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Seasonal Patterns of Forage Selection by Wapiti (Cervus elaphus) in Relation to Land Reclamation

Alberta
ENVIRONMENTAL CENTRE

SEASONAL PATTERNS OF FORAGE SELECTION BY WAPITI (*Cervus elaphus*) IN RELATION TO LAND RECLAMATION

by

Patrick J. Fargey and Alex W.L. Hawley
Wildlife Biology Branch
Animal Sciences Division
Alberta Environmental Centre
Vegreville, Alberta

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SUMMARY

The selection by captive wapiti of 14 grasses and 4 legumes in land reclamation was measured during the winter, spring and summer. Statistically significant differences in selection among plant species were apparent in every season. During the winter, creeping red fescue was the most frequently eaten species, although sainfoin, brome, timothy and sheep fescue were also selected. Timothy, brome and sainfoin were most frequently selected during the spring. During the summer, the legumes (alfalfa, cicer milkvetch, sainfoin and alsike clover) along with timothy, brome and Russian wild rye were selected more often than other species.

Winter and early spring were identified as the times of year when free-ranging wapiti would most benefit from additional high quality forage. Therefore, plant species preferred in these seasons were also assessed for their ability to meet the energy and protein requirements of a pregnant wapiti cow. Based on these results, forages were recommended for reseeding strategies that have the objective of improving foraging opportunities of wapiti on revegetated pipeline rights-of-way or seismic cut-lines. Forages recommended for improving winter foraging were red fescue, timothy, white clover and cicer milkvetch. Forages recommended for improving spring foraging were brome, timothy and white clover. In addition, it was suggested that the winter and spring seed mixes be applied separately to prevent undesired interspecific competition, thereby optimizing the foraging benefits to wapiti within each season.

Selection of summer forages occurred in 2 distinct groups that corresponded to whether plants were frequently or infrequently eaten. Mean cell wall thickness (MCWT) and forage resistance to mechanical shearing (SF) best explained this forage selection pattern. Both MCWT and SF are related to handling time, which supports the hypothesis that wapiti use handling time to discriminate between plant species. Moisture content was related to forage selection, indicating that succulence may also be important. The proportion of leaf comprising the available biomass was not correlated to plant species selection. Examination of the relationship among plant attributes revealed that differences occurred between grasses and legumes in their structure and physical properties. Grasses appeared to have more interstitial space and less cell contents between cell walls. In addition, grasses and legumes differed in the amount of variance in the resistance to shearing that was not accounted for by quantitative measurements of fiber content.

The botanical composition of rumen contents often provides a biased estimate of diet and this is generally thought to be due to plant species differences in rumen mean retention time (MRT). A technique was tested wherein large particles were isolated from rumen contents in an effort to reduce the bias in estimating diet composition induced in rumen samples by plant species differences in rumen mean retention time (MRT). Wet-sieving of rumen samples collected immediately after the animals had eaten disclosed that partial separation of the large and small particle sizes could be achieved with a 4 mm sieve. Unfortunately, the separation did not remove large biases that still remained in diet estimates obtained using this technique.

ACKNOWLEDGEMENTS

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The study site was located on the Athabasca Ranch and we express our warmest gratitude to the people at both the Athabasca and Entrance Ranches for their hospitality, understanding and support.

We commend Kirby Smith, Fish and Wildlife Division, Alberta Forestry, Lands and Wildlife, for initiating this study; it was largely through his efforts that the project was undertaken.

Many personnel of the Alberta Environmental Centre contributed to this project. We would particularly like to emphasize the technical support and advice provided by Al Kolenosky and the fine animal care provided by Kristi Roy. The scanning electron microscopy, for which we are most grateful, was expertly done by Arlene Oatway, Electron Microscopy Services Section, Alberta Environmental Centre.

Analyses of forage quality were done without charge by the Soil and Feed Testing Laboratory, Alberta Agriculture. Instruction on the use of the Ottawa Texture Measuring System and the Kramer shear cell was gratuitously provided by Phyllis Shand, Home Economics Department, University of Alberta. Zenia Hawrysh, also of the Home Economics Department, provided use of her laboratory. A Boreal Alberta Research Grant from the Boreal Institute was used to partially fund the analyses of diet composition. To all these people and agencies we express our thanks.

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PROJECT TEAM

Joanne Barbeau
Pam Cole
Pat Fargey
Alex Hawley
Al Kolenosky
Kristi Roy

1. GENERAL INTRODUCTION

1.1 Wapiti and Land Reclamation in Alberta

Surface coal mining and the exploration and transportation of petroleum products often result in surface disturbances in areas where wapiti occur in Alberta. Examination of the distribution of wapiti in the province (Nietfeld _et al_. 1984) in relation to the locations of surface coal mines (Alberta Energy Resources Conservation Board 1984), reveals that 5 mines are operating in areas inhabited by wapiti. Coal mining is typically an intensive, long-term disturbance, the impact of which is likely to be small or only locally important to wapiti. In contrast, activities associated with the petroleum industry since 1980 have generated 498,800 km of seismic cut-lines (H.Selcho, personal communication) in the non-settled, forested region of the province called the Green Zone (Alberta Energy and Natural Resources 1981a) and 58,800 km of pipeline throughout the province (J. Owen, personal communication).

Current statistics on the number of hectares affected in regions inhabited by wapiti are unavailable. They can, however, be estimated by extrapolating from historic activity levels. Until 1979, 37.5 % of the seismic activity in the Green Zone occurred in the Whitecourt, Edson, Rocky-Clearwater, and Bow-Crow Forests (Alberta Energy and Natural Resources 1981b). These regions collectively cover the majority of wapiti range in the province (Figure 1.1). If it is assumed that seismic lines averaged 5 m in width, then in excess of 93,500 ha of land would likely have been disturbed since 1980. When pipeline rights-of-way are included, the amount of land that was disturbed in areas inhabited by wapiti was likely in excess of 100,000 ha.

Surface disturbances resulting from industrial activities in Alberta are required to undergo reclamation. The Alberta Forest Service (AFS) has primary responsibility for the administration of land reclamation in the Green Zone (Alberta Energy and Natural Resources 1981a). The AFS objectives for land reclamation are:

1) to establish a self-sustaining vegetative cover which stabilizes the soil;
2) to reclaim the land to a forest environment which is consistent to the region with respect to land forms, vegetative pattern and hydrology; and
3) to reclaim the land to a productivity at least comparable to the undisturbed condition (Alberta Energy and Natural Resources 1984a) .

The creation of wildlife habitat, commercial timber production and recreational activities were also mentioned as possible end uses of reclaimed sites.

Research into the effects of oil and gas exploration and production on wildlife has concentrated largely on the physiological and behavioral effects of noise, increases in human access, landscape alterations and the ingestion of toxic substances (Bromley 1985).

Figure 1.1 Wapiti range in relation to forest management areas in Alberta. Wapiti distribution is according to Nietfeld _et_ _al_. (1984).

Wildlife managers in Alberta have responded by implementing policy to mitigate the detrimental effects of the petroleum industry on wildlife (Stubbs and Markham 1979). Not all the environmental consequences to wildlife of the petroleum industry are negative, however, and there is potential for designing reclamation strategies specifically to benefit wildlife. There has been a growing appreciation for the increases in both habitat diversity (Downing 1983; Revel et al. 1984) and forage availability, particularly for wapiti (Brusnyk and Westworth 1985), that have accrued from the reclamation of pipeline rights-of-way and seismic lines in Alberta. Parallel to this has been the recognition that the habitat modifications resulting from oil and gas production and exploration can be designed to enhance wildlife habitat (Prism Environmental Consulting Services 1984) and that reclamation strategies that have use by wildlife as a major goal should focus on key wildlife species (Green and Salter 1987).

Wapiti are an important big game species in Alberta and the Alberta Fish and Wildlife Division would like to double the population by the year 2000 (Alberta Energy and Natural Resources 1984b). Emphasizing the enhancement of wapiti range when reclaiming pipeline rights-of-way and seismic cutlines could facilitate this objective.

1.2 Project Objectives

There were 2 main objectives to this study. The first was to identify plant species that could be used in land reclamation to improve the foraging opportunities for wapiti. This was to be achieved by quantitatively measuring the seasonal changes in both forage quality and wapiti foraging preferences for selected grass and legume species. The second objective was to examine specific forage attributes and to look for possible explanations for the observed pattern of forage selection. Particular attention was directed at testing a hypothesis proposed by Spalinger et al. (1986) that handling time (time spent ingesting or ruminating the forage) influences forage selection.

1.3 Project History

The study proceeded in 2 phases. Phase I of the project was initiated in 1982 by the Fish and Wildlife Division, Alberta Forestry, Lands and Wildlife (then called Energy and Natural Resources), and involved an examination of the establishment and productivity of 22 plant species on a private ranch near Hinton, Alberta (David Walker and Associates 1983; 1984). The second phase evaluated feeding selection of these plant species by wapiti and was conducted by the Alberta Environmental Centre at the request of Alberta Forestry, Lands and Wildlife. The results of the forage selection study are presented herein.

2. WAPITI SELECTION OF 18 PLANT SPECIES AND THEIR POTENTIAL USE IN LAND RECLAMATION

2.1 Introduction

Environmental disruption from the exploitation of natural resources frequently requires reclamation of land in areas inhabited by wapiti. In particular, disturbances such as oil and gas pipeline rights-of-way and seismic cut-lines from geo-physical exploration are common in Alberta (Chapter 1). The reseeding of these types of disturbances can be viewed as an opportunity to improve wapiti range.

Wapiti, like other ungulates in northern temperate climates, experience large seasonal fluctuations in forage quality (Collins and Urness 1983; Hobbs _et_ _al_. 1983; Nietfeld 1983; Hanley 1984). Land reclamation could improve productivity of wapiti populations by providing forage in the seasons in which the animals may be nutritionally constrained. Devising reclamation strategies that will successfully address these constraints requires a detailed knowledge of wapiti seasonal preferences for, and nutritional quality of, potential reclamation plant species.

Inferences about foraging preferences are frequently based on the definition of preferred forage as being plant species that are "proportionately more frequent in the diet than in the available environment" (Petrides 1975). This distinction is normally made by mathematically adjusting the relative abundance of each plant species in the diet by its availability (availability is normally synonymous with standing biomass) to produce a forage preference index (Krueger 1972). Estimates of availability on a large scale may not accurately reflect plant biomass composition in the area in which animals are foraging (Loehle and Rittenhouse 1982). More sophisticated assessments attempt to approximate availability from the perspective of the animal (Owen-Smith and Cooper 1987).

Researchers frequently ascribe variation in forage preference to some combination of plant characteristics that either positively or negatively influence foraging decisions made by the animal. The cumulative expression of these characteristics is commonly described as plant palatability. Attempts to identify the important forage characteristics affecting animal selection, even in simplified experimental situations, leave at least one third of the variability in animal preferences unexplained (Chapter 3). Consequently, accurate prediction of the foraging response of an animal requires that assessments of plant species preference be done directly.

Several reviews have been made of the literature on the food habits of wapiti both throughout their range (Kufeld 1973; Nelson and Leege 1982) and within Alberta specifically (Morgantini 1986). Unfortunately, there is little quantitative information on wapiti feeding preferences of plant species used in land reclamation. This project was initiated to identify plant species that could be used to improve the foraging opportunities of wapiti on reclamation sites in Alberta. The specific objectives of this study were to:

1) estimate quantitatively the seasonal diet preferences of wapiti for selected reclamation plant species;
2) assess the relative forage quality of these plant species;
3) use these results to suggest modifications to current reseeding practices in Alberta.

2.2 Materials and Methods

2.2.1 Experimental Design

The study site was located near Hinton, Alberta (53° 23' latitude and 117° 40' longitude) in the Boreal Foothills ecoregion (Strong and Leggat 1981) on a grass meadow dominated by Festuca rubra. Vegetation plots were established in 1982 by Alberta Fish and Wildlife Division (David Walker and Associates 1983) and consisted of 3 adjacent and contiguous replicates totalling approximately 0.5 hectares (Figure 2.1). Each replicate contained 22 plots measuring 3 m by 25 m, each of which contained 1 of 18 plant species (Table 2.1) or was barren. The assignment of plant species to plots within the replicates was random. Details on the establishment and initial productivity of all 22 plant species were reported by David Walker and Associates (1984). There were initially 22 plant species in the experiment but 4 were dropped because of poor productivity.

The plots were surrounded on 3 sides by a buffer zone 2.5 m wide. The buffer zone on the south side was extended to 10 m to encompass an animal restraint system and handling pen (Figure 2.1). An alley led

Table 2.1 Grasses and legumes used in the wapiti forage selection study.

Scientific Name	Common Name	Variety
Onobrychis viciifolia Scop.	sainfoin	Melrose
Astragalus cicer L.	cicer milkvetch	Oxley
Trifolium hybridum L.	alsike clover	Aurora
Medicago sativa L.	alfalfa	Peace
Agropyron dasystachyum (Hook.) Scribn.	northern wheat grass	Elbee
Agropyron intermedium (Host) Beauv.	intermediate wheat grass	Clarke
Agropyron pectiniforme R. & S.	crested wheat grass	Parkway
Agropryon smithii Rydb.	western wheat grass	Walsh
Agropyron riparium Scribn. & Smith	streambank wheat grass	Sodar
Agropyron trachycaulum (Link) Malte	slender wheat grass	Revenue
Festuca ovina L.	hard sheep fescue	Durar
Festuca rubra L.	creeping red fescue	Boreal
Poa pratensis L.	Kentucky bluegrass	Banff
Poa compressa L.	Canada bluegrass	Reubens
Alopecurus pratensis L.	meadow foxtail	common
Elymus junceus Fisch.	Russian wild rye	Swift
Phleum pratense L.	timothy	Climax
Bromus inermis Leyss.	smooth brome grass	Magna

from the animal restraint system to an adjacent holding pen where salt and water were provided ad libitum. The entire area was enclosed by a page wire fence 2 m high and all vegetation within the fence or holding pen, but not on the plots containing vegetation, was removed by application of herbicide or rotovation. Herbicide application was discontinued after the first summer because rotovation was found to be more effective at removing extraneous vegetation. The plots were rigorously weeded by hand immediately before every trial, except for the winter trial when the weeding took place during September and October of the preceding fall. Each spring of the study, prior to any new growth emerging, the plots were mown to a height of 1 cm and the mown residue was removed from the plots.

Two male and 2 female adult wapiti, fitted with either a 7.6 cm (males) or 10 cm (females) ruminal cannula, were used in the forage selection trials. Body weights of the animals during the 7 months of experimentation averaged 272 and 289 kg for the males and 233 and 223 kg for the females. The animals were kept at the Alberta Environmental Centre between trials on grass pasture sown with a mixture comprised of 15 % crested wheat grass (Agropyron pectiniforme), 15 % pubescent wheat grass (A. trichophorum), 10 % meadow foxtail (Alopecurus pratensis), 25 % smooth brome grass (Bromus inermis), 10 % timothy (Phleum pratense) and 25 % Russian wild rye (Elymus junceus). Alfalfa-grass hay and alfalfa-barley pellets were supplemented as required. The animals were transported to the study

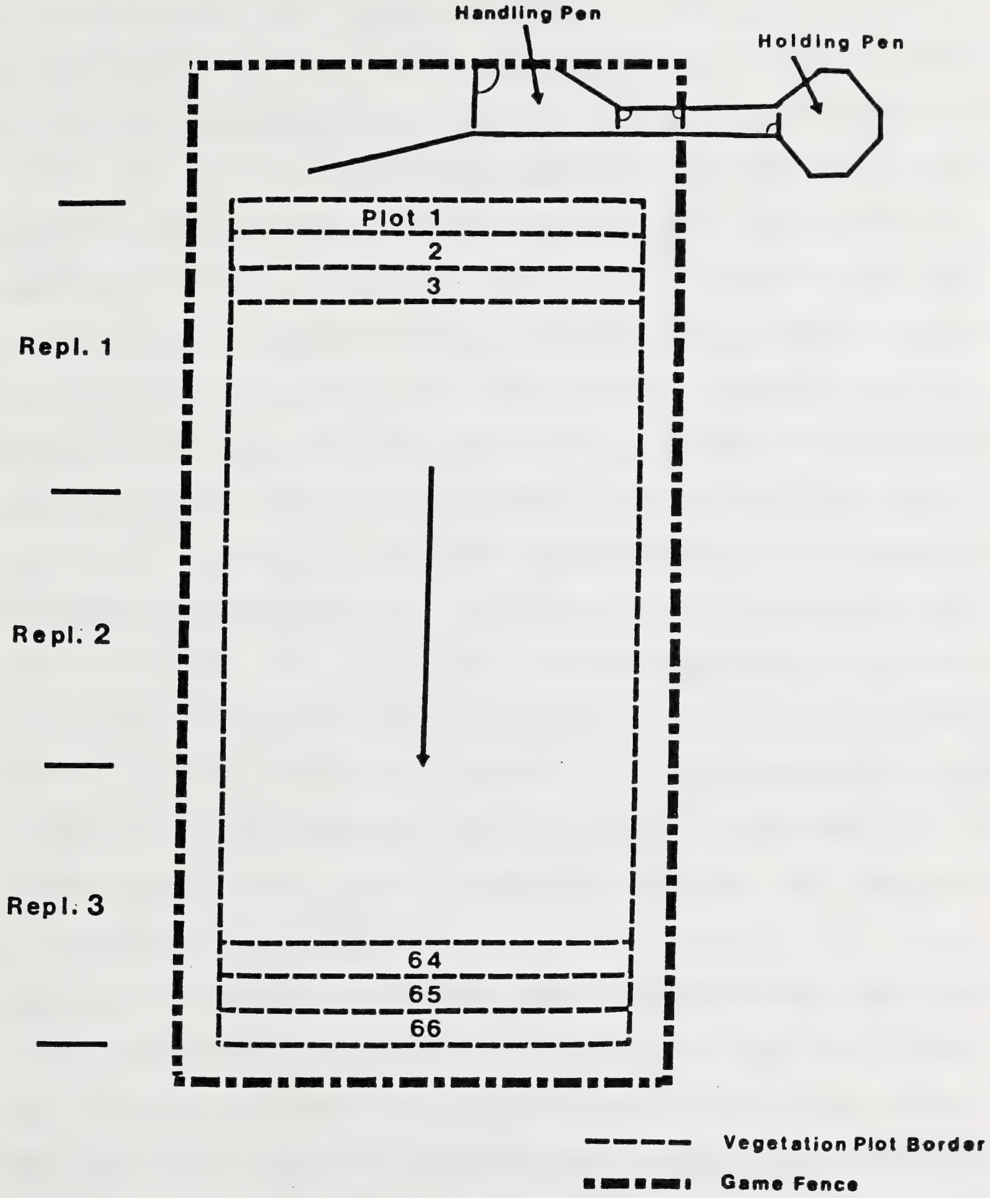

Figure 2.1 A diagrammatic representation of the study site.

site on the day before a trial was to begin. Plot vegetation was the only source of food for the animals during each trial except for the winter trial during which 1.5 kg/animal of alfalfa-barley pellets were fed on two nights when the temperature fell to -40°C.

Three forage selection trials were conducted in 1986, one in each of winter (February 14-27), spring (June 12-18) and late summer (August 20-September 2). These dates were selected to represent major seasonal differences in animal behavior, physiology, climate and plant phenology. The duration of each trial was selected to maximize the time the animals spent grazing on the plots without seriously depleting the preferred species. The spring trial was limited to 7 days in order to minimize the impact of grazing on plant production for the trial in August.

2.2.2 Plant Selection

In each trial, the animals were allowed to forage in 2 distinct foraging bouts (morning and evening) that were at least 6 hours apart. The starting times varied with season but were designed to maximize the time between bouts within the constraint of daylight. This approximated the crepuscular foraging patterns of free-ranging wapiti (Gates 1980), although it did not allow the animals as many foraging bouts as would normally occur. A foraging bout ended when any animal bedded down or when all animals had discontinued foraging for at least 8 minutes. The animals were held in the holding pen between foraging bouts.

The amount of time spent foraging on each plant species was estimated by one observer using an instantaneous scan with a 2 minute time interval between scans (Hull et al. 1960; Jacobsen and Wiggins 1982). The plot that the head of each animal was over or in and the activity the animal was engaged in were recorded during each scan. Plant species that were eaten significantly more often than other plant species were considered to be preferred. Forage selection estimates were not adjusted for differences in standing biomass. It was felt that the effect of availability on forage selection should not be removed from the data because plant species differences in productivity should be considered when choosing plant species for revegetating disturbed sites. Furthermore, only the first 4 days of each trial were used to calculate plant species selection to ensure that depletion of preferred plant species was not influencing foraging behavior. This decision was based on a visual assessment of the depletion of plot vegetation during the trials, combined with the examination of daily trends in mean feeding times of the 5 most frequently selected species.

In addition to the foraging scans described above, a second observer conducted bite counts over intervals ranging from 30 seconds to 2 minutes. These counts were taken opportunistically in order to obtain data for all possible plots used by the animal during the foraging bout. The results were examined to compare plant species differences in biting rates and to determine whether a significant change in biting rate occurred between the first and second halves of each trial.

