National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform 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.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme 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.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

NUTRITIONAL ECOLOGY OF WAPITI AND CARRYING CAPACITY OF LATE WINTER AND SPRING RANGE IN THE YUKON

BY

ROBERT F. FLORKIEWICZ ©

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 1994

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

ISBN 0-315-95029-3

UNIVERSITY OF ALBERTA
RELEASE FORM

NAME OF AUTHOR: Robert F. Florkiewicz

TITLE OF THESIS: Nutritional ecology of wapiti and carrying capacity of late winter and spring range in the Yukon

DEGREE: Master of Science

YEAR THIS DEGREE GRANTED: 1994

Robert F. Florkiewicz

Box 747
Watson Lake, Yukon, Y0A 1C0

April 28, 1994

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 NUTRITIONAL ECOLOGY OF WAPITI AND THE CARRYING CAPACITY OF LATE WINTER AND SPRING RANGE IN THE YUKON submitted by ROBERT FRANK FLORKIEWICZ in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

Robert J. Hudson

Robert J. Christopherson

Stan A. Boutin

April 22, 1994

This work is dedicated

to the memory of my father

"Gus"

ABSTRACT

Free ranging wapiti (*Cervus elaphus*) introduced into the Yukon Territory in the early 1950's, have been static since monitoring was initiated in 1961. These wapiti, at the northern limit of the species distribution, must endure greater climate extremes, shorter growing season and delayed spring forage emergence relative to their southern conspecifics. This study was undertaken to assess seasonal forage and range availability and forage nutritional quality as factors potentially limiting population growth and range carrying capacity.

South slope habitat was least abundant on winter range but was consistently selected ($P<0.05$) by wapiti. Wapiti diets were significantly correlated (1988 $P=0.03$; 1989 $P=0.046$) with species composition on south slope grassland habitats where principal forages, bent reedgrass (*Calamagrostis purpurascens*), sedges (*Carex* spp.), sage (*Artemisia frigida*), and forbs (*Anemone patens*) were most abundant. South slope habitats supported the greatest area specific nutrient levels and were clearly most advantageous as foraging habitat for wapiti.

Modeled requirements for energy and protein and activity patterns of mature female wapiti were used with estimates of forage biomass to assess winter range nutritional carrying capacity. Winter diet quality and composition suggested that protein contents of 6.3% in 1988 and 5.9% in 1989 were marginal to inadequate. Protein requirements were met only at the longest observed daily foraging duration (10.8 h/d) when either browse (*Salix* spp, *Populus tremuloides*), sage or both were included in the diet. Although basic maintenance energy requirements could be met in the shortest foraging duration (7.9 h/d), the incremental energy costs for locomotion in snow and gestation probably resulted in negative energy balance.

Although nutritionally advantageous, south slope habitats supported low biomass of all winter forages. The traditional assessment of carrying capacity relative to population level provided little insight into the current situation in the Yukon. However, foraging logistics suggest the low biomass availability could restrict wapiti dry matter and nutrient intake during winter. Spring forage emergence on south facing aspects is critical to ending late winter negative energy balance on northern wapiti ranges.

Acknowledgements

This study was funded with the assistance of the following agencies: the Canada/Yukon Economic Development Agreement, the Yukon Fish and Game Association, the Yukon Department of Renewable Resources, a Boreal Institute Grant to the author, the University of Alberta Department of Animal Science, and an NSERC operating grant to Dr. R. J. Hudson.

There is an ever growing list of persons to whom I am indebted for assistance, moral support and interest. Manfred and Hannah Hoefs for encouragement and support, without which this study would not have materialized. Manfred, whose persistence ensured financial and logistical support for field portion of the study. The department of Renewable Resources particularly those among the habitat section who, over the years, have patiently tolerated my presence and the associated absence of most anything not bolted down. It was and continues to feel like home. I thank-you all and would like to particularly mention Vickey Aschacher for her smile and always cheerful assistance in early drafts of tables and data entry. Many other of my associates in the Yukon provided invaluable comments on many drafts of the study design, helpful suggestions, and encouragement in early stages of the study for which I am extremely grateful. I would like to particularly acknowledge the contribution of Jean Carey and Philip Merchant, both of whom provided inordinate amounts of personal and professional support over the entire study. I have gained much from their friendship and learned much from their experience, thank-you.

There are many who have assisted in the field and lab portions of the study with many hours and days of vegetation sampling and sorting. Thanks to Jennifer Staniforth, Nancy Kwok, Troy Charlton, Frances Naylen, Jason Marshal, Danielle Chasse' and many others shall remain unnamed but whose assistance I appreciate no less. I owe a particular debt of gratitude to David Bakica, who persevered for the 2 full summer field seasons. David maintained his sense of humour long after mine took leave. Thank-you Dave, you have and are the true spirit of the Yukon.

I have benefitted greatly from my associates and fellow students in the Department of Animal Science. Many thanks to my cohort who made the time a truly learning experience. I would also like to thank Janet Detrich and Pat Marceau for assistance with lab work, always above the call of duty. Many thanks to Chris Olsen and Lyle Renecker for enlightening discussion and critical advice, and especially to Jan Adamczewski whose personal interest and advice was and continues to be inspirational. Thanks also to Gavin Godby, Ray Weingardt, and Bob Hardin for statistical and computing expertise.

Many thanks go to my supervisor, Dr. Bob Hudson whose perennial good nature and humour have kept me on track from this projects' inception. He has provided me with the resources for learning and with ideas when I most needed them. He was also most patient when other parts of "living" interfered with timely completion of this project.

I would thank my family for support throughout the lengthy tenure of this project, particularly the unfailing support and love of my mother, Ilse.

Finally, I would like offer my love and gratitude to Mary Gamberg for her help, patience and love through the write-up when the path looked long and I found it difficult to handle my share of the load. Thank-you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1.0 Introduction

Translocation of North American elk or wapiti (*Cervus elaphus*) to areas beyond the current North American distribution has met with limited success. Introductions into Alaska (Troyer 1960, Batchelor 1965, Burris and McKnight 1973), Yukon (Hoefs 1980), Alberta (Rippin 1983) and British Columbia (J.P. Elliot 1987: pers. comm.) have either failed or yielded inconclusive results. The notable exception is the introduction of Roosevelt wapiti (*C. e. roosevelti*) to Afognak Island in the Alaskan Gulf (Burris and McKnight 1973). However, the initial post liberation productivity and current abundance of this subspecies likely is due to the absence of competition for forage and a maritime climate and consequent influence on vegetation production (Troyer 1960).

Wapiti were introduced to the Yukon to increase the number and diversity of big game species and occurred as the result of lobbying by the Yukon Fish and Game Association (YFGA). A brief reconnaissance survey conducted by the Canadian Wildlife Service (CWS) prior to the introductions suggested the Hutshi Lake-Nordenskiold river valley had climate and vegetation most similar to other wapiti ranges (Soper 1950). Based on this report wapiti from Elk Island National Park (Alberta), 19 in 1951 (5 males, 14 females) and 30 in 1954 (8 males, 22 females), were released near Braeburn lake north of Whitehorse. Within a decade the wapiti from these 2 releases had established in apparently distinct ranges, the Hutshi valley and the Takhini River-Ibex-Stony Creek region along the Alaska Highway (Figure 1)(Pearson 1967). However, to the present time, neither population has increased to levels initially anticipated (Hoefs 1980).

The Yukon is the northern distributional limit for wapiti. By one definition, the limit or the edge of the range is an "isopleth" of zero population increase (Andrewartha and Birch 1954). Caughley et al. (1988) suggested that on the edge of the range there are either insufficient resources for an individual even when sharing with other individuals, or that other components of the environment (predators, disease, climate) raise mortality rates beyond birth rates despite adequate resources. If wapiti are in fact at their northern limit in the Yukon, they should not be expected to flourish. Either mortality equal to or greater than the birth rates or inadequate resources would limit population growth. However, pregnancy and birth data are difficult to determine for free-ranging wapiti in small populations. Consequently, it is necessary to examine other environmental and behavioral indices to evaluate the potential for growth in this population.

As with most free-ranging ungulate populations, determination of proximal causes of mortality in wapiti are also difficult to make. Even when determined for small populations, their

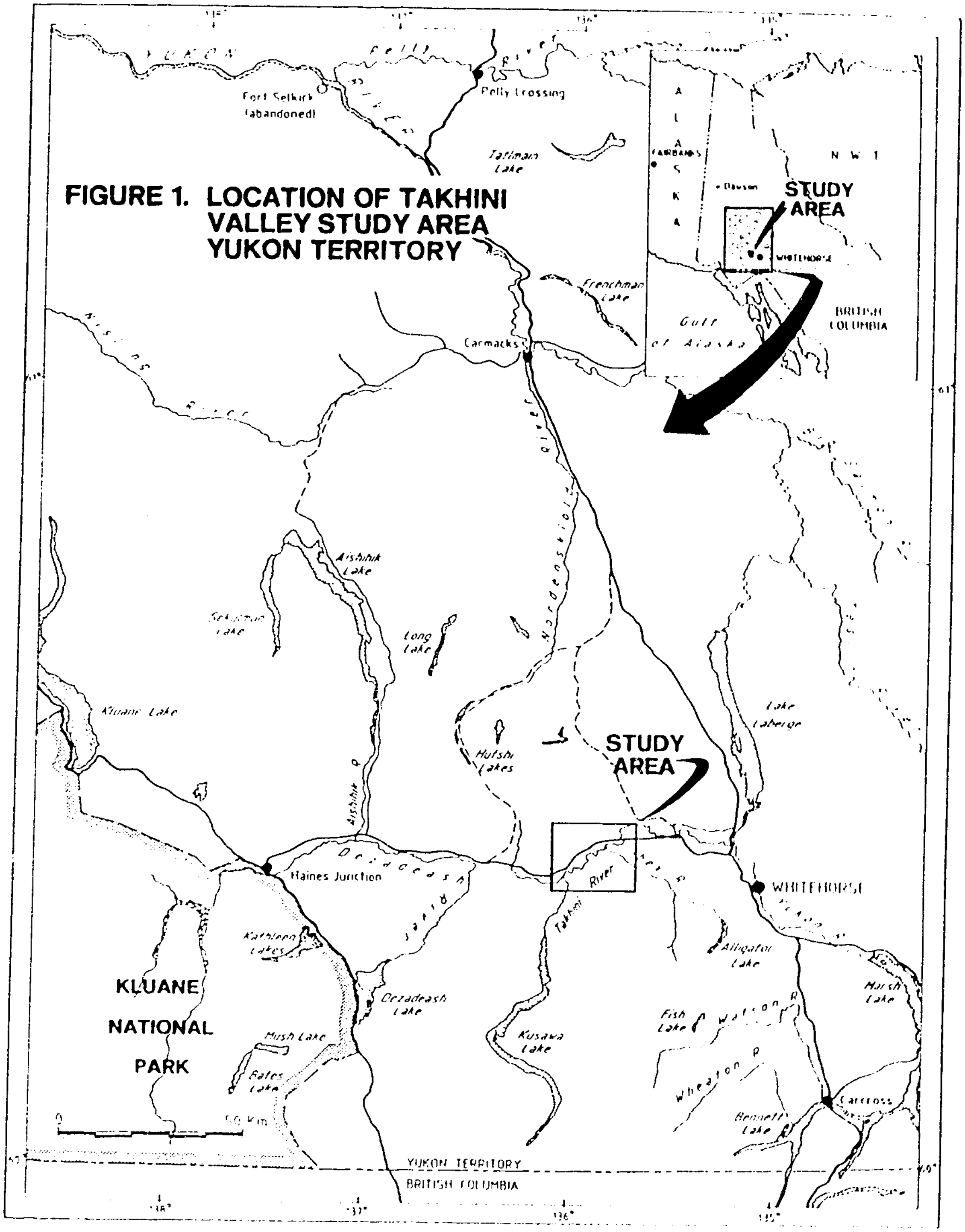

FIGURE 1. LOCATION OF TAKHINI VALLEY STUDY AREA YUKON TERRITORY

significance is uncertain unless they can be assessed over an extended time period. However, predation of moose and caribou by black (*Ursus americanus*) and grizzly bears (*U. arctos*) and by wolves (*Canus lupus*) in areas surrounding wapiti ranges is well documented (Larsen et al. 1989, YFWB 1992). Predation of wapiti is probably opportunistic, unpredictable, and supported by "switching" (Bergerud 1983) within this ecosystem. Predation will likely remain a stochastic mortality factor as long as the wapiti remain within such narrow limits of geography and population.

An earlier study explored the prevalence and role of disease (Hoefs 1980). Tuberculosis and brucellosis were the primary agents evaluated and neither were found in wapiti introduced into the Yukon. Moreover, although mature females appeared small, wapiti were in good physical condition suggesting that chronic heavy parasitism or disease have not been present or are important factors limiting population size.

Local climate on wapiti ranges is strongly influenced by their proximity to the Coast Mountains and may be both beneficial and detrimental to wapiti. Annual precipitation is 25-30% lower than other wapiti ranges in North America, whereas mean winter snow accumulations, ranging between 30 and 47 cm in typical habitat types, are within tolerance levels for wapiti (Beall 1974, Leege and Hickey 1977, Adams 1982). Yukon ranges receive only 60% of the growing degree days (Stewart et al. 1977) common to wapiti ranges in central Alberta. Consequently, winter access to forage may not be hindered by snow but forage production on wapiti ranges in the Yukon may be restricted by lack of moisture and shorter duration of the growing season.

Forage production and availability and their influence on nutritional status are considered critical to the size and density of herbivore populations (Wynne-Edwards 1970, Moen 1978, White 1978). Nutrition of individual animals is determined by their foraging behaviour relative to the distribution and abundance of forage (Hanley 1982) and by their ability to extract nutrients from forages selected (Van Soest 1982). Winter reduction in forage quality and abundance and the presence of anti-nutritive substances limit nutrient availability and determine the limits of range carrying capacity (Klein 1968, Robbins 1983). Further, snow cover increases the energy cost of locomotion (Parker et al. 1984) and impairs the ability to improve nutrition by interfering with selective foraging (Wickstrom et al. 1984, Hanley and McKendrick 1985). Nutrient balance also must be sustained because of winter duration (Wallmo et al. 1977) and, in gravid females, increasing production costs for offspring and associated tissues (Oftedal 1985).

At northern range limits, ungulates including wapiti must obtain sufficient nutrients to restore body condition and support productive functions during a relatively shorter growing season (White 1983, Geist 1983, Guthrie 1984) and endure a relatively longer period of low quality forage and depletion of body reserves. Traditional means of assessing the ability of a habitat or range to support ungulates involve comparisons of available biomass or associated nutrients, relative to requirements for those nutrients (Hobbs et al. 1982, Hobbs and Swift 1985). However, in making such assessments, the ability to use measured "available" forage resources is implicit. Moreover, the strong correlation between forage biomass and rates of forage (and therefore nutrient) intake (Arnold and Dudzinski 1967, Collins et al. 1978, Hudson and Watkins 1986) suggest that systems with low net primary productivity could impair foraging intake rates beyond seasonal reductions in forage quality and abundance.

In this study, I evaluated the range attributes and resource use behaviour of free-ranging wapiti to assess whether nutrient availability could be limiting population growth, and to provide recommendations for future management of wapiti in the Yukon.

Specifically, I tested whether wapiti in the Yukon remain at a stable low density because they are at the nutritional carrying capacity of their range. This hypothesis would be rejected by the following evidence:

1) Modelled nutrient (energy and protein) requirements of "typical" breeding female wapiti are met under winter foraging and nutrient availability regimes;
2) Given the requirements of a "typical" wapiti are met during the late winter period then the availability of forage biomass and nutrients exceed the total winter requirements of the current population.

To construct these tests, I organized my field study according to the following objectives:

1) To determine the range and habitat features selected by wapiti in the Yukon.
2) To determine the nutritional quality and abundance of forages seasonally available to wapiti in the Yukon.
3) To evaluate the influence of snow cover and winter duration on nutritional status based on estimated diets and predicted requirements for wapiti in the Yukon.
4) To provide estimates of nutritional carrying capacity upon which management of free-ranging wapiti can be based.

2.0 Study area and study population

2.1 Study area

Wapiti ranges in the Yukon lie on the southern edge of the Dawson Range Ecoregion within the scattered discontinuous permafrost zone (Oswald and Senyk 1977). The two known population centres are the Hutshi Lake- Nordenskiold River valley (61°.10'N, 136°.36'W) and the Takhini River valley (60°.48'N, 135°.55'W) (Figure 1). The intensive portion of this study was conducted on the Takhini Valley range.

Regional geology is largely metamorphic quartzite that is sporadically intruded with igneous quartzite and granodiorite (Templeman-Kluit 1974). Surface geology reflects glaciation during the most recent advance of the Cordilleran ice sheet of the Wisconsin period. Shallow morainal and glaciofluvial deposits line the Hutshi/Nordenskiold and Takhini River valleys while valley bottoms are overlain with fine textured glaciolacustrine deposits. The climate is cold continental with mean annual temperatures below freezing (-3 to -4 °C). Precipitation (and climate in general) is influenced by the Coast Mountain range immediately south of the study area. Mean annual precipitation (measured from the Braeburn and Canyon Lake weather stations) is near 300 mm, with 65% falling as rain (AES 1982). Winter snow accumulations range from 30 to 60 cm (from 94.5 cm mean annual snowfall) persisting into early April (AES 1985). Snow melt occurs through April with little carryover into May.

Both wapiti ranges lie within the Boreal Forest Region (26b) of Rowe (1972). Black spruce stands (*Picea mariana*) predominate northern exposures and wet low areas whereas white spruce (*Picea glauca*) is lightly to moderately stocked on elevated terraces and dry benches. The dominant forest cover is regeneration to aspen (*Populus tremuloides*), due to extensive forest fires in 1958, although growth rarely exceeds 3 to 4 metres in height. Draws and gullies, frequently interspersed along south facing grassland slopes, have also been colonized by aspen. Willow (*Salix* spp.) tends to regenerate on sheltered and north facing sites. Understorey vegetation in upland sites is dominated by purple reedgrass (*Calamagrostis purpurascens*) with localized concentrations of bluegrass (*Poa* spp.). Other gramineae (*Carex* spp., *Agropyron* spp., *Festuca* sp., *Bromus* sp.) are sparsely distributed through xeric to mesic sites between 940 m and 1430 m in elevation. Principal forbs include crazyweed (*Oxytropis* sp.), Gormans' penstemon (*Penstemon gormanii*), goldenrod (*Solidago* sp.), groundsel (*Senecio* sp.), siberian aster (*Aster sibericus*), and cut leaf anemone (*Anemone multifida*). Shrubs other than aspen and willow include rose (*Rosa acicularis*), bearberry (*Arctostaphylos uva-ursi*) and Juniper (*Juniperus communis*). Hygric valley bottoms and riparian areas are densely stocked with sedges (*Carex* spp., *Eriophorum* spp).

2.2 Study population

Wapiti, originating from Elk Island National Park (EINP), were transplanted to the Braeburn area of the Yukon about 100 km North of Whitehorse. Nineteen wapiti, 5 bulls and 14 cows, were released in 1951 and 30, 8 bulls and 22 cows, were subsequently released in 1954. Post liberation monitoring was initiated by the Canadian Wildlife Service (CWS) in 1964 and continued to 1967. Since their release, the wapiti settled into 2 distinct ranges, the Hutshi/Nordenskiold valley and the Takhini valley. There are few records of wapiti from the groups released prior to 1964. However, parts of both ranges burned during the extremely dry summer of 1958. Apparently, wapiti first colonized the Takhini valley by the second year following the burn (R. Stevens, pers. commun.). As the ranges are only separated by 80 km and only the extreme northern and extreme southern areas of the Hutshi valley burned in 1958, it is probable that most of the animals remained within the extensive south facing grassland/forest complex around the Hutshi lakes in the first 10 years post-liberation.

Surveys conducted intermittently since wapiti were liberated consistently noted low calf proportions in female groups (Pearson 1967) (Appendix 1). Over the first 20 years of intermittent monitoring, principal ranges, estimated population sizes, and incidence of predation and or mortality were documented. Poor productivity and juvenile recruitment were noted and predation was suggested as a potential limiting factor. Low calf numbers persisted to the time of this study (Yukon Fish and Wildlife Branch, unpubl. survey reports). Investigations into the agents responsible for the lack of population growth involved testing for tuberculosis and brucellosis in addition to a limited program of wolf control (Hoefs 1980). Although concerns had been expressed regarding habitat and forage limitations by CWS biologists (unpubl. corresp. 1977) no detailed investigation had been conducted into the suitability of the environment for wapiti.

