National Library of Canada
Bibliothèque nationale du Canada

Canadian Theses Service
Services des thèses canadiennes

Ottawa, Canada
K1A 0N4

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ MICROFILMÉE TELLE QUE NOUS L'AVONS REÇUE

NL 339 (r. 86/01)

Canada

0-315-26895-6

National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Division

Division des thèses canadiennes

Ottawa, Canada
K1A 0N4

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

- Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

Marie Theresa Nietfeld

Date of Birth — Date de naissance Nov 30, 1957	Country of Birth — Lieu de naissance Canada

Permanent Address — Résidence fixe

Dept. Animal Science
University of Alberta
Edmonton, Alberta

Title of Thesis — Titre de la thèse

Foraging Behavior of Wapiti in the Boreal Mixed Wood Forest, Central Alberta

University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

Masters of Science

Year this degree conferred — Année d'obtention de ce grade 1980 - 1983	Name of Supervisor — Nom du directeur de thèse Dr. R. J. Hudson

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date October 17 / 83	Signature Marie Nietfeld

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

Foraging Behavior of Wapiti in the Boreal Mixed-Wood Forest, Central Alberta

by

© , **Marie T. Nietfeld**

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF **Master of Science**
IN
Wildlife Productivity and Management

Department of Animal Science

EDMONTON, ALBERTA
Fall, 1983

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR	Marie T. Nietfeld
TITLE OF THESIS	Foraging Behavior of Wapiti in the Boreal Mixed-Wood Forest, Central Alberta

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED Fall, 1983

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Marie Nietfeld

PERMANENT ADDRESS:

Department of Animal Science
University of Alberta
Edmonton, Alberta T6G 2P5

DATED October 13 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Foraging Behavior of Wapiti in the Boreal Mixed-Wood Forest, Central Alberta submitted by Marie T. Nietfeld in partial fulfilment of the requirements for the degree of Master of Science in Wildlife Productivity and Management.

....
Supervisor

....

Jan O. Murie
....

....

Date ...October 13, 1983......

Abstract

Food habits of wapiti (*Cervus elaphus nelsoni*) in the boreal mixed-wood forest of central Alberta were examined in five habitat types: poplar forest, willow, upland grassland, lowland grassland, and sedge meadow. Diets were sampled using the bite count method from October (1980) to August(1981). Few differences in the use of forage classes (grass, browse, forbs) were found among different sexes and ages of wapiti. Significant differences in the use of forage classes occurred among seasons and among habitats ($P<.05$). Grasses dominated the grassland and sedge meadow diets for much of the year, though forbs were important components in the summer. Forbs remained important in the winter diet in the lowland. Browse generally dominated diets selected in poplar forests. Use of grass in this habitat was greatest in spring and fall, and forbs were important in the spring and summer diets. In the willow habitat, browse was the major component of the diet during winter and summer, while grasses dominated the diet in spring and fall.

Forage quality, based on crude protein, was significantly greater in spring and summer than in fall and winter ($P<.05$). Forbs generally contained more protein than other forage classes, except in summer when no differences were evident. Digestibility of winter forage samples ranged from 35-45%, while summer samples ranged from 60-75%. Forbs tended to have the highest overall digestibility. Dietary crude protein followed seasonal trends similar to that of forages. It was significantly greater in the spring and summer than fall and winter. Dietary crude protein ranged from 4.5% in the sedge meadows during winter to 25.3% in the lowland grassland in summer. Dietary crude protein was considered to be sufficient to meet requirements of wapiti throughout the year, except in the sedge meadows in winter.

Foraging rates (bite rate, consumption rate, rate of movement) varied among sex and age classes, habitats, and seasons. Foraging rates were generally greatest in summer and lowest in winter. Within a season, rates tended to be the lowest where selection was the greatest, in areas of high species and structural diversity. Adult females had higher consumption rates than other wapiti during the summer, while adult males exhibited slower rates of movement during this period.

Acknowledgements

This thesis is dedicated to those people who have instilled in me a strong rewarding interest in research, and to those who have encouraged my progression in this study.

I thank Lynn Jebson and Doreen Bayne for their enthusiastic assistance in the field and their friendship during the summer phases of the study, and hope they have gained from this experience. Greatfully I acknowledge all who helped out during the fall-winter phases, especially those who volunteered their time, often during inclement weather. To Gavin Godby and Ray Weingardt, I express sincerest thanks for their endless assistance and advice on data input and analyses. Similarly, I appreciate assistance from laboratory personnel, noteably Terry Fenton and Orest Pulnyak.

I am grateful to my committee members, Dr. J. Murie, Dr. R. Christopherson, Mr. W. Wishart, and my supervisor, Dr. R. J. Hudson, for their helpful comments on this manuscript. I also thank my supervisor for his advice and for his patience during the write-up. Magi Nams and Nike Goodson also provided useful comments on the manuscript.

The moral support given by my family and friends was much needed and much appreciated. I extend many thanks to them.

This study was funded by the Alberta Fish and Wildlife Division, and by the Natural Sciences and Engineering

Research Council of Canada (operating grant to Dr. R. J. Hudson and a post-graduate scholarship to the author). Their support, as well as the support of the Department of Animal Science, is gratefully acknowledged.

To the wapiti!: who accepted me as one of them and freely gave their companionship, may lush grass be beneath your feet, always.

Table of Contents

Chapter Page

List of Tables

List of Figures

Introduction

Large herbivores spend much of their time foraging to obtain adequate food to meet nutritional requirements. Diet selection, a process which governs the amounts and varieties of food consumed (Ellis *et al*. 1976), is a means by which herbivores can attenuate fluctuations in forage quality, and avoid chemical defenses of plants (see Freeland and Janzen 1974). Diet selection is influenced by quality and quantity of available foods, which are influenced by the location and time of feeding (Hobbs 1979). Animal characteristics (physiological requirements, anatomical and morphological features, and their behavior) and environmental conditions (eg. snow conditions) also influence diet choice.

The consequences of diet selection occur at the individual level (animal condition), and at the population level (productivity). Quality of forages in the diet can affect growth rate, body size, age of sexual maturity, reproductive potential, and survival (Klein 1970, Sinclair 1974). Consequences of diet selection also occur at the ecosystem level, influencing energy and nutrient flow from herbage to herbivores, the partitioning of food resources between species, and habitat condition (Klein 1970, Sinclair 1974, Ellis *et al*. 1976, McNaughton 1979).

The boreal mixed-wood forest regions (Rowe 1972) contain forage resources particularly suited to supporting populations of native ungulates (Telfer and Scotter 1975).

Much of this forest is marginal agricultural land and its productivity as "natural" habitat for native ungulates has received increasing interest. The profitability of game ranching in these areas was initially assessed by Telfer and Scotter (1975), and intensively managed systems (game farming) are gaining interest in Western Canada. Determination of optimal stocking rates of ungulates on these ranges is important to the economic viability as well as sound ecological management of this resource base. Estimates of forage and diet quality, as well as forage quantity, are important in assessing productivity and predicting range carrying capacity for native herbivores (Wallmo *et al*. 1977, Robbins 1977). Diet selection throughout the year is important to the welfare of the animal. Summer forages provide fat stores, while winter forages provide a portion of the overwinter maintenance requirements (Hobbs 1979). Thus, diet selection is important in determining optimal stocking on both summer and winter ranges.

As nutritional requirements vary with sex and age as well as with season (Nelson and Leege 1982), diet selection by these classes may also vary (see Geist 1982). Smaller animals would be expected to feed more selectively than larger ones. Larger wapiti would be expected to forage on more fibrous plants. Wapiti under increased energy demands would be expected to forage differently than those without added requirements. To avoid competition between adult males and females, males may be expected to use different parts of the range. Thus, range suitability may change in relation to population structure.

At the Ministik Wildlife Research Station, a mixed-species (wapiti, moose, bison) grazing system in the boreal mixed-wood forest of Alberta has been established for a number of years. Studies have attempted to define animal requirements and patterns of resource use on a seasonal basis. The present study was conducted at this research station to investigate the food habits of wapiti in relation to available forage resources. An investigation of resource-use by wapiti had been conducted by Gates (1980).

Objectives

Determination of the capacity for wapiti production in specific areas requires measurements of the available food resources, their patterns of use, and an estimation of their effect on the nutritional status of the animal. Since nutritional requirements vary with season, age and sex (Nelson and Leege 1982), these factors also must be considered in area evaluations.

The overall objective of this study was to examine and compare seasonal food habits and foraging behavior of adult and young wapiti of both sexes in five main habitats identified by Gates (1980) as important to wapiti in the mixed-wood boreal forest region: willow, poplar forest, upland and lowland grasslands, and sedge meadows.

Specific objectives which provided a structure for the study were:

1) to describe plant species composition and estimate plant biomass in the five habitat types.

2) to determine the quality of the most prominent forage items in the wapiti diet throughout the year.

3) to determine and compare the botanical composition of the diet of male and female, adult and young wapiti seasonally in the five habitat types.

4) to examine dietary preferences of wapiti in the five habitat types.

5) to estimate and compare quality of the wapiti diets in the five habitats during different seasons of the year.

6) to examine and compare foraging efficiency of the four sex and age classes of wapiti seasonally in the five habitat types.

Study Area

The study was conducted at the Ministik Wildlife Research Station, 50 km southeast of Edmonton, Alberta (NW Sec 25 TP 50 R 21). The study area was approximately 60 ha in size, and was enclosed by 2-meter high game fence.

Geology and Topography

The Ministik area is underlain by the Edmonton Formation, an Upper Cretaceous bedrock of shales, sandstones, clays and coal interbedding (Bayrock 1972). The Cooking Lake Moraine, composed of glacial debris formed during the retreat of the Wisconsin ice sheet, overlies the Edmonton Formation. The area exhibits gently rolling to rolling hills and shallow depressions, typical of hummocky dead-ice moraine. Numerous sloughs are characteristic of the area.

Soils

Soils of the Ministik area are mainly Luvisols, and lie within the grey wooded soil zone. The Cooking Lake loam, which predominates in the region (Bowser *et al*. 1962), is a fairly well-drained orthic grey wooded soil developed on glacial till of the Edmonton formation, underlying treed areas. The Uncas loam, an orthic dark grey wooded soil also developed from glacial till, is found on less densely treed areas. This soil is fairly well-to well-drained. Sandy loams are also present on the area, though in low proportions.

Climate

The Ministik region exhibits a cool, continental climate characterized by short warm summers and long cold winters (Wonders 1969). Temperatures range from about -40°C to 32°C. The frost-free period averages 100 days, although considerable yearly variation occurs. The average annual precipitation is 450 mm, and about 125 cm of snow falls annually. The average wind velocity is less than 26 kph. Appendix 1 describes weather conditions during the study periods (1980-1981) as recorded at the Edmonton International Airport.

Vegetation

Rowe (1972) classified the Ministik area as being the southern fringe of the boreal mixed wood forest zone. The site of the study area was homesteaded early in the twentieth century, which created greater interspersion of habitat types than found on undisturbed sites. The interspersion of grasslands and forests, and the scarcity of conifers gives the area some characteristics of aspen parkland.

Gates (1980) classified the vegetation cover of Ministik Research Station into five types: willow, poplar forest, upland grassland, lowland grassland, and sedge meadows (Figure 1).

Poplar forest was the dominant cover type, occupying 47% of the area. Trembling aspen (*Populus tremuloides*) dominated drier sites, while balsam poplar (*P. balsamifera*) dominated the more mesic sites. A fire in this area in the 1890's resulted in white spruce (*Picea glauca*), the dominant climax species of this forest zone, being poorly represented on the study area (Gates 1980). The most common shrubs in the understory of the poplar forest were beaked hazelnut (*Corylus cornuta*), rose (*Rosa acicularis* and *R. woodsii*), raspberry (*Rubus melanolasias*), and saskatoon (*Amelanchier alnifolia*). Numerous seasonally abundant forbs were present as well as brome grass (*Bromus pumpellianus*) and bluegrass (*Poa* spp.).

The willow habitat occupied about 12% of the study area, forming a band around the sedge meadows. Willow (*Salix* spp.) was the dominant cover species, although balsam poplar was present in some areas. Sedges (mainly *Carex antheroides*) and reedgrass (*Calamagrostis canadensis*) were the main understory species.

Sedge meadows occurred on 11.5% of the area, with *Carex antheroides* as the principal species. Cattails (*Typha latifolia*) occurred along the open water edge of the sedge meadows, and reedgrasses occurred near the shore edge of the

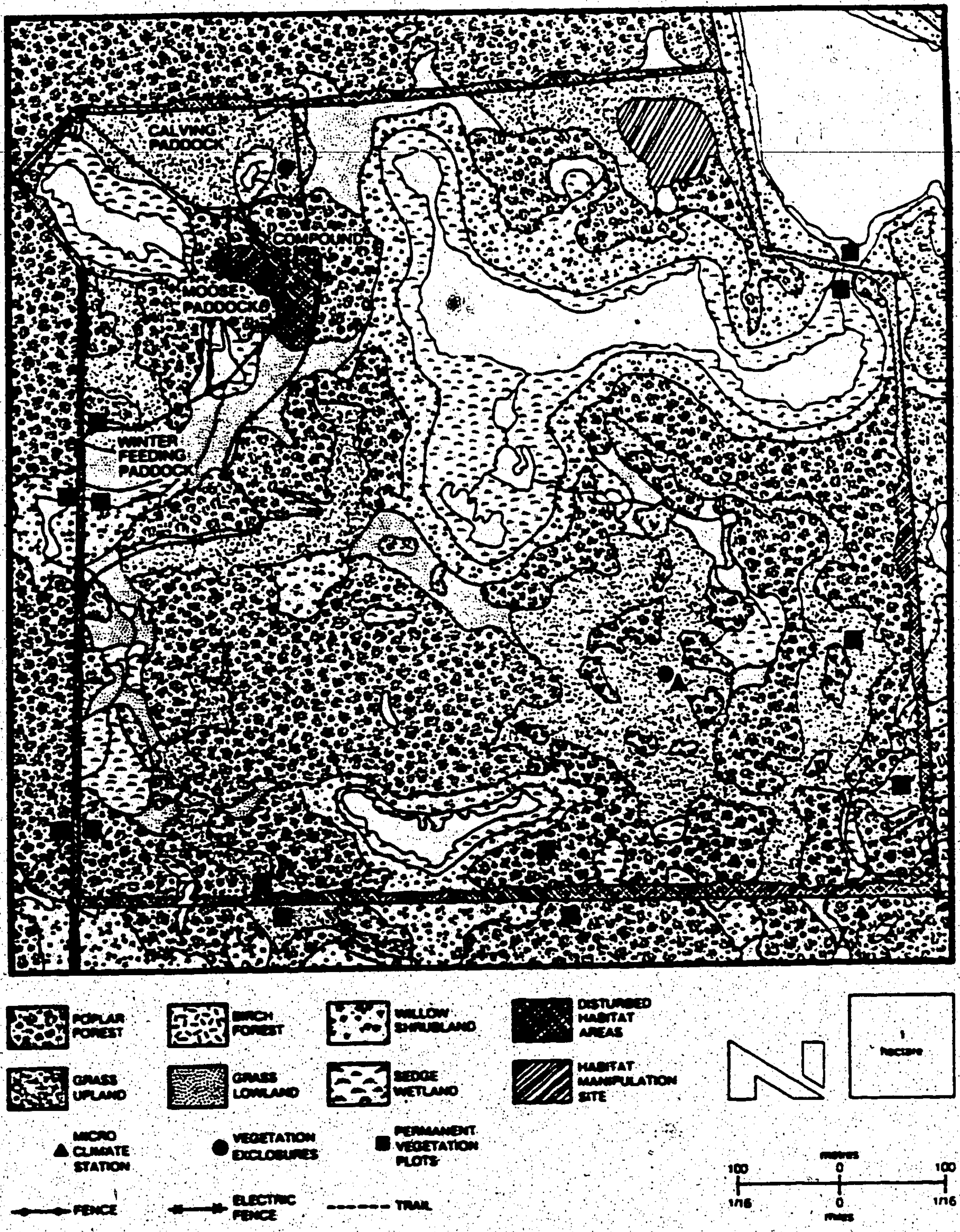

Figure II.1 Vegetation cover types at Ministik Wildlife Research Station; willow, poplar forest, upland grassland, lowland grassland, and sedge meadow.

meadows. Forbs occurred mainly at the shore edge.

Upland grasslands occurred in cleared upland forest areas, and occupied 19.1% of the study area. These areas were seeded in the early 1900's, and native species have not yet replaced those introduced. Bluegrass and brome were the dominant grass species. Forbs included clover (*Trifolium* spp.), dandelion (*Taraxacum officinale*), and strawberry (*Fragaria virginiana var. glauca*). Shrubs, snowberry (*Symphoricarpos* spp.) and rose, were frequent on only a few sites. Poplar regeneration was infrequent on the upland.

Lowland grasslands occupied 4.4% of the area. The major lowland grassland site had also been seeded. Bluegrass, brome, wheatgrass (*Agropyron cristatum*), and reedgrass were the major species present. Thistle (*Cirsium arvense*) was the predominant forb.

History

The Ministik Wildlife Research Station was established by the Alberta Wildlife Production Research Committee in 1976. A quarter section of the reserve was fenced in 1977, and hand-reared wapiti, bison, moose, and deer were introduced into the compound from foundation stock at the University of Alberta. Wild moose and deer are capable of entering the compound. The stocking rates of these species for the winters of 1977-1981 are given in Table II.1.

Table II.1: Winter stocking rates (ungulates/60 ha) Ministik Research Station for 1977-78 to 1980-81.

	Cervus elaphus	Alces alces	Bison bison	Odocoileus spp.
1977-78	9	2(+)	0	?
1978-79	12	3(+)	3	2(+)
1979-80	9	2(+)	5	?
1980-81	17	4	5	5(+)

Study Animals

During this study, 12 wapiti - three adult males, three adult females, three male calves, and three female calves - were observed. The adult animals had been hand-reared and were free-ranging residents of the Ministik study area for four to five years prior to the study. Two of the female calves were received from Elk Island National Park in June of 1980 and were hand-reared. The other calves were born in 1980 to resident females placed in a calving pen. These calves were maternally reared and habituated to human presence before being allowed to free-range with the herd. Habituation had a taming effect that facilitated close observation of the calves. One adult female was pregnant at the start of the study, and calved in May 1981.

Animals were supplemented with small amounts of alfalfa pellets from January to April 1981. Schwartz and Nagy (1973) and Regelin *et al.* (1976) found no effect of artificial feeding on the diets selected by tame animals.

The use of tame animals for food habit studies has several advantages over other methods. Tame animals facilitate accurate description of the plant species and plant parts consumed. Representative samples of forage which reflect the chemical composition of the diet can be collected (Hobbs 1979). Fecal analysis (Sparks and Malechek 1968) and rumen samples (Rice *et al.* 1971) underestimate the quantity of species of higher digestibilities (McInnis *et al.* 1977, Vavra *et al.* 1978). The feeding-site method

(McCulloch 1955) and foraging minutes method (Buechner 1950) overestimate importance of shrubby species and underestimate forbs and grasses in the diet (Wallmo *et al.* 1973). The use of tame animals also allows the investigation of diet selection within specific habitats, which can not be determined using fecal samples (Collins 1979).

METHODS

Vegetation Composition and Biomass

Herbaceous Vegetation

Herbaceous vegetation was sampled each month in all five habitats during snow-free periods, October and November 1980, April through August 1981. Thirty 25cm x 50cm plots were randomly sampled in each habitat, except in the sedge meadow in November, where 20 plots were used. Plant species, genera, or plant group (grasses) in each plot were recorded, as were their height, a visual estimate of their percentage cover, and their phenological stage. Ten plots within each habitat were clipped at ground surface, then the plant species or groups were separated, dried at 65°C for 2 to 4 days, and weighed to obtain an estimate of biomass. When components of litter (eg. fallen leaves) were consumed by the wapiti, these were also collected from the plots, separated, dried, and weighed. During the summer months, the number of plots in the poplar forest was increased to 60 to account for the great plant diversity there. Of these plots, 20 were clipped for biomass estimation.

One-way analyses of variance (ANOVA) were used to compare herbaceous vegetation biomass (dry weight) among habitats during each month. Differences among means were evaluated using the Least Significant Difference (LSD) test (Sokal and Rohlf 1969). Differences at P=.05 were considered statistically significant.

Shrubs

In the spring of 1980, a browse inventory was conducted by technical personnel at the station. Previously, a reconnaisance survey was undertaken to determine the location of representative stands within the forest and the willow cover types. Eleven stands were selected for sampling in the poplar forest and 2 stands were selected in the willow habitat. In each forest stand, 4-2mx2m plots, 10m apart, were established. In the willow stands, 7 plots were established. In each plot, the average heights, the number of stems, and the number of browsed and unbrowsed twigs of each species were recorded. These data provided information on species frequency of occurrence and the yield of twigs (twigs/hectare) of the predominant shrubs.

Foraging Behavior

The bite count method (Neff 1974) was used to estimate diet composition. Each distinct removal of a plant, plant part, or a number of plants was considered to be a bite. Diets were sampled during the 7th to 23rd day of each month from October 1980 through August 1981. Based on plant phenology and snow cover, the months were grouped into seasons: fall (October and November), winter (December, January, February, and March), spring (April and May), and summer (June, July, and August). Data were not collected in

September due to the rut and breeding period. Adult males were not included in the October sample as they were still in rut. The wapiti were allowed to free-range over the study area at all times, therefore no pre-trial adaptation periods were necessary. Since all animals had been exposed to natural vegetation when young, or for a number of years after being reared in pens, the forage selection exhibited by the wapiti should be representative for that area.

The herd was followed during morning and evening feeding bouts. Using a tape recorder, an observer recorded the foraging sequence of a focal animal. Choice of the focal animal was governed by its habitat usage and the amount of data previously recorded from that animal in that habitat. The duration of any one recording session ranged from 3 to 45 minutes. A new foraging sequence was initiated if the focal animal changed habitats. An attempt was made to obtain similar total recording time for each animal in each habitat. If sufficient data could not be collected from a particular wapiti, additional data were recorded from other animals of the same sex and age class. Due to seasonal habitat preferences, it was impossible to obtain equal recording times from all habitats in any one season.

The recorded foraging sequence of an animal consisted of its movement (steps), feeding behavior (the finding, cropping, and chewing of food items), and non-foraging behavior (eg. grooming, social interactions). Information recorded on the forage items included species or group, (ie.

grasses), and the plant part ingested. During each recording session, records were kept of location, weather conditions (ambient temperature, precipitation, cloud cover, wind), as well as general observations on the foraging behavior and habitat usage of the wapiti. In winter, records were kept of snow conditions in the different habitats. Snow depth was measured with a meter stick in each habitat during the start, middle, and end of each recording period.

Diet Composition

The contribution of each forage item to the diet was determined as a percentage of the total number of bites. Forage classes considered were graminoids, browse, forbs, lichens, and fungi. Graminoids included all grasses, reedgrass, sedges, and cattails. Browse refers to any part of shrubs or trees, including fallen leaves, that was consumed. A diversity index (Harris 1972): $N=\sum pi \log pi$ where N=index value and pi=the proportion of each species in the diet, was calculated for all the diets. This index gives an indication of the number of species included in the diet, as well as the relative proportion of each species. High indices indicate that a variety of species were included in the diet, with no one species dominating.

ANOVAs were used to test for differences in the use of grasses, forbs, and browse, as well as for plant species or groups, among sex and age classes of wapiti within each habitat each season. Wapiti were considered as a group when testing for habitat differences within a season, and seasonal differences within a habitat. These same analyses were used to test for differences in the diversity index among sex and age classes, seasons, and habitats. The LSD test was used to evaluate significant differences at the P=.05 level.

Foraging Selectivity

The degree of foraging selectivity exhibited by the wapiti was examined by determining the ratio of the percentage diet biomass to the percentage habitat biomass of the most abundant herbaceous forages in each habitat during snow-free periods.

Selection for shrub species was examined by determining the ratio of the percentage frequency of each shrub in the diet to the percentage frequency of the occurrence of the shrub in the habitat.

These ratios have been used by Chamrad and Box (1968) and van Dyne and Heady (1965), respectively, as preference indices.

Forage Quality

Fifty grams or more of the major forage items consumed by the wapiti were collected during each month's recording session. Samples were hand-picked as "bites", duplicating as closely as possible the parts and amounts of forage items that wapiti were observed to ingest. These forage samples were collected from a number of plants at various locations on the study area. The number of simulated "bites" of each item was recorded. Samples were dried at 60-65°C for 2-4 days, and the bite size (grams per bite) of the forages was calculated on a dry weight basis. Dried samples were stored in bags until final collections were made in August. Samples were then ground through a 1-mm screen of a Model-4 Wiley mill and stored at 5°C until analyzed.

Fresh feces were collected from all animals at the mid-point of the recording sessions for the months of October, November, December, May, June, July, and August. Feces were not collected during late winter and early spring due to supplemental feeding of wapiti with alfalfa pellets. Fecal samples were dried at 60°C for 2-4 days, ground, and stored in vials until analyzed for crude protein.

Crude protein content of triplicate forage samples was calculated from total nitrogen determined by the macro-Kjeldahl (Nx6.25) method (A.O.A.C. 1965).

In vitro digestibilities of major forage items in the diet were determined by the Tilley and Terry (1965) two-stage method, with some modifications suggested by Minson and McLeod (1972). Samples (0.5 gm) were inoculated with a mixture of rumen fluid and McDougall's buffer solution and then incubated at 39-40°C for 48 hours. Rumen inoculum was collected from two fistulated wapiti steers fed on a diet of browse and alfalfa hay. Samples of rumen contents were squeezed through layers of cheesecloth into separate containers maintained at 39°C. These samples were strained through a cheesecloth a second time before equal volumes of sample from each animal were mixed and added to the buffer solution. Capillary tubes fitted into test tube stoppers allowed for the release of fermentation gases. Samples were analyzed in duplicate, running blanks (of buffer solution and inoculum) and a standard sample of known *in vivo* digestibility in each trial. Following the fermentation period, residues of the sample were digested with acid pepsin for 48 hours. The indigestible residue was then washed into tared containers, dried at 100°C, and reweighed. The percentage dry matter (D.M.) digestibility was calculated as:

$$\frac{100(D.M.\ sample - (D.M.\ residue - D.M.\ blank))}{D.M.\ sample}$$

Crude protein content of individual fecal samples was also determined by the macro-Kjeldahl method (Nx6.25), and was used as an additional indication of forage and diet quality (see Gates 1980). Monthly composite samples of feces from all individuals were sent to the Soil and Feed Testing Laboratory, Edmonton for the determination of acid detergent fiber, lignin, cellulose, and ash content.

Seasonal variation in forage class crude protein and *in vitro* digestibility, and fecal crude protein content were analyzed by an ANOVA. The crude protein content and *in vitro* digestibility values of the forage classes within each season were also compared with an ANOVA. Significant differences among means were evaluated with the LSD test (P=0.05).

Diet Quality

Diet quality, based on crude protein content of forages, was calculated as the sum of forage crude protein concentrations multiplied by weighted diet percentages. Weighted percentages were calculated by multiplying bite frequency by the estimated bite weight, then normalizing these values to 100 (Schwartz *et al*. 1977, Hobbs 1979). Forages comprising 1% or more of the average wapiti diet for one month were included in the diet quality values. In instances where crude protein values were missing, values were interpolated, using the average value of the preceding and following month. In a few cases where a plant species (contributing little to the diet) had not been collected, the average monthly values for that forage class was used.

Diet quality differences among habitats for each season, and seasonal differences for each habitat were analyzed by ANOVA. the LSD test at P=0.05 was used to evaluate significant differences.

Foraging Efficiency

For each foraging sequence recorded on an animal, the average consumption rate (bites per minute), rate of movement (steps per minute), the number of feeding stations per minute (that area that an wapiti forages on while not moving its forefeet), the overall time spent foraging (seconds per minute), and the time spent in other activities (seconds per minute) were calculated. Variations in these measurements among the four sex and age classes of wapiti within each habitat for each season were analyzed by one-way analyses of variance. The wapiti were considered as one group when comparing the foraging sequence rates among habitats each season, and among seasons for each habitat with one-way ANOVA. The LSD test (P=0.05) was used to evaluate significant differences.

Consumption rates (grams/minute) of wapiti on the different habitat segments over the year were calculated by multiplying the average bite size (grams/bite) for an individual in a habitat by its average bite rate (bites/minute) in that habitat. Variation in consumption rates among habitats and seasons was analyzed by ANOVA.

RESULTS

Snow Conditions

The first permanent snowfall of 1980 occurred in early December (Table IV.1). Snow depth varied widely during the winter, and was negatively associated with warming trends and positively associated with cooling trends. Differences in snow depth among habitats were small. Snow depths in all habitats remained less than 30 cm, and at no time hindered movement of wapiti or prevented foraging behavior. Crusting conditions of the snow were related to aging, wind conditions, and trampling by animals. Heavy use of some regions caused a layer of ice to form near the ground surface, and prevented the extraction of forage by wapiti. As spring approached snow melted first on south facing slopes and areas of steep topography. Snow remained longest in forested areas. By April, the snow cover had completely disappeared.

Vegetation Composition and Biomass

Herbaceous Vegetation

Biomass of herbaceous vegetation is presented by forage class (Figures IV.1-IV.5). Species specific data are given in Appendix 3-7. Total herbage biomass was significantly greater ($P<.05$) in the sedge meadow than other habitats for all months. This biomass ranged from 1,949 Kg/ha in April to

Table IV.1: Snow depths in the major habitats at Ministik Wildlife Research Station, 1980-1981.

		Willow (cm)	Poplar Forest (cm)	Upland Grassland (cm)	Lowland Grassland (cm)	Sedge Meadow (cm)
December	9	23.0	22.0	20.0	24.0	23.0
	15	19.5	19.0	18.0	19.0	19.0
	21	17.5	16.5	15.0	17.0	16.5
January	7	19.0	18.0	14.0	20.5	18.0
	14	19.2	19.0	18.0	21.0	19.0
	21	12.0	9.7	9.3	9.2	10.4
February	7	16.0	16.0	15.0	18.0	15.0
	15	11.9	10.2	11.4	10.1	9.3
	21	9.8	7.7	8.1	7.7	8.3
March	7	14.0	14.0	14.0	16.0	13.0
	14	10.5	8.8	7.9	12.1	6.7
	21	11.4	10.1	11.5	14.7	9.3

7,045 Kg/ha in August (Figure IV.1). *Carex* spp. dominated the sedge meadows, with forbs, mainly asters (*Aster* spp.), water smartweed (*Polygonum amphibium*), and mint (*Mentha arvensis*), forming only a minor portion of the summer biomass. The willow habitat, in which *Carex* was also the predominant herbaceous plant, had the second highest biomass during the year, reaching 5,562 Kg/ha in August (Figure IV.2). Forb diversity was high in this habitat (Appendix 4), although forb biomass was relatively low in relation to graminoids. However, when forb biomass was compared among habitats, the willow habitat was second only to the lowland grassland.

The upland grassland, as well as some portions of the lowland areas, were heavily grazed during late spring, summer, and fall. As a result, the vegetation was maintained in a state of regrowth for much of the year. This resulted in a much lower biomass there than in the *Carex* dominated areas; (*Carex* was seldom consumed during the late spring and summer). Herbaceous biomass ranged from 437 to 4,946 Kg/ha in the lowland (Figure IV.4), and from 365 to 1,739 Kg/ha in the upland grasslands (Figure IV.3). Forbs accounted for large proportions of the biomass in the grassland habitats during summer. Abundant forbs on the uplands were clover, dandelion, strawberry, aster, yarrow (*Achillea millefolium*), and thistle. Thistle was the major forb in the lowlands. Since it was avoided by the wapiti and bison during much of the growing season, it proliferated in these areas. Nettle

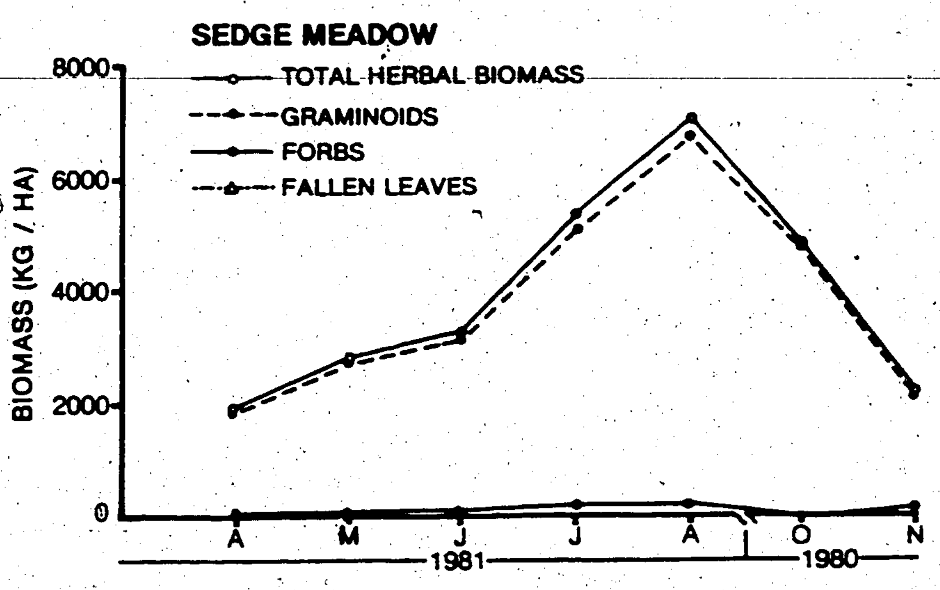

Figure IV.1 Herbaceous (graminoids and forbs) biomass (kg/ha) in the sedge meadows for October and November 1980, April through August 1981.

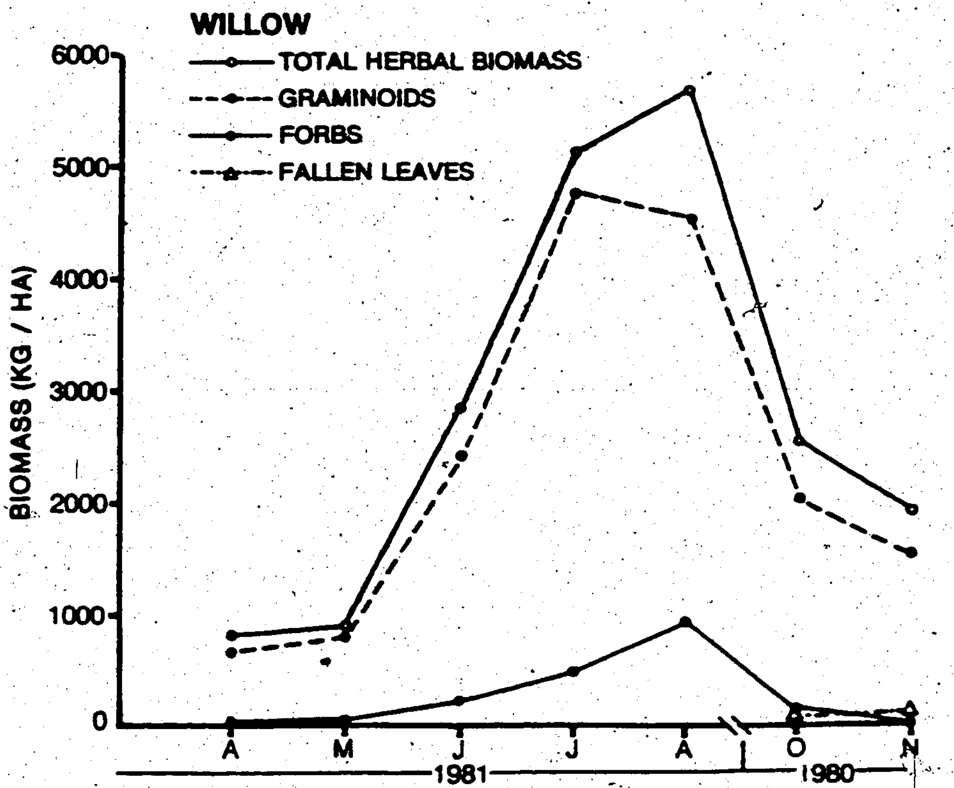

Figure IV.2 Herbaceous (graminoids and forbs) biomass (kg/ha) in the willow habitat for October and November 1980, April through August 1981. Leaf litter (browse) included in estimates during months of use by wapiti.

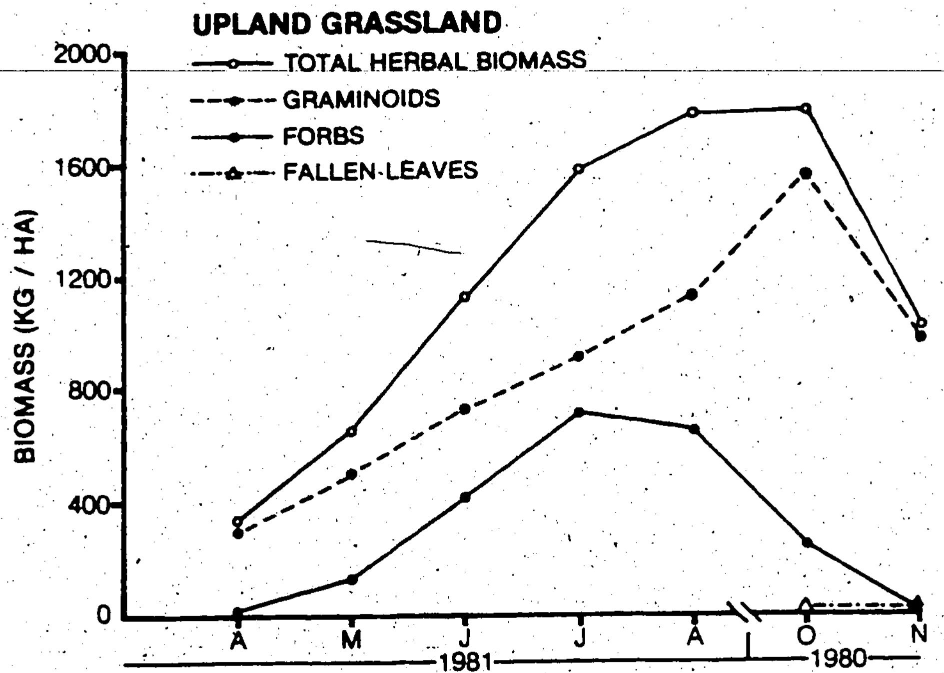

Figure IV.3 Herbaceous (graminoids and forbs) biomass (kg/ha) in the upland grassland for October and November 1980, April through August 1981. Leaf litter (browse) included in estimates during months of use by wapiti.

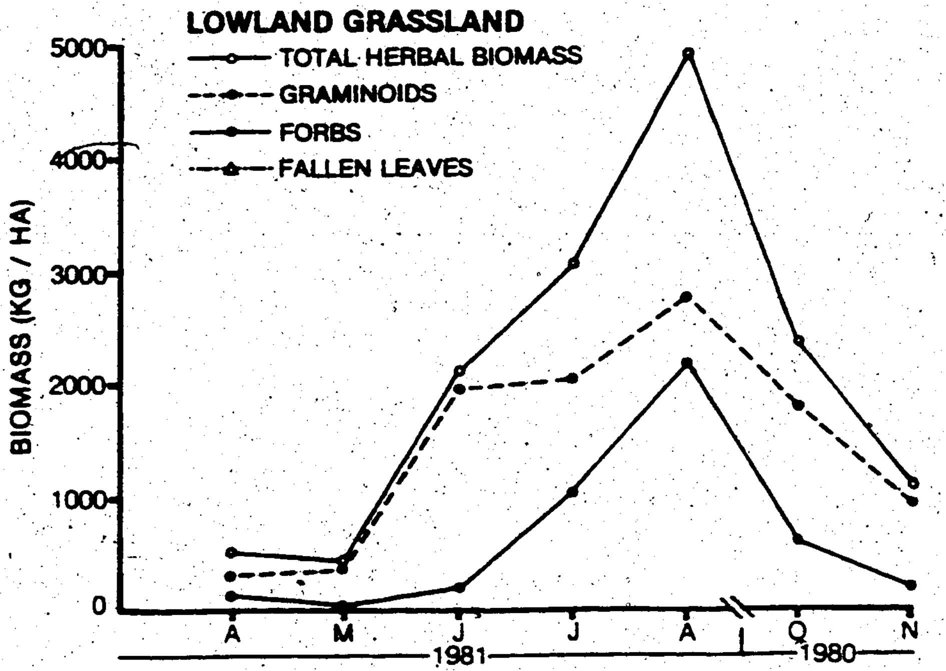

Figure IV.4 Herbaceous (graminoids and forbs) biomass (kg/ha) in the lowland grassland for October and November 1980, April through August 1981.