2.2.3 Plant Yield and Quality

Standing biomass estimates for the winter trial were taken in October by randomly locating 5 quadrats, each 0.1 m^2, in each plot and clipping all the vegetation to a height of 1 cm. These samples were frozen immediately and stored in plastic bags at -20°C. The material from all quadrats clipped from each plot was pooled to form one sample per plot. Each sample was weighed and oven-dried at 60°C to determine dry matter content. The total amount of biomass was averaged among plots for each species to calculate available biomass on a dry matter basis. The biomass estimates for the spring and summer trials were collected the day before the trial was to begin using procedures similar to those described above, except that 3 quadrats, each 0.2 m^2 in size, were used. The change to fewer quadrats of larger size was made to decrease the effort required to do the clippings.

Material obtained from the biomass estimates in the spring and summer trials were used for nutritional analyses and, when necessary, the sample was augmented with additional material clipped on the first day of the trial. For the winter trial, vegetation for nutritional analyses was collected on January 15 to allow sufficient time to process the samples for the nylon bag dry matter disappearance (NBDMD) analysis conducted during the foraging trial in February.

The dried vegetation samples were ground through a Wiley Mill equipped with a 2 mm screen. A subsample was taken for measurement of NBDMD as described below. The remainder of the sample was further ground through a 1 mm screen and analysed for crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium (Ca) and phosphorus (P) by the Soil and Feed Testing Laboratory, Alberta Department of Agriculture. Additionally, from the winter and summer samples, five species were separated into their leaf and stem components and analysed on that basis. The species examined in this way were brome, intermediate wheat grass, timothy, cicer milkvetch, western wheat grass (winter only) and alfalfa (summer only). Chemical analyses of these species were conducted only on whole plant samples for the spring trial because of logistical constraints. Furthermore, it was felt that differences in nutrient content between leaves and stems would be less important during this period.

Of the material ground only through the 2 mm screen, 2 g was used in *in situ* NBDMD analyses using techniques described by Hawley *et al*. (1981). The bag dimensions were 10 cm by 5.5 cm with a pore size of 50 µm. Measurements of NBDMD were conducted with winter vegetation samples during the winter feeding trial because the winter samples were collected 1 month before the feeding trial, which allowed sufficient time for sample preparation. The vegetation collected for the spring trial was tested during the summer trial while the summer vegetation samples were tested in a penned feeding trial during which the animals were fed good quality alfalfa-grass hay and 2 kg of alfalfa pellets daily. There were 2 types of NBDMD trials conducted. In one, NBDMD samples of whole plants were compared. In the second, the NBDMD of the leaf and stem fractions were compared for the 5 species listed above. Whole plant samples were divided among 3 animals such that each animal had samples from 2 of the three replicates (32 samples). The fourth animal received all the samples (30 samples) of the leaf and stem samples. The bags were suspended around a 50 cm loop of tygon tubing that was filled with lead shot (Neathery 1969) and placed unattached in the rumen for 48 hrs.

2.2.4 Statistical Analysis

Data on plant selection, biting rate, available biomass and forage quality were analysed statistically using the computer software package SPSSX (SPSS 1986) in combination with the SPSS user procedure UANOVA (Taerum 1987). The main effects in the plant selection and biting rate analyses were animal and plant species. The biting rate results were also compared for differences in the first and second halves of each trial. For the nutritional and available biomass results, plant species and replicate were the main effects. In the NBDMD analysis, the effect of replicate was confounded by animal so they were treated as a block with plant species as the other main effect. Differences between plant species means in all analyses were tested with Student-Newman-Keuls' multiple range test (Steel and Torrie 1980) using UANOVA (Taerum 1987). A Chi-squared goodness-of-fit test (Steel and Torrie 1980) with the total number of times all animals occurred in a particular replicate as the observed frequency, and one-third of the total observations as the expected frequency, was used to test if animals were equally distributed among plot replicates. Linear correlations were determined using the microcomputer program Statgraphics (STSC 1986).

2.3 Results

2.3.1 Available Biomass

There was considerable variation in biomass within plant species. The standard errors (SE) were large, often in excess of 25 % of the mean (Table 2.2). Alsike clover had only patchy growth for the fall and late summer trials and no biomass above 1 cm during the spring trial. Sainfoin suffered a high degree of winter kill on 2 of the 3 plots and was so patchy in its growth that there was no measurable biomass on these 2 plots during the spring trial. In addition, an unknown animal dug up many of the sainfoin plants the preceding autumn. Crested wheatgrass, brome, meadow foxtail, timothy and Canada bluegrass began to grow earlier in the spring than the other species and this was reflected in relatively higher amounts of available biomass at the time of the spring trial (Table 2.2). Sainfoin also began to grow rapidly in early spring and had 336 g/m^2 of available biomass on the undamaged plot.

Table 2.2 Mean and standard error of available biomass (g/m^2), on a dry matter basis. Samples were collected before each forage selection trial (n = 3).

	Winter[1]			Spring			Summer		
Plant species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
cicer milkvetch	67	abc[2]	1.9	190	a	54.6	132	bcd	7.6
alfalfa	97	abc	25.6	203	a	72.1	127	bcd	29.5
sainfoin	85	abc	18.1	112	a	115.8	66	ab	33.0
alsike clover	28	a	7.6	0[3]	–	–	24	a	12.9
crested WG[4]	164	bcd	13.3	225	a	13.9	159	bcd	17.0
northern WG	139	abcd	1.0	86	a	0.3	228	de	16.1
intermediate WG	181	cd	26.3	144	a	41.1	166	bcd	19.2
streambank WG	140	abcd	26.5	110	a	13.6	191	cd	10.2
western WG	129	abcd	21.3	117	a	19.0	139	bcd	38.3
slender WG	224	d	58.0	152	a	44.5	237	de	28.9
meadow Foxtail	163	bcd	28.1	236	a	11.3	186	cd	11.5
brome	122	abcd	18.2	281	a	57.9	109	abc	15.3
Russian wild rye	63	abc	17.0	57	a	11.7	71	ab	34.3
sheep fescue	176	dc	5.3	162	a	24.4	211	cde	31.9
red fescue	173	cd	18.5	166	a	16.4	239	de	19.8
timothy	139	abcd	8.2	222	a	14.3	188	cd	18.1
Canada bluegrass	228	d	31.2	256	a	60.4	313	e	11.2
Kentucky bluegrass	51	ab	21.3	45	a	13.8	112	abc	22.2

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[1] Collection dates were for winter, October 12; spring, June 11; summer, August 19, 1986.

[2] Means within seasons that do not share a common letter were significantly different ($P<0.05$).

[3] No measurable biomass.

[4] WG = wheat grass.

2.3.2 Animal Behavior on the Plots

The mean ± SE amount of time the animals spent daily on the plots during the winter, spring and late summer trials was 161.6 ± 15.0 min, 135.7 ± 9.8 min and 213.9 ± 7.6 min, respectively. Overall, the animals used replicate 1 significantly ($P<0.005$) less often, and replicates 2 and 3 more often than would be expected if the animals had spent equal time on all replicates. This pattern still occurred, though to a slightly lesser degree, when sainfoin (2 out of 3 replicates were damaged) was excluded from the analysis. The most extreme deviation from equal distribution of the animals occurred in the spring when replicates 1, 2 and 3 were used 19, 38 and 43 % of the time, respectively.

2.3.3 Plant Species Selection

During the winter trial, creeping red fescue was selected significantly more often than all other species except sainfoin (Figure 2.2). In the case of sainfoin, the animals appeared to be principally eating green leaves near the base of the plant but, to a lesser extent, also ate the old, coarse stems. Brome, timothy and hard sheep fescue were also consumed frequently.

During the spring trial, timothy, brome and sainfoin were the most frequently selected species, collectively accounting for over 60% of the time spent feeding (Figure 2.3). Other plant species received relatively little grazing attention. It is noteworthy that alsike clover was grazed as frequently as the grasses, with the exception of

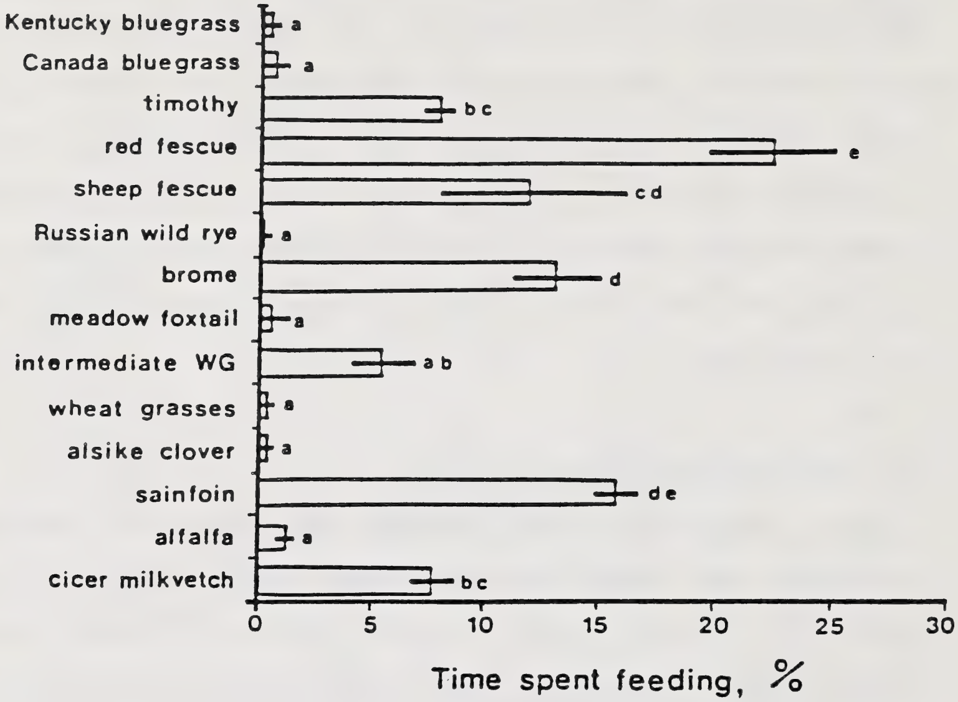

Figure 2.2 The mean (horizontal bars represent 1 SE) proportion of time spent feeding on each plant species during the first 4 days of the winter forage selection trial (n=4). The means for northern, western, crested and slender wheat grass were not significantly different and were presented as an aggregate mean. Plant species that do not share a common letter were significantly different ($P<0.05$). WG=wheat grass.

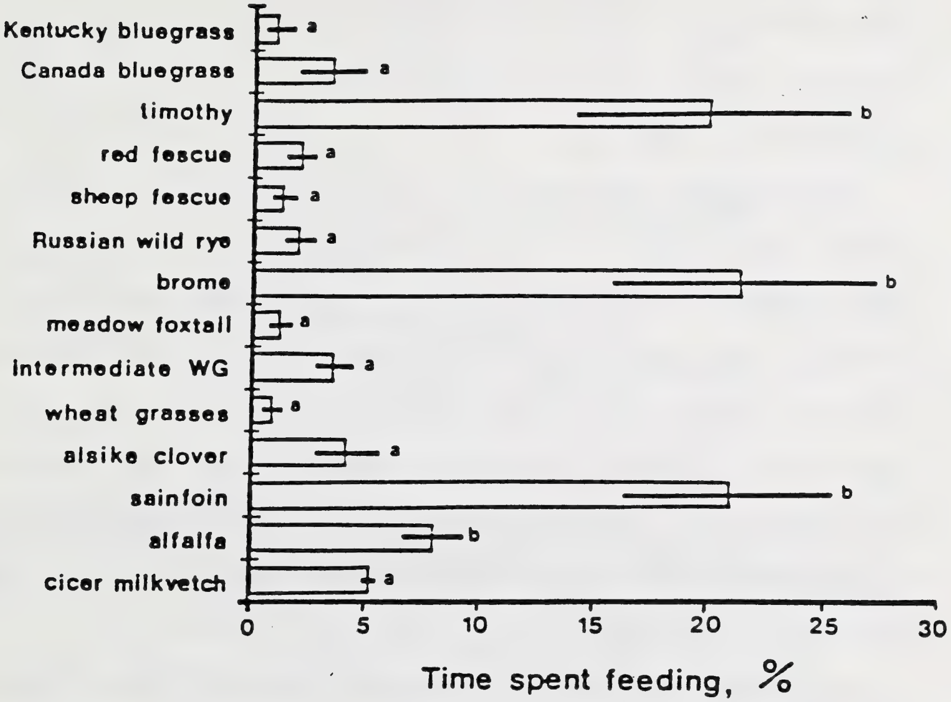

Figure 2.3 The mean (horizontal bar represents 1 SE) proportion of time spent feeding on each plant species during the first 4 days of the spring forage selection trial (n=4). The means for northern, western, crested and slender wheat grasses were not significantly different and were presented as an aggregate mean. Plant species that do not share a common letter were significantly different (P<0.05). WG=wheat grass.

timothy and brome, even though there was no measurable available biomass.

In the summer trial, the animal use of the legumes was extensive (Figure 2.4), accounting for approximately half of the time spent feeding. Timothy, brome and Russian wild rye were also selected frequently, while the other grasses were selected significantly less frequently (less than 3 %).

Seasonal differences in plant use were distinct for several plant species. Red fescue, and to a lesser extent hard sheep fescue, were used frequently in the winter but at much lower rates during the spring and late summer trials. Cicer milkvetch was rarely selected in the spring but was selected at moderate levels in the late summer and winter trials. Russian wild ryegrass was used heavily only during the late summer trial. The legumes collectively were selected most often in late summer. The exception to this was sainfoin which was grazed extensively in all seasons.

Correlations between available biomass and plant species selection for the winter and spring trials were not significant ($P>0.17$ and $P>0.80$, respectively), while a significant negative correlation ($r=-0.62$; $P<0.007$) was obtained for the summer trial. Correlations between other plant characteristics and selection are discussed in Chapter 3.

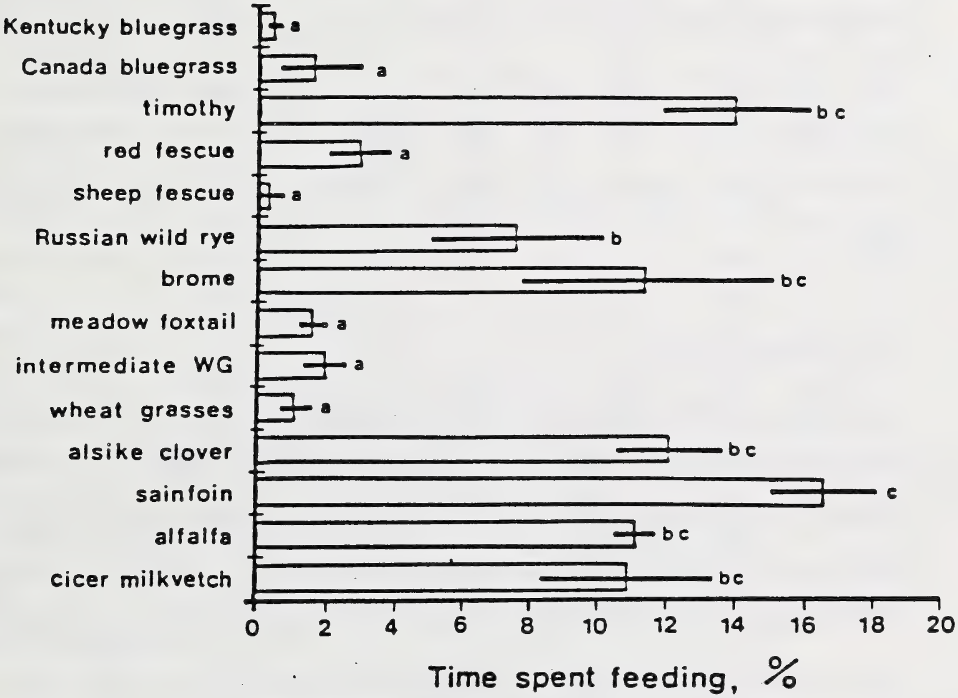

Figure 2.4 The mean (horizontal bar represents 1 SE) proportion of time spent feeding on each plant species during the first 4 days of the summer forage selection trial (n=4). The means for northern, western, crested and slender wheat grasses were not significantly different and were presented as an aggregate mean. Plant species that do not share a common letter were significantly different ($P<0.05$). WG=wheat grass.

2.3.4 Biting Rates

A significant difference in the biting rates between the first and second halves of a feeding trial was observed only during the winter trial, in which biting rate was lower ($P<0.001$) in the second half. There were differences in biting rate among plant species (Table 2.3). In the winter trial, only streambank wheat grass tended to have a lower value than most of the other species, while during the summer trial, biting rate was significantly lower for sainfoin and higher for Kentucky bluegrass than for other species (Table 2.3). Biting rates did not differ significantly among individual plant species during the spring.

2.3.5 Forage Quality

Forage collected before the winter trial was generally characterized by low NBDMD, low CP and high fiber (Table 2.4). The CP content of legumes was 2 to 4 times greater than that of grasses. Fiber made up the majority of the dry matter for all species, although cicer milkvetch and alsike clover had significantly less NDF than other species. The NBDMD of both alfalfa and sainfoin were very low. Calcium content was much higher in legumes than in grasses, while P was low for all species. Leaves tended to be of higher quality than stems in the forage components measured and this difference was much larger for cicer milkvetch than for other species (Table 2.5).

Table 2.3 Mean, standard error and sample size of wapiti biting rates (bites per minute) during each forage selection trial.

	Winter				Spring				Summer			
Plant Species	$\bar{x}$		SE	n	$\bar{x}$		SE	n	$\bar{x}$		SE	n
cicer milkvetch	30.5	b[1]	1.47	4	40.2	a	2.12	3	42.6	ab	1.61	4
alfalfa	25.4	b	3.45	4	39.4	a	1.26	4	42.6	ab	1.43	4
sainfoin	25.3	b	1.29	4	33.3	a	1.42	4	35.1	a	1.11	4
alsike clover	25.6	b	1.31	4	40.0	a	3.05	2	44.6	abc	1.43	4
crested WG[2]	30.0	b	–	1	49.3	a	4.01	2	39.6	ab	0.88	4
northern WG	20.8	ab	1.31	4	48.2	a	7.64	2	40.0	ab	2.24	4
intermediate WG	26.7	b	1.94	4	48.7	a	3.48	4	40.0	ab	1.68	4
streambank WG	13.1	a	1.39	3	49.5	a	0.86	2	45.8	abc	2.15	4
western WG	27.8	b	3.30	3	31.8	a	–	1	48.5	bc	1.07	4
slender WG	23.3	ab	–	1	46.8	a	2.76	3	45.7	abc	2.33	4
meadow foxtail	22.3	ab	3.92	3	41.7	a	2.24	3	38.9	ab	1.44	3
brome	28.8	bc	2.04	4	42.5	a	2.31	4	45.3	abc	2.69	4
Russian wild rye	22.3	ab	1.72	3	33.4	a	2.40	4	47.8	abc	1.10	4
sheep fescue	29.5	b	0.83	4	41.9	a	1.02	2	35.4	ab	2.64	3
red fescue	30.0	b	0.55	4	51.5	a	1.86	3	45.2	abc	2.62	4
timothy	30.4	b	0.85	4	48.2	a	2.21	4	47.6	abc	1.94	4
Canada bluegrass	23.3	ab	3.96	3	48.2	a	2.89	3	42.7	ab	2.38	4
Kentucky bluegrass	26.7	b	1.28	3	39.0	a	4.78	3	55.9	c	6.90	4

[1] Means within a season that do not share a common letter were significantly different ($P<0.05$).

[2] WG = wheat grass.

Table 2.4 Mean and standard error of nylon bag dry matter disappearance (NBDMD), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium and phosphorus values, on a dry matter basis, of whole plant samples (n = 3) collected before the winter trial.