At the time this investigation was initiated the 2 known populations were estimated to contain approximately 50 animals each. Available information on the physical stature of wapiti in the Yukon is limited to a small sample of weights and external linear measurements for animals that were immobilized for Brucellosis testing (Hoefs 1980) and animals immobilized for the current study. Weight and chest girth measurements for 6 female wapiti from the Yukon were within the 95% CI of mean size for animals from Banff National Park (Flook 1970). However, mean weights did appear substantially lower than a sample from Elk Island National Park. The sample of male wapiti weights is too small for comparison (Appendix 1).

3.0 Materials and Methods

3.1 Range attributes

3.1.1 Forage biomass

Vegetation sampling and site selection followed Mueller-Dombois and Ellenberg (1974), Oldemeyer and Regelin (1980), and Hobbs et al.(1981). Either 3 or 4 rectangular 1 ha macro plots were randomly allocated to vegetation polygons within 4 habitat types. Major forage species were hand plucked from 20 1 m^2 quadrats located using a grid reference and random co-ordinates. Shrub and browse current annual growth (CAG) and associated twigs to 4 mm in diameter, between 0.5 and 2.5 m in height, were clipped from ten 1x5 m plots located at alternate forage sampling quadrats within each macro plot. Ground cover was evaluated as percent cover for herbaceous vegetation and low growing shrubs, bare ground, rock and deadfall.

Standing biomass of principal forages was evaluated in July and August. Samples were sorted to species and air dried in paper bags. Air dried samples were cleaned, oven dried at 50°C and weighed to 0.1 g on an electronic balance.

3.1.2 Nutrient analysis

Forage and fecal sampling periods were divided into intervals representing changes in the physical and the nutritional environment of wapiti. Periods included late winter (February and March), early herbaceous emergence (April 1-16), late emergence (April 17-April 30), browse leaf out (May), leaf expansion (June 1-June 18), and leaf maturation (June 19-July 31).

Major forage plant species, identified primarily from fecal analysis and by visual inspection of feeding craters, were collected in 1988 and in 1989, sorted to species and air dried in the field. All samples were oven dried and stored in plastic bags until processed. Prior to analysis, samples were ground in a Wiley mill (2 mm screen) and stored in airtight plastic containers.

Forage samples were analyzed in duplicate according to A.O.A.C. (Horwitz 1980). Crude protein was determined by macro-kjeldahl nitrogen x 6.25. Neutral detergent fibre (NDF), acid detergent fibre (ADF), and acid lignin (ADL) were determined according to Goering and Van Soest (1970). Soluble fractions were evaluated as the ash and fibre free dry matter, hemicellulose was estimated as the difference between NDF and ADF, and cellulose as the difference between

ADF and lignin. Dry matter was determined by drying overnight in a forced draft oven at 110°C.

In situ digestibility (NBDMD) was determined for selected 1989 forages using the nylon bag technique (Orskov et al. 1980, Fargey 1988, von Keyserlingk and Mathison 1989). Representative forage samples of 1 g DM were heat sealed into 3x7 cm nylon bags, placed into weighted lingerie bags and incubated for 48 hours in the rumens of three mature beef steers. The trials were conducted in winter using animals that were maintained outdoors and fed a daily ration of 1 kg grain supplement and *ad lib* moderate quality grass hay. Upon removal, bags were rinsed twice, once individually by hand until the rinse water ran clear, and a second time, enclosed in nylon stockings, in a commercial washing machine. Dry matter disappearance was determined as the sample dry matter weight loss, to the nearest 0.1 mg, after drying 24 hours at 110°C.

A subsample of winter forages was analyzed using the *in vitro* technique described by Tilley and Terry (1963) and Pearson (1970). Rumen inoculum was prepared from a mixture of equal parts rumen fluid and strained solid fractions combined in a waring blender according to Fay et al. (1980). Duplicate samples were incubated in a mixture of buffer medium (Goering and Van Soest 1970) and rumen fluid collected from a free ranging adult male wapiti on a winter diet of browse and grass.

Fecal protein and ash content were determined for individual fecal samples collected through the season. Macro-kjeldahl nitrogen and ash analysis were conducted according to A.O.A.C. (Horwitz 1980). Fecal crude protein (N x 6.25) was used as an index of the temporal variation in diet quality and of winter duration. Inflection in fecal protein levels, representing animal response to new forage, was considered the end of winter. Winter range occupation and hence the initiation of the winter period was considered to occur with permanent snow cover.

3.2 Resource-use behaviour

3.2.1 Habitat use

Radio-collars (Telonics Inc., Mesa Arizona) were placed on 5 females in the Takhini Valley range (TV), 3 in March 1988 and 2 in March 1989. A sixth female was marked with eartags for permanent recognition. Mature females were immobilized by helicopter using a Cap-Chur rifle (Palmer Chemical Co. Ltd., Douglasville Georgia) and a cocktail of M-99 (etorphine hydrochloride) and Rompun (xylaxine hydrochloride) (Bayuet Division, Miles Laboratories, Mississauga Ontario). Immobilization was reversed using M 50-50 (Diprenorphine) (D-M pharmaceutical Ltd., Rockville M.D.).

Although mature female wapiti were selected for radio-collaring from both the TV and the HN ranges, intensive ground monitoring was restricted to the 5 radio-collared animals on the TV range. Periodic aerial location of animals in the HN range was conducted to corroborate general findings on wapiti ecology in the Yukon.

Radio-collared animals were monitored during late winter, spring and summer of 1988 and 1989. Wapiti were located a minimum of twice weekly during late winter (February, March), once every 2 days in spring (April, May), and once every 3 days in summer (June, July). Location periods were in the morning (0600 to 1200 hrs) or the evening (1700 to 2400 hrs) when foraging was most intense and likely to dominate the activity pattern. When actively foraging, wapiti were visible from a greater distance and therefore potential for disturbance was reduced. Habitat preference data were analyzed using 24 hour and 48 hour location intervals. Because no difference in habitat preference or avoidance among any of the seasonal periods studied was observed between the 2 intervals, the 24 hour interval data were used in assessing habitat selection.

Each location was noted with time, map position, and group composition, and was plotted onto 1:20,000 scale air photographs. When the precise location could not be verified visually, predominantly in summer after leaf flush, location and habitat type were assigned after the location was determined by walking around three sides of the transmitter. Each location was considered 1 point regardless of the number of animals or radio-collars within a group as recommended by Thomas and Taylor (1990). Visual location of animals not associated with radio-collared females were recorded but were not used to analyze habitat selection. Observations were pooled within season and year to assess seasonal habitat selection.

The TV range boundary was delineated using a modification of the minimum convex polygon (Mohr 1947). Habitat types selected by wapiti, and contiguous with polygons in which wapiti were actually located, circumscribed the outer boundary of the TV range. Vegetation polygons within the range were outlined on 1:40,000 scale air photographs and composition verified using 1:20,000 scale colour and false colour infra-red aerial photographs and ground reconnaissance. Individual polygons were classified according to the dominant cover species, physiographic, and topographic features (Aatelma 1988). Polygons were transferred to 1:50,000 base maps where the area of each polygon was determined using a digital planimeter. Vegetation polygons were grouped into habitat types based on covertype similarity and patterns of use by wapiti. The total area of each habitat was determined by summing the constituent polygon areas. Major habitat types selected by wapiti were included in detailed vegetation analysis (Table 1).

Table 1. Summary of habitat types within the Takhini Valley wapiti range, Yukon

Habitat type	Proportion of range (%)		Site characteristics	Principal cover and forage species
	Total	Winter		
Dense Aspen Regeneration (DA)	32.5	25.9	canopy cover 26% to >50% level to moderate south slope moist to dry aspect S, SW, SE ground cover 68% (±4%)	*Populus tremuloides* *Anemone multifida* *Solidago decumbens* *Calamagrostis purpurascens* *Agropyron trachycaulum*
Open Aspen Regeneration (OA)	15.6	11.7	canopy cover 5% to 25% level dry ground cover 59% (±6%)	*P. tremuloides* *Salix* spp *Epilobium angustifolium* *Fragaria virginiana* *C. purpurascens* *A. trachycaulon*
Conifer Regeneration (CR)	22.9	37.5	canopy cover 5% to 50% level to moderate north slope moist to wet aspect W, N, E ground cover 64% (±7%)	*Picea glauca* *Pinus contorta* *Salix* spp *E. angustifolium* *Anemone multifida* *A. trachycaulon*
Conifer Residual (CRe)	2.8	3.4	canopy cover >20% level moist to wet ground cover >80%	*P. glauca* *Salix* spp *E. angustifolium* *Festuca altaica*
South Slope (SS)	5.2	8.9	canopy cover <5% south slopes from slight to 45° dry aspect SW,S,SE ground cover 47% (±3%)	*P. tremuloides* *Anemone patens* *Artemisia frigida* *C. purpurascens* *Carex* spp
Proportion of total range (%)	79.0	87.4		
Total area (ha)	17791.8	9954.6		

3.2.2 Forage selection

Principal forages (Petrides 1975) were considered to be species constituting 2% or more of the estimated winter diets. Fecal fragment analysis (Sparks and Malechek 1968, Holecheck et al. 1982, Gill et al. 1983) was used to identify the major forage species selected during winter, spring, and summer. Because bias in the fecal analysis technique has been attributed to diets of forages with high differential digestibility, particularly forbs (Fargey 1988), winter diets were considered to be most accurate and realistically assessed by fecal analysis. Fecal plant composition in spring and summer were similarly determined but were used more broadly, as an indication of diet class preference rather than for quantification of forage species consumption. Some species such as browse foliage may be under-represented in fecal analysis (Charles Schwartz, 1990 pers.comm.). The technique is generally considered to be imprecise when highly digestible forages such as foliage are being consumed with other less digestible forages such as browse twigs.

A second bias generally attributed to the technique, based on detection and recognition of forage fragments, was minimized by using technicians familiar with northern plant species and by provision of plant species list and reference specimens for species not already available. Fecal analysis was the primary means of determining wapiti diets although supplemental observations were made at snow craters and during observations on foraging radio-collared animals. Wapiti on the TV range were extremely wary of humans and thus direct monitoring of forage species selection using bite count methods (Hudson and Nietfeld 1985) was not practical.

Fecal samples were collected from groups of mature female wapiti 1 to 2 times per week between March and July 1988, and January and July 1989. Samples were bagged individually and frozen until composite samples representing winter, spring and early summer foraging periods were made. Individual fecal samples were oven dried at 50°C for 48 hours. Triplicate composite samples of 5 g from at least 20 separate animals were forwarded to the Composition Analysis Lab (CAL) at Colorado State University. Five slides and 20 fields per slide were read for each sample. Species percent frequency was interpolated as relative dry weight percent of forage species in the diet.

3.2.3 Activity patterns

Seasonal activity patterns were determined for 3 wapiti using radio-collars modified according to Garshelis et al. (1981) and Green (1982). Telemetry signals were recorded using a

TR-2 receiver scanner system connected to a TDP-2 advanced digital data processor (Telonics Inc., Mesa Arizona) and recorded using a Rustrack dual channel strip chart recorder (Gulton, Manchester N.H.). Animals were selected randomly for weekly scans of at least 24 hours. Periods of up to 48 hours were included, where possible, to ensure representative measurement of activity bouts. Additional data on duration of active and inactive periods were obtained from partial recordings less than 24 hours duration. Signal strength and period, based on mercury tip-switch positions within the radio-collars, differentiated between inactivity (bedded), head up activity (standing, walking-feeding) and head down activity (grazing-feeding). Active and resting periods were analyzed as bouts of 15 minutes or longer in duration. Bouts between 5 and 15 minutes were considered breaks in activity and were incorporated into either the preceding or the following activities. Activity patterns were confirmed visually, periodically while activity scans were being recorded.

3.3 Nutrient requirements and carrying capacity

Range carrying capacity for the late winter period was assessed by contrasting range supply of energy and crude protein with the predicted animal requirements for maintenance and reproduction (zero weight change) following the procedure of Hobbs et al. (1982). Nutrient requirements were determined from relationships summarized by Robbins (1983) and NRC (1984). Energy and nitrogen requirements were based on an average weight of 225 kg for mature female wapiti on Yukon winter range (Appendix 2). Daily energy requirements for maintenance were calculated using activity data collected during telemetry scans from female wapiti in February and March in 1989. The energy cost (kJ/h.kg$^{0.75}$) associated with specific activities of lying (20.7), feeding (26.4) and walking (27.1) follow Pauls et al. (1981) and Hudson et al. (1985) (for animals at maintenance). Energy costs were summed for winter activity patterns to provide an estimate of the daily ME requirement. The energy requirement for gestation was estimated as the energy in the fetus and associated tissues (Robbins and Moen 1975, Robbins and Robbins 1979) and the efficiency of energy use for pregnancy (k_p= 0.133) from ARC (1980:88).

The incremental cost of foraging in snow was estimated using the relationship developed by Parker et al. (1984) and daily travel rates based on forage biomass developed by Wickstrom et al. (1984). Similar to Wickstrom et al. (1984), I assumed no change in the rate of travel for this approximation. The range of forage biomass available in the Yukon was used to produce a range of winter travel rates and from the regressions of Parker et al. (1984) expected energy increments for travel under snow conditions in the Yukon were examined. Fifty percent of the foraging activity was considered slow travel and the increment was applied to that proportion of foraging energy cost.

Requirements for protein were determined as the sum of metabolic fecal (MF), endogenous urea (EU), scurf loss (S), tissue deposition (T) (assumed zero for winter), and conceptus (C) requirements divided by the product of true protein digestibility (TD) and the biological value (BV).

Protein required = (MFP+EUP+S+T+C)/(BV*TD) (after NRC 1984)

Metabolic fecal protein is a constant proportion of intake and is approximated as 35 g/kg DM intake (Mould and Robbins 1981). Endogenous urea nitrogen is lost in proportion to body weight and represented as $0.16 \times W^{0.75}$ g/day. Protein was determined by multiplying nitrogen by 6.25. Scurf, skin, and hair loss was determined as $0.2 \times W^{0.6}$ g/day. Requirements for the conceptus and associated tissues follow the formulation of Hudson and White (1985). Biological value prediction was based on Robbins (1983) formula:

BV = 94.9 - 2.2 (CP%) where CP% is the protein content of the diet

True protein digestibility was considered to be 95% (Robbins 1983:283).

The carrying capacity of the winter range was assessed by contrasting the mean biomass for each major forage with the associated nutrient concentration. Protein was measured directly and digestible energy was determined as:

DE = Species biomass * NBDMD * 18.0 Kj/g

where NBDMD is the *in situ* digestibility measured for the principal forage species and 18.0 is the approximate energy content of digested organic matter (Hudson and White 1985) corrected for ash content. The total area of each habitat and the product of the nutrient composition of forages and the relative composition of forages in each habitat were used to determine availability. Animal requirements and duration of range occupation were contrasted with available nutrient to determine the total number of animals that could be supported during winter. Variability of biomass estimates for the principal forage species was used to determine 95% confidence limits for carrying capacity of individual habitats and the total range. Metabolizable energy (ME) was considered to be 0.82 * DE to account for obligate losses from incompletely metabolized compounds in the urine and losses of heat and fermentation gases from the rumen (Van Soest 1982).

3.4 Statistical analysis

Analysis of variance (ANOVA) was used to compare species biomass among 4 habitat types, and Student-Newman-Keuls (SNK) multiple range tests (Steel and Torrie 1980) were used in habitat specific comparisons.

Differences in chemical composition and apparent digestibility among forage species within months were evaluated by ANOVA and SNK multiple range tests. Species specific regressions for apparent NBDMD and IVDMD were determined by linear regression (Steel and Torrie 1980, SAS Institute 1982).

Habitat selection was evaluated by comparing the relative proportion of animal locations within each major habitat and the relative availability of the habitat over the entire range. Significant differences, assessed using a Chi-squared statistic, were determined using a Bonferroni Z distribution, comparing the 95% confidence band for use with the availability of specific habitats (Neu et al. 1974, Byers et al. 1984). A level of significance of 5% was used unless otherwise indicated.

4.0 Results

4.1 Range attributes

4.1.1 Forage biomass

Vegetation biomass dry matter (DM) at the end of the 1989 growing season was used to estimate forage availability on the winter range. Contrasts were not made with the 1988 sampling year because the difference between the timing of the collection periods was too great. When all forage classes were included, forage production values ranged from 471 kg/ha in conifer regeneration (CR) habitats to 278 kg/ha in south slope grassland (SS) habitats. With the exception of SS habitats, biomass was dominated by foliage of *Salix* spp. and *Populus tremuloides*. Fireweed (*Epilobium angustifolium*) was significantly more abundant in CR habitats than open aspen regeneration (OA) and dense aspen (DA) habitats (P=0.01) but was not considered a valuable winter forage because the foliage dropped and deteriorated rapidly before snowfall. Therefore this species was not considered part of the available winter biomass. When browse foliage was excluded from the available winter forage (see section 4.2.2), SS habitats were the most productive habitats assessed (Table 2). Many species occurred in higher quantities on SS habitats than other habitats whereas a single species provided most biomass in each of the other habitat types.

Spring biomass was measured immediately following snow melt each year (Table 3). No differences were observed between years in the available spring biomass of preferred forages (sum of preferred forages excluding browse) (P = 0.20), or all forages sampled (sum of herb and shrub biomass excluding browse) (P = 0.41) in SS habitats. Because plot sizes were increased from 0.25 m^2 to 1.0 m^2 in 1989 for non-SS habitats, biomass values from 1988 were multiplied by 4. No difference was found in spring biomass of preferred forages in OA (P=0.17), DA (P=0.33), and CR (P=0.99) habitat types. Dense aspen was the only habitat that had between year differences in available forage biomass (P=0.036).

4.1.2 Forage phenology and quality

Forage nutritional phenology was assessed for key species from late winter and monthly through the growing season. Few of the key winter and/or spring forages occurred in habitats other than south facing grasslands in large quantities and therefore few among habitat comparisons were made. The SS habitats were first to clear as overwinter snow accumulation was light and the southern exposure resulted in rapid melting and evaporation. New growth of purple reedgrass (*C. purpurascens*) increased from 4.2% to 21.0% of the total available *Calamagrostis* foliage through April and to 54.6% by June 1989 (Figure 2). The ratios of new to cured foliage were similar in the aspen regeneration (DA, OA) habitats although the rate of emergence of new foliage was delayed relative to SS grasslands. Protein content of harvestable *Calamagrostis* increased gradually in spring as new growth was initiated on the lower portions of marcescent foliage. Available protein was therefore diluted by the attached dried foliage. Even so, protein quality peaked sooner and at a higher level in SS habitats than in DA and OA regeneration habitats.

Total biomass and protein content of *Carex* spp. and *Artemisia frigida* remained relatively stable between years (Figure 3, Figure 4). The proportion of old foliage and stems relative to new growth was high and likely diluted protein content of the new growth. The crocus (*Anemone patens*) on SS habitats was among the first species to emerge on the winter and spring range but

Table 2. Standing live forage biomass (kg/ha) assessed in July/August 1989 representing the available winter forage within each habitat type used by wapiti

Species	Habitat type				
	South Slope	Open Aspen Regeneration	Dense Aspen Regeneration	Conifer Regeneration	Prob
Agropyron spp.	5	30	15	3	0.1808
Anemone spp.	27	9	8	7	0.1266
Artemisia frigida	45 A	1 B	tr B	0	0.0001
Bromus pumpellianus	2 B	17 A	8 AB	0 B	0.0298
Calamagrostis purpurascens	91 A	27 AB	56 AB	9 C	0.0348
Carex spp.[1]	16 A	tr B	tr B	1 B	0.0003
Festuca saximontana	1	5	0	0	0.2172
Fragaria virginanus	0	25	14	0	0.3428
Poa glauca	3	4	2	0	0.3677
Poa cusickii	3 A	0	tr B	0	0.0027
Unidentified graminoids	tr B	4 A	tr B	2 AB	0.0320
Mixed forbs[2]	28	24	17	1	0.0772
Populus tremuloides[3]	17 B	26 B	53 A	5 B	0.0001
Salix spp.[3,4]	4 B	14 B	1 B	84 A	0.0025
Total available biomass	242	186	175	112	
Biomass of preferred species	181	77	113	98	
Preferred as a proportion of available winter biomass	74.8%	41.3%	64.6%	89.9%	

[1] includes *C. concinna*, *C. rupestris*, *C. obtusata*

[2] includes *Achillea millifolium*, *Antennaria rosea*, *Erigeron cespitosus*, *Gallium boreale*, *Penstemon* spp., *Potentilla* spp., *Solidago* spp.