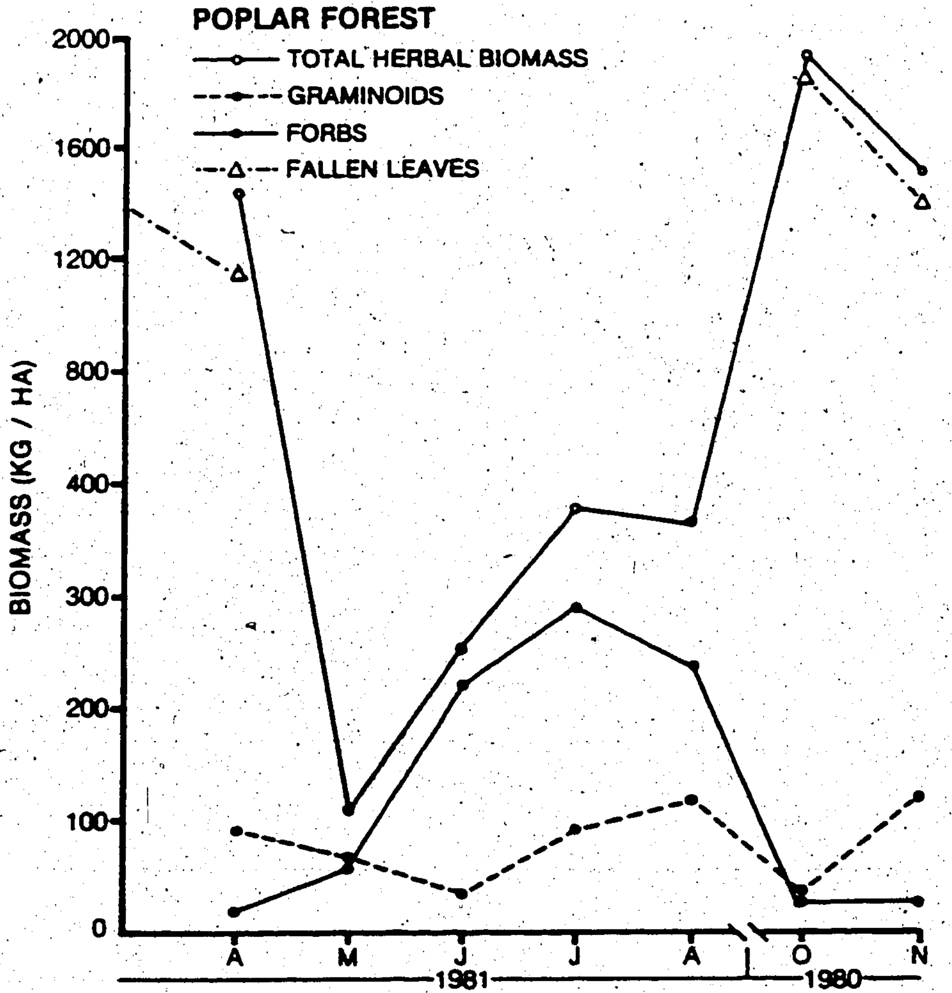

Figure IV.5 Herbaceous (graminoids and forbs) biomass (kg/ha) in the poplar forest for October and November 1980, April through August 1981. Leaf litter (browse) included in the estimates during months of use by wapiti.

(*Urtica gracilis*) dominated a few small areas of the lowland grassland habitat.

Herbaceous vegetation was poorly represented in the forest habitat for most of the year, ranging from 111 kg/ha to 369 kg/ha (Figure IV.5). Grass biomass in this habitat was very low in comparison to the other habitats. Forbs dominated the herbaceous understory in spring and summer. Numerous forb species were present (Appendix 7), giving the forest the highest herbage species diversity of any habitat. Dominant forbs included asters, bunchberry (*Cornus canadensis*), peavine (*Lathyrus* spp.), sarsaparilla (*Aralia nudicaulis*), violet (*Viola* spp.), strawberry, and tall lungwort (*Mertensia paniculata*).

Shrubs

Hazel was the predominant shrub in the poplar forest habitat, accounting for 41.5% of all stems (Table IV.2). Other common shrub species included rose, raspberry, saskatoon, and snowberry. Shrub species which wapiti preferred when first introduced into the area, such as dogwood (*Cornus stolonifera*) and cherry (*Prunus* spp.) (Gates' 1980), were poorly represented. Heavy browsing on aspen and balsam poplar saplings and seedlings resulted in these being infrequent in the forest understory, and also prevented the encroachment of forest onto the grasslands.

Table IV.2 Shrub species, their frequency and twig yield in the poplar forest habitat.

Species	% of All Stems	Stems per Hectare	Total Yield (twigs/hectare)
Populus tremuloides	.76	737.5	113.6
Betula papyrifera	.58	567.5	4431.8
Populus balsamifera	1.75	1705.0	2784.1
Amelanchier alnifolia	6.07	5907.5	29886.3
Cornus stolonifera	4.32	4205.0	14040.9
Corylus cornuta	41.51	40397.5	150682.0
Lonicera spp.	.88	852.5	2215.9
Prunus virginiana	3.21	3125.0	20056.8
Ribes spp.	1.46	1420.0	?
Rosa spp.	19.44	18920.0	63250.0
Rubus hirtellum	2.80	2727.5	2329.5
Rubus melanolasius	11.97	11647.5	8806.8
Shepherdia canadensis	.23	277.5	?
Symphoricarpos spp.	5.60	5455.0	?
TOTAL		97325.0	

Fallen leaves, mainly from mature poplar trees, were an important component of the autumn through early spring biomass in the forest habitat. In October, leaf litter was estimated at 1,833 Kg/ha, and in April a considerable amount, 1,130 Kg/ha, remained (Figure IV.5).

In the willow habitat, *Salix* spp. comprised 69.2% of all the stems (Table IV.3). Balsam poplar and raspberry were the next most common species. After leaf abscission, leaf litter contributed a small amount to the overall biomass in the willow habitat. Heavy browsing on low shrub willow produced hedging, and these shrubs appeared to be quite productive. However, heavy browsing on willow above 4 meters in height produced a distinct browse line and many stems of these stands of willow were dead.

Forage Quality

Crude Protein

Values for crude protein content of major forage items are representative of the plant parts consumed by wapiti. Values varied significantly among forage classes, and among seasons ($P<.0001$) (Table IV.4). Forage protein values for all forage classes were significantly higher in spring and summer than in fall and winter ($P<.05$) (Figure IV.6-IV.8). May values, representing the initiation of new growth, were significantly higher than those for all other months. Protein values declined with further growth and maturation

Table IV.3: Shrub species, their frequency and twig yield in the willow habitat.

Species	% of All Stems	Stems per Hectare	Total Yield (twigs/hectare)
Betula papyrifera	.20	86.2	?
Populus balsamifera	16.53	6077.6	27672.0
Populus tremuloides	2.04	862.0	3103.4
Salix spp.	69.20	29224.0	186637.7
Cornus stolonifera	1.02	344.8	1034.5
Corylus cornuta	.41	172.4	344.8
Rubus hirtellum	3.06	1034.5	344.8
Rubus melanolasius	7.55	3189.7	13017.0
TOTAL		40991.0	219150.0

Table IV.4: Percent crude protein (N x 6.25) of major forage items included in wapiti diets.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
GRAMINOIDS											
Upland grass	9.76	7.76	7.15	5.64	6.5	8.97	14.92	20.37	14.34	12.84	14.26
Lowland grass	15.1	12.4	11.62	6.9	7.05	12.9	15.51	25.57	19.6	14.92	17.63
Forest grass	7.2	6.04			6.0	7.35	12.4	18.4		11.7	
Carex spp.	10.4	9.78	4.48	4.4	4.48	5.72	11.98	19.14	16.4		
BROWSE											
Betula papyrifera											
Twigs	7.61	7.7	7.48		6.66						
Leaves								25.0	20.0	19.52	18.96
Populus balsamifera											
Twigs	7.5	7.28	6.34	6.71	6.82	7.06					
Bark		3.81	4.0	3.3	3.6	3.9	3.5				
Branch	5.23		5.3		5.03	4.69					
Leaves								21.6	15.44	15.26	16.02
Populus tremuloides											
Twigs	8.52	7.75	7.02	7.24	7.2	7.87	8.4				
Bark		3.4	4.28	3.18	4.8	4.6	4.0				
Branch	7.02			6.47		6.15					
Leaves								22.7	16.52	15.04	14.62
Salix spp.											
Twigs	7.96	7.6	7.54	7.6	7.6	7.64	8.51				
Bark					6.5	5.7	4.8				
Branch			5.9		4.56						
Leaves								24.41	18.45	17.85	15.15
Amelanchier alnifolia											
Twigs	6.28	6.18	5.6	6.2	5.9	5.7					
Leaves									16.62	16.68	15.55
Cornus stolonifera											
Twigs	6.19	5.58	6.76	5.29	3.45	5.85	6.28				
Leaves									16.35	14.32	14.14
Corylus cornuta											
Twigs	5.75	5.01	5.73	5.62	5.67	6.11	7.1				
Leaves								25.04	17.38	16.95	16.33
Lonicera dioica leaves								25.19	15.5	12.36	11.14
Lonicera involucrata											
Twigs	4.95				4.92	4.89	5.7				
Leaves								22.82	15.31	13.49	12.45

Table IV.4: Percent crude protein (Nx6.25) of major forage items included in wapiti diets, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Prunus virginiana											
Twigs	5.8					6.60					
Leaves								30.38		23.23	20.65
Ribes spp. leaves									20.48	17.22	15.09
Rosa spp.											
Twigs	4.57			4.4		4.76					
Leaves								26.06	16.89	13.38	12.48
Rubus hirtellum											
Twigs	7.52	7.66	5.9	4.7	5.85	5.51	7.59				
Leaves								24.1			13.06
Rubus melanolasius											
Twigs					7.31		6.76				
Leaves								26.22	23.22	16.9	19.3
Symphoricarpos spp.											
Twigs	6.3	4.63	4.82		5.1						
Leaves								26.25	13.07	11.72	10.86
Viburnum edule leaves									19.06		
Fallen leaves	8.9	7.33	7.2		7.68	7.15	8.58				
FORBS											
Achillea millefolium	7.5							23.58			13.33
Anemone canadensis									13.21		10.7
Aralia nudicaulis									17.26	13.84	13.8
Aster spp.	10.94	9.42	8.75	8.48		6.9		24.75	19.4	16.23	16.0
Cirsium arvense	16.0	15.79	13.19	11.1	5.5	7.42	11.39				
Cornus canadensis	8.2	7.1					8.16				
Disporum trachycarpum									18.45	15.52	12.50
Equisetum spp.									18.12	13.18	
Erigeron spp.									15.13	11.55	
Fragaria glauca	9.2							19.35	11.57	11.37	13.48

Table IV.4: Percentage of crude protein (Nx6.25) in major forage items in wapiti diets, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Galeopsis tetrahit	9.51							23.98	26.18	21.59	17.32
Galium boreale								24.24	15.02		
Geum allepicum								20.46	14.12	12.08	
Heracleum lanatum								31.68	21.22	16.9	17.81
Lathyrus spp.								32.52	22.66	20.03	22.11
Maianthemum canadense								20.77			11.61
Mertensia paniculata								23.1	23.2	11.36	13.6
Petasites spp.								19.4			
Plantago major									16.00	14.86	15.25
Polygonum amphibium									21.59	21.88	13.37
Rubus pubescens								19.1		10.17	
Sanicula marilandica									11.76	10.78	12.0
Solidago spp.									19.3	17.02	16.2
Sonchus arvensis									15.8	13.75	15.20
Stachys palustris									19.04	14.3	
Taraxacum officinale	11.1							20.1	15.79	14.84	14.34
Trifolium spp.	22.2							25.18	25.62	21.38	24.08
Urtica gracilis	16.04	17.72								25.58	27.08
Vicia americana									24.7	23.12	25.6
Viola spp.								21.5	14.25	14.08	14.88

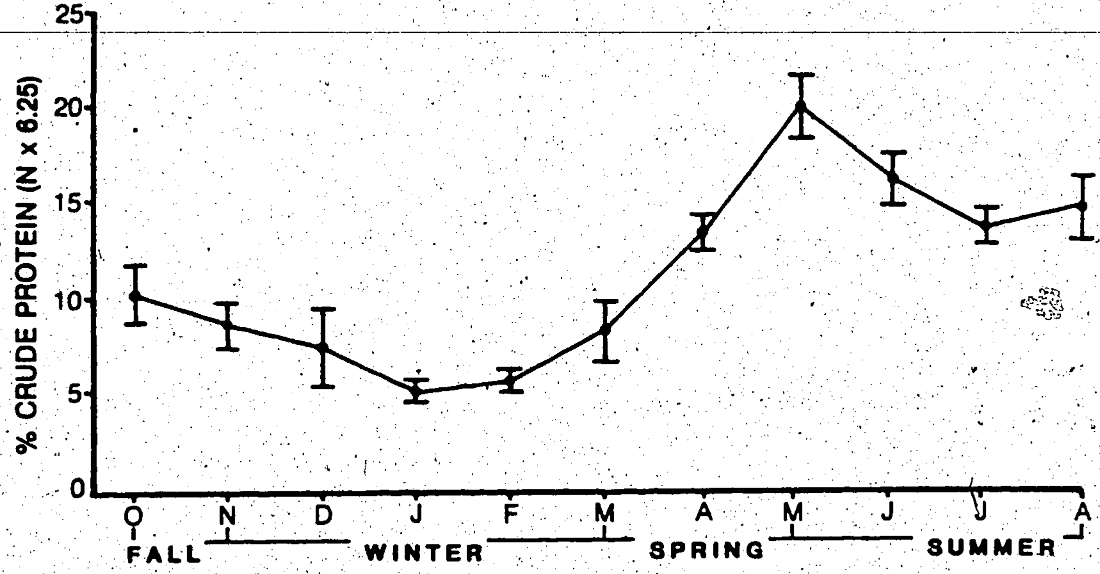

Figure IV.6 Monthly variation in crude protein content (Nx6.25) of graminoid samples (means and S.E.).

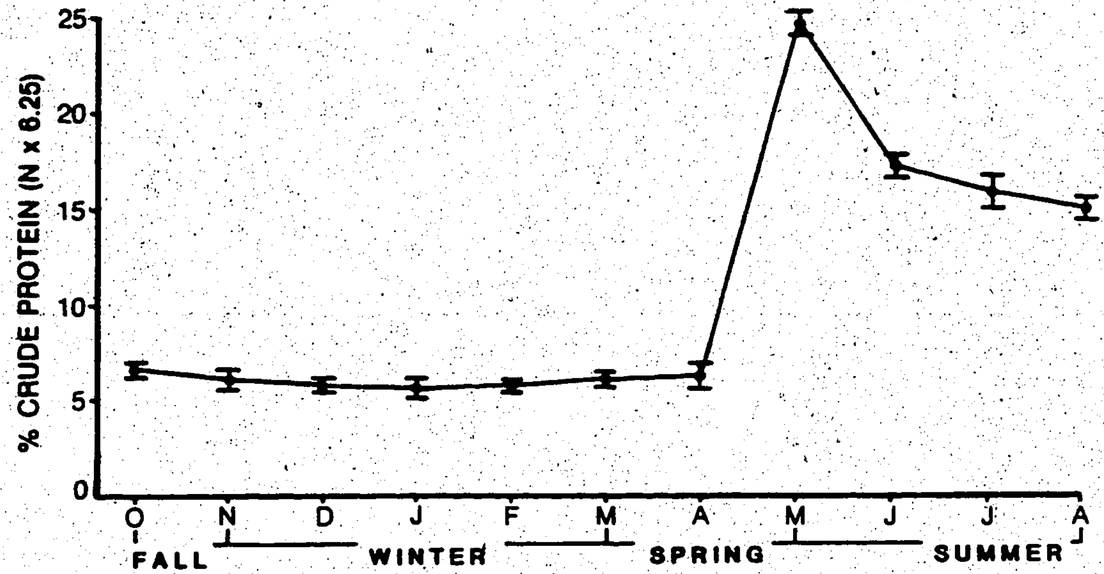

Figure IV.7 Monthly variation in crude protein content (Nx6.25) of browse samples (means and S.E.).

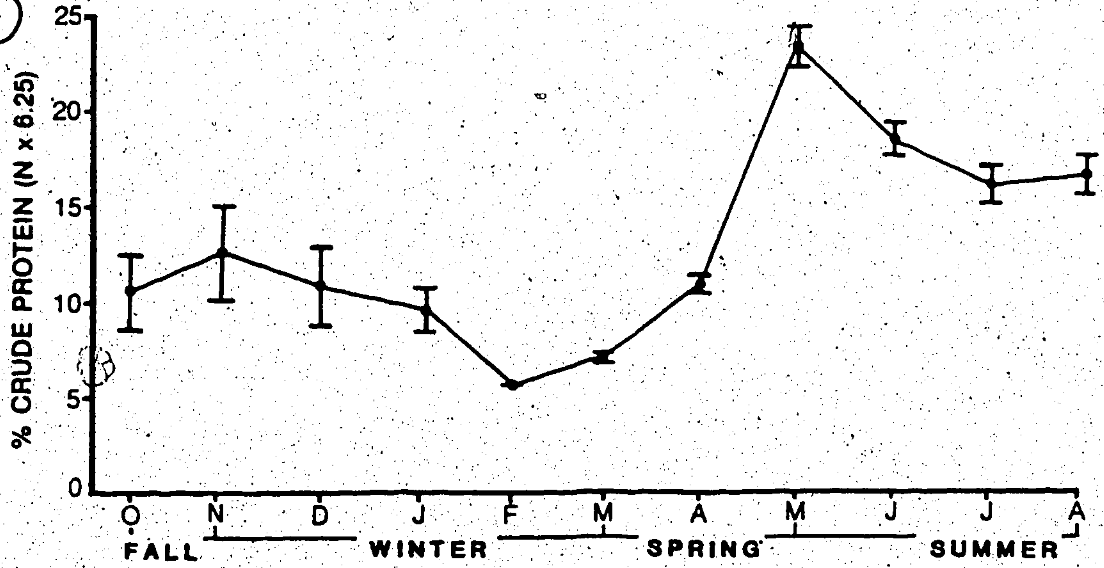

Figure IV.8 Monthly variation in crude protein content (Nx6.25) of forb samples (means and S.E.).

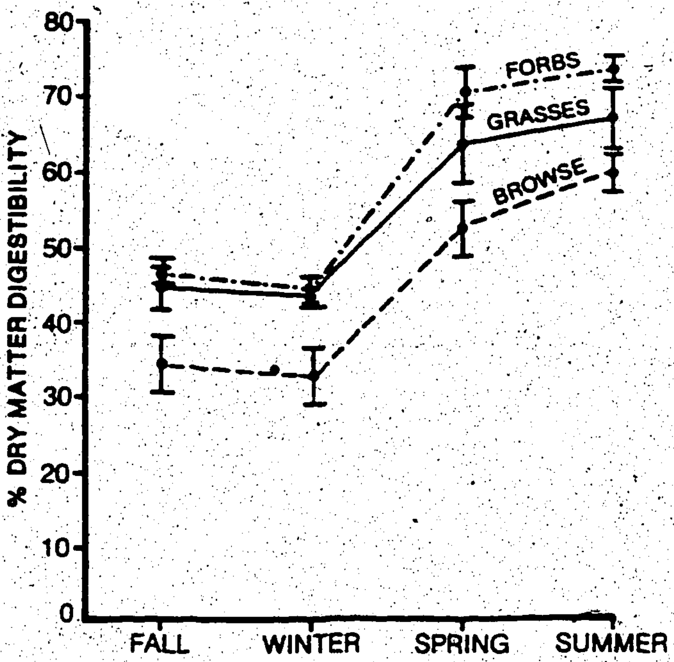

Figure IV.9 Seasonal variation in the in vitro dry matter digestibility of graminoids, browse, and forb samples (means and S.E.).

during summer, and then again with senescence in fall. Change in protein content during winter was variable, though generally less than at other seasons.

The protein content of grasses, browse, and forbs varied during the year from 5.6% to 21.0%, 5.8% to 25.0%, and 5.5% to 21.7%, respectively. During fall, grasses and forbs had significantly higher protein content than did browse ($P<.05$). In winter and spring, forbs contained more crude protein than the other forage classes. However, in late spring, after leafing out, browse protein values were the highest. There were no significant differences among forage classes during the summer.

Grasses maintained in a state of regrowth (upland and lowland areas) had higher crude protein values from summer through winter than mature grasses and *Carex* in the willow and sedge meadow habitats.

Winter browse values included items such as tree bark and branches, which were lower in crude protein content than cured leaves or twigs, thus decreasing the overall value for browse. Fallen leaves maintained a relatively high crude protein content (~7%) during winter.

In Vitro Digestibility

In vitro digestibilities of forage items are presented by forage class on a seasonal basis (Figure IV.9, Appendix 8). *In vitro* digestibility values were significantly higher

(P<.05) for all forage classes during spring and summer compared with fall and winter. Digestibility values of all classes declined by about 25-30% from summer to early winter. The digestibility of forbs was significantly greater than grasses and/or browse from spring through fall (P<.05). In winter no differences in digestibility were found between forage classes. However, the digestibility of browse was lower than that of grasses and forbs. The winter digestibility values for browse were calculated from December samples. A few samples collected during late winter suggested that browse digestibility declined further by about 10-15%. Digestibility of browse items in declining order were fallen leaves> twigs> branches> and bark.

Botanical Diet Composition

Diet composition of wapiti is expressed as percentages of total bites. Since few significant differences among the sex and age classes of wapiti were found at the forage class (browse, forbs, grasses) level, the results are presented as the average for all animals. Diets of the four sex-age classes are given in Appendix 9-11, recording times and number of bites the data is based on are given in Appendix 17 and 18, respectively. Differences in the use of forage species among the classes of wapiti occurred, although there was as much variation within a group as among groups. Diets

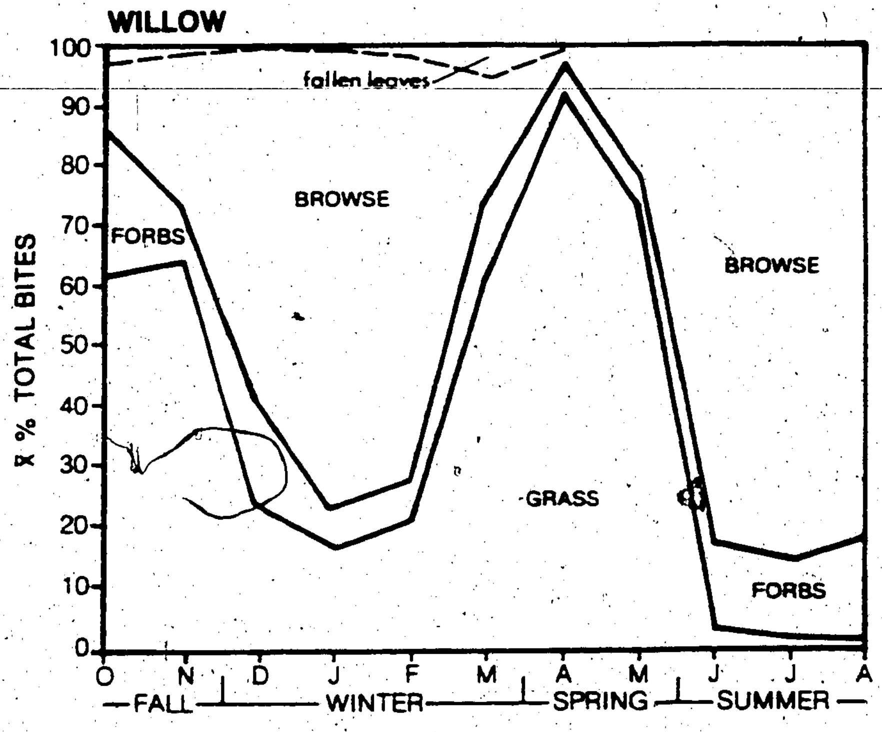

Figure IV.10 Forage class composition (graminoids, forbs, browse) of wapiti diets in the willow habitat.

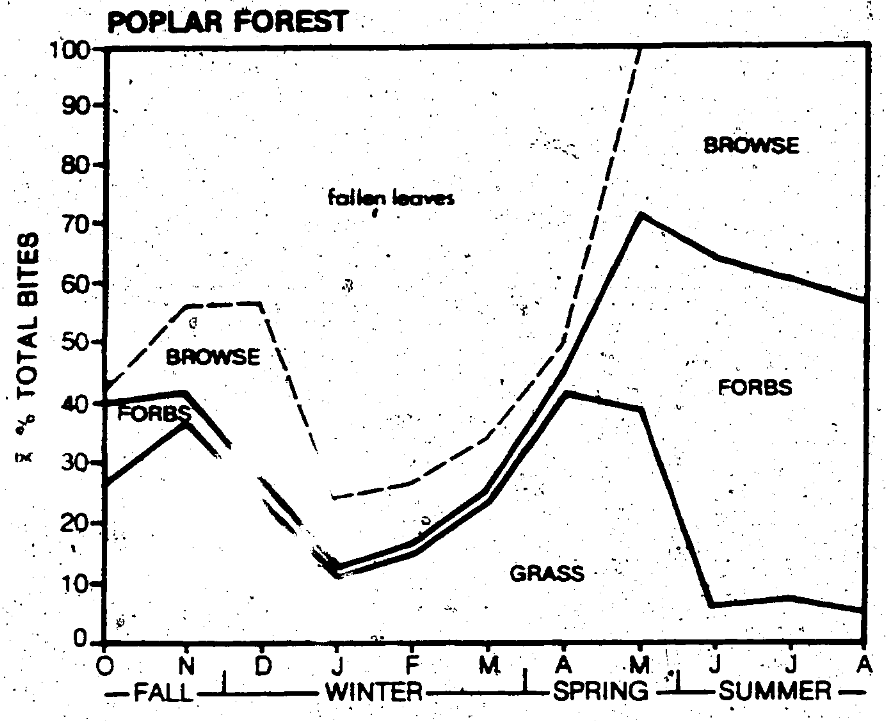

Figure IV.11 Forage class composition (graminoids, forbs, browse) of wapiti diets in the poplar forest habitat.

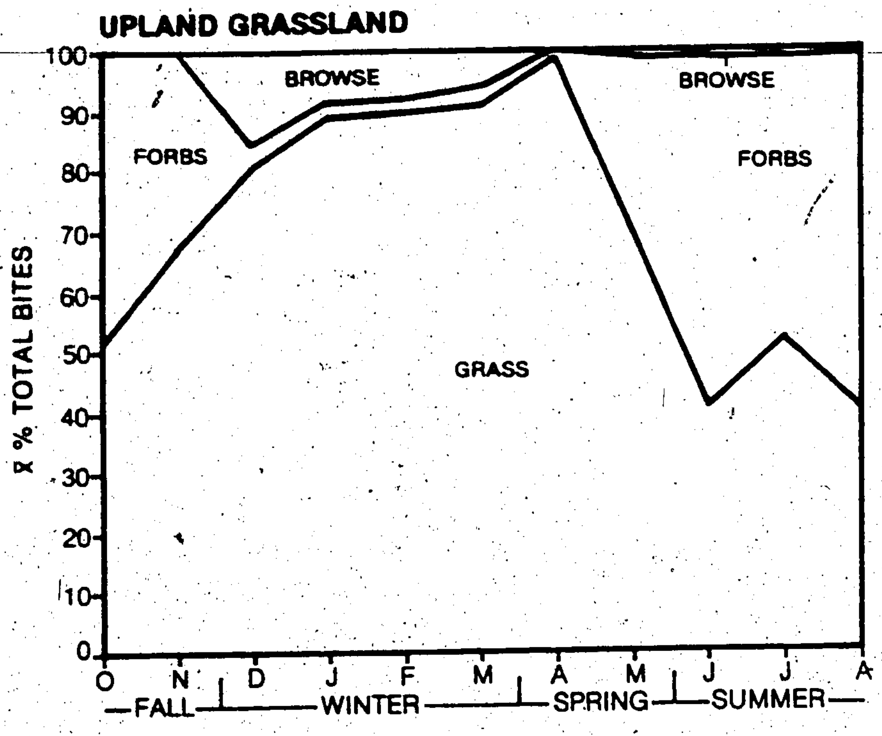

Figure IV.12 Forage class composition (graminoids, forbs, browse) of wapiti diets in the upland grassland.

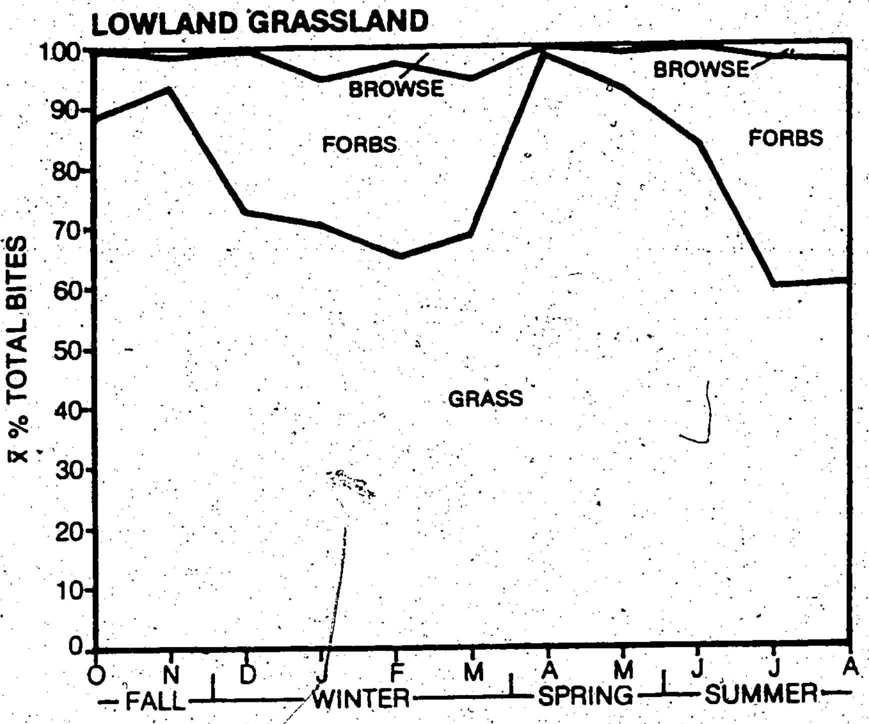

Figure IV.13 Forage class composition (graminoids, forbs, browse) of wapiti diets in the lowland grassland.

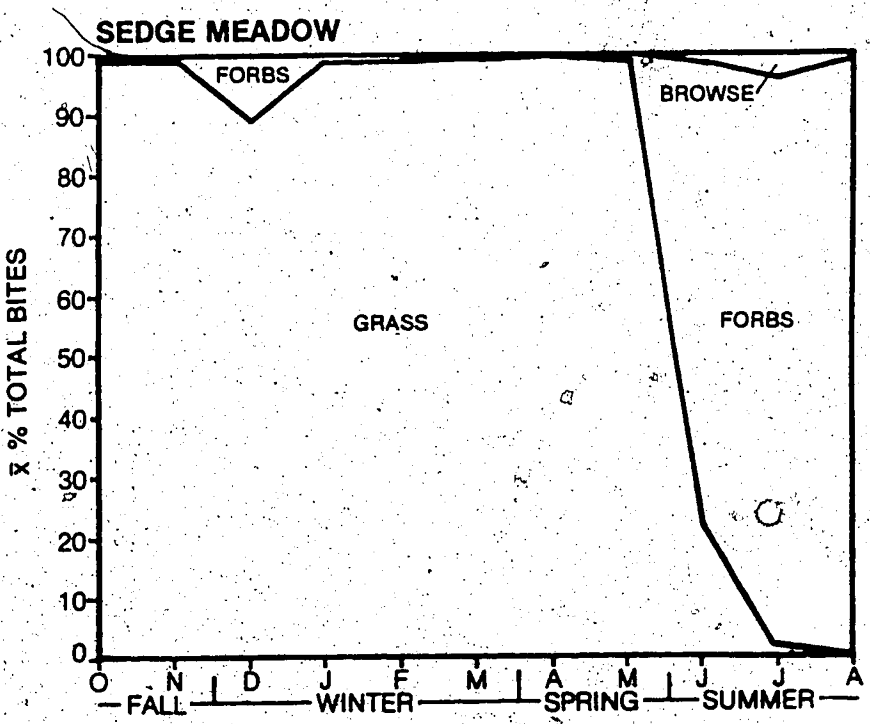

Figure IV.14 Forage class composition (graminoids, forbs, browse) of wapiti diets in the sedge meadows.

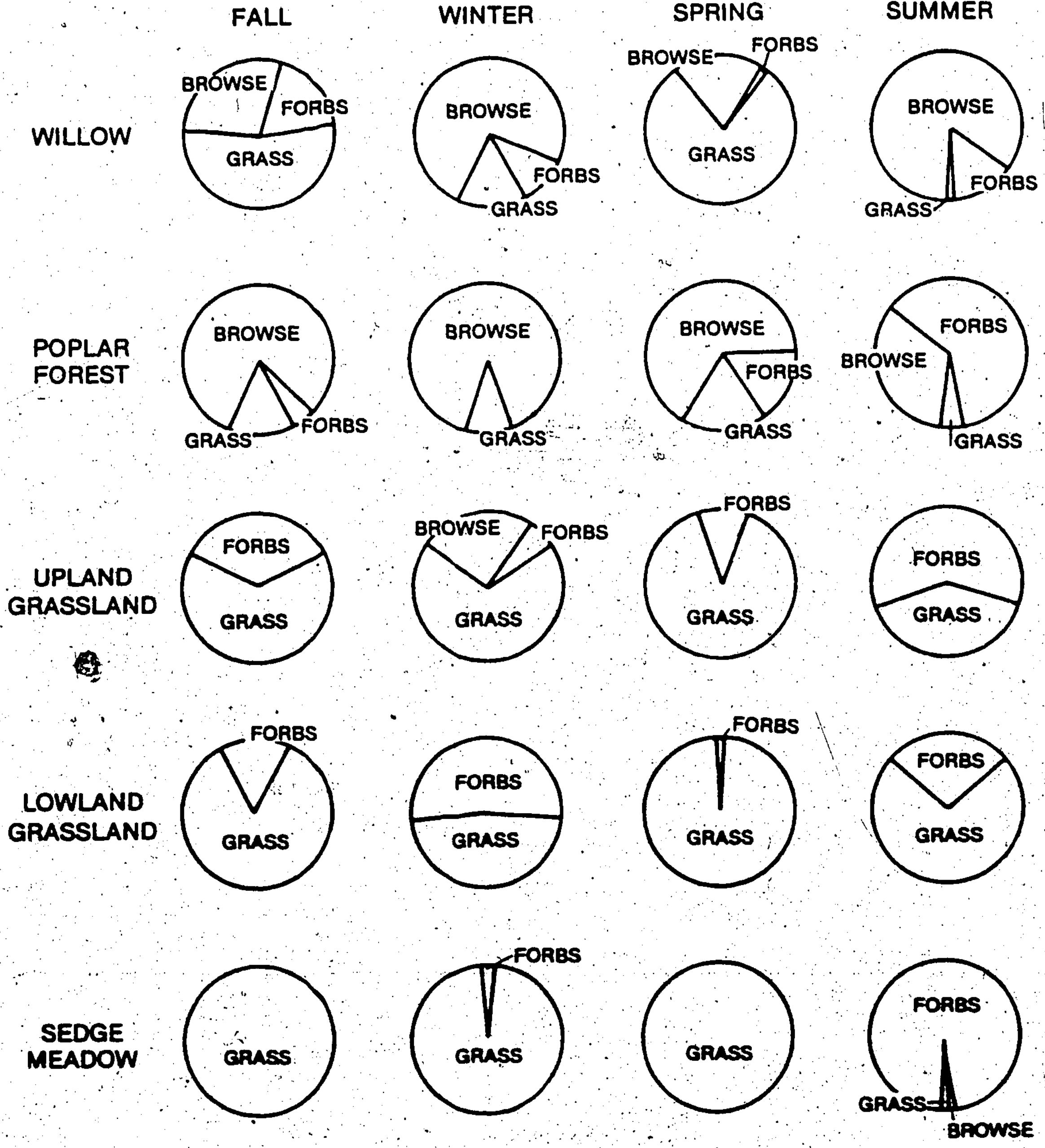

Figure IV.15 Seasonal dry weight diet composition of wapiti in the five habitats.

varied significantly among seasons and habitats ($P<.001$). A significance level of $P=.05$ was used to evaluate the following differences among diet composition in relation to season and habitat.

Browse consumption was significantly greater in the poplar forest and willow habitats than other habitats during all seasons (Figure IV.10-IV.14). Graminoids were consumed significantly more in the sedge meadow and lowland grassland during fall to spring than in other habitats. Use of grasses on the upland areas during winter was also significantly greater than in the willow and poplar forest habitats. During summer, use of grasses was greatest in the grassland areas. Forb consumption was more variable, being significantly greater in the upland grassland and willow habitats during fall, in the lowland grassland and willow areas during winter, in the poplar forest and upland grasslands during spring, and in the sedge meadows, upland grassland, and poplar forest during summer.

Seasonal diet composition, expressed as a percentage of dry weight of forage classes is presented in Figure IV.15. Trends are similar to those based on percentage of bites. Forbs, however, comprised a larger portion of the lowland grassland diet in winter.

Seasonal trends in diet selection are discussed below.

Willow Habitat

Spring

Graminoids (predominantly new growth of sedge) dominated the majority of the wapiti's spring diet in the willow habitat, averaging 78% of the total forage consumed (Table IV.5). Use of browse was limited in April as leaf flush had not yet occurred. Browse use increased in May to form 24.4% of the diet; most frequently consumed was willow. Honeysuckle (*Lonicera involucrata*), raspberry, and gooseberry (*Rubus hirtellum*) were of secondary importance. Forbs contributed 3% of the spring diet in April. Numerous forbs contributed small amounts to the May diet; yellow avens (*Geum allepicum*) appeared to be the most important new growth.