	NBDMD, %			CP, %			NDF, %			ADF, %			Calcium, %			Phosphorus, %		
Plant Species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
cicer milkvetch	53.6	cdef	3.8	12.0	f	0.57	54.6	a	2.6	44.7	d	1.9	2.94	e	0.198	0.11	hi	0.009
alfalfa	14.3	a	4.6	9.1	d	0.29	72.0	efg	1.1	57.0	d	1.4	2.01	d	0.042	0.077	efgh	0.007
sainfoin	27.0	b	0.4	8.3	d	0.19	69.8	def	1.1	58.2	d	3.2	1.48	c	0.070	0.073	defg	0.001
alsike clover[1]	44.4	cdef	6.3	10.4	e	0.01	58.3	b	0.4	51.2	d	0.5	2.20	d	0.204	0.11	i	0.001
crested WG[3]	41.1	cd	1.6	2.5	a	0.10	78.4	hi	0.4	45.5	d	0.5	0.49	a	0.023	0.047	abcd	0.003
northern WG	56.0	def	4.2	2.9	ab	0.34	78.3	hi	0.3	46.2	d	0.6	0.70	ab	0.075	0.043	abc	0.005
intermediate WG	54.4	cdef	1.2	2.9	ab	0.08	71.2	ef	0.4	39.7	abcd	0.1	0.56	ab	0.042	0.057	bcdef	0.003
streambank WG	57.0	ef	3.6	3.0	ab	0.14	78.3	hi	0.7	46.2	d	1.1	0.64	ab	0.041	0.043	abc	0.001
western WG	58.0	f	0.5	2.7	a	0.08	77.1	hi	0.3	41.7	bcd	0.4	0.66	ab	0.036	0.057	bcdef	0.003
slender WG	44.2	cde	1.3	2.9	ab	0.25	80.6	i	0.4	44.7	d	0.6	0.51	ab	0.020	0.057	bcdef	0.006
meadow foxtail	42.4	cde	3.9	3.4	ab	0.30	68.7	cde	0.7	38.5	abc	0.4	0.86	b	0.083	0.050	abcde	0.003
brome	46.8	cdef	1.7	2.4	a	0.14	72.7	efgh	0.9	40.8	abcd	0.6	0.68	ab	0.040	0.030	ab	0.003
Russian wild rye	54.8	cdef	5.6	4.8	c	0.08	75.6	ghi	0.6	44.0	cd	0.5	0.76	ab	0.067	0.097	ghi	0.007
sheep fescue	39.8	c	1.7	4.0	bc	0.55	72.1	efg	2.1	40.7	abcd	2.0	0.69	ab	0.043	0.073	defg	0.016
red fescue	43.6	cde	2.3	2.9	ab	0.09	65.1	c	0.5	35.3	a	0.4	0.78	ab	0.047	0.060	cdef	0.003
timothy	40.5	c	1.6	2.4	a	0.10	73.5	efgh	1.7	43.4	cd	1.1	0.51	ab	0.015	0.040	abc	0.004
Canada bluegrass	48.1	cdef	0.6	2.4	a	0.18	73.1	efgh	0.8	39.1	abc	0.7	0.52	ab	0.033	0.027	a	0.006
Kentucky bluegrass	42.5	cde	2.7	4.0	bc	0.22	66.1	cd	0.6	36.3	ab	0.7	0.75	ab	0.020	0.080	ghi	0.006

[1] n = 2.
[2] Means that do not share a common letter were significantly different ($P<0.05$).
[3] WG = wheat grass.

Table 2.5 Mean and standard error of nylon bag dry matter disappearance (NBDMD), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium and phosphorus values, on a dry matter basis, for leaf and stem samples (n = 3) of 5 species collected before the winter trial.

	NBDMD, %			CP, %			NDF, %			ADF, %			Calcium, %			Phosphorus, %		
Plant Species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
Leaves																		
western WG[2]	60.1	d[1]	1.9	2.8	bc	0.08	74.5	e	0.2	40.8	bc	0.6	0.76	b	0.022	0.057	cd	0.001
brome	54.6	cd	2.3	2.8	bc	0.14	64.2	bc	1.5	37.2	a	0.8	0.95	b	0.031	0.030	ab	0.004
intermediate WG	60.6	d	1.0	3.3	cd	0.10	67.8	cd	0.5	37.6	ab	0.4	0.77	b	0.043	0.057	cd	0.001
timothy	52.6	cd	3.7	3.6	d	0.05	62.4	b	1.6	37.1	a	1.1	0.84	b	0.007	0.050	c	0.003
cicer milkvetch	60.0	d	2.9	15.1	f	0.22	44.6	a	1.0	36.0	a	0.7	4.02	d	0.139	0.14	e	0.004
Stems																		
western WG	42.6	b	0.9	2.5	b	0.11	81.0	f	0.5	42.9	cd	0.5	0.50	a	0.043	0.043	bc	0.003
brome	40.6	b	0.9	1.8	a	0.21	83.3	f	1.1	45.3	de	0.9	0.34	a	0.047	0.027	a	0.006
intermediate WG	46.4	bc	2.4	2.6	b	0.08	74.8	e	0.4	41.9	c	0.1	0.34	a	0.020	0.053	cd	0.003
timothy	28.1	a	0.7	1.9	a	0.19	80.8	f	1.0	47.6	e	0.5	0.36	a	0.018	0.030	ab	0.002
cicer milkvetch	39.8	b	2.9	7.2	e	0.16	69.5	d	2.2	57.7	f	1.6	1.30	c	0.030	0.070	d	0.005

[1] Means that do not share a common letter were significantly different ($P<0.05$).
[2] WG = wheat grass.

During the spring trial, legumes had the highest CP content overall while the wheat grasses and Russian wild ryegrass were significantly higher than other grasses (Table 2.6). Legumes also had significantly lower NDF and ADF and higher Ca contents than grasses. Phosphorus levels were numerically, but not significantly, higher in legumes compared to grasses. All NBDMD values were similar except for the fescues, which were significantly lower. Acid detergent fiber content was similar among grasses. The NDF content of timothy was significantly lower than that of other grasses, while NDF of wheat grasses tended to be higher.

As in the other trials, legumes in the summer trial had significantly higher CP contents than did grasses (Table 2.7). Russian wild rye had a significantly higher CP content than other grasses. Cicer milkvetch and alsike clover had significantly higher, and sheep fescue significantly lower, NBDMD values than the other species. Although NDF content was significantly lower in the legumes, most of the fiber was ADF. As a consequence, the ADF values for grasses and legumes were similar. The legumes had significantly more Ca and tended to have more P (Table 2.7). Calcium and P levels were generally similar among grasses, although Russian wild ryegrass had significantly more P than other grass species. Leaves had significantly higher values than stems for NBDMD and CP, and lower values for NDF and ADF (Table 2.8). Intermediate wheatgrass was an exception in that the NDF content of its leaves was not significantly different from that of its stems. Leaf and stem Ca and P levels were

Table 2.6 Mean and standard error of nylon bag dry matter disappearance (NBDMD), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium and phosphorus values, on a dry matter basis, of whole plant samples (n = 3) collected before the spring forage selection trial.

	NBDMD, %			CP, %			NDF, %			ADF, %			Calcium, %			Phosphorus, %		
Plant Species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
cicer milkvetch	81.5	c[1]	1.02	21.0	g	0.57	23.0	a	0.62	22.5	a	0.30	1.38	c	0.010	.30	e	0.012
alfalfa	76.8	c	2.57	18.1	f	0.53	29.1	b	0.49	23.4	a	0.9	2.24	c	0.068	.25	cde	0.004
sainfoin	72.4[2]	bc	–	17.3	f	–	24.3	a	–	22.5	a	–	1.73	c	–	.26	cde	–
alsike clover	–[3]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
crested WG[4]	73.9	bc	0.53	9.4	b	0.14	56.9	g	0.85	31.9	ab	4.58	0.28	ab	0.085	.24	bc	0.005
northern WG	76.6	c	0.45	10.9	cd	0.22	62.4	h	0.51	43.5	b	0.62	0.34	ab	0.007	.23	bc	0.004
intermediate WG	76.7	c	0.46	10.9	cd	0.20	53.1	de	0.54	33.8	ab	0.35	0.47	ab	0.026	.27	cde	0.012
streambank WG	77.4	c	1.59	11.2	d	0.39	61.1	h	0.27	33.6	ab	0.98	0.30	ab	0.072	.22	ab	0.010
western WG	76.8	c	0.38	10.8	cd	0.11	56.6	g	0.55	31.9	ab	4.72	0.21	a	0.018	.24	bc	0.008
slender WG	76.7	c	0.72	11.8	de	0.42	55.3	efg	0.44	34.6	ab	4.7	0.40	ab	0.055	.25	bcd	0.018
meadow foxtail	77.1	c	0.33	8.2	a	0.21	56.3	fg	0.47	28.3	ab	0.70	0.33	ab	0.022	.21	ab	0.005
brome	78.7	c	1.32	9.9	bc	0.16	53.5	de	0.46	25.8	a	0.64	0.34	ab	0.041	.23	bc	0.004
Russian wild rye	77.8	c	0.84	12.9	e	0.12	57.7	g	0.28	27.7	a	1.61	0.34	ab	0.031	.30	de	0.016
sheep fescue	64.2	a	1.11	7.3	a	0.04	54.6	def	0.67	28.2	a	0.73	0.33	ab	0.038	.18	a	0.007
red fescue	70.0	b	0.18	7.8	a	0.23	53.6	de	0.76	28.8	ab	1.05	0.26	ab	0.016	.21	ab	0.015
timothy	80.1	c	2.58	8.1	a	0.16	50.3	c	0.47	25.3	a	1.11	0.37	ab	0.108	.21	ab	0.009
Canada bluegrass	77.2	c	1.20	7.4	a	0.33	55.2	efg	0.64	25.7	a	0.61	0.20	a	0.068	.20	ab	0.006
Kentucky bluegrass	73.2	bc	1.55	8.4	a	0.25	52.4	d	1.23	25.1	a	0.93	0.50	b	0.069	.20	ab	0.010

[1] Means that do not share a common letter were significantly different ($P<0.05$).
[2] n = 1.
[3] Insufficient available biomass to sample for nutritional analysis.
[4] WG = wheat grass.

Table 2.7 Mean and standard error of nylon bag dry matter disappearance (NBDMD), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium and phosphorus values, on a dry matter basis, of whole plant samples (n = 3) collected before the summer forage selection trial.

	NBDMD, %			CP, %			NDF, %			ADF, %			Calcium, %			Phosphorus, %		
Plant Species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
cicer milkvetch	82.5	h[1]	0.54	13.5	de	0.54	29.5	a	0.51	26.7	a	0.70	3.07	d	0.105	0.19	b	0.018
alfalfa	67.6	cde	0.27	15.0	de	0.38	41.6	b	0.50	33.2	abc	1.15	2.29	c	0.380	0.19	b	0.009
sainfoin	72.1	efg	1.09	12.6	d	0.89	40.4	b	1.11	36.3	abc	1.29	1.42	b	0.208	0.19	b	0.007
alsike clover	81.3	h	1.58	15.8	e	0.80	31.9	a	0.88	28.2	ab	1.39	1.84	bc	0.037	0.26	c	0.009
crested WG[2]	62.7	b	1.38	4.5	a	0.25	62.8	d	0.70	34.8	abc	0.86	0.47	a	0.019	0.12	a	0.008
northern WG	73.8	fg	0.81	5.3	ab	0.23	70.3	f	0.39	40.7	bc	0.29	0.42	a	0.041	0.13	a	0.009
intermediate WG	71.0	efg	1.20	4.9	ab	0.14	60.2	d	0.21	33.3	abc	0.68	0.49	a	0.043	0.14	ab	0.011
streambank WG	73.1	fg	0.67	5.3	ab	0.13	69.7	ef	0.30	40.5	bc	0.54	0.28	a	0.008	0.12	a	0.005
western WG	73.4	fg	1.11	6.3	ab	0.71	61.4	d	0.60	33.2	c	0.45	0.49	a	0.098	0.13	a	0.008
slender WG	64.1	bc	0.74	5.2	ab	0.14	64.7	de	0.96	35.9	abc	1.06	0.40	a	0.038	0.12	a	0.006
meadow foxtail	68.4	cdef	0.72	4.7	ab	0.14	56.3	c	0.58	29.7	ab	0.42	0.66	a	0.016	0.12	a	0.004
brome	69.5	defg	0.72	7.2	bcd	1.51	53.6	c	4.14	29.9	abc	2.41	0.82	a	0.072	0.14	ab	0.018
Russian wild rye	75.0	g	3.53	9.3	c	0.42	66.5	def	0.82	36.7	abc	0.35	0.56	a	0.036	0.26	c	0.017
sheep fescue	53.9	a	0.50	4.5	a	0.28	63.5	d	1.18	35.5	abc	0.82	0.49	a	0.037	0.12	a	0.007
red fescue	65.0	bcd	0.99	5.4	ab	0.56	55.6	c	0.38	30.6	abc	0.21	0.70	a	0.107	0.16	ab	0.018
timothy	74.9	g	1.57	5.5	ab	0.40	55.8	c	1.60	30.2	abc	0.97	0.47	a	0.048	0.14	ab	0.009
Canada bluegrass	64.6	bc	1.98	4.2	a	0.39	63.3	d	0.99	31.9	abc	1.60	0.33	a	0.014	0.10	a	0.013
Kentucky bluegrass	70.1	efg	0.51	6.1	ab	0.21	56.3	c	0.44	28.8	ab	0.98	0.59	a	0.055	0.15	ab	0.015

[1] Means that do not share a common letter were significantly different ($P<0.05$).

[2] WG = wheat grass.

Table 2.8 Mean and standard error of nylon bag dry matter disappearance (NBDMD), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), calcium and phosphorus values, on a dry matter basis, for leaf and stem samples (n = 3) collected before the summer forage selection trial.

	NBDMD, %			CP, %			NDF, %			ADF, %			Calcium, %			Phosphorus, %		
Plant Species	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE	$\bar{x}$		SE
Leaves																		
intermediate WG[2]	77.4	c[1]	1.3	7.8	b	0.35	57.6	cd	0.2	30.6	d	0.2	0.82	a	0.194	0.17	bc	0.011
brome	78.9	c	0.4	6.6	b	1.01	53.5	c	4.2	29.2	d	1.3	1.00	a	0.203	0.14	ab	0.007
timothy	84.5	d	0.8	7.5	b	0.34	48.1	b	1.1	26.4	c	0.8	0.58	a	0.147	0.15	abc	0.004
cicer milkvetch	87.2	d	1.6	14.6	d	0.43	24.5	a	0.4	22.4	b	0.6	3.58	b	0.106	0.19	c	0.017
alfalfa	84.5	d	0.3	20.2	e	0.02	27.0	a	0.8	18.1	a	0.5	2.84	b	0.767	0.23	d	0.008
Stems																		
intermediate WG	67.2	b	1.0	4.6	a	0.14	61.9	d	0.7	34.3	e	0.3	0.46	a	0.104	0.15	abc	0.002
brome	62.5	b	1.9	3.4	a	0.20	63.8	d	0.5	35.2	e	1.1	0.36	a	0.030	0.11	a	0.007
timothy	64.6	b	0.4	3.7	a	0.48	63.0	d	0.6	34.3	e	0.3	0.35	a	0.129	0.13	ab	0.004
cicer milkvetch	75.1	c	4.0	9.6	c	0.25	47.5	b	1.2	41.9	f	0.9	1.18	a	0.139	0.18	bc	0.008
alfalfa	53.8	a	2.1	9.9	c	0.35	56.4	cd	0.2	48.5	g	1.6	1.71	a	0.193	0.15	bc	0.011

[1] Means that do not share a common letter were significantly different ($P<0.05$).
[2] WG = wheat grass.

similar among species, except for alfalfa and cicer milkvetch leaves, which had higher Ca contents than did leaves of other grasses.

2.4 Discussion

Time spent feeding on each plant species as a relative measure of selection had the advantage of being easily estimated and also permitted resolution of temporal changes in foraging behavior. The method quantified the amount of foraging effort the animals were willing to invest in feeding on each species and this provided a strong basis for assessing wapiti grazing preferences. Selection of plant species did not account for the unequal use of replicates by wapiti and it is possible that the animals occupied the third replicate most frequently as a consequence of avoidance of the handling area. This should not have affected our interpretation of differential selection of plant species because all species occurred randomly in each of the replicates. The method did not measure the relative proportions of plant species actually consumed. It was not possible to estimate these proportions because rumen samples provided an inaccurate estimate of the diet (Chapter 4).

Alsike clover was the only species for which selection was obviously affected by lack of forage biomass, and this was true only during the spring trial. Wapiti spent 4% of their feeding time grazing alsike clover. In spite of this plant species having no measureable biomass during the spring trial (Table 2.2), it appeared that the animals would have selected alsike clover more often if more plant material had been available.

The effect of constraining the animals to 2 foraging bouts per day did not appear to be significant. The amount of time that animals were held without access to food was well below that which has been shown to affect diet selection of sheep (Sidahmed _et_ _al_. 1977). Furthermore, fasting would have caused the animals to be less discriminating, which would have made identification of differences in animal preference more conservative.

Inter-study comparisons of plant species selection can be difficult because selection measurements are relative and studies differ in the plant species available. Researchers must be cautious when extrapolating forage selection data to other circumstances because of the relativity of food preferences. The advantage of evaluating forage selection with confined animals is that a wider variety of plant species, many of which are common in the literature, can be compared in conditions that allow for fair comparisons to be made. Thus, plant species not normally found in the literature on wapiti food habits can be evaluated by comparing them with other plant species known to be preferred by wapiti.

Kufeld (1973) and Nelson and Leege (1982) standardized the results of a wide variety of food habit studies by assigning an importance rating (values 1 to 3) to each plant species in each season. Major trends in foraging preferences observed in the present study were similar to those identified in the literature. For instance, seasonal patterns of use for alfalfa, clover, smooth brome, Kentucky bluegrass, timothy and the wheat grasses identified by Kufeld (1973) and Nelson and Leege (1982) were similar to those observed in the present study. There were only 2 exceptions. These same authors reported that crested wheatgrass was moderately selected in the spring and that Canada bluegrass received moderate use in every season except summer. This was in contrast to the present study in which these 2 species were rarely used in any season.

Crested wheatgrass grows rapidly in the spring and has been used successfully to increase production of cattle on native range that was slow to begin growing in the spring (Hart _et_ _al_. 1983). Wapiti have also been reported as using this species in the spring (Kufeld 1973). It was possible that greater use of this species in the spring could have been observed in the present study if the spring trial had been held earlier. In addition, cattle have also been shown to avoid sainfoin throughout the spring and summer (Gesshe and Walton 1981). This contrasts sharply with the results of both this study and research on sheep (Wilman and Asiedu 1983; Smoliak and Hanna 1975) and underscores the variability in foraging preferences that can occur between animal species.

2.4.1 Meeting Nutritional Requirements

In north temperate rangelands, winter and early spring are the two times of the year when productivity of wapiti populations would most likely be improved by an increase in the availability of high quality forage. Early spring can be a particularly critical time for pregnant wapiti cows because of increased energy and CP requirements for fetal growth and milk production. The plant species that were preferred by wapiti in this study were assessed for their ability to meet the metabolizable energy (ME) and CP requirements of a pregnant wapiti cow during the winter and spring seasons.

The daily ME requirement of a pregnant wapiti cow during the winter (November to April) was estimated to be 8.63 Mcal. This value was calculated by assuming that the animal spent 47 % of its time feeding, 42 % resting and 11 % moving (Green 1982) and that the energy expenditure of a pregnant cow for each of these activities was 6.6, 5.0 and 6.4 kcal/h/$kg^{0.75}$, respectively, (Pauls _et_ _al_. 1981).

The ME content of each of the forages in this study was estimated using the equation:

$$\text{ME content} = \text{NBDMD} * 3.9\ \text{Mcal/kg} * 0.87$$

where NBDMD was our best estimate of digestibility, 3.9 Mcal/kg was the approximate energy content of 1 kg of roughage (Van Soest 1982) and 0.87 is the proportion of digestible energy that was ME (Simpson _et_ _al_. 1978). The relationship between NBDMD and digestibility is controversial. It has been reported to both over-estimate (Scales _et_ _al_. 1974) and under-estimate (Neathery 1972) _in_ _vivo_ digestibility by as much as 10-15 percentage units. Consequently, conclusions generated from this equation must be interpreted cautiously.

The most frequently selected species during the winter forage selection trial were red and sheep fescue, timothy, brome and cicer milkvetch. Based on the above equation, the ME content of each of these plant species was 1.48, 1.35, 1.37, 1.59 and 1.82 Mcal/kg, respectively. Therefore, the daily dry matter intake (DMI) of each of these plant species necessary to meet the energy requirements of a pregnant, 240 kg cow would be 5.8, 6.4, 6.3, 5.4 and 4.7 kg, respectively. If it is assumed that the animals will only eat leaves, the intake requirements for maintenance decrease to 4.7, 4.8 and 4.2 kg/day of brome, timothy and cicer milkvetch, respectively.

The vegetation from the winter was visibly leached and weathered and this was reflected in low NBDMD and CP and high NDF values for most of the plant species (Table 2.4). Maximum voluntary intake of extremely poor quality grass hay has been shown to be less than 4 kg/day for adult wapiti cows (L.A. Renecker and R.J. Hudson, personal communication). Even if free-ranging animals increase their DMIs by selective foraging (Heaney 1973), the forage quality of the grasses was sufficiently poor that it is unrealistic to expect the animals to consume more than 4.5 - 5.0 kg/day. Voluntary intake of low quality alfalfa-grass hay, on the other hand, is as high as 6 kg/day (L.A. Renecker and R.J. Hudson, personal communication), suggesting that voluntary intake of cicer milkvetch should be higher than that of grasses, perhaps as high as 6.0 - 6.5 kg/day. The low ME content and expected voluntary intakes of the preferred grasses suggest that a pregnant cow would at best just meet her energy requirements by eating these species during the winter months. In contrast, the ME content and expected voluntary intake of cicer milkvetch indicated that this species should easily meet the ME requirements of the same cow.