[3] excluding foliage

[4] includes *S. glauca* and *S. bebbiana*

tr production less than 0.5 kg/ha

Means within a row followed by dissimilar letters differ significantly.

Table 3: Habitat specific spring forage biomass (kg/ha) on wapiti range in the Yukon.

Habitat type	Prefered forages		All forages	
	1981	1989	1988	1989
South slope (SS)	73.9±14.7	110.5±20.1	89.7±15.7	119.3±18.5
Open aspen (OA)	76.9± 3.6	34.0±17	84.8±10.5	90.3±6.6
Dense aspen (DA)	69.6±18.7	46.4±12.3	88.9 A ±8.9	64.4 B ±3.7
Conifer regen (CR)	6.8±3.3	6.8±3.3	6.8±3.4	17.8±13.5

Means within a row followed by dissimilar letters differ significantly.

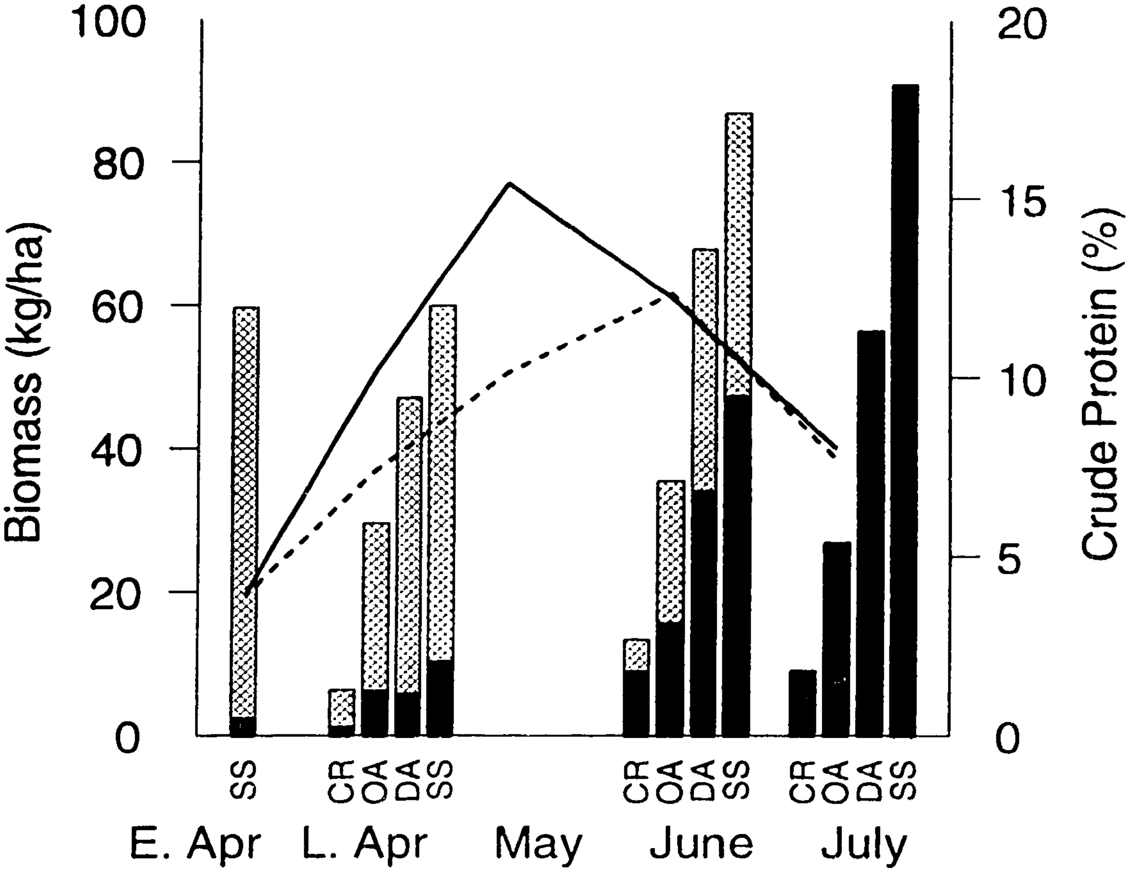

Figure 2: Monthly changes in biomass (kg/ha) for new growth (■) and previous (▨) years foliage of purple reedgrass (*Calamagrostis purpurascens*) in south slope (SS), conifer regeneration (CR), open aspen (OA) and dense aspen (DA) regeneration habitats in the Takhini Valley, Yukon. Crude protein content (%) of new growth in SS (———) and DA (- - - - -) habitats in the 1989 sampling year.

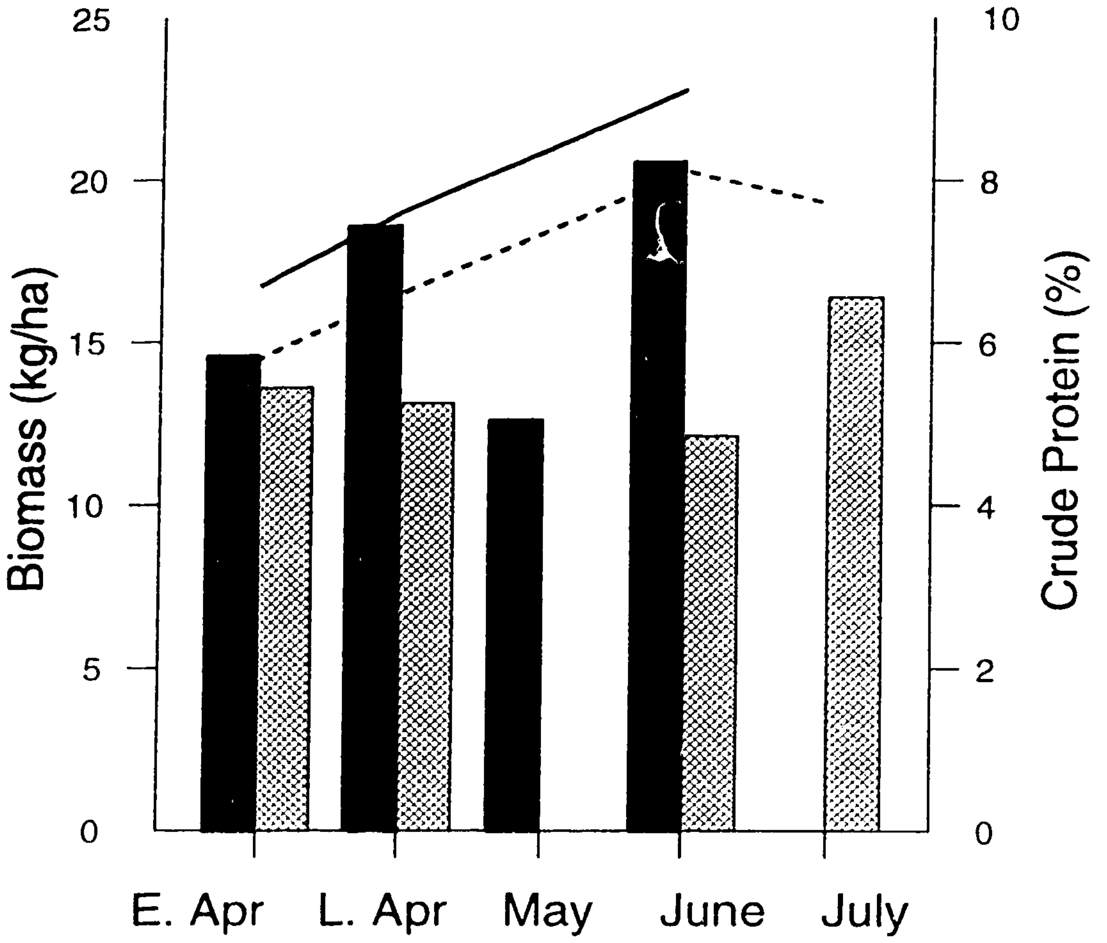

Figure 3: Monthly changes in biomass (kg/ha) and crude protein (%) of sedges (*Carex* spp.) in SS habitats in 1988 (■ , ————) and 1989 (▨ , - - - - -).

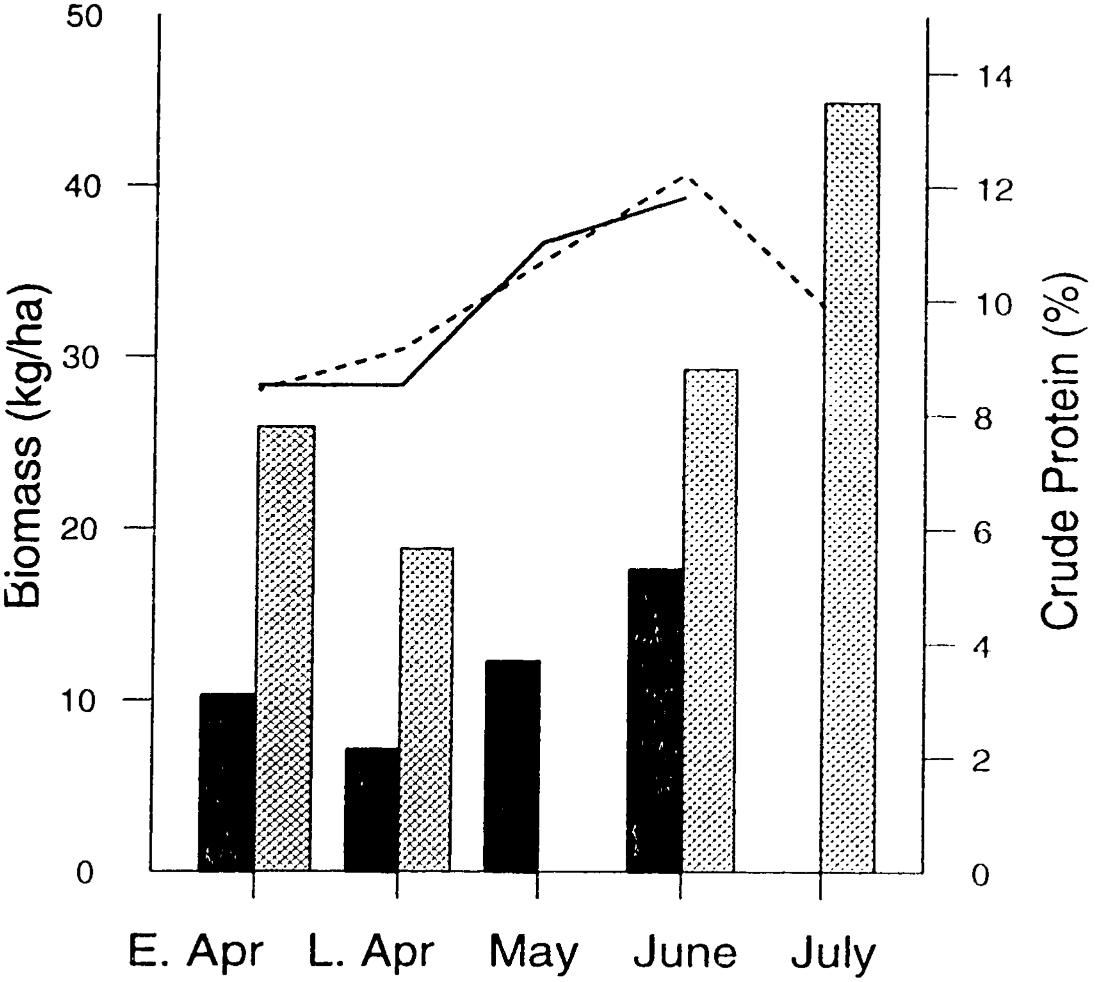

Figure 4: Monthly changes in biomass (kg/ha) and crude protein (%) of sage (*Artemisia frigida*) in SS habitats in 1988 (■ , ———) and 1989 (▨ , - - - - - -).

the available biomass during the early and late April sampling periods was low (Figure 5). The large flower stalks and buds that emerged early, were specifically "hunted" by wapiti and therefore the total biomass for this species is probably higher than was determined from sampling. This species was low in fibre and extremely high in protein. Three samples of combined foliage and flowers demonstrated a mean NBDMD of 84.8% (SE=1.8) (unpubl. data).

The protein content of browse current annual growth (CAG) twigs remained relatively stable through the growing season (Figure 6). However for willow, significant increases in protein ($P = 0.0001$) and reduction in NDF ($P = 0.005$) in May 1989, coincided with bud swelling and foliage emergence. Advanced phenological development in 1988 resulted in separation of measurable quantities of foliage distinct from browse twigs. Samples collected in 1989 varied in phenological development from the initial swelling to broken leaf buds. However, these could not be separated from the twig CAG and likely produced the transient increase in quality observed in May. Similar phenological advance was observed for aspen, where catkins emerged in the first week of May 1988, followed by foliage in the second week. Although aspen catkins were not produced on the Takhini Valley range in 1989, foliage emergence was similar to 1988.

4.1.3 Seasonal nutritional quality of forage

Nutritional quality of forages are summarized in Tables 4-8. Nutritional differences among principal winter browse, shrub, graminoid and forb classes were observed in fibre ($P = 0.0001$), protein ($P = 0.0001$), and digestibility ($P = 0.0001$). Fibre content as neutral detergent fibre (NDF) was highest in the graminoids, lowest in crocus and willow bark, and intermediate in shrub and browse twigs. Although forage fibre was highest in the graminoids, almost 50% was composed of hemicellulose (NDF-ADF). Graminoids were significantly lower in lignin but were similar in ADF relative to other forage classes and therefore higher proportions of potentially digestible fibre. However, moderate cell soluble content and low crude protein content may have reduced their *in situ* (NBDMD) digestibility. Graminoids had the lowest apparent digestibility in spite of the apparently low indigestible fraction. Browses had lower apparent digestibility than *Artemisia frigida* and, with the exception of lignin, were similar in fibre content. The current year twig growth was higher in protein ($P < 0.005$) relative to older twigs to 4 mm in diameter, particularly for willow. Although differences in fibre content were not apparent, there was a difference in willow NBDMD. *Artemisia frigida* had the highest estimated digestibility, it was among the highest in protein content, but was intermediate in fibre content.

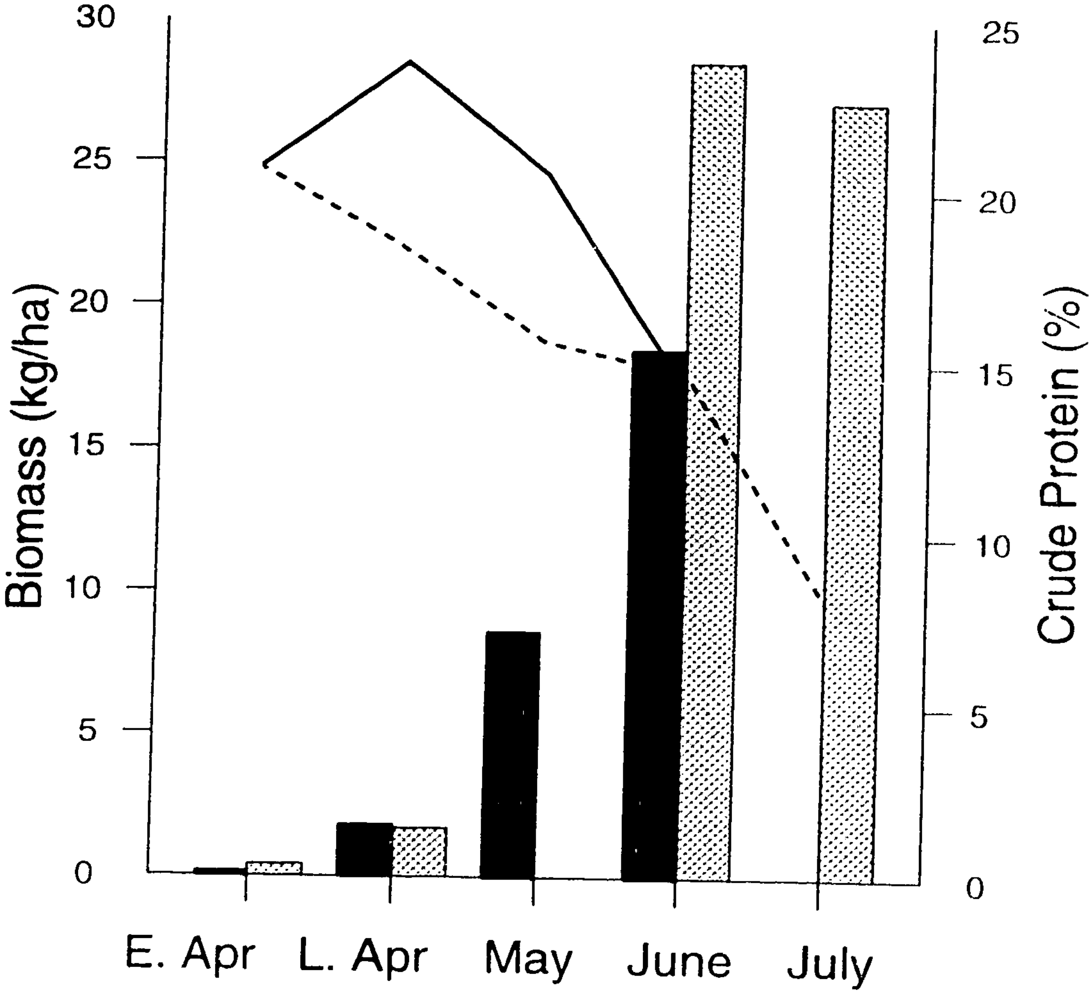

Figure 5: Monthly changes in biomass (kg/ha) and crude protein (%) of wild crocus (*Anemone patens*) in SS habitats in 1988 (■ , ———) and 1989 (▨ , - - - - - -).

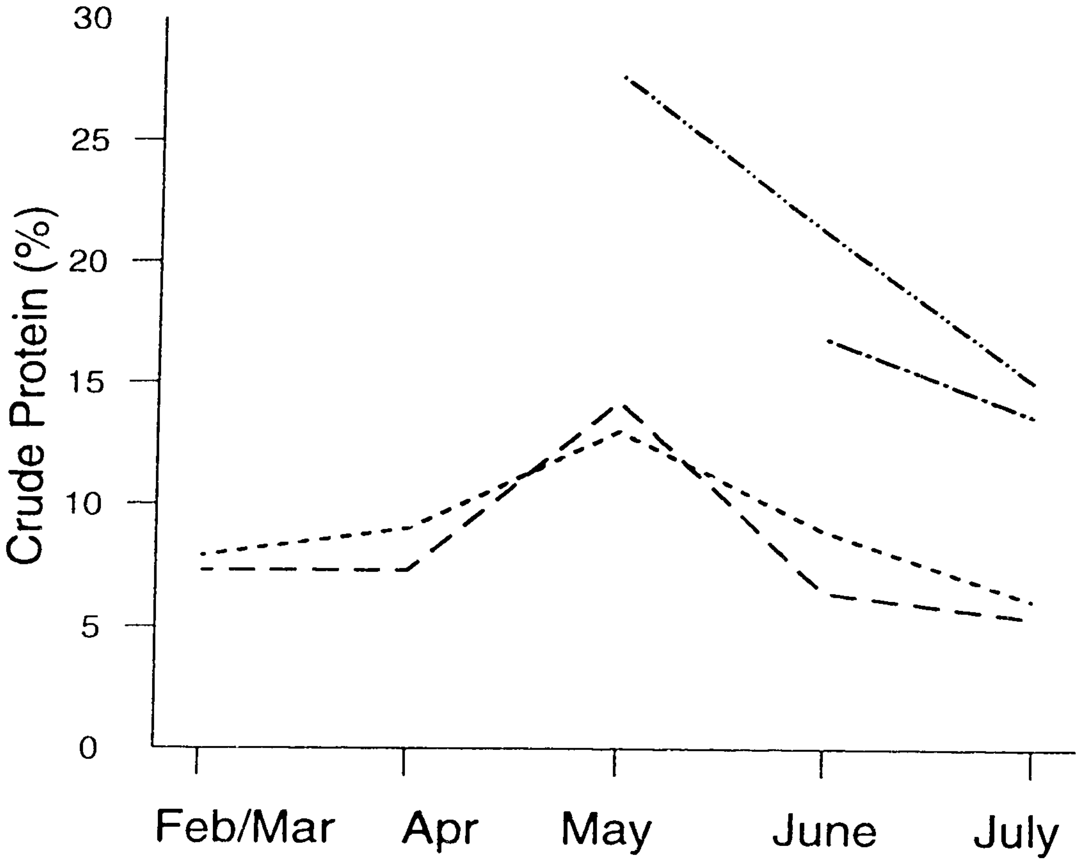

Figure 6: Monthly changes in crude protein content (%) of browse and foliage of aspen (*Populus tremuloides*) (- - - - - , ·—··—··) and willow (*Salix* spp.) (— — — , ·—·—·).