Summer

By summer, consumption of sedge and grasses in the willow habitat had declined greatly, averaging 1.9% of the diet. This decline in use, especially of sedge, is attributable to its advanced growth stage, rendering it relatively unpalatable to wapiti. Leaf flush of browse species (willow and balsam) occurred during late spring-early summer. The result was a shift in diet composition of mainly graminoids in spring to browse (83.6%) in summer. Willow dominated the overall diet,

Table IV.5: Wapiti diets in the willow habitat as a percentage of total bites.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
GRAMINOIDS											
Grasses	6.78	9.42	7.73	5.72	10.43	13.72	10.42	21.61	2.18	1.45	1.47
Carex spp.	61.94	53.72	15.25	9.20	9.4	48.05	83.53	51.25	0.16	0.02	0.02
Total	68.72	63.14	22.98	14.92	19.84	61.77	93.95	78.26	2.56	1.47	1.49
BROWSE											
Betula papyrifera		0.18	0.15	0.33	0.38			0.96	1.92	1.49	2.10
Populus balsamifera	0.1	3.83	7.83	3.78	7.01	3.26	0.40	0.46	0.69	2.32	1.15
Populus tremuloides		0.44	0.26	2.81	1.74	2.09	0.11	0.03	0.97	0.68	1.68
Salix spp.	9.84	21.74	50.90	68.28	62.72	15.52	2.57	15.4	76.68	77.7	76.19
Amelanchier alnifolia			0.05						0.13	0.05	0.02
Cornus stolonifera		0.15	0.90	0.33	0.16	0.05	0.02	0.01	0.28	0.39	0.35
Corylus cornuta				0.03							
Lonicera involucrata	0.07	0.03	0.03			0.05		3.53	0.20	0.32	0.04
Lonicera dioica									0.01		0.07
Prunus virginiana											0.03
Ribes spp.								0.01	0.25	0.12	0.09
Rosa spp.								0.07		0.01	0.17
Rubus hirtellum		0.23	0.38	0.56	0.05	0.19		1.84	0.06	0.04	0.02
Rubus melanolasius	0.31	0.03						1.91	1.05	0.87	0.78
Symphoricarpos spp.	1.43	0.03		0.66	0.11		0.02	0.14	0.01	0.05	0.02
Leaves (fallen)	3.44	1.26	0.95	0.93	1.74	5.45	0.7			0.01	0.15
Unknown browse							0.02				
Total	15.19	27.91	61.45	77.70	73.91	26.61	3.82	24.37	82.26	84.02	82.86
FORBS											
Achillea millefolium								0.06		0.02	
Agrimonia striata											0.04
Aralia nudicaulis								0.01	0.06		
Aster spp.	6.36	2.02	3.89	1.75	0.71	0.73	0.11	0.35	7.62	4.08	4.74
Cirsium arvense	7.37	6.14	11.05	5.62	4.95	10.8	1.9	0.08	0.05	0.01	
Cornus canadensis								0.01			
Disporum trachycarpum								0.01			
Epilobium angustifolium									0.01		

Table IV.5: Wapiti diets in the willow habitat as a percentage of total bites, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Equisetum spp.								0.05	1.57	0.27	0.02
Erigoron spp.								0.03	0.21	0.59	0.01
Fragaria glauca	0.42	0.06					0.12	0.11	0.09	0.05	0.10
Galeopsis tetrahit	0.14	0.06			0.16			0.10	1.14	4.76	6.15
Galium boreale								0.01	0.01	0.01	0.03
Geum allepicum							0.06	0.80	0.60	0.23	0.21
Heracleum lanatum								0.11	0.11	0.03	
Hieracium canadense											0.02
Lathyrus spp.								0.03	0.01	0.03	0.02
Lysimachia ciliata										0.01	
Maianthemum canadense								0.01			
Mentha arvensis										0.01	0.01
Mertensia paniculata								0.11	0.28	0.01	0.04
Mitella nuda										0.01	0.01
Petasites spp.		0.12						0.23	0.03		
Plantago major										0.06	
Polygonum amphibium								0.15	0.86	1.04	0.64
Potentilla anserina											0.07
Pyrola spp.	0.14										
Ranunculus sceleratus									0.06	0.05	
Scutellaria galericulata									0.08	0.01	0.02
Solidago spp.		0.03			0.05			0.01	0.06	0.03	0.18
Sonchus arvensis	0.52							0.05	0.55	1.37	2.65
Stachys palustris								0.05	0.41	0.53	0.10
Stellaria spp.										0.02	0.03
Taraxacum officinale	0.24							0.35	1.23	0.27	0.24
Trifolium spp.										0.03	
Urtica gracilis	0.80	0.53	0.64		0.05			0.01	0.01	0.77	0.13
Vicia americana	0.03								0.03	0.06	0.02
Viola spp.								0.03	0.06	0.05	
unidentified forbs	0.03					0.05	0.03	0.64	0.06	0.03	0.08
Total	16.09	8.95	15.58	7.37	5.92	11.58	2.22	2.76	15.18	14.42	15.58
Lichen spp.					0.33						
Fungi spp.						0.05					
Unidentified									0.01	0.02	0.09

averaging 76.9%. Birch, balsam, and aspen contributed small amounts to the diet. Use of forbs increased from spring to summer (15.1% of the diet). Although numerous forbs (~41 species) were consumed by wapiti, those most frequently ingested were aster, hemp nettle, and sow thistle.

Fall

Grasses comprised the major portion of the fall diet in the willow habitat. Curing of forbs, and matured grass and sedge, and the abscission of browse leaves probably all contributed to the heavy use of sedge shoots which were continuously growing throughout this period. Sedge shoots constituted 57.8% of the diet. Consumption of browse declined to 21.6%. Willow contributed 15.8% of the diet; about 2% of this occurred as the ingestion of fallen leaves. Snowberry and balsam were consumed in small amounts. The use of forbs declined to 12.5% of the diet, and the number of species of forbs included in the diet declined to 12. Thistle and aster were consumed most frequently.

Winter

Consumption of graminoids declined during winter, to 29.9% of the diet. Their greatest use (61.8%) was in March when most areas were becoming snow-free, exposing new growth of *Carex*, which comprised 48.1% of the March diet. Use of browse increased during the months of permanent snow cover (December, January, February) to 71% of the diet. During this period, willow comprised 60.6% of the diet, but use declined to 15.5% in March. Balsam and aspen rece[illegible]tle use during winter. Initially, only twigs [illegible] branches of browse were consumed, but by Fe[illegible] March large pieces of branches of willow and balsam were also consumed. Elk were observed to test twigs and branches, by mouthing them or breaking them off, before ingesting them. Only green material was consumed. Few forbs (mainly thistle and aster) were taken in winter, and contributed to only 10% of the diet.

Overall, browse use was significantly greater in summer and in winter than spring and fall, while consumption of grasses was significantly greater in spring and fall than in summer and winter. Forbs comprised a greater proportion of the diet in summer than at other periods of the year.

Poplar Forest

Spring

Grasses comprised an average of 39.0% of the spring diet in the poplar forest (Table IV.6). Elk selected for

Table IV.6: Wapiti diets in the poplar forest as a percentage of total bites.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
GRAMINOIDS											
Grasses	25.96	34.63	21.70	10.80	13.75	22.65	40.24	37.54	5.26	6.20	5.15
Carex spp.		0.02	0.02					0.16	0.15	0.02	0.01
Total	25.96	34.65	21.72	10.80	13.75	22.65	40.24	37.70	5.41	6.22	5.16
BROWSE											
Betula papyrifera			0.05			0.05			0.08	0.36	0.42
Populus balsamifera	0.97	1.57	2.95	1.20	4.59	1.42	0.16	0.12	0.53	0.90	0.82
Populus tremuloides	0.23	3.79	4.80	6.00	3.43	4.43	2.84	0.21	3.24	6.16	3.78
Salix spp.		0.21	0.35	0.1		0.15	0.16	0.24	1.32	2.19	2.24
Amelanchier alnifolia		2.69	2.02	0.85	0.31	0.81	0.05	0.15	3.61	7.67	7.24
Cornus stolonifera	0.04	0.77	0.48		0.13	0.12	0.18	0.02	2.33	0.87	2.66
Corylus cornuta	0.06	5.91	14.1	2.0	1.13	1.96	0.66	2.98	17.82	10.71	2.33
Lonicera involucrata		0.03	0.05	0.15	0.05	0.12	0.04	11.58	1.01	1.79	2.41
Lonicera dioica								1.24	0.41	0.90	0.81
Prunus virginiana		0.02				0.02		0.95	0.35	1.72	2.15
Ribes spp.								0.66	1.88	0.23	0.20
Rosa spp.	0.11	0.15	0.26	0.03		0.17	0.02	3.87	1.06	3.70	14.17
Rubus hirtellum		0.57	1.70	1.41	0.40	0.41	0.09	2.40	0.20	0.22	0.16
Rubus melanolasius	0.08	0.12	0.02	0.07				4.33	1.36	1.55	3.34
Shepherdia canadensis		0.02	0.03	0.07	0.11						
Symphoricarpos spp.		0.16	0.57	0.55			0.26	2.09	0.41	0.53	1.58
Viburnum edule		0.10				0.02		0.03	0.82	0.54	0.30
Leaves (fallen)	59.14	45.36	44.98	76.60	74.83	67.19	51.49	0.09			
unidentified browse		0.05			0.12		1.59				0.01
Total	60.63	61.52	72.48	89.03	85.10	76.87	57.54	30.96	36.43	40.04	44.62
FORBS											
Achillea millefolium	0.04							0.13	0.02	0.01	0.04
Actaea rubra									0.01	0.04	0.03
Agrimonia striata										0.05	0.13
Anemone canadensis								0.25	0.19	0.50	0.12
Apocynum androsaemifolium									0.04	0.27	0.08
Aralia nudicaulis								0.09	6.27	1.85	1.64
Aster spp.	0.34	0.08	4.74	0.05	0.02	0.02		1.66	6.33	8.87	10.95
Cirsium arvense	0.86	0.62	0.62	0.08	0.24	0.14	0.32	0.06			

Table IV.6: Wapiti diets in the poplar forest as a percentage of total bites, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Cornus canadensis	11.29	2.5	0.26		0.05	0.25	0.93	0.03	0.06	0.17	0.25
Disporum trachycarpum								0.07	0.70	0.58	1.01
Epilobium angustifolium									0.02	0.05	0.01
Equisetum spp.								0.03	0.34	0.48	0.25
Erigeron spp.								0.03		0.01	0.02
Fragaria glauca	0.11	0.06	0.02			0.02	0.29	5.39	2.09	1.43	2.28
Galeopsis tetrahit	0.08	0.01		0.03				0.38	0.32	0.78	0.60
Galium boreale								0.78	0.48	0.51	0.43
Galium triflorum									0.01	0.04	0.05
Geum allepicum								0.29	0.02	0.03	0.02
Heracleum lanatum							0.04	0.84	2.35	0.59	0.32
Hieracium canadense											0.01
Lathyrus spp.	0.02							3.33	17.74	17.45	12.68
Linnaea borealis					0.04	0.02	0.05				0.01
Lysimachia ciliata											0.05
Maianthemum canadense								2.48	0.16	0.19	0.62
Mertensia paniculata	0.11							7.82	4.03	4.09	1.44
Mitella nuda							0.09				0.01
Osmorhiza spp.										0.02	0.01
Petasites spp.								0.10			
Plantago major										0.03	
Pyrola spp.	0.19	0.08		0.01	0.16	0.03	0.26				
Rubus pubescens									0.05		0.31
Sanicula marilandica								0.06	0.28	0.41	0.56
Scutellaria galericulata									0.02		0.01
Sium suave								0.03			
Smilacina racemosa								0.01	0.02		
Solidago spp.			0.02				0.02	0.15	0.11	0.28	
Sonchus arvensis								0.01	0.02		0.01
Stachys palustris									0.16	0.08	0.06
Stellaria spp.										0.02	

Table IV.6: Wapiti diets in the poplar forest as a percentage of total bites, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Taraxacum officinale	0.27							4.60	10.29	5.42	5.90
Thalictrum spp.										0.05	0.01
Trifolium spp.								0.07	0.19	0.85	2.77
Urtica gracilis	0.06	0.1	0.09					0.06		0.15	0.02
Vicia americana	0.02		0.02					0.18	2.94	3.28	2.11
Viola spp.	0.02							2.08	2.76	4.89	4.14
unidentified forb		0.01	0.05				0.02	0.28	0.17	0.13	
Total	13.41	3.47	5.81	0.17	0.51	0.48	2.02	31.29	58.17	53.6	49.16
Lichens		0.01			0.57						
Fungi		0.34			0.07		0.04	0.04	0.02	0.11	1.07
Unidentified										0.04	

grass blades that had remained green over winter and for new growth. A trace amount of sedge, which occurred in some of the depressional areas, was also consumed. In early spring, browse comprised the major part of the diet, 57.5%. Fallen leaves accounted for 51.5% of this amount, as leafing out of browse species had not yet occurred. Elk tended to move quickly through forested areas, spending little of their overall early spring foraging time there. With leaf flush in May, wapiti rarely consumed old leaves. New browse growth averaged 31% of the diet. Honeysuckle, one of the earliest species to leaf out, comprised 11.6% of the diet in May. Raspberry, rose, hazel, gooseberry, and snowberry were also important in the diet. Forb consumption was low in April, and consisted mainly of cured or evergreen species. In May, use of forbs increased to comprise 31.3% of the diet. About 34 forbs were observed in the diet. Tall lungwort, strawberry, dandelion, peavine, lily (*Maianthemum canadense*), and violet were the most frequently consumed items. Morel mushrooms were infrequently included in the diet.

Summer

Use of the poplar forest for foraging continued to increase from later spring into summer. With the increase in availability of new browse leaves and forbs, use of grasses declined to 5.6% of the summer diet.

Browse increased gradually in the diet during summer, averaging 41.4% of the diet. The number of browse species included in the summer diet (16) remained about the same as in the spring diet. Hazel received heaviest use in early (17.8%) and mid (10.7%) summer, declining in late summer to only 2.3% of the diet. Saskatoon averaged 6.2% of the diet, receiving greater use in the latter parts of the summer. Rose averaged 6.3% of the summer diet, and was the most frequently consumed species in August (14.2%). Aspen, raspberry, dogwood, and willow contributed small amounts to the diet. Low availability of aspen may have limited its consumption, as wapiti selected strongly for aspen leaves. During summer storms, when terminal twigs and branches of aspen and balsam were broken by wind, wapiti moved through the forest selecting for leaves of these species. Even after the leaves were dried, wapiti generally consumed them whenever they were encountered. Aspen leaves were taken in preference to balsam leaves. Adult males were occasionally observed to break down small aspen trees and consume the leaves, and adult females were infrequently observed to stand on their hind legs to reach aspen leaves.

The frequency of occurrence of forbs in the diet peaked in June at 58.2%, then gradually declined during the summer to 49.2%. Although numerous forb species were included in the diet, few contributed more than 1% of the diet. The most common forbs in the summer diet were peavine, aster, dandelion, violet, sarsaparilla, tall lungwort, vetch, and strawberry.

Mushrooms were generally consumed when encountered and actively sought. The wapiti appeared to be capable of smelling mushrooms which had not yet emerged; these were exposed with the muzzle, and then ingested. The low abundance of mushrooms, however, prevented any significant contribution to the diet. Palleson (1979) found mushrooms included in wapiti diets to be highly digestible and high in protein and phospherous. Being 70-90% water, however, large volumes would have to be consumed to obtain substancial benefit from this forage source.

Fall

Browse dominated the fall diet in the poplar forest, averaging 61.1%. With leaf abscission in October, abundant leaves (mainly aspen and balsam) covered the forest floor. The high availability of this forage supply was reflected in the diet, as fallen leaves comprised 52.3% of the diet. The leaves were licked up non-selectively, though wapiti often foraged around tree trunks where leaves were more abundant. In October, little browsing on twigs occurred. During November, use of twigs increased. The most frequently ingested species were hazel, aspen, saskatoon, and balsam poplar. Fallen twigs were occasionally ingested.

Grasses, mainly brome and bluegrass, averaged 30.3% of the fall diet. Green grasses were selected over cured grasses. Forb use dropped to an average of 16.9%, and could be related to the curing of most forbs, and by the cover of leaf litter. Bunchberry, a relatively abundant forb that cured later than other species, averaged 6.9% of the diet. Although 14 other forb species were recorded in the diet, they contributed only minor amounts to the diet. Wintergreen (*Pyrola* spp.) and twinflower (*Linnaea borealis*), despite their evergreen foliage and abundance, were rarely consumed. Lichens and fungi were consumed in trace amounts.

Winter

Browse consumption increased during winter to comprise 80.9% of the diet. The increase in the use of browse could not be related to snow cover, as fallen leaves were still the predominant form of browse ingested, 65.9% of the diet. When foraging in the poplar forest, wapiti spent much of their time cratering for leaves. Foraging activities were centered in areas of high leaf abundance (around tree trunks) or accessibility (previous craters, snow-free areas). Heavy browsing pressure inflicted on the area by wapiti, moose and deer, and shallow snow depths that allowed efficient cratering were probably the main factors resulting in low use of other browse forms (twigs, branches). Browse species contributing to 1% or more of the diet were aspen and balsam poplar, hazel, saskatoon, and gooseberry. In early winter only the current annual growth of most shrubs was consumed. As winter progressed, and browse availability declined, portions of stems and branches were also consumed. Besides the consumption of fallen leaves, aspen and balsam poplar twigs and branches were included in the diet mainly as a result of adult males bending and breaking down small trees. Generally, all ingestible parts of the trees were consumed. Branches extending 3 m or more in length and up to 2 cm in diameter were ingested. Cows and calves were often observed at broken tree sites, feeding on twigs and branches. A sample of 20 aspen and 20 balsam trees, with similiar diameters to those broken down by wapiti, were cut down and the portion of dry weight available to the wapiti was estimated (373 gm/tree for aspen and 325 gm/tree for balsam). Trees broken down by moose were also used by wapiti.

Wapiti occasionally stripped bark from aspen and balsam trees. Although barking sites were distributed over the entire study area, excessive barking resulting in damage to trees only occurred in a small stand behind the corrals. During idle periods, the wapiti were often observed to bark trees for ingestive and grooming purposes. As wapiti were supplementally fed at the corrals during winter, those areas in close proximity to the corrals received the greatest use.

Consumption of grasses declined in the winter to 17.2% of the diet. The most frequent foraging on grasses was recorded in December and March. Grasses were generally ingested along with fallen leaves. Forbs were a minor portion (1.7%) of the winter diet. Aster and thistle were the most commonly consumed forbs. Lichens and fungi were consumed in trace amounts.

The contribution of browse to the diet was significantly higher in winter and fall than in the other seasons. Forb use was significantly higher in the summer and the spring, while grasses were consumed significantly more in spring and winter than other seasons.

Upland Grassland

Spring

Grasses, mainly bluegrass, comprised 84.0% of the spring diet in the upland habitat (Table IV.7). The low height of new grasses on this area prevented any selection for green leaf in the spring diet. Thus, cured grasses still comprised a large portion of the early spring diet. Due to their low availability in early spring, forbs comprised less than 1% of the April diet.

Table IV.7: Wapiti diets in the upland grassland as a percentage of total bites.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
GRAMINOIDS											
Grasses	50.93	67.2	81.74	89.17	89.43	90.72	98.57	68.59	40.36	54.19	40.61
Total	50.93	67.2	81.74	89.17	89.43	90.72	98.57	69.59	40.36	54.19	40.61
BROWSE											
Betula papyrifera									0.01	0.01	
Populus balsamifera			1.20	0.25	0.04	0.13	0.04	0.06	0.07	0.15	0.35
Populus tremuloides			0.15	0.14	0.02	0.09	0.13	0.06	0.48	0.57	0.27
Salix spp.						0.03				0.03	
Amelanchier alnifolia			0.2	0.05		0.01	0.03		0.01	0.01	0.02
Cornus stolonifera			0.03								
Corylus cornuta					0.04			0.01	0.01	0.03	0.01
Prunus virginiana								0.01			
Rosa spp.						0.04		0.06	0.18	0.06	0.13
Rubus hirtellum						0.04		0.07	tr.		
Rubus melanolasius								0.09	0.03	0.01	0.01
Symphoricarpos spp.	0.15		0.41	0.02	0.08			0.27	0.05	0.09	0.38
Leaves (fallen)			13.81	8.72	8.89	5.61	0.73	0.02			
Unidentified browse				0.02		0.01	0.01				
Total	0.15		15.8	9.20	9.07	5.93	0.94	0.65	0.84	0.96	1.18
FORBS											
Achillea millefolium	0.42	0.31	0.38	0.07	0.02	0.11	0.01	1.76	0.53	0.38	0.78
Aralia nudicaulis									0.01		
Aster spp.	3.19	3.0	0.06				0.05	1.29	4.63	6.18	4.36
Cirsium arvense	0.67	0.60	0.96	1.55	1.43	3.22	0.37	0.04			
Cornus canadensis									0.01		
Fragaria glauca	2.20	0.36		0.02	0.04	0.01	0.06	4.19	1.65	2.27	2.06
Galeopsis tetrahit									0.01	0.01	0.03
Galium boreale								0.95	0.50	0.13	0.05
Geum allepicum								0.07	0.03	0.07	0.03
Heracleum lanatum									0.01		
Lathyrus spp.								0.60	0.92	0.28	0.22
Malanthemum canadense								0.06			

Table IV.7: Wapiti diets in the upland grassland as a percentage of total bites, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Mertensia paniculata								0.02	0.01		
Petasites spp.									0.01		
Plantago major											0.01
Polygonum amphibium											0.01
Solidago spp.								0.03	0.58	0.43	0.15
Sonchus arvensis								0.01	0.04	0.08	0.02
Stachys palustris									0.01	0.02	0.20
Taraxacum officinale	11.71	9.20					0.01	18.10	36.15	20.42	18.81
Trifolium spp.	30.73	20.05	1.06					3.20	12.55	23.66	31.29
Urtica gracilis											0.01
Vicia americana								0.21	0.96	0.19	0.30
Viola spp.								0.21	0.21	0.08	0.05
unidentified forb						0.01		0.01			0.01
Total	48.92	32.80	2.46	1.64	1.49	3.35	0.50	30.75	58.82	54.20	58.21

However, they increased in the May diet to 30.8%. Dandelion accounted for 18% of the diet in May, followed by strawberry, clover, aster, and yarrow. Browse contributed trace amounts to the diet due to low availability. The upland grasslands were only occasionally used in early spring due to the low forage availability. With an increase in forage abundance in late spring, the uplands became a preferred foraging area.

Summer

The uplands continued to be a preferred habitat for wapiti foraging during the summer. The consumption of grasses declined to 45%. This coincided with increased selection for forbs (57% of the diet). Dandelion was the most frequently consumed forb in June (36.2%); comprising 25% of the summer diet. Clover constituted 22.5% of the summer diet, reaching a high in August of 31.1%. Aster and strawberry comprised 5% and 2% of the diet, respectively. Browse consumption remained low (1%).

Fall

Wapiti continued to spend much of their foraging time on the upland grasslands during the fall. Consumption of grasses increased in the fall to 59% of the diet. Forbs comprised 40.9% of the diet and use of forb species was related to curing. Clover, which continued to grow during fall, contributed 25.4%, while dandelion, which cured earlier, decreased to 10.2% of the diet. Consumption of browse remained low, and the only species used was snowberry which retained its leaves longer than most other species.

Winter

Foraging in the uplands decreased during winter, and occurred mainly during periods of shallow snow or on snow-free areas. When snow was deep, wapiti concentrated their cratering activities at the grassland-forest border where forage abundance appeared to be greater than on the grassland. The proportion of grasses in the diet increased during winter to 87.8% of the diet. The consumption of browse was greatest during winter, comprising 10% of the diet. The increase was largely due to the ingestion of fallen aspen and balsam poplar leaves. The occurrence of forbs in the diet declined sharply with permanent snow cover to 2% of the diet. This estimate may be conservative, as more forbs may have been consumed along with the grass and leaves than could be accurately observed.

Overall, on the upland grasslands consumption of grasses was significantly greater in spring and winter, and significantly lower in summer. Consumption of forbs was significantly greater in summer and fall, and lower in winter. Browse use, though always low, was significantly greater in winter, due to the ingestion of fallen leaves.

Lowland Grassland

Spring

Grasses formed the major portion, 95%, of the spring diet in the lowland grasslands (Table IV.8). Grass growth began earlier in the lowlands than on the upland grassland. Elk selected new, scattered blades of grass from amongst weathered vegetation. Consumption of forbs was low, averaging 3.3% of the diet. Although many forb species contributed to the May value (~23%), dandelion and hemp nettle accounted for over 50% of the bites. Little browse was available, resulting in browse comprising <1% of the diet.

Summer

During the summer, the lowland grassland received sporadic heavy use by wapiti. The frequency of grasses in the diet declined during summer, to 68.5%. Most grass consumption occurred on regrazed regions. The consumption of forbs reached a maximum in July (38.6% of

Table IV.8: Wapiti diets in the lowland grassland habitat as a percentage of total bites.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug
GRAMINOIDS											
Grasses	84.99	93.34	73.12	68.54	70.1	66.14	98.37	91.59	84.86	59.88	60.80
Carex	0.60	0.12	0.02	0.11	0.36	0.46	0.41	0.10	0.01		
Total	85.59	93.46	73.14	68.65	70.46	66.60	98.78	91.69	84.87	59.88	60.80
BROWSE											
Betula papyrifera									0.03		
Populus balsamifera		0.02	0.07	0.64	0.96	1.09	0.11	0.08	0.01	0.26	0.46
Populus tremuloides					0.18	0.14		0.01	0.08	0.08	0.22
Salix spp.				0.16	0.18	0.05	0.06	0.03	0.12	0.19	0.11
Amelanchier alnifolia									0.03	0.25	0.89
Cornus stolonifera											0.02
Ribes spp.										0.02	
Rosa spp.								0.03	0.23	0.21	0.27
Rubus hirtellum			0.12		0.12			0.06	0.03	0.10	0.01
Rubus melanolasius		0.01						0.49	0.09	0.22	0.13
Symphoricarpos spp.	0.06	0.01					0.01	0.11	0.19	0.21	0.70
Leaves (fallen)		0.18	0.76	4.76	3.74	1.21	.06	0.02			
Total	0.06	0.22	0.95	5.56	5.37	2.49	0.24	0.82	0.78	1.54	2.81
FORBS											
Achillea millefolium	0.29	0.08	0.07	0.21	0.06	0.02	0.01	0.24	0.15	0.13	0.18
Aralia nudicaulis	0.01									0.01	
Aster spp.	1.08	0.13		0.27	0.24		0.01	0.26	0.81	1.26	1.47
Chenopodium album										0.03	0.04
Cirsium arvense	8.43	5.82	25.81	24.77	23.11	30.87	0.73	0.24	0.05	0.03	
Descurainia sophics									0.02	0.01	0.01
Equisetum spp.									0.03		0.01
Erigeron spp.								0.01		0.02	
Fragaria glauca						0.02		0.44	0.08	0.10	0.11
Galeopsis tetrahit	0.04				0.12		0.02	1.16	3.51	12.94	2.92
Galium boreale								0.03	0.01		
Geum allepicum							0.17	0.34	0.25	0.34	0.16

Table IV.8: Wapiti diets in the lowland grassland as a percentage of total bites, continued.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Heracleum lanatum								0.05	0.04	0.04	
Lathyrus spp.								0.07	0.04	0.04	0.18
Mentha arvensis									0.02	0.01	0.01
Mertensia paniculata								0.25	0.06	0.28	0.12
Mitella nuda									0.01	0.01	
Petasites spp.								0.04	0.06		
Plantago major								0.01	0.25	0.50	1.05
Polygonum amphibium											0.01
Potentilla anserina									0.03		0.01
Rubus pubescens										0.01	
Scutellaria galericulata									0.01	0.02	0.01
Solidago spp.				0.21				0.09	1.03	1.26	0.10
Sonchus arvense								0.43	1.18	5.84	4.73
Stachys palustris	0.04							0.06	0.17	0.31	0.07
Stellaria spp.									0.01		
Taraxacum officinale	0.12					0.02		1.9	5.42	3.25	5.18
Trifolium spp.	3.95	0.22					0.01	0.16	0.86	3.56	16.82
Urtica gracilis	0.39	0.07	0.03	0.16	0.18			0.15	0.02	8.46	2.64
Vicia americana								0.01	0.07	0.07	0.25
Viola spp.								0.03			
unidentified forb							0.02	0.05	0.06	0.04	0.31
Total	14.35	6.32	25.91	25.63	23.72	30.92	0.97	5.72	14.25	38.57	36.39
Lichens					0.42						
Fungi					0.12						
Unidentified								0.01	0.01		

the diet). Forbs averaged 29.7% of the summer diet. Clover, aster, hemp nettle, dandelion, thistle, and nettle were the most commonly consumed forbs. Consumption of browse increased slightly to 1.7% of the diet.

Fall

Foraging in the lowland grasslands increased during fall. Grasses comprised 89.5% of the fall diet. Wapiti selected for green grass leaf when possible. Forb consumption declined to 10.3% of the diet. Thistle was the most abundant forb and also the most commonly used forb. Both green and cured thistle were consumed, and leaves were selected over stems. Only trace amounts of browse were taken.

Winter

Consumption of grasses decreased over winter to 69.5% of the diet coincident with a decline in availability of grasses. Wapiti selected thistle patches for foraging, resulting in thistle composing 26.1% of the diet. Few other forbs were consumed. Use of browse was low (3.6% of the diet). Balsam poplar twigs and fallen aspen and balsam leaves were the most frequent browses consumed.

Browse consumption was significantly greater in winter than at other times of the year, and ~~significantly lower in spring and fall than in winter~~ and summer. Forb use was significantly greater in summer and winter than in spring and fall, while use of grasses was significantly greater in spring and fall than in winter or summer.

Sedge Meadows

Spring.

Wapiti concentrated much of their early spring foraging in the sedge meadows. Growth of vegetation began in this habitat earlier than in others. Sedge shoots comprised almost the entire spring diet (98.3%) (Table IV.9). Consumption of forbs and browse was minimal.

Summer

Foraging in the sedge habitat declined sharply as summer progressed. *Carex* formed 15% of the June diet, but was not consumed in late summer. Decline in use of *Carex* coincided with advancing growth stage. Cattail shoots were occasionally consumed in the sedge meadows. Browse (willow) contributed 2.4% to the summer diet. Twenty-one forb species formed 89% of the diet. Asters

Table IV.9: Wapiti diets in the sedge habitat as a percentage of total bites.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
GRAMINOIDS											
Grasses	0.04	0.44	1.59		0.43	0.11	0.02	2.01	0.97		
Carex spp.	99.88	98.54	88.22	98.44	99.29	99.78	99.98	96.59	15.03		
Typha latifolia								0.24	7.42	2.92	
Total	99.93	98.97	89.81	98.44	99.71	99.89	100.00	98.84	22.15	2.98	
BROWSE											
Populus balsamifera			0.48								
Salix spp.		0.68		0.24		0.01		0.60	1.86	4.17	1.12
Corylus cornuta								0.08			
Ribes spp.											
Rubus melanolasius								0.02			
Leaves (fallen)			0.16		0.14						
Total		0.68	0.64	0.24	0.14	0.01		0.70	1.86	4.17	1.12
FORBS											
Aster spp.		0.13	4.94	0.12				0.06	34.14	69.38	77.15
Cirsium arvensis	0.04	0.06	4.62	1.[illegible]	0.14			0.01			
Equisetum spp.									0.56	0.42	
Erigeron spp.									2.78		
Fragaria glauca								0.01		0.21	0.22
Galeopsis tetrahit								0.06	1.48		1.34
Geum allepicum								0.07			
Heracleum lanatum								[illegible]			
Mentha arvensis											0.22
Petasites spp.		0.14						0.06	6.86	0.21	
Plantago major								0.01			
Polygonum amphibium									14.84	13.[illegible]	12.53
Rananculus sceleratus									1.67	0.[illegible]	
Scutellaria galericulata									1.90	2.29	1.14

Table IV.9: Wapiti diets in the sedge habitat as a percentage of total bites, continued

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug
Sium suave									0.19		
Solidago spp.									0.19		0.67
Sonchus arvense								0.03	4.08	4.38	4.25
Stachys palastris								0.01	3.34	1.67	3.36
Stellaria spp.									1.14		
Taraxacum officinale								0.05	0.19	0.21	
Urtica gracilis		0.01									
Vicia americana								0.06			
Total	0.04	0.35	9.55	1.32	0.14	0.10		0.46	75.33	92.92	98.88
Unidentified	0.03										

comprised over half of the diet, followed by water smartweed, sow thistle, and hedge nettle.

Fall

Low abundance and curing of grasses on the grasslands resulted in a return to the consumption of sedge shoots in the meadows during fall. New growth of sedge was avidly consumed (99% of the fall diet). Curing forbs were consumed infrequently. Browse contributed only 1% to the fall diet.

Winter

In winter, the sedge habitat was generally used as a walkway between forest habitats. Exposed sedge blades were consumed as the wapiti passed through the area. Cratering for forage was infrequent. Sedge blades averaged 97.0% of the diet. Forbs averaged 2.8% of the diet, with the highest forb use recorded in December. Thistle and asters were the most commonly consumed forbs.

The consumption of forbs in the sedge habitat was significantly higher in the summer than in all other seasons. The reverse was true for grasses, which were used significantly more in spring, fall, and winter than in summer. The overall use of browse in the sedge meadows was low.

Diet Diversity Index

Diet diversity indices ranged from 0 to 3 (Table IV.10). Overall, there were no significant differences among sex and age classes of wapiti. For comparisons among habitats and seasons, wapiti sex-age classes were combined. Diets from the poplar forest regions had significantly higher values than other habitats during all seasons (P<.05). That is expected, since the forest areas were the most diverse in plant species composition and structure. The diet indices in the willow habitat were also significantly higher (P<.05) than those from the upland and lowland grasslands, and the sedge meadows during all seasons except summer when *Salix* comprised the majority of the diet in the willow habitat. During summer, the upland grassland diets were the second most diverse.

Diversity indices within each habitat varied significantly with season (P<.0001). High indices were associated with high species diversity in the habitat, which generally occurred during the summer (Figure IV.16). Diet diversity in the poplar forest, upland grassland, lowland grassland, and sedge meadows were all significantly higher in summer than at other times of the year (P<.05). Lowest diversity values occurred during winter in the poplar forest

Table IV.10. Diversity indices (N=Σpi log pi) of monthly wapiti diets in the five habitats at Ministi

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October	1.2845	.0805	.9525	.0665	1.1714	.0384	[illegible]84	.0923	.0075	0035
November	1.4602	.2455	1.3612	.0637	.7792	.0143	.2482	.0437	.0754	0224
December	1.4841	.0784	1.4927	.0798	.5848	.0372	.5784	0325	4759	1288
January	1.1220	.1195	.8967	.0995	.4004	.0225	.8205	0307	.0405	.0319
February	[illegible]1112	.1870	.8233	.0577	.3747	.0335	.8275	4293	.0354	0286
March	1.4653	.0617	.9987	.0543	.3641	.390[illegible]	.7423	0511	.0131	0051
April	.6205	.0494	1.0403	.0286	.0846	.0245	.0929	.0193	0019	.0191
May	1.3947	.0643	2.2857	.0616	1.0616	.0391	.4478	0421	.1759	.0286
June	1.0517	.0736	2.5942	.0843	1.4049	.0299	.6867	.0858	1.4886	.0874
July	1.0030	.0822	2.6656	.0561	1.4124	.0417	1.3765	0742	7387	0954
August	1.0030	.0897	2.7531	.0509	1.4086	.0208	1.3207	0749	.7427	1034

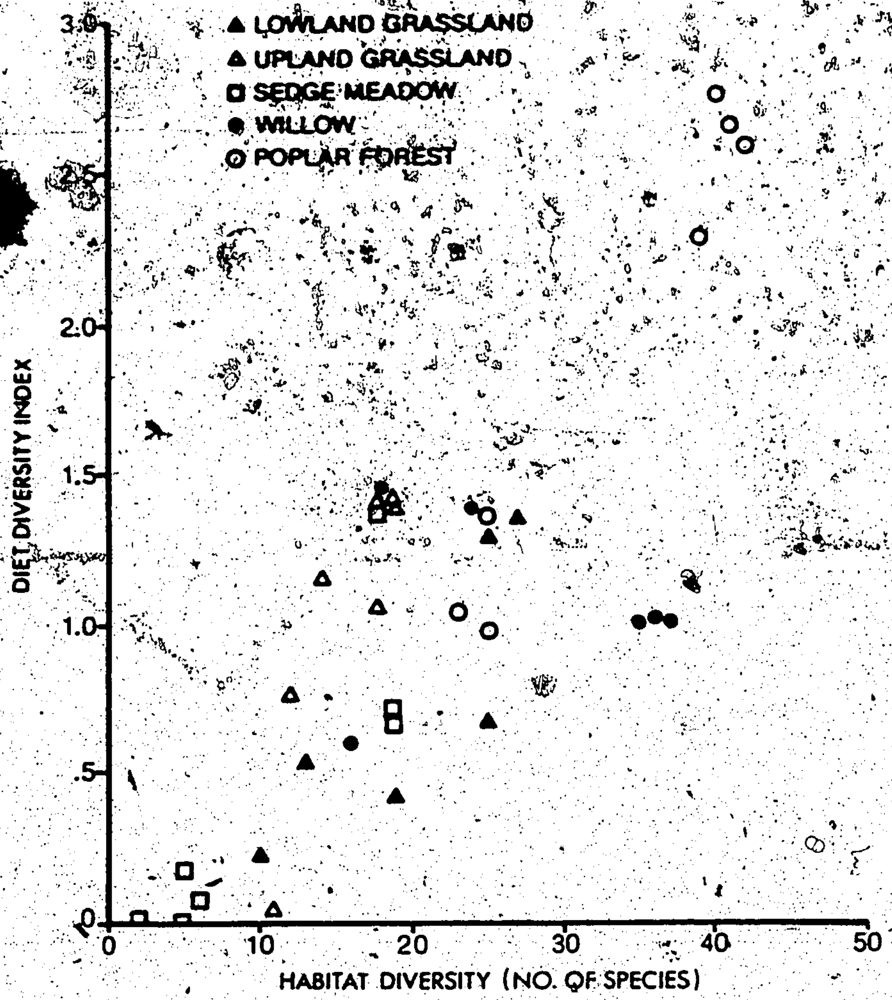

Figure IV.16 The relationship between diet diversity index, N=ξpi log pi, and the number of species or groups within a habitat.

and upland grassland, during the spring in the lowland grassland, and during the fall in the sedge meadows. In the willow habitat, strong selection for *Salix* leaves during summer resulted in a diet diversity index which was significantly lower than that of fall and winter, despite higher forage diversity during the summer. Heavy browsing pressure in the willow habitat during the winter may have prevented such intense selection, resulting in a wider use of forage items.

Foraging Selectivity.

In the willow habitat, sedges (*Carex*) were consumed almost in proportion to availability during spring and fall (Table IV.11). At those times, sedges comprised over 90% of the diet. During summer, however, wapiti exhibited a strong selection for asters. Water smartweed and sow thistle were also consumed in greater amounts than they were available in the herbage layer. Sedges and grasses were seldom eaten during the summer period, despite their large biomass.

In the poplar forest, grasses were not selected during spring and summer when more preferred forb species were available (Table IV.12). Peavine was the forb most consistently selected for during the summer. Other forbs that were selected included tall lungwort, dandelion, and sarsaparilla. However, in fall when grasses and bunchberry

Table IV.11: Proportion of herbage biomass in the diet (a) to the proportion of herbage biomass (b) in the willow habitat.

	April		May		June		July		Aug		Oct		Nov	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Carex spp.	82.9	68.9	70.9	73.3	0.00	77.0	00.0	83.5	00.0	71.7	55.7	76.8	47.0	77.1
grasses	5.2	21.6	12.2	23.0	1.7	14.4	0.9	7.7	0.8	11.8	2.8	14.3	3.7	10.9
Aster spp.	00.0	2.4	00.0	0.8	7.1	1.3	4.3	2.3	6.5	2.8	8.6	0.6	2.7	1.2
Cirsium arvense	8.5	4.6	00.0	1.3	00.0	3.4	00.0	2.5	00.0	7.3	13.3	6.1	10.7	2.0
Galeopsis tetrahit							2.6	0.1	5.8	0.2				
Mentha arvensis							0.0	1.4	0.0	1.5				
Sonchus arvensis					0.8	0.7	2.7	0.5						

Table IV.12: Proportion of herbage biomass in the diet (a) to the proportion of herbage biomass (b) in the poplar forest habitat.

