9	2.38
		Saskatoon	39.0	30.0	.300	15.5	2.50
		Western snowberry	30.4	24.7	.259	10.4	1.67
Heavy June, 1981.	before grazing	Aspen	33.3	37.5	.312	16.7	2.68
		Rose	35.1	19.0	.297	16.4	2.62
		Saskatoon	38.0	34.8	.334	16.8	2.70
		Western snowberry	35.0	22.0	.290	14.0	2.30

Appendix F (continued).

Treatment	Sample	Browse species	%DM	%ADF	%P	%CP	%N
Light October, 1980.	before grazing	Aspen	49.6	39.1	.132	6.2	0.99
		Rose	44.0	23.0	.335	8.5	1.35
		Saskatoon	49.0	31.0	.400	9.8	1.53
		Western snowberry	39.6	29.9	.188	7.5	1.19
Light October, 1981.	before grazing	Aspen	46.4	40.2	.129	9.1	1.45
		Rose	44.8	22.8	.330	8.6	1.38
		Saskatoon	48.4	30.4	.419	10.0	1.59
		Western snowberry	42.0	29.8	.206	6.7	1.07

Appendix F (continued).

Treatment	Sample	Browse species	%DM	%ADF	%P	%CP	%N
Heavy October, 1980.	before grazing	Aspen	49.6	42.3	.122	6.7	1.07
		Rose	49.9	24.0	.225	6.3	1.00
		Saskatoon	50.0	40.0	.240	6.9	1.15
		Western snowberry	38.3	28.2	.225	6.6	1.06
Heavy October, 1981.	before grazing	Aspen	44.9	39.5	.166	10.2	1.62
		Rose	45.2	21.0	.249	9.3	1.49
		Saskatoon	44.9	38.9	.268	8.9	1.42
		Western snowberry	45.0	30.5	.247	8.4	1.34

10.7 Appendix G. Weekly herbaceous biomass levels in the forest edge phase grassland (20 quadrats/week).

Treatment	Day of grazing	Herbaceous biomass (kg/ha)					
		Live	std. dev.	Dead	std. dev.	Total	std. dev.
Light June, 1980.	0	1700	377	516	213	2216	497
	8	1365	404	870	338	2235	597
	17	1035	342	723	375	1758	583
	23	1189	502	497	296	1686	657
	28	1283	501	626	231	1909	639
Light June, 1981.	0	2168	394	505	400	2673	543
	8	2237	530	516	230	2753	667
	15	2136	428	478	265	2614	612
	22	2202	468	393	134	2595	499
	28	1933	326	657	304	2590	473

Appendix G (continued).

Treatment	Day of grazing	Herbaceous biomass (kg/ha)					
		Live	std. dev.	Dead	std. dev.	Total	std. dev.
Heavy June, 1980.	0	971	289	514	261	1485	492
	7	773	310	522	353	1295	527
	15	499	212	443	241	942	305
	23	326	197	294	185	620	280
	28	465	187	350	240	815	334
Heavy June, 1981.	0	1610	472	191	207	1801	552
	7	1397	428	228	122	1625	486
	15	1168	438	222	107	1390	494
	22	798	240	246	106	1044	252
	28	687	125	232	126	919	137

Appendix G (continued).

Treatment	Day of grazing	Herbaceous biomass (kg/ha)					
		Live	std. dev.	Dead	std. dev.	Total	std. dev.
Light October, 1980.	0	1740	742	1824	867	3564	1112
	7	1674	481	1651	755	3325	787
	20	1059	315	1681	557	2740	641
	30	1008	515	1934	627	2942	859
Light October, 1981.	0	2260	775	2062	866	4322	1136
	8	2101	710	3355	1642	5456	2111
	16	1476	391	3270	1568	4746	1741
	24	1059	542	2551	1134	3610	1721

Appendix G (continued).

