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# Ecological and Morphophysiological Constraints on Foraging by Wapiti (*Cervus elaphus*)

by

Zhigang Jiang

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy

in

Wildlife Productivity and Management

Department of Animal Science

Edmonton, Alberta

Fall 1993

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**Re: Zhigang Jiang's PhD thesis**

Several chapters comprising Zhigang Jiang's PhD thesis have been published under joint authorship with me. For the record, I confirm that he is deservedly first author on these publications and rightful owner of the information from the standpoint of the thesis. My role has been one of general supervision. The creative aspects as well as the field and analytical work are overwhelmingly his.

Sincerely

R.J. Hudson
Professor
Wildlife Productivity & Management

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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 **Ecological and Morphophysiological Constraints on Foraging by Wapiti (*Cervus elaphus*)**, submitted by **Zhigang Jiang** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Wildlife Productivity and Management**.

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DATE: September 29, 1993

*To my parents and to my wife*

*for their support and sacrifice*

# ABSTRACT

The multiple constraint hypothesis posits that ecological and digestive constraints interact in hierarchical fashion with metabolic requirements to limit forage intake of wapiti in seasonal environments. To test this hypothesis, I first adapted a single-dose marker method to estimate intakes of forage by free-ranging wapiti facing the interaction of these three factors. I compared these results to seasonal intakes of penned wapiti fed hand-cut herbage (relieving the logistic constraint) or pelleted diets (relieving both logistic and digestive constraints) offered *ad libitum* . Two groups of animals were used in these studies: 12 yearlings from August 1989 to August 1990 and 12 adult hinds from September 1990 to September 1991.

To explore ecological constraints (logistics of foraging), I studied the timing of foraging bouts and habitat selection in relation to thermal environment, rumination requirement and food availability. I also studied the occurrence of different foraging postures in different habitats. In patches and at feeding stations, I studied factors which may shape giving-up decisions. Based on the relationships among bite depth, biomass and sward height, I modeled expected bite size and predicted changes of dietary protein and fiber as bite depth increased. To quantify the digestive capacity constraint, I studied seasonal diet-specific digestion rates, passage rates, and gut fills. To assess the seasonal metabolic requirement, I measured fasting heat production and determined seasonal maintenance and growth requirements by balance trials.

Low food consumption of wapiti in winter was determined primarily by low metabolic demand due to growth acquiescence and low activity; such dormancy can not be revoked by high quality food supplementation. The spring resurgence of the growth impetus and grazing costs elevated metabolic requirements However, free-ranging wapiti could not ingest enough food due to foraging logistics. When high quality green pasture forage became available as the growing season progressed, logistic constraints were relieved. The digestive system of wapiti can process 2-3 times more food in summer than in winter due to the higher digestion and passage rates. The intake of free-ranging wapiti apparently met their demand during this period. Foraging in heterogeneous pastures with mature swards in late summer was time-consuming and less profitable in terms of energy expenditure and gain. In the year of the study, foraging logistics on summer pasture prevented yearlings from ingesting enough food to meet their metabolic demand.

# ACKNOWLEDGMENTS

I am especially grateful to my supervisor, Dr. Robert J. Hudson, for his encouragement, guidance, assistance in my study and critical review of my thesis. Dr. Hudson stimulated my study interests in the field of Wildlife Management and Productivity. I also thank the members of my supervisory committee: Dr. Willem Saur and Dr. Jan Murie, for advise and critical reviews of the dissertation.

I thank Dr. Anne Naeth and Dr. Iain Gordon for serving as my oral examination committee members and for their useful comments on the dissertation. Dr. John Feddes chaired my dissertation defense.

I acknowledge financial support from the Natural Science and Engineering Research Council of Canada, Alberta Agriculture Research Council (Farming for the Future), and Canadian Circumpolar Institute.