	April		May		June		July		Aug		Oct		Nov	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
grasses	10.4	19.0	28.5	53.6	11.6	12.5	[illegible]	[illegible]	2.0	33.2	10.4	2.3	17.2	6.2
Aralia nudicaulis					12.0	[illegible]	[illegible]	7.4	5.1	9.0				
Aster spp.					6.0	15.5	7.0	8.4	7.6	7.7				
Cornus canadensis	0.0	0.4	0.0	4.3	0.0	11.4	0.0	12.8	0.0	7.4	7.5	0.7	3.0	0.7
Fragaria glauca			2.7	0.8	1.2	6.1	[illegible]	[illegible]	0.4	9.3				
Lathyrus spp.			5.1	1.0	29.4	11.0	0.7	8.4	26.4	5.3				
Mertensia paniculata			13.1	4.4	5.1	5.4	3.7	2.9	1.5	0.0				
Taraxacum officinale			4.2	0.0	6.3	0.0	4.6	3.2	2.1	3.3				
Viola spp.			1.8	0.0	1.7	7.3	2.4	2.8	2.3	3.5				

cured later than other herbaceous vegetation, they were consumed in greater quantities than expected. Fallen poplar leaves, which dominated the forest floor during fall were consumed less than would be predicted by their biomass. Saskatoon and honeysuckle were the only shrubs which occurred more frequently in the diet than their frequency of occurrence in the habitat for an extended time period (Table IV.13). Hazel, raspberry, rose, gooseberry, chokecherry, dogwood, and snowberry were all selected for at some point in late spring or summer.

Forbs (dandelion, clover, and aster) were selected in the upland habitat during the summer (Table IV.14) while strawberry was consumed less than it was available in the habitat. Grasses were generally consumed less than expected.

Grasses, in the lowland habitat, tended to be consumed in slightly larger amounts than they occurred in the habitat (Table IV.15). This selection decreased when more preferred forbs (dandelion, sow thistle, clover, and hemp nettle) were available. Thistle, though comprising a significant proportion of the lowland biomass, was generally not included in the summer diet. During fall, thistle was consumed less than expected.

In the sedge habitat, *Carex* was consumed almost in proportion to its availability in spring and fall (Table IV.16). In the summer, however, *Carex* was rarely consumed despite its predominant biomass. A few species of forbs - aster, smartweed, and sow thistle - were strongly selected.

Table IV.13: Relationship between frequency of occurrence of shrub species in the poplar forest habitat and their frequency in the browse proportion of the diet during late spring and summer 1981.

Species	% frequency in habitat	% May diet	% June diet	% July diet	% August diet
Amelanchier alnifolia	6.07	.46	9.91	19.16	16.23
Lonicera involucrata	.88	35.53	2.77	4.47	5.40
Cornus stolonifera	4.32	.06	6.40	2.17	5.96
Corylus cornuta	41.51	9.14	48.92	26.75	5.22
Rosa spp.	19.44	11.87	2.91	9.24	31.76
Prunus virginiana	3.24	2.92	.96	4.30	.00
Rubus hirtellum	2.80	7.36	.55	[illegible].55	.36
Rubus melanolasius	11.97	13.29	3.73	6.37	7.49

Table IV.14: Proportion of herbage biomass in the diet (a) to the proportion of herbage biomass (b) in the upland habitat.

	April		May		June		July		Aug.		Oct		Nov.	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
grasses	98.6	95.9	73.8	80.5	38.1	64.0	54.7	56.3	46.8	68.0	52.0	90.5	77.6	94.6
Aster spp.	0.7	0.2	3.6	0.6	5.0	2.1	2.4	0.9	1.7	0.0				
Cirsium arvense	0.0	3.7					0.0	4.0	0.0	2.5	0.0	2.9	0.0	1.2
Fragaria glauca			2.5	3.4	1.9	3.9	1.3	4.3	0.7	3.0	0.7	0.7	0.0	1.4
Trifolium spp.	0.0	0.4	2.4	3.0	9.1	9.7	18.3	16.6	38.1	18.9	36.0	3.0	14.5	1.5
Taraxacum officinale			20.1	8.4	44.6	17.7	20.6	7.0	12.0	4.2	9.2	1.3	0.7	0.0

Table IV.15. Proportion of herbage biomass in the diet (a) to the proportion of herbage biomass (b) in the lowland habitat.

	April		May		June		July		Aug.		Oct.		Nov.	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
grasses	98.4	65.6	91.6	87.1	93.1	86.6	58.4	65.4	64.4	55.9	84.6	73.5	87.8	73.6
Cirsium arvense	0.0	33.9	0.0	0.5	0.0	8.7	0.0	22.1	0.0	31.3	15.4	15.8	12.2	21.9
Galeopsis tetrahit			0.8	2.4	1.4	1.1	11.0	1.8	5.2	2.5			0.0	0.7
Sonchus arvensis			0.0	2.8	0.9	0.9	5.7	1.0	9.4	1.3				
Trifolium spp.							2.0	0.7	14.7	1.0	2.7	1.0		
Taraxacum officinale			1.2	2.7	3.4	0.4	3.7	1.3	2.4	1.0				
Urtica gracilis	0.0	0.4			0.0	1.3	0.0	4.2	3.5	2.0	0.0	6.9	0.0	3.5

Table IV.16: Proportion of herbage biomass in the diet (a) to the proportion of herbage biomass (b) in the sedge habitat.

	April		May		June		July		Aug.		Oct.		Nov.	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b
Carex spp.	99.9	1 0.0	96.6	1 0.0	12.3	97.4	0.0	96.8	0.0	93.4	99.9	100.0	98.5	98.8
grasses					0.0	0.3	0.0	0.5	0.0	3.5			0.0	0.8
Aster spp.					12.7	1.1	71.5	1.4	79.8	1.1				
Galeopsis tetrahit					0.0	0.3	0.0	0.2	1.0	0.0				
Mentha arvensis					0.0	0.2	0.0	0.2	0.0	0.2				
Polygonum amphibium					17.5	0.2	17.5	1.2	12.2	1.1				
Sonchus arvensis					2.7	0.1	2.6	0.1	3.5	0.1				
Stachys palustris							1.0	0.3	0.0	0.2				

Other species, such as mint, were generally not included in the diet despite their availability.

Diet Quality

Dietary Crude Protein

Dietary crude protein exhibited seasonal (Table IV.17, Figure IV.17) trends similar to forage crude protein levels (Table IV.5, Figure IV.6-8). Diet quality varied significantly with season and habitat ($P<.0001$), being greater in spring and summer than in fall and winter($P<.05$). Dietary protein increased greatly during spring, to 16.9% for all habitats. Increases in diet quality during spring corresponded to new growth of grasses and sedge shoots. Wapiti diets in the poplar forest diet contained many fallen leaves in April and had a significantly lower quality value than the other habitats. With green-up occurring in all habitats in May, diet quality reached its peak, with little difference among habitats.

Crude protein concentrations of summer diets in the poplar forest (18.0%), and sedge meadows (17.9%), were significantly greater than values for the willow diet (16.7%), and the upland grassland diet (16.5%) ($P<.05$).

Diet quality declined across habitats by 16% during fall to average 10.9%. Fall dietary crude protein levels were significantly higher in the lowland grassland (14.1%), followed by the upland grassland (12.5%), habitats than in

Table IV.17: Annual variation in diet quality (% crude protein; Nx6.25) in the five habitats.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October	10.65	.2203	8.73	.7235	14.39	.2969	15.40	.0679	10.40	.0
November	9.50	.1158	6.87	.0556	10.59	.7010	12.83	.068	9.78	.005
December	7.55	.0666	6.66	.0226	7.35	.2786	12.31	.1066	5.41	.1891
January	7.35	.0866	7.11	.0911	6.57	.0746	8.84	.1125	4.46	.055
February	6.37	.0437	7.22	.2165	6.68	.0363	6.44	.0348	4.48	.0
March	6.86	.0293	7.01	.0614	8.45	.1077	9.43	.1321	5.72	.0
April	11.72	.0477	9.23	.1522	14.85	.0675	15.45	.0383	11.98	.0
May	19.54	.0602	21.00	.8224	20.47	.0104	25.26	.1217	19.33	.0635
June	16.85	.0718	19.30	.2626	16.45	.0435	19.52	.0471	19.31	.0635
July	17.80	.0662	17.66	.4130	15.13	.0727	17.71	.5707	18.59	.8685
August	15.33	.0692	17.12	.2450	18.00	.1293	18.46	.1066	15.67	.0625

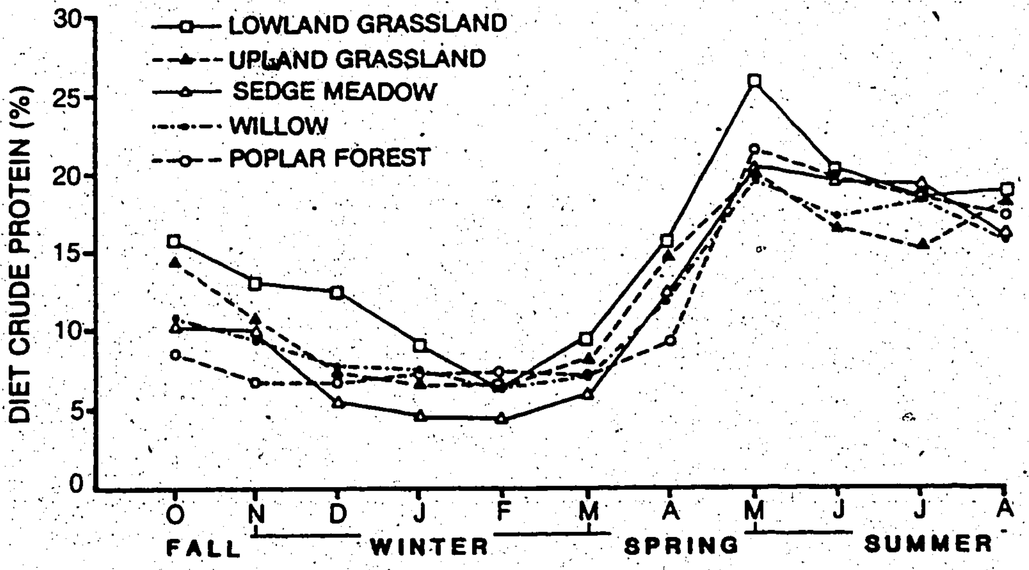

Figure IV.17 Annual variation in dietary crude protein (Nx6.25) in the five habitat types.

other habitats (P<.05). Poplar forest diets were significantly lower in crude protein (7.8%) at this time.

During winter, diet quality in most habitats remained relatively constant. The greatest variation occurred in the lowland grassland where protein content declined by about 48% from December to February. Despite this, the lowland grassland winter diet quality (9.3%) was significantly greater than the diet quality in the other habitats (P<.05). Thistle, which contained large amounts of crude protein during much of the winter, comprised a large proportion of the lowland diet. Diet quality in the sedge meadows was significantly lower than in the other habitats, and was reflected in the low use of this habitat during winter. No significant differences were found among forest, upland grassland, and willow diet quality values during winter, which averaged 7.1% crude protein.

Fecal Protein

Fecal crude protein peaked in June then declined through the remainder of the year, being significantly higher in spring and summer than fall and winter (P<.0001) (Figure IV.18). Although fecal crude protein followed the same seasonal trend as diet quality, it consistantly overestimated dietary crude protein except in May. However, the degree of overestimation among months was variable.

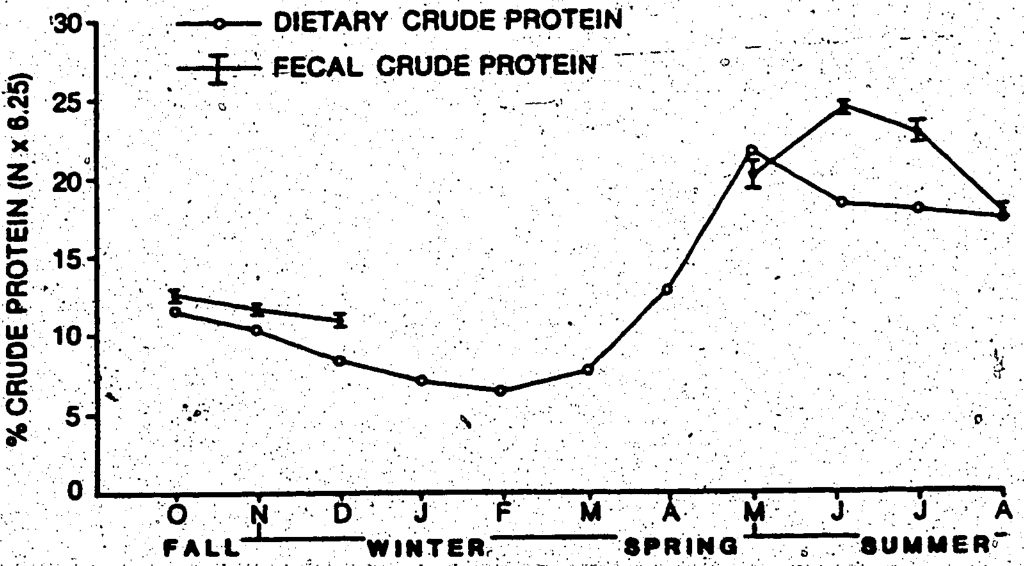

Figure IV.18 Monthly variation in fecal crude protein (Nx6.25), means and S.E., as compared with monthly variation in dietary crude protein (Nx6.25).

Acid detergent fiber content of the feces was greater in the fall and winter months than in the spring and summer (Table IV.18). Lignin content increased from spring through summer, then declined during fall. However, the largest value was recorded for the December sample. Cellulose content was variable, though fall and winter cellulose values were generally higher than those of spring and summer. Acid detergent fiber, cellulose, and lignin concentrations tended to increase during fall and early winter when dry matter digestibility of forages decreased. Ash content declined from late spring to mid summer, then increased through fall before declining again in the December sample.

Foraging Efficiency

Animals may employ different foraging strategies to satisfy food requirements, and at least some features of these contrasting strategies can be deduced from a comparison of characteristic patterns of foraging (Novellie 1978). Rate of consumption and rate of movement of foraging wapiti were examined for variation among habitats, seasons, and sex and age classes which may reflect differences in foraging strategies.

Bites/Minute

Bite rate varied significantly among seasons (P<.001) and habitats (P<.001). Wapiti averaged 14.6 bites/minute

Table IV.18: Fecal fiber, ash, and crude protein (Nx6.25) content of fall, early winter, late spring, and summer samples.

	May	June	July	Aug.	Oct.	Nov.	Dec.
acid detergent fiber	40.0	39.3	53.2	49.0	56.1	58.5	63.7
lignin	17.3	18.3	28.9	31.1	29.7	22.1	36.9
cellulose	17.0	19.9	23.4	18.6	20.6	22.7	23.9
ash	5.7	1.7	0.9	2.1	5.8	5.6	2.9
crude protein: mean	18.6	23.2	21.4	17.4	11.9	10.8	10.3
S.E.	.713	.195	.579	.316	.127	.214	.278

(b/m) in the willow habitat over the year, representing the lowest overall bite rate in any habitat. Bite rate was significantly greater in spring and summer (P<.05), declining through fall and winter to a low of 4.7 b/m in February (Figure IV.19).

In the poplar forest, wapiti averaged 16.6 b/m over the year. Bite rate was significantly greater in spring than other seasons, and the summer rate was significantly greater than that in fall and winter (P<.05) (Figure IV.20). The lowest value was recorded for December (11.1 b/m), coinciding with the first major snowfall. Bite rate tended to increase during winter and spring.

The average bite rate of wapiti on the upland grassland (33.3 b/m) was the highest overall rate recorded in any habitat. Bite rates were significantly higher in summer than any other season (P<.05), though rates remained high from late spring to late fall (Figure IV.21). The highest rate was recorded in August (49 b/m). Elk exhibited significantly lower bite rates during winter. The lowest rate occurred in early winter and was related to the wapiti cratering through snow for forage. An increase in the bite rate during late winter was attributed to wapiti foraging on small, snow-free areas of grassland.

The second greatest overall bite rate (25.6 b/m) was observed in the lowland grasslands. Spring and summer rates were significantly higher than fall and winter rates, and the lowest rate was recorded in mid winter (P<.05) (Figure

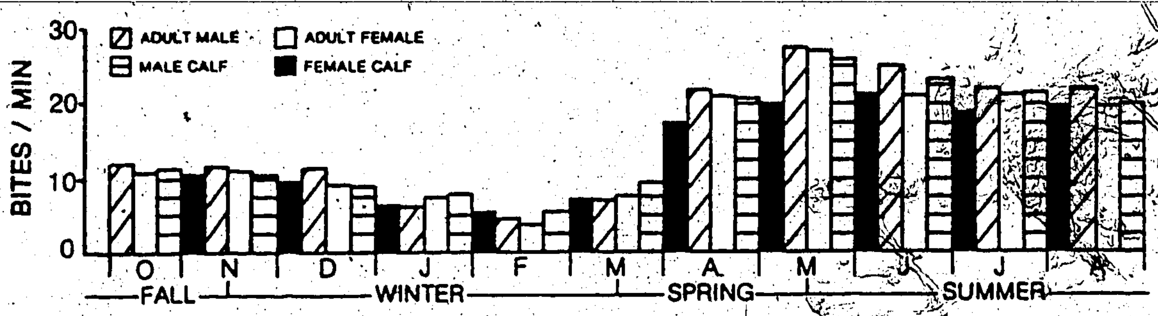

Figure IV.19 Seasonal variation in bite rates (bites/minute) of the sex and age classes of wapiti in the willow habitat.

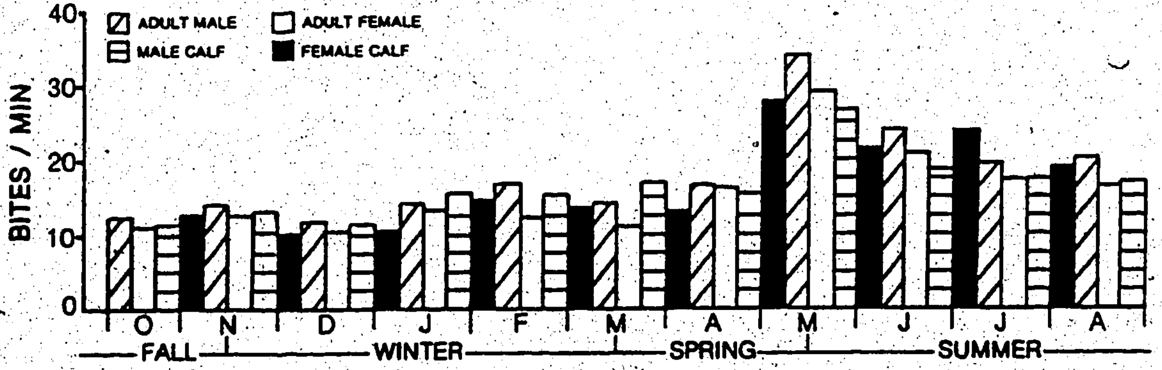

Figure IV.20 Seasonal variation in bite rates (bites/minute) of the sex and age classes of wapiti in the poplar forest.

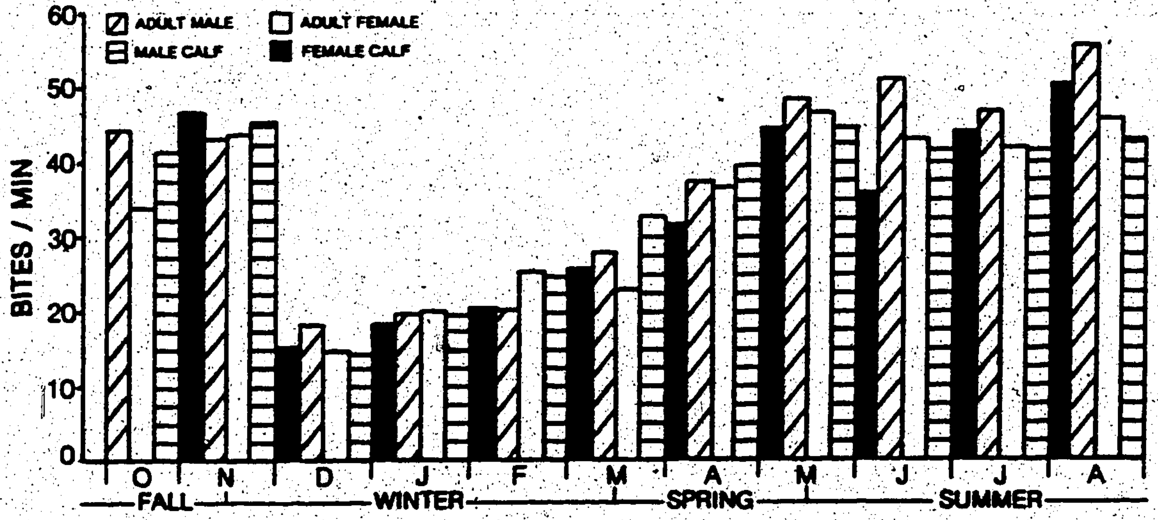

Figure IV.21 Seasonal variation in bite rates (bites/minute) of the sex and age classes of wapiti in the upland grassland.

IV.22).

The seasonal foraging rate of wapiti varied most in the sedge habitat, where it ranged from 33.3 b/m in late spring to a low of 5.1 b/m during December (Figure IV.23). Significantly greater rates were associated with wapiti foraging on green sedge shoots (spring and fall) (P<.05). Low rates were associated with wapiti foraging on cured sedge blades while crossing over this habitat during winter. No rates were obtained for the summer as wapiti spent too little time foraging in the sedge habitat to obtain representative data.

Bite rates were significantly lower in the willow and poplar forest than other habitats over most seasons, and significantly greater on the upland grasslands than other habitats during all seasons (P<.05).

Feeding Stations

The number of feeding stations per minute followed the same pattern as consumption rates (Figure IV.24-IV.28). Values were generally significantly higher in spring and summer than in fall and winter (P<.001) and lowest in winter. The average number of feeding stations per minute were 3.8/min, 3.9/min, 5.6/min, 4.3/min, and 3.0/min in the willow, poplar forest, upland, lowland, and sedge meadows, respectively. Significantly greater values occurred on the upland grasslands for much of the year (P<.01), though in

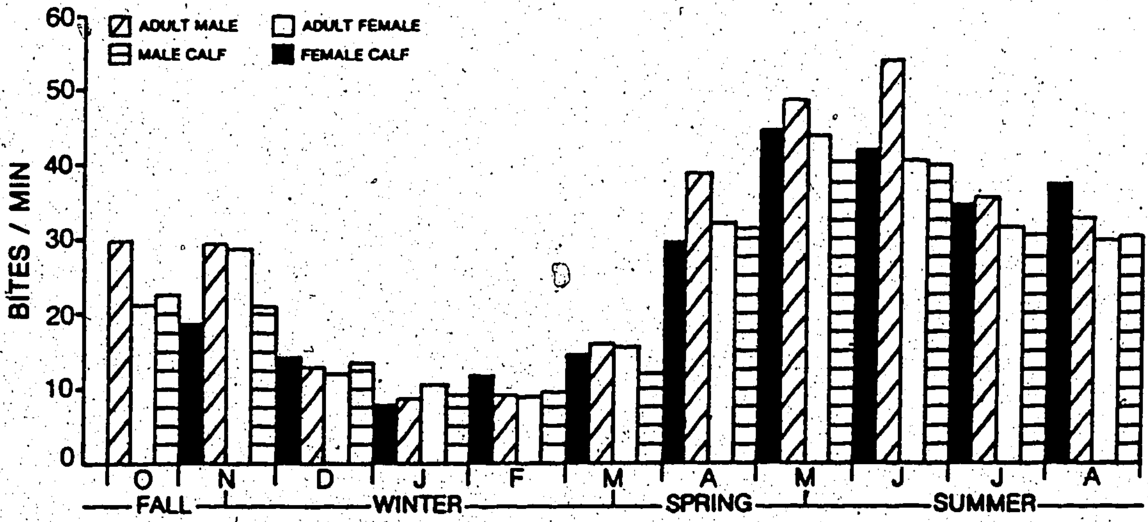

Figure IV.22 Seasonal variation in bite rates (bites/minute) of the sex and age classes of wapiti in the lowland grassland.

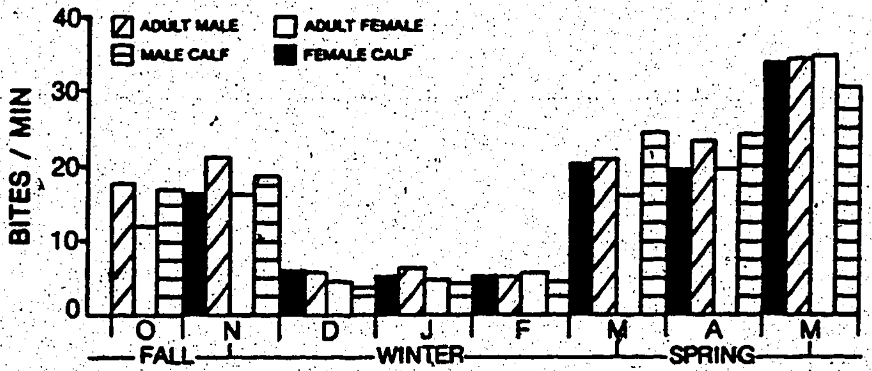

Figure IV.23 Seasonal variation in bite rates (bites/minute) of the sex and age classes of wapiti in the sedge meadows.

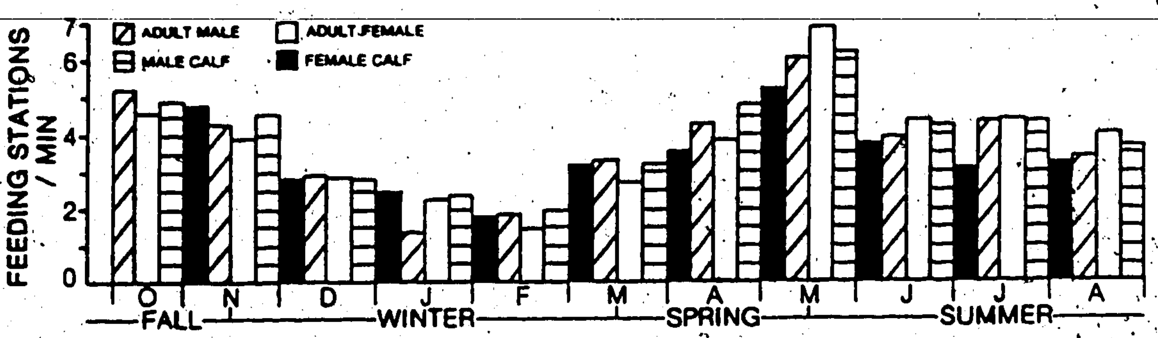

Figure IV.24 Seasonal variation in feeding station rates of the sex and age classes of wapiti in the willow habitat.

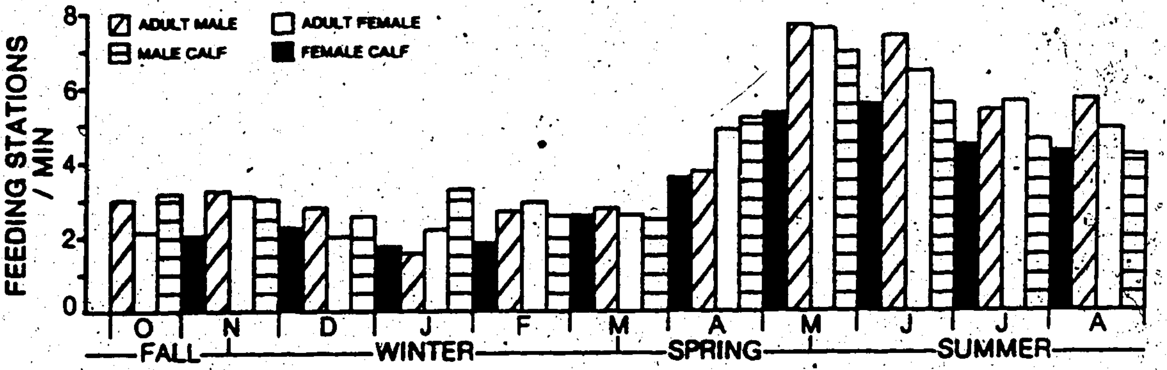

Figure IV.25 Seasonal variation in feeding station rates of the sex and age classes of wapiti in the poplar forest.

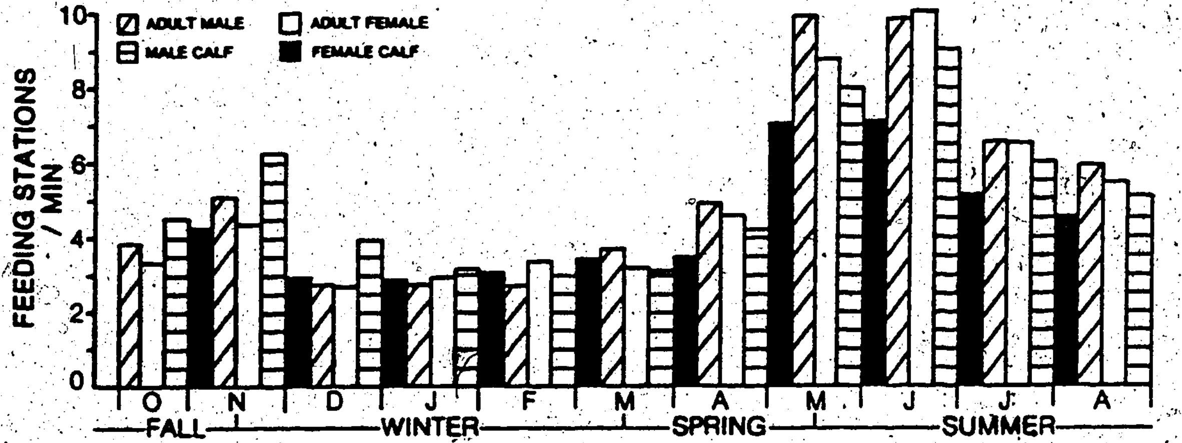

Figure IV.26 Seasonal variation in feeding station rates of the sex and age classes of wapiti in the upland grassland.

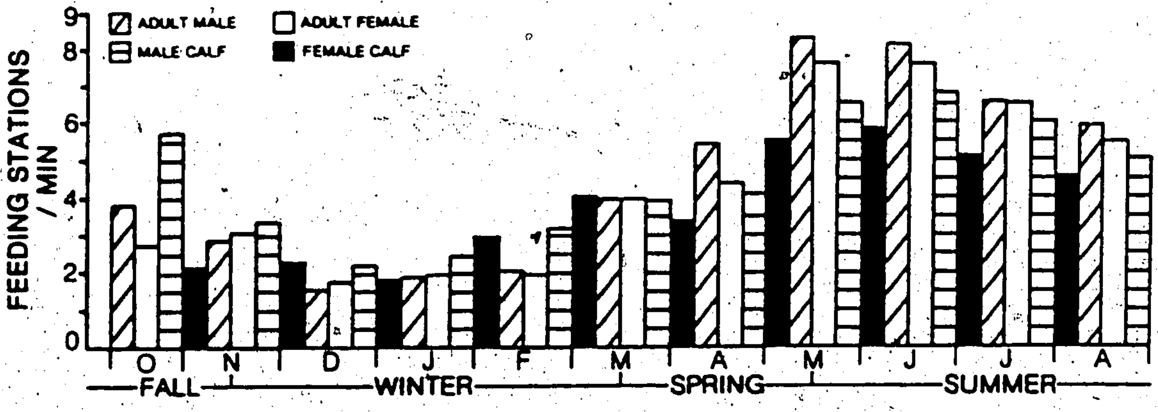

Figure IV.27 Seasonal variation in feeding station rates of the sex and age classes of wapiti in the lowland grassland.

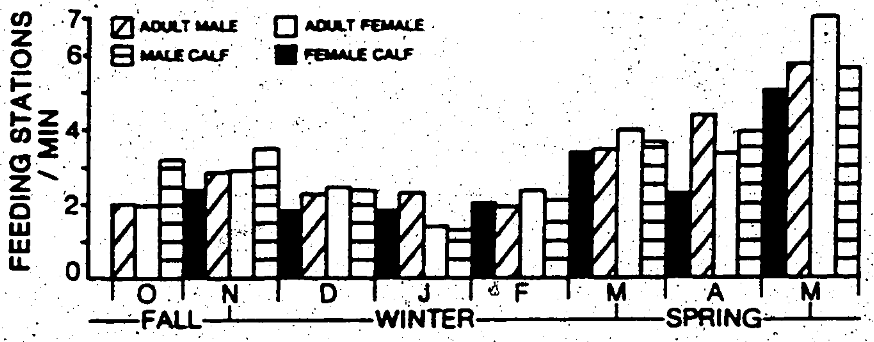

Figure IV.28 Seasonal variation in feeding station rates of the sex and age classes of wapiti in the sedge meadows.

fall the values were the greatest in the willow.

Steps/Minute

Average rates of movement while foraging were 8.8 steps/minute (s/m) in the willow habitat, 8.6 s/m in the poplar forest, 9.5 s/m in the upland grassland, 8.9 s/m in the lowland grassland, and 8.4 s/m in the sedge meadows. Foraging movement tended to be significantly greater in the summer and/or spring than in the fall and/or winter ($P<.001$) (Figure IV.29-IV.33). Greater rates of movement corresponded with greater bite rates. Snow conditions resulted in a reduction in the rate of movement, as wapiti had to crater for ground level vegetation or browse. Both these activities require more time than grazing on snow-free areas.

Movement in the sedge meadows differed from the other areas in being greater in winter. Animals spent considerable time walking between scattered clumps of sedge blades protruding above the snow. Lowest rates of movement in this habitat were recorded in late winter, early spring, and fall when the wapiti were grazing intensively on sedge shoots. Movement during foraging was apparently related to the dispersion of forage items. Concentrated food sources were associated with a decrease in the rate of movement, while scattered forage items during winter caused greater movement.

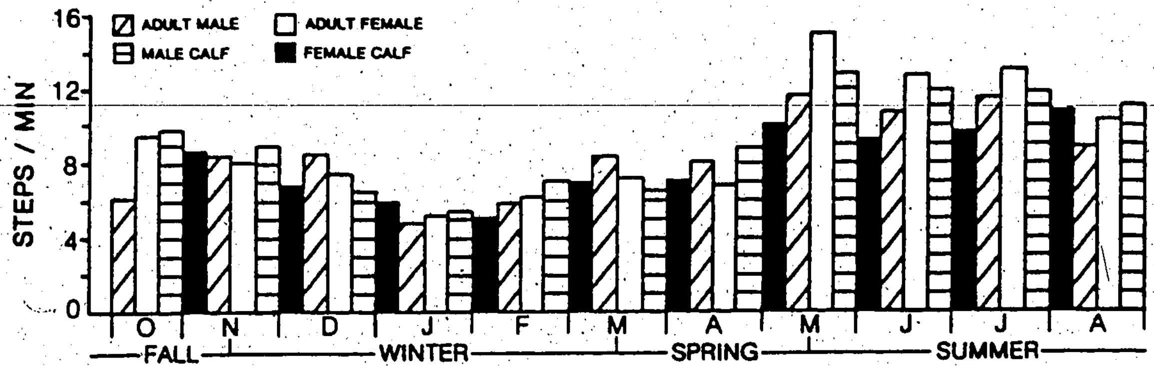

Figure IV.29 Seasonal variation in rate of movement (steps/minute) during foraging of the sex and age classes of wapiti in the willow habitat.

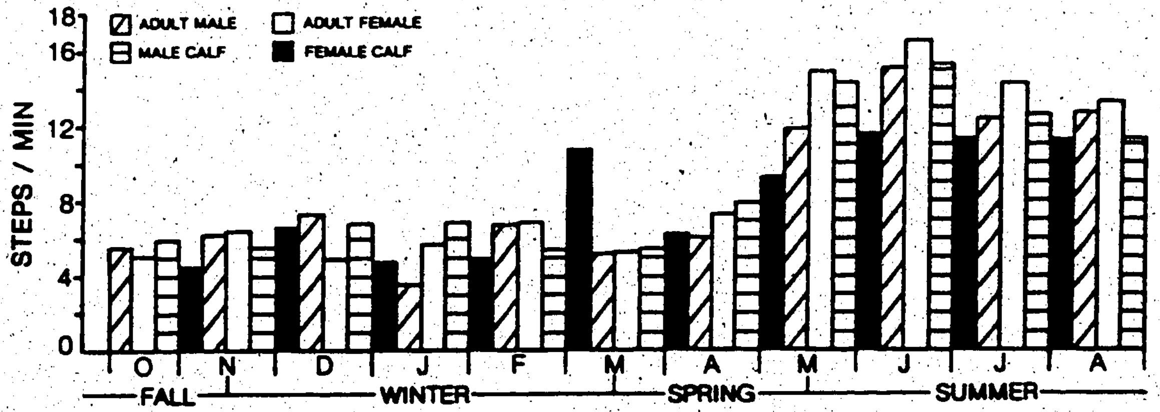

Figure IV.30 Seasonal variation in rate of movement (steps/minute) during foraging of the sex and age classes of wapiti in the poplar forest.

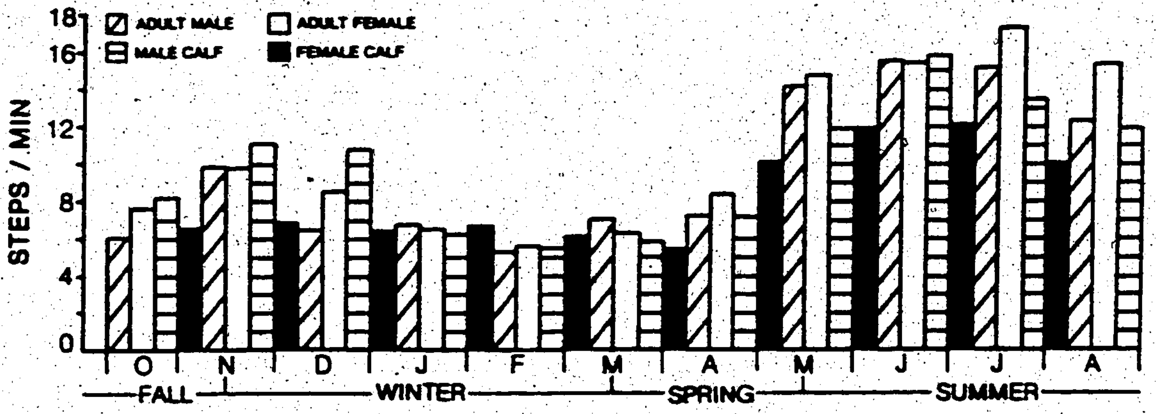

Figure IV.31 Seasonal variation in rate of movement (steps/minute) during foraging of the sex and age classes of wapiti in the upland grassland.