Winter differences in forage quality between cicer milkvetch and the preferred grass species were further emphasized when CP requirements are examined. The minimum dietary CP content that would meet the winter maintenance requirements of a 240 kg cow would be approximately 5-7 % (Mould and Robbins 1981), assuming that this animal can eat only 4.0-5.0 kg/day of low quality winter forage. Only cicer milkvetch would meet these CP requirements at this level of feed intake.

The daily ME requirements of a pregnant wapiti cow in the spring (May and June, during the last trimester of pregnancy or in early lactation) were calculated to be 20.5 Mcal, assuming that the proportions of time spent feeding, resting and moving were 56, 33 and 11 %, respectively, (Green 1982), and that the energy expenditure for each of these activities during the same period was 15.0, 10.8 and 18.8 kcal/h/kg$^{0.75}$, respectively, (Pauls et al. 1981).

Timothy, brome and sainfoin were frequently selected during the spring. The intake rates of each of these species required to meet daily ME requirements of a pregnant cow would be 7.5, 7.7 and 8.3 kg/day. It is realistic to expect animals to be able to consume high quality spring forage at these rates. Furthermore, the animal would readily meet its predicted CP requirement during lactation at these consumption rates (Nelson and Leege 1982). All plant species that were preferred by the wapiti during the spring forage selection trial should meet the CP and ME requirements of wapiti during the spring months.

2.5 Reseeding Strategies

The plant species currently recommended by the Alberta Forest Service (AFS) for the reseeding of disturbed areas in the more northern forests of Alberta are creeping red fescue, timothy, crested wheat grass, white clover (*Trifolium repens*) and alsike clover. The AFS plant species recommendations for reseeding disturbed areas in the south part of Alberta are the same as for the north, except Canada bluegrass is substituted for crested wheat grass (Alberta Energy and Natural Resources 1984a). This group of plant species will be collectively called the AFS seed mix for ease of reference.

The results of the present study suggest modifications to the AFS seed mix. These modifications are based on the premise that a primary end use of the reclaimed site is to provide forage for wapiti. As discussed in the previous section, winter and spring are the primary seasons in which wapiti would benefit most from additional, high quality forage. Separate reseeding strategies are recommended for providing forage in these seasons. This was done in order to prevent undesired interspecific plant competition and to optimize the foraging benefits to wapiti within each of these seasons.

The recommendations are based on a single season of forage selection at one site. Climatic effects on vegetation may differ from year to year and could have differential effects on plant selection. However, climate will broadly influence all plants in an area and yearly variation in climate will most likely shift the phenology of all species. In contrast, the effect of micro-site on plant growth, morphology and composition could be important in determining differential selection of plant species. This effect will be site-specific and was not tested in the present study.

2.5.1 Enhancing Winter Forage

Creeping red fescue was the most highly preferred species during the winter trial. On the other hand, this species was infrequently used during the spring and summer trials. This suggests that the annual phytomass production of red fescue would accumulate over the growing season and be available for winter use. Therefore, red fescue should remain in seed mixes used to provide winter forage for wapiti (winter seed mix). Timothy was also preferred during the winter trial and should be kept in the winter seed mix. Crested wheat grass and Canada bluegrass, the other 2 grasses in the AFS seed mix, were rarely selected by wapiti during the winter trial and should not be used in the winter seed mix.

Creeping red fescue and timothy were seriously deficient in CP and other species, such as legumes, should be used in the winter seed mix to compensate for this deficiency. Of the 2 legumes normally found in AFS seed mixes (alsike and white clover), only alsike clover was investigated in the present study. Alsike clover had a relatively high CP content, but was infrequently selected by the wapiti during the winter trial. Furthermore, it is a short-lived perennial (Watson et al. 1980) that would not persist on reseeded sites. White clover in contrast, is a long-lived perennial that is reported to be nutritious and palatable but is often low yielding (Watson et al. 1980). In fact, it was originally to be included in this study but was omitted because of low yield. Because white clover is a legume, its CP content can be expected to be higher and its continued inclusion in the winter seed mix should be beneficial.

The winter seed mix would be greatly enhanced by the addition of a plant species that was both productive and high in CP. Cicer milkvetch was productive and had excellent nutritional characteristics during the winter trial. In addition, it is a long-lived perennial that is hardy and persistent (Watson et al. 1980). While it was not one of the most preferred species, it received moderate use during the winter trial. The main limitations to use of this species are that it often takes up to 2 years to establish, the seed requires scarification and the seed bed requires careful preparation (Watson et al. 1980). Despite these difficulties, the nutritional benefits of cicer milkvetch to wapiti are such that every effort should be made to include this species in the winter seed mix.

In summary, red fescue, timothy and white clover should compose the winter seed mix. In addition, every effort should be made to establish cicer milkvetch in areas where it would be desirable to enhance the winter foraging opportunities of wapiti.

2.5.2 Enhancing Spring Forage

The AFS seed mix already contains timothy, which was one of the species identified in this study as being best suited for enhancing spring range. Smooth brome grass was also well suited for this purpose and, while not contained in the AFS seed mixes, has no limitations precluding its inclusion (Watson et al. 1980). Maintaining a legume in the spring seed mix may be beneficial and there is no reason to exclude white clover. Crested wheat grass, Canada bluegrass and creeping red fescue were infrequently selected during the spring trial and are not recommended for spring seed mixes. Red fescue has the additional disadvantage of out-competing other species seeded with it on seismic cut-lines (Downing 1983). Thus, special emphasis should be given to excluding it from spring seed mixes in order to prevent it from competing with timothy and brome.

In summary, timothy, brome and white clover are recommended for the spring seed mix.

2.5.3 Other Strategies

Russian wild ryegrass was frequently eaten in the late summer trial and could play a role in extending the productive summer grazing period. The NBDMD, CP, Ca and P values of this species were relatively high at this time of year. Unfortunately, this species grew poorly in this study and was one of the least productive grasses. Streambank wheatgrass was rarely selected in any season.

Therefore, this species might have potential for use where the incidence of wapiti grazing is to be minimized, such as on reclaimed sites sensitive to erosion or in roadside ditches.

2.5.4 General Considerations

The implementation of spring and winter forage enhancement strategies would not necessitate inordinate amounts of additional effort or cost to the petroleum industry, and some of the recommended plant species are already contained in the AFS seed mix. It would be common in Alberta to use reseeding strategies to enhance wapiti nutrition in both winter and spring because it would often be unknown in which season a specific wapiti population would benefit more from enhanced foraging. Winter and spring seed mixtures could be applied alternately, perhaps every 500 m, along pipeline rights-of-way and cutlines. Alternatively, or in addition, the spring seed mix could be applied on slopes with southern aspects in order to encourage early spring growth.

The utility of the recommended seed mixtures to improve the foraging opportunities of wapiti depends in part upon how well the forage preferences of captive wapiti approximate those of wild populations. Foraging experience has been shown to influence diet selection (Arnold and Maller 1977; Bartmann and Carpenter 1982). In addition, research has shown that tame pronghorns (*Antilocapra americana*) selected diets different from wild animals when both were foraging in free-ranging conditions (Schwartz and Nagy 1976). Lack of experience should not have affected the foraging behavior of the animals in the present study because all animals were adults and had foraging experience on both native and cultivated ranges. Furthermore, the selection patterns observed for the plant species in the present study were similar to those reported in food habit studies of wild wapiti (Kufeld 1973; Nelson and Leege 1982).

Of broader concern is whether wild wapiti populations will use the recommended plant species on the revegetated site, given the wide variety of alternative food plants that will be available on native range. Further experimentation will be required to determine whether wild populations will graze on reseeded areas. However, since the areas are to be reseeded anyway, there is every reason to use plant species that will enhance wapiti nutrition, if enhancing wapiti nutrition is considered desirable.

2.6 Summary

Captive wapiti were used to measure selection of 14 grass and 4 legume species during the winter, spring and summer seasons. Statistically significant patterns in plant species selection were apparent in every forage selection trial. During the winter, red fescue was the most frequently eaten species although sainfoin, brome, timothy and sheep fescue were also selected. Timothy, brome and sainfoin were the most frequently selected species during the spring. During the summer, the legumes (alfalfa, cicer milkvetch, sainfoin and alsike clover) along with timothy, brome and Russian wild rye were selected more often than other species.

Winter and early spring were identified as the 2 times of year when wapiti would most benefit from additional high quality forage. Plant species that were preferred in these seasons were assessed for their ability to meet the energy and CP requirements of a pregnant wapiti cow. Based on these results, reseeding strategies directed towards improving the foraging opportunities of wapiti during the winter were recommended to use red fescue, timothy, white clover and cicer milkvetch in the seed mixes. Seed mixes for improving the spring foraging opportunities were recommended to contain brome, timothy and white clover. In addition it was recommended that red fescue be excluded from the spring seed mix in order to prevent it from competing with brome and timothy.

3. FORAGE ATTRIBUTES AFFECTING DIET SELECTION BY WAPITI

3.1 Introduction

Considerable effort has been directed towards studying the nutritional ecology of ruminants. A prominent theory proposes that the cell wall content and the nutrient concentration of the diet normally selected by a ruminant is determined by body size (Demment and Van Soest 1985) and by morphology of the jaw and gastro-intestinal tract (Bell 1969; Hoffmann 1973; Bunnell and Gillingham 1985). This theory originated from research on African ungulates and has since been supported by comparative research on wild North American ungulates (Schwartz and Ellis 1981; Hobbs _et_ _al_. 1983). This research has identified the general types of diets animals choose, but it has not been effective in identifying the vegetation components that animals use to discriminate among plant species (Hanley 1982).

Studies examining specific forage attributes have shown that dry matter digestibility and crude protein and fiber contents are often significantly correlated to ruminant diet selection (Coleman and Barth 1973; Vangilder _et_ _al_. 1982; Gesshe and Walton 1981). However, interpretation of these relationships is problematic because there is no evidence that animals can detect these components directly (Arnold and Hill 1972). The physical structure of forages has also been related to selection. For example, ruminants have been shown to select leaves over stems (Arnold 1960; Field 1976), new green growth over old brown material (Hamilton _et_ _al_. 1973) and for plant species higher in moisture content over drier material (Radwan and Crouch 1974; Gesshe and Walton 1981).

Taste may be an important determinant of forage selection (Arnold and Dudzinski 1978). Soluble carbohydrates (Cowlishaw and Alder 1960) and organic acids (Jones and Barnes 1967) have been positively correlated to sheep selection of grasses. However, Radwan and Crouch (1974) found no clear relationship between soluble carbohydrates and deer browse preferences. Strong tasting or aromatic secondary plant chemicals, such as water soluble phenolics and terpenoids, have been shown to be negatively correlated with the selection of forage by ruminants (Schwartz et al. 1980a; Cooper and Owen-Smith 1985; Personius et al. 1987). These compounds are also known to interfere with nutrient digestion (Oh et al. 1967; Schwartz et al. 1980b) and absorption (Robbins et al. 1987).

Spalinger et al. (1986) hypothesized that ruminants use handling time as a major forage selection criteria. The concept of handling time was originally conceived for monogastric animals and was defined as the amount of time required to ingest a food item. Spalinger et al. (1986) have included the amount of time spent ruminating in their definition of handling time in order to make it more applicable to ruminant animals. The concept of handling time has important implications with respect to nutrient intake by ruminants. The resistance of plant fiber to physical breakdown during chewing and rumination (Trudell-Moore and White 1983; Chai et al. 1984; Kennedy 1985) is the primary constraint on the passage of material from the reticulo-rumen (Thorton and Minson 1973; Poppi et al. 1981b). Passage rate, in turn, is the primary factor determining the voluntary intake of forages (Laredo and Minson 1973; Poppi et al. 1981a). Consequently, an animal maximizes daily nutrient intake if it selects forages with lower handling times. Even small increases in intake would have important consequences on animal fitness because of the large effect intake has on animal production (White 1983). It can be argued that the resistance of forage to chewing during ingestion could be the forage attribute that best represents handling time. This paper assesses the relative importance of a variety of forage attributes, including two that are related to either forage resistance to chewing or to rumen MRT, as determinants of plant species selection by wapiti.

3.2 Materials and Methods

The study was conducted in conjunction with the summer forage selection trial described in Chapter 2. Only the results from the summer trial were used in the present study because plant material was not available from the other seasons for measurement of the forage attributes described below. Details of the study site were described in Chapter 2. In brief, the site comprised 18 plant species seeded in 3 contiguous replicates. The plant species used were: sainfoin (Onobrychis viciifolia), cicer milkvetch (Astragalus cicer), alsike clover (Trifolium hybridum, alfalfa (Medicago sativa), crested wheat grass (Agropyron pectiniforme), northern wheat grass

(*A*. *dasystachyum*), intermediate wheat grass (*A*. *intermedium*), western wheat grass (*A*. *smithii*), streambank wheat grass (*A*. *riparium*), slender wheat grass (*A*. *trachycaulum*), hard sheep fescue (*Festuca ovina*), creeping red fescue (*Festuca rubra*), Kentucky bluegrass (*Poa pratensis*), Canada bluegrass (*Poa compressa*, meadow foxtail (*Alopecurus pratensis*), Russian wild rye (*Elymus junceus*), timothy (*Phleum pratense*) and smooth brome grass (*Bromus inermis*).

The procedures used to measure wapiti selection, neutral detergent fiber (NDF), acid detergent fiber (ADF), crude protein (CP), nylon bag dry matter disappearance (NBDMD) and available biomass were described in Chapter 2.2. Forage selection was represented by the amount of time that animals spent feeding on each species, expressed as a percentage of the total amount of time spent foraging. In addition to the above measurements, a portion of the material collected at the time of the summer trial was fresh frozen at -20°C and kept for use in the measurements described below.

The percentage of leaf material comprising the total available biomass was measured for each plant species. This was accomplished by separating and weighing the leaf and stem components of 5 g of oven-dried material from each replicate. Floral parts were included with the stem fraction.

The physical resistance to shearing of the forage samples was used as an estimate of plant frangibility and was measured with the Ottawa Texture Measuring System (Voisey 1971) equipped with a 454 kg load cell and a standard shear compression cell (Kramer *et al*. 1951) using a deformation rate of 15 cm/min. Vegetation samples were thawed, cut into 5 cm lengths, placed in a plastic bag with a damp paper towel and kept refrigerated until sheared, normally within 3 - 5 hrs. Five samples, approximately 0.5 g each, of leaves, stems and the whole plant were taken from each of 3 replicates and sheared. Four species had such a small proportion of their total biomass made up of either leaves or stems that plant parts were not tested separately. Red fescue, sheep fescue and Kentucky bluegrass were considered to have only leaves while Canada bluegrass had only stems. The measurements made on whole plant samples of Canada bluegrass were used when comparisons of leaf measurements were made with the other plant species. A measurement consisted of laying the sample perpendicular to the blades of the shear cell and recording the peak shear force (SF) required to shear the sample expressed as newtons per gram (N/g).

Representative samples of leaves and stems were taken for each species (the fescues and bluegrasses were exceptions and were treated as described for the SF measurements) from each of the 3 replicates and prepared for scanning electron microscopy (SEM) by the Electron Microscopy Services Section, Alberta Environmental Centre. Samples were soaked in glutaraldehyde fixative for 24 hrs, vacuum dried for 2-3 hrs and washed briefly in cacodylate buffer. Samples were then cut to provide a cross-sectional view for mounting, dehydrated in 3 changes of ethyl alcohol (50-100 %), soaked in 3 changes of amyl acetate, critical point dried in CO_2 and sputter-coated with gold. Photo-micrographs were taken through the center of the sample at 600X magnification. Mean cell wall thickness (MCWT) was measured from the photo-micrographs using procedures described by Spalinger et al. (1986). A second variable (XSACW) represented the amount of cell wall as a percentage of the cross sectional area of the sample. This measurement was made using the same photo-micrographs used to calculate MCWT by recording along a linear transect through the middle of the micrographs the number of 0.5 cm intervals that intersected cell wall. This number was expressed as a percentage of the total number of intervals. No measurements were taken from the pithy region that occurred in the centers of the stems of most species.

The mean value across the 3 replicates was used for each plant species and plant part in correlations, linear regressions and step-wise multiple regressions performed using the micro-computer statistics program Statgraphics (STSC 1986). Forward step-wise multiple regression was done using an F-ratio to enter and remove of 4.0. Testing for statistical differences between slopes of 2 linear regressions was done using procedures described by Steel and Torrie (1980).

3.3 Results

Shear force, NBDMD, NDF, MCWT, XSACW and CP were all significantly correlated to forage selection (Table 3.1). The amount of leaf comprising the available biomass was not correlated to selection. Correlations between selection and NDF or moisture were calculated on

Table 3.1 Correlation coefficients between forage selection and the chemical and physical attributes of 18 plant species.

Attributes[1]	Correlation coefficient
crude protein (CP)	0.725***
neutral detergent fiber (NDF)	-0.740***
acid detergent fiber (ADF)	-0.282
nylon bag dry matter disappearance (NBDMD)	0.518***
shear force (SF)	-0.685***
shear force (leaves)	-0.766***
available biomass	-0.617***
moisture content	0.797***
% leaf of total biomass	-0.127
cell wall thickness (MCWT)	-0.676***
cell wall thickness (leaves)	-0.808***
cross sectional area of cell wall (XSACW)	-0.626***
cross sectional area of cell wall (leaves)	-0.697***

[1] Measured using whole plant unless otherwise indicated.
***P<0.001

a whole plant basis because these compositional data were not available for the plant parts of all species. On a whole plant basis, both NDF and moisture tended to be more highly correlated to selection than either SF or MCWT. In general, the diets that the animals selected were high in CP, NBDMD and moisture content and low in SF, NDF and MCWT. Of these variables, a high degree of co-variation ($r^2 \geq 0.5$) occurred between moisture, NDF, MCWT, XSACW and SF (Table 3.2). A step-wise multiple regression with plant species selection as the dependent variable and all plant attributes in Table 3.1 as independent variables resulted in the selection of only leaf MCWT and moisture content, in that order, as significant terms ($R^2=0.684$, $P<.001$). The resulting equation was:

$$\text{Selection} = 0.0155 + 0.201\ \text{Moisture} - 3.402\ \text{Leaf MCWT}$$

The simple linear relationship between feeding time and moisture content (Figure 3.1) reflected a pattern that was repeated to varying degrees with the other variables that were highly correlated with selection. MCWT (Figure 3.2) and SF (Figure 3.3) were exceptions to this pattern because the plant species were arranged in 2 distinct groups. Russian wild rye was an outlier in both cases. The slopes of separate regressions through each group were not significantly different from zero ($P>0.4$).

Examination of the relationship between NDF and one of MCWT, XSACW or SF revealed that in each case the slope of the legume regression

Table 3.2 Correlation coefficients among chemical or physical attributes of 18 plant species.

Forage Attribute	Moisture	Crude Protein	Neutral Detergent Fiber	Acid Detergent Fiber	Nylon Bag Dry Matter Disappearance	Mean Cell Wall Thickness	Cross Sectional Area of Cell Wall	Shear Force
moisture		***	***	***	***	***	***	***
crude protein	0.845		***	***	***	***	***	***
neutral detergent fiber	-0.938	-0.880		***	***	***	***	***
acid detergent fiber	-0.358	-0.430	0.621		***	***	***	***
nylon bag DMD	0.603	0.618	-0.630	-0.619		***	*	***
cell wall thickness	-0.751	-0.685	0.808	0.601	-0.610		***	***
X-S area of cell wall	-0.693	-0.509	0.763	0.452	-0.298	0.791		***
shear force	-0.772	-0.645	0.866	0.679	-0.478	0.755	0.800	

*P<0.05; ***P<0.001

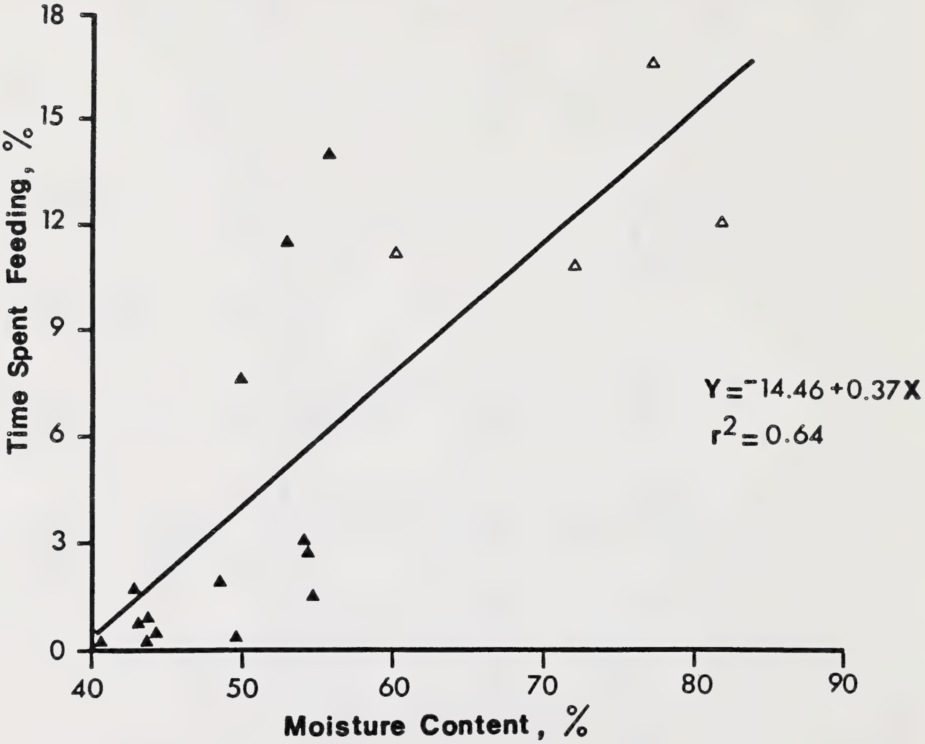

Figure 3.1 Linear regression between the proportion of total feeding time spent consuming each of 18 plant species and their moisture content. Grass = ▲; legume = △.