Table 4. Nutrient composition of principal forages selected by wapiti on the Takhini Valley winter range, Yukon Territory. Analysis includes samples collected in February and March 1989.

		NDF (%)			ADF (%)			Lignin (%)			CP (%)			NBDMD (%)		
Forage species	Forage class	x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Calamagrostis purpurascens	cured foliage	59.1 A	1.05	2	30.4 B	0.55	2	3.3 E	0.35	2	3.9 EF	0.58	2	57.2 D	0.53	3
	> CAG[A] foliage	59.7 A	0.25	4	31.5 B	0.34	4	2.1 E	0.25	4	3.0 F	0.47	4			
Carex spp.	cured foliage	55.4 A	2.14	3	28.2 B	1.17	3	3.5 E	0.32	3	4.7 E	0.45	3	50.3 E	2.10	2
Anemone patens	cured foliage	28.6 D	2.40	2	20.0 D	1.63	3	4.4 E	0.93	3	6.5 CD	0.26	3			
Artemisia frigida	dormant	39.2 C	1.16	3	27.9 B	1.05	3	7.3 D	1.04	3	8.4 A	0.46	3	71.2 A	0.56	3
Populus tremuloides	> CAG twigs	40.2 C	1.21	4	29.6 B	0.80	4	15.4 B	0.29	4	6.3 CD	0.06	4			
	CAG twigs	41.4 BC	0.40	5	32.2 B	0.69	5	19.8 A	0.55	5	7.9 AB	0.19	4	63.2 BC	0.68	4
Salix spp.	> CAG twigs	46.3 B	1.81	5	38.4 A	1.32	5	20.0 A	0.42	5	5.7 D	0.10	5	60.7 CD	1.59	3
	CAG twigs	43.5 BC	1.23	6	36.8 A	1.14	6	20.5 A	0.53	6	7.3 BC	0.08	6	66.6 B	1.07	4
	bark	29.4 D	1.35	2	23.7 C	1.35	2	12.4 C	1.00	2	3.6 F	0.20	2			

[A] current annual growth

dissimilar letters within columns indicate means differ significantly

Table 5. Nutrient composition of principal forages selected by wapiti on the Takhini Valley winter range, Yukon Territory. Analysis for period includes early April (1-16) and late April (17-30) collections combined.

Forage species	Forage class	NDF (%)			ADF (%)			Lignin (%)			CP (%)			NBDMD (%)		
		x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Calamagrostis																
purpurascens	foliage	58.1 A	1.14	4	27.9 AB	0.59	4	1.8 C	0.07	4	10.2 BC	1.21	4	70.8 A	3.38	3
Carex spp.	foliage	55.4 A	0.57	3	26.8 B	0.50	3	2.5 C	0.12	3	6.1 D	0.31	2	54.3 B		1
Anemone patens	buds, foliage	28.8 C	2.10	2	18.5 C	1.15	2	1.9 C	0.10	2	19.5 A	1.14	3			
Artemisia frigida	foliage, stem	40.1 B	0.03	2	28.5 AB	0.17	2	6.5 B	0.02	2	8.8 BCD	0.18	7	71.0 A	0.44	5
Populus tremuloides	CAG twigs	38.3 B		1	29.7 AB		1	15.9 A		1	10.5 B		1	64.6 A		1
Salix spp.	CAG twigs	38.4 B	1.20	4	31.2 A	0.88	4	16.7 A	1.18	4	7.3 CD	0.16	4	65.1 A	0.46	3

[A] current annual growth

dissimilar letters within columns indicate means differ significantly

Table 6. Nutrient composition of principal forages selected by wapiti on the Takhini Valley winter range, Yukon Territory. Analysis for period includes samples collected in May 1989.

		NDF (%)			ADF (%)			Lignin (%)			CP (%)			NBDMD (%)		
Forage species	Forage class	x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Anemone patens	foliage	25.0 AB		1				2.2 C		1	15.6 B	1.31	3			
Populus tremuloides	CAG twigs	35.6 A	2.12	3	27.7 A	20.3	3	15.2 A	1.05	3	13.0 B	2.62	3	70.8 A	1.87	1
	foliage	19.8 B	3.11	2	14.6 B	2.24	2	7.3 B	1.03	2	27.6 A	7.08	2	89.8 A	1.57	2
Salix spp.	CAG twigs	32.1 AB	1.89	3	25.7 A	1.38	3	12.8 A	0.93	3	14.2 B	1.05				

dissimilar letters within columns indicate means differ significantly

Table 7. Nutrient composition of principal forages selected by wapiti on the Takhini Valley winter range, Yukon Territory. Analysis for collections from June 1989.

Forage species	Forage class	NDF (%)			ADF (%)			Lignin (%)			CP (%)			NBDMD (%)		
		x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Calamagrostis purpurascens	foliage	55.6 A	0.46	6	26.9 B	0.17	6	1.6 F	0.14	6	11.2 DE	0.16	6	74.3 C	0.55	3
Carex spp.	foliage	55.8 A	0.95	4	26.4 B	0.54	4	3.2 EF	0.24	4	8.1 EF	0.29	4	64.5 E	0.96	4
Anemone patens	buds, foliage	19.5 C	1.30	3	12.9 D	0.70	3	3.0 EF	0.16	3	14.7 BC	1.01	3			
Artemisia frigida	foliage, stem	36.8 B		1	26.7 B		1	5.5 DE		1	12.2 CD		1	77.4 BC		1
Populus tremuloides	CAG twigs	38.8 B	1.87	2	28.0 B	0.77	2	13.7 B	0.97	2	8.9 DEF	0.17	2	71.2 CD	1.76	2
	foliage	20.7 C	0.81	2	15.2 CD	0.73	2	7.3 CD	1.03	2	21.2 A	1.51	2	89.0 A	0.35	2
Salix spp.	CAG twigs	41.0 B	2.54	3	33.0 A	2.40	3	16.3 A	1.18	4	6.4 F	0.20	3	67.4 DE	0.44	2
	foliage	23.9 C	1.79	3	18.5 C	1.44	3	9.3 C	0.77	3	16.8 B	1.87	3	82.6 B	2.53	3

dissimilar letters within columns indicate means differ significantly

Table 8. Nutrient composition of principal forages selected by wapiti on the Takhini Valley winter range, Yukon Territory. Analysis for collections from June 1989.

		NDF (%)			ADF (%)			Lignin (%)			CP (%)			NBDMD (%)		
Forage species	Forage class	x	SE	N	x	SE	N	x	SE	N	x	SE	N	x	SE	N
Calamagrostis purpurascens	foliage	55.6 A	1.27	4	28.5 A	1.06	4	2.7 E	0.39	4	8.0 BC	0.47	4			
Carex spp.	foliage										7.7 C	0.35	3	63.0 C	2.40	2
Anemone patens	buds, foliage										8.1 BC	0.23	3			
Artemisia frigida	foliage, stem	40.9 B		1	29.5 A		1	9.7 C		1	9.9 B	0.00	2	72.3 B	0.54	2
Populus tremuloides	CAG twigs	43.3 B	1.89	2	33.3 A	1.49	2	18.9 A	0.19	2	6.1 CD	0.28	2	62.9 C	0.92	2
	foliage	23.9 C	0.66	2	16.3 B	0.10	2	7.3 D	0.21	2	15.0 A	0.18	2	82.7 A	0.87	2
Salix spp.	CAG twigs	39.5 B	2.40	3	31.1 A	1.80	3	16.5 B	0.07	3	5.4 D	0.38	3	69.2 BC	2.88	3
	foliage	21.4 C	0.88	3	16.1 B	0.79	3	8.0 C	0.59	3	13.6 A	0.97	3	82.9 A	0.18	3

dissimilar letters within columns indicate means differ significantly

Digestibility of winter forages was highly correlated with the cell soluble fraction in a multiple linear regression ($r^2 = 0.77$, $P = 0.0002$). Inclusion of cellulose (ADF - lignin) in the regression increased the accounted variation to 81% of the *in situ* results. Digestibility of forb and browse species was equivalent to the cell content fraction (DM - NDF) whereas dry matter loss in graminoids and *Artemisia* was equivalent to the soluble and a larger proportion of the digestible fibre. *In vitro* (IVDMD) digestion trials conducted on winter forage samples were correlated with the NBDMD in 4 of 5 species evaluated (Table 9). However, the *in vitro* digestibility estimates were consistently lower, from 3.5 and 16 digestibility units, than the *in situ* estimates. Willow browse demonstrated poor correlation between methods, ranging from 14.8 to 25.5 digestibility units lower for the *in vitro* technique.

4.2 Resource-use behaviour

4.2.1 Habitat use

Five radio-collared wapiti cows were located 391 times in the periods of April to August 1988 and January to August 1989. Of these locations, 46% were confirmed visually but this varied from 93% in spring to 29% in summer when wapiti were either screened by foliage or were isolated for calving.

Location data for the period between the end of January and the end of March 1989 were used to determine late winter habitat use. The winter range habitat types used by radio-collared wapiti encompassed 79% of the total TV range (Table 10). SS habitat types were selected and OA avoided during winter. CR, conifer residual (CRe) and DA were used in proportion to their availability. Foraging in CR habitats was often observed when adjacent to SS habitats or along travel corridors between SS habitat patches. However, a large proportion of the CR habitat type remained unused during winter and therefore the true importance of CR is likely underestimated by the use/availability assessment.

No difference was found in habitat selection during spring between 1988 and 1989. Intense foraging activity on SS continued although some within period differences were noted. Combining April and May into spring, obscured a temporal shift in foraging pattern and habitat use. Significant selection for SS ($P < 0.05$) was observed for part of the spring observation period. However, 28.6% of the animal observations in 1988 and 31.9% in 1989 were in DA although use of this type for the entire April/May period was not significant ($P > 0.05$). Female wapiti selected DA habitats almost exclusively during summer. The specific use of a mosaic of small meadows,

Table 9. Simple linear regression for the comparison between the NBDMD and IVDMD digestibilities for selected winter forages of wapiti. Samples were collected in 1989 on the Takhini Valley range, Yukon.

Forage species	N	a	b	SEb	(ADJ) r^2
Calamarostis purpurascens	5	-14.15	1.18	0.52	0.50
Carex spp.	5	-24.09	0.97	0.12	0.96^A
Artemisia frigida	6	-19.14	1.08	0.20	0.84^B
Populus tremuloides	5	-35.33	1.35	0.63	0.47
Salix spp.	7	34.70	0.12	0.09	0.09

Carex spp. include *C. concinna*, *C. rupestris*, and *C. obtusata*

Salix spp. include *S. glauca* and *S. bebbiana*

^{A} P = 0.0012

^{B} P = 0.0061

Table 10. Seasonal habitat selection by female radio-collared wapiti in the Takhini Valley range, Yukon, 1988-1989.

Habitats used	Relative habitat availability (%)	distribution of animal locations (%)				
		1988		1989		
		Apr-May (77)^A	June-July (64)	Feb-Mar (47)	Apr-May (105)	June-July (98)
Dense aspen regen.	(41.1)	28.6	76.6$^+$	19.1	33.3	68.8$^+$
Open aspen regen.	(19.7)	9.1$^-$	9.4$^-$	0.0$^-$	3.8$^-$	13.5
Conifer regeneration	(29.0)	13.0$^-$	14.1$^-$	34.0	13.3$^-$	13.6$^-$
South slope grassl.	(6.6)	46.8$^+$	0.0$^-$	42.6$^+$	49.2$^+$	2.1$^-$
Conifer residual	(3.5)	2.6	0.0	4.3	6.7	2.1

^{A} number of locations

$^-$ habitat use is less than available ($P<0.05$)

$^+$ habitat use is greater than available ($P<0.05$)

sink holes and small creeks interspersed among the DA habitat could not be assessed although individual components may have supplied larger proportions of summer forage on this range.

4.2.2 Forage selection

Principal forages, those identified as being 2% or greater by fecal composition analysis, constituted 89% of the estimated winter diet in 1988 (Table 11) and 95% in 1989 (Table 12). Wapiti diets were similar in both years. The dominant forages included a single grass species (*Calamagrostis purpurascens*), low growing sedges (*Carex* spp.), fringed sage (*Artemisia frigida*) a shrub-like forb, and the CAG and bark of willow (*Salix* spp.). Winter diets were significantly correlated with forage biomass in SS habitat types (P = 0.03 in 1988, P = 0.046 in 1989, Spearmans rank correlation) (Table 13). No correlation was evident for diet and forage production among the other habitats sampled although both DA and CR habitats contained 1 preferred forage whose biomass exceeded levels found in SS habitats. Aspen browse biomass was higher in DA habitats and willow browse in CR habitats.

The transition between winter and spring diets occurred as a shift in the proportion of the major winter forage species selected where increasing proportions of newly emergent forbs and low growing sedges became more prevalent in the diet. These changes reflected the exposure of low growing sedge with the receding snowline, the emergence of forbs (*Anemone patens, Potentilla sp.*), and the advanced growth of graminoids on SS. *Artemisia frigida* continued to constitute a relatively large proportion of the transitional diet. Spring diet selection may have also been influenced by the emergence of catkins in both aspen and willow browse. Advanced emergence of browse catkins and foliage in 1988 was followed by an earlier increase in use of aspen and willow by wapiti. Because of delayed foliage emergence and the absence of catkins on aspen in 1989, spring diets contained less browse and more forbs.

Summer diets determined by fecal analysis were dominated by willow foliage in both years. However, summer foraging activity and habitat selection patterns favoured DA habitats. The use of aspen was supported by observation of large fragments of aspen in fecal pellets. It is doubtful therefore that identification and quantification of aspen foliage within summer feces was successful using this technique and probable that willow was over-represented in that year.

4.2.3 Activity patterns

Fourteen continuous 24-hour activity patterns were recorded from 3 mature female wapiti

Table 11. Diets (%) of wapiti on the Takhini Valley range, based on microhistological analysis of composite fecal samples for each period in 1988.

Forage species (%)		Sampling period and phenological stage				
		February March late winter	Early April early emergence	Late April late emergence	May/Early June leaf out	July leaf extension
Agropyron sp.		tr	1	0	0	0
Bromus pumpellianus		1	1	1	tr	1
Calamagrostis purpurascens	**	32	14	4	1	1
Carex spp	**	14	22	4	1	1
Deschampsia caespitosus		tr	tr	tr	tr	tr
Festuca saximontana	**	1	5	2	2	1
Poa sp.	**	3	10	6	4	2
Unidentifiable graminoids		1	1	1	0	tr
Total gramioids		52	55	31	13	17
Anemone spp.		tr	6	7	7	7
Artemisia frigida	**	23	20	tr	tr	0
Equisetum scirpoides		tr	6	4	0	0
Fragaria virginiana		tr	0	tr	5	13
Identifiable forbs[1]		1	2	tr	tr	tr
Unidentifiable forbs		tr	1	1	tr	tr
Total forbs		26	35	13	14	16
Lichen/Moss		tr	1	0	0	0
Arctostaphylos uva-ursi		1	2	0	tr	0
Populus tremuloides	**	1	tr	5	13	13
UID bark	**	3	1	8	4	3
Salix spp.	**	16	6	43	56	51
Salix bark	**	tr	0	0	tr	0
Identifiable shrubs and trees[2]		0	1	0	1	0
Total shrubs and trees		22	12	57	74	67

---

[1] Identifiable Forbs: *Draba* sp., *Gallium boreale*, *Potentilla* spp., *Oxytropis* spp., *Antennaria* sp., *Senecio* sp., *Solidago yukonense*

[2] Identifiable shrubs and trees: *Picea* spp., *Pinus contorta*, *Sheperdia canadensis*, *Amelanchier* sp..

tr Species occurrence less than 0.5% of the diet

** Principal winter forages

Table 12. Diets (%) of wapiti on the Takhini Valley range, based on microhistological analysis of composite fecal samples for each period in 1980

Forage species (%)		Sampling period and phenological stage				
		February March	Early April	Late April	May	Late June early July
		late winter	early emerg.	late emerg		leaf maturation
Agropyron sp.		tr	tr	0	tr	1
Bromus pumpellianus		tr	1	0	0	0
Calamagrostis purpurascens	**	32	11	2	7	tr
Carex spp.	**	8	6	6	4	5
Deschampsia caespitosus		0	tr	0	1	0
Festuca saximontana	**	tr	0	1	0	0
Poa sp.	**	1	tr	0	1	0
Unidentifiable graminoids		1	2	1	1	tr
Total gramioids		42	20	10	14	6
Anemone spp.		0	4	81	66	2
Artemisia frigida	**	32	72	1	tr	0
Equisetum scirpoides		0	0	tr	0	0
Fragaria virginana		tr	0	0	2	1
Identifiable forbs[1]		tr	0	0	0	1
Unidentifiable forbs		tr	1	0	1	1
Total forbs		33	77	82	69	5
Lichen/Moss		tr	0	0	0	tr
Arctostaphylos uva-ursi		tr	0	0	0	0
Populus tremuloides	**	tr	0	tr	0	0
UID bark	**	6	2	5	6	1
Salix spp.	**	17	0	3	0	86
Salix bark	**	tr	0	0	0	0
Identifiable shrubs and trees[2]		1	0	tr	tr	0
Total shrubs and trees		25	2	9	16	87

[1] Identifiable Forbs: *Draba* sp., *Gallium boreale*, *Potentilla* spp., *Oxytropis* spp., *Antennaria* sp., *Senecio* sp., *Solidago yukonense*

[2] Identifiable shrubs and trees: *Picea* spp., *Pinus contorta*, *Sheperdia canadensis*, *Amelanchier* sp..

tr Species occurence less than 0.5% of the diet.

** Principal winter forage

Table 13. Spearman rank correlation coefficient between habitat forage species composition and estimated late winter diets of wapiti.

Collection period		Habitat South Slope	 Open Aspen	 Dense Aspen	 Conifer Regeneration
Winter	r	0.538	-0.150	-0.100	0.254
1988	test	2.119^{A}	-0.502	-0.332	0.871
Winter	r	0.489	-0.010	0.023	0.245
1989	test	1.859^{B}	-0.032	0.075	0.836

^{A} P = 0.030
^{B} P = 0.046

between February 11 and July 3 1989 (Table 14). The duration of primary activity bouts (walking, grazing, browsing) did not differ between winter and summer although there was a significant change in the total daily time active (P = 0.02). Activity cycles within a 24 hour period were generally determined from 1200 hrs to 1200 hrs the following day and in most cases, an equal number of active and bedded periods were completed during this period. The number of cycles increased from a mean of 4 in winter to 6-7 in spring and summer (P = 0.039). Summer bedding periods were significantly shorter than winter periods (P = 0.0003). Although the proportions of the day active (and bedded) tended to differ between seasons in this small sample, they were not significant (P = 0.065 winter-spring, P = 0.11 spring-summer).

Standing did not occur as a distinct activity in periods longer than 15 minutes. Standing bouts were most often between 5 and 15 minutes and were recorded as a total for 24 hours. Bouts shorter than 5 minutes were incorporated into the previous or subsequent activity type. Few standing bouts were recorded during winter scans and, although differences in the daily time standing were evident when comparing winter and summer activities, standing generally averaged less than 5% of the daily activity budget.

The largest deviations in day to day activity patterns occurred when movements between foraging sites occurred. These generally took place during part of what would otherwise have been a resting period. Similar variations have been reported for roe deer (*Capreolus capreolus*)(Cederlund 1981) and moose (*Alces alces*) (Risenhoover 1986).

4.3 Fecal indicators

Fecal protein levels, corrected for ash content, were similar in 1988 and 1989 and followed a pattern of gradual increase in spring. During late winter 1989, levels were lower and lagged by 5 days over 1988. Fecal protein levels were equivalent by May although the seasonal peak and summer mean level was higher in 1988 (Figure 7).

Fecal ash levels were similar between years with spring maxima coinciding with the period of intense grazing activity on SS habitats. Correction for ash content in faeces increased the mean fecal protein values by 14.7% (SE =0.7) during winter, 19.2% (SE = 1.5) during spring, and 14.6% (SE = 0.6) during summer.