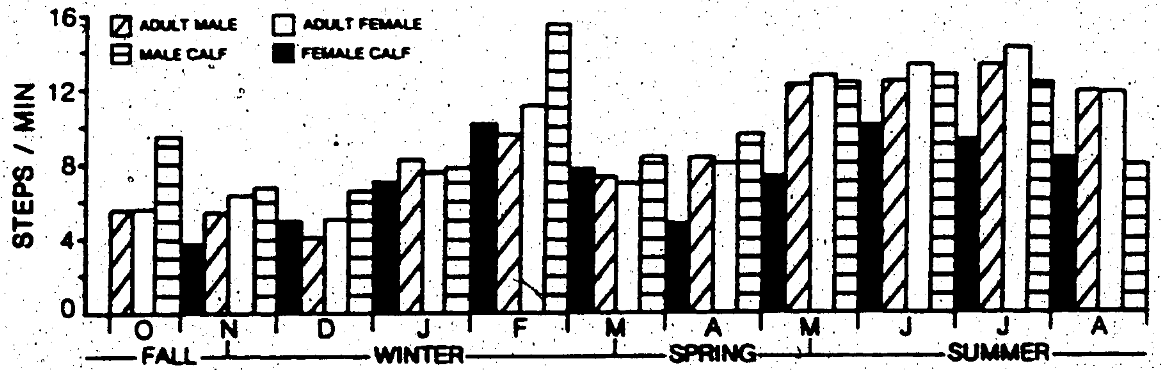

Figure IV.32 Seasonal variation in rate of movement (steps/minute) during foraging of the sex and age classes of wapiti in the lowland grassland.

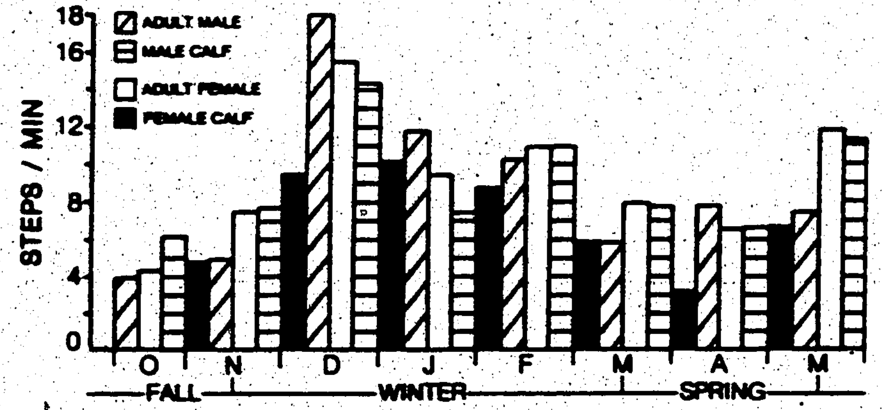

Figure IV.33 Seasonal variation in rate of movement (steps/mimute) during foraging of the sex and age classes of wapiti in the sedge meadows.

Other Activity

While foraging, wapiti spent little time involved in other activities (Table IV.19). In most habitats, the least amount of time spent in nonforaging activities occurred in fall or winter, and the most time in summer or spring. Elk in the sedge meadows were again an exception. Here, the least amount of time devoted to other activites while foraging occurred in the spring.

Differences in the overt foraging behavior occurred among the sex and age classes of wapiti, however, few consistently significant results were found. Adult females tended to have the greatest bite rate during the summer and fall. Adult males tended to have the lowest number of feeding stations per minute and the lowest rate of movement over the year.

Consumption Rates

Consumption rates (grams/minute;g/min) were significantly greater in summer (7.8 g/min) than other seasons for all habitats (P<.0001) (Table IV.20). Winter values were the lowest, averaging 1.8 g/min across all habitats. Differences among habitats varied with season. Species abundance, diversity, and phenology (which affect both bite size and bite rate) influenced these differences.

Table IV.19: Time wapiti spent in other activities during monthly foraging sessions at Ministik.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October	.378	.1367	1.688	.2750	2.501	.3265	2.563	.4485	3.390	.5843
November	.573	.3902	1.647	.3522	2.585	.3261	2.958	.5727	2.346	.4450
December	.736	.1457	1.578	.3841	2.178	.5759	.799	.1884	4.79	1.3442
January	.648	.3191	2.281	.3731	.617	.2035	1.191	.3655	8.170	1.2496
February	1.443	.4170	2.872	.4756	.788	.2771	2.018	.5387	6.371	1.3679
March	3.111	.7576	1.721	.2523	2.842	.3808	2.814	.3349	2.014	.5000
April	1.818	.4119	1.640	.3850	3.835	.9113	4.829	.7390	2.243	1.1083
May	2.749	.4363	3.256	.3913	2.244	.2992	3.686	.4218	1.573	.3245
June	3.824	.5917	4.269	.5973	3.890	.3647	5.113	.5219		
July	3.121	.3699	3.588	.4479	4.108	.4573	4.839	.3562		
August	3.096	.392	5.102	.5639	3.218	.3803	4.722	.4375		

Table IV.20: Annual variation of wapiti consumption rates (grams/minute) in the five habitat types.

	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October	2.86	.1701	2.79	.2619	5.18	.4082	5.57	.2452	3.11	.3571
November	3.00	.2261	2.43	.1082	3.17	.0606	5.00	.2917	3.68	.2223
December	2.87	.2435	2.65	.2578	1.57	.1181	2.18	.1386	1.47	.1863
January	1.99	.0222	2.74	.0961	1.44	.0214	1.36	.0635	1.27	.1196
February	1.39	.0826	1.84	.0590	1.26	.0517	1.18	.1009	1.35	.0745
March	1.39	.0642	1.72	.1662	1.63	.0559	2.66	.1694	1.67	.1349
April	2.55	.1401	2.23	.0695	2.12	.0932	1.99	.1101	2.59	.1560
May	4.27	.2215	2.58	.1851	2.58	.0686	4.11	.2074	7.23	.3396
June	9.31	.3175	6.36	.4798	5.74	.9335	12.54	.8600		
July	8.15	.3806	6.71	.2306	6.83	.1657	8.32	.4267		
August	8.87	.3602	5.65	.3700	7.88	.4270	7.82	.6951		

The interrelationships of bite rate, bite size, and consumption rate with herbaceous biomass were examined for the upland and lowland grasslands for the snow-free period. Correlation and regression analyses were used to establish appropriate relationships. Correlation and regression coefficients for bite rates with biomass were nonsignificant for both grassland areas, bite rates remaining relatively constant as biomass increased (Figure IV.34). In summer and fall, bite rate declined in the lowland probably due to selection of forbs and green leaf, respectively. Bite size increased with biomass (Figure IV.35), though in the lowland it declined slightly over summer and fall. Correlation coefficients showed a good relationship between biomass and bite size ($R=.84$ upland; $R=.74$ lowland). Regression coefficients for these were significant ($R^2=.71$, $P<.01$, $Y=.02751+.00007X$ for upland and $R^2=.54$, $P<.05$, $Y=.11556+.0298X$ for lowland). Consumption rates also tended to increase with increasing biomass (Figure IV.36), showing a strong correlation for the upland. Regression coefficient for the upland was significant at $P<.005$ ($R^2=.77$, $Y=-.6397+.00356X$). In the upland grassland consumption rates continued to increase to the maximum biomass (2,000 Kg/ha). In the lowland the highest rate was reached at about 2,300 Kg/ha, and leveled off at 3,000 Kg/ha. Consumption rates during the rut were lower than other periods at comparable biomass.

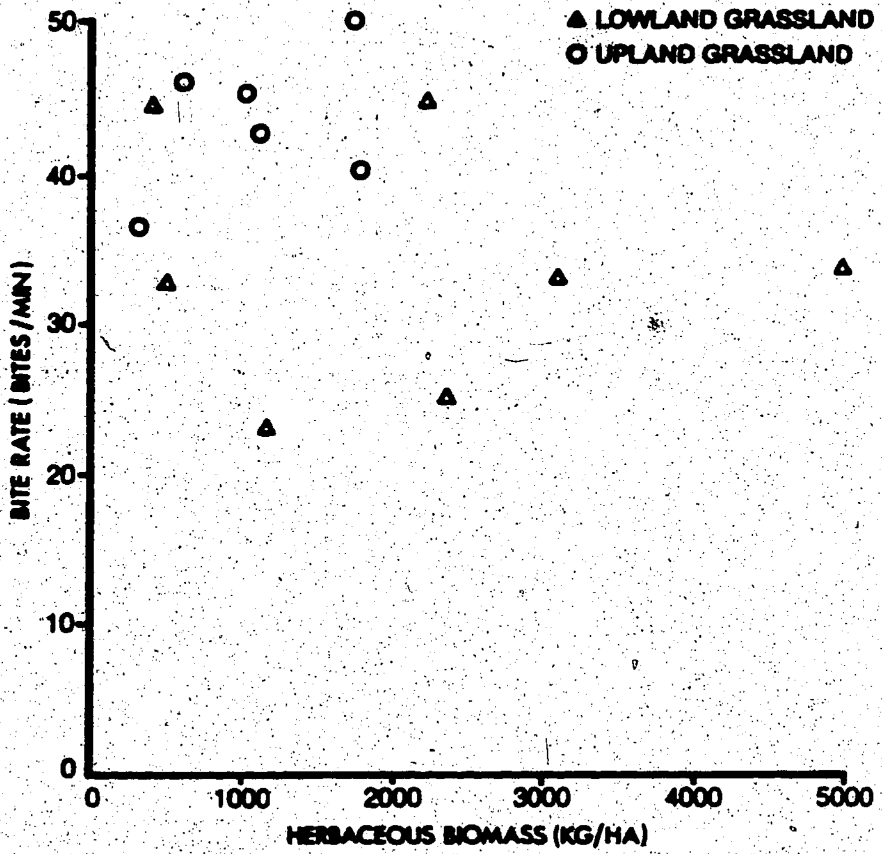

Figure IV.34 Relationship between bite rate (bites/minute) and herbaceous biomass (kg/ha) in the upland and lowland grasslands during snow-free periods.

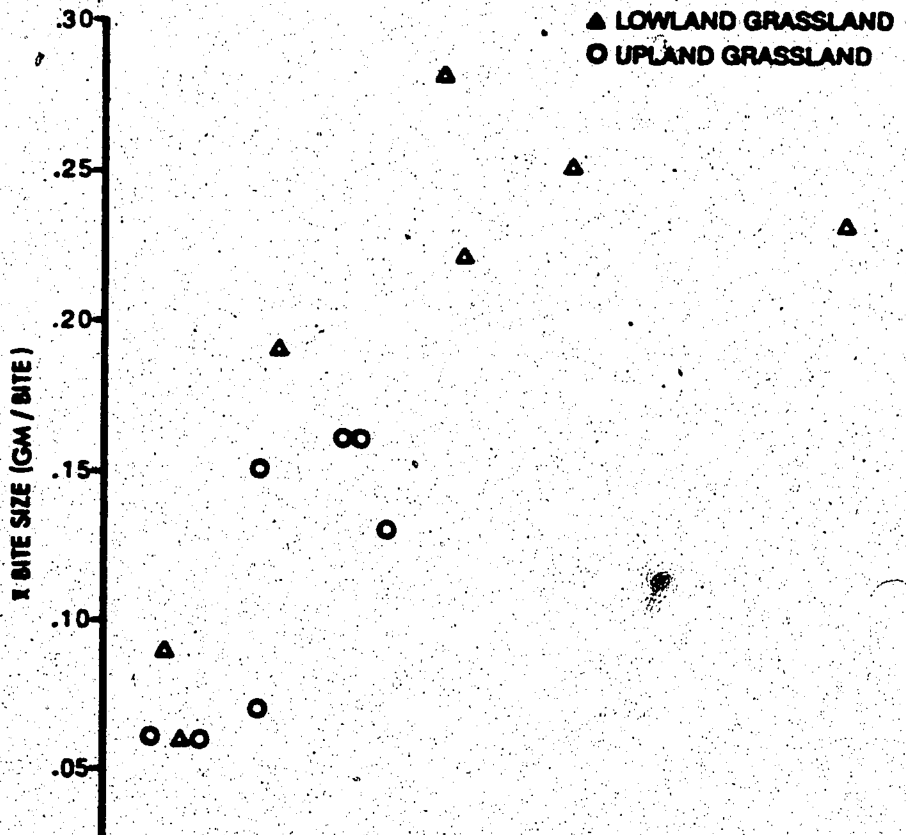

Figure IV.35 Relationship between bite size (grams/bite) and herbaceous biomass (kg/ha) in the upland and lowland grasslands during snow-free periods.

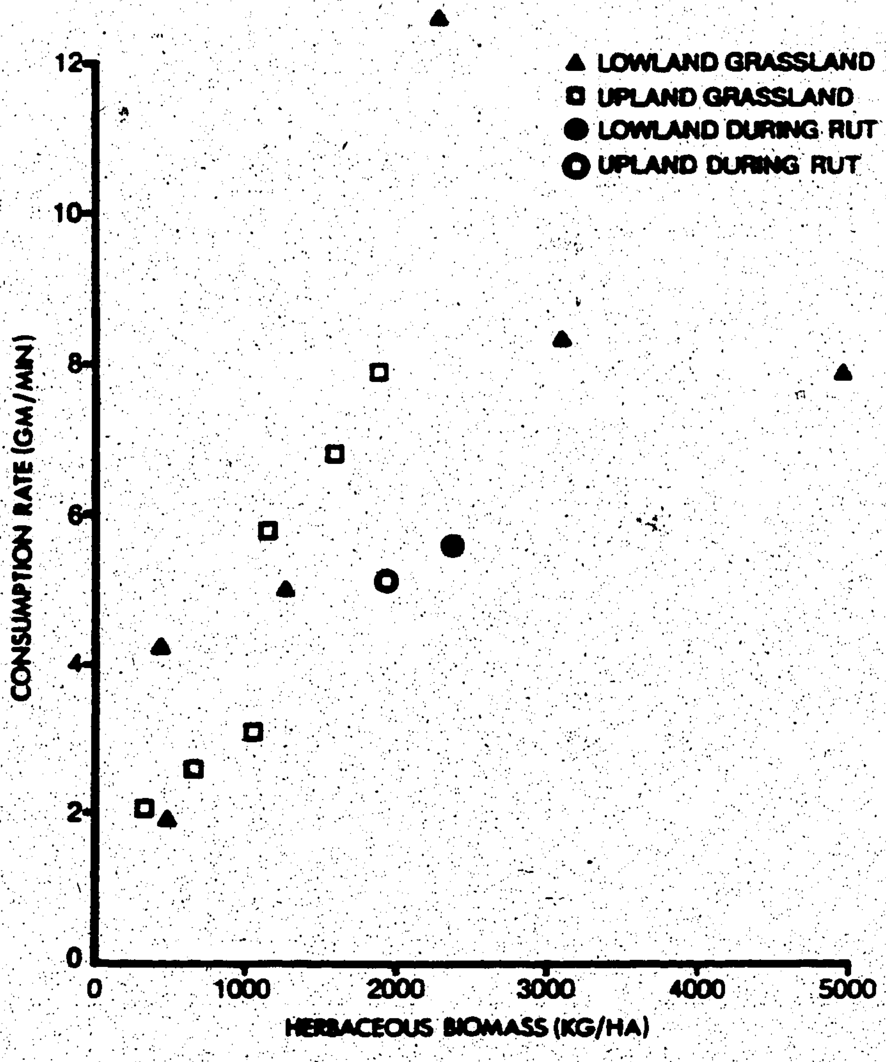

Figure IV.36 Relationship between consumption rates (grams/minute) and herbaceous biomass (kg/ha) in the upland and lowland grasslands during snow-free periods.

Correlation and regression coefficients between estimated consumption rate and eating measurements indicate that bite size was the major factor influencing gram/min intake ($R=.97$, $R^2=.94$ for upland; $R=.88$, $R^2=.78$ for lowland: $P<.005$) (Figure IV.37).

Snow

Snow influenced diet selection and foraging rates. Snow hindered foraging on the heavily grazed grasslands. Elk rarely cratered on these areas, as the vegetation was short and difficult to extract. When snow was shallow enough to be muzzled out of the way or when patches were snow-free, wapiti shifted to using these areas. Browsing increased in winter, but did not appear to be related to snow depth as Gates (1980) found. Snow depths remained below 30 cm and wapiti generally cratered through it without difficulty. The increase in browsing was mainly due to the inclusion of fallen leaves in the diet. Cratering in the forest was efficient as the leaves were readily accessible. However, the following year when greater snow depths were recorded wapiti appeared to be browsing above the snow more and cratering less.

Snow resulted in a decrease in foraging rates, and rates were lower when wapiti had to crater than muzzle snow out of the way. As a result, winter consumption rates declined greatly from that of summer (Figure IV.38).

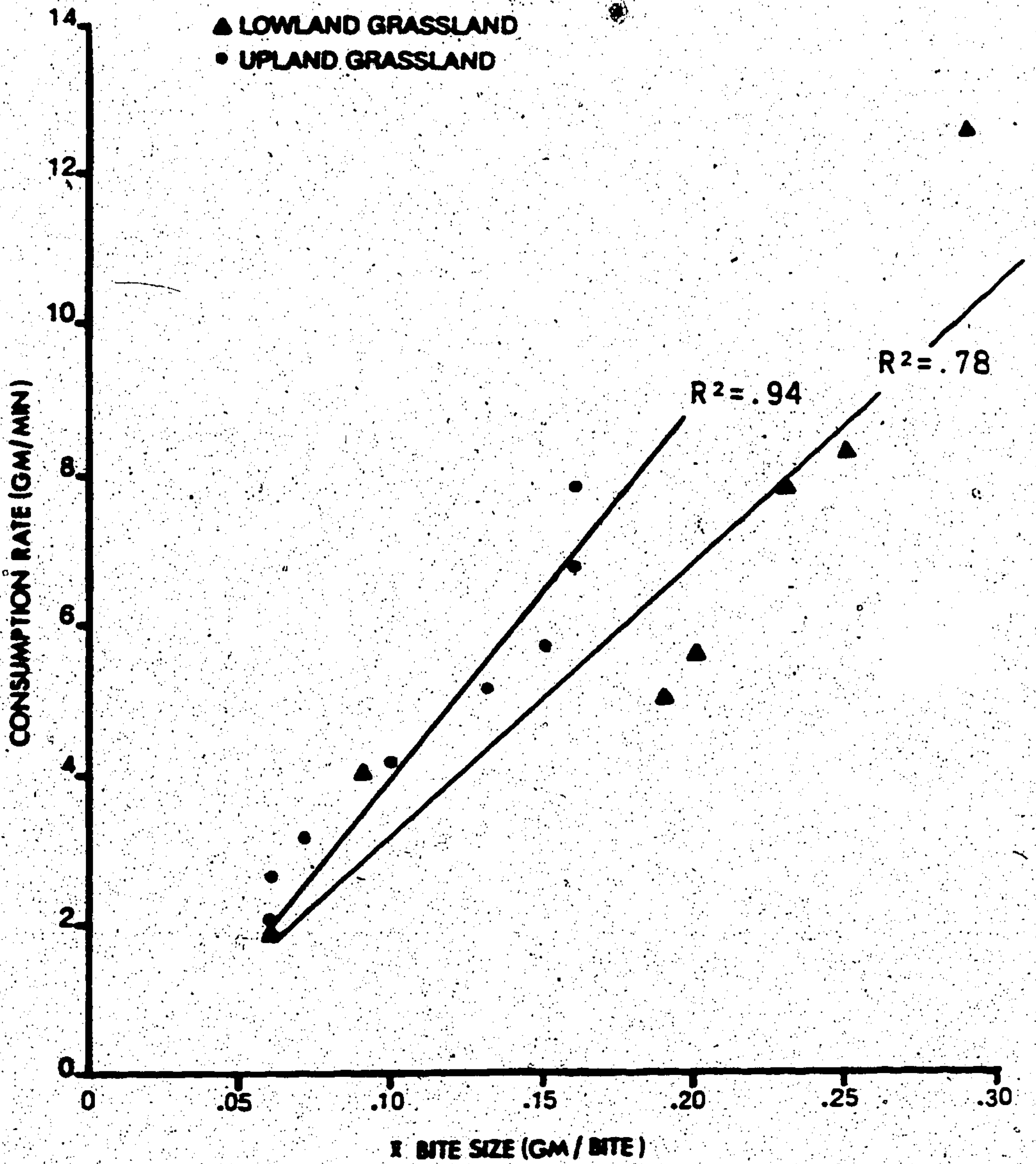

Figure IV.37 Relationship between bite size and gram/minute intake in the upland and lowland grasslands during snow-free periods.

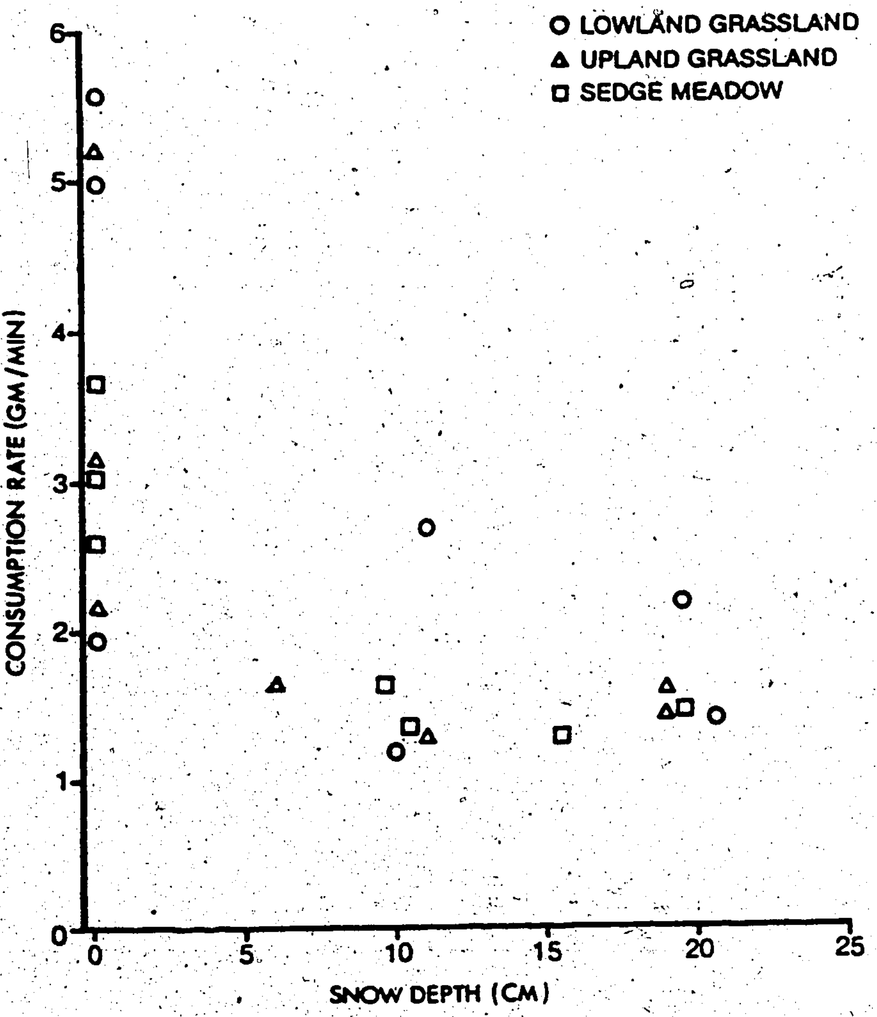

Figure IV.38 The effect of snow on consumption rates of wapiti.

Snow removal by wapiti has been discussed by Gates (1980). Young animals were initially less efficient at cratering than adults. They removed snow by straight foreward and backward strokes, rather than at an angle. The result was for snow to fall back into the crater. Cratering behavior improved with experience. Cratering efficiency of wapiti was measured as the ratio of crater strokes to grams of forage obtained. The variation in cratering efficiency among habitats was evaluated using an ANOVA. Cratering efficiency varied significantly with habitat (P<.001). Wapiti in the forest averaged .35 grams forage per crater stroke (1.8 bites/stroke) (Table IV.21). Wapiti exhibited much the same cratering efficiency in the willow, lowland, and sedge habitats. Although wapiti in the upland grassland obtained a relatively high ratio of bites per stroke, their small bite size on this area resulted in an average of .09 grams per stroke.

There was no altrustic behavior observed at crater sites as observed in caribou (Bergerud 1972). Adults displaced calves, and cows were observed to displace their own calves; though they would tolerate the presence of their own calf at a crater site more than other animals. Adult males tended to be dominant over females and calves, and all four sex and age classes had separate dominance hierarchies.

Table IV.21: Cratering efficiency (grams intake/crater stroke) of wapiti in the five habitat types.

HABITAT	December	January	February
Willow	.23	.19	.23
Poplar Forest	.34	.40	.31
Upland Grassland	.13	.12	.01
Lowland Grassland	.24	.20	.14
Sedge Meadow	.19	.20	.21

DISCUSSION

Wapiti in boreal habitats live in a strongly seasonal environment. They must contend with large fluctuations in forage availability and quality to meet nutritional requirements. Their adaptive foraging strategies enable them to adjust best to available forage resources (Geist 1982). The diet selection process is one means by which animals, within limits of anatomical and physiological constraints, can choose diets to obtain the required nutrients. In this study, diet selection and foraging patterns of wapiti were documented and were examined in view of the quantity and quality of available forages.

Vegetation Composition and Biomass

Herbaceous vegetation biomass tended to be the greatest in areas of greatest moisture availability - the sedge meadow, willow, and lowland habitats. These were also areas where graminoids dominated the herbaceous composition. In the poplar forest, grasses were insignificant in biomass. Forbs dominated the herbaceous layer in the poplar forest during summer. Despite a high diversity of forbs, their biomass was small and much of the forest floor was bare soil. Forbs were also important components of most other habitats during summer.

Forage biomass values for Ministik and other boreal mixed-wood forest regions (Bishoff 1981, Telfer and Scotter 1975, Blood 1966) are comparable or higher than information on wapiti ranges in Utah (Collins 1979) and Colorado (Hobbs 1979). Since wapiti used all habitat types, and concentration of foraging activity varied among habitats throughout the year, the boreal mixed-wood forest has much potential for supporting wapiti.

Grazing pressure reduced the height of herbaceous vegetation. Heavily grazed grassland regions (upland grasslands and portions of the lowland grassland) supported less biomass than other graminoid-dominated habitats where the herbaceous vegetation was little used during the latter growing stages. As *Carex* spp. matured in the sedge meadows and willow habitats, they were rarely consumed. Reedgrass, also occurring in these areas, was a non-preferred graminoid during the growing season. As a result, these dominant graminoids forms grew unobstructed, for the most part, during the summer.

Grazing patch differences in one habitat were also noticeable. Grazed regions of the upland and lowland grasslands were lower in biomass than comparable areas that received little use. Areas of low use were associated with old standing grasses or seasonally unselected species (thistle) which obscured and hindered consumption of forage items.

Species composition of grassland areas could also be related to grazing pressure. Heavy grazing of lowlands appears to have decreased the competitive ability of grasses and decreased their ground cover. This reduction has allowed thistle, an opportunistic invader, to form a significant portion of the standing biomass at the end of the growing season. Once established on a site, thistle was rarely eaten until fall, resulting in proliferation of this species. During fall and winter, thistle formed a significant portion of the diet selected by wapiti in these areas. In this case, thistle invasion appeared to be benefical to wapiti, as it increased the amount of biomass available for winter use.

The upland grasslands bear much of the grazing pressure of both wapiti and bison during spring through fall (Gates 1980; personal observation). The result has been the formation of a plant community (bluegrass-clover-dandelion) that is maintained in a state of regrowth for much of the growing season. Forage quality on these areas was probably increased as a result of regrazing (Anderson and Scherzinger 1975). However, when forages began to cure, animals rapidly depleted this forage resource. The low pre-winter biomass on upland grasslands probably influenced the low winter useage by wapiti in comparison to when they were first introduced (Gates 1980).

Browsing pressure, by both wapiti and moose, can also affect the phenology and composition of browse species. Shrubs inside the compound were lower in height and hedged in comparison to those outside the compound, reflecting the intensity of use. Young aspen and balsam poplar were almost eliminated from the forest understory, and the encroachment of these species onto the grasslands was prevented. Cairns

(1976) also found that browsing pressure at Elk Island National Park prevented encroachment of poplar forests onto grasslands.

Forage Quality

Patterns of change of forage quality at Ministik were related to plant phenology. All plants exhibit annual cyclic fluctuations in growth, nutrient content, texture, and palatability (Nelson and Leege 1982).

Forage crude protein and digestibility were greatest during early stages of plant growth. The proportion of meristematic tissue, which is high in protein content, is greater in early growth stages and the fiber content of the plant is lower than in more advanced growth stages (Dietz *et al*. 1958). As the plant matures, the proportion of structural carbohydrates increases, resulting in a decrease in the concentration of protein and an increase in the fiber components of the plant (Dietz *et al*. 1962, Olberg 1956, Burzlaff 1970, Cook 1972, Willard and Schuster 1973, Short *et al* 1974). Thus, as forage production increases, nutritional quality tends to decline. A large decrease in crude protein content of all forages occurred from late spring to summer, a period of rapid maturation. During summer, forage crude protein content declined, though to a far lesser extent and some forages exhibited slight increases in August. This can be explained in terms of plant phenology and animal selection. Since heavy grazing maintained the grassland areas in a state of regrowth, forage protein concentration on these areas would be expected to be greater than on similar areas in advanced growth stages (Mackie 1970, Hebert 1973, Anderson and Scherzinger 1975).

Also, many forage items exhibited staggered growth stages. That is, early growth forms to advanced reproductive stages were interspersed throughout the habitats. As forage quality was based on plants and plant parts that wapiti were observed to ingest, selection for early growth forms and specific plant parts (leaves) reduced the expected changes in the crude protein content. Forage crude protein content and digestibility continued to decline through fall and winter. Mature, senescent grasses, which dominated the sedge meadows and willow habitats, had lower protein concentrations than grasses on heavily grazed areas. Yet these lower quality grasses were included in the diet more as the biomass on the grasslands declined.

Browse varied in protein content and digestibility in relation to the plant part consumed. Cured leaves contained a higher concentration of crude protein and were more digestible during winter than other parts (twigs, stems, branches, bark).

Forage crude protein values for summer at Ministik and Elk Island (Bishoff 1981) were comparable or slightly lower than values recorded on summer ranges in Utah (Collins 1979, Palleson 1979), Washington (Schommer 1978, McReynolds 1977), and Colorado (Hobbs 1979). The digestibility of forages was generally comparable to that in Utah (Collins 1979, Palleson 1979) and Washington (Schommer 1978). Summer ranges in boreal mixed-wood and montane areas generally provide enough digestible energy and protein to meet the requirements of wapiti. Schommer (1978), however, found a mid-late summer period where deficiences were evident for cow wapiti.

In winter, digestibility of forages, overall, was comparable among ranges. The crude protein content of boreal mixed-wood forages remained higher than that of most montane regions. McReynolds (1977) found forage crude protein to exceed minimum requirements year round, though Hobbs (1979) and Schommer (1978) found forage crude protein to be close to or below critical levels (5%). Bishoff (1981) and results from my study suggest that boreal mixed-wood forest contains forage of adequate quality to provide for winter requirements (see Nelson and Leege 1982). Bishoff (1981) points out, however, that overstocking can lead to overbrowsing. The inclusion of 2-3 year old wood (of lower forage quality) in the diet would probably not provide adequate winter nutrition.

Seasonal Diet

Elk consumed a wide variety of forage species throughout the year. However, only a few forages were major items in the diets in each habitat. Forage selection varied with forage availability, and with species diversity and relative abundances in the habitats over the year. The seasonal diet of wapiti at Ministik followed similar trends to previous diet studies in the boreal forest regions (Holsworth 1960, Blood 1966, Telfer and Cairns 1979, Gates 1980). In comparison to Montane ranges (Boyd 1970, Constan 1972, Cowan 1947, Hansen and Reid 1975, Kirsh 1962, Knight 1970, Mackie 1970, Marcum 1979, Morris and Schwartz 1957, Murie 1951, Singer 1979, Stevens 1966), wapiti in the boreal mixed-wood tend to include more browse in their diets, and browse becomes the major component in winter.

Spring

Grasses were the major components in the spring diets in most habitats. In the forest habitat, where grass biomass was small, grasses formed a lesser portion of the diet. Sedges were most heavily used in early spring. Sedges initiate growth earlier than other forages, and the shoots can be selected from the surrounding cured, and rotting vegetation. As grasses, mainly bluegrass and brome, green-up, wapiti consumed these in preference to sedges.

Summer

Browse and forbs were important components in the summer diets of wapiti in habitats where their availability was high. In heavily forested regions, browse may dominate the summer diet (Blood 1966, Hunt 1979), whereas in habitats similar to Ministik (Elk Island) Holsworth (1960) estimated forbs to comprise the majority of the diet. Forb species that were selected at other locations, as well as Ministik, include asters, peavines, dandelion, and sow thistle. Clover was frequently consumed on open, grazed-grassland areas at Ministik and at Elk Island (Holsworth 1960).

Willow (*Salix* spp.) was strongly selected in the willow habitat during the summer. At other locations where willow is present, wapiti also include it in their diet (Kufeld 1973). Aspen, which is an important browse in similar areas (Holsworth 1960, Blood 1966, Hunt 1979), was not a major component of the summer diet at Ministik. Low availability of young trees was probably the limiting factor. Most small trees in the size range that could be browsed by wapiti were broken down or previously heavily browsed by moose and wapiti. When aspen leaves were made available (blown down by winds), they were actively selected. Shrubs which were browsed the most frequently were those which occurred most frequently in the understory (hazel, rose, raspberry, saskatoon). Gates (1980) reported that dogwood and chokecherry were important browse species at Ministik when wapiti were first introduced. Although wapiti avidly consumed these species when encountered, they contributed little, overall, to the diet. Heavy use in the past may have resulted in these species being overbrowsed.

Fall

Blood (1966) and Hunt (1979) reported browse to be the major component of the wapiti fall diet in eastern parts of the boreal mixed-wood forest. However, at Ministik grasses were the major diet components in most habitats. Green sedge shoots were again consumed in the sedge meadows and willow habitat. On grassland areas, grasses increased in importance in the diet as forbs began to cure. Browse, however, was the main forage class consumed in the poplar forest. Fallen leaves, mainly those of aspen and balsam, comprised the majority of the forest diet. Although observations of wapiti consuming fallen leaves had not been reported before at Ministik, Holsworth (1960) found that the winter diets of wapiti at Elk Island included 20% litter which included fallen leaves. Hobbs (1979) also reported that wapiti in Colorado frequently consumed aspen leaves when in the aspen forest habitat. Moose at Ministik also spent much of the early winter 1982 foraging on fallen leaves (personal observation). The relatively large biomass and forage quality of fallen leaves suggest that they are a valuable diet component.

Winter

Grasses were the major components of the diets in the grassland and meadow areas during winter. Gates (1980) reported that, overall, wapiti spent more time grazing in the winter than browsing. However, wapiti foraging was largely concentrated in willow and forest habitats during the 1980-1981 winter, probably as a result of low biomass on the preferred grassland areas. Thus, browse appeared to be the most important winter forage, as was found to be the case in most boreal mixed-wood forest studies (Blood 1966, Hunt 1979, Telfer and Cairns 1979). Fallen leaves, again, were the most frequent browse consumed.

Aggregate Seasonal Diet

A total diet was estimated for each season using Gate's (1980) habitat selection data for wapiti at Ministik. Seasonal diet composition for each habitat was multiplied by the fraction of time wapiti spent foraging in these habitats. Values were then added for all habitats within one season (Figure V.1). Grasses dominated the diet over most of the year. Forbs became the major component of the diet during summer. Browse consumption was relatively low (≈20%) except during winter when it accounted for one-third of the diet. Caution must be taken when interpreting these results. Changes in habitat selection since Gates' (1980) study were evident during the 1980-1981 winter. Wapiti spent less time foraging on the upland grasslands and more in the forest and willow areas. Thus, the importance of browse in the winter diet is underrepresented here.

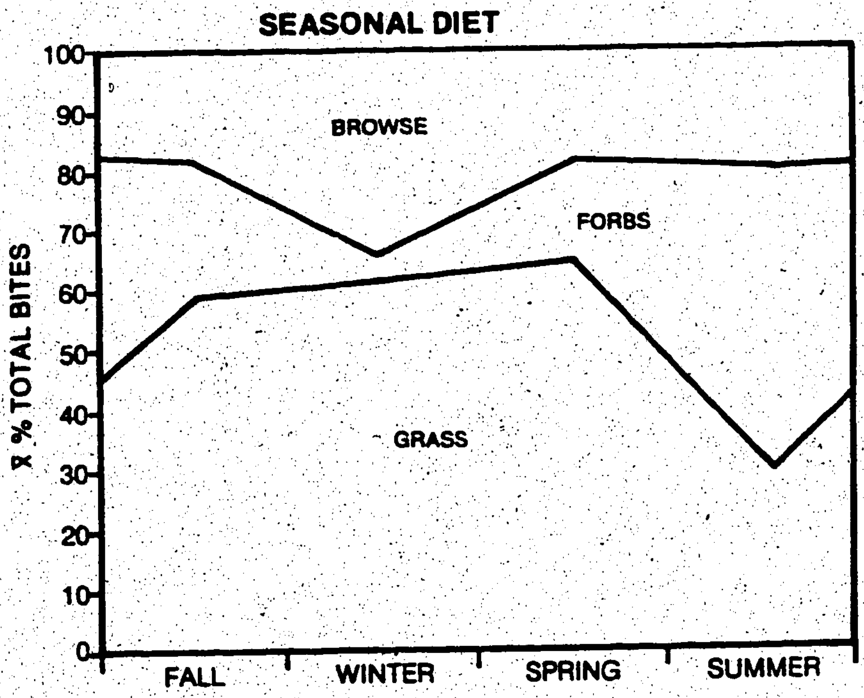

Figure V.1 Aggregate seasonal diet of wapiti in the boreal mixed-wood forest region of Ministik based on % of total number of bites and time spent foraging in each habitat (Gates 1980).

Selectivity

Despite including mostly common forages in the diet, wapiti exhibited preferences for a number of forage items. A preferred species may be defined as one which occurs proportionately more in the diet of an animal than it occurs in the environment (Petrides 1975). Preference for a plant species reflects the quantity and also the rate of consumption of that species (Ivins 1962). Preference ratings (see Krueger 1972) attempt to measure the degree of selectivity that is exhibited for specific forage items (Hobbs 1979).

The degree of selectivity during foraging varied with season, and among habitats depending on vegetation abundance and diversity, and the relative abundances of preferred and non-preferred forage types. The ability of wapiti to exhibit wide variation in selectivity (also reported by Hobbs 1979 and Collins 1979) allows for considerable alteration of the dietary components. Hobbs (1979) found that wapiti were capable of selecting diets of similar quality and similar portions of forage classes despite differences in availability. This ability to selectively alter the diet allows for an attenuation of the nutritional fluctuations in forages. By selecting browse in late winter, wapiti on Hobbs' (1979) study area were able to maintain a crude protein intake above 5%. Hobbs *et al*. (1980) state that the wapiti are foraging in an optimal manner.

The theory of optimal foraging (developed by McArthur and Pianka 1966, and Emlen 1966; reviewed by Schoener 1971, Krebs 1977, Pyke *et al*. 1977) attempts to formulate the basis of selection by an optimally efficient forager, and from this to predict diet choice. The theory is based on the assumption that natural selection acts on animals to maximize their foraging efficiency. Foraging efficiency is measured in terms of a "currency" (Schoener 1971); energy being the most common. This theory has generally not been applied to large herbivores (though see Belovsky 1978) due to limitations of foraging constraints (bulk intake and passage time) discussed by Westoby (1974). Hypotheses developed from the theory (see Ellis *et al*. 1976), however, have been applied to large herbivores.