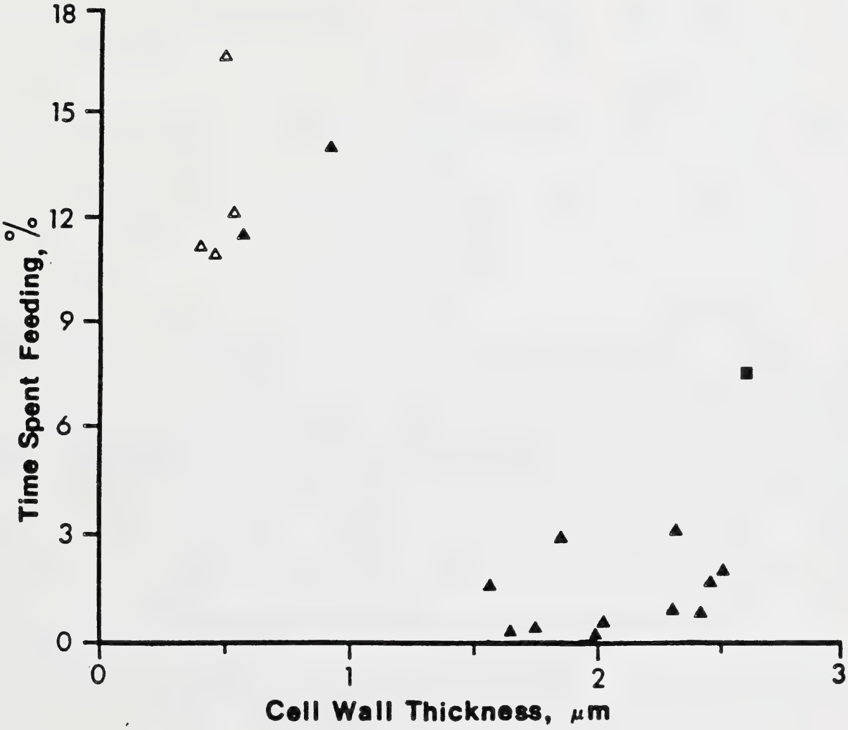

Figure 3.2 Proportion of total feeding time spent consuming each of 18 plant species plotted against their leaf mean cell wall thickness. Grass = ▲; Russian wild rye = ■; legume = △.

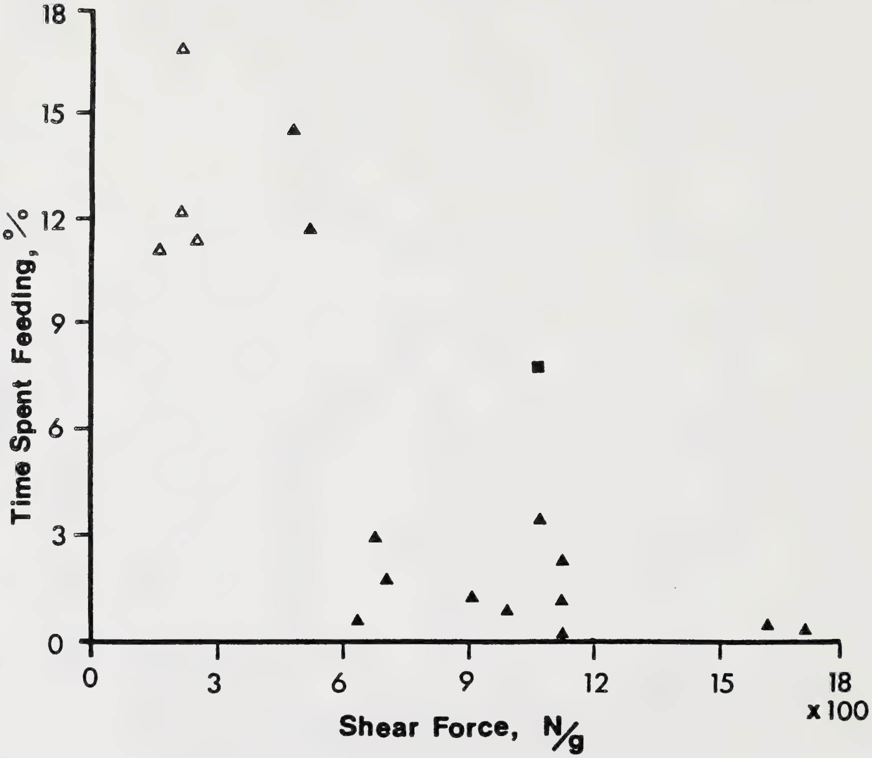

Figure 3.3 Proportion of total feeding time spent consuming each of 18 plant species plotted against the force required to shear the leaves. Grass = ▲; Russian wild rye = ■; legume = △.

was significantly (P<0.01) greater than that of grasses (Figures 3.4, 3.5 and 3.6, respectively). In contrast, no significant differences were observed between legumes and grasses in the relationship of SF with MCWT (Figure 3.7) or XSACW (Figure 3.8). As a consequence, single regressions were used to test these relationships (Figures 3.7 and 3.8).

Considerable differences among plant species were obtained in the amount of variation of MCWT, XSACW and SF. The overall coefficients of variation for each technique, when averaged within plant parts, were 8.5, 18.8 and 13.4 %, respectively.

3.4 Discussion

Plant species occurred in 2 distinct groups of selection in the summer forage selection trial namely, those that were grazed frequently and those that were grazed infrequently (Figure 3.9). The first group comprised plant species that were eaten more than 10 % of the time and the second group species that were eaten less than 3 % of the time. The differences in feeding times between these 2 groups were significant, while differences among plant species within each group were not (Figure 3.9). Only Russian wild rye grass was selected an intermediate amount, although it was more closely allied with the frequently eaten plant species. Other ruminants (e.g. Kudus [_Tragelaphus strepsiceros_]), have also displayed a forage response pattern comprised of favored and neglected plant species, with few plant species that are intermediate (Owen-Smith and Cooper 1987).

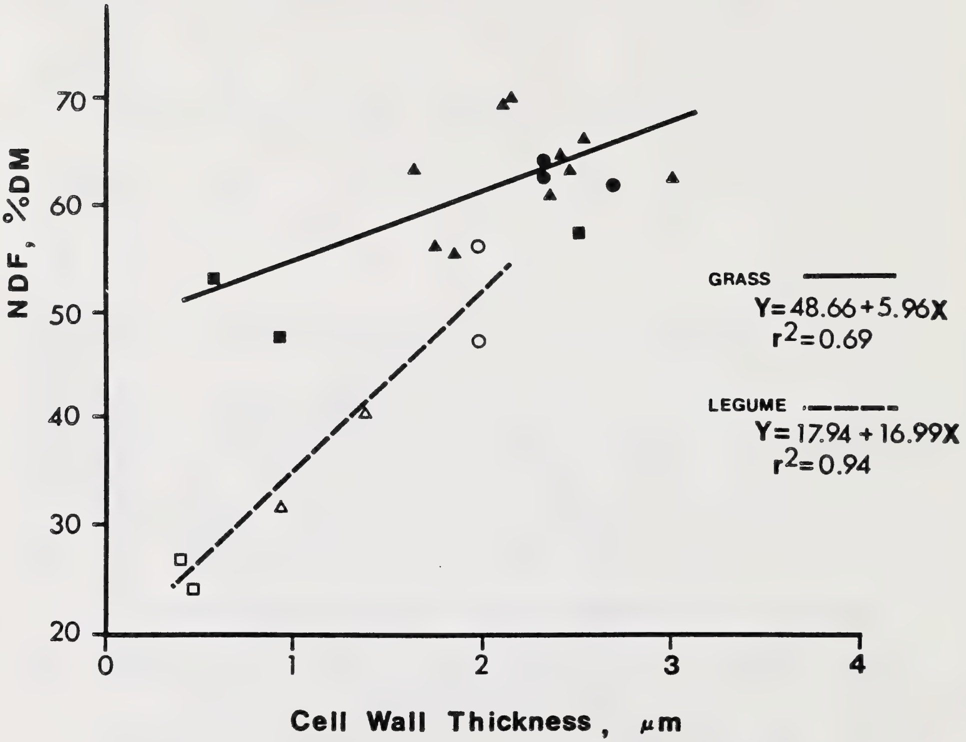

Figure 3.4 Linear regressions between neutral detergent fiber (NDF) as a percentage of dry matter and mean cell wall thickness. Whole plant = triangle; leaf = square; stem = circle. Grasses solid (n=17); legumes hollow (n=6).

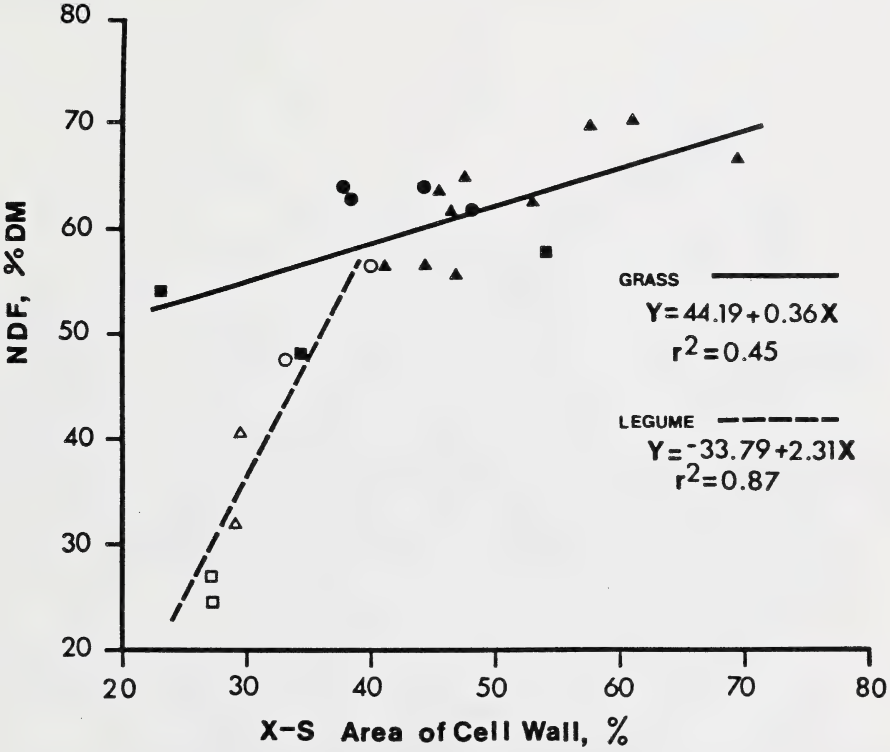

Figure 3.5 Linear regressions between neutral detergent fiber (NDF) as a percentage of dry matter and the cross sectional (X-S) area occupied by cell wall expressed as percentage of total area. Whole plant = triangle; leaf = square; stem = circle. Grasses solid (n=17); legumes hollow (n=6).

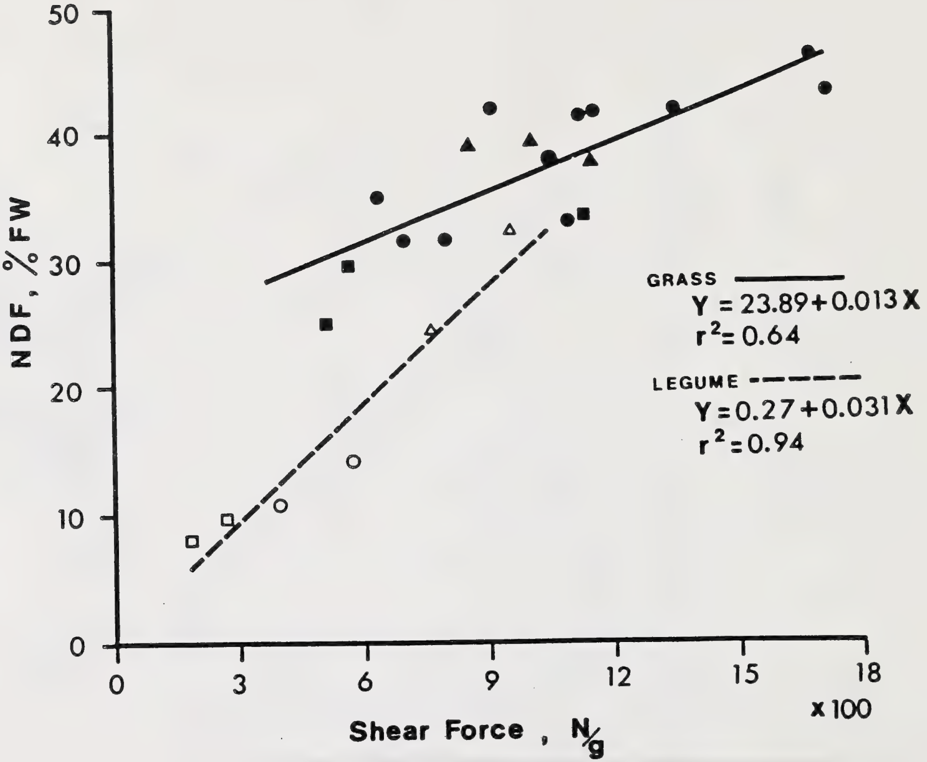

Figure 3.6 Linear regressions between neutral detergent fiber (NDF) as a percentage of fresh weight and the amount of force required to shear each sample. Whole plant = triangle; leaf = square; stem = circle. Grasses solid (n=17); legumes hollow (n=6).

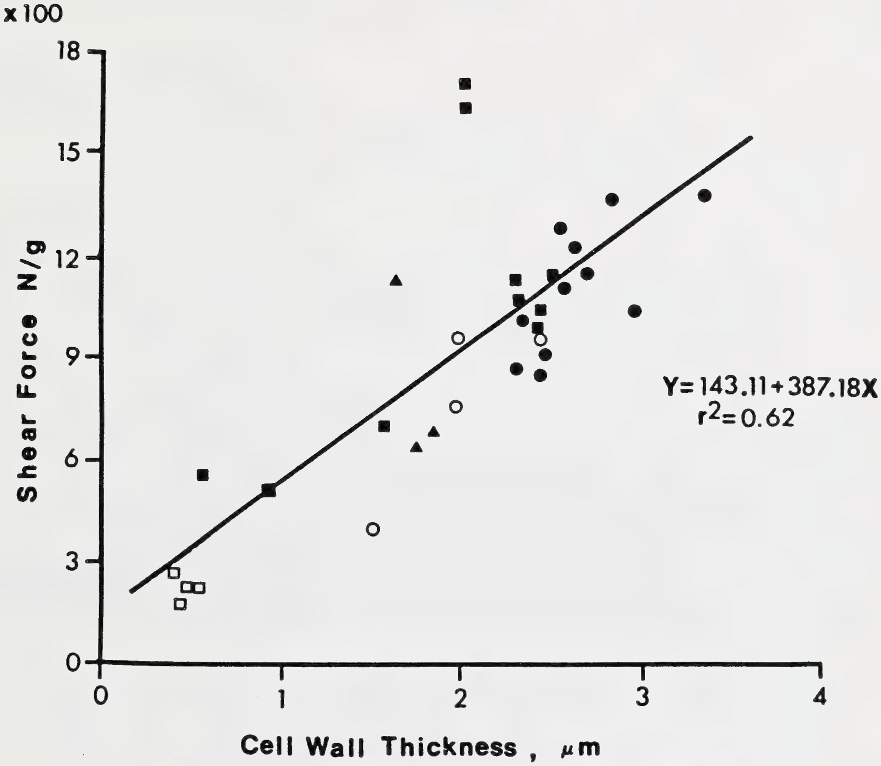

Figure 3.7 Linear regression between the amount of force required to shear each sample and mean cell wall thickness n=32). Whole plant = triangle; leaf = square; stem = circle. Grasses solid; legumes hollow.

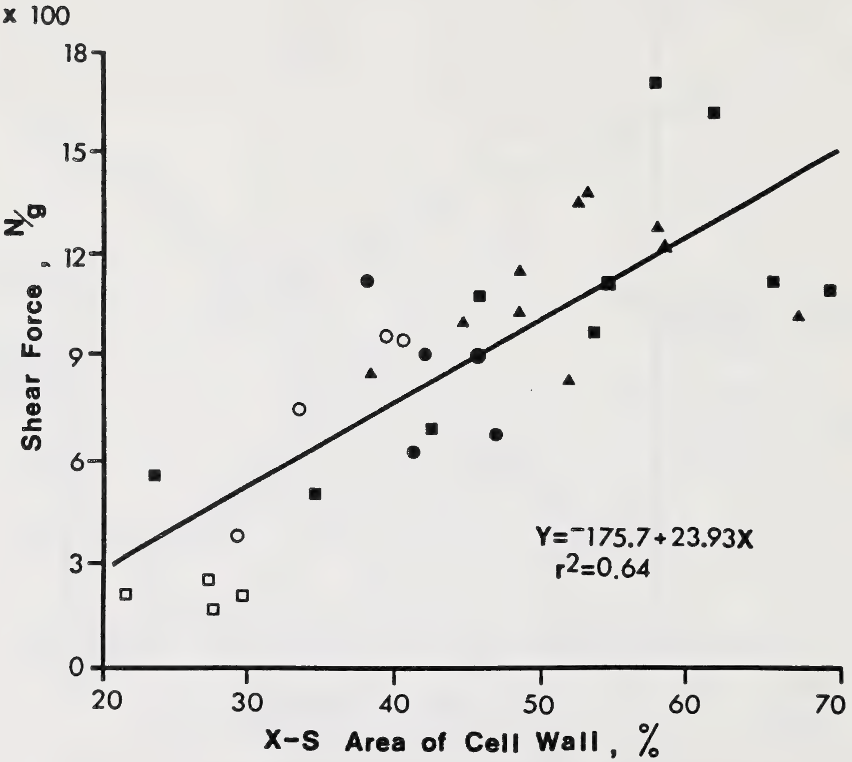

Figure 3.8 Linear regression between the amount of force required to shear each sample and the cross sectional (X-S) area of the cell wall expressed as a percentage of the total area (n=32). Whole plant = triangle; leaf = square; stem = circle. Grasses solid; legumes hollow.

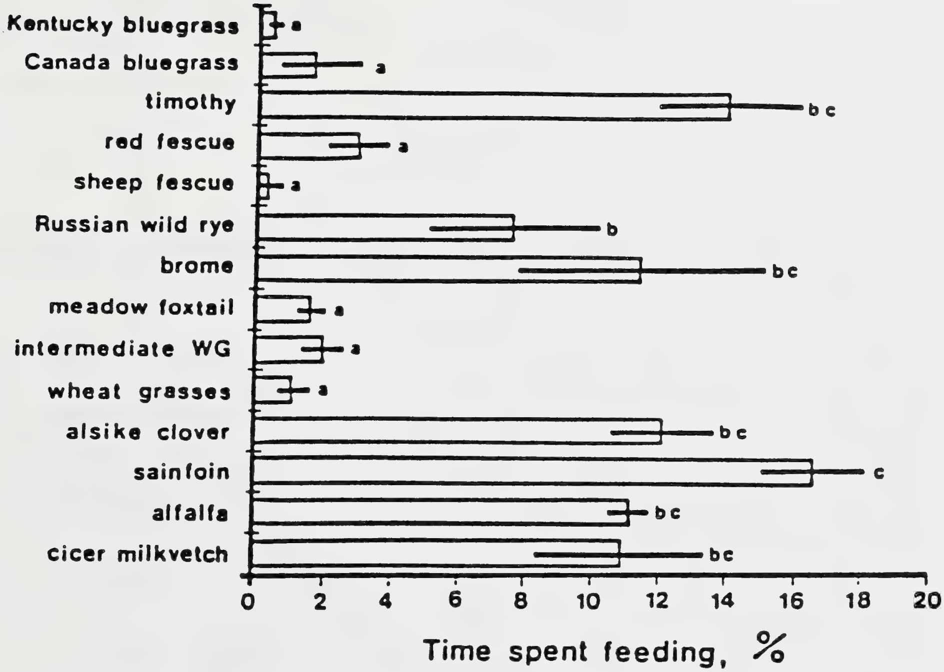

Figure 3.9 The mean (horizontal bars represent 1 SE) proportion of time spent feeding on each plant species during the first 4 days of the summer forage selection trial (Chapter 2). The means for northern, western, crested and slender wheat grasses (WG) were not significantly different and were presented as an aggregate mean. Plant species that do not share a common letter were significantly different ($P<0.05$). WG=wheat grass.