The effective end of winter foraging conditions, as estimated by the spring inflection in fecal protein levels, occurred within the first week of April in both 1988 and 1989. Radio-collared wapiti in the TV range generally return to SS habitats with permanent snow accumulations. This

Table 14. Seasonal activity patterns (±SE) of radio-collared female wapiti during 1989, Takhini Valley wapiti range, Yukon.

Period	N	Daily activity period (hrs/24 hr day)			Bouts/day		Mean bout duration (min)		N
		Active	Bedded	Standing	Active	Bedded	Active	Bedded	
Winter	5	9.4 A ± 0.5	14.4 A ± 1.2	0.08 A ± 0.05	4.1 A ± 0.1	4.4 ± 0.2	130.2 ± 8.9	205.3 A ± 11.0	20
Spring	6	11.4 AB ± 0.9	12.3 AB ± 0.9	0.37 AB ± 0.9	6.7 B ± 0.9	6.7 ± 1.1	116.6 ± 20.2	136.6 AB ± 30.9	36
Summer	3	13.8 B ± 0.9	9.8 B ± 1.2	0.58 B ± 0.3	7.3 B ± 0.3	7.3 ± 0.9	124.6 ± 19.2	77.1 B ± 1.2	21

means in the same column followed by dissimilar letters differ significantly P <0.025.

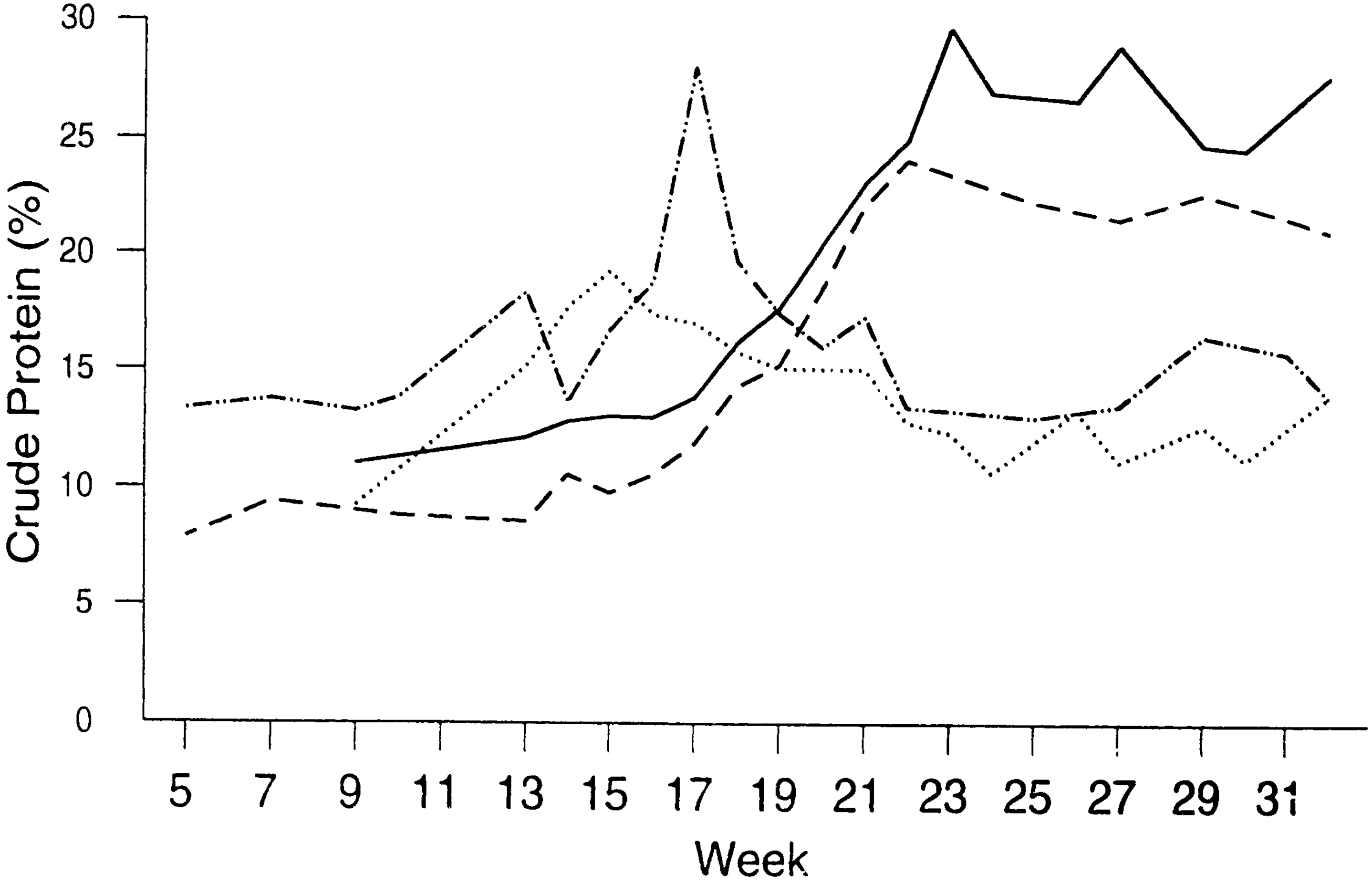

Figure 7: Weekly variation in fecal protein and fecal ash levels between winter and early summer 1988 (———— ....) and 1989 (— — —, —··—··—).

period occurs through October, therefore wapiti on the TV range experience an effective winter duration between 151 and 182 days. A mean of 164 days was used for carrying capacity determinations.

4.4 Nutrient requirements and carrying capacity

Maintenance energy requirements of a typical wapiti female were determined as the sum of energy expenditure for each activity and the duration of each activity. The incremental energy costs for an average snow cover of 32 cm was determined to be 10% greater than the snow free foraging cost. Baseline metabolizable energy (ME) requirements for maintenance ranged from 31.32 MJ/day to 32.33 MJ/day for low and high foraging duration, respectively. The incremental requirement for locomotion in snow over the same range was between 0.67 MJ/d (2.1% of maintenance) and 0.915 MJ (2.8% of maintenance). The daily incremental ME cost of gestation was 0.78 MJ/d (2.4% of maintenance) by January 1 and 4.416 MJ/d (13.9% of maintenance) by April 1.

At high intake levels, the predicted daily digestible energy intake by wapiti on the Takhini Valley winter range would meet or exceed requirements at both high and low biomass levels (Table 15). However, at low biomass and intermediate and short foraging duration, daily energy requirements would not be met beyond early January.

Daily dry matter intake during winter was estimated to range between 3 and 5 kg DM (1.3% to 2.2% of body weight) for a 225 kg wapiti. The associated maintenance protein requirements were estimated to range between 7.3% and 6.2% of the diet dry matter. Dietary protein content of 5.9% in 1988 and 6.3% in 1989, indicated that dietary protein intake was marginal to inadequate. Protein nutrition was adequate only under the highest intake levels and diet composition was high in browse and/or sage during late winter.

The carrying capacity of the Takhini Valley winter range was calculated to exceed current and historic population levels of 50 individuals (Table 16). The DA and CR habitats could support the highest number of animals on the winter range based on total range supply of either energy or protein. However, the biomass of these habitat types was dominated by a single browse species and so they would be of limited value because other dominant forages were not available. The SS habitat was the least abundant but had the highest area specific nutrient density of any habitat type. Based on area specific energy content, SS habitats were 39% more productive than DA habitats and 63-65% more productive than CR or OA habitat types. Similarly, SS habitats were

Table 15: Energy intake relative to requirements for wapiti on winter ranges in the Yukon. Digestible energy determined from forage fiber components and the formulae of Robbins et al. (1987), modified for differences in NDF digestibility as found in Mould and Robbins (1982). Base ME cost 31.84 MJ/d @ 9.4 h/d foraging and biomass 242 kg/ha. ME=DE*0.82

	Daily intake of dry matter, protein and energy						Total ME Requirements[1] (MJ/day)					
Forage biomass	242 kg/ha			339 kg/ha			Jan 1	Feb 1	Mar 1	Apr 1	Apr 15	May 1
Foraging time (hrs)	DM(kg)[2]	CP(g)[3]	ME(MJ)	DM (kg)	CP (g)	ME(MJ)						
7.9	2.9	180	26.75	3.65	224	33.30	32.78	33.38	34.47	36.41	37.89	40.59
9.4	3.5	216	31.82	4.40	266	39.62	33.42	34.03	35.11	37.06	38.54	41.24
10.8	4.0	246	36.56	4.99	309	45.52	34.02	34.63	35.72	37.66	39.14	41.84

[1] including gestation ME (MJ/d) energy requirements Jan 1 - Apr 15 and May 1 (0.780, 1.387, 2.475, 4.416, 5.899, 8.600)

[2] intake estimated as Hudson and Watkins (1986)

[3] protein intake was fixed by species composition and averaged 6.13% for the two winters. Reduction in sage and increased sedge between 1988 and 1989 decreased dietary protein intake from 6.3 to 5.9%.

Table 16. Availability of energy and protein on the Takhini Valley winter range relative to animal requirements. Incremental energy requirement for movement in snow was also included. Carrying capacity estimates derived as the total number of animals each habitat may support during a winter of 164 days, with a forage utilization level of 50%. ME=0.82*DE.

	Habitat type				
	South Slope	Open Aspen	Dense Aspen	Conifer Regen.	
Total area (ha)	885	1165	2580	3731	
Biomass (kg/ha)	242	186	175	112	
Available Protein (kg/ha)	10.0	4.4	7.0	6.9	
Available DE (MJ/ha)	2192	767	1290	827	
Carrying capacity (animal numbers):					Total
Energy (ME requirement 32.6 MJ/d)	149	68	255	237	709
Protein (6.7%)	106	61	216	307	690

5.0 Discussion

5.1 Range attributes

5.1.1 Forage biomass

Forage biomass on winter ranges in the Yukon is lower than on other North American wapiti ranges. Mean levels of biomass ranged between 112 and 242 kg/ha and were not different among habitats. Similar levels were confirmed in a subsequent investigation (Bailey and Willoughby 1990). Forage biomass on other wapiti ranges varies widely with habitat type and with season. Nietfeld (1983) found biomass values exceeding 1000 kg/ha in the aspen boreal forest of central Alberta. Wapiti have successfully colonized an arid shrub-steppe environment where grassland forage production ranged between 230 and 2330 kg/ha although 89% of the grassland habitat supported a forage biomass of 800 kg/ha or greater (McCorquodale 1991). Similarly, Hudson and Nietfeld (1985) reported biomass values for grassland habitats in the aspen parkland of 2300 kg/ha. Watkins et al. (1991) reported between 840 and 935 kg/ha for heavily grazed upland habitats of the same range.

Critical lower limits of forage production are required to maintain dry matter intake and have been assessed for deer, wapiti, and caribou (Wickstrom et al. 1984, Trudell and White 1981, Hanley and Mckendrick 1985). On ranges where forage is below these limits, dry matter intake declines as compensation normally achieved through increased feeding duration, bite rate, or bite size is incomplete. At low biomass levels caribou (or reindeer) restrict almost all active time to foraging whereas an increasing amount of search time is used under more favourable conditions (Trudell and White 1981). Smaller ungulates are better adapted to low biomass ranges because of lower absolute forage requirements despite a higher weight specific requirement. Wickstrom et al. (1984) speculate that this relative difference may have contributed to the failure of wapiti introductions in Alaska. McCorquodale et al. (1991) suggested that 600 to 800 kg/ha were the range of apparent minimum levels of forage production required to maintain wapiti.

For biomass levels between 200 kg/ha and 500 kg/ha, forage consumption rates of wapiti decline to 5 or 6 g/min (Collins et al. 1978, Wickstrom et al. 1984, Hudson and Nietfeld 1985). At this intake rate, wapiti would need to forage in excess of 12 hours/day to meet winter maintenance requirements. Wapiti in the Yukon foraged on average 9.4 hours/day (range 7.9 - 10.8 hrs) during winter at forage biomass levels of 242 kg/ha (145 - 339 kg/ha) on SS habitats. Intake rates of 8.0 g/min would be required to maintain an average daily intake of 4.5 kg forage dry matter. Therefore, the apparent requirement of increased foraging duration was not observed on winter ranges in the Yukon. In specific cases where longer than average daily foraging durations were recorded, wapiti moved discrete foraging sites rather than increased foraging duration. This movement occurred at the expense of bedding rather than foraging time and has been observed elsewhere for wapiti and other ungulates (Cederlund 1981, Risenhoover 1986, Watkins et al. 1991).

The apparent discrepancy between daily foraging duration in winter and the available forage biomass for wapiti in the Yukon may be a consequence of the forage distribution and physical characteristics. Hudson and Watkins (1986) found that wapiti foraging rates were slower but bites were larger when consuming cured ratner than fresh vegetation. Foliage tended to release from the leaf base rather than the biting point as was common for summer vegetation. This relationship therefore is likely to be more representative of winter than other relationships derived from wapiti foraging during summer (Collins et al. 1978). Under snow-free conditions, herbivores may forage more selectively, enhancing the differences between habitats because of selection for forage species or plant parts. However, when selectivity is reduced by snow cover, bite sizes are likely to be more consistent and a function of plant morphology. Goodson et al. (1991) found that differences in bite size and the proportion of green forage in bighorn sheep (*Ovis canadensis*) diets from 2 different habitats were eliminated with snow cover. The relationship between biomass and intake is inconsistent in forested habitats (Hudson and Watkins 1986) or when forages at low biomass levels are consumed (Trudell and White 1981, Wickstrom et al. 1984). This inconsistency may be the consequence of forage distribution on the winter range. Forage that is dispersed in clumps is more available at equivalent biomass levels than are evenly distributed forages (Arnold and Dudzinski 1967, Hudson and Nietfeld 1985). Therefore, in the Yukon wapiti may forage at an effectively higher biomass when cratering on clumped forages of the winter range. Although the most productive SS grasslands are more than 50% unvegetated (Mean = 52.6%, N = 80), the most productive and heavily used grass species (purple reedgrass) grows from a central root mass or tussock. It appears that wapiti are therefore able to select among patches or individual tussocks to forage, in effect, at a higher biomass level. The largest portion of wapiti foraging activity and apparent diet is concentrated from within a single habitat type and within the same forage stratum where this forage is predominant.

Forage biomass could be limiting if regeneration habitats are available in the absence of south slope or other productive grasslands. Adjacent mature forests appeared to have few of the preferred winter forage species and with the exception of some forbs, biomass also appeared to be lower than the more open grassland and regeneration habitats.

5.1.2 Forage phenology and nutritional value

Concentration on winter range during early spring and subsequent movement to transitional ranges are common behavioral strategies for wapiti (Knight 1970, Baker 1982, Morgantini and Hudson 1989). Increased forb consumption early in this transition period is essential to ending winter forage restriction and to meeting the increasing nutrient demands of gestation or antlerogenesis. Emergent plant tissue is high in energy and CP but the available biomass of new tissue is limited either by growth habit or, in the case of some forbs and graminoids, dilution of the new green foliage by the previous years growth (Hobbs and Sopwatt 1984). Therefore, the opportunity to improve the early spring diet through selective foraging is limited and diets continue to be dominated by staple grasses and shrubs. This was similarly noted by Hoefs (1975) for Dall sheep in the Yukon.

Foraging patterns changed during spring green-up, with greater search intensity and increased foraging duration at the expense of bedding periods. Wapiti concentrated foraging activity along the receding snow line and on open patches (also Hanley 1982), a time when cratering activity has stopped almost completely. The initial foraging effort during green-up was concentrated on the relatively robust newly emergent crocus (*A. patens*) flower stalks, followed by other forbs, graminoids, and emergent browse foliage in sheltered sites. The dense *Carex* spp. and *Poa* sp. "grazing lawns" common on sheep ranges (Hoefs and Cowan 1979) were limited in extent, although heavily used where available. These features were highly attractive to wapiti, as the older lignified sedges are removed and the high quality new growth is completely available. *Poa cusickii* was also highly attractive in early spring due to a similar growth habit.

Goodson et al. (1991) suggested significant nutritional benefits of green-up were often delayed beyond the peak of diet quality resulting from an apparent plateau in foraging effort. However, the short lag between the emergence of new green foliage, foraging behavioral response, and increasing fecal protein levels, would suggest otherwise. Fecal protein levels remained relatively constant through winter, gradually increasing within 1 to 2 weeks following the emergence of new growth on the SS habitats. Seip and Bunnell (1985) found that a 7-10 day advance in phenology on burned relative to unburned range was evident in fecal protein levels for stone sheep (*Ovis dalli stonei*). Although calibration of fecal protein levels with dietary intake is controversial (Leslie and Starkey 1985, 1987, Hobbs 1987, Robbins et al. 1987a), it is a sensitive index to winter/spring diet transition and increasing diet quality (Morgantini and Hudson 1989, this study). The nutritional advantage from high quality forages in phenologically advanced habitat types is generally short lived as, by May (mid May in the Yukon), the quality of forages in other habitats is also increased (Hobbs and Sopwart 1984). However, this short lived advantage of advanced phenology can be significant in the early adaptation of rumen microbial populations in the shift to higher quality summer forages (Freeland and Janzen 1974, Westoby 1978). A shift in foraging rather than habitat on the winter/spring range may be critical to the survival and population growth for wapiti on northern ranges.

5.2 Resource-use behaviour

5.2.1 Habitat selection

Habitat selection patterns for wapiti in the Yukon were consistent within seasons and between years. During the winter and 2 spring periods covered in this study, female wapiti relied on SS habitat types as occurs elsewhere within mountainous wapiti ranges (Lovaas et al. 1966, Knight 1970, Sweeney 1975, Ward et al. 1975). The use of southern exposures has been attributed to physical and biological variables as well as increased quantity and quality of relatively available forage (Mackie 1970).

In most of the northwestern United States, wapiti winter range is dominated by bunch grass communities (Knight 1970, Sweeney 1975, Houston 1982, Skovlin et al. 1983, Thomas et al. 1988). European red deer also preferentially select grassland habitats among forested winter ranges (Welch et al. 1990). In boreal forest habitats of Alberta, wapiti selected for grassland and wet meadow habitats although these were of a smaller micro-topographic scale than was selected by wapiti on western rangelands (Gates and Hudson 1981, Nietfeld 1983, Morgantini 1988). When snow accumulation increased beyond 30 cm, forested subunits became increasingly important to wapiti in Alberta. Similar shifts have been documented in Saskatchewan (Hunt 1979) and in Manitoba (Blood 1966, Rounds 1981). Wapiti appear to increase the level of dietary browse in forested habitats although, where available, they preferentially select grasslands, shrublands and recent burns as winter range (Rounds 1981). Selection of grassland winter range is consistent with wapiti preference for grass or grass dominated mixed diets. Hobbs et al. (1981) found that wapiti in Colorado selected among habitats to provide a mixed diet that contained 50% or more grass forage. Wapiti in the Yukon also utilize mixed diets in winter with similar proportions of gramineous forage and browse and shrubs.

The SS habitat was the only type actively selected by radio-collared wapiti during winter and spring. Other habitats were either avoided or used in proportion to their availability. Almost 50% of the radio-collared animal locations were associated with SS that constituted 9% (885 ha) of the 9955 ha winter range. The extent of the winter range is an important and perhaps primary determinant of carrying capacity (Skogland 1986) and must be critically evaluated if estimates are to have meaning. For example, if Hobbs et al. (1981) had not qualified their estimate of winter range extent (6000 ha) for wapiti in Colorado, with the subsequent estimates of winter range as 4000 ha and "primary" winter range as 2000 ha (Hobbs et al. 1982), the population would have differed substantially with their estimated carrying capacity rather than the general agreement that was found.

In this study, the vegetation polygon boundary of the outer-most animal location was used, rather than the animal location itself, to determine the extent of the range. This slightly expanded the range bounds to include a larger proportion of the CR habitat type. This was considered reasonable given this covertype was used frequently by wapiti, particularly when associated with SS habitats. However, the additional area may account for the lack of statistical significance in the selection for the CR habitat type.

Radio-collared wapiti were used to assess habitat selection, primarily to avoid sightability bias (Biggins and Jackson 1984, Samuel et al. 1987, Thomas and Taylor 1990). Although the total number of radio-collared animals was small, 3 in the first year and 5 in the second year, all were female and the remaining mature females in the population (9 in 1988 and 4 in 1989) were often closely associated with the marked animals. The low number of marked individuals may have violated assumptions regarding statistical reliability (Alldredge and Ratti 1986, 1992). However, this group was well represented because of the association of the animals and that a relatively large proportion of the female population was marked.