Special thanks to Mr. Chris Olsen, manager of the Ministik Wildlife Research Station, and Mr. Shaun Kallal for their help during the field phase of the study. Thanks also are extended to fellow students who worked at the Ministik Wildlife Research Station: Ray Nixdorf, Ray Case, Norm Cool, Saphida Wairimu and John Wilmshurst. I also appreciate help from other fellow students and friends inside and outside the Department of Animal Science.

I would also like to thank Mr. Terry Fenton, supervisor of the central laboratory in this department, for his advice and assistance during the period of sample analysis . I also thank Ms Pat Marceau for her assistance in the laboratory.

Finally, I sincerely thank my wife, Hongxia Fang, for her understanding and support during my study. I also thank my parents and my family for their moral support.

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# CHAPTER I GENERAL INTRODUCTION

Wapiti (North American subspecies of *Cervus elaphus*) once occurred from New York State to Vancouver Island and from New Mexico to northern Alberta (Flook, 1970). Although severely depleted by commercial hunting and agricultural settlement, the wapiti is returning to the prairies and parklands of western Canada in its new role as an agricultural animal. Wapiti farming in western Canada generally follows the New Zealand model, except that the short grazing season requires heavy winter supplementation (Friedel, 1993). Native pasture comprises the major food source of wapiti from mid April to November.

Deer farming and ranching is part of a world-wide trend towards rational use of wildlife (Hudson *et al.*, 1989; Renecker and Hudson, 1991). Besides tapping specialty markets, commercial deer farming has been promoted as a new opportunity for sustainable animal production. Owing to the current lack of information on wapiti, farmers, veterinarians and extension agents must refer to research on red deer (*Cervus elaphus*), which is about half the size of wapiti, conducted under quite different conditions in Britain and New Zealand. Thus, we need studies on seasonal energetics and performance of wapiti in western Canada (Haigh and Hudson, 1993).

## The Seasonal Energetic Cycle

Northern wild ruminants, particularly *Cervidae*, show strong seasonal cycles of growth, appetite and energy metabolism (Bandy *et al.*, 1970; Hudson and White, 1985; Hudson *et al.*, 1985; Pauls *et al.*, 1981). These cycles are entrained by photoperiod and associated with seasonal endocrine profiles (Shi and Barrell, 1992 ), and they are expressed even in stable nutritional environments (Kay, 1979; Adam *et al.*, 1986). Wapiti share this seasonal rhythm of appetite and growth, which matches the availability of seasonal food resources (Pauls *et al.*, 1981).

The underlying mechanism is not clear. Most of the early research assumed that energy expenditure was the driving force and that metabolic cycles represented a form of winter dormancy which reduced requirements during the lean winter period. However, what is unusual about seasonal metabolic rates is the exceptionally high summer values rather than low winter values which are close to the interspecific mean (Hudson and Christopherson, 1985).

## The Multiple-Constraint Hypothesis

Whether to understand the role of wapiti in ecosystems or to tap the species' potential as an agricultural animal, an important step in modeling energy budgets is understanding foraging constraints. Hudson and White (1985) proposed a multiple-constraint hypothesis of forage intake by wapiti. Presumably, wapiti eat to satisfy their nutrient requirements. However, ecological factors such as timing and duration of foraging bouts, selection of habitat and bite size, as well as morphophysiological factors such as rate of passage, rate of digestion and gut fill may prevent wapiti from achieving their metabolic objective. Based on the hypothesis, Hudson and White (1985) simulated dry matter intake as the minimum of intakes calculated on the basis of the metabolic requirement (the animal's objective) and two constraints: the ecology of foraging and digestive capacity. I designed a study to test the multiple constraint hypothesis under field conditions, exploring the interactions of foraging ecological (foraging logistics), digestive and metabolic factors (Fig. I.1).

### Foraging ecology and environmental hierarchy

Foraging in patchy environments is a classic problem of optimal foraging (Charnov, 1976; Pyke, 1984). Foraging presumably is guided by the trade-off of gains and costs. Wapiti face three basic problems: "where to eat?", "what to eat?" and "when to eat?". The frequency of decision-making by herbivores depends on the level in the environmental hierarchy, ranging from 10 per year at the landscape region level to $10^7$ per year at the subunit within community level (Senft *et al.*, 1987).