Frequently and infrequently eaten plant species tended to separate along the moisture content axis (Figure 3.1). This separation was much more complete along the MCWT and SF axes (Figures 3.2 and 3.3, respectively). In the latter cases, the frequently eaten group was distinguished by having much thinner cell walls and lower resistance to shearing. The separation of the frequently and infrequently eaten groups by MCWT was particularly distinct in that neither group had species with MCWTs in the range of 1.0 to 1.5 µm that separated the two groups.

An explanation for the abruptness of the transition between these 2 groups became apparent when the plot of feeding time and leaf MCWT was compared to the curvilinear relationship between MCWT and the rate of plant fiber breakdown in the rumen as predicted by Spalinger et al. (1986)(Figure 3.10). The leaf MCWTs of the frequently eaten plant species were typically in the relatively steeper region of the breakdown curve. As a result, the predicted ruminal breakdown rate of plant material of the frequently selected group was over 1.5 times higher than that of the infrequently selected group. It appears that the location and abruptness of the separation of the 2 plant species groups may be a response to the curvilinear relationship between MCWT and fiber breakdown in the rumen.

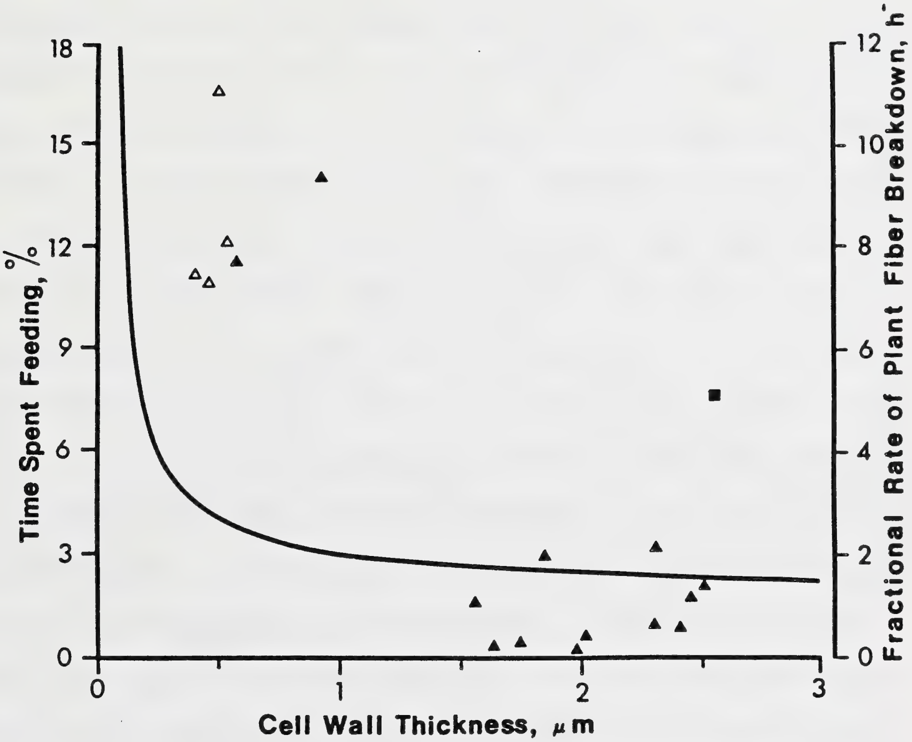

Figure 3.10 Proportion of the total foraging time spent consuming 18 plant species plotted against the leaf mean cell wall thickness (CWT). The solid line represents predicted rumen mean retention time as a function of CWT (Spalinger *et al*. 1986). Grass = ▲; Russian wild rye ■; Legume = △.

The above discussion does not imply that animals can determine MCWT or the rate of plant material breakdown. Rather, proximal sensory cues related to these forage attributes, such as how difficult the forage was to chew, were probably employed by the animals to detect the plant species with faster rates of breakdown. Sensory cues such as forage toughness would require the animals to chew the food item in order to assess it. This is consistent with the observation that every species in the summer forage selection trial was eaten at least part of the time. It is also worth noting that the feeding times among plant species within the frequently and infrequently selected groups were not significantly different from each other, nor were they correlated with either leaf MCWT or SF. This suggests that the animals were either unable, or disinclined, to discriminate between plant species within each group.

Both MCWT and SF should be related to plant species differences in handling time. For example, MCWT was correlated by Spalinger et al. (1986) with the rate of breakdown of each plant species in the rumen. Changes in the rate of plant fiber breakdown (i.e.passage rate) has been identified in section 3.1 as one the important consequences of plant species differences in handling time. In addition, forage resistance to mastication is directly related to handling time because resistance of plant fiber to physical breakdown will control how much time is spent ingesting and ruminating the forage. Therefore, SF should be a good index of forage resistance to mastication and hence, a good indicator of handling time. Other researchers have also related selection to forage attributes linked with handling time. For instance, Theron and Booysen (1966) found that the leaf tensile strength of grasses was significantly correlated to forage selection. In general, our results support the hypothesis of Spalinger _et_ _al_. (1986) which proposed that wapiti use handling time to discriminate among plant species.

Support for the hypothesis of Spalinger _et_ _al_. (1986) does not preclude the possibility that other forage attributes were important. Moisture content explained a significant portion of the variation left unaccounted for by leaf MCWT in a step-wise multiple regression equation predicting forage selection. It is reasonable to suggest that the animals may have been partially using succulence to discriminate between plant species. In addition, none of the forage attributes could be used to explain why Russian wild rye lay outside the two groups. Perhaps other forage attributes not measured in this experiment would be able to explain this deviation. Several possibilities are suggested and discussed in Chapter 5.

In contrast to the studies of Arnold (1960) and Field (1976), the proportion of leaf comprising the available biomass of each plant species was not correlated to selection in the present study. The lack of correlation was due largely to the wheat grasses, all of which were infrequently eaten despite having a high proportion of their total biomass composed of leaves. It appears that wapiti were selecting for forage attributes other than leafiness. The wheat grasses had relatively large leaf MCWT, SF and NDF values, sometimes even higher than their respective stems, suggesting that the animals were selecting for intrinsic plant attributes (eg. resistance to chewing) rather than morphological features such as leafiness.

Regressions using NDF as the dependent variable and either MCWT (Figure 3.4) or XSACW (Figure 3.5) as the independent variable resulted in separate regressions for legumes and grasses. The significantly steeper slope for legumes in both regressions indicated that increases in either MCWT or XSACW resulted in a more rapid decrease in the amount of cell solubles in legumes than in grasses.

A decrease in NDF content indicated an increase in the proportion of the dry biomass containing cell contents and a corresponding decrease in cell walls. Measurement of XSACW and MCWT, on the other hand, referred directly (XSACW) or indirectly (MCWT) to the proportion of area of a leaf or stem cross section that was occupied by cell wall. The area between the cell walls could have been occupied by either the cell contents or interstitial space (presumably air).

Two explanations for the steeper slope of the legumes in these regressions can be suggested. The first is that the solute concentration of the cell contents of the legumes was higher. As a consequence, the amount of cell solubles would have decreased faster for legumes than for grasses when cell contents were displaced by thickening of the cell walls. The second explanation is that grasses had more interstitial space and less cell contents between cell walls. Consequently, the amount of cell contents would have decreased faster for legumes than for grasses as the cell walls thickened because more cell contents and less interstitial space would be displaced. Forage moisture content explained 88 % of the variation in NDF (Table 3.2) with no apparent difference between grasses and legumes in this relationship. This suggests that the solute concentrations of their respective cell contents were similar. Thus, it appears that the best explanation of the observed results was that legumes had proportionally more interstitial space and less cell contents between their cell walls than did grasses.

Differences between grasses and legumes were also observed in a regression of NDF with SF (Figure 3.6). This suggests that qualitative differences existed between the resistance of grass and legume fiber to shearing that were not reflected in quantitative changes in cell wall content. This difference was not observed in the regressions of SF with MCWT or XSACW (Figures 3.7 and 3.8), contrary to what would be expected if qualitative differences in fiber existed. Perhaps the techniques used to measure XSACW and MCWT were not precise enough to detect a difference. This was supported by the relatively high coefficients of variation observed for MCWT and XSACW. Furthermore, measurements of SF were more representative of the plant sample because the whole plant or plant part was sheared, while MCWT and XSACW were both measured only at the middle of a leaf or stem sub-sample.

Michaud et al. (1984) employed a similar shearing technique to measure the structural strength of oven-dried tropical grasses and obtained an insignificant correlation between NDF and SF. The range in NDF values they encountered was less than half that encountered in the present study. Statistical analysis of our results over the same range still resulted in a positive and significant regression ($r=0.70$, $P<0.005$). The use of oven-dried instead of fresh material could have contributed to the differences between the studies, but poor correlations between voluntary intake and cell wall content have also been reported for tropical grasses (Laredo and Minson 1973; 1975). This is noteworthy because voluntary intake of forages is highly negatively correlated to the resistance of plant fiber to physical degradation (Troelson and Bigsby 1964; Welch 1982). Perhaps large qualitative differences in fiber quality, comparable to those observed between legumes and grasses in this study, exist among the tropical grass species.

3.5 Summary

Selection by wapiti of 14 grasses and 4 legumes occurred in 2 distinct groups corresponding to whether the plant was frequently or infrequently eaten. Mean cell wall thickness and SF were the plant attributes that best explained this forage selection pattern. Both SF and MCWT were related to handling time, thereby supporting the hypothesis of Spalinger _et al_. (1986), which proposed that wapiti use handling time to discriminate between plant species while making foraging decisions. Moisture content was also related to forage selection, suggesting that succulence was also important to selection. The proportion of leaf comprising the available biomass was not correlated to plant species selection.

Differences were observed between legumes and grasses in their structure and physical properties. Grasses appeared to have more interstitial space and less cell contents between cell walls. Differences also occurred between grasses and legumes in the resistance of fiber to shearing and these differences were not accounted for by quantitative measurements of fiber content.

4. ANALYSIS OF WAPITI RUMEN CONTENTS TO DETERMINE THE BOTANICAL COMPOSITION OF THE DIET

4.1 Introduction

Sampling from an esophageal fistula is the most accurate method of quantifying the food habits of free-ranging ruminants (Rice 1970; McInnis et al. 1983). A major disadvantage of this technique is that only a small portion of the foraging session can be sampled and this can lead to an unreliable estimate of diet under heterogeneous grazing conditions (Loehle and Rittenhouse 1982). A much more difficult problem is the short life expectancy of esophageally fistulated animals due to fistula deterioration from pressure necrosis around the cannula (Veteto et al. 1972).

The diet of a ruminant can also be accurately represented by rumen content samples taken through a rumen fistula, provided that the rumen has been evacuated prior to foraging (Lesperance et al. 1960). While this results in an accurate representation of what the animal has consumed, the effects of rumen evacuation on foraging behavior is likely to be severe because of the role that rumen distention plays in determining appetite (Baile and Della-Fera 1981). When rumen contents were sub-sampled without prior evacuation, the occurrence of forbs in the diet is significantly under-estimated relative to grasses (Rice 1970; McInnis et al. 1983). Gaare et al. (1977) has suggested that this is due to plant species differences in rumen mean retention time (MRT) in that plant species with longer rumen MRTs are over-represented in the rumen contents.

The potentially high mortality and morbidity rates for esophageally fistulated animals made esophageal fistulation unacceptable for the food habit study discussed in Chapter 2. The present study was initiated to determine if a modification of the rumen sub-sampling technique would make rumen content samples more representative of the actual diet. The modification was based on the observation that most of the reduction in the size of feed particles occurs during rumination, with only 15-30 % of the total reduction attributable to mastication during ingestion (Trudell-Moore and White 1983; Chai _et al_. 1984; Kennedy 1985). If animals thoroughly ruminate feed particles between foraging bouts, the rumen contents immediately after eating should be composed of 2 particle size pools: a large particle pool corresponding to the most recently consumed meal and a small particle pool corresponding to the particles that have been subjected to rumination. It was hypothesized that sieving with the correct mesh size would separate these 2 particle pools. The composition of the meal would then be determined from the botanical composition of the large particle pool. It was hoped that biases in diet estimation due to differences in MRT would thereby be attenuated, because MRT should affect the composition of only the small particle pool. The specific objectives of this project were to select a sieve size that isolated primarily the large particle pool and to determine whether the particles belonging to this pool provided an accurate estimate of diet composition.

4.2 Materials and Methods

The experimental animals were 2 male and 2 female adult wapiti that were ruminally fistulated and fitted with either a 7.6 cm (males) or 10 cm (females) ruminal cannula. Animals were fed two different types of diets in three studies. Sampling for both diets involved allowing the animals to feed in the morning and evening with at least 6 hours between meals. This was to ensure that the animals had ample time to ruminate before feeding. Rumen content samples were collected from each animal immediately before and after every meal and stored fresh frozen at -20°C. A sample consisted of five 100 ml sub-samples, each taken from 1 of 5 different locations in the rumen (Figure 4.1). The sub-samples from the ventral sac were taken with the device shown in Figure 4.2.

The first type of diet was comprised of range forage. All 4 animals grazed on a pasture in 3 separate feeding trials consisting of 14 days during the winter (trial 1), 7 days during the spring (trial 2) and 14 days during the summer (trial 3). Details on the dates of each trial, the feeding routine and the description of the pasture were given in Chapter 2. The plant species comprising the pasture were: northern wheat grass (*Agropyron dasystachyum*), intermediate wheat grass (*A. intermedium*), crested wheat grass (*A. pectiniforme*), western wheat grass (*A. smithii*), streambank wheat grass (*A. riparium*), slender wheat grass (*A. trachycaulum*), sheep fescue (*Festuca ovina*), red fescue (*F. rubra*), Kentucky bluegrass (*Poa pratensis*), Canada bluegrass (*P. compressa*), meadow foxtail

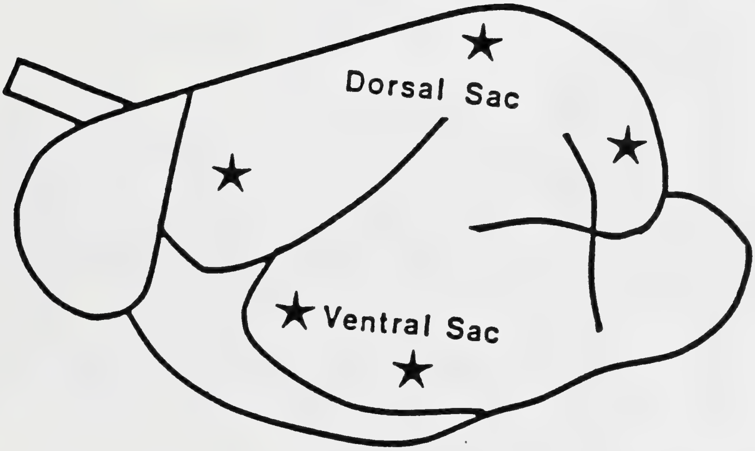

Figure 4.1 Locations of rumen sub-sampling. Sites of sub-sampling are represented by stars.

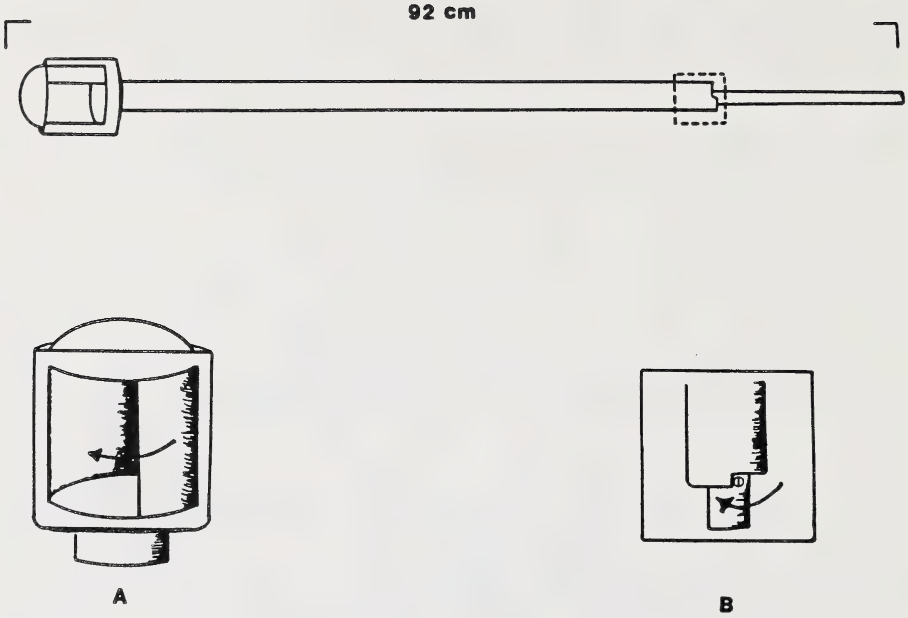

Figure 4.2 Device used to sub-sample rumen contents within the ventral sac. A rumen content sample was taken by inserting the closed sample chamber into the ventral sac. The sample chamber was then opened, allowed to fill, closed again and extracted from the rumen. A=100 ml sample chamber; B=mechanism for opening and closing sample chamber.

(*Alopecurus pratensis*), Russian wild rye (*Elymus junceus*), timothy (*Phleum pratense*), brome (*Bromus inermis*), sainfoin (*Onobrychis viciifolia*), cicer milkvetch (*Astragalus cicer*), alsike clover (*Trifolium hybridum*) and alfalfa (*Medicago sativa*).

The second type of diet was long hay comprised of 500 g (as fed) of each of alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*), timothy (*Phleum pratense*) and brome (*Bromus inermis*). One female and two male wapiti were held in separate pens with concrete floors and fed this ration twice daily (0700 and 1800 h) for 9 days (August 3 to 12, 1985). Animals were removed from their feeding pens as soon as one animal had discontinued feeding for a least 15 minutes. Between meals, the animals were housed individually in roofed, open-air pens in which water and Co-I salt were available *ad libitum*.

Four samples of each hay species were taken opportunistically over the course of the second experiment and the average dry matter content (DM) determined by oven-drying at 60°C. To facilitate separation of the orts, timothy and alfalfa were fed in the opposite corner of the pen from brome and red clover. The orts from the morning meal were left in the feeding troughs and fed with the evening meal. At the end of each day the floors were swept and all orts collected. The orts were later separated to species, oven-dried at 60°C and weighed. The amount of each plant species ingested each day by each animal was calculated on a DM basis.

4.2.1 Study 1: Determining Particle Size Distribution

A subset of all the rumen samples collected before and after feeding were analysed for the relative distribution of different sized particles. The samples analysed were from the winter (day 9) and summer (day 6) trials when diet 1 was fed and day 9 of the trial when diet 2 was fed. These samples were selected to illustrate the full effect of diet type on particle size distribution. From each sample, approximately 50 g (fresh weight) of thawed material was sieved serially through screen mesh sizes of 11.5, 7.4, 4.0 and 2.0 mm using techniques described by Mudgal _et_ _al_. (1982). The material remaining on each screen and the material passing through the final 2.0 mm screen were collected, oven-dried at 60°C, weighed and expressed as a percentage of total dry weight. A screen size of 4.0 mm was determined by visual inspection of the data (Figure 4.3) as that best able to separate the larger particles that belonged to the most recent meal from the smaller particles that were theoretically the remnants of previous meals. This screen size was used to sieve rumen samples in the remaining 2 studies.