The location of radio-collared animals within groups was common during the winter period. To avoid potential dependency problems, a single location point was used for marked animals within a group (Alldredge and Ratti 1992). Dependency among successive locations or auto-correlation can also invalidate the conclusions of habitat selection tests (Dunn and Gipson 1977, Byers et al. 1984). A minimum location interval of 48 hours is commonly used in habitat selection studies on large herbivores (McCorquodale 1987). When shorter relocation intervals are selected (eg Carson and Peek 1987, Kufeld et al. 1989), the criterion of accessability of the entire range within that interval has been used (Leptich and Gilbert 1989). In this study, no difference was found when habitat selection was evaluated using either 48 hr or 24 hr location intervals, consequently the latter sampling interval was used for the analysis.

5.2.2 Snow as a limiting factor

Snow cover is an important factor governing winter habitat selection and range use by wapiti. Selective foraging by ungulates is reduced and the foraging energy cost is increased exponentially with snow depth (Parker et al. 1984, Wickstrom et al. 1984, Dailey and Hobbs 1989). However, snow-free winter ranges are subject to reductions in forage quality from weathering and nutrient leaching (Tukey 1970, Hobbs et al. 1981).

Hanley and McKendrick (1985) found that deer wintering on the islands of southeastern Alaska, faced a significant decline in forage availability following a 3 week snow accumulation. Similarly, resource limitation was greater for white-tailed deer and wapiti during winter, based solely on snow distribution (Jenkins and Wright 1988, Jenkins 1985). Winter foraging by wapiti is influenced primarily by snow depths and available forage biomass, often resulting in the selection of south aspects during winter. Snow depths between 45 cm to 60 cm caused wapiti to seek shallower depths, while forage availability determined the wintering location (Leege and Hickey 1977). Similar response depths of 40 cm to 46 cm cause a shift to more exposed winter range (Beall 1974, Sweeney 1975, Adams 1982). Sweeney (1975) suggested that depths in excess of 70 cm were critical, eliciting an avoidance reaction. In Alberta boreal forest habitats, wapiti respond to snow depths above 30 cm by moving from grassland and meadow habitats to more heavily forested sites and forest margins (Gates and Hudson 1981). Because extensive grasslands or wind swept habitats were not available within this forest complex, a shift in foraging habitat to more available forage sources, such as browse, was observed. Increasing dietary browse or shrub components as availability of graminoids decreases has been noted for other wapiti populations (Sweeney and Steinhoff 1976, Nelson and Leege 1982).

Long term snow cover information obtained from the Whitehorse airport weather station (AES 1991) was representative of the TV wapiti range. Two different sources of snow information, month end snow depth and a forested snow course, represented snow depths in open and regeneration habitats, respectively. Mean month end snow depths from exposed sites for 40 years of record were 31, 30, 22, and 3 cm for January through April. Snow depths in regeneration habitat types were 42, 47, 46, and 9 for the same months. Snow depths measured on the TV range verified that exposed SS habitats retained about half of the mid-winter snow cover found in aspen and conifer regeneration habitats. (These were 13.0 cm and 20.7 cm for SS habitats in 1988 and 1989, and 25.2 [SE = 2.5] in 1988 and 41.1 [SE = 2.2] in 1989 for regeneration habitats.) Periodic deep snow winters occur at approximately 10 year intervals, where snow accumulation may attain 65 cm in regeneration habitats. In 45 years of recorded snow depths, only nine had accumulations higher than 40 cm and one with accumulations greater than 65 cm measured in areas equivalent to SS habitat types. Therefore it appears that, on average, snow accumulation would not cause undue hardship to wapiti in the Yukon.

The incremental energy cost to wapiti foraging at snow depths of 30 cm were estimated to be 10% based on linear regressions presented by Parker et al. (1984). Wapiti in the Yukon were observed to forage at a relatively consistent and brisk pace both in winter and in spring when grasslands were snow free. Because of the relatively low forage biomass and clumped distribution of winter forages on Yukon ranges, foraging travel rates should remain relatively high. Wickstrom et al. (1984) demonstrated that increased rates of travel were required when forage biomass decreased. Foraging travel rates were estimated between 3 and 5 m/min based on forage biomass. This estimate was nearer the 1.1 m/min rate of travel for winter ranges found in Alberta by Gates and Hudson (1981) than the 20 m/min to 120 m/min locomotion rates evaluated by Parker et al. (1984). Using the higher travel rates and the relative sinking depths, the exponential function developed by Parker et al. (1984) predicts an increase locomotion costs of 54% for sinking depth of 32 cm instead of 10% found for the much slower rate. It appears that the exponential function is more relevant to energy expenditure in flight responses and long movement through fresh snow rather than movement associated with foraging. Travel costs on snow covered winter ranges must be evaluated carefully. Although foraging energy costs are increased, ungulates adapt by travelling slower (Mattfeld 1974 cited in Parker et al. 1984) and therefore the influence on total energy cost is small (Hobbs 1989).

Although snow accumulation on SS habitats should incur only limited increased energy cost (10% increase in locomotion cost and 2.2% increase in the total energy requirement) increased snow depths to 58 cm, as would be encountered in regeneration habitats, would increase the energy expenditure for locomotion by an additional 10% over the SS increment (Parker et al. 1984). Regeneration habitats have fewer preferred forages and with increased energy cost of foraging, they would become a nutritional liability. Wapiti in the Yukon are probably forced to rely on the SS habitats because of limited foraging returns in other habitats. Restriction to a portion of the range from snow cover can result in the depletion of preferred forages, forcing herbivores to rely on more abundant lower quality forage. Biomass is an important determinant of the ability of grazing herbivores to compensate for snow cover and forage burial. Seip (1983) suggested that on northern winter ranges, Stone sheep experienced absolute shortages of food when snow restricted foraging activity. Similar restrictions have been observed for wapiti, deer, and caribou because of deep or heavy snow pack (Severinghaus and Cheatum 1956, Telfer 1970, Prescott 1974, Telfer 1978, Adamczewski et al. 1988). Under these conditions, progressive defoliation of available and palatable species severely limits annual forage carryover.

5.2.3 Forage selection

Temperate and arctic ungulates characteristically consume a limited number of key or staple forages during winter (Hoefs 1975, Hobbs et al. 1981, Dailey et al. 1984) even though they may frequently sample other forages. Dietary sampling also occurs in summer or on snow free winter ranges, where maximum discrimination is possible, resulting in diets that often include species contributing little to the nutrient balance (Collins et al. 1978, Hoefs 1975, Hobbs et al. 1981). Sampling has been viewed as an important strategy used in assessing the relative foraging profitability of other habitats (Ellis et al. 1976, Robbins 1983:325).

Winter diets of wapiti in the Yukon were correlated with the dry weight production of plant species on SS grasslands and, although other habitats selected by wapiti contained preferred forages, they were usually a single species. Moreover, consumption of high proportions of graminoids and sage indicate they were principal forages even though they may not be, by definition, preferred or selected (Petridies 1975). Forage species composition of the winter and spring diets of wapiti were very similar to the principal forages selected by Dall sheep in the Yukon. Over an annual cycle Hoefs and Cowan (1979) recorded 110 plant species used by sheep but 4 provided more than half of the annual diet (51.2%). Using the bite count method they determined that *Artemisia frigida*, *Carex filifolia*, *Calamagrostis purpurascens*, and grayleaf willow (*Salix glauca*) constituted between 61.9% and 68.3% of the winter diet, and considered them to be "stable" forage species. These same 4 species were "stable" or staple forages for wapiti in the TV range. With the exception of wheatgrass (*Agropyron yukonense*) comprising between 4.6% and 9.5% of the winter diet, the remaining species consisted of forbs and grasses each constituting 2% or less of the recorded bites in Dall sheep diets.

Wapiti winter ranges were rarely snow-free and therefore cratering through moderate snow depths was required. Foraging in SS habitats, with a relatively higher available biomass, would improve the foraging efficiency (intake per unit time). Wapiti may have been able to further improve foraging efficiency by cuing on exposed culms of *Calamagrostis purpurascens* to aid in location of the basal foliage and thereby decreasing search effort. Ungulates are also apparently able to detect volatile oils (Bergerud and Nolan 1970, Helle 1982 cited in White [1983]) from beneath snow cover. Wapiti appeared to use this ability when searching for *Artemisia frigida* as they were observed pushing noses along the snow surface and stopping to crater on this species.

Artemisia frigida comprised a major proportion of the winter diet in both 1988 and 1989. Although not commonly reported as a forage species of wapiti (Kufeld 1973), it is important in the winter diets of mule deer, bighorn sheep, and antelope (Cooperider and Bailey 1984). Dall sheep in the Yukon took up to 29.6% of the foraging bites of the winter diet as *Artemisia frigida* (Hoefs and Cowan 1979). The relatively heavy use of this species, determined by the bite count method, is noteworthy as it is apparently overestimated using the fecal analysis technique (Gill et al. 1983). Plant fragments for this species are easily recognized and relatively abundant in rumen and fecal contents (Howard and Samuel 1979). Experimental work on deer conducted by Gill et al. (1983) suggested that *Artemisia frigida* was overestimated by a factor of 4 when consumed at approximately 6% of the foraging bites. However, when it composed 32% of the foraging bites, it was marginally lower than was estimated by fecal analysis. Although dramatic, these differences were inconclusive and additional calibration of the fecal analysis technique is required. Error in their work was introduced by not correcting for the different bite weights of grasses and forbs. Differences may have been introduced as a result of the higher dry matter intake of forbs relative to graminoids, as was demonstrated by Trudell and White (1981) for reindeer. Although further experimental work is required fecal analysis appears to be a reasonable indicator of winter diet quality, when the error associated with differential digestibility is minimized.

Spring diets continued to include substantial quantities of *Calamagrostis purpurascens* and *Artemisia frigida* despite intensive foraging on emergent forbs. Hoefs (1975) noted during green up on exposed grasslands (in April) sheep continued to select these two species to 50% of the diet. This was also evident in the TV, where new growth in *Carex* spp., *Calamagrostis purpurascens* and *Artemisia frigida* was initiated on the dormant plants or on existing cured tillers. The result of older foliage being consumed as wapiti or sheep foraged for new growth would be in effect a dilution of the new plant tissue.

Dried browse foliage was consumed in winter when it remained attached to shrubs or where leaves had been caught on conifer foliage. This was also the case for Dall sheep, moose, and wapiti consuming *Salix* spp. and *Populus tremuloides* foliage (Hoefs 1975, Hobbs et al. 1981, Gates and Hudson 1983, Nietfeld 1983, Renecker 1987). Risenhoover (1987) found that moose in Alaska, occasionally selected cured foliage where attached to browse stems, but amounted to less than 1% of forage biomass consumed between January and April. Browse foliage taken from the ground and as they cured on current annual growth twigs, were among the lowest quality forages evaluated. Although including browse foliage as available forage would result in a substantial increase in the standing crop for regeneration habitats, fallen cured foliage was lower in nutritional quality than any forage examined.

5.2.4 Forage and diet nutritional quality

Wapiti are one of the most adaptable mixed feeding herbivores in both behaviour and morphophysiology (Hofmann 1985). Kufeld (1973) summarized a wide variety of forage species consumed seasonally by wapiti. Winter diets of wapiti in the Yukon were extremely diverse with roughly equal proportions as graminoids, forbs and browse. Each group has variable levels of nutrients but also compounds that could impair the nutritional quality and consequently their value to wapiti. The interaction between growth form and winter weather are important determinants of the stability of nutrients in forage. The quality of forage species on winter ranges in the Yukon was assumed to be relatively stable because of the insulating influence of snow cover that prevents nutrient leaching (Tukey 1970). Hobbs et al. (1981) noted that on snow free winter ranges, forages declined in quality although wapiti were able to maintain stable nutrient intakes, presumably by varying species composition of the diet. Because of the relatively limited species availability on the winter range in the Yukon, much of the nutrient intake of wapiti is a function of few available species.

The digestible energy of forages consumed by wild herbivores is regularly assessed using the *in vitro* microdigestion technique (IVDMD) (Ward 1971, Oldemeyer et al. 1977, Milchunas et al. 1978, Hobbs et al. 1981). This technique is considered accurate on grass hay diets (Baker and Hansen 1985) but it has been found to both over and underestimate *in vivo* dry matter digestion of other forages (Mould and Robbins 1982, Hjeljord et al. 1982). Robbins et al. (1987b) suggested aspects of ruminant digestion are poorly mimicked using *in vitro* digestion techniques. Specifically, the differences included absorbtion and differential flow of fibrous, volatile, and soluble forage materials from the rumen, extensive dilution of allelochemics, addition and mixing of saliva, and the difference between solubility *in vitro* and absorbability *in vivo*.

Estimated digestibility differed between the *in vitro* and *in situ* digestion techniques for different forage classes similar to the findings of Person et al. (1980). Graminoid digestibility was higher by *in vitro* digestion while shrubs and browse were higher using nylon bag estimates. Other work has determined that low quality grass diets were predicted more reliably using the *in vitro* technique but as the forage quality increased, the *in situ* technique was a better predictor of *in vivo* digestibility (Monson et al. 1969). Vigourous digestion of higher quality diets would result in more rapid accumulation of metabolic end products causing an earlier depression of digestion for *in vitro* systems. This may also be the case for the differences observed in the browse digestion trials of Hjeljord et al. (1982). Although the 2 techniques are known to approximate each other (Mould and Robbins 1982) and digestibility estimates varied in magnitude depending on forage class, *in situ* digestion estimates were consistently higher than *in vitro*.

The higher apparent digestibility for browse and sage using the *in situ* technique may be associated with sample processing. Browse samples were re-ground using a 20 mesh screen to reduce sample heterogeneity, resulting from the presence of larger stem fragments. Greater escape of indigestible fragments may have spuriously elevated the *in situ* DMD determinations. Person et al. (1980) also found that DMD of browses tended to be higher using this technique (also using a 20 mesh screen). The NBDMD for *Artemisia frigida* may have been high for reasons similar to browse twigs although the IVDMD digestibility was also high relative to published estimates (Milchunas et al. 1978, Cooperrider and Bailey 1984). The potency of digestion inhibiting terpenes in this species may have been reduced through volatilization during drying and processing (Robbins 1983:245) as all forage species were similarly processed. The correlation between microdigestion techniques for sage suggest both techniques are measuring similar aspects of digestion.

Senescent grasses and winter twigs are generally considered to be low in secondary compounds (Rhoades and Cates 1976, Bryant et al. 1983). Wapiti diets in the Yukon are low in these compounds with the exception of terpenoids in sage. Crude terpenoids reduce IVDMD of big sage brush (*Artemisia tridentata*) (Striby et al. 1987). Cluff et al. (1982) observed a large difference between rumen levels of monoterpenoids and levels predicted from the plant species consumed by mule deer. Adaptations may exist for the consumption of forages with high proportions of essential oils although they contribute little to the energy budget because of high urinary losses (Harris et al. [1959] cited in Nelson and Leege [1982]). There is some controversy regarding the *in vivo* influence of secondary compounds. They are known to be bacteriostatic (terpenes) and to complex bacterial and other protein (tannins) *in vitro* but *in vivo* reductions in fibre digestion have yet to be demonstrated for deer or other ruminant species regularly consuming such forages (Mould and Robbins 1982, Robbins et al. 1987b). Detoxification of secondary compounds such as tannins may occur as early as the processes of mastication and insalivation (Burritt et al. 1987). Provenza and Malechek (1984) measured a 50% reduction in the tannin content and higher IVOMD of oesophageal extrusa relative to the original browse consumed by goats. Solublization and the potential retention of the reflex closure of the ventricular grove in adult animals (Church 1988:32, Hofmann 1989) and production of salivary binding proteins (Hagerman and Robbins 1987, Austin et al. 1989, Robbins et al. 1991) are mechanisms potentially enabling herbivores to regularly consume forages high in secondary plant compounds.

Detoxification of sage would make it an abundant source of crude protein and energy for wapiti in the Yukon. Protein forages otherwise occur as relatively disparate *Anemone* spp. and browse CAG. Browse CAG in this study had lower levels of fibre and was more digestible than similar species in Alaska (Oldemeyer et al. 1977, Risenhoover 1989). Differences in browse quality on wapiti range may be attributable, in part, to growth habitat. Because precipitation is relatively low and sites are located in upland habitats, slower growth due to moisture limitation may have resulted increased carbohydrate production and decreased cell wall lignification as suggested by Van Soest et al. (1978).

The nutritional quality of browse foliage was relatively low. Protein content of yellowing *Salix* spp. was similar to current annual growth twigs, whereas leaf litter digestibility was among the lowest for any forage examined (41%-43%, unpubl. data). Nutritional quality was similarly low for winter foliage in other studies (Renecker and Hudson 1988, Klein and Bay 1990). Given the relatively poor nutritional quality of old browse foliage and deeper snow accumulation in regeneration habitats, where foliage biomass is highest, foliage is not an important winter forage for wapiti in the Yukon.

Despite the low protein content of *C. purpurascens*, wapiti (and Dall sheep) used large proportions of this species as a staple winter forage. This is most likely a consequence of the high biomass and low lignin content and with sufficient protein otherwise available, *C. purpurascens* would provide a large proportion of dietary digestible energy to wapiti.

Fibre analysis has been used to estimate forage digestibility with reasonable success (Van Soest 1967, Renecker and Hudson 1988, Von Keyserlingk and Mathison 1989). *In vitro* digestion trials often report dry matter disappearance values lower than is suggested by the fractions of apparently digestible fibre (Hobbs et al. 1981, Schwartz and Hobbs 1985) or they report values that vary from the true digestibility at different rates (Hjeljord et al. 1982). Digestibility estimates from *in situ* trials more closely resemble the composition of soluble, slowly degradable and non-degradable fractions in forages (Von Keyserlingk and Mathison 1989) and although some have found *in situ* to be accurate (Monson 1969, Neathery 1972), in other cases variability has reduced the reliability of this technique (Milchunas et al. 1978, Van Soest 1982:94).

In vivo digestion of the cell soluble fraction is essentially complete (Van Soest 1982:82). However, the apparent digestibility, determined as the difference between dry matter and NDF digestibility (Van Soest 1967), is considerably lower than is suggested *in vivo*. A number of values for soluble fraction digestibility have been considered. Robbins et al. (1987b) determined a loss of 16 g/100 g soluble fraction, based on a combined regression using the NDF digestibility for grass, legumes and browse stems fed to deer. Estimates of fibre dry matter digestion, if accurate, are considered true digestibility because there is no structural fibre of metabolic origin (Van Soest 1982:45). The remaining fecal dry matter is composed of the indigestible components of the soluble fraction, metabolic fecal dry matter, and endogenous losses. Soluble fraction digestibility varies with true forage digestibility for wapiti and deer (Mould and Robbins 1982, Robbins et al. 1987b).

Prediction equations for the digestibility of both fibre and soluble fractions of a range of forages typically consumed by mule deer and wapiti were contrasted with the *in vitro*/*in situ* results of this study. The formulae of Mould and Robbins (1982) and Robbins et al. (1987b) were modified to reflect the differences in NDF digestion between wapiti and mule deer (Mould and Robbins 1982, Baker and Hansen 1985, Baker and Hobbs 1987). As soluble fraction digestibility is similar for both species, the estimation formulae for this fraction were not altered (Baker and Hansen 1985, Baker and Hobbs 1987).

Although the prediction equations suggest the DMD of grass forages could be higher, the agreement of other forage classes with microdigestion results suggest a realistic assessment can be made based on forage fibre fractions. Differences observed among graminoid species are most likely attributable to relatively slower digestion of the slowly degradable fraction and the low protein content. Renecker (1987:92-93) found asymptotic digestibility to be higher and relative digestion rates lower for timothy-brome hay relative to alfalfa or aspen twigs fed to wapiti, moose, and cattle. *In vivo* competition between digestion and passage limit the rumen residence time of slowly digested forages and ultimately mastication and particle breakdown would result in passage prior to complete digestion of cellulose (Welsh 1982, Ulyatt et al. 1986). However, on mixed diets, a reduction in the rate of passage and increase NDF digestibility has been observed (Baker and Hobbs 1987) suggesting digestible energy content of grass forages consumed by wapiti may be more available than would be determined either *in vitro* or *in situ*.