According to the theory of optimal foraging, selectivity should increase with increasing forage abundance (Emlen 1966). Hobbs (1979) found that wapiti were more selective during the start of winter when forages were more abundant than during late winter. Wapiti at Ministik exhibited the greatest degree of selectivity during the summer, when forage diversity as well as forage abundance was highest. Selectivity appeared to be the greatest where forage quality differences between forage items were the largest. In the sedge and willow habitats, forbs (mainly asters) were selected from among mature reedgrass and sedges. Although these graminoids dominated these areas, they were non-preferred, and of lower quality. On the upland grasslands, in which quality differences between forbs and regrazed grasses were less, forbs were selected but grasses still formed a large portion of the diet.

Selectivity declined during the fall and winter, as would be predicted by the optimal foraging theory (Emlen 1966). As species diversity, abundances, and forage quality declined, species and plant parts that were rarely included in the summer diet were frequently ingested.

Although large herbivores tend to select diets of higher quality than the surrounding vegetation, the preference for a particular forage often cannot be consistently related to forage characteristics (Ivins 1962, Scotter 1965, Radwin and Crouch 1974, Tucker *et al*. 1976). In Radwin and Crouch's study forage characteristics included protein content, fiber characteristics, sugars, dry matter, mineral content, essential oils, moisture, and dry matter and cellulose digestibility. Hobbs (1979) suggested that if the unit considered is the plant part (what the animals ingest) rather than the entire plant, a consistent relation might be found. At Ministik, forages representative of those consumed by wapiti were analyzed for crude protein content. In some instances, wapiti preferred species which contained greater amounts of crude protein (peavine, aster) than other species. However, this was not a consistent finding, and wapiti often consumed large amounts of forage with lower protein values. Secondary compounds, which act as toxins to rumen-micro-organsims (Freeland and Janzen 1974), play an important role in winter forage selection of subarctic herbivores (Bryant and Kuropat 1980). Bryant and Kuropat (1980) found that moose forage preferences were not well correlated with crude protein content of browse but were strongly negatively correlated with the resin content. Preferred browse species such as willow and aspen contained less resin (reflecting levels of plant secondary compounds). Resins lower rumen microbe numbers, leading to increased rumen turnover times (Bryant and Kuropat 1980). Thus starvation can occur despite a full rumen. The value of being a generalist feeder is that the effects of toxic plant chemical defenses is reduced (Freeland and Janzen 1974). It is likely that wapiti choose their diets based on a number of nutritional criteria, resulting in partial preferences (Westoby 1974).

Plant Phenology and Spatial Distribution

Plant phenology was an important factor influencing diet selection of wapiti. Species that greened-up before others in spring were those most heavily used. As more preferred forages inititated growth, wapiti shifted to these. Early growth forms or plants maintained in an early phenological stage were selected over mature or cured forms. If mature plants were consumed, the leaves or leaves and upper portions of the stems were stripped from the lower portions of the plant. In browse species, leaves were selected over twigs and branches.

The seasonal pattern of use of many species could be related to the phenological stage of that species and of the surrounding species. For example, thistle was rarely consumed during early growth stages, but in the fall both green and cured thistle was consumed. Curing and decline in abundance of more preferred species may have influenced the inclusion of thistle in the diet.

Spatial distribution of forages may also influence plant availability and use. Krueger (1972) stated that uniformly distributed plants may occur more frequently in the diet than plants with irregular distributions. That appeared to be the case for wapiti at Ministik. The wapiti fed continuously over an area, selecting for specific items as they came to them, rather than moving between dispersed patches.

Vertical distribution of plants and plant size also affect forage consumption (Hobbs 1979, Collins 1979). Matured grasses and sedge tend to interfere with the selection of forbs and early stages of grass growth. Shrubs, and thistle also hindered consumption of plants that grew in proximity to them. Small plant size may also prevent selection from surrounding forages, as was also noted by Hobbs (1979).

Diet Quality

Diet quality is an indication of the nutritive value of the diet in relation to the nutritional requirements of an animal, which vary with season, age and sex. Diet quality is greatly influenced by forage quality. Yet, ruminants tend to select diets of higher nutritional quality than found in the environment (Arnold 1964, Klein 1970). Selection for specific plant parts, or alteration of the proportion of forage classes in the diet can compensate for changes in forage quality (Hobbs 1979).

Since the forages collected were intended to duplicate those ingested by wapiti, diet quality exhibited seasonal trends similar to that of forage quality. Crude protein content of the diet was highest in spring and summer, declining through fall and winter. Much of the winter foraging occurred in the poplar forest regions, and little occurred in the sedge meadows. Thus the overall winter diet quality (based on nitrogen levels) would probably be greater than 7% crude protein. McReynolds (1977) also found that wapiti winter diets in Washington exceeded 7% crude protein. In both cases, diet quality exceeds values estimated for the maintenance requirements of wapiti. McCullough (1969) concluded, based on studies of deer and domestic ruminants, that diets containing 7% protein are adequate for wapiti during winter. Nelson and Leege (1982) estimated, from wapiti feeding trial data, that crude protein content of forage required for wapiti maintenance would be about 5.7%.

They also concluded that wapiti on browse ranges would require higher crude protein levels, due to a reduction in consumption rates and lower digestibility.

Hobbs (1979, 1981), however, found wapiti winter diets in Colorado to contain on the average 5.4% crude protein. Red deer (*Cervus elaphus*) were capable of maintaining body weights on diets containing 5% crude protein (Maloiy *et al.*). Robbins *et al.* (1975) predicted that when forages consumed by deer (*Odocoileus* spp.) contained less than 4.8% crude protein, the apparent digestibility of the diet would be negative. Hobbs (1979) and Nelson and Leege (1982) conclude that wapiti diets containing much less than 5% crude protein would be protein deficient, and would also decrease the rate of carbohydrate digestion. At Ministik, the diet quality was below 5% only in the sedge meadow during the winter. Therefore, the diets in the poplar forest, willow, and grassland habitats should have provided sufficient protein throughout the winter.

Hobbs (1979) found that when grass and browse were equal in protein content, animals consumed primarily grass and thereby maintained relatively high protein intake and diet digestibility. When grass protein fell to a critical level (≈ 5%), wapiti shifted to browse which contained higher protein levels at that time. Elk were limited by the availability of forages which contained adequate protein content and not absolute forage biomass. At Ministik, habitat usage, and therefore diet selection, appeared to be influenced by both quality and quantity of forage. Regrazed grasslands had the highest protein quality but also the lowest prewinter biomass. Elk tended to use these areas only when snow depths were shallow and cratering was not necessary for snow removal. The sedge meadows, with a large prewinter biomass but low forage quality (≈5%), were only occasionally used. The forest area of intermediate forage quality and biomass, and also the cover type largest in area, was used the most during winter.

Hobbs (1979) used winter diet quality data (crude protein content, cell wall components, and *in vitro* digestibility) in a simulation model of wapiti energy and nitrogen balance. He found that in habitats where wapiti energy status was most favorable, nitrogen balance was most negative. In most habitats, predicted energy requirements exceeded energy gains. Predicted weight losses were greatest where herbage biomass was the largest, as Wallmo *et al.* (1977) also found. Thus, carrying capacity estimates based on forage quality are different from those based on forage quantity (Hobbs 1979).

Spring diets contained 20% crude protein or more, a figure comparable to McReynolds' (1977) total spring diet quality of 23% crude protein for wapiti in Washington. Nelson and Leege (1982) estimated that a diet of 20% crude protein, with a protein digestion coefficient of about 0.7, would provide nearly three times the protein required for maintenance and pregnancy (Nelson and Leege 1982).

Summer diet quality contained from 16.5% to 18.6% crude protein in the different habitats at Ministik. These values are comparable to other studies. Hobbs (1979) found summer diets in Colorado to average 16.2% crude protein. Collins (1979), working in Utah, reported wapiti summer diets averaging 18.9% crude protein. These summer diets all exceed the level of 13% that French *et al.* (1955) recommend for optimal growth and reproduction of white-tailed deer. As well, these diets exceed the protein demands of lactation as estimated for wapiti by Nelson and Leege (1982).

During spring and summer wapiti were capable of increasing the forage quality on the upland and lowland grassland areas by maintaining them in a state of regrowth. As a result diet quality from these regrazed areas was probably higher than similar ungrazed areas. Bedell (1971) found that both cattle and sheep were able to select diets higher in protein and lower in fiber on grazed areas than that which was present as ungrazed forage. Streeter *et al.* (1974) found that cattle selectively graze bluegrass regrowth so as to maintain a high dietary nutrient intake throughout the growing season.

Dietary Constraints and Differences Among Wapiti Classes

Ruminants exhibit anatomical, physiological, and ecological constraints on diet selection. The anatomy of the digestive tract, to a large extent, determines the efficiency of utilization of food items. Larger ruminants tend to have larger rumens per unit body weight than smaller ruminants (Hofmann 1973), permitting greater rumen fill. Rumen fill and retention time largely determine intake (Baile and Forbes 1974). The passage rate through the digestive tract is influenced by the number of physical barriers present in the rumen and omasum, and this varies considerably according to the kinds of foods eaten (Hofmann 1973). Hofmann divided African ruminants into groups based on their stomach structure. Bulk and roughage feeders, which subsist mainly on grasses, have a large subdivided rumen which delays coarse fibrous foods and allows for more complete fermentations of ingested forages. Selective feeders (which feed on browse tips and forbs) have a simple, relatively small rumen which allows for quick turnover of food and a high rate of fermentation. Feeders of intermediate selectivity (consuming both grasses and browse) exhibit intermediate characteristics in anatomy and rate of fermentation.

That wapiti exhibit an intermediate feeding style is suggested by their rumen structure (Church and Hines 1978) and their food habits (Hobbs 1979, Hobbs *et al*. 1983). The inclusion of mainly common foods in the diet, and the ability of wapiti to shift relative use of forage classes seasonally and also within a season in different habitats supports their classification as mixed feeders. This feeding style allows wapiti to be generalistic and opportunistic feeders, capable of using a wide variety of plant species and habitat types. Thus, wapiti are able to feed on the most nutritious food items at any given time of the year (Hanley 1980).

In a comparison of winter food habits of wapiti, mule deer, and bighorn sheep, Hobbs *et al*. (1983) found that wapiti consumed diets with the lowest concentration of cell solubles and the largest proportion of unlignified cell wall. Wapiti were the least selective of the three species. Collins (1979) compared the summer diets of wapiti and mule deer. He found that wapiti diets contained a greater percentage of common forages, and were higher in fiber content.

Energy and nutrient requirements, which are functionally related to animal body weight ($W^{0.75}$) (Kleiber 1961), also predict that common forages should make up a large proportion of the diet of large herbivores (Bell 1971, Geist 1974, Jarman 1974, Janis 1976). Absolute maintenance requirements (per animal per unit time) increase with increasing body size. Thus, larger animals must ingest greater quantities of forage and therefore spend more time feeding. The large amount of intake required necessitates that common forages comprise much of the diet. Since this requirement is less for small animals, they ingest less and can afford more time to be selective. In relation to relative maintenance requirements (per unit weight per unit time), smaller animals, with their higher metabolic rates require more protein and energy per unit weight per day than larger animals. As they also have a smaller gut, they compensate for these constraints by selecting for a lower fiber/protein ratio in their diet.

Theoretically, younger wapiti, with their smaller body size and therefore different energy requirements, would be expected to feed more selectively than adults (Geist 1982). Younger animals also possess morphological features, such as a narrow jaw, which would allow for the selection of plants and plant parts which cannot be selected by animals with larger jaws (Field 1970, Hofmann 1973, Jarman 1974). Dietary differences attributable to age have been reported in ungulates (Bergerud 1972, Tucker *et al*. 1977, Willms *et al*. 1980). However, a number of studies reported no age differences in diet selection (Dudzinsiki and Arnold 1973, Johnson 1980, Kie *et al*. 1980, and Hobbs *et al*. 1983). Hobbs *et al*. found no significant differences between the diets of wapiti as calves and as yearlings in the same area in Colorado.

At Ministik, age was not a major influence of diet selection at the forage class level. Sporadic differences occurred in habitats of high plant diversity, though the differences followed no particular pattern. During winter, the low forage diversity and abundance may have limited the selection of a different diet by young animals. During spring and summer, when all forages were relatively high in protein content, foraging in a less selective manner than possible may not have penalized young wapiti in terms of nutritional requirements.

Harper (1962) found that diets of cows and calves differed, as calves foraged on a greater number of species and fed in a discontinuous manner. Although calves exhibit this exploratory foraging behavior when very young, they were feeding in a continuous manner similar to adults when their diets were first sampled, at 4.5 months of age.

It would also be expected that pregnant and lactating females, with their increased energy requirement, would exhibit differences in dietary selection. According to theory of optimal foraging, these animals should forage less selectively, increasing their diet breadth (Schoener 1971). Although there were few animals to compare, no differences were noted in the diets of pregnant or lactating cows compared with nonpregnant cows of the same age. A decrease in foraging selectivity is not the only means by which these cows can compensate for greater energy requirements. During two activity scans of lactating and non-lactating females in August (1981), lactating females started their foraging bouts before nonlactating females and often continued foraging longer. Since calves were already beginning to spend a considerable amount of time feeding on vegetation at this time, differences in length of foraging bouts may have been even greater during the earlier stages of lactation. Increased length of the foraging period during pregnancy and lactation has been recorded for domestic sheep (Arnold and Dudzinski 1967), waterbuck (*Kobus deffassa*) (Spinage 1968), and impala (*Aepyceros melampus*) (Jarman and Jarman 1973). Increasing the number of feeding bouts would have similar results.

Adult males had a larger bite size. On some areas, such as the upland grasslands where the major plant species formed an integrated pattern, a higher proportion of their bites included a greater number of species. However, this did not significantly alter the proportions of forage classes in the diet as compared to the other wapiti.

In winter the size and strength of adult males allowed them to bend and break down small aspen and balsam trees, making more forage available for use. Similar foraging behavior has been observed in moose (Telfer and Cairns 1978). This activity accounted for little of the wapiti diet in the poplar forest. Consumption of large branches may have been related to rumen fill, rather than nutritional benefit: Fallen leaves, which comprised the majority of the forest winter diet, were higher in crude protein and more digestible than the branches.

The lack of observed dietary differences among the wapiti can also be related to their herding behavior. Jarman (1974) predicted that individuals in large aggregations can not be as selective in their diet choice as more solitary animals due to competition for forage items. Herding behavior of wapiti at Ministik was strongest in the winter and loosest in the summer, as Gates (1980) also found. Although adult females and calves generally remained together throughout the year, adult males were often observed foraging alone. However, the diets that cows and bulls chose in each habitat remained similar. Harper (1962) also found that dietary differences between bull and cow wapiti were a result of them using different portions of range. When the bulls and cows foraged on the same range, their diets were similar.

Learning may also play a role in the development of food habits (Leuthold 1977). Direct imitation of the mother or another social member may be on mechanism by which young animals recognize palatable foods, thus influencing preferences (Edwards 1976). Arnold and Maller (1977), working with sheep, found that early experiences influenced diet selection at a later time.

Snow

During winter, when forage is lower in nutritional quality and abundance, snow further decreases availability of forage and hinders ungulate movement. That snow influences distribution, habitat selection, and forage selection by wapiti has been frequently documented (Gaffney 1941, Craighead *et al*. 1973, Beall 1974, Ward *et al*. 1975, Martinka 1976, Leege and Hicken 1977). Elevational migrations, and the use of southerly aspects are related to selection for areas with shallow snow depths.

Telfer (1978) found that snow depth was more related to wapiti winter distributions in Alberta than local abundance of browse. Hornbeck (1979), however, found snow depth to be an unimportant factor in his study, and the winter distribution of wapiti in Manitoba was related to vegetational features. The shallow snow depths at Ministik during the study were not sufficient to influence movement or habitat utilization patterns. When snow depths are under 20 cm, wapiti can muzzle the snow out of the way (Gates 1980). At greater snow depths, wapiti crater for ground forage. Since snow depths were always under 30 cm, and varied little between habitats, snow depths alone could not explain the patterns of forage use at Ministik during the winter.

Habitat usage and the use of specific areas within habitats appeared to be influenced by a combination of forage availability and snow conditions. The upland grasslands, which had a relatively low prewinter biomass, were seldom used when wapiti had to crater through snow to expose the forage. Use was generally restricted to the grassland-forest border where forage availability was greatest and fallen leaves were also present. Gaffney (1941) also observed wapiti cratering in areas of higher vegetation availability. When snow depths were only a few centimeters or snow-free patches occurred on the uplands, foraging on these areas increased.

Wapiti spent the majority of their winter foraging time in the forest regions, and in the willow habitat. In the forest, wapiti cratered for abundant fallen leaves.

Cratering was common in close proximity to tree trunks, ~~where leaf availability was greatest. Wapiti were often~~ observed to reuse previous craters. During warming periods when the vegetation at the base of tree trunks or on steep slopes was exposed, wapiti concentrated their foraging in these areas. In the willow habitat, wapiti cratered in areas where herbage abundance was high and generally only browsed on twigs in areas where ground cover was low. Thus, wapiti appeared to forage in a manner in which they expended the least amount of energy possible in order to fulfill their energy requirements. Geist (1982) has termed this behavior the law of minimum.

Crusted or hard-packed snow decreases the snow depth at which herbaceous vegetation is accessible (Gaffney 1941, Ward *et al*. 1975, Gates 1980). Heavy grazing by wapiti and bison in the lowland grassland area resulted in dense packing of snow. At some regions, an ice layer at ground level restricted foraging on those areas.

Many studies indicate that wapiti browse more during the winter than at other seasons. In some areas, this increase in winter browsing has been related to increased snow depths (Rouse 1957, Gates 1980). Gates (1980) found that the time wapiti at Mi[illegible]s K spent browsing increased with increasing snow depth. Although browsing increased during the 1980-81 winter, it was more a result of shifts in habitat selection due to forage availability rather than snow depths.

Since snow conditions vary greatly from year to year, and wapiti exhibit flexible foraging behavior, annual variations in habitat selection and diet composition are to be expected.

Foraging Efficiency

Foraging patterns of herbivores change to cope with seasonality of quantity and quality of food supplies (Novellie 1978). These changes should be reflected in overt foraging behavior. Wapiti at Ministik exhibited seasonal and habitat variations in consumption rates, rate of movement, and time spent in other activities during foraging periods.

The rate of feeding, as indicated by the number of bites per minute and, to a lesser extent, the number of feeding stations per minute, was greater in spring and/or summer than other seasons. This coincided with periods of increased availability of high quality forage. During periods of abundance, wapiti may relax selection (Hobbs 1979). Since forage quality is uniformly high during summer, the inclusion of species of relatively lower quality would not penalize the wapiti in terms of nutrient requirements, and thus search intensity may be lower. New growth can be quickly harvested from each feeding station (Novellie 1978). In response to declining abundance of high quality forage during fall, wapiti selected for green plant material over senescent plants. Gates (1980) found that foraging time of wapiti at Ministik increased during the fall, providing an opportunity for greater selectivity and allowing diet quality to remain higher than if foraging time had not been altered. Novellie (1978) found that the time spent at a feeding station (feeding station interval; FSI) by springbok (*Antidorcas marsupialis*) and blesbok (*Damaliscus dorcus phillipsi*) was inversely correlated with forage quality. High FSI's were associated with mature or dry coarse swards of poor nutritional quality. These animals could have been either selecting for better quality forage or consuming more of the forage at each station, thus increasing the time spent at each station.

Foraging rates were lowest during winter. Low food abundance and snow cover appeared to influence foraging rates the most. Snow decreased the availability and accessibility of food resources. Wapiti were forced to muzzle or crater to obtain herbaceous vegetation or leaf litter. Snow removal exerted time and energy costs. Wapiti responded to these conditions by lowering their plane of selection and consuming most of the exposed vegetation. Wapiti fed on snow-free areas, or used old craters whenever possible; both these activities allowed an increased rate of consumption.

Within a season, feeding rates tended to be the greatest on areas where biomass and species diversity were low. This was the case on the upland grasslands, where vegetation was short and prominent species were evenly distributed. The lowland grassland, with somewhat similar characteristics to the uplands, also permited higher foraging rates. The poplar forest and willow habitats exhibited the lowest bite rate of the habitats over most of the year. Greater species diversity and more complex structure of these habitats probably contributed to the more selective foraging behavior. When selectively feeding, animals spent a greater amount of their foraging time moving between acceptable food items. Novellie (1978) found that for both springbok and blesbok the mean FSI was higher on unburnt veld in comparison to burnt veld for much of the year. He attributed this to the greater selectivity exhibited by the animals on the unburnt veld, which was more complex in structure.

Novellie (1978) observed a negative correlation between step rate and mean FSI. The longer a foraging animal spent at each feeding station, the lower its overall movements. As well, an increased rate of movement during foraging was positively related to bite rates and station rates at Ministik. Rate of movement was greatest in spring and summer and lowest in winter in all habitats except the sedge meadows where animals fed at clumps of vegetation dispersed over the habitat. In contrast, Owen-Smith (1979) found that a dry season drop in food intake rates was coupled with an increase in movement rate, and hence in the energetic costs of foraging in the kudu (*Tragelaphus strepsiceros*).

Novellie (1978) found little differences in foraging behavior between sexes of either springbok and blesbok.

Differences in foraging rates and movement rates existed among the different sex and age classes of wapiti at Ministik. However, most of the time few consistent trends existed. Adult females had higher bite rates in some of the habitats over summer. Adult males tended to have a slower rate of movement while foraging in the summer. This could be attributed to the adult males more solitary foraging behavior at this time. Their movement was not influenced by other animals as it was in the herd.

Consumption Rates

Productivity of the animal (growth rate, reproduction, lactation) may be controlled by the amount of food consumed as well as forage quality (Trudell and White 1981). Food intake is influenced by the time devoted to foraging each day, the time spent in search during foraging, the biting rate, and the size of bite (Allden and Whittaker 1970, Chacon and Stobbs 1976, Arnold 1964, Arnold and Dudzinski 1967). Bite size of wapiti at Ministik generally increased with increasing biomass. Bite rate was more variable, generally being the greatest in summer and the lowest in winter. Changes in both bite size and bite rate, which were influenced by vegetation diversity, compostition, and phenology, influenced consumption rates. Allden and Whittaker (1970) found that for sheep on grass swards both biting rate and bite size were important in accounting for a constant food intake with changing food availability at high plant biomass. Sheep (Allden and Whittaker 1970), Jersey cows (Chacon and Stobbs 1976), and reindeer feeding on lichens (Trudell and White 1981) increased bite size and decreased biting rate with increases in biomass. However, reindeer foraging on vascular plants had a constant bite size irrespective of biomass, while bite rate increased in relation to the biomass of selectively eaten grasslike plants and browse.

Consumption rates (grams/minute) of cattle (Chacon and Stobbs (1976), sheep (Allden and Whittaker 1970), and reindeer (Trudell and White 1980) tended to increase with increasing biomass though reaching a maximum level at which the animal could not further increase intake. This maximum level varied with species and with forage composition and structure (eg. height, % leaf). Larger bodied herbivores, with their greater intake requirements, reached their maximum intake levels at greater vegetation biomass. Chacon and Stobbs (1976) found cattle grazed on pastures yielding 7,440 kg/ha in autumn and 3,800 kg/ha in spring to consume 8.7 kg/day and 6.1 kg/day, respectively. Intake decreased with defoliation to 1.9 kg/day in fall (pasture 3,600 kg/ha) and 2.8 kg/day in spring (pasture 2,400 kg/ha). At different herbage availability, sheep obtained a maximum rate of intake at 1,800 kg/ha (Allden and Whittaker 1970). Consumption rate declined with decreases in tiller length. Trudell and White (1981) found reindeer maximum intake of willow (4.8 kg/day) and lichen (2.8 kg/day) to occur at

2,000 kg/ha.

Consumption rates for wapiti tend to vary widely among habitats. Collins (1977, 1979) found intake to range from 3.7 to 17.6 grams/minute. Highest consumption rates occurred in habitats with the greatest forage production, these tending to be preferred foraging areas. Collins (1977, 1979) found the average daily summer intake of wapiti to be about 8.3 kg/day. Wapiti at Ministik exhibited lower consumption rates, averaging 7.8 grams/minute in the summer and only 1.8 grams/minute in winter. Using Gates (1980) activity data, daily intake rates for wapiti at Ministik would be 3.6 kg/day and 1.4 kg/day in the summer and winter, respectively.

Collins (1977) suggest that consumption rates can determine whether or not a habitat segment will be grazed at all. The threshold for acceptance of a segment as a forage source may depend on minimum daily forage requirments. Based on diet data from the Colockum Creek wapiti herd, Washington, Nelsen and Leege (1982) calculate a 236 kg wapiti cow to have a daily intake of 4.1 kg in winter and 3 kg in summer for maintenance and activity requirements. Energy required for gestation and lactation was 0.31 kg/day and 5 kg/day over and above maintenance, respectively. Hobbs (1979), using a simulation model, found winter intake to vary from 4.5 to 5.5 kg/day.

Based on 20 gram intake required per kg body weight (Nelsen and Leege 1982), the average daily intake for the sex and age classes of wapiti at Ministik should have been about 3.7, 3.6, 3.6, and 6.1 kg/day for fall through summer, respectively. Thus, the observed intakes were lower than expected. A number of factors could have contributed to the observed values. Bite size, taken as an average for all animals, may have been underestimated due to the mixed structure of the population. Vegetation biomass may also have imposed limitations on intake. Chacon and Stobbs (1976) found low leaf densities prevented animals from harvesting large quantities of herbage. Sheep (Allden and Whittaker 1970) and reindeer (Trudell and White 1981) also exhibit marked decreases in intake with decreasing biomass. During fall, winter, and spring, vegetation biomass at Ministik was generally below that at which maximum intake of wapiti occurred (≈3,000 kg/ha). When accessibility of herbage imposes limitations on the rate which food can be consumed, herbivores can partially compensate by increasing foraging time (Allden and Whittaker 1970). It is possible that wapiti, under the heavy grazed conditions at Ministik, foraged longer periods than when they were first introduced into the area. Since foraging times determined by Gates (1980) were used to determine daily intakes, this may have contributed to the low consumption rates calculated.

As was done by Wallmo *et al.* (1977) and Hobbs (1979), carrying capacity was estimated on the basis of forage quantity by calculating the number of wapiti required per unit time to remove one-half the total winter biomass. An average intake of 5 kg/day, based on Hobbs (1979) data, was used. The sedge meadow, and willow habitat could support more wapiti than the forest or grassland habitats (Table V.1). However, the capacity to which wapiti can utilize the available forage resource would appear to be influenced by a variety of factors, thus affecting the carrying capacity of an area. Not all available vegetation is acceptable as forage to the animals. Of the acceptable forage, not all will contain the nutritional quality required. The sedge dominated habitats could support the greatest number of wapiti based on biomass, but sedge contained protein below suggested levels during winter. Variation in yearly precipitation and snow conditions can cause dramatic changes in forage availability and foraging effort required. The complexity of factors influencing carrying capacity and their dynamic nature suggests that stocking rates should be conservative. Estimates based on .3 or .25 of the total winter biomass may be more realistic.

Mixed stocking rates of 10 animals/Km (moose and wapiti) at Elk Island National Park resulted in overutilization (Bishoff 1981). Bishoff suggests a stocking rate below 8.5 animals/Km. Since wapiti are opportunistic and generalistic foragers, a higher stocking rate of just wapiti should be possible. Heavy stocking, however, should be avoided as this limits free choice of forage, placing constraints on diet expansion and ultimately on habitat selection (Bishoff 1981).

Table V.1: Estimated carrying capacity (elk-days/ha) for the Ministik habitats based on one-half of the prewint[illegible]mass and an intake rate of 5 Kg/day.

Habitat	Biomass (Kg/[illegible])	[illegible]e rate ([illegible]g/day)	Carrying capacity (elk-days/ha)
Sedge meadow	2086.7	5	208.7
Willow	1898.6	5	189.9
Poplar Forest	1519.6	5	152.0
Upland Grassland	1022.2	5	102.2
Lowland Grassland	1273.1	5	127.3

SUMMARY

A study was conducted at the Ministik Wildlife Research Station on the foraging behavior of wapiti. The purpose of the study was to estimate diet composition of four sex and age classes of wapiti, diet quality, and foraging patterns of these animals in five habitat types (willow, poplar forest, upland grassland, lowland grassland, and sedge meadows). Results were related to forage quality and quantity.

Herbaceous biomass in the sedge meadows ranged from 1,949 kg/ha in April to 7,001 kg/ha in August, and was significantly greater than other habitats. In the willow habitat, herbaceous biomass reached 6,000 kg/ha. Willow was the dominant shrub with 186,638 twigs/ha. Herbaceous biomass in the grasslands was significantly lower than the *Carex* dominated habitats, and was due in part to the continuous grazing on these areas. Biomass ranged from 433 to 4,949 kg/ha in the lowland and 329 to 1,738 kg/ha in the upland grassland. Forbs accounted for much of the biomass at the end of the summer.

The poplar forest had a significantly lower herbaceous biomass than other habitats, ranging from 106 to 366 kg/ha. Forbs dominated the biomass during summer. Leaf litter (browse) was an important component of forage from fall (1,833 kg/ha) through spring (1,130 kg/ha). Hazel was the prominent shrub in the understory, averaging 150,682 twigs/ha. Other commonly occurring shrub species were rose, raspberry, saskatoon, and snowberry. Browse utilization was heavy resulting in preferred species, dogwood and chokecherry (Gates 1980), being poorly represented. Encroachment of forest onto grasslands was prevented by browsing pressure.

Crude protein content and dry matter digestibility of major forage items were determined. These generally varied significantly among forage classes. The average crude protein content of grasses, browse, and forb samples varied during the year from 5.6 to 21%, 5.8 to 25%, and 5.5 to 22%, respectively. During fall, grasses and forbs had significantly higher crude protein contents than did browse. Forbs continued to contain more protein from winter through spring, while no significant differences among forage classes occurred in the summer. Digestibilities of winter and summer samples ranged from 44 to 67% for grasses, 45 to 74% for forbs, and 35 to 60% for browse. Digestibility of forbs were significantly greater than grasses and/or browse from spring through fall. In winter browse was significantly lower than both forbs and grasses.

Diet composition of wapiti varied among habitats and seasons. Few significant differences in forage class composition occurred among the sex and age classes of wapiti. Graminoids comprised the spring diets in most habitats. In the poplar forest leaf litter was also consumed in early spring.

Browse and forbs became important dietary components during summer and availability was a major factor in determining their usage. Grasses remained an important dietary component on the grasslands. *Carex* was seldom consumed in either the sedge meadows or willow habitat during summer, probably as a result of advanced growth. In fall, wapiti shifted back to foraging mainly on graminoids in most habitats. In the poplar forest, fallen leaves dominated the diet while grasses were of secondary importance to the diet. In winter, wapiti concentrated foraging in the poplar forest and willow habitats. Fallen leaves constituted the majority of the forest diet, whereas browse and graminoids contributed much to the willow diet. Grasslands were mainly used when snow depths were shallow.

Diet diversity indices varied among habitats and seasons. Indices were generally highest in the summer when forage diversity and abundance was the highest. Habitats with the largest species diversity and complexity in vegetation structure had the highest indices.

Diet quality exhibited seasonal trends similar to forage crude protein. Dietary crude protein was significantly greater in spring and summer than fall and winter. Diet quality ranged from 16 to 18% among habitats in the summer and 4.8 to 8.8% among habitats in winter. Crude protein in the diet was generally enough to provide maintenance and reproductive requirements. Fecal crude protein followed the same trends as diet quality, but generally overestimated these values.

Foraging rates varied among seasons, habitats, and classes of wapiti. Foraging rates tended to be the greatest in summer and lowest in winter. Low foraging rates were generally associated with areas of greater plant complexity, and also with snow cover. Consumption rates were significantly greater in summer (7.8 g/min) than other seasons, winter being the lowest (1.8 g/min). Consumption rates tended to follow trends similar to changes in herbaceous biomass on the grassland areas during the snow-free period.

REFERENCES

Allden, W.G. and I.A. Whittaker. 1970. The determinants of herbage intake on grazing sheep: the interrelationship of factors influencing herbage intake and availability. Aust. J. Agric. Res. 21:755-766.

Anderson, E.W. and R.J. Scherzinger. 1975. Improving quality of winter forage for elk by cattle grazing. J. Range Manage. 28:120-125.

A.O.A.C. 1965. Official methods of analysis, 10th ed. Association of Official Agricultural Chemists, Washington, D.C. 957 pp.

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

Arnold, C.W. 1964. Factors within plant associations affecting the behavior and preformance of grazing animals. IN: D.J. Crisp, ed., GRAZING IN TERRESTRIAL AND MARINE ENVIRONMENTS. Blackwell Scientific, Oxford. 407pp.

Arnold, C.W. and N.A. Dudzinski. 1967. Studies on the diet of the grazing animal. II. The effect of physiological status in ewes and pasture availability of herbage intake. Aust. J. Agric. Res. 18:349-359.

Arnold, C.W. and R.A. Maller. 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 J.M. Forbes. 1974. Control of feed intake and regulation of energy balance in ruminants. Physiol. Rev. 54:160-214.

Bayrock, L.A. 1972. Surficial geology, Edmonton. NTS 83H. Alberta Res. Council. 1:250,000 map.

Beall, R.C. 1974. Winter habitat selection and use by a western Montana elk herd. Ph.D. Dissertation. Univ. of Mont., Missoula, 197pp.

Bedell, T.E. 1971. Nutritive value of forage and diets of sheep and cattle from Oregon subclover-grass mixtures. J. Range Manage. 24:125-133.

Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. Sci. Am. 225:86-93.

Belovsky, G.E. 1978. Diet optimization in a generalist herbivore, the moose, with implications for life history strategies. Theor. Pop. Biol.

Bergerud, A.T. 1972. Food habits of Newfoundland caribou. J. Wildl. Manage. 36:913-923.

Bishoff, W. 1981. Yield, use and chemical composition of forage in Elk Island National Park, Alberta. M.Sc. Thesis, Univ. Alberta, Edmonton. 139 pp.

Blood, D.A. 1966. Range relationships of elk and cattle in Riding Mountain National Park, Manitoba. Canadian Wildl. Serv. Wildl. Manage. Bull., Series 1, no. 19 62 pp.

Bowser, W.E., A.A. Kjearsgaard, T.W. Peters, and R.E. Wells. 1962. Soil Survey of Edmonton Sheet (83-H). Alberta Soil Survey Rep. No.21. Canada Dept. of Agriculture.

Boyd, R.J. 1970. Elk of the White River plateau, Colorado. Colo. Div. Game, Fish, and Parks Tech. Bull. no.25 126pp.

Bryant, J.P. and P.J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Ann. Rev. Ecol. Syst. 11:261-285.

Buechner, H.K. 1950. Life history, ecology and range use of pronghorn antelope in Trans-Pecos, Texas. Am. Midl. Nat. 43:257-354.

Burzlaff, D.E. 1971. Seasonal variation of the in vitro dry matter digestibility of three sandhill grasses. J. Range Manage. 24:60-63

Cairns, A. 1976. Distribution and food habits of moose, wapiti, deer, bison, and snowshoe hare in Elk Island National Park, Alberta. M.S. Thesis, Univ. of Calgary 171pp.

Chamrad, A.D. and T.W. Box. 1968. Food habits of white-tailed deer in south Texas. J. Range Manage. 21:158-164.

Chacon, E. and T.H. Stobbs. 1976. Influence of progressive defoliation of a grass sward on the eating behavior of cattle. Aust. J. Agric. Res. 27:709-727.

Church, D.C. and W.H. Hines. 1978. Rumino-reticular characteristics of elk. J. Wildl. Manage. 42:654-659.

Collins, W.B. 1977. Diet composition and activity of elk on different habitat segments in the lodgepole pine type.

Uinta Mountains, Utah. M.S. Thesis Utah State Univ., Logan. 74pp.

Collins, W.B. 1979. Feeding behavior and habitat selection of deer and elk on northern Utah summer ranges. Ph.D. Thesis, Utah State Univ. 107 pp.

Collins, W.B., P.J. Urness, and D.D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Manage. 42:799-810.

Constan, K. J. 1972. Winter foods and range use of three species of ungulates. J. Wildl. Manage. 36(4):1068-1076.

Cook, C.W. 1972. Comparative nutritive value of forbs, grasses, and shrubs. Pages 303-318 IN: C.M. McKell, J.P. Blaisdell, and J.R. Goodin, eds., Wildland shrubs-their biology and utilization. USDA Forest Ser. Gen. Tech. Rep. Int-1.

Cowan, I. McT. 1947. Range competition between mule deer, bighorn sheep, and elk in Jasper Park, Alberta. Trans. N. Amer. Wildl. Conf. 12:223-227.

Craighead, J.J., F.C. Craighead, R.L. Ruff, and B.W. O'Gara. 1973 Home ranges and activity patterns of non-migratory elk of the Madison Drainage herd as determined by biotelemetry. Wildl. Monogr. 33:50pp.

Dietz, D.R., R.H. Udall, H.R. Shepard, and L.E. Yeager. 1958. Seasonal progression in chemical content of five key browse species in Colorado. Soc. Amer. Forest. Proc. 117-122.

Dietz, D.R., R.H. Udall, and L.E. Yeager. 1962. Chemical composition and digestibility by mule deer of selected forage species, La Pouche range, Colorado. Colo. Game and Fish Dept. Tech. Pub. 14. 89pp.

Dudziniski, M.L. and G.W. Arnold. 1973. Comparison of diets of sheep and cattle grazing together on sown pastures on the New South Wales by principal component analysis. Aust. J. Agric. Res. 24:899-912.

Edwards, J. 1976. Learning to eat by following the mother in moose calves. Am. Midl. Nat. 96:229-232.

Ellis, J.E., J.A. Weins, C.F. Rodell, and J.C. Anway. 1976. A conceptual model of diet selection as an ecosystem process. J. Theor. Biol. 60:93-108.

Emlen, J.M. 1966. The role of time and energy in food preferences. Am. Nat. 100:611-617.

Emlen, J.M. 1973. ECOLOGY: An evolutionary approach. Addison-Wesley Pub. Co., Reading Mass.

Field, C.R. 1970. Observations on the food habits of tame warthog and antelope in Uganda. E. Afr. Wildl. J. 8:1-17.

Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of secondary plant compounds. Am. Nat. 108:874-875.

French, C.E., L.C. McEwan, N.D. Magruder, R.H. Ingraham, and R.W. Swift. 1955. Nutritional requirements of white-tailed deer for growth and antler development. Penn. State Col. Agr. Exp. Stat. Bull. 600. 50pp.

Gaffney, W.S 1941. The effects of winter elk browsing, South Fork of the Flathead River, Montana. J. Wildl. Manage. 5:427-453.

Gates, C.C. 1980. Patterns of behavior and performance of American elk in the boreal mixed wood forest. Ph.D. Dissertation, Univ. of Alberta.

Geist, V. 1974. On the relationship of social evolution and ecology of ungulates. Am. Zool. 14:205-220.

Geist, V. 1982. Adaptive behavioral strategies. IN: Elk of North America ecology and management. J.W. Thomad and D.E. Toweill, eds. Stackpole Books. pp 219-277.

Hanley, T.A. 1980. Nutritional constraints on food and habitat selection by sympatric ungulates. Ph.D. Thesis, Univ. Washington. 176 pp.

Hansen, R.M. and L.D. Reid. 1975. Diet overlap of deer, elk, and cattle in southern Colorado. J. Wildl. Manage. 28:43-47.

Harper, J.A. 1962. Daytime feeding habits of Roosevelt elk on Boyes Prairies, California. J. Wildl. Manage. 26:97-100.

Harris, L.D. 1972. An ecological description of a semi-arid east African ecosystem. Range Science Depart. Science Series No. 11. Colorado State Univ. 80 pp.