4.2.2 Study 2: Botanical Composition of Rumen Contents Compared to Foraging Time

Samples of rumen contents collected when diet 1 was fed (winter: days 2, 4, 6, 10 and 14; spring: days 1, 3 and 7; summer:days 1, 3, 5, 9 and 13) were examined for botanical composition. These days were

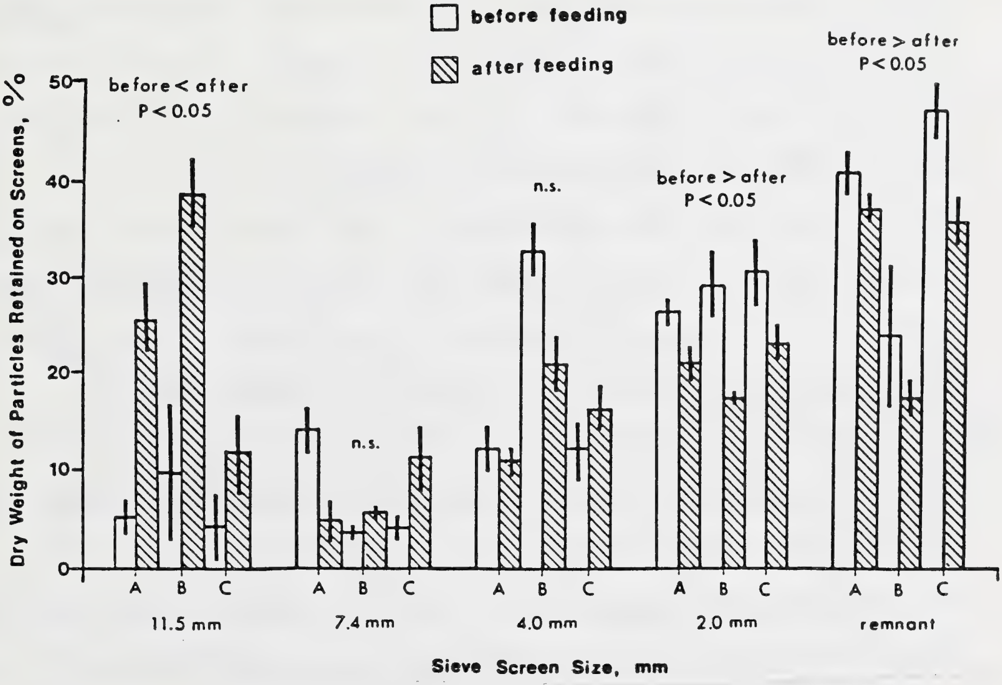

Figure 4.3 The percentage of total dry weight of feed particles (mean ± SE) in rumen contents collected immediately before or after feeding that were retained by, or passed through (remnant), 4 different sieve screen sizes. A=winter pasture (diet 1) n=4; B=summer pasture (diet 1) n=4; C=grass-legume hay (diet 2) n=3.

selected in order to minimize the number of samples actually examined while still maintaining a representative sample from each season. Samples were processed by thawing and sieving the entire sample, 50 g at a time, using a 4.0 mm screen. The material retained on the screen was oven-dried and sent to the Composition Analysis Laboratory (CAL), Colorado State University, for determination of botanical composition using microhistological analysis of plant cuticle fragments. Microhistological analysis could only accurately identify congeneric species to genus. Therefore, data for the wheat grasses, fescues and bluegrasses were presented as generic aggregates.

Data on the time spent feeding on each plant species, expressed as percentage of the total amount of time spent foraging (foraging time), was collected while the animals received diet 1 (see Chapter 2) and were compared to the results of the rumen content analysis.

4.2.3 Study 3: Botanical Composition of Rumen Contents Compared to Dry Matter Intake

The botanical composition of the rumen content samples collected immediately after the animals had fed on diet 2 were determined. The first 4 days were used as a conditioning period in order to give the animals time to become accustomed to the diet and to minimize the number of feed refusals. The rumen samples collected during the last 5 days were sieved and analysed for botanical composition using the techniques described in study 2. Legumes other than alfalfa and red clover were often mistakenly reported by CAL to be present in the rumen contents. Consequently, all occurrences of legumes in the rumen contents were reported as a single category called 'legumes'.

The botanical composition estimates from the morning and evening meals of each day were averaged for each animal. This allowed the diet estimates from the rumen contents to be compared with the daily DMIs of each plant species or plant species category expressed as a percentage of the total DMI (%DMI).

4.2.4 Statistical Analysis

All results were analysed using analysis of variance (ANOVA) procedures (Steel and Torrie 1980) with the mainframe statistics program SPSSX (SPSS 1986) in combination with the user procedure UANOVA (Taerum 1987).

The main effects of study 1 were screen size, type of diet, sampling time (before and after feeding) and meal time (morning and evening). The primary aim of this study was to determine if the relative proportion of rumen contents retained on each sieve mesh size changed before and after feeding. It was also important to determine if this was affected by the diet consumed. Thus, the primary factors of concern in the ANOVA were screen size, the screen size by sampling time interaction and the screen size by diet interaction. The screen size by meal time interaction was also tested to determine if the results from the morning and evening meals were different. Note that because the results were calculated as percentages, the mean value of each category within all the main effects except screen size were summed to constant. Consequently, the only main effect that could be tested was screen size.

The results were then examined with the variation from diet and meal time pooled in order to determine whether any differences still existed in the particle size distributions between before and after feeding that were applicable to all the diets. The cell means associated with the screen size by sampling time interaction were compared using Student-Newman-Keuls' (SNK) multiple range test in the program UANOVA. Means from before and after feeding were compared for each screen size to see if they were significantly different.

The influence of plant species on the relationship between rumen content analysis and foraging time was tested in study 2 by examining the plant species by method (rumen content analysis and foraging time) interaction for each season individually. The cell means from the plant species by method interaction were compared using SNKs' multiple range test and the results examined to determine whether the means from rumen content analysis or foraging time were significantly different within a plant species. Study 3 was analysed in a similar fashion except that season was not a part of the experiment and rumen content analysis was compared to %DMI instead of foraging time.

4.3 Results

In study 1, the amount of material retained on each screen was significantly affected ($P<0.001$) by screen size and by both the screen size by diet and screen size by sampling time interactions. In contrast, the meal time by screen size interaction was not significant ($P>0.48$). After feeding, significantly more material was retained on the 11.5 mm screen and significantly less was either retained on, or passed through, the 2.0 mm screen (Figure 4.3). It appeared that the recently eaten particles were, on average, larger than those that were in the rumen prior to feeding. Visual comparison of the particle size distributions from before and after feeding (Figure 4.3) suggested that the 4.0 mm screen was best able to isolate the larger recently eaten particles. A mean ± SE of 67.2 ± 12.8 % of the rumen contents that were in the rumen prior to feeding passed through this sieve.

In study 2, there was a significant interaction ($P<0.001$) between plant species and method of estimating diet. Comparisons of the results from the rumen content analysis and foraging time demonstrated that the fescues were significantly over-represented while timothy and sainfoin were under-represented in the rumen contents relative to foraging time in all seasons (Table 4.1). The wheatgrasses were significantly over-estimated in the spring and summer by more than 26 and 45 %, respectively. Brome tended to be under-estimated in every season and the difference was significant in winter and summer. Alfalfa and red clover were significantly under-estimated on the summer pasture while alsike clover tended to be under-estimated in all 3 seasons, significantly so in summer. Russian wild rye was significantly under-estimated only on the summer pasture while the bluegrasses were over-estimated on the winter pasture. Examination of

Table 4.1 Mean and standard error of the amount of time spent feeding on each plant species (foraging time) and the botanical composition of the rumen contents (n=4).

	Winter Pasture					Spring Pasture					Summer Pasture				
	Foraging Time (%)		Rumen Contents (%)		Difference (rumen-time)	Foraging Time (%)		Rumen Contents (%)		Difference (rumen-time)	Foraging Time (%)		Rumen Contents (%)		Difference (rumen-time)
Plant Species	$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE	
wheat grasses	10.8	2.54	12.6	3.38	1.8	13.4	3.07	40.2	2.04	26.8*	10.8	0.66	56.5	1.33	45.6*
meadow foxtail	0.8	0.41	2.6	0.28	1.8	5.7	1.91	0.1	0.02	-5.6	3.0	1.39	0.1	0.05	-2.9*
brome	7.1	1.27	1.4	0.10	-5.7*	14.8	3.47	8.7	0.97	-6.1	10.3	2.66	1.7	0.13	-8.6*
Russian wild rye	2.0	1.25	0.2	0.06	-1.8	1.9	1.10	0.2	0.06	-1.8	9.0	1.55	0.2	0.06	-8.8*
fescues	46.3	5.77	72.5	3.94	26.2*	6.8	1.68	21.1	2.59	14.3*	3.3	0.52	21.2	1.68	17.9*
timothy	8.2	1.04	0.0	0.00	-8.2*	19.0	5.97	0.0	0.00	-19.0*	10.3	2.19	0.0	0.01	-10.3*
bluegrasses	2.6	1.28	10.2	0.62	7.7*	3.2	0.84	5.9	1.25	2.7	8.7	1.92	6.5	0.44	-2.2*
cicer milkvetch	5.5	0.40	0.4	0.15	-5.1*	8.0	1.35	6.6	1.10	-1.4	13.2	1.94	8.4	2.13	-4.8
alfalfa	2.5	1.02	0.1	0.06	-2.4	8.1	1.40	12.3	3.50	4.2	12.9	0.33	5.1	0.70	-7.8*
sainfoin	9.9	3.31	0.1	0.01	-9.8*	15.0	3.16	5.0	2.28	-10.0*	10.1	1.42	0.3	0.08	-9.8*
alsike clover	4.3	1.30	0.0	0.00	-4.3	4.1	1.96	0.0	0.00	-4.1	8.3	2.01	0.0	0.02	-8.3*

*Means for methods within species and seasons were significantly different ($P<0.05$).

the raw data from the results of study 2 revealed that a particular animal would reportedly have 10-20 % of its rumen contents composed of the bluegrasses (winter) or the fescues (summer), even though the animal had not been observed eating these species for two days prior to the collection of the rumen sample. Only meadow foxtail and cicer milkvetch were not significantly over or under-estimated in any season, although cicer milkvetch was numerically under-estimated in all 3 seasons.

In study 3, there was a significant ($P<0.001$) interaction between plant species and the method of estimating diet. Comparisons between rumen contents and the known %DMI revealed that rumen contents tended to over-estimate the grasses relative to legumes (Table 4.2). This difference was significant ($P<0.05$) for brome and the legumes but not for timothy.

4.4 Discussion

The results from study 1 indicated that the proportion of large particles in the rumen was consistently greater after the animals had eaten. For example, the proportion of particles retained on the 11.5 mm screen increased by approximately 29 percentage units after feeding on summer pasture (Figure 4.3). The difference was affected by diet as was demonstrated by the smaller increase (less than 8 percentage units) in the proportion of particles retained on the 11.5 mm screen after the animals ate the hay diet. The results generally supported the hypothesis that freshly ingested feed

Table 4.2 Mean and standard error of the dry matter intake (DMI) of each plant species or species group and the botanical composition of the rumen contents (n=3).

Plant type	DMI, %		Rumen contents, %		Difference (rumen - DMI)
	$\bar{x}$	SE	$\bar{x}$	SE	
brome	22.6	0.31	43.7	3.03	21.0*
timothy	24.9	0.12	31.3	1.84	6.4
legumes	52.5	0.27	25.0	2.02	-27.5*

*Means for methods within species and seasons were significantly different ($P<0.05$).

particles were larger than the particles from earlier meals. Thus, the rumen contents immediately after feeding did appear to be composed of large and small particle pools.

The 4.0 mm screen was used to separate these 2 particle pools. On average, this screen was able to eliminate approximately two-thirds of the weight of particles present in the rumen before feeding. It was not possible with this method to determine what proportion of the pre-feeding particles were retained on this screen when post-feeding samples were sieved. Our results suggest that sieving with the 4.0 mm screen did not adequately separate the two particle pools. Large biases, similar to those reported by other researchers who examined unsieved samples (Rice 1970; McInnis _et al_. 1983), still remained in the diet estimate based on rumen contents. For instance, in study 2 large discrepancies existed in every season between the results received from rumen content analysis and foraging time.

Comparisons between rumen contents and foraging time must be made cautiously because foraging time does not account for plant species differences in the rate of ingestion and may not be exactly correlated with relative consumption. However, it seems unlikely that differences in rate of ingestion would explain why plant species that were rarely eaten often made up a large proportion of the rumen contents. For example, in every season at least 1 species was over or under-represented by at least 25 %. In fact, during the summer trial with diet 1, the wheat grasses were reported by CAL to compose 56.5 % of the rumen contents, even though they were eaten less than 11 % of the time. In addition, large differences, (e.g. 20-30 %), existed between the plant species composition of the rumen contents compared to the known %DMIs of these plant species.

One explanation for the bias associated with the rumen sampling method is that a large number of the particles that were retained on the 4.0 mm screen were from previous meals. Thirty percent of the pre-feeding particles were retained by this screen. These particles would be primarily composed of plant species with longer MRTs and would bias the diet estimate by causing these species to be over-estimated. Differences among plant species in susceptibility to comminution during ingestion could have also contributed to the bias. Plant species more susceptible to comminution during ingestion would have more particles pass through the 4.0 mm screen and thus would be under-estimated in the diet.

Using a screen size different from 4.0 mm would not improve the diet estimate determined from the rumen contents. For instance, a larger screen size would cause more of the recently eaten particles to pass through and the species corresponding to these particles would be under-estimated. Similarly, a smaller screen size would retain more of the particles from previous meals and the plant species corresponding to these species would be over-estimated. Thus, it appears that sieving is an ineffective approach to improving the estimate of diet composition determined from rumen contents. No technique currently exists that provides a reliable estimate of diet from sub-samples of rumen contents. It is recommended that this technique not be used in food habit studies where other, more reliable techniques are applicable. Future research should be directed towards alternatives such as developing correction factors calculated from direct measurements of rumen MRT to adjust rumen botanical composition estimates (Gaare et al. 1977).

Problems also existed in using microhistological analysis of plant cuticle fragments to determine botanical composition of rumen contents. For instance, in study 2 substantial amounts of some plant species were reported in the rumen contents even though the animal had not been observed eating these species for several days. Furthermore, in study 3 red clover and alfalfa were mistaken for other legumes that were not available to the animals during the studies. Some of the biases observed in rumen content may have been due to the inability to accurately distinguish some species using the microhistological technique.

4.5 Summary

Using a 4.0 mm screen to sieve rumen content samples did not correct the biases previously reported by other researchers in the estimate of diet composition determined from rumen contents. Future research in this area should concentrate on developing correction factors calculated from direct measurements of rumen MRT to adjust rumen botanical composition estimates (Gaare _et al_. 1977).

5. GENERAL DISCUSSION: SELECTION OF INDIVIDUAL FOOD ITEMS BY RUMINANTS

Optimal foraging theory (OFT) has been used extensively during the last 20 years in research examining diet selection by animals (Shoener 1987). The theory is based on the premise that foraging behavior is a heritable trait that is subject to natural selection. From this it is argued that natural selection has honed foraging behavior such that when the population is in evolutionary equilibrium, the animals are maximizing their Darwinian fitness by foraging optimally (Shoener 1971; Pyke _et_ _al_. 1977).

Net energy intake is the criterion normally assessed when determining if animals are foraging optimally. Mathematical models are used to predict the optimum diet based on the energy content and abundance of each potential food item and on the amount of time the animal takes to pursue, handle and swallow the food. The validities of the models are tested by comparing the results of the model to the observed foraging behavior of the animal. Although the appropriateness and the validity of the assumptions underlying OFT have been criticized (Gray 1987), it appears that OFT has made some significant contributions to the study of foraging behavior, particularly for some predators, nectivores and granivores (Krebs _et_ _al_. 1983; Shoener 1987).

The application of OFT to the study of how ruminants select their diets has met with limited success. Linear programming models have been used to approximate the observed consumption pattern of major forage categories (i.e. aquatic vegetation, deciduous browse and forbs) exhibited by moose (Alces alces) and the relative proportions of monocots and dicots in the diets of 14 sympatric herbivores (Belovsky 1978; 1986). Owen-Smith and Novellie (1982) attempted to predict the diet selection patterns of a kudu (Tragelaphus strepsiceros) using OFT. However, the model proposed by these authors was unsatisfactory because it predicted a much less diverse diet than that selected by the animals. Researchers are invariably left trying to account for why ruminants forage in such a diversified fashion (Freeland and Janzen 1974; Westoby 1978). To date, OFT has not been successful in explaining how ruminants distinguish between the individual units of the forage resource.

There are several reasons why classical OFT may not be the most appropriate conceptual model for ruminants. It may not be possible for the animal to distinguish the differences between food items that would be necessary for it to forage optimally. The concept of handling time for ruminants, as discussed in Chapter 3, is more complex than in the case of monogastrics because handling time for ruminants includes differences in the amount of time spent ruminating. To minimize handling time, a ruminant would have to select forages that were faster to ingest and also required less rumination. It is unlikely that ruminants are able to accurately assess how much time is spent ruminating individual food items.

An even more daunting task for a ruminant animal is the detection of the energy content of the forage. While the gross energy content of forages tend to be similar (Van Soest 1982) the factors that determine what proportion of this energy is digestible are both subtle and variable. Cell contents are uniformly digestible but the digestibility of cell walls varies substantially among plant species and is strongly and negatively correlated to lignin content (Van Soest 1967). Furthermore, lignin content within a plant species can be affected by environmental factors such as temperature (Van Soest *et al*. 1978).

The inability of ruminants to accurately distinguish between food items on the basis of handling time or digestible energy content may explain why classical OFT has not been able to account for how ruminants select between individual food items. Adaptations and alternatives to traditional OFT have been proposed to account for the patterns of diet selection of large generalist herbivores such as ruminants. These ideas separate into 4 general hypotheses that are discussed below.

1. *Toxic Chemical Dilution*. Freeland and Janzen (1974) argue that diet diversity is an adaptation to minimize the consequences of ingesting toxic and anti-nutritive plant compounds. By feeding on a variety of species, the concentration of any particular compound is kept below the threshold at which toxicity occurs or digestive capacity is impaired.

2. Optimal Foraging Theory Using Proximate Decision Rules. Krebs *et al*. (1983) distinguish between ultimate and proximate decision rules governing foraging behavior. They argue that the classical OFT models provide only ultimate explanations and, as such, can only provide general predictions. A good example of this would be the successful prediction by OFT of the general forage classes consumed by herbivores (Belovsky 1978; 1986). To explain foraging behavior with more resolution requires a more proximate perspective. Krebs *et al*. (1983) suggested that this could best be done by determining what "rules of thumb" (ROT) animals employ when making foraging decisions. These ROT should reflect the sensory input that an individual animal uses to make foraging decisions. If the researcher can measure the ROTs that animals are using, then these rules can be included in more complex OFT models as additional constraints. From this perspective, the diverse food habits of ruminants would be a result of imprecise ROT and the animals are foraging as optimally as their ROT will allow.

3. Risk Aversion. Traditional OFT models have been adapted to accommodate the concept of risk in stochastic foraging models (Caraco 1980). This type of analysis recognizes that the animal may not detect variation in the size of the food reward (i.e. energy or nutrients) and hence may make foraging mistakes while trying to select the optimal diet. In other words, the ROT that the animals apply are inaccurate. As a result, a highly selective foraging strategy would have a larger variance in the size of the food reward received than would a less selective strategy. Some animals are said to follow a

risk-aversion foraging strategy (Caraco 1980) in which they forage less selectively in order to have a higher probability of always meeting their maintenance requirements even though the mean quality of their diet will be lower. Belovsky (1984) argued that foraging strategies of large generalist herbivores are risk-aversion and that this accounts for the diversified foraging strategy of ruminants.

4. Satisficing. Some authors have suggested that large generalist herbivores do not use decision rules that are consistent with OFT. For instance, Bunnell and Gillingham (1985) have adapted the concept of "satisficing" from the field of economics (Winter 1971; Radner 1975) to describe how ruminant animals choose food items. The satisficing theory argues that animals will not continue to pursue an optimal foraging strategy into infinity. Instead, once a certain acceptability threshold is reached, the individual will stop sampling and consume the selected food item. To determine whether a food item is above this threshold, the herbivore would use some type of ROT. The difference between OFT and satisficing is that OFT predicts that the animal tries to optimize its intake using its ROT, while satisficing theory predicts that the animal would use its ROT to determine whether a food item passes its acceptability threshold. No effort would be made to discriminate between food items once they were deemed acceptable. They would simply be eaten.

All 4 of these hypotheses can be used to explain conceptually why the diets of ruminants are so diverse. However, the toxic chemical dilution hypothesis is quite limited. It does not explain why some species are eaten more than others, only that the diet will be diverse. There is no evidence that the plant species used in the forage selection experiments in Chapter 2 contain any toxic or anti-nutritive compounds. Nevertheless, the animals ate some species much more often than others. It is more likely that animals detect the presence of toxic compounds by smell or taste (Chapman and Blaney 1979) and use this as an ROT to discriminate between food items.

It is unclear which, if any, of the 3 remaining hypotheses best explains the patterns of foraging behavior of ruminants. More attention needs to be paid to the ROT that animals use to make their foraging decisions before these 3 hypotheses can be tested. Indeed, not only do the ROT need to be identified, but an assessment of how accurately and precisely they are applied is also required to determine whether ruminants employ optimizing, risk aversion or satisficing foraging strategies.

The main sensory cues used by ruminant animals to distinguish between food items probably result from ingesting a sample of the forage. This contention is based on the observation that ruminants eat at least small amounts of most plant species they encounter (Chapter 2; Owen-Smith and Cooper 1987). The results of the present study were used to suggest some ROT that the ruminants may be using to select between food items.

The relationship between handling time and voluntary intake by ruminants was discussed in Chapter 3. It seems logical that animals would try to eat species that have lower handling times in order to increase their nutrient intake. Differences between plant species in their resistance to mastication is a likely sensory cue that the animals use as a ROT to select plant species with lower handling times. The mechanical measurement of shear force would be a good research technique for assessing differences in the physical toughness of plant fiber (see Chapter 3).