Treatment	Day of grazing	Herbaceous biomass (kg/ha)					
		Live	std. dev.	Dead	std. dev.	Total	std. dev.
Heavy October, 1980.	0	1696	464	1211	635	2907	780
	7	1096	303	1074	600	2170	667
	15	1117	463	991	534	2108	804
	24	929	431	1076	506	2005	824
	30	662	394	749	479	1411	860
Heavy October, 1981.	0	1358	312	436	193	1794	413
	8	1017	402	1197	589	2214	816
	16	647	282	1480	816	2127	1009
	24	359	160	887	557	1246	658

10.8 Appendix H. Attributes affecting the number of browsings and mortality rate of aspen (25 suckers and 2 quadrats/area).

Treatment	Area#	Dependant Var.		Plant Attributes			Area Attributes				
		# times browsed (n/plant)	mort. rate (%)	Height (cm.)	#Branch (n/pl.)	Age (yrs)	Snow-berry cover (%)	Aspen density (n/m²)	Live herb. (kg/ha)	Dead herb. (kg/ha)	Total herb. (kg/ha)
Light June, 1980.	101	75	6[illegible]5	20.2	1.16	2.00	5	10.3	2176	380	2556
	102	.49	19.0	29.9	1.96	2.22	30	5.1	2332	1176	3508
	103	.29	12.5	35.8	1.68	2.36	0	14.3	2074	382	2456
	104	.46	32.0	25.7	1.36	2.04	0	12.5	1364	1248	2612
	105	.08	83.0	53.8	2.68	2.16	30	3.3	1850	846	2696
	106	.52	25.0	31.0	1.40	1.40	55	11.3	1408	238	1646
	107	.33	13.0	41.9	2.16	1.44	15	2.1	1460	836	2296
	108	.30	15.0	30.9	1.88	1.20	15	4.4	2076	1306	3382
	109	.29	20.0	53.2	2.20	1.88	25	2.6	1802	1168	2970
	110	.82	33.3	34.5	1.24	1.08	25	4.6	1192	1062	2254
Overall mean		.43	24.3	35.9	1.78	1.78	20	7.1	1773	864	2637
Std. deviation		.21	15.2	10.4	.47	.44	17	4.5	394	399	549

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	# times browsed	mort. rate	Height	#Branch	Age	Snow-berry cover	Aspen density	Live herb.	Dead herb.	Total herb.
		(n/plant)	(%)	(cm.)	(n/pl.)	(yrs)	(%)	(n/m²)	(kg/ha)	(kg/ha)	(kg/ha)
Light June, 1981.	201	1.05	16.0	45.5	1.76	2.76	50	3.5	3010	394	3404
	202	.64	45.8	43.7	1.50	2.83	50	3.9	3264	430	3694
	203	.41	33.3	60.9	2.22	3.59	60	1.0	2544	1750	4294
	204	.70	48.0	23.9	1.31	1.85	0	1.0	2430	518	2948
	205	1.01	34.6	17.2	1.19	1.73	10	8.0	2628	574	3202
	206	.92	44.0	23.8	1.36	2.28	6	5.9	3102	364	3466
	207	.55	75.0	22.3	1.40	2.12	5	2.9	2908	284	3192
	208	1.39	77.3	27.4	1.84	2.96	0	5.4	1928	406	2334
	209	.65	36.0	51.4	2.08	2.96	38	2.8	1904	98	2002
	210	.99	52.4	32.9	1.16	2.20	25	2.0	1974	286	2260
Overall mean		.82	45.5	35.4	1.60	2.55	24	3.6	2569	510	3079
Std. deviation		.28	17.6	14.1	.36	.57	23	2.2	506	455	710

Appendix H (continued).