Hebert, D.M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis, Univ. British Columbia. 375 pp.

Hobbs, N.T. 1979. Winter diet quality and nutritional status of elk in the upper montane zone, Colorado. Ph.D. Dissertation. Colorado State Univ., Fort Collins. 131pp.

Hobbs, N.T., D.L. Baker, J.E. Ellis, and D.M. Swift. 1979. Composition and quality of elk diets during winter and summer- a preliminary analysis. IN: M.S. Boyce and L.D. Hayden-Wing, eds., North American elk: ecology, behavior and management. Univ. of Wyoming Press.

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

Hofmann, R.R. 1973. The ruminant stomach. East African Monogr. in Biology vol. 2. East African Literature Bureau. 354pp.

Holsworth, W.N. 1960. Interractions between moose, elk, and buffalo in Elk Island National Park, Alberta. M.S. Thesis. Univ. B.C. 92pp.

Hornbeck, G. 1979. Elk distributions and habitat selection in Manitoba. M.S. Thesis. Fort Collins, Colorado.

Hunt, H.M. 1979. Summer, autumn, and winter diets of elk in Saskatchewan. The Can. Field-Nat. 93:283-287.

Ivins, J.O. 1962. The relative palatability of herbage plants. J. Brit. Grassl. Soc. 7:43-54.

Janis, C. 1976. The evolutionary stategy of the Equidae and the origins of rumen and cecal digesta. Evolution 30:757-774.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. Behavior 48:215-267.

Jarman, M.V. and P.J. Jarman. 1973. Daily activity of impala. E. Afr. Wildl. J. 11:75-92.

Johnson, B.K. 1980. Bighorn sheep food habits, forage preferences, and habitat selection in alpine and subalpine communities. Ph.D. Thesis, Colorado State Univ., Fort Collins. 170 pp.

Kie, J.G., L. Drawl, and G. Scott. 1980. Changes in diet and nutrition with increased herd size in Texas white-tailed deer. J. Range Manage. 33:28-34.

Kirsh, J.B. 1962. Little Belt elk food habits and range use investigations. Big Game Research Project W-98-R-2 Job. no B-8 44pp.

Klieber, M. 1961. THE FIRE OF LIFE. John Wiley and Sons Ltd., New York. 454pp.

Klein, D.R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. Pages 25-44 IN: A. Watson, ed., Animal Populations in Relation to Their Food Resources. Sym. Brit. Ecol. Soc. No. 10. Blackwell Sci. Publ., Oxford. 478pp.

Knight, R.R. 1970. The Sun River elk herd. Wildl. Monogr. No. 23 66pp.

Krebs, J.R. 1977. Optimal foraging theory and experiment. Nature 268:583-584.

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 Wildl. Manage. 26:106-113.

Leege, T.A. and W.D. Hickey. 1977. Elk-snow habitat relationships in the Pete King Drainage, Idaho. Idaho Dep. Fish and Game Wildl. Bull. No.6 23pp.

Leuthold, W. 1977. African Ungulates: A Comparative Review of Their Ethology and Behavioral Ecology. New York Press. 307pp.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100:603-609.

Mackie, R.J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Manage. 20 79pp.

Maloiy, G.M.D., R.N.B. Kay, and E.D. Goodall. 1970. Digestion and nitrogen metabolism in sheep and red deer given large or small amounts of water and protein. Brit. J. Nutr. 24:843-855.

Marcum, C.L. 1979. Summer-fall food habits and forage preferences of a western Montana elk herd. IN: M.S. Boyce and L.D. Hayden-Wing, eds., North American elk: ecology, behavior, and management. Univ. of Wyoming Press.

Martinka, C.J. 1976. Fire and elk in Glacier National Park. Pro. Tall Timber Fire Ecology Conf. No.14 :377-389.

McCulloch, C.Y. 1955. Utilization of winter browse on wilderness big game range. J. Wildl. Manage. 19:206-215.

McCullough, D.R. 1969. The Tule elk: its history, behavior, and ecology. Univ. Calif. Publ. Zool. Vol 88. Berkley and Los Angeles: Univ. Cal. Press. 209 pp.

McInnis, M.L., M. Vavra, and W.C. Krueger. 1977. A comparison of techniques to determine the diets of grazing herbivores. Abstract of Papers. 13th annual meeting of the Society fo Range Management. Portland Oregon.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113:691-703.

McReynolds, S.J. 1977. Seasonal elk food habits and diet quality in central Washington. M.S. Thesis. Washington State Univ. 79pp.

Minson, D.J. and M.N. McLeod. 1972. The in vitro technique: its modification for estimating digestibility of large numbers of tropical pasture samples. Division of Tropical Pastures Tech. Paper No. 8 , 15 pp.

Morris, M.S. and J.E. Schwartz. 1957. Mule deer and elk food habits on the National Bison Range. J Wildl. Manage. 21:189-193.

Murie, O.J. 1951. THE ELK OF NORTH AMERICA. The Stackpole Co., Harrisberg, Penn. 376pp.

Neff, O.J. 1974. Forage preferences of trained mule deer on Beaver Creek watersheds. Arizona Game Fish Dept. Spec. Rep. 4. 61 pp.

Nelson, J.R. and T.A. Leege. 1982. Nutritional requirements and food habits. IN: Elk of North America ecology and management. J.W. Thomas and D.E. Toweill, eds. Stackpole Books. pp 323-367.

Novellie, P.A. 1978. Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. S. Afr. Wildl. Res. 8:137-144.

Oelberg, K. 1956. Factors affecting the nutritive value of range forage. J Range Manage. 9:220-225.

Owen-Smith, N. 1979. Assessing the foraging efficiency of a large herbivore, the kudu. S. Afr. J. Wild. Res. 9:102-110.

Palleson, J.D. 1979. Nutritive value of mule deer and elk diets and forages on lodgepole pine summer range in Utah. M.Sc. Thesis, Utah State Univ. 108 pp.

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

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

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

Regelin, W.L., R.M. Bartmann, D.W. Reichert, and P.H. Neil. 1976. The influence of supplemental feed on food habits of tamed deer. U.S.D.A. For. Ser. Res. NOte RM316. 4 pp.

Rice, R.W., D.R. Cundy, and P.R. Weyerts. 1971. Botanical and chemical composition of esophageal and rumen fistula samples of sheep. J. Range Manage. 24:121-124.

Robbins, C.T. and A.N. Moen. 1975. Composition and digestibility of several deciduous browses in the northeast. J. Wildl. Manage. 39:337-341.

Robbins, C.T., P.J. Van Soest, W.W. Mautz, and A.N. Moen. 1975. Feed analysis and digestion with reference to white-tailed deer. J. Wildl. Manage. 39:67-79.

Rouse, R.A. 1957. Elk food habits, range use and movements, Gravelly Mountains, Montana. M.S. Thesis, Montana State College, Bozeman.

Rowe, J. S. 1972. Forest regions of Canada. Dept. Environ. Can. Forest Serv. Pub. No. 1300. 172pp.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 11:369-404.

Schommer, T.J. 1978. Seasonal coeffecients for energy and protein of central Washington elk diets. M.Sc. Thesis, Washington State Univ. 57 pp.

Schwartz, C.C. and J.G. Nagy. 1973. Pronghorn food habits studies, 1970-1972. US/IBP Grassland Biome Tech. Rep. No. 231. Colorado State Univ., Fort Collins. 32 pp.

Schwartz, C.C., J.G. Nagy, and R.W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. J. Wildl. Manage. 41:161-168.

Scotter, G.W. 1965. Chemical composition of forage lichens from northern Saskatchewan as related to use by barren ground caribou. Can. J. Plant Sci. 45:246-250.

Short, H.L., R.M. Blair, and L. Burkart. 1972. Factors affecting nutritive values. Pages 311-318 IN: C.M.

McKell, ed., Wildland shrubs-their biology and utilization. USDA Forest Serv. Gen. Tech. Rep. Int-1

Short, H.L., R.M. Blair, and C.A. Selequist. 1974. Fiber composition and digestibility by small ruminants. J. Wildl. Manage. 38:197-209.

Sinclair, A.R.E. 1974. The natural regulation of buffalo populations in East Africa I. Introduction and resource requirements. E. Afr. Wildl. J. 12:135-154.

Singer, F.J. 1979. Habitat partitioning and wildfire relationships of cervids in Glacier National Park, Montana. J. Wildl. Manage. 30:349-363

Sokal, and Rohlf. 1969. Biometry. W.H. Freeman Press, San Fransisco. 776 pp.

Sparks, D.R. and J.C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. J. Range Manage. 21:264-265.

Spinage, C.A. 1968. A quantitative study of the daily activity of the Uganda defassa waterbuck. E. Afr. Wildl. J. 6:89-93.

Stevens, D.R. 1966. Range relationships of elk and livestock, Crow Creek Drainage, Montana. J. Wildl. Manage. 30:349 -363.

Streeter, C.L., C.B. Rumberg, T.H. Hall,. and E.G. Siemer. 1974. Meadow forage quality, intake, and milk production of cows. J. Range Manage. 27: 133-136.

Telfer, E.S. 1978. Cervid distribution, browse, and snow cover in Alberta. J. Wildl. Manage. 42:352-361.

Telfer, E.S. and A. Cairns. 1978. Stem breakage by moose. J. Wildl. Manage. 42:639-642.

Telfer, E.S. and A. Cairns. 1979. Bison-wapiti interrelationships in Elk Island National Park, Alberta. Pages 114-121 IN: M.S. Boyce and L.D. Hayen-Wing, eds., North American elk: ecology, behavior and management. Univ. of Wyoming Press.

Telfer, E.S. and G.W. Scotter. 1975. Potential for game ranching in boreal aspen forest regions of western Canada. J. Range. Manage. 28:172-180.

Tilley, J.M.A. and R.A. Terry. 1965. A two stage technique for the in vitro digestion of forage crops. J. Brit. Grassl. Soc. 18:104-111.

Trudell, J. and R.G. White. 1981. The effect of forage structure on food intake, biting rate, bite size and daily eating time of reindeer. J. Appl. Ecol. 18:63-81.

Tucker, R.E., M. Majok, D.D. Parkinson, and A. McLean. 1976. Palatability of Douglas fir foliage to mule deer in relation to chemical and spatial factors. J. Range Manage. 29:486-489.

Tucker, R.E., A. McLean, and D.E. Waldren. 1977. Relative preference by mule deer for six shrubs near Kamloops, British Columbia. Can. J. An. Sci. 57:373-377.

van-Dyne, G. and H.F. Heady 1965. Botanical composition of sheep and cattle diets on a mature annual range. Hilgardia 36:465-492.

Vavra, M., R.W. Rice, and R.M. Hansen. 1978. A comparison of esophageal fistula and fecal material to determine steer diets. J. Range Manage. 3:11-13.

Wallmo, O.C., L.H. Carpenter, W.L. Regelin, R.B. Gill, and D.L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122-127.

Wallmo, O.C., R.B. Gill, L.H. Carpenter, and D.W. Reichert. 1973. Accuracy of field estimates of deer food habits. J. Wildl. Manage. 37:556-562.

Ward, A.L., K.L. Diem, and R.W. Weeks. 1975. The impact of snow of elk. Pages 105-174 IN: D.H. Knight et al., eds., The Medicine Bow Ecology Project. Univ. of Wyoming.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108:290-304.

Wilfard, E. and J.L. Schuster. 1973. Chemical composition of six great plains grasses as related to season and precipitation. J. Range Manage. 26:37-38.

Willms, W., A. McLean, R.E. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British Columbia. J. Range Mange. 33:55-59.

Wonders, W.C. 1969. Atlas of Alberta. Gov't. of Alberta and Univ. of Alberta, Edmonton.

APPENDICES

Appendix 1: Meteorological data obtained from the Edmonton International Airport, Edmonton, during study periods 1980-1981.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Temperature(C)											
mean maximum	11.62	4.03	-9.80	1.48	-1.45	4.95	11.06	18.14	17.80	21.40	27.38
mean minimum	-.59	-6.40	-19.00	-10.60	-13.86	-7.34	-3.70	4.30	4.40	9.65	10.11
mean	6.48	-.05	-14.80	-4.58	-7.75	-.68	3.70	11.20	11.10	15.57	18.80
Relative Humidity											
maximum	90.50	90.60	80.76	88.18	77.76	84.24	86.24	84.71	87.70	88.00	90.20
minimum	46.40	59.00	59.76	67.80	52.00	52.65	36.06	37.65	42.50	56.00	37.60
Precipitation											
rainfall(mm)	4.9	.2	2.8	---	tr	2.0	tr	4.1	26.7	101.4	.4
snowfall(cm)	tr	.4	29.9	.8	4.5	1.8	3.6	--	--	--	--
total (mm)	4.9	.6	32.7	.8	4.5	3.8	3.6	4.1	26.7	101.4	.4
x snow depth	--	tr	14.06	10.11	11.6	1.88	.18				
Wind											
average speed	10.32	11.20	14.03	11.24	13.79	13.10	15.80	14.98	12.4	10.88	10.05
prevailing direction	S,W	S	S	S	S	S	S	SE	W	W,NW	S

Appendix 2: List of species occurring in wapiti diets and their associated abbreviations, shrub identification from Gates (1980).

FORBS		
Achillea millefolium	Ac.mi.	yarrow
Actacea rubra	Ac.ru.	baneberry
Agrimonia striata	Ag.st.	agrimony
Anaphalis margaritacea	An.ma.	pearly everlasting
Anemone canadensis	An.ca.	anemone
Apocynum androsaemifolium	Ap.an.	dogbane
Aralia nudicaulis	Ar.nu.	wild sarsaparilla
Aster species	As.sp.	asters
Bidens cernua	Bi.ce.	nodding beggar ticks
Chenopodium album	Ch.al.	lambsquarter
Cirsium arvense	Ci.ar.	thistle
Cornus canadensis	Co.ca.	bunchberry
Descuraina sophia	De.so.	tansy mustard
Disporum thrachycarpum	Di.tr.	fairy berry
Epilobium angustifolium	Ep.an.	fireweed
Equisetum spp.	Eq.sp.	horsetail
Erigeron philadelphicus	Er.ph.	fleabane
Fragaria virginianus var. glauca	Fr.gl.	strawberry
Galeopsis tetrahit	Ga.te.	hemp nettle
Galium boreale	Ga.bo.	bedstraw
Galium triflorum	Ga.tr.	sweet bedstraw
Geum allepicum	Ge.al.	yellow avens
Heracleum lanatum	He.la.	cow parsnip
Hieracium canadense	Hi.ca.	hawkweed
Lathyrus spp.	La.sp.	peavine
Linnaea borealis	Li.bo.	twinflower
Lysimachia ciliata	Ly.ci.	fringed loosestrife
Maianthemum canadense	Ma.ca.	lily
Mentha arvensis	Me.ar.	common mint
Mertensia paniculata	Me.pa.	tall lungwort
Mitella nuda	Mi.nu.	bishop's cap
Osmorhiza spp.	Os.sp.	sweet cicley
Petasites spp.	Pe.sp.	coltsfoot
Plantago major	Pl.ma.	common plantain
Polygonum amphibium	Po.am.	water smartweed
Potentilla anserina	Po.an.	silverweed
Pyrola spp.	Py.sp.	wintergreen
Ranunculus cymbalaria	Ra.cy.	creeping buttercup
Ranunculus sceleratus	Ra.sc.	celery-leafed buttercup
Rubus pubescens	Ru.pu.	dewberry
Sanicula marilandica	Sa.ma.	snakeroot
Scutellaria galericulata	Sc.ga.	common skullcap
Sium suave	Si.su.	water parsnip

Appendix 2: List of species occurring in wapiti diets and their associated abbreviations continued.

Smilacina racemosa	Sm.ra.	false Solomon s seal
Solidago spp.	So.sp.	goldenrod
Sonchus arvensis	So.av.	sow thistle
Stachys palustris	St.pa.	hedge nettle
Stellaria spp.	St.sp.	chickweed
Taraxacum officinale	Ta.of.	dandelion
Thalictrum spp.	Th.sp.	meadow rue
Trifolium spp.	Tr.sp.	clover
Urtica gracilis	Ur.gr.	common nettle
Vicia americana	Vi.am.	vetch
Viola spp.	Vi.sp.	violet
BROWSE		
Betula papyrifera		paper birch
Populus balsamifera		balsam poplar
Populus tremuloides		trembling aspen
Salix spp.		willow
Amelanchier alnifolia		saskatoon
Cornus stolonifera		red osier dogwood
Corylus cornuta		hazel
Lonicera dioica		twining honeysuckle
Lonicera involucrata		bracted honeysuckle
Prunus virginiana		chokecherry
Ribes spp.currant		currant
Rosa spp.rose		rose
Rubus hirtellum		gooseberry
Rubus melanolasius		raspberry
Shepherdia canadensis		buffaloberry
Symphoricarpos spp.		snowberry
Viburnum edule		low bush cranberry
GRAMINOIDS		
Agropyron cristatum		wheatgrass
Bromus		brome
Calamagrostis spp.		reedgrass
Carex spp.	Ca.sp.	sedge
Poa spp.		bluegrass

Appendix 3: Herbaceous biomass (kg/ha) in the sedge habitat during snowfree periods, means and S.E.

	Oct.		Nov.		Apr		May		June		July		Aug	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
GRAMINOIDS														
Grass			16.0	10.1					10.8	7.1	25.0	18.6	266.7	219.2
Ca.sp.	4737.5	621.5	2060.5	[illegible]04.6	1948.8	221.2	2780.7	360.7	3091.5	626.9	5156.0	562.6	65[illegible].6	1240.6
FORBS														
Ta.of.									5.8	2.7	15.1		0.3	0.2
Eq.sp.													[illegible]	3.7
Ga.te.									9.8	9.6	12.8	12.8	[illegible]	[illegible]
So.ar.									0.1	0.1	6.7	6.7	[illegible]	[illegible]
Cl.ar.			7.2	7.2					0.4	0.4	4.6	3.1	[illegible]	[illegible]
Sc.[illegible]									0.5	0.5	7.1	4.1	[illegible]	[illegible]
St.sp.									0.1	0.1	2.8	1.3	69.5	63.2
Ra.sc.									0.1	0.1			0.1	0.1
Me.ar.									6.2	6.2	9.5	6.5	16.7	16.7
St.pa.									3.8	3.8	14.6	13.6	14.2	14.2
Po.am.									53.2	[illegible]	61.4	37.3	77.0	77.0
Ge.al.											0.2	0.2		
So.sp.											2.5	2.5		
Ra.cy.	0.3	0.2	0.7	0.7					0.1	0.1			1.0	0.5
Py.sp.			0.7	0.7					1.4	1.4			2.8	2.4
As.sp.			1.6	1.6					34.4	25.1	[illegible]	21.8	5.3	5.0
Si.su.													2.0	2.0
Bl.ce.													11.7	11.7
un.fb.													0.1	0.1
TOTAL	4737.8	621.7	2086.7	324.9	1948.8	221.2	2780.7	360.7	317[illegible].2	689.2	534[illegible]	[illegible]	7044.5	1668.[illegible]

Appendix 4: Herbaceous biomass (kg/ha) in the willow habitat during snowfree periods; means and S.E.

	Oct.		Nov.		Apr.		May		June		July		Aug	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.		S.E.
GRAMINOIDS														
Grass	372.0	159.6	206.0	83.7	160.0	58.5	186.9	[illegible]	[illegible]	117.9	[illegible]	129.0	717.4	241.1
Ca.sp.	2000.8	584.7	1463.4	570.7	511.2	181.6	594.6	230.7	[illegible]	516.4	4631.6	1584.7	4302.2	1066.3
FORBS														
Vi.sp.											0.6	0.6		
Er.sp.											6.5	5.9	16.0	15.0
So.sp.									3.0	2.4				
Ta.of.							3.2	0.8	5.8	2.7	15.1	10.6	28.6	13.8
Fr.gl.	0.2	0.2	0.2	0.2			1.6	1.6					4.8	0.5
Eq.sp.									21.7	15.6	36.9	[illegible]	37.0	37.0
Ur.gr.	0.6	0.6	6.7	5.0					0.2	0.2				
Ga.te.	8.8	8.8	3.2	3.2	0.2	0.2	0.3	0.3	19.6	10.4	10.7	9.5		
So.ar.	0.2	0.2					0.2	0.2	11.1	6.1	28.6	18.8		
Cl.ar.	157.8	69.6	53.2	22.9	33.8	13.9	10.4	9.5	[illegible]	53.3	140.5	07.3	440.6	304.7
He.la.							6.4	6.4	3.5	3.5			0.4	0.4
Sc.ga.									30.3	18.4	11.6	7.8	[illegible]	24.1
St.sp.							0.2	0.2	2.1	2.0	0.4	0.4	0.3	0.2
Ra.sc.	0.1	0.1					0.1	0.1			0.2	[illegible]	0.9	0.1
Me.ar.									11.3	5.0			[illegible]	[illegible]
Tr.sp.											0.1	0.1	4.2	4.2
St.pa.							0.4	0.4	0.9	0.5	4.1	3.1	43.5	24.6
Ge.al.					0.3	0.2	7.3	5.6	36.3	18.7	[illegible]	4.4	7.0	7.0
Po.am.									8.0	8.0			9.4	9.4
Ra.cy.	0.3	0.2	0.7	0.7					0.1	0.1			1.0	0.5
Ru.pu.							0.2	0.2						
Py.sp.			0.4	0.4			0.1	0.1	4.4	4.4			2.8	2.4
As.sp.	15.0	10.7	23.1	12.6	17.9	11.9	6.8	4.4	68.9	24.3	[illegible]	13.5	181.4	66.0
BROWSE														
Leaves	50.1	14.5	141.7	55.1	20.3	8.0								
TOTAL	2605.7	849.0	1898.6	754.3	743.6	274.4	806.1	[illegible]	[illegible]	806.9	4918.7	1830.4	5582.8	778.5

Appendix 5: Herbaceous biomass (kg/ha) in the upland grassland habitat during snowfree periods, means and S E

	Oct.		Nov.		April		May		June		July		Aug	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S E	x	S E
GRAMINOIDS														
Grass	1584.1	271.9	967.7	101.4	263.1	28.1	500.4	86.5	716.3	118.5	900 5	115.5	1177 2	146.9
FORBS														
Vi.sp.							0.2	0.2			0.3	0.3	1.2	
So.sp.											98.4	87 1		
Ta.of.	23.1	9.2	0.2	0.1			52.3	8.9	194.1	38 8	112.4	25.5	79.2	16.1
Fr.gl.	11.4	6.1	14.2	9.3	0.1	0.1	21.4	9.5	16.4	11.9	68.0	31 2	51.3	22 1
So.ar.							0.6	0.4						
Ci.ar.	49.9	33.4	12.7	9.7	101.1	60.2	1.1	0.8	7.8	5.6	63 5	54 3	43 4	29.5
Tr.sp.	45.4	18.1	4.2	2.5	1.1	0.7	18.5	7.5	99.0	45.1	272 8	99 3	329 6	90 1
Ge.al.							1.7	1.7			1.0	1 0	0 3	0 3
As.sp.	3.0	2.4	0.6	0.4			1.3	1.3	6.3	6.3	28 0	19.5	15 5	8 6
La.sp.							2.7	1.7	8.8	5.0	17 3	10 3	3 8	2 1
Ar.mi.			4.2	4.0			14.6	7.6	19.2	8.3	34 6	22.0	21 6	16 8
Vi.am.							0.2	0.2	1.4	0.8	1 2	0 8	2.8	1.7
Ga.bo.							6.5	5.3	5.6	5.4	4.2	4.2	12 7	11 1
Ma.ca.							0.3	0.3					1 0	1 0
An.ma.									3.2	3.2				
Pl.ma.									1.2	1.2				
BROWSE														
Leaves			18.4	9.4										
TOTAL	1716.9	341.2	1022.2	136.8	365.4	89.1	621.8	131.9	1079.5	250.0	1602 3	480 9	1739.7	3[illegible]

Appendix 6: Herbaceous biomass (kg/ha) in the lowland grassland habitat during [illegible]free periods, means and S.E.

	Oct.		Nov.		Apr.		May		June		July		Aug	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E	x	S.E
GRAMINOIDS														
Grass	1747.9	213.5	937.7	163.2	333.3	42.5	377.0	34.5	1977.0	116.7	2017.1	[illegible]	2764.7	637.0
Ca.sp.	3.9	3.9	3.2	3.2										
FORBS														
So.sp.							0.6	0.6	6.2	4.4	18.5	18.5	1.6	1.6
Ta.of.	0.4	0.4					11.8	7.0	5.8	3.9	50.0	15.0	53.8	25.8
Fr.gl.							0.6	0.6	1.7	1.7	22.3	22.3	1.0	1.0
So.ar.							12.0	5.9	20.6	20.6	11.7	11.7	62.4	22.0
Ch.ar.	375.7	142.9	279.4	109.9	172.3	74.2	2.1	1.6			682.4	314.4	1549.6	854.3
Tr.sp.	1.6	1.6					0.4	0.4	0.0	0.0	21.5	21.5	88.7	26.6
As.sp.											33.2	22.0	54.2	43.1
Ar.mi.							6.5	4.9	7.3	6.0	6.1	6.1	79.1	52.4
Vi.am.											0.3	0.3		
Pl.ma.													4.5	4.2
Po.an.							6.8	6.8					3.4	3.4
Ga.te.			8.8	8.8			10.5	6.0	24.7	13.8	50.3	23.8	124.2	92.8
De.so.									2.2	2.1	10.6	10.6	48.8	48.8
Ut.gr.	164.8	117.5	44.0	38.0	2.0	1.3	3.5	2.5	28.6	21.0	129.8	97.6	149.6	101.9
Me.ar.											16.1	14.9		
He.la.							0.2	0.2						
St.sp.									0.9	0.9				
Ge.al.							5.4	5.4	0.4	0.4				
TOTAL	2294.3	479.8	1273.1	324.1	507.6	118.1	437.2	76.3	2075.3	191.5	306 96	927.8	4945.8	1914.9

Appendix 7: Herbaceous biomass (kg/ha) in the poplar forest during snowfree periods, means and S.E.

	Oct.		Nov.		Apr.		May		June		July		Aug.	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
GRAMINOIDS														
Grass	43.4	18.4	93.5	32.0	283.3	117.2	65.4	16.6	30.9	10.0	92.3	36.1	137.5	67.9
BROWSE														
Leaves	1832.9	127.6	1398.7	66.2	1130.8	251.4								
FORBS														
Co.ca.	13.9	9.4	11.0	4.3	5.4	2.8	5.5	2.5	28.3	7.5	46.9	25.7	26.4	6.0
Vi.sp.							2.3	1.1	18.1	11.6	10.4	8.7	12.5	6.1
Ta.of.	0.2	0.2			0.3	0.2	0.4	0.2			11.8	5.6	5.4	3.0
Fr.gl.	1.6	1.0	0.4	0.4	1.5	0.7	5.6	2.3	15.1	7.1	30.4	11.9	32.3	12.5
Eq.sp.													1.1	0.8
Cl.ar.	0.2	0.2												
He.la.							0.7	0.4	9.0	7.3	0.7	0.7		
St.sp.							0.2	0.2			1.5	1.1	0.2	0.1
Tr.sp.							0.1	[illegible]			0.2	0.2	0.7	0.7
Ge.al.					1.3	0.9								
Py.sp.	8.8	5.4	3.6	1.8	4.9	3.7	1.1	0.9	5.2	2.8	4.6	2.4	14.1	7.7
As.sp.	2.7	2.4	3.3	3.3			3.3	1.6	38.3	13.3	30.6	10.1	27.5	7.5
Li.bo.	5.2	3.2	3.0	1.9	1.2	0.8	5.3	3.1	3.5	4.6	9.4	4.5	6.7	3.2
Ar.nu.									20.4	12.3	27.3	12.4	32.0	16.4
Ru.pu.							3.5	2.4	5.2	3.9	29.0	8.7	25.3	11.4
Me.pa.							5.5	4.0	13.5	7.9	10.6	5.0	2.7	1.7
An.ca.							0.7	0.5	8.5	4.3	3.5	2.4	2.9	1.8
Mi.nu.	2.5	[illegible]	3.7	2.4			0.6	0.6	4.7	3.1	1.5	1.2	3.1	2.1
Ma.ca.							4.3	[illegible]	13.6	4.2	7.8	3.6	7.3	3.0
Di.tr.											[illegible]	6.6	0.4	0.3
Vi.am.							0.2	0.2	7.3	6.2			1.6	1.6
La.sp.			0.1	0.1			4.0	1.8	27.2	13.3	30.6	9.9	19.1	6.9
Ga.sp.							1.0	0.5	2.1	1.4	6.8	3.7	6.2	2.3
Sa.ma.							1.2	1.2					3.6	3.2
Ac.ru.									7.0	5.0				
Os.sp.									0.7	0.7				
Pl.ma.											3.2	3.2		
Ra.sc.	1.2	1.0	2.2	1.5										
TOTAL	1912.5	169.3	1519.6	113.8	1427.9	377.7	110.7	41.9	258.7	123.3	368.9	[illegible]	368.5	166.7

Appendix 8: Seasonal in vitro dry matter digestibility values of grasses, browse, and forbs in the diet.

	Grasses		Browse		Forbs	
	x	S.E.	x	S.E.	x	S.E.
Season						
s[illegible]	63.28	4.728	52.52	3.712	70.21	2.928
s[illegible]	66.52	4.221	59.89	2.583	73.53	1.828
fall	44.10	3.100	35.79	3.253	47.42	1.899
winter	43.60	0.900	33.67	3.778	44.63	0.199

Appendix 9: Percentage of graminoids contained in monthly diets of the four sex and age classes of wapiti in each habitat; 1=adult males, 2=adult females, 3=male calves, and 4=female calves.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October										
Group 1										
Group 2	69.00	3.898	26.23	8.321	50.63	1.594	84.97	4.673	99.93	0.067
Group 3	65.33	1.567	29.58	2.587	48.23	1.281	95.90	3.70	99.83	0.167
Group 4	71.84	[illegible]	21.53	8.372	52.93	8.080	80.34	5.443	100.00	0.0
Mean	68.72	[illegible]	25.96	3.785	50.93	2.733	85.59	3.663	99.22	0.057
November										
Group 1	65.63	5.991	24.49	8.596	68.50	0.862	95.97	1.506	99.13	0.593
Group 2	64.93	2.391	44.77	7.969	65.47	0.722	95.47	2.302	98.67	1.048
Group 3	57.74	2.515	35.67	8.457	68.88	1.762	91.77	2.887	99.03	0.590
Group 4	64.27	6.652	33.67	2.794	65.97	1.932	90.63	3.749	99.07	0.884
Mean	63.14	2.368	34.65	3.913	67.20	0.754	93.46	1.414	98.97	0.348
December										
Group 1	22.80	8.279	20.53	6.181	84.41	[illegible]	[illegible]	9.219	91.53	6.747
Group 2	16.00	7.330	16.43	2.791	82.03	[illegible]	[illegible]	8.967	90.60	8.127
Group 3	25.50	8.266	24.37	3.285	79.87	[illegible]	[illegible]	15.426	88.70	6.180
Group 4	27.63	10.650	25.53	10.335	80.67	[illegible]	84.97	2.979	88.36	14.666
Mean	22.98	3.996	21.72	3.263	81.74	1.561	73.14	4.936	89.81	4.369
January										
Group 1	24.05	6.950	10.30	4.060	85.97	0.784	62.84	7.600	100.0	0.0
Group 2	5.50	2.074	11.60	3.361	88.63	2.025	70.37	2.979	95.77	3.877
Group 3	18.73	2.019	11.74	6.503	90.97	1.117	73.97	2.649	100.0	0.0
Group 4	11.4	2.685	[illegible]	0.203	91.11	1.386	67.60	2.089	100.0	0.0
Mean	14.92	2.909	10.80	1.842	89.17	0.876	68.69	2.408	98.44	0.108
February										
Group 1	20.13	2.333	13.17	4.401	88.10	1.069	71.47	4.173	100.0	0.0
Group 2	18.70	2.572	17.73	4.781	86.54	3.250	70.80	7.597	100.0	0.0
Group 3	18.93	6.241	12.60	2.406	90.67	3.205	70.73	1.539	99.57	1.233
Group 4	21.60	6.908	11.50	3.653	92.40	1.955	68.87	2.034	100.0	0.0
Mean	19.84	2.472	13.75	1.936	89.43	1.293	70.46	1.463	99.71	0.308
March										
Group 1	57.27	10.262	30.99	4.699	87.03	3.889	65.32	13.146	100.0	0.0
Group 2	59.69	13.055	17.23	2.942	93.23	0.484	63.63	7.630	99.93	0.033
Group 3	63.00	7.223	20.77	5.335	86.93	0.677	71.67	4.405	99.73	0.267
Group 4	67.10	7.199	21.60	3.401	95.67	0.994	65.77	2.727	99.17	0.033
Mean	61.77	4.410	22.65	2.536	89.43	1.564	66.60	2.716	99.89	0.065

Appendix 9. Percentage of graminoids contained in monthly diets of the four sex and age classes of wapiti in each habitat; 1=adult males, 2=adult females, 3=male calves, and 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	95.60	1.752	32.45	9.351	98.75	0.3383	99.52	0.251	100.0	0.0
Group 2	95.67	0.291	42.90	5.755	99.17	0.733	98.97	0.10	100.0	0.0
Group 3	93.77	1.979	42.33	5.081	97.20	1.510	97.87	0.145	100.0	0.0
Group 4	91.37	0.555	43.27	1.981	98.97	0.984	98.77	0.353	99.82	0.0
Mean	93.95	0.784	40.24	3.016	98.57	0.475	98.78	0.251	99.96	0.0
May										
Group 1	73.00	5.600	27.67	2.974	73.90	1.770	90.83	2.826	98.33	0.649
Group 2	74.13	7.082	42.90	6.912	69.47	3.417	92.80	1.419	99.13	0.120
Group 3	70.77	5.741	46.63	2.948	67.20	4.216	92.30	1.473	98.14	0.950
Group 4	73.57	3.176	31.60	4.461	67.60	3.879	90.83	0.809	99.23	0.426
Mean	72.87	2.5[illegible]5	37.70	3.109	69.59	1.770	91.69	0.807	98.84	0.285
June										
Group 1	3.90	0.603	5.33	0.639	42.45	3.091	78.09	1.539	10.09	3.307
Group 2	2.07	0.821	4.67	1.157	42.33	1.410	91.03	1.683	23.60	0.757
Group 3	2.11	0.897	4.55	0.709	38.97	0.176	81.40	5.024	13.10	3.589
Group 4	2.17	1.354	7.10	5.107	37.70	1.914	89.03	4.480	36.77	9.084
Mean	2.56	0.484	5.41	1.272	40.36	1.047	84.87	2.210	22.15	4.556
July										
Group 1	3.80	1.079	6.10	3.099	43.18	3.275	59.83	4.273	0.19	0.0
Group 2	0.73	0.260	6.77	3.788	47.23	1.965	53.33	7.446	2.27	0.0
Group 3	0.50	0.264	6.33	4.94	44.00	7.868	55.37	11.084	4.12	0.0
Group 4	0.83	0.338	5.68	3.209	45.03	4.902	66.97	3.113	5.03	5.033
Mean	1.47	0.495	6.22	1.395	44.84	4.365	59.88	3.426	2.98	1.258
August										
Group 1	2.13	0.491	10.08	5.136	39.40	1.514	65.47	2.797	0.0	0.0
Group 2	1.33	0.865	5.02	1.391	42.17	1.257	55.33	5.045	0.0	0.0
Group 3	1.13	0.570	2.57	1.660	40.47	1.257	61.83	4.054	0.0	0.0
Group 4	1.37	1.168	3.11	0.406	40.39	0.664	60.55	10.489	0.4	0.0
Mean	1.49	0.367	5.16	1.604	40.61	0.547	60.80	3.090	0.1	0.0

Appendix 10: Percentage of browse contained in monthly diets of the four sex and age classes of wapiti in each habitat; 1=adult males; 2=adult females, 3=male calves, and 4=female calves.