5.2.5 Diet energy and crude protein during winter

Dry matter intake varies as a function of environmental conditions, diet quality, and physiological condition (Mould and Robbins 1981, Robbins et al. 1981, Suttie et al. 1983, Arnold 1985). However, mature wapiti consume medium quality forages at a rate of about 15 to 20 g DM/kg W or 1.5% to 2.0% of body mass (Mould and Robbins 1981, Hudson and White 1985, Baker and Hansen 1985, Baker and Hobbs 1987). Therefore, a 225 kg wapiti will consume between 3.4 and 4.5 kg of forage dry matter per day. This intake range agrees with values modelled using a relationship derived by Hudson and Watkins (1986).

SS grassland habitats produced a mean forage biomass of 242 kg/ha, ranging between 145 kg/ha and 339 kg/ha (95% CL). Based on foraging durations observed for wapiti in the Yukon, energy requirements could not be met at the lower limit of forage biomass in any of the 4 habitat types evaluated. At mean biomass levels, energy requirements of wapiti were met only on SS habitats at the highest daily activity periods of 10.8 hours/day. The mean active duration of 9.4 hours would have been sufficient to meet energy requirements at the upper confidence limit of 339 kg/ha on SS habitats.

These variations demonstrate an important limitation in the application of forage biomass assessments. Because forage standing crop is an important determinant of the rate at which forage can be harvested, determination of the "effective biomass" ie biomass in tussocks rather than uniformly distributed, would be of value. Also, the relationship between forage biomass and forage intake rate is predicated upon herbivores grazing uniform swaths within a forage class, and so extrapolation to intakes on tussock form grasslands or mixed diets of shrubs and browse requires further evaluation. Recently, Spalinger and Hobbs (1992) and Shipley and Spalinger (1992) have examined foraging rate as a function of cropping and chewing rate and bite size relative to asymptotic intake rate. Intake rates are asymptotic when a herbivore can reach the next bite as it is processing the last bite and then become a function of the competition between processing forage and taking the next bite. If bite size and cropping rate are the factors determining intake rate, then on ranges where swards are uniform the cropping rate can approach a maximum but bite sizes would be reduced. Conversely, if forages are clumped then bite sizes can be maximal, particularly in winter when tillers release from the basal rosette. However, location and cratering for the next bite would impose a greater limit on intake. It is reasonable that wapiti would gain a considerable advantage in foraging SS habitats over other available habitats where forage is relatively more dispersed or, as in the case of CR habitats, select browse that is spatially aggregated but are better protected by anti-nutritional compounds.

Dietary protein intake estimates of 5.9% and 6.3% for 1988 and 1989 were considered to be representative of the entire winter. Snow cover would ensure minimal selectivity among forage species and also ensure relatively consistent forage quality. Maintenance protein requirements for ruminants range between 5-7% (Murphy and Coates 1966, Thorne et al. 1976, Nelson and Leege 1982). The protein requirements of wapiti in the Yukon, estimated factorially (Robbins 1983, NRC 1984), were met only at the highest intake levels in 1989. These levels could be attained during the longest rather than the mean foraging day duration. Therefore, under conditions experienced on wapiti ranges in the Yukon, where wapiti may potentially forage more efficiently on forage than is indicated by plant biomass, wapiti likely meet minimum energy requirements. However, because of obligate protein loss, only a change in ratio of high protein forages could increase the protein content of diet. Consequently, it appeared that wapiti consume diets that are marginal to sub-maintenance in crude protein.

Digestive efficiency is a function of both energy and protein content of the diet and deficiencies in either could result in an overall reduction in nutrient availability. Both nutrients have been found to be primary limiting factors on ungulate winter range. Deficiencies of digestible nitrogen become critical when forages drop below 5% CP (Deitz et al. 1962, Nagy et al. 1974, Mould and Robbins 1981) and possibly at higher levels as well. Van Soest (1982:240, 280-281) suggested protein intakes below 6-8% would impair the digestion efficiency due to a shortage of N for rumen microbial functions. Cellulolytic bacteria are most commonly limited by nitrogen shortage (Van Glyswyk 1970). Sinclair (1974) suggested that under conditions of poor nutritional quality, protein is the most critical nutrient determining animal abundance. Maintenance of viable rumen microbial population is essential to ensure digestive capacity during periods of nutritional deprivation (de Calesta et al. 1975). Limitations in nitrogen intake could precipitate energy deficiencies through a reduction of feed intake and dry matter digestibility (Weston and Hogan 1967, Leibholz and Hartmann 1972; both cited in Milchunas et al. 1978).

5.2.6 Forage selection relative to habitat selection

Hobbs et al. (1981) found that although wapiti selected from a number of different winter forages the quality of the winter diet remained relatively stable. They suggested that wapiti were habitat generalists as they selected a balance of grass and browse among a number of habitats. Rather, during winter, wapiti in the Yukon appear to be forage generalists, at least in their primary feeding habitat. Because the diet composition is related to forage species composition within SS habitats, they appear to forage non-selectively on the most available forages. The other habitats, whether selected or not, received some foraging activity in relatively specific forage classes or a single forage species abundant within that specific habitat type. The 3 most heavily used forage species on a Dall sheep winter range were also the 3 most abundant (Hoefs 1984). This form of dietary generalism has been observed elsewhere in sheep and mountain goat (*Oreamnos americana*), also known to be mixed feeders (Keating et al. 1985, Fox and Smith 1988).

Nudds (1980) suggested that temperate latitude herbivores experience decreased plant diversity and abundance during winter, consequently the diet is dominated by the most abundant forages. Although Jenkins (1982) pointed out limitations in the data re-analyzed by Nudds (1980), the thesis is reasonable and appears to follow for many northern herbivores. Selection may, through social factors such as experience or tradition, or through physical factors such as forage biomass or snow cover, occur at the level of habitat (habitat specialists) whereas the diet may be generalized, relying on the most abundant species, when the ability to forage selectively is low. This form of generalism occurs in deer or moose that occupy seasonal habitats such as winter yards (Verme 1965, Ozoga and Gysel 1972, Crete 1989) or in species that have established seasonal migration patterns (Hebert 1973, Baker 1982, Morgantini and Hudson 1988).

5.3 Nutritional carrying capacity

Based on the range supply/animal demand model, an assessment of the carrying capacity of different habitats was evaluated within the TV wapiti range. The SS habitat types had carrying capacities (animal days per ha) between 45% and 125% higher than other habitats for both energy and crude protein. The protein availability in other habitat types was lower per unit of area and in most cases resulted in lower estimated carrying capacity. The CR habitat could support higher overall animal numbers based on protein rather than energy, due to the prevalence of willow browse. However, accessing this relatively abundant source of protein would be at the expense of increased foraging energy cost and reduced daily dry matter intake. Therefore, under winter conditions in the Yukon, wapiti have little alternative but to seek the largest part of their dietary protein intake from SS habitat types. In the absence of the SS habitat type, it is unlikely that this or other similar ranges in the Yukon, would provide suitable winter range for wapiti.

Energy was considered most critical in deer carrying capacity models (Potvin and Huot 1983, Hanley and McKendrick 1985). On snow free winter ranges, increased protein requirements were more critical to total carrying capacity than increased energy cost of activity and bedding (Hobbs et al. 1982). In this study, either energy or protein could be lower than maintenance requirements within the range of intakes and forage nutritional values observed. However, protein was more likely to be limiting.

6.0 Conclusions and management implications

Wapiti in the Yukon currently exist below winter range carrying capacity even though the winter range is relatively limited. The SS grassland habitat type is critical to the persistence of wapiti because of relatively high production, quality, and availability of staple forages.

Protein intake was lower than estimated requirements under Yukon conditions although within the range of 5-7% often considered as the maintenance requirement for ruminants. Dietary protein content varied largely with diet species composition because of protein content differences among the staple forages and the low biomass of alternative forage species. Wapiti were able to harvest forage at levels that provide winter energy requirements within foraging durations common to wapiti in other areas at biomass levels lower than are documented for any other wapiti range. Forage spatial distribution and growth habit were important factors in permitting wapiti to harvest forage at rates equivalent to sites with higher biomass levels.

Wapiti have been observed sporadically in locations other than the 2 current ranges but no additional population centres are known. The persistence of these 2 small populations in the Yukon suggest their existing range, the complex of SS grasslands, burn regeneration, and closely associated regeneration habitats common to both, provide the year round requirements of wapiti. Winter reductions in forage abundance and quality are apparently mitigated through the low snow accumulation and the relative abundance of a few nutritionally important forages. Heavy use of *Artemisia frigida* is one adaptation critical to maintaining levels of both protein and energy in the winter diet of wapiti in the Yukon.

Spring habitat selection and diet composition varied little from winter periods with the exception of an apparently small increase in forb biomass consumption. However, the 2 to 3 week advance in phenology experienced in SS habitats is critical to wapiti and northern ungulates in general. Advanced phenology is particularly critical to mature females, and population productivity, where the added requirement of the rapidly growing fetus further stresses protein and energy reserves. The winter and summer diet of wapiti is dominated by forages that are similar in digestibility and nutrient quality. However, the pursuit of relatively rare but extremely high quality emergent forages in spring is likely the only time when forage competition is evident for wapiti on Yukon ranges. Emerging forbs are rare and eagerly "hunted" by wapiti and other smaller herbivores. This "competition" is likely exacerbated by the relatively low productivity of northern ranges. Until the emergence of additional forb, browse and shrub foliage occurs in late April and early May, wapiti are likely to be in competition for limited resources. It is during this brief period that wapiti on winter/spring ranges may be nutritionally limited by population density (Hobbs and Swift 1985). By increasing populations on these ranges, the rate of improvement in spring diets would be delayed as would the improvement in nutritional status during a potentially critical period.

Under current conditions, extreme nutritional limitation is likely to occur only as an unusual event where excessive snow depths or unusually long winter and delayed spring increase reliance on diminished nutrient body reserves. These events appear relatively rare on wapiti ranges in the Yukon. However, as wapiti have persisted but not increased appreciably, in either of the two known population centres, for 30 or more years post liberation, periodic nutritional stress influencing productivity could be an important co-factor to other proximal sources of mortality. However, the tendency towards smaller body size relative to their EINP founder stock suggests some potential for early life nutritional restriction, although, additional data are required to evaluate this hypothesis.

The key role of SS habitat types in the winter and spring foraging dynamics of wapiti in the Yukon, and the limited abundance of this habitat type, necessitate the protection of these habitats from disposition and disturbance. In the Takhini Valley 885 ha of SS grassland exists on the range and based on this habitat, the carrying capacity is limited to about 100 animals. Because the most abundant forages are also the most heavily used by wapiti any competing land use should be evaluated based on the potential impact to SS habitats and the staple forages. Any use will reduce the potential of this range to support wapiti. Selective use of some forage species alter the ability of wapiti to obtain winter nutrients particularly protein. Reduction of *Calamagrostis* *purpurascens* could increase the required foraging duration or the travel distance required to maintain energy intake. However, reduction in the availability and consumption of forbs such as *Artemisia frigida* would reduce protein intake to substantially below maintenance levels. Habitats used as bedding or winter feeding areas adjacent to SS foraging habitats should also benefit from protection to ensure that winter foraging areas are maintained as an intact ecological unit.

Sporadic and inconsistent mortality in adults and juveniles in conjunction with variable productivity are likely to have a large influence in the overall population growth rate of wapiti in the Yukon. This form of demographic stochasticity in small populations is probably the major limitation to population growth. The nucleus breeding herd in each range may be too small to gain reproductive momentum required to increase recruitment of young females into the population. Management activities are best directed toward experimental manipulation, which is to enhance the core breeding herd in one population, and monitoring the response in manipulated and unmanipulated populations. As population growth is monitored, range forage should be monitored to ensure that forage species composition and production are not adversely influenced.

7.0 Literature cited

Aatelma, H. 1988. Distribution of cover types on the Takhini River elk range. Government of Yukon internal report. 30pp.

Adamczewski, J.Z., C.C. Gates, B.M. Soutar, and R.J. Hudson. 1988. Limiting effects of snow on season habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Can. J. Zool. 66:1986-1996.

Adams, A.W. 1982. Migration. Pages 301-321 in J.W. Thomas and D.E. Toweill, eds. Elk of North America. Ecology and management. Stackpole Books, Harrisburg, Pa.

Agricultural Research Council. 1980. The nutrient requirements of ruminant livestock. Commonwealth agricultural bureaux, Farnham Royal, England. Chapter 3 Requirements for Energy pp. 73-119.

Alldredge, J.R., and J.T.Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manage 50:157-165.

Alldredge, J.R., and J.T.Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. J.Wildl. Manage 56:1-9.

Andrewartha, H.G., and L.C. Birch. 1954. The distribution and abundance of animals. Chicago University Press, Chicago.

Arnold, G.W. 1985. Regulation of forage intake. In Bioenergetics of Wild Herbivores. R.J. Hudson and R.G. White. (eds.) CRC Press, Boca Raton, Fl. pp 81-102.

Arnold, G.W. and M.L. Dudzinski. 1967. Studies on the diet of the grazing animal. III. The effect of pasture species and pasture structure on the herbage in take of sheep. Aust. J. Agric. Res. 18:657-666.

Atmospheric and Environment Service. 1982. Canadian Climate Normals: Volume 3. Precipitation, 602pp

Atmospheric and Environment Service. 1985 Canadian Climate Normals: Annual snow summary, Yukon Territory.

Atmospheric and Environment Service. 1991. Summary of weather data for Whitehorse Airport for years of record. Unpubl. file.

Austin, P.J., L.A. Suchar, C.T. Robbins, and A.E. Hagerman. 1989. Tannin binding proteins in the saliva of deer and their absence in the saliva of sheep and cattle. J. Chem. Ecol. 15:1335-1347.

Bailey, A.W.. and M.G. Willoughby. 1990. Range plant communities, recommended stocking rate, and herbage production for the Yukon. Final Report. Western Rangeland Consultants Ltd., Edmonton AB. 89pp.

Baker, D.L., and D.R. Hansen. 1985. Comparative digestion of grass in mule deer and elk. J. Wildl. Manage. 49:77-79.

Baker, D.L. and N.T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can. J. Zool. 65:1978-1984.

Baker, R. 1982. Migration. Paths through time and space. Hodder and Stoughton Ed. Ltd. London. 248pp.

Batchelor, R.F. 1965. The Roosevelt elk in Alaska: it's ecology and management. Alaska dept. of Fish and Game. Vol V:Project W-6-R-5. Work plan D. Federal aid in wildlife restoration Project report : Juneau AK.

Beall, R.C. 1974. Winter habitat selection and use by a western Montana elk herd. PhD. Thesis. University of Montana. 197 pp.

Bergerud, A.T. 1983. Prey switching in a simple ecosystem. Scientific American. Dec. 1993:130-141.

Bergerud, A.T., and M.J. Nolan. 1970. Food habits of hand-reared caribou *Rangifer tarandus* L. in Newfoundland. Oikos 21:348-350.

Biggins, D.E., and M. R. Jackson. 1984. Biases in aerial surveys of mule deer. In Proc. symp. of issues and technology in management of impacted western wildlife. Thorne Ecol. Inst., Boulder, Colo. pp 60-65.

Blood, D.A. 1966. Range relationships of elk and cattle in Riding Mountain National Park, Manitoba. Wildl. Manage. Bull. 1(19). Ottawa; Can. Wildl. Serv. 62pp.

Bryant, J.P., F.S. Chapin,III, and D.R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to herbivory. Oikos 40:357-368.

Burris, O.E., and D.E. Mcknight. 1973. Game transplants in Alaska. Alaska Dept. Fish and Game. Technical Bulletin No 4. Dec 1973.

Burritt, E.A., J.C. Malechek, and E.D. Provenza. 1987. Changes in concentrations of tannins, total phenolics, crude protein, and *in vitro* digestibility of browse due to mastication and insalivation by cattle. J. Range. Manage. 40:409-411.

Byers, C.R., R.K. Steinhorst, and P.R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050-1053.

Carson, R.G., and J.M. Peek. 1987. Mule deer habitat selection patterns in north-central Washington. J. Wildl. Manage. 51:46-51.

Caughley, G., D. Grice, and R. Brown. 1988. The edge of the range. J. Anim. Ecol. 57:771-785.

Cederlund, G. 1981. Activity patterns in moose and roe deer in a northern boreal forest. 12:39-45.

Church. D.C. 1988. Digestive physiology and nutrition of ruminants. Vol. 1 Digestive physiology. O&B Books, Corvallis, OR. 564pp.

Cluff, L.K., B.L. Welch, J.C. Pederson, and J.D. Brotherson. 1982. Concentration of monoterpenoids in the rumen ingesta of wild mule deer. J. Range. Manage. 35:192-194.

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.

Cooperrider, A.Y., and J.A. Bailey. 1984. Fringed sage brush (*Artemisia frigida*)-a neglected forage species of western ranges. INT-200.

Crete, M. 1989. Approximation of K carrying capacity for moose in Eastern Quebec. Can. J. Zool. 67:373-380.

Dailey, T.V. and N.T. Hobbs. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. Can. J. Zool. 67:2368-2375.

Dailey, T.V., N.T.Hobbs, and T.N.Woodard. 1984. Experimental comparisons of diet selection by mountain goats and mountain sheep in Colorado. J. Wildl. Manage. 48:799-806.

De Calesta, D.S., J.G. Nagy, and J.A. Bailey. 1975. Starving and refeeding mule deer. J. Wildl. Manage. 39:663-669.

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

Dunn, J.E. and P.S. Gipson. 1977. Analysis of radio telemetry data in studies of home range. Biometrics 33:85-101.

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

Fargey, P.J. 1988. Seasonal patterns of forage selection by wapiti (*Cervus elaphus* L.) in relation to land reclamation. M.Sc. Thesis. University of Alberta. 90pp.

Fay, J.P., K.-J. Cheng, J.W. Costerton, M.R. Hanna, and R.E. Howarth. 1980. *In vitro* digestion of bloat-safe and bloat-causing microorganisms: gas and foam production. J. Dairy Sci. 63:1273-1281.

Flook, D.L. 1970. Causes and implications of an observed sex differential in the survival of wapiti. CWS report series No 11. 71 pp.

Fox, J.L. and C.A. Smith. 1988. Winter mountain goat diets in SE Alaska. J. Wildl. Manage. 52:362-365.

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

Garshelis, D.L., H.B. Quigley, C.R. Villarrubia, and M.R. Delton. 1981. Assessment of telemetric motion sensors for studies of activity. Can. J. Zool. 60:1800-1805.

Gates C.C. and R.J. Hudson. 1981. Habitat selection by wapiti in a boreal forest enclosure. Naturaliste Can. 108:153-166.

Gates, C.C. and R.J. Hudson. 1983. Foraging behavior of wapiti in a boreal forest enclosure. Nat. Can. 110:197-206.

Geist, V. 1983. On the evolution of ice age mammals and its significance to an understanding of speciations. ASB Bulletin Vol 30:109-133.

Gill, R.B., L.H. Carpenter, R.M. Bartman, D.L. Baker, and G.G. Schoonveld. 1983. Fecal analysis to estimate mule deer diets. J. Wildl. Manage. 47:902-915.

Goering, H.K. and P.J. Van Soest. 1970. Forage fibre analysis (apparatus, reagents, procedures, and some applications). Agric. Hdbk. 379. Agric. Res. Serv. USDA Wash. D.C. 20 pp.

Goodson, N.J., D.R. Stevens, and J.A. Bailey. 1991. Winter-spring foraging ecology and nutrition of bighorn sheep on montane ranges. J. Wildl. Manage. 55:422-433.

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

Guthrie, R.D. 1984. Alaskan megabucks, megabulls and megarams: The issue of pleistocene gigantism. Special publication Carnegie Institute.

Hagerman, A.E. and C.T. Robbins. 1987. Implications of soluble tannin-protein complexes for tannin analysis and plant defence mechanisms. J. Chem. Ecol. 13:1243-1258.

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

Hanley, T.A., and J.D. Mckendrick. 1985. Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeast Alaska. J. Wildl. Manage 49:103-199.

Hebert, D.M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis, University of British Columbia, Vancouver. 357pp.

Hjeljord, O., F. Sundstol, and H. Haagenrud. 1982. The nutritional value of browse to moose. J. Wildl. Manage. 46:333-343.

Hobbs, N.T. 1987. Fecal indices to dietary quality: a critique. J. Wildl. Manage. 51:317-320.

Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildl. Monogr. 101:1-39.

Hobbs, N.T. and R.A. Sopwart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551-560.

Hobbs, N.T. and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J. Wildl. Manage. 49:814-822.

Hobbs, N.T., D.L.Baker, J.E. Ellis, and D.M. Swift. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45:156-171.