Treatment	Area#	Dependant Var.		Plant Attributes			Area Attributes				
		# times browsed	mort. rate	Height	#Branch	Age	Snow-berry cover	Aspen density	Live herb.	Dead herb.	Total herb.
		(n/plant)	(%)	(cm.)	(n/pl.)	(yrs)	(%)	(n/m^2)	(kg/ha)	(kg/ha)	(kg/ha)
Heavy June, 1980.	111	1.41	80.0	30.4	1.08	1.48	0	10.2	1518	404	1922
	112	1.01	48.0	28.0	1.56	2.20	10	4.8	1018	538	1556
	113	2.16	84.0	22.3	1.04	1.56	10	.8	674	836	1510
	114	1.38	37.5	45.7	1.36	2.36	15	10.5	1172	1772	2944
	115	1.44	54.2	34.2	1.40	2.24	0	8.5	1570	702	2272
	116	1.49	52.0	37.1	1.20	1.84	20	9.5	1014	260	1274
	117	1.29	58.3	32.4	1.52	2.16	15	4.0	804	1630	2434
	118	1.54	28.0	48.2	1.52	2.16	10	5.2	534	358	892
	119	1.26	79.2	35.3	1.32	1.96	15	8.5	780	188	968
	120	1.21	64.0	31.0	1.12	2.00	10	13.7	750	506	1256
Overall mean		1.39	58.5	35.4	1.33	2.03	11	7.6	983	719	1702
Std. deviation		*.25*	*17.7*	*7.4*	*.18*	*.26*	*6*	*3.8*	*349*	*553*	*674*

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	# times browsed (n/plant)	mort. rate (%)	Height (cm.)	#Branch (n/pl.)	Age (yrs)	Snow-berry cover (%)	Aspen density (n/m^2)	Live herb. (kg/ha)	Dead herb. (kg/ha)	Total herb. (kg/ha)
Heavy June, 1981.	211	1.46	56.5	26.5	1.24	2.12	9	11.8	1388	126	1514
	212	1.43	62.5	24.1	1.32	2.24	0	13.1	2250	232	2482
	213	1.05	87.5	22.9	1.40	2.12	23	3.0	2120	94	2214
	214	1.25	54.2	28.7	1.16	2.20	3	10.8	1654	74	1728
	215	1.63	23.1	48.6	1.62	2.50	21	9.3	554	34	588
	216	1.13	36.0	39.0	1.48	2.28	11	13.6	2082	48	2130
	217	1.93	68.0	59.8	1.80	2.92	0	5.9	1668	90	1758
	218	1.45	48.0	45.0	1.68	2.64	25	18.3	846	88	934
	219	1.71	92.0	35.8	1.32	2.36	6	6.9	1828	266	2094
	220	1.55	48.0	36.1	1.40	2.44	3	5.1	1252	400	1652
Overall mean		1.46	57.3	36.7	1.44	2.38	10	9.8	1564	145	1709
Std. deviation		.25	20.4	11.4	.19	.24	10	4.7	558	117	585

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	# times browsed	mort. rate	Height	#Branch	Age	Snow-berry cover	Aspen density	Live herb.	Dead herb.	Total herb.
		(n/plant)	(%)	(cm.)	(n/pl.)	(yrs)	(%)	(n/m²)	(kg/ha)	(kg/ha)	(kg/ha)
Light October, 1980.	131	.06	0.0	52.8	1.35	1.75	7	.8	3260	3342	6602
	132	.22	0.0	72.2	1.95	2.65	3	5.0	2598	1218	3816
	133	.11	5.6	62.4	2.15	2.50	2	1.3	1918	1482	3400
	134	.25	5.3	49.3	1.65	2.55	0	3.5	2092	3740	5832
	135	.49	6.3	63.0	1.37	2.37	0	1.5	872	4520	5392
	136	.55	16.7	49.5	1.75	2.50	0	1.8	1598	2506	4104
	137	.27	5.6	86.7	1.55	3.05	0	0.1	1980	2044	4024
	138	.10	0.0	133.8	2.65	3.95	0	1.3	1260	2944	4204
	139	.06	0.0	118.8	2.20	3.60	1	1.0	1360	838	2198
	140	.16	0.0	103.8	2.30	3.65	1	0.5	1224	1400	2624
Overall mean		.21	4.9	81.2	1.93	2.91	1	1.7	1816	2403	4219
Std. deviation		.15	5.0	29.4	.41	.66	2	1.5	716	1215	1381