Month	Willow x	Willow S.E.	Poplar Forest x	Poplar Forest S.E.	Upland Grassland x	Upland Grassland S.E.	Lowland Grassland x	Lowland Grassland S.E.	Sedge Meadow x	Sedge Meadow S.E.
October										
Group 1										
Group 2	13.90	1.646	56.67	1.850	00.0	0.0	0.0	0.0	0.0	0.0
Group 3	20.77	2.241	61.33	4.332	0.20	0.1	0.0	0.0	0.0	0.0
Group 4	12.63	0.318	62.51	6.094	0.21	0.133	0.20	0.186	0.0	0.0
Mean	15.19	1.736	60.63	2.769	0.15	0.063	0.06	0.074	0.0	0.0
November										
Group 1	24.07	4.889	71.84	6.646	00.0	0.0	0.10	0.100	0.77	0.498
Group 2	25.57	1.668	50.70	6.965	00.0	0.0	0.03	0.033	1.03	1.033
Group 3	31.97	3.588	60.37	7.794	00.0	0.0	0.40	0.400	0.20	0.0
Group 4	30.03	4.772	63.17	3.541	00.0	0.0	0.35	0.418	0.70	0.700
Mean	27.91	2.002	61.52	3.694	00.0	0.0	0.22	0.137	0.68	0.309
December										
Group 1	58.13	9.963	72.71	5.060	11.94	1.002	1.27	0.938	1.20	1.200
Group 2	70.17	8.369	72.73	11.811	16.60	3.958	0.63	0.448	0.00	0.0
Group 3	59.27	12.268	72.80	3.458	17.93	2.170	0.50	0.208	0.00	0.0
Group 4	58.30	10.842	71.67	10.335	16.73	4.039	1.39	1.091	1.36	1.481
Mean	61.45	4.708	72.48	3.611	15.80	[illegible]	0.95	0.347	0.64	0.537
January										
Group 1	65.10	5.141	89.57	3.976	11.63	[illegible]	7.30	1.513	0.12	0.0
Group 2	92.14	2.230	87.00	3.341	10.40	[illegible]	7.12	2.237	0.43	0.433
Group 8	73.03	1.991	89.23	6.697	7.60	[illegible]	3.93	0.524	0.27	0.0
Group 4	80.47	7.388	90.30	0.265	7.17	1.868	3.90	1.709	0.13	0.0
Mean	77.70	3.947	89.08	1.866	9.20	0.969	5.56	1.745	0.24	0.108
February										
Group 1	74.17	3.526	86.77	4.396	11.03	1.202	3.00	0.473	0.0	0.0
Group 2	73.27	6.508	[illegible]	3.781	10.72	[illegible]	4.60	1.300	0.0	0.0
Group 3	85.20	9.752	[illegible]	2.288	8.23	[illegible]	7.25	1.802	0.57	0.633
Group 4	68.12	26.370	84.03	3.735	6.30	[illegible]	6.63	0.696	0.0	0.0
Mean	73.90	6.892	85.10	1.929	9.07	1.225	5.37	0.807	0.14	0.158
March										
Group 1	30.83	10.31	68.54	4.636	10.75	5.245	5.59	4.756	0.0	0.0
Group 2	21.13	4.814	[illegible]	2.981	4.17	1.789	0.73	0.384	0.0	0.0
Group 3	30.70	4.535	78.77	5.388	6.20	1.387	1.67	0.903	0.03	0.033
Group 4	23.93	6.953	77.90	3.512	2.60	1.332	1.97	0.984	0.0	0.0
Mean	26.61	1.578	76.87	2.540	5.93	1.622	2.49	1.262	0.01	0.083

Appendix 10: Percentage of browse contained in monthly diets of the four sex and age classes of wapiti in each habitat; 1=adult males; 2=adult females, 3=male calves, and 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	3.00	[illegible].317	65.27	10.209	1.10	0.322	0.0	0.0	0.0	0.0
Group 2	2.72	0.788	54.80	5.225	0.77	0.767	0.13	0.088	0.0	0.0
Group 3	3.90	1.411	55.83	5.466	1.46	0.436	0.30	0.153	0.0	0.0
Group 4	5.11	1.213	54.27	2.824	0.43	0.384	0.53	0.289		0.0
Mean	3.82	0.587	57.54	3.208	0.94	0.247	0.24	0.092	0.0	0.0
May										
Group 1	25.00	3.659	41.83	7.593	0.67	0.285	0.83	0.348	0.83	0.467
Group 2	23.50	7.414	24.50	3.840	0.40	0.100	0.80	0.416	0.60	0.088
Group 3	26.53	5.434	24.60	2.488	0.37	0.273	0.33	0.176	0.70	0.404
Group 4	2[illegible].90	2.954	32.93	5.658	1.15	0.120	1.30	0.551	0.67	0.481
Mean	24.37	2.303	30.96	3.742	0.65	0.142	0.82	0.198	0.70	0.170
June										
Group 1	78.97	5.160	[illegible]67	2.074	1.33	0.433	1.10	0.371	5.80	8.818
Group 2	85.73	2.085	27.89	2.161	0.60	0.153	0.47	0.328	1.63	1.433
Group 3	81.82	7.172	43.64	7.825	0.83	0.260	0.73	0.533	0.0	0.0
Group 4	82.50	3.116	34.50	10.265	0.61	0.088	0.80	0.361	0.0	0.0
Mean	82.26	1.776	36.43	3.777	0.84	0.157	0.78	0.192	1.86	1.880
July										
Group 1	77.47	3.982	39.03	18.556	1.17	0.491	2.50	0.451	0.0	0.0
Group 2	82.62	2.924	44.47	5.015	0.97	0.433	2.00	0.635	1.60	1.600
Group 3	85.80	1.290	36.13	5.617	1.10	0.400	0.89	0.203	10.27	10.267
Group 4	90.20	2.042	40.51	2.331	0.60	0.265	0.77	0.318	4.8	0.0
Mean	84.02	1.885	40.04	4.519	0.96	0.185	1.54	0.309	4.17	2.562
August										
Group 1	81.57	3.175	43.33	12.855	1.10	0.463	1.55	0.437	0.0	0.0
Group 2	81.27	6.912	37.40	12.701	0.90	0.100	3.40	0.231	0.3	0.367
Group 3	82.30	3.963	50.23	4.161	1.03	0.219	[illegible]	0.6659	0.0	0.0
Group 4	86.30	3.523	47.53	9.071	1.70	1.147	[illegible]	0.328	4.18	3.470
Mean	82.86	2.078	44.62	[illegible].150	1.18	[illegible]	[illegible]	[illegible]	1.12	0.771

Appendix 11: Percentage of forbs contained in monthly diets of the four sex and age classes of wapiti in each habitat; 1=adult males, 2=adult females, 3=male calves, 4=female calves.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E
October										
Group 1										
Group 2	18.10	2.376	17.13	9.872	49.37	1.594	15.03	4.673	0.0	0.0
Group 3	15.75	2.028	12.68	4.017	51.57	1.309	5.52	3.700	0.16	0.167
Group 4	14.90	3.538	10.43	4.215	45.84	8.135	22.50	5.350	0.0	0.0
Mean	16.09	1.506	13.41	3.629	48.92	2.757	14.35	3.626	0.04	0.056
November										
Group 1	10.30	1.250	3.30	2.084	31.50	0.862	3.20	1.488	0.10	0.100
Group 2	9.60	1.100	8.77	1.842	34.29	0.722	4.50	2.329	0.27	0.176
Group 3	10.81	1.795	3.75	1.084	31.20	1.762	7.83	2.551	0.77	0.623
Group 4	5.30	2.875	3.07	0.745	34.07	1.910	8.90	4.038	0.27	0.219
Mean	8.95	1.052	3.47	0.666	32.80	0.752	6.32	1.393	0.35	0.165
December										
Group 1	19.07	3.319	2.67	1.147	3.57	1.686	30.07	9.572	7.03	5.565
Group 2	14.83	4.281	13.90	12.611	1.37	1.017	30.70	9.361	10.00	8.127
Group 3	14.77	4.013	4.63	0.233	2.23	0.727	29.26	15.48	11.17	6.180
Group 4	13.63	0.410	5.13	0.033	2.67	0.833	13.60	1.922	10.12	13.310
Mean	15.58	1.306	5.81	3.160	2.46	0.640	25.91	5.031	9.55	4.015
January										
Group 1	10.93	1.841	0.13	0.231	1.88	0.265	30.42	8.940	0.0	0.0
Group 2	2.13	1.041	0.07	0.033	0.97	0.484	22.07	1.302	4.40	4.06
Group 3	8.27	3.733	0.29	0.203	2.07	0.696	21.50	2.524	0.88	0.0
Group 4	8.17	4.781	0.20	0.200	1.63	0.518	28.53	2.739	0.0	0.0
Mean	7.37	1.745	0.17	0.075	1.64	0.272	25.63	2.490	1.32	1.038
February										
Group 1	5.73	1.299	0.27	0.067	1.40	0.145	24.17	4.667	0.0	0.0
Group 2	7.50	3.459	1.30	0.231	2.13	1.203	24.63	3.444	0.0	0.0
Group 3	3.80	3.172	0.37	0.067	1.10	0.569	[illegible]	0.985	0.55	0.633
Group 4	6.63	1.666	0.42	0.067	1.33	0.318	[illegible]	3.267	0.0	0.0
Mean	5.92	0.417	0.51	0.562	1.49	0.327	23.72	1.526	0.14	0.158
March										
Group 1	6.97	0.788	0.43	[illegible]	3.07	2.07	29.97	3.033	0.08	0.0
Group 2	21.92	10.958	0.50	0.153	2.63	1.304	34.67	7.172	0.07	0.033
Group 3	8.35	3.013	0.50	0.173	5.98	1.637	26.73	4.788	0.23	0.233
Group 4	9.00	0.289	0.50	0.252	1.70	0.777	32.30	2.802	0.03	0.033
Mean	11.58	3.247	0.48	0.092	3.35	2.070	30.92	2.262	0.10	0.058

Appendix 11: Percentage of [illegible]ained in monthly diets of the four sex and age classes of wapiti in [illegible]bitat; 1=adult males, 2=adult females, 3=male calves, 4=fe[illegible], continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	1.55	0.441	1.58	0.929	0.27	[illegible]	0.47	0.133	0.0	0.0
Group 2	1.60	0.529	2.33	0.617	0.10	0.058	0.90	0.551	0.0	0.0
Group 3	2.33	0.649	1.70	0.611	1.23	1.100	1.77	0.285	0.0	0.0
Group 4	3.40	0.666	2.25	1.126	[illegible].60	0.60	0.73	0.273	0.0	0.0
Mean	2.22	0.349	2.02	0.383	0.50	0.296	0.97	0.222	0.0	0.0
May										
Group 1	6.15	2.659	27.82	5.154	25.43	1.017	6.30	2.650	0.40	0.200
Group 2	1.93	0.393	32.63	3.021	34.28	3.350	5.36	1.217	0.33	0.088
Group 3	1.30	0.322	29.20	1.724	34.97	4.317	5.37	1.271	1.00	0.625
Group 4	3.47	0.884	35.47	3.405	31.10	3.866	5.83	0.623	0.10	0.058
Mean	2.76	0.774	31.29	1.969	30.75	1.769	5.72	0.723	0.46	0.173
June										
Group 1	17.10	5.341	55.00	1.646	56.10	2.658	20.42	1.405	85.15	12.125
Group 2	14.17	2.293	67.63	3.251	57.03	1.281	8.53	1.734	75.00	1.559
Group 3	16.43	3.372	51.77	7.305	60.2	0.252	17.87	4.972	79.42	3.604
Group 4	15.43	3.206	58.27	8.528	61.93	1.877	10.17	4.139	[illegible]	9.084
Mean	15.81	1.684	58.17	3.312	58.82	1.031	14.25	2.120	[illegible]	4.539
July										
Group 1	18.63	3.372	54.90	20.55	55.37	3.312	37.70	4.042	88.56	0.0
Group 2	17.17	2.976	48.60	4.392	52.15	2.378	41.23	9.032	98.40	1.600
Group 3	11.8	1.102	55.87	4.184	54.87	7.467	43.09	11.100	89.73	10.267
Group 4	10.16	1.795	55.04	0.874	54.40	4.631	32.27	2.918	95.00	5.00
Mean	14.42	1.563	53.60	4.768	54.20	2.106	38.57	3.495	92.92	5.459
August										
Group 1	16.73	2.733	45.33	10.066	59.70	1.505	33.50	2.471	100.0	0.0
Group 2	17.33	6.068	59.23	11.126	56.97	1.260	41.27	4.953	99.71	0.333
Group 3	13.50	3.453	42.20	2.674	58.53	0.418	33.97	4.524	100.00	0.0
Group 4	14.75	3.883	50.03	8.910	57.63	1.105	36.83	10.684	95.83	3.470
Mean	15.58	1.905	49.16	4.597	58.21	0.578	36.39	3.042	98.88	0.771

Appendix 12: Bite weight (grams/bite) of forage species or groups included in wapiti diets.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug
Upland grass	.13	.08	.06	.06	.048	.043	.057	.058	.13	.17	.18
Lowland grass	.21	.18	.12	.10	.09	.096	.06	.09	.30	.23	.23
Forest grass	.09	.09	.07	.07	.67	.058	.07	.09			
Carex spp. (blades)			.25	.25	.25	.25				.25	
(shoots)	.2	.2					.079	.12	.22		
Betula papyrifera											
Twigs	.36	.36		.36							
Leaves								.05	.13	.25	.25
Populus balsamifera											
Twigs	.8	.85	.95	.9	.97	1.3					
Bark		.17	.17	.17	.17	.17					
Leaves								.3	.6	.7	.7
Populus tremuloides											
Twigs	.42	.51	.65	.57	.4	.26					
Bark		.14	.14	.14	.14	.14					
Leaves								.14	.35	.37	.4
Salix spp.											
Twigs	.2	.21	.27	.25	.3	.47	.4				
Bark		.17	.17	.17	.17	.17					
Leaves								.12	.44	.4	.43
Corylus cornuta											
Twigs	.2	.3	.27	.24	.15	.18	.18				
Leaves								.1	.22	.3	.3
Cornus stolonifera											
Twigs		.2	.14	.15	.17	.14	.6				
Leaves									.2	.25	.4
Lonicera involucrata											
Twigs							.24				
Leaves								.14	.33	.3	.4
Lonicera dioica											
Leaves								.05	.23	.2	.21
Viburnum edule											
Leaves										.23	
Rubus melanolasius											
Leaves								.062	.18	.25	.32
Rosa spp.											
Leaves								.054	.14	.12	.22
Rubus hirtellum											
Twigs		.48	.53	.47	.42	.48	.75				
Leaves								.09			.2

Appendix 12: Bite weight (grams/bite) of forage species or groups included in wapiti diets, continued.

Ribes spp.											
Leaves								.081	.25	.35	.37
Prunus virginiana											
Twigs		.2	.24	.2	.2	.18					
Leaves								.17		.31	.28
Amelanchier alnifolia											
Twigs	.2	.28	.26	.23	.21	.22	.28				
Leaves									.25	.25	.32
Symphoricarpos spp.											
Twigs	.1		.1			.07					
Leaves								.05	.25	.24	.23
Fallen leaves	.3	.21	.21	.19	.12	.12	.20				
Anemone canadensis									.11	.11	
Cornus canadensis	.15	.22	.29				.176				
Mertensia paniculata								.11	.35	.29	.3
Maianthemum canadense								.05			.112
Viola spp.								.056	.17	.16	.16
Erigeron spp.									1.16	.19	
Solidago spp.								.37	.33	.3	
Taraxacum officinale	.1	.05						.06	.17	.17	.1
Fragaria glauca	.05	.02						.032	.16	.1	.05
Equisetum spp.									.2	.26	-
Aralia nudicaulis									.53	.57	.89
Urtica gracilis	.30	.23								.49	.29
Galeopsis tetrahit								.06	.11	.2	.39
Sonchus arvensis									.2	.23	.43
Cirsium arvense	.4	.4	.31	.27	.2	.35	.22				
Heracleum lanatum								.08	.53	.51	.32
Lathyrus spp.								.1	.46	.74	.59
Vicia americana									.4	.4	.35
Galium boreale								.05	.17		
Aster spp.	.18	.17	.2	.2	.2	.2		.03	.15	.33	.45
Trifolium spp.	.15	.05	.02					.04	.1	.13	.19
Achillea millefolium								.017			.13
Stachys palustris									.2	.23	.2
Plantago major									.1	.064	.07
Geum allepicum								.2	.28	.33	
Polygonum amphibium									.4	.53	.51
Disporum trachycorpum									.78	.51	.62
Sanicula marilandica									.46	.42	.42

Appendix 13: Bite rate (bites/minute) of the four sex and age classes of wapiti in the five habitats; 1=adult males, 2=adult females, 3=male calves, 4=female calves.

Month	Willow x	Willow S.E.	Poplar Forest x	Poplar Forest S.E.	Upland Grassland x	Upland Grassland S.E.	Lowland Grassland x	Lowland Grassland S.E.	Sedge Meadow x	Sedge Meadow S.E.
October										
Group 1										
Group 2	12.40	0.416	13.54	1.568	44.78	4.579	27.25	5.061	17.56	2.322
Group 3	11.43	0.318	10.07	0.640	33.89	3.394	26.14	10.53	12.18	1.220
Group 4	11.55	0.149	12.75	0.192	41.85	3.228	21.82	1.264	17.19	0.779
Mean	11.79	0.219	12.12	0.720	40.17	2.495	25.07	3.492	15.64	1.174
November										
Group 1	11.32	0.791	13.17	1.455	47.06	4.220	15.82	6.584	16.78	0.946
Group 2	12.48	0.621	13.57	0.802	44.07	3.499	28.00	2.468	21.41	0.635
Group 3	11.76	0.771	12.57	0.661	43.66	1.220	27.71	2.908	16.70	1.438
Group 4	11.18	0.936	13.237	0.994	45.62	1.569	21.39	1.340	18.35	1.558
Mean	11.69	0.369	13.14	0.450	45.10	1.309	23.23	2.239	18.31	0.771
December										
Group 1	9.49	0.328	10.10	0.601	16.25	1.712	14.22	1.065	5.90	1.482
Group 2	11.86	0.872	12.25	1.216	18.10	1.903	12.37	2.594	5.57	1.168
Group 3	9.38	0.836	10.70	0.646	14.99	1.375	12.35	2.218	4.25	0.204
Group 4	9.24	0.307	11.53	0.520	15.12	2.557	12.60	1.073	2.84	0.925
Mean	9.99	0.427	11.14	0.418	16.11	0.097	12.89	0.830	4.44	0.563
January										
Group 1	7.52	1.034	10.80	0.605	18.74	0.604	8.01	0.716	5.19	0.414
Group 2	6.65	2.690	14.00	1.235	19.70	0.255	8.35	0.862	6.39	0.300
Group 3	7.23	0.433	12.88	2.315	20.15	1.322	10.63	0.623	4.44	0.409
Group 4	7.66	0.973	15.34	1.149	19.33	0.257	9.59	2.910	4.30	0.146
Mean	7.32	0.514	13.25	0.801	19.48	0.355	9.15	0.739	5.08	0.288
February										
Group 1	5.38	1.117	14.69	1.996	20.97	1.209	11.97	2.257	5.80	0.710
Group	4.55	0.681	17.03	1.229	20.46	1.562	9.09	0.490	5.45	0.225
Group 3	3.89	0.311	12.71	0.811	24.12	3.097	8.70	0.271	5.81	0.543
Group 4	5.17	0.327	15.11	1.268	25.05	3.771	9.24	1.040	3.35	1.181
Mean	4.75	0.342	14.89	0.719	22.65	1.270	9.75	0.669	5.00	0.468
March										
Group 1	7.06	1.852	13.52	0.707	26.48	0.655	14.42	1.436	21.97	2.514
Group 2	7.78	2.369	14.07	1.036	27.82	0.702	16.53	0.914	21.17	1.872
Group 3	7.75	0.890	11.43	0.601	25.89	1.066	15.75	1.176	16.23	5.873
Group 4	9.13	0.435	18.26	3.699	33.13	7.096	12.77	0.337	24.21	4.046
Mean	7.93	0.712	14.32	1.126	28.33	0.654	14.87	0.620	20.90	1.878

Appendix 13: Bite rate (bites/minute) of the four sex and age classes of wapiti in the five habitats; 1=adult males, 2=adult females, 3=male calves, 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	17.38	0.599	13.44	1.074	32.35	0.352	29.7	0.756	19.45	1.198
Group 2	21.91	2.157	16.65	0.775	39.35	5.091	38.38	3.026	23.78	2.493
Group 3	22.26	3.432	16.24	1.825	36.20	2.818	31.96	1.134	19.24	1.028
Group 4	20.67	0.113	15.15	0.690	39.54	1.169	31.67	1.081	23.94	1.452
Mean	20.56	1.049	15.37	0.627	36.86	1.544	32.93	1.234	21.60	0.978
May										
Group 1	21.27	1.654	27.36	1.413	44.52	1.338	44.91	2.318	33.32	2.572
Group 2	26.95	3.356	34.66	3.777	48.65	1.666	48.43	1.173	33.87	3.456
Group 3	26.75	3.259	28.64	1.381	46.51	1.208	46.34	0.713	34.60	2.688
Group 4	25.56	1.775	26.52	0.876	45.03	1.841	40.13	1.252	31.27	1.831
Mean	25.13	1.654	29.29	1.336	46.18	0.813	44.95	1.1172	33.26	1.217
June										
Group 1	21.31	0.832	22.16	0.780	36.67	1.892	39.83	4.829		
Group 2	24.10	1.299	23.93	1.483	50.33	1.121	54.13	1.185		
Group 3	21.17	1.234	21.41	1.483	42.67	0.183	41.29	7.306		
Group 4	23.32	1.825	18.41	2.424	42.18	1.168	45.26	2.590		
Mean	22.48	0.689	21.48	0.878	42.96	1.560	44.68	2.779		
July										
Group 1	18.63	0.677	22.99	2.263	43.60	3.462	34.16	1.548		
Group 2	22.01	1.109	18.94	1.447	46.24	2.551	35.88	2.008		
Group 3	21.28	1.905	17.16	1.293	42.46	2.583	33.37	6.219		
Group 4	21.70	0.642	17.61	0.680	41.98	1.156	30.34	1.327		
Mean	29.27	0.677	19.17	0.952	43.57	1.205	33.44	1.548		
August										
Group 1	20.09	1.693	19.72	2.992	50.55	0.751	40.85	5.735		
Group 2	22.20	1.943	20.43	2.903	55.62	4.216	32.23	1.584		
Group 3	21.93	5.363	16.37	0.887	45.63	2.727	29.59	3.036		
Group 4	18.99	1.663	17.10	0.191	43.40	3.571	30.90	4.704		
Mean	20.80	1.376	18.41	1.045	48.80	1.940	33.39	2.191		

Appendix 14: The number of feeding stations/minute of the four sex and age classes of wapiti in the five habitat types; 1=adult males, 2=adult females, 3=male calves, 4=female calves.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October										
Group 1										
Group 2	5.21	0.1742	3.05	0.2619	3.94	0.5444	3.46	0.563	2.05	0.3339
Group 3	4.62	0.28	2.33	0.3759	3.34	0.4278	2.66	0.1135	1.98	0.2677
Group 4	5.86	0.3235	3.14	0.4038	4.53	0.4245	5.58	0.3061	3.22	0.2797
Mean	5.23	0.2233	2.84	0.2619	3.93	0.2906	3.90	0.4744	2.42	0.2501
November										
Group 1	4.74	0.106	2.27	0.2454	4.33	0.2381	2.23	0.0706	2.41	0.1778
Group 2	4.26	0.5914	3.32	0.4791	5.94	0.6433	3.01	0.2103	2.92	0.4031
Group 3	4.00	0.5741	3.18	0.2108	4.81	0.1604	3.11	0.1391	2.97	0.1211
Group 4	4.58	0.2368	3.13	0.4319	6.31	0.4748	3.58	0.7783	3.46	0.3134
Mean	4.40	0.2036	2.97	0.1982	5.35	0.3035	2.98	0.2277	2.94	0.1628
December										
Group 1	2.79	0.2340	2.32	0.11	2.83	0.5186	2.27	0.391	1.84	0.475
Group 2	2.99	0.6646	2.79	0.1808	2.84	0.3102	1.54	0.2459	2.36	0.355
Group 3	2.97	0.251	2.02	0.1281	2.77	0.4851	1.72	0.3143	2.73	0.525
Group 4	3.10	0.5392	2.64	0.2184	4.19	0.7105	2.39	0.2106	1.91	0.4748
Mean	2.96	0.1993	2.44	0.1143	3.16	0.2871	1.98	0.1671	2.17	0.2273
January										
Group 1	2.37	0.2238	1.81	0.3297	2.79	0.1729	1.75	0.2222	1.80	0.1065
Group 2	1.23	0.160	1.64	0.4278	2.75	0.1065	1.84	0.3755	2.24	0.2293
Group 3	2.32	0.2991	2.20	0.3457	2.96	0.4937	1.86	0.5064	1.34	0.1068
Group 4	2.31	0.5028	3.31	0.3218	3.27	0.7609	2.60	0.4041	1.28	0.0839
Mean	2.13	0.2003	2.24	0.2485	2.94	0.2077	2.01	0.1751	1.67	0.1321
February										
Group 1	1.81	0.3361	1.86	0.1408	3.12	0.3835	2.98	0.1531	2.12	0.2654
Group 2	1.77	0.2388	2.64	0.2386	2.65	0.3285	1.96	0.2834	1.98	0.1592
Group 3	1.35	0.3783	2.92	0.0536	3.32	0.2226	1.96	0.0706	2.35	0.1775
Group 4	1.91	0.4377	2.55	0.4757	3.02	0.2218	3.19	0.0753	1.89	0.5055
Mean	1.71	0.1645	2.49	0.167	3.03	0.1469	2.56	0.1764	2.09	0.1479
March										
Group 1	2.96	0.777	2.73	0.3699	3.45	0.0934	4.11	0.6592	3.04	0.4713
Group 2	3.87	0.8393	2.73	0.1435	3.69	0.3579	4.04	0.6126	3.45	0.2346
Group 3	2.68	0.0484	2.63	0.4511	3.25	0.4436	3.96	0.0376	3.90	0.1485
Group 4	3.26	0.411	2.47	0.2318	3.21	0.227	3.92	0.3118	3.65	0.0458
Mean	3.19	0.2914	2.64	0.141	3.40	0.1443	4.01	0.2044	3.51	0.1505

Appendix 14: The number of feeding stations/minute of the four sex and age classes of wapiti in the five habitat types; 1=adult males, 2=adult females, 3=male calves, 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	3.58	0.1734	3.96	1.083	3.45	0.1975	3.43	0.1495	2.26	0.1301
Group 2	4.37	0.318	3.76	0.1742	5.18	0.8716	5.60	0.7034	4.34	0.5944
Group 3	3.88	0.2664	4.87	1.0835	4.62	0.3314	4.23	0.2298	3.34	0.6428
Group 4	4.64	0.1538	5.22	0.5801	4.24	0.1823	4.12	0.0794	3.80	0.3691
Mean	4.12	0.1734	4.45	0.3959	4.376	0.2809	4.34	0.2871	3.44	0.3085
May										
Group 1	5.38	0.5082	5.26	0.7902	7.13	0.691	5.55	0.0982	4.55	0.1323
Group 2	6.01	0.214	7.63	0.202	9.75	0.6579	8.50	0.7533	5.18	0.3984
Group 3	6.83	0.561	7.56	0.423	8.80	0.3138	7.54	0.4842	7.04	0.5918
Group 4	6.23	0.1639	6.88	0.0625	7.98	0.7001	6.47	0.4022	5.73	0.3155
Mean	6.11	0.2324	6.83	0.3483	8.42	0.3919	7.02	0.3952	5.63	0.3242
June										
Group 1	3.64	0.3369	5.60	0.6295	7.02	0.5204	5.80	0.3828		
Group 2	3.98	0.1258	7.36	0.3428	9.34	1.0939	7.97	1.364		
Group 3	4.53	0.2533	6.36	0.0968	10.31	0.7981	7.61	0.3988		
Group 4	4.20	0.1761	5.54	0.2166	8.98	0.6906	6.57	0.6205		
Mean	4.08	0.1402	6.21	0.2739	8.91	0.4969	6.92	0.4312		
July										
Group 1	3.19	0.1498	4.55	0.9415	6.29	0.9049	5.26	0.5324		
Group 2	4.36	0.4214	5.36	0.0273	8.49	0.4623	6.71	0.2888		
Group 3	4.47	0.6504	5.75	0.4275	9.24	0.5098	6.52	0.1386		
Group 4	4.44	0.1541	4.61	0.2454	8.10	0.5227	6.05	0.5798		
Mean	4.12	0.4713	5.07	0.2733	8.03	0.422	6.14	0.2474		
August										
Group 1	3.41	0.2558	4.66	1.172	5.81	0.6133	4.93	0.4875		
Group 2	3.49	0.2311	5.71	0.3841	7.43	0.503	5.82	0.3314		
Group 3	4.30	0.4346	4.82	0.5457	7.75	0.3898	5.48	0.3178		
Group 4	3.75	0.4504	4.17	0.3804	6.52	1.1517	5.11	0.7013		
Mean	3.74	0.1881	4.84	0.3425	6.88	0.3857	5.33	0.231		

Appendix 15: Rate of movement (steps/minute) during foraging sessions by the four sex and age classes of wapiti; 1=adult males, 2=adult females, 3=male calves, 4=female calves.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October										
Group 1										
Group 2	6.52	0.9346	5.65	0.1405	6.06	0.8085	5.62	0.2917	4.04	0.5324
Group 3	9.53	0.3347	5.73	0.8376	7.63	0.4194	6.08	0.9945	4.29	0.1894
Group 4	9.79	0.5862	5.77	0.9093	8.22	0.5442	9.22	0.4998	6.10	0.8062
Mean	8.61	0.6186	5.72	0.3596	7.31	0.4445	6.97	0.6557	4.81	0.4313
November										
Group 1	8.68	0.1719	4.66	0.3334	6.78	1.1561	3.79	0.1354	4.85	0.1607
Group 2	8.46	0.8101	6.24	0.3314	10.14	1.2127	5.79	0.7416	7.50	0.8135
Group 3	8.24	0.8568	6.50	1.0970	9.93	0.6614	6.41	0.7062	7.50	0.8135
Group 4	8.98	0.5742	5.47	0.404	11.07	0.6735	7.00	1.2385	7.43	1.2995
Mean	8.59	0.2940	5.72	0.345	9.48	0.6367	5.75	0.5005	6.20	0.5377
December										
Group 1	6.89	0.3227	6.75	0.4262	6.94	1.3482	4.92	0.8054	9.63	4.06
Group 2	8.79	1.6962	7.32	0.9252	6.53	0.2581	4.39	1.8223	17.57	2.43
Group 3	7.37	0.6122	5.08	0.4933	8.51	1.599	5.20	1.075	16.80	3.200
Group 4	7.12	1.2735	6.76	0.8433	11.50	2.0102	7.06	0.6294	9.93	4.472
Mean	7.54	0.5254	6.48	0.7872	8.37	0.8554	5.39	0.586	13.09	2.0646
January										
Group 1	5.76	0.2425	4.86	0.4335	6.32	0.8303	7.11	0.3931	9.92	0.8266
Group 2	4.57	0.1500	3.65	0.9786	6.72	0.7246	8.30	0.5936	11.77	0.6697
Group 3	5.26	0.2410	5.66	0.7777	6.71	1.4853	7.53	1.8509	9.36	0.3982
Group 4	5.33	0.5724	6.96	0.4258	6.39	1.2188	8.15	1.8866	7.53	0.9702
Mean	5.29	0.2007	5.29	0.4685	6.54	0.4754	7.77	0.6012	9.65	0.5561
February										
Group 1	5.18	0.0681	4.81	1.0011	6.83	1.7207	10.17	0.8769	8.99	1.0982
Group 2	5.97	0.1652	6.72	0.1763	5.34	0.2070	9.67	1.1287	10.52	1.0084
Group 3	6.11	1.156	6.91	0.4842	5.39	0.3427	11.19	0.710	11.22	1.5366
Group 4	6.89	0.7398	5.34	0.5544	5.45	0.5838	15.82	1.3527	8.27	3.7886
Mean	6.04	0.347	5.95	1.0011	5.75	0.4392	11.71	0.8569	5.00	0.468
March										
Group 1	6.91	0.5446	11.81	5.5825	6.10	0.9924	7.85	0.8577	5.93	0.0681
Group 2	8.75	1.2908	5.09	0.4157	7.04	0.4403	7.31	0.0505	5.91	0.5363
Group 3	7.25	0.2879	5.26	0.9107	6.29	0.7535	6.93	0.6261	7.93	0.4795
Group 4	6.72	1.1238	5.50	0.9060	5.70	0.2954	8.39	0.6274	7.77	0.4170
Mean	7.41	0.4560	6.92	1.492	6.28	0.3141	7.63	0.3096	6.89	0.3415

Appendix 15: Rate of movement (steps/minute) during foraging sessions by the four sex and age classes of wapiti; 1=adult males, 2=adult females, 3=male calves, 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	7.21	0.9802	6.69	1.1345	5.28	0.2833	4.81	0.3541	3.27	0.3688
Group 2	8.40	1.3259	6.18	0.3055	7.45	0.7687	8.57	0.7163	7.86	0.8555
Group 3	7.11	0.8055	7.35	0.8263	8.35	0.3193	7.73	0.6199	6.49	1.40
Group 4	8.72	0.113	7.94	0.5886	7.17	0.5025	9.60	1.1552	6.62	0.6197
Mean	7.86	0.4811	7.04	0.3871	7.06	0.3996	7.68	0.6291	6.06	0.638
May										
Group 1	10.57	1.6874	9.22	1.476	10.26	1.196	7.34	0.0346	6.71	0.2804
Group 2	11.59	0.3078	12.85	0.9577	14.01	1.1775	12.52	1.1787	7.41	0.2751
Group 3	14.97	0.3493	15.12	0.9652	14.76	0.3408	12.83	0.4085	11.80	0.9406
Group 4	12.76	0.5677	14.40	0.417	11.91	1.6795	12.28	0.7239	11.46	0.4409
Mean	12.47	0.6307	12.90	0.8137	12.74	0.7392	11.24	0.7481	9.35	0.7335
June										
Group 1	8.89	0.928	12.17	2.1598	12.03	0.6013	10.52	0.8942		
Group 2	10.93	0.8574	14.99	1.2989	15.04	1.573	12.28	1.715		
Group 3	12.75	0.7922	16.50	0.4364	15.76	1.6485	13.59	1.1733		
Group 4	11.39	1.5455	15.28	0.3271	15.76	1.6485	12.90	1.7636		
Mean	10.99	0.6194	14.73	0.7286	14.76	0.8756	12.12	0.6765		
July										
Group 1	10.08	0.8324	10.72	1.752	12.31	2.0551	9.56	1.6128		
Group 2	11.50	0.5284	12.35	0.8215	15.12	0.6502	13.87	1.0964		
Group 3	13.06	1.5685	14.63	1.1153	17.04	1.3959	14.04	0.6392		
Group 4	11.82	0.247	12.66	0.1035	13.71	0.8716	12.38	0.3058		
Mean	11.62	0.5109	12.59	0.6351	14.55	0.7796	12.45	0.7049		
August										
Group 1	11.36	1.7752	12.24	3.144	10.15	0.8041	9.34	1.4052		
Group 2	8.91	0.8556	12.77	0.652	12.33	0.972	11.86	0.2055		
Group 3	10.67	0.6609	13.36	1.3647	15.49	0.984	11.79	1.0802		
Group 4	11.11	0.3816	11.36	0.239	12.30	2.311	7.97	1.3259		
Mean	10.51	0.5355	12.43	0.7776	12.57	0.8301	10.24	0.6888		

Appendix 16: Time spent in other activity by the four sex and age classes during foraging sessions in each habitat; 1=adult males, 2=adult females, 3=male calves, 4=female calves.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
October										
Group 1										
Group 2	0.370	0.180	2.273	0.679	2.383	0.9068	2.217	0.1405	3.19	0.8528
Group 3	0.520	0.3972	1.717	0.1506	2.640	0.2914	2.880	0.5855	3.090	1.187
Group 4	0.243	0.1220	1.073	0.2521	2.480	0.5957	2.593	1.393	3.890	1.330
Mean	0.378	0.1367	1.688	0.2750	2.501	0.3265	2.563	0.4485	3.390	0.5843
November										
Group 1	0.260	0.1739	1.493	0.1147	2.483	1.2032	3.137	1.3418	1.480	0.4025
Group 2	1.713	1.5416	2.200	0.9969	2.857	0.4693	2.030	0.8701	1.200	0.2761
Group 3	0.317	0.2162	1.200	0.5316	1.780	0.1358	2.737	0.6129	3.600	1.0425
Group 4	0.0	0.0	1.693	1.0831	3.220	0.2910	3.930	1.8274	3.103	0.9624
Mean	0.573	0.3902	1.647	0.3522	2.585	0.3261	2.958	0.5727	2.346	0.4450
December										
Group 1	0.390	0.1588	1.830	1.4191	4.420	1.8042	1.243	0.0779	6.450	2.523
Group 2	0.637	0.1367	0.807	0.5960	1.067	0.4804	0.310	0.0651	8.155	1.555
Group 3	0.677	0.1369	1.967	0.5239	2.093	0.3186	1.220	0.5903	0.0	0.0
Group 4	1.240	0.459	1.707	0.4354	1.130	0.1609	0.423	0.2188	4.000	3.5119
Mean	0.736	0.1457	1.578	0.3841	2.178	0.5759	0.799	0.1884	4.79	1.3442
January										
Group 1	0.353	0.2474	2.190	0.1380	1.230	0.639	3.000	0.647	7.277	2.332
Group 2	2.390	1.037	2.913	0.8253	0.667	0.1846	0.600	0.1365	4.323	2.2134
Group 3	0.173	0.0784	3.413	0.1835	0.237	0.2367	0.127	0.1267	10.107	2.8982
Group 4	0.257	0.1322	0.607	0.2869	0.333	0.3334	1.037	0.3096	10.973	1.4202
Mean	0.648	0.3191	2.281	0.3731	0.617	0.2035	1.191	0.3655	8.170	1.2496
February										
Group 1	1.073	1.009	3.003	1.3859	1.000	0.7047	0.223	0.1126	9.485	5.842
Group 2	0.667	0.1715	3.400	1.1539	1.160	0.595	1.333	1.0134	4.055	2.6332
Group 3	1.620	0.9054	2.873	0.8628	0.750	0.750	4.030	0.7994	6.353	1.0194
Group 4	2.410	1.0511	2.210	0.7821	0.240	0.1833	2.483	0.8537	5.857	2.638
Mean	1.443	0.4170	2.872	0.4756	0.788	0.2771	2.018	0.5387	6.371	1.3679
March										
Group 1	3.167	2.529	1.577	0.6282	2.493	0.9093	2.867	0.2843	1.020	0.4244
Group 2	5.200	1.373	1.783	0.3233	3.547	0.5990	2.113	0.7114	3.617	1.7631
Group 3	2.293	0.6886	1.503	0.8512	2.910	1.2007	3.310	1.1824	1.640	0.3733
Group 4	1.783	0.6876	2.020	0.5378	2.417	0.4014	2.967	0.3192	1.780	0.4428
Mean	3.111	0.7576	1.721	0.2523	2.842	0.3808	2.814	0.3349	2.014	0.5000

Appendix 16: Time spent in other activity by the four sex and age classes during foraging sessions in each habitat; 1=adult males, 2=adult females, 3=male calves, 4=female calves, continued.

Month	Willow		Poplar Forest		Upland Grassland		Lowland Grassland		Sedge Meadow	
	x	S.E.	x	S.E.	x	S.E.	x	S.E.	x	S.E.
April										
Group 1	2.010	1.0318	2.470	0.8588	7.863	1.4381	6.467	1.6175	1.027	0.3019
Group 2	1.527	0.7084	0.803	0.6775	1.180	0.5274	3.620	1.367	1.097	0.3789
Group 3	1.090	0.5459	0.833	0.3562	3.920	1.340	3.687	1.6299	2.570	1.1254
Group 4	2.647	1.095	2.453	0.775	2.377	1.1922	5.543	1.3762	4.277	1.318
Mean	1.818	0.4119	1.640	0.3850	3.835	0.9113	4.829	0.7390	2.243	1.1083
May										
Group 1	1.933	0.4511	3.270	1.1941	2.603	0.2691	4.573	0.8409	2.163	0.6071
Group 2	3.060	0.8876	3.173	1.1195	1.950	0.3812	3.103	0.1963	1.117	0.5401
Group 3	1.680	0.3995	3.327	0.1592	3.020	0.6317	3.090	1.0576	0.587	0.1639
Group 4	4.323	0.9191	3.253	0.8111	1.403	0.7685	3.973	1.1268	2.427	0.7075
Mean	2.749	0.4363	3.256	0.3913	2.244	0.2992	3.686	0.4218	1.573	0.3245
June										
Group 1	3.547	1.373	3.210	0.694	4.370	1.03	5.935	1.3669		
Group 2	4.103	1.4031	3.250	0.5446	3.673	0.547	3.533	0.417		
Group 3	5.263	1.2302	4.950	0.9097	4.420	0.8764	5.113	1.067		
Group 4	2.383	0.4278	5.667	1.9886	3.097	0.4518	5.840	0.0408		
Mean	3.824	0.5917	4.269	0.5973	3.890	0.3647	5.113	0.5219		
July										
Group 1	3.700	0.9704	2.927	1.5034	4.803	1.493	3.830	0.4899		
Group 2	3.437	0.7981	4.023	0.6366	3.643	0.6077	6.413	0.2717		
Group 3	3.640	0.2011	4.090	1.0262	5.063	0.5217	5.210	0.4524		
Group 4	1.717	0.7981	3.310	0.4652	2.923	0.4709	3.903	0.1392		
Mean	3.121	0.3699	3.588	0.4479	4.108	0.4573	4.839	0.3562		
August										
Group 1	3.383	0.5892	5.590	1.3202	2.103	0.3986	3.8533	0.6409		
Group 2	3.373	0.9934	4.373	0.5710	3.637	0.6291	5.707	1.017		
Group 3	3.060	0.7863	5.050	0.4966	4.663	0.5130	5.387	0.5100		
Group 4	2.567	1.0988	5.393	2.0621	2.470	0.5757	3.940	1.0566		
Mean	3.096	0.392	5.102	0.5639	3.218	0.3803	4.722	0.4375		

Appendix 17: Minutes of data recorded from the habitats during each season.

Habitat	Fall	Winter	Spring	Summer
Willow	520	1399	890	2021
Poplar Forest	508	2112	1064	2458
Upland Grassland	641	1095	1165	2122
Lowland Grassland	852	1098	925	2173
Sedge Meadow	842	806	1106	260
TOTAL	3363	6510	5150	9034

Appendix 18: Number of bites recorded from the habitats during each season.

Habitat	Fall	Winter	Spring	Summer
Willow	6109	10276	21208	41207
Poplar Forest	6544	28568	27066	48096
Upland Grassland	35987	24341	48718	94859
Lowland Grassland	20340	14514	37682	79921
Sedge Meadow	14470	11649	30796	1354
TOTAL	83450	89348	165470	265437