Environmental heterogeneity is both temporal and spatial. The temporal hierarchy involves the seasonal and diurnal thermal environment, which affects foraging costs by thermal regulation. Other random factors such as storms or predators interrupt normal behavior. The spatial hierarchy considered in this study encompassed habitats, patches, feeding stations and swards. Wapiti can increase food intake rate or diet quality by selecting a habitat of high food availability or quality. Within habitats, food is distributed in patches. In a patch with limited food resources, the trade-off of foraging effort decreases as the food resource is depleted. Optimal departure from a feeding station will save locomotive and searching costs. The sward is the smallest hierarchical unit considered in this study. The vertical quality profiles of swards may influence the diet selection.

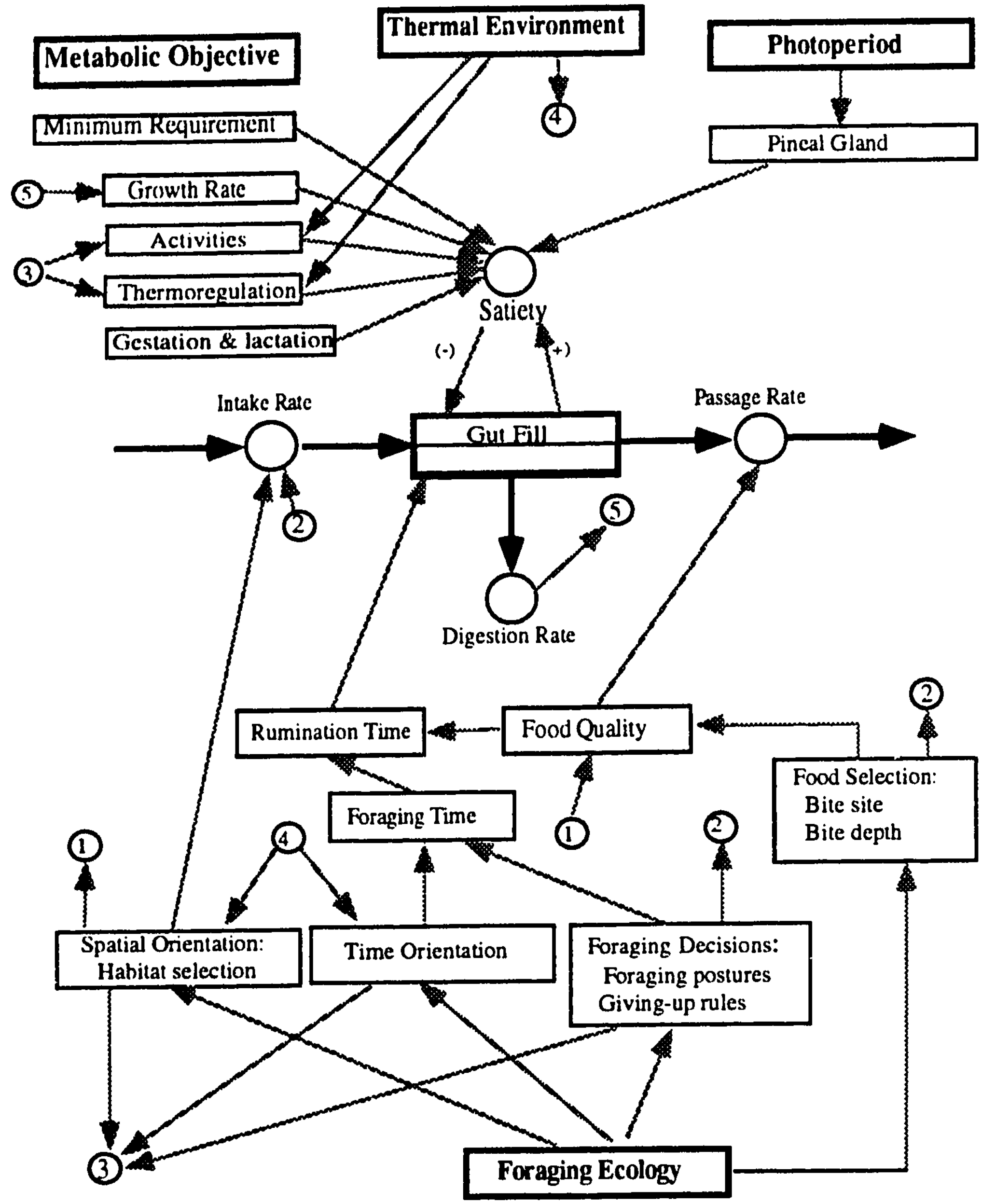

**Fig. I.1** Multiple constraints on foraging by wapiti showing the hierarchical structure of metabolic objective and ecological, digestive constraints. Solid arrows indicate food flow. Gray arrows represent the interactions. Circled numbers denote links between arrows.

### Digestive capacity

Digestive capacity is determined by gut fill, the amount of digesta dry matter in the alimentary tract. Gut fill is the outcome of competing rates of intake, digestion and passage. Gut fill is increased by either increasing intake or decreasing digestion and passage rates. Seasonal forages and digestive physiology of animal interact on the digestibility and retention time of forage. Presumably, gut fill constrains food intake, especially when wapiti feed on coarse forage.

Holleman and White (1989) developed a technique to calculate digesta passage rate and gut fill with a single dose of non-absorbable digestive marker. They found close agreement of calculated and measured digesta fill in domestic sheep. They pointed out that digestive markers have not been used to their analytical potential, particularly in nondomestic species.

### Metabolic objective

Recent studies on seasonal fasting metabolic rate, a measure of minimum metabolism, measured in white-tailed deer and reindeer question whether fasting metabolic rates (hence energy requirements) change from winter to summer (Tyler and Blix, 1990; Pekins *et al.*, 1992).