Hobbs, N.T., D.L. Baker, J.E. Ellis, D.M. Swift, and R.A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. J. Wildl. Manage. 46:12-21.

Hoefs, M.A. 1980. Elk in Yukon. North, winter 1980, pp. 52-55.

Hoefs, M.A. 1984. Productivity and carrying capacity of a subarctic sheep winter range. Arctic 37:141-147.

Hoefs, M.A. 1975. Ecological investigation of Dall sheep and their habitat. Ph.D. thesis. University of British Columbia. Vancouver. B.C. 495 p.

Hoefs, M.A. and Cowan, I.McT. 1979. Ecological investigations of a population of Dall sheep (*Ovis dalli dalli*). Syesis, 12 (suppl. 1):1-83.

Hofmann, R.R. 1985. Digestive physiology of the deer, their morphophysiological specialization and adaptation. In Biology of deer production. P. Fennessy and K. R. Drew (eds.). R. Soc. N.Z. Bull. 22:393-407.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Holechek, J.L., M. Vavra, and D. Arthur. 1982. Relationships between performance, intake, diet nutritive quality and fecal nutritive quality of cattle on mountain range. J. Range Manage. 35:741-744.

Horwitz, W.J. 1980. ed. Official methods of analysis. 13th edition. Association of Analytical Chemists. Washington D.C. 975pp.

Houston, D.B. 1982. The northern Yellowstone elk: ecology and management. Macmillan Publ. Inc. New York. N.Y. 474pp.

Howard, G.S. and M.J. Samuel. 1979. Atlas of epidermal plant species fragments ingested by grazing animals. U.S. Dep. Agric. Tech. Bull. 1582. 143 pp.

Hudson, R.J. and W.G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64:1705-1708.

Hudson, R.J. and R.G. White. 1985. Computer simulation of energy budgets. In Bioenergetics of wild herbivores. R.J.Hudson and R.G. White (eds.). pp 261-290. CRC Press, Boca Raton, Fl.

Hudson, R.J. and M.T. Nietfeld. 1985. Effect of forage depletion on the feeding rate of wapiti. J. Range. Manage. 38:80-82.

Hudson, R.J., W.G. Watkins, and R.W. Pauls. 1985. Seasonal bioenergetics of wapiti in western Canada. In Biology of deer production. P. Drew and K. R. Fennessy (eds.). R. Soc. N.Z. Bull. 22:447-452.

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

Jenkins, K.J. and R.G. Wright. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. J. App. Ecol. 25: 11-24.

Jenkins, K.J. 1985. Winter habitat and niche relationships of sympatric cervids along the north fork of the Flathead River, Montana. Ph.D. thesis, University of Idaho, Moscow.

Jenkins, S.H. 1982. Management implications of optimal foraging theory: a critique. J. Wildl. Manage. 46:255-257.

Keating, K.A., L.R. Irby, and W.F. Kasworm. 1985. Mountain sheep winter food habits in the upper Yellowstone valley. J. Wildl. Manage. 49:156-161.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. J. Wildl. Manage. 32:350-367.

Klein, D.R. and C. Bay. 1990. Foraging dynamics of muskoxen in Peary Land, northern Greenland. Hol. Ecol. 13:269-280.

Knight, D.R. 1970. The sun river elk herd. Wildl. Mono. No 23. 66pp.

Kufeld, R.C., D.C. Bowden and D.L. Schrupp. 1989. Distribution and movements of female mule deer in the Rocky Mountain foothills. 871-877.

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

Larsen, D.G., D.A. Gauthier, and R.L. Markel. 1989. Causes and rates of moose mortality in the southwest Yukon. J. Wildl. Manage. 53:548-557.

Leege,T.A. and W.O. Hickey. 1977. Elk-snow-habitat relationships in the Pete King Drainage, Idaho, Idaho Dept. Fish and Game. Wildl. Bull. No. 9. Boise Idaho. 23pp.

Leptich, D.J. and, J.R. Gilbert. 1989. Summer home range and habitat use by moose in northern Maine. J. Wildl. Manage. 53:880-885.

Leslie, D.M. and E.F. Starkey. 1987. Fecal indices to dietary quality: A reply. J. Wildl. Manage. 51:321-325.

Leslie, D.M. and E.F. Starkey. 1985. Fecal indices to dietary quality of cervids in old growth forests. J. Wildl. Manage. 49:142-146.

Lovaas, A.L., J.L. Egan, and R.R. Knight. 1966. Aerial counting of two Montana elk herds. J. Wildl. Manage. 30:364-369.

Mackie, R.J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20:1-79.

McCorquodale, S.M. 1987. Fall-winter habitat use by elk in the shrub-steppe of Washington. Northwest Sci. 61:171-173.

McCorquodale, S.M. 1991. Energetic considerations and habitat quality for elk in arid grasslands and coniferous forests. J. Wildl. Manage. 55:237-242.

Milchunas, D.G., M.I.Dyer, O.C. Wallmo, and D.E. Johnson. 1978. In vivo-in vitro relationships of Colorado mule deer forages. Colo. Div. Wildl. Spec. Rep. 43:1-44.

Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. J. Wildl. Manage. 42:715-738.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

Monson, W.G., R.S. Lowrey, and I. Forbs. 1969. *In vivo* nylon vs two stage *in vitro* digestion. Comparison of two techniques for estimating dry matter digestibility of forages. Agronomy J. 61:587-589.

Morgantini, L.E. 1988. Behavioral adaptive strategies of wapiti in the Canadian rocky mountains. Ph.D. Thesis. University of Alberta, Edmonton. Alberta. 193 pp.

Morgantini, L.E. and R.J. Hudson. 1988. Migratory patterns of the wapiti, *Cervus elaphus* in Banff National Park, Can. Field-Nat. 102:12-19.

Morgantini, L.E. and R.J. Hudson. 1989. Nutritional significance of wapiti *Cervus elaphus*, migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Res. 21:288-295.

Mould, E.D. and C.T. Robbins. 1981. Evaluation of detergent analysis in estimating nutritional value of browse. J. Wildl. Manage. 45:937-947.

Mould, E.D. and C.T. Robbins. 1982. Digestive capabilities in elk compared to white-tailed deer. J. Wildl. Manage. 46:22-29.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods in vegetation ecology. J. Wiley and Sons. N.Y. 547 pp.

Murphy, D.A. and J.A. Coates. 1966. Effects of dietary protein on deer. North. Am. Wildl. Conf. 31:129-139.

Nagy, J.G., H.W. Steinhoff, and G.M. Ward. 1974. Effects of essential oils of sagebrush on deer rumen microbial function. J. Wildl. Manage. 28:785-790.

National Research Council. 1984. Nutrient requirements of beef cattle. National Academy Press. Washington D.C. 90pp.

Neathery, M.W. 1972. Conventional digestion trial vs nylon bag technique for determining season differences in quality of midland bermudagrass forage. J. Anim. Sci. 34:1075-1084.

Nelson, J.R. and T.A. Leege. 1982. Nutritional requirements and food habits. pp 323-368. In Elk of North America: ecology and management. J.W. Thomas and D.E. Toweill (eds.) Stackpole books, Harrisburg Pa. 698p.

Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization availability data. J. Wildl. Manage. 38:541-545.

Nietfeld, M.T. 1983. Foraging behavior of wapiti in the boreal mixed wood forest, central Alberta. M.Sc. thesis, Univ. Alberta. 185pp.

Nudds, T.D. 1980. Forage preference, theoretical considerations of diet selection by deer. J. Wildl. Manage. 44:735-740.

Oftedel, O.T. 1985. Pregnancy and lactation. pp 215-238 In Bioenergetics of wild herbivores. R.J.Hudson and R.G. White (eds.). CRC Press, Boca Raton, Fl.

Oldemeyer, J.L., A.W. Franzmann, A.L. Brondage, P.D. Arneson, and A. Flynn. 1977. Browse-quality and the Kenai Moose population J. Wildl. Manage. 41:533-542.

Oldemeyer, J.L. and W.L. Regelin. 1980. Comparison of 9 methods for estimating density of shrubs and saplings in Alaska. J. Wildl. Manage. 44:662-666.

Orskov, E.R., F.D. Debhovell, and F. Mould. 1980. The use of the nylon bag technique for evaluation of feedstuffs. Trop. Anim. Prod. 5:195-213.

Oswald, E.T. and J.P. Senyk. 1977. Ecoregions of Yukon Territory. Canadian Forestry Service, Fisheries and Environment Canada. Victoria. 1977. 116p.

Ozoga, J.J. and L.W.Gysel. 1972. Response of white-tailed deer to winter weather. J. Wildl. Manage. 36:892-896.

Parker, K.L., C.T. Robbins, and T.A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.

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

Pearson, H.A. 1970. Digestibility trials: *in vitro* techniques. pp: 85-92 In: Range and wildlife habitat evaluation: a research symposium. U.S. Dept. Agric. For. Serv. Misc. Publ. 1147.

Pearson, A. 1967. Annual file report. Project M5-1-1. Elk survey in Yukon Territory. 10pp.

Person, S.J., R.E. Pagau. R.G. White, and J.R. Wick. 1980. In-vitro and nylon bag digestibilities of reindeer and caribou forages. J. Wildl. Manage 44:613-622.

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

Potvin, F. and J. Huot. 1983. Estimating carrying capacity of a white-tailed deer wintering area in Quebec. J. Wildl. Manage. 47:463-474.

Prescott, W.H. 1974. Interrelationships of moose and deer of the genus Odocoileus. Natur. Can. 101:493-504.

Provenza, F.D. and J.C. Malechek. 1984. Diet selection by domestic goats in relation to blackbrush twig chemistry. J. Appl. Ecol. 21: 831-841.

Renecker L.A. and R.J. Hudson. 1988. Seasonal quality of forages used by moose in the aspen-dominated boreal forest. central Alberta. Holarct. Ecol. 11:111-118.

Renecker, L.A. 1987. Bioenergetics and behavior of moose in the aspen boreal forest. Phd thesis. Univ. Alberta, Edmonton. 210pp.

Rhoades, D.F. and R.G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. pp 168-213. In Recent advances in phytochemistry, Vol. 10. Biochemical interaction between plants and insects. J.W. Wallace and R. L. Mansell (eds) Plenum, New York.

Rippin, B. 1983. History and performance of elk transplant projects in northeastern Alberta. Alberta Fish and Wildlife report. 22p.

Risenhoover, K.L. 1986. Winter activity patterns of moose in interior Alaska. J. Wildl. Manage. 50:727-734.

Risenhoover, K.L. 1989. Composition and quality of moose winter diets in interior Alaska. J. Wildl. Manage. 53:568-577.

Risenhoover, K.L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis. Michigan Tech. Univ. Houghton, Michigan.

Robbins, C.T., S. Mole, A.E. Hagerman, and T.A. Hanley. 1987a. Role of tannins in defending plants against ruminants: Reduction in protein availability. Ecology 68:98-107.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68:1606-1615.

Robbins, C.T. and A.N. Moen. 1975. Uterine composition and growth in pregnant white-tailed deer. J. Wildl. Manage. 39:355-360.

Robbins, C.T., R.S. Podbielankik-Norman, D.L. Wilson, and E.D. Mould. 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. J. Wildl. Manage. 45:172-186.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Academic Press, N.Y. 343 pp.

Robbins, C.T. and B.L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. Am. Nat. 114:101-116.

Robbins, C.T., A.E. Hagerman, P.J. Austin, C. McArthur, and T.A. Hanley. 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. J. Mammal. 72:480-486.

Rounds, R.C. 1981. First approximation of habitat selectivity of ungulates on extensive winter ranges. J. Wildl. Manage. 45:187-196.

Rowe, J.S. 1972. Forest Regions of Canada. Dept. of the Env. Can. For. Serv., Publ. No. 1300, Ottawa 172pp.

Samuel, M.D., E.O. Garton, M.W. Schlegel, and R.G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. J. Wildl. Manage. 51:622-630.

SAS Institute. 1982. SAS users guide: statistics. 1982 edition. SAS Institute, North Carolina. 584 pp.

Schwartz, C.C. and N.T. Hobbs. 1985. Forage and range evaluation. In Bioenergetics of wild herbivores. R.J.Hudson and R.G. White (eds). pp 25-52. CRC Press, Boca Raton, Fl.

Seip, D.R. and F. Bunnell. 1985. Nutrition of stone sheep on burned and unburned ranges. J Wildl. Manage. 49:397-405.

Seip, D.R. 1983. Foraging ecology of Stone Sheep. Ph.D. Thesis. Univ. British Columbia. Vancouver. 175pp.

Severinghaus, C.W. and E.L. Cheatum. 1956. Life and times of the white-tailed deer. In The deer of North America. W.P. Taylor (ed), Stackpole Co. Harrisburg Pa. pp 57-186.

Shipley, L.A. and D.E. Spalinger. 1992. Mechanics of browsing in dense food patches: effects of plant and animal morphology. Can. J. Zool. 70:1743-1752.

Sinclair, A.R.E. 1974. The natural regulation of buffalo populations in East Africa. IV: The food supply as a regulating factor and competition. E. Afr. Wildl. J. 12:291-311.

Skogland, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. J. Wildl. Manage. 50:314-319.

Skovlin, J.M., P.J. Edgerton, and B.R. McConnell. 1983. Elk use of winter range as affected by cattle grazing, fertilizing, and burning in southeastern Washington. J. Range. Manage. 36:184-189.

Soper, J.D. 1950. Proposed introduction of American wapiti and plains bison to Yukon Territory, Canada. CWS report 11-50.

Spalinger, D.E. and N.T. Hobbs. 1992. Mechanics of foraging in mammalian herbivores: new models of functional response. Am. Nat. 140:325-348.

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

Steel, R.D.G. and J.H. Torrie. 1980. Principles and procedures of statistics, A biometrical approach. McGraw Hill Books, N Y. 633pp.

Stewart, R.R., R.R. MacLennan and J.D. Kinnear. 1977. The relationship of plant phenology to moose. Tech. Bull. No 3. Sask. Dept. Tour. and Ren. Res. 20 pp.

Striby, K.D., C.L. Walmbolt, R.G.Kelsey, and K.M. Haustad. 1987. Crude terpenoid influence on in vitro digestibility of sage brush. J. Range. Manage. 40:244-248.

Suttie, J.M., E.D. Goodall, K. Pennie, and R.N.B. Kay. 1983. Winter food restriction and summer compensation in red deer stags (*Cervus elaphus*). Br. J. Nutr. 50:737-747.

Sweeney, J.M. and H.W. Steinhoff. 1976. Elk movements and calving as related to snow cover. In Ecological impacts of snowpack augmentation in the San Juan Mountains, Colorado, H.W. Steinhoff and J.D. Ives (eds.) pp 415-436. Ft. Collins: Colorado State Univ. Publ.

Sweeney, J.M. 1975. Elk movements and calving as related to snow cover. Ph.D Thesis. Colorado State Univ., Ft. Collins. Co. 95pp.

Swenson, J.E. 1987. The tradeoffs of managing for trophy bull elk (*Cervus elaphus canadensis*). Annals Biol. 3:1-6.

Telfer, E.S. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34:553-559.

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

Tempelman-Kluit, D.J. 1974. Reconnaissance geology of Aishihik Lake, Snag and part of the Stewart River map-areas, west-central Yukon (115A, 115F, 115G and 115K). Geological survey of Canada, Dept. Energy, mines and resources. Paper M44-73-41.

Thomas, J.W., D.A. Leckenby, M. Henjum, R.J. Pedersen, and L.D. Bryant. 1988. Habitat-effectiveness index for elk on blue mountain winter ranges, Oregon and Washington U.S.A., U.S. For. Serv. Gen. Tech. Rep. PNW. Vol. 218.

Thomas, D.L. and E.J. Taylor. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54:322-330.

Thorne, E.T., R.E. Dean, and W.G. Hapworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. J. Wildl. Manage. 40:330-335.

Tilley, J.M.A. and R.A. Terry. 1963. A two-staged technique for the in vitro digestion of forage crops. J. Br. Grass. Soc. 18:104-111.

Troyer, N.A. 1960. The roosevelt elk on Afognak Island, Alaska. J. Wildl. Manage. 24:15-21.

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

Tukey, H.B. 1970. The leaching of substances from plants. Ann. Rev. Plant. Physiol. 21:305-324.

Ulyatt, M.J., D.W. Dallow, A.John, C.S.W. Reid, and G.C. Waghorn. 1986. The contribution of chewing, during eating and rumination, to the clearance of digesta from the rumino-reticulum. In Control of Digestion and metabolism in Ruminants. L.P. Milliagan, W.L. Grovum and A. Dobson, (eds.), Prentice Hall, Inglewood Cliffs, N.J. p.498-515.

Van Soest, P.J. 1982. Nutritional ecology of the ruminant. O and B books, Corvalis, Or. 374 pp.

Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan, their ecology and management. J. For. 63:523-529.

Van Glyswyk, N.O. 1970. The effect of supplementing a low-protein hay on the cellulolytic bacteria in the rumen of sheep and on the digestibility of cellulose and hemicellulose. J. Agric. Sci. Camb. 74:169-180.

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

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

Von Keyserlingk, M.G. and G.W. Mathison. 1989. Use of the *in situ* technique and passage rate constants in predicting voluntary and apparent digestibility of forages by steers. Can. J. Anim. Sci. 69:973-987.

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.

Ward, A.L., K. Diem, and R. W. Weeks. 1975. The impact of snow on elk. In Final Rep. Medicine Bow Ecol. Proj., ed. D. Knight, pp. 105-174. Laramie Univ. Wyoming. 380pp.

Ward, A.L. 1971. *In vitro* digestibility of elk winter forage in southern Wyoming. J. Wildl. Manage. 35:681-688.

Watkins, W.G., R.J. Hudson, and P.L.J. Fargey. 1991. Compensatory growth of wapiti (*Cervus elaphus*) on aspen parkland ranges. Can. J. Zool. 69:1682-1688.

Welch, D., B.W. Staines, D.C. Catt and D. Scott. 1990. Habitat usage by red deer (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer in a scottish sitka spruce plantation. J. Zool. Lond. 221:453-476.

Welch, J.G. 1982. Rumination, particle size and passage from the rumen. J. Anim. Sci. 54:885-893.

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

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity on northern ungulates. Oikos 40:337-384.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berl) 33:71-86.

Wickstrom, W.L., C.T. Robbins, T.A. Hanley, D.E. Spalinger, and S.M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48:1285-1301.

Wynne-Edwards, V.C. 1970. Feedback from food resources to population regulation. pp 413-427. In Animal populations in relation to their food resources. A. Watson (ed.) British Ecological Soc. Blackwell Scientific Publ. Oxford.

Yukon Fish and Wildlife Branch. 1992. An experiment designed to test wolf regulation of ungulates in the Aishihik Area, Southwest Yukon. Draft proposal. Oct 92. Unpubl. Rep. 67pp.

Appendix 1: Physical measurements of wapiti in the Yukon.

Reference[1]	Id.[2]	Sex	Age	Date (mm/yy)	Hind Food (mm)	Total length (mm)	Weight (kg)
1	.	M	≥ 3	10/76	630	1690	296
	.	M	≥ 2	10/76	625	1450	.
	.	F	≥ 3	10/76	610	1600	243
	.	F	≥ 3	10/76	620	1540	249
	.	F	≥ 3	10/76	590	1570	267
	.	F	≥ 3	10/76	590	1560	240
	.	F	≥ 3	10/76	630	1660	254
	.	F	0.5	10/76	550	1220	109
2	130	F	≥ 3	7/87	620	1465	213
	370	F	8	3/88	630	1560	218
	550	F	9	3/88	600	1510	.
	270	F	9	3/88	620	1580	210
	190	F	4	3/88	660	1570	210
	241	F	9	3/88	630	1630	263
	460	F	9	3/88	.	1580	236
	670	F	6	3/88	580	1530	220
	410	F	1.5	3/89	600	1460	160
	930	F	3.5	3/89	590	1550	213
	YY	F	4.5	3/89	610	1540	228
	570	M	≥ 3	7/87	650	1640	313
3	1055	F	0.5	12/89	540	1290	.
	1092	F	0.5	12/89	520	1190	.
	1105	F	0.5	12/89	540	1250	.
	.	F	0.5	1/90	.	.	.
	.	M	0.5	1/90	.	.	.

---

[1] Reference No. 1 = Hoefs 1980, 2 = this study, 3 = calf mortality study 1990

[2] Unique animal identification number or radio-collar frequency