Cell contents represent the most digestible and nutrient-rich fraction of forages (Van Soest 1982) and it is probable that ruminant animals select plant species that have proportionally more cell solubles. The solute concentration of the cell contents did not vary significantly among the 18 species examined in the present study. Consequently, moisture content covaried with the total cell solubles. An animal selecting for succulent food items would, therefore, be increasing its intake of cell contents. However, the observation that ruminants express obvious preferences for some species of dry hay suggests that differences in succulence may be of secondary importance. Other potential indicators of the cell soluble content of forages include simple tastes like sweetness (simple carbohydrates) or sourness (organic acids), and ruminants can distinguish between these simple tastes (Goatcher and Church 1970; Arnold and Hill 1972; Arnold _et al_. 1980). Furthermore, significant correlations have been demonstrated between the selection of plant species and the soluble carbohydrate (Cowlishaw and Alder 1960) or organic acid content of grasses (Jones and Barnes 1967) or solutions (Arnold _et al_. 1980).

The taste of Russian wild rye may account for why this species was an outlier in the relationship between feeding time with either the resistance of fiber to shearing or the cell wall thickness (Chapter 3). In both cases, this grass was selected more often than expected given its high resistance to shearing and thick cell walls. Perhaps some taste attribute, such as sweetness or sourness, contributed to its selection.

Future research on the ROT that animals use when foraging should examine each potential ROT in isolation and assess the accuracy and precision with which the animals are able to apply it. Each prospective ROT could then be analysed in association with other ROT and their interactions and the degree of covariance assessed. An experimental system that could exercise this degree of control would not be difficult to design. Different forages could be washed in neutral detergent solution to remove the cell contents. Cafeteria style penned feeding experiments could be used to determine how differences in fiber resistance to chewing affects diet selection. The mechanical resistance to shearing (Chapter 3) could be used as an index of fiber toughness. In similar experiments, taste components such as sugars, organic acids or secondary plant compounds could be added to a standard plant fiber ration to assess how taste affects the selection of food items.

A more complete understanding of the ROT that ruminant animals apply in order to select among food items will require further research. An understanding of these decision rules will allow the resolution of the more "ultimate" debate concerning the objective (i.e. optimizing, risk aversion or satisficing) of the foraging strategy pursued by ruminant animals.

6. LITERATURE CITED

Alberta Energy and Natural Resources. 1981a. Alberta public lands. Public Lands Division, Alberta Energy and Natural Resources, Edmonton.

Alberta Energy and Natural Resources. 1981b. Forest depletion by energy development in the Green Area of Alberta. Hardy and Associates Ltd., Calgary.

Alberta Energy and Natural Resources. 1984a. The resource handbook operational guidelines for industry. Forest Land Use Branch Tech. Rep. No. 75, Alberta Energy and Natural Resources, Edmonton.

Alberta Energy and Natural Resources. 1984b. Status of the fish and wildlife resource in Alberta. Fish and Wildlife Division, Alberta Energy and Natural Resources, Edmonton.

Alberta Energy Resources Conservation Board. 1984. Alberta's coal industry annual statistics. Energy Resources Conservation Board Ann. Stat. Ser. 85-29, Energy Resources Conservation Board, Calgary.

Arnold, G.W. 1960. Selective grazing by sheep of two forage species at different stages of growth. Aust. J. Agric. Res. 11: 1026-1033.

Arnold, G.W., de Boer, E.S. and Boundy, C.A.P. 1980. The influence of odour and taste on the food preferences and food intake of sheep. Aust. J. Agric. Res. 31: 571-587.

Arnold, G.W. and Dudzinski, M.L. 1978. Ethology of free-ranging domestic animals. Elsevier Scientific Publishing Company, New York.

Arnold, G.W. and Hill, J.L. 1972. Chemical factors affecting selection of food plants by ruminants. In J. Harborne (ed.). Phytochemical ecology. Academic Press, New York.

Arnold, G.W. and Maller, R.A. 1977. Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. Appl. Anim. Ethol. 3: 5-26.

Baile, C.A. and Della-Fera, M.A. 1981. Nature of hunger and satiety control systems in ruminants. J. Dairy Sci. 64: 1140-1152.

Bartmann, R.M. and Carpenter, L.H. 1982. Effects of foraging experience on food selectivity of tame mule deer. J. Wildl. Manage. 46: 813-818.

Bell, R.H.V. 1969. The use of the herb layer by grazing ungulates in the Serengeti. Ph. D. Thesis, University of Manchester, England.

Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. Theoret. Pop. Biol. 14: 105-134.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. Am. Nat. 124: 97-115.

Belovsky, G.E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70: 35-52.

Bromley, M. 1985. Wildlife management implications of petroleum exploration and development in wildland environments. U.S. Department of Agriculture Forest Service Gen. Tech. Rep. INT-191, U.S. Department of Agriculture, Ogden.

Brusnyk, L.M. and Westworth, D.A. 1985. An assessment of post-construction use of a pipeline corridor by ungulates. Nova Corporation, Calgary.

Bunnell, F.L. and Gillingham, M.P. 1985. Foraging behavior: dynamics of dining out. In R.J. Hudson and R.G. White (eds.). Bioenergetics of wild herbivores. CRC Press, Inc., Boca Raton.

Caraco, T.A. 1980. On foraging time allocation in a stochastic environment. Ecology 61: 119-128.

Chai, K., Kennedy, P.M. and Milligan, L.P. 1984. Reduction of particle size during rumination in cattle. Can J. Anim. Sci. 64: 339-340.

Chapman, R.F. and Blaney, W.M. 1979. How animals perceive secondary compounds. In G.A. Rosenthal and D.H. Janzen (eds.). Herbivores and their interaction with secondary plant metabolites. Academic Press, New York.

Coleman, S.W. and Barth, K.M. 1973. Quality of diets selected by grazing animals and its relation to quality of available forage and species composition of pastures. J. Anim. Sci. 36: 754-761.

Collins, W.B. and Urness, P.J. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47: 646-663.

Cooper, S.M. and Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. Oecologia 67: 142-146.

Cowlishaw, S.J. and Alder, F.E. 1960. The grazing preferences of cattle and sheep. J. Agric. Sci. 54: 257-265.

David Walker and Associates. 1983. The Athabasca Ranch elk winter range improvement study IV. David Walker & Associates, Edmonton.

David Walker and Associates. 1984. The Athabasca Ranch elk winter range improvement study V. David Walker & Associates, Edmonton.

Demment, M.W. and Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. 125: 641-672.

Downing, D.J. 1983. Seismic line revegetation and management near Rocky Mountain House, Alberta. M.Sc. Thesis, University of Calgary, Calgary.

Field, C.R. 1976. Palatability factors and nutritive values of the food of buffaloes (Syncerus caffer) in Uganda. E. Afr. Wildl. J. 14: 181-201.

Freeland, W.J. and Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Am. Nat. 108: 269-289.

Gaare, E., Sorensen, A. and White, R.G. 1977. Are rumen samples representative of the diet? Oikos 29: 390-395.

Gates, C.C. 1980. Patterns of behavior and performance of wapiti (Cervus elaphus nelsoni) in the boreal mixed wood forest. Ph.D. Thesis, University of Alberta, Edmonton.

Gesshe, R.H. and Walton, P.D. 1981. Grazing animal preferences for cultivated forages in Canada. J. Range Manage. 34: 42-45.

Goatcher, W.D. and Church, D.C. 1970. Review of some nutritional aspects of the sense of taste. J. Anim. Sci. 31: 973-981.

Gray, R.D. 1987. Faith and foraging: a critique of the "paradigm argument from design". In A.C. Kamil, J.R. Krebs and H.R. Pulliam (eds.). Foraging behavior. Plenum Press, New York.

Green, R.A. 1982. Elk habitat selection and activity patterns in Rocky Mountain National Park, Colorado. M.S. Thesis, Colorado State University, Fort Collins.

Green, J.E. and Salter, R.E. 1987. Methods for reclamation of wildlife habitat in the Canadian prairie provinces. Alberta Recreation, Parks and Wildlife Foundation, Edmonton.

Hamilton, B.A, Hutchinson, K.J., Annis, P.C. and Donnelly, J.B. 1973. Relationships between the diet selected by grazing sheep and the herbage on offer. Aust. J. Agric. Res. 24: 271-277.

Hanley, T.A. 1982. The nutritional basis for food selection by ungulates. J. Range Manage. 35: 146-151.

Hanley, T.A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in coastal montane coniferous forest. J. Appl. Ecol. 21: 423-436.

Hart, R.H., Waggoner, J.W. Jr., Clark, D.H., Kaltenbach, C.C. Hager, J.A. and Marshall, M.B. 1983. Beef cattle performance on crested wheatgrass plus native range vs. native range alone. J. Range Manage. 36: 38-40.

Hawley, A.W.L., Peden, D.G., Reynolds, H.W. and Stricklin, W.R. 1981. Bison and cattle digestion of forages from the Slave River lowlands, Northwest Territories, Canada. J. Range Manage. 34: 126-129.

Heaney, D.P. 1973. Effects of the degree of selective feeding allowed on forage voluntary intake and digestibility assay results using sheep. Can. J. Anim. Sci. 53: 431-438.

Hobbs, N.T., Baker, D.L. and Gill, R.B. 1983. Comparative nutritional ecology of montane ungulates during winter. J. Wildl. Manage. 47: 1-16.

Hoffmann, R.R. 1973. The ruminant stomach. East African Monographs in Biology Vol. 2. East African Literature Bureau, Nairobi.

Hull, J.L., Lofgreen, G.P. and Meyer, J.H. 1960. Continuous versus intermittent observations in behavior studies with grazing cattle. J. Anim. Sci. 19: 1204-1207.

Jacobsen, N.K. and Wiggins, A.D. 1982. Temporal and procedural influences on activity estimated by time-sampling. J. Wildl. Manage. 46: 313-324.

Jones, E.C. and Barnes, R.J. 1967. Non-volatile organic acids of grasses. J. Sci. Food Agric. 18: 321-323.

Kennedy, P.M. 1985. Effect of rumination on reduction of particle size of rumen digesta by cattle. Aust. J. Agric. Res. 36: 819-828.

Kramer, A., Burkhardt, G.J. and Rogers, H.P. 1951. The shear press, a device for measuring food quality. Canner 112: 34.

Krebs, J.R., Stephens, D.A. and Sutherland, W.J. 1983. Perspectives in optimal foraging. In A.H. Brush and G.A. Clark, Jr. (eds.). Perspectives in ornithology. Cambridge University Press, Cambridge.

Krueger, W.C. 1972. Evaluating animal forage preference. J. Range Manage. 25: 471-475.

Kufeld, R.C. 1973. Foods eaten by the Rocky Mountain elk. J. Range Manage. 26: 106-113.

Laredo, M.A. and Minson, D.J. 1973. The voluntary intake, digestibility, and retention time by sheep of leaf and stem fractions of five grasses. Aust. J. Agric. Res. 24: 875-888.

Laredo, M.A. and Minson, D.J. 1975. The effect of pelleting on the voluntary intake and digestibility of leaf and stem fractions of three grasses. Br. J. Nutr. 33: 159-169.

Lesperance, A.L., Bohman, V.R. and Marble, D.W. 1960. Development of techniques for evaluating grazed forage. J. Dairy Sci. 43: 682-689.

Loehle, C. and Rittenhouse, L.R. 1982. An analysis of forage preference indices. J. Range Manage. 35: 316-319.

McInnis, M.L., Vavra, M. and Krueger, W.C. 1983. A comparison of four methods used to determine the diets of large herbivores. J. Range Manage. 36: 302-306.

Michaud, M.W., Diehl, K.C., Hussey, M.A. and Holt, E.C. 1984. Use of the FTC CS-1 (Kramer type) cell and instron machine for testing structural strength in forages. Proc. Forage Grassl. Conf.: 213-217.

Morgantini, L.E. 1986. Elk winter food habits and forage quality along the eastern slopes of Alberta; a review. In C.B. Powter, R.J. Fessenden and D.G. Walker (eds.). Proceedings of the 1985 and 1986 Alberta Reclamation Conference. Canadian Land Reclamation Association Report #87-1, Canadian Land Reclamation Association Alberta Chapter, Edmonton.

Mould, E.D. and Robbins, C.T. 1981. Nitrogen metabolism in elk. J. Wildl. Manage. 45: 323-334.

Mudgal, V.D., Dixon, R.M., Kennedy, P.M. and Milligan, L.P. 1982. Effect of two intake levels on retention times of liquid, particle and microbial markers in the rumen of sheep. J. Anim. Sci. 54: 1051-1055.

Neathery, M.W. 1969. Dry matter disappearance of roughages in nylon bags suspended in the rumen. J. Dairy Sci. 52: 74-78.

Neathery, M.W. 1972. Conventional digestion trials versus nylon bag technique for determining seasonal difference in quality of midland bermuda grass forage. J. Anim. Sci. 34: 1075-1084.

Nelson, J.R. and Leege, T.A. 1982. Nutritional requirements and food habits. In J.W. Thomas and D.E. Toweill (eds.). Elk of North America: ecology and management. Stackpole Books, Harrisburg.

Nietfeld, M.T. 1983. Foraging behavior of wapiti in the boreal mixed-wood forest, Central Alberta. M.Sc. Thesis, University of Alberta, Edmonton.

Nietfeld, M., Wilk, J., Woolnough, K. and Hoskin, B. 1984. Wildlife habitat requirement summaries for selected wildlife species in Alberta. Fish and Wildlife Division, Alberta Energy and Natural Resources, Edmonton.

Oh, H.K., Sakai, T., Jones, M.B. and Longhurst, W.M. 1967. Effects of various essential oils isolated from Douglas fir needles upon sheep and deer rumen microbial activity. Appl. Microbiol. 15: 777-784.

Owen-Smith, N. and Cooper, S.M. 1987. Assessing food preferences of ungulates by acceptability indices. J. Wildl. Manage. 51: 372-378.

Owen-Smith N. and Novellie P. 1982. What should a clever ungulate eat? Am. Nat. 119: 151-178.

Pauls, R.W., Hudson, R.J. and Sylven, S. 1981. Energy expenditure of free-ranging wapiti. University of Alberta Feeders' Day Report 60: 87-91.

Personius, T.L., Wambolt, C.L., Stephens, J.R. and Kelsey, R.G. 1987. Crude terpenoid influence on mule deer preference for sagebrush. J. Range Manage. 40: 84-88.

Petrides, G.A. 1975. Principal foods versus preferred foods and their relations to stocking rate and range condition. Biol. Conserv. 7: 161-169.

Poppi, D.P., Minson, D.J. and Ternouth, J.H. 1981a. Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. Aust. J. Agric. Res. 32: 99-108.

Poppi, D.P., Minson, D.J. and Ternouth, J.H. 1981b. Studies of cattle and sheep eating leaf and stem fractions of grasses. III. The retention time in the rumen of large feed particles. Aust. J. Agric. Res. 32: 123-137.

Prism Environmental Consulting Services. 1984. Habitat enhancement and the petroleum industry. Fish and Wildlife Division, Alberta Energy and Natural Resources, Edmonton.

Pyke, G.H., Pulliam, H.R. and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Radner, R. 1975. Satisficing. J. Math. Econ. 2: 253-262.

Radwan, M.A. and Crouch, G.L. 1974. Plant characteristics related to feeding preference by black-tailed deer. J. Wildl. Manage. 38: 32-41.

Revel, R.D., Dougherty, T.D., and Downing, D.J. 1984. Forest growth and revegetation along seismic lines. University of Calgary Press, Calgary.

Rice, R.W. 1970. Stomach content analysis: a comparison of rumen versus esophageal techniques. In Range and wildlife habitat evaluation - a research symposium. U.S. Department of Agriculture Misc. Publ. No. 1147, U.S. Department of Agriculture, Washington.

Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L. Schwartz, C.C. and Mautz, W.W. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68: 98-107.

Scales, G.H., Streeter, C.L., Denham, A.H. and Ward, G.M. 1974. A comparison of indirect methods of predicting in vivo digestibility of grazed forage. J. Anim. Sci. 38: 192-199.

Schwartz, C.C. and Ellis, J.E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18: 343-353.

Schwartz, C.C. and Nagy, J.G. 1976. Pronghorn diets relative to forage availability in northeastern Colorado. J. Wildl. Manage. 40: 469-478.

Schwartz, C.C., Nagy, J.G. and Regelin, W.L. 1980b. Juniper oil yield, terpenoid concentration, and antimicrobial effects on deer. J. Wildl. Manage. 44: 107-113.

Schwartz, C.C., Regelin, W.L. and Nagy, J.G. 1980a. Deer preference for juniper forage and volatile oil treated foods. J. Wildl. Manage. 44: 114-120.

Shoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.

Shoener, T.W. 1987. A brief history of optimal foraging ecology. In A.C. Kamil, J.R. Krebs and H.R. Pulliam (eds.). Foraging behavior. Plenum Press, New York.

Sidahmed, A.E., Mooris, J.G., Weir, W.C. and Torell, D.T. 1977. Effect of the length of fasting on intake, in vitro digestibility and chemical composition of forage samples collected by esophageally fistulated sheep. J. Anim. Sci. 46: 885-890.

Simpson, A.M., Webster, A.J.F., Smith, J.S. and Simpson, C.A. 1978. The efficiency of utilization of dietary energy for growth in sheep (Ovis ovis) and red deer (Cervus elaphus). Comp. Biochem. Physiol. 59: 95-99.

Smoliak, S. and Hanna, M.R. 1975. Productivity of alfalfa, sainfoin and cicer milkvetch on subirrigated land when grazed by sheep. Can. J. Plant Sci. 55: 415-420.

Spalinger, D.E., Robbins, C.T. and Hanley, T.A. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. Can. J. Zool. 64: 312-321.

SPSS. 1986. Statistical package for the social sciences X. SPSS Inc., Chicago.

Steel, R.G.D. and Torrie, J.H. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York.

Strong, W.L. and Leggat, K.R. 1981. Ecoregions of Alberta. Resource Evaluation and Planning Division, Alberta Energy and Natural Resources, Edmonton.

STSC. 1986. Statgraphics. STSC Inc., Rockville.

Stubbs, C.W.B. and Markham, B.J. 1979. Wildlife mitigative measures for oil and gas activity in Alberta. U.S. Department of Agriculture Forest Service Gen. Tech. Rep. RM-65, U.S. Department of Agriculture, Washington.

Taerum, T. 1987. Efficient algorithm for analysis of variance. Computing Services Gen. Publ., University of Alberta, Edmonton.

Theron, E.P. and Booysen, P. De V. 1966. Palatability in grasses. Proc. Grassl. Soc. S. Afr. 1: 111-120.

Thorton, R.F. and Minson, D.J. 1973. The relationship between apparent retention time in the rumen, voluntary intake, and apparent digestibility of legume and grass diets in sheep. Aust. J. Agric. Res. 24: 889-898.

Troelson, J.E. and Bigsby, F.W. 1964. Artificial mastication - a new approach for predicting voluntary forage consumption by ruminants. J. Anim. Sci. 23: 1139-1142.

Trudell-Moore, J. and White, R.G. 1983. Physical breakdown of food during eating and rumination in reindeer. Acta Zool. Fenn. 175: 47-49.

Van Soest, P.J. 1967. Development of a comprehensive system of feed analysis and its application to forages. J. Anim. Sci. 26: 119-128.

Van Soest, P.J. 1982. Nutritional ecology of the ruminant. O & B Books, Corvallis.

Van Soest, P.J., Mertens, D.R. and Deinum, B. 1978. Preharvest factors influencing quality of conserved forage. J. Anim. Sci. 47: 712-720.

Vangilder, L.D., Torgerson, O. and Porath, W.R. 1982. Factors influencing diet selection by white-tailed deer. J. Wildl. Manage. 46: 711-718.

Veteto, G., Davis, C.E., Hart, R. and Robinson, R.M. 1972. An esophageal cannula for white-tailed deer. J. Wildl. Manage. 36: 906-912.

Voisey, P.W. 1971. The Ottawa texture measuring system. Can. Inst. Tech. J. 4: 91-103.

Watson, L.E., Parker, R.W. and Polster, D.F. 1980. Manual of species suitability for reclamation in Alberta. Alberta Land Conservation and Reclamation Council Report #RRTAC 80-5, Alberta Land Conservation and Reclamation Council, Edmonton.

Welch, J.G. 1982. Rumination, particle size and passage from the rumen. J. Anim. Sci. 54: 885-894.

Westoby, M. 1978. What are the biological bases of varied diets? Am. Nat. 112: 627-631.

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40: 377-384.

Wilman, D. and Asiedu, F.H.K. 1983. Growth, nutritive value and selection by sheep of sainfoin, red clover, lucerne and hybrid ryegrass. J. Agric. Sci. 100: 115-126.

Winter, S.G. 1971. Satisficing, selection, and the innovating remnant. Quart. J. Econ. 85: 237-261.