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	# times browsed	mort. rate	Height	#Branch	Age	Snow-berry cover	Aspen density	Live herb.	Dead herb.	Total herb.
		(n/plant)	(%)	(cm.)	(n/pl.)	(yrs)	(%)	(n/m^2)	(kg/ha)	(kg/ha)	(kg/ha)
Light October, 1981.	231	.30	0.0	46.2	1.65	2.25	7	0.7	2274	3698	5972
	232	.20	5.0	71.8	2.45	2.75	0	1.5	2226	3484	5710
	233	.25	5.0	50.6	2.20	3.00	0	2.3	1250	2420	3670
	234	.45	15.0	67.1	2.05	3.40	3	1.2	1824	1498	3322
	235	.21	0.0	94.2	2.90	3.75	0	1.2	2592	5280	7872
	236	.00	0.0	97.4	2.85	4.15	0	3.0	3292	2688	5980
	237	.26	10.0	39.7	1.85	2.05	0	0.3	3440	2992	6432
	238	.00	5.0	84.9	3.35	4.00	3	3.5	4892	1970	6862
	239	.17	0.0	74.4	2.80	3.00	0	1.5	2422	3194	5616
	240	.05	0.0	85.6	2.85	3.55	13	1.8	2228	4330	6608
Overall mean		.19	4.0	71.7	2.50	3.21	3	1.7	2644	3160	5804
Std. deviation		.14	4.9	19.0	.51	.66	4	1.0	1014	1123	1385

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	times browsed (n/plant)	mort. rate (%)	Height (cm.)	#Branch (n/pl.)	Age (yrs)	Snow-berry cover (%)	Aspen density (n/m²)	Live herb. (kg/ha)	Dead herb. (kg/ha)	Total herb. (kg/ha)
	121	.39	30.0	66.5	2.75	3.40	7	1.5	1690	356	2046
	122	.05	5.0	66.0	2.45	2.85	3	5.5	2106	1494	3600
	123	.22	12.5	64.4	1.80	2.40	3	3.5	1302	1760	3062
	124	.30	5.3	60.3	1.95	2.05	1	3.0	1754	412	2166
	125	.10	5.0	61.8	1.90	2.45	0	3.5	1878	556	2434
	126	.30	10.0	54.7	2.10	2.10	0	2.0	1346	580	1926
	127	.10	5.0	53.0	2.00	2.40	0	1.5	1592	1484	3076
	128	.11	0.0	63.8	1.70	2.25	27	1.0	1180	2384	3564
	129	.10	5.0	77.0	1.80	2.45	32	1.0	1410	2084	3494
	130	.00	0.0	91.6	2.60	3.20	15	2.5	758	1816	2574
Overall mean		.17	7.8	66.0	2.11	2.55	9	2.5	1502	1293	2795
Std. deviation		.12	8.3	10.8	.35	.43	12	1.4	386	752	647

Appendix H (continued).

		Dependant Var.		Plant Attributes			Area Attributes				
Treatment	Area#	# times browsed (n/plant)	mort. rate (%)	Height (cm.)	#Branch (n/pl.)	Age (yrs)	Snow-berry cover (%)	Aspen density (n/m²)	Live herb. (kg/ha)	Dead herb. (kg/ha)	Total herb. (kg/ha)
Heavy October, 1981.	221	.21	5.0	64.4	3.10	3.10	0	1.0	1220	402	1622
	222	.31	20.0	34.4	1.10	1.80	2	2.8	1988	640	2628
	223	.05	0.0	50.6	1.55	2.40	3	1.5	1660	744	2404
	224	.40	0.0	71.2	2.65	3.55	22	1.7	1706	688	2394
	225	.60	5.0	60.7	1.90	2.65	32	1.2	1434	918	2352
	226	.59	21.1	29.8	1.40	2.00	13	1.0	1206	1132	2338
	227	.50	36.8	48.0	2.25	3.00	2	1.7	1208	752	1960
	228	.10	20.0	99.7	3.25	4.25	3	4.0	1358	866	2224
	229	.05	5.0	34.8	1.75	1.90	0	4.0	1064	332	1396
	230	.40	25.0	68.0	2.11	2.05	20	1.7	1824	556	2380
Overall mean		.31	13.6	56.4	2.11	2.67	10	2.1	1467	703	2170
Std. deviation		.20	11.8	20.5	.69	.78	11	1.1	310	239	390