Maintenance requirements refer to the amount of energy needed for each animal to maintain body weight or, more precisely, energy equilibrium. For free-ranging animals, the maintenance requirement is called ecological maintenance (Moen, 1985). Depending on age, sex and ambient temperature, wapiti need additional energy for growth, gestation, lactation and thermoregulation. When logistic and digestive factors do not constrain intake, the metabolic requirement may ultimately regulate intake, presumably by adjusting the satiety set-point. As a consequence of natural selection, the metabolic requirement has been modulated in relation to the availability of food resources. Environment cues such as photoperiod may synchronize those cycles.

## Dissertation Organization and Objectives

The dissertation is presented in research paper format. The organizing question involves interactions of ecological and digestive constraints and metabolic objective on foraging by wapiti in seasonal environments. For the foraging ecology constraint and environmental hierarchy, I was interested in how wapiti adjust their foraging behavior in response to photoperiod and seasonal habitats, how they respond to diurnal thermal environment by timing their foraging bouts, and by what rules they depart from patches at different levels, and how do wapiti adjust their bite depth to seasonal swards. For the digestive constraint, I explored whether the digestive kinetics of wapiti were affected by seasonal diet and in which season food intake was limited by gut fill. For the metabolic objective, the question was whether energy requirements for maintenance and body weight gain change among seasons.

The specific objectives in relation to these three interacting factors were:

1) For the foraging ecology constraint:
    - to study proximate factors guiding orientation in time and space.
    - to study the foraging strategy in seasonal habitats.
    - to determine the rules wapiti used to terminate foraging in patches and feeding stations.
    - to simulate how bite depth in seasonal swards affects dietary quality and bite size.
2) For the digestive constraint:
    - to determine food consumption of wapiti on a standard ration and native forages.
    - to determine digestibilities and passage rates of seasonal forages.
    - to calculate digestion rates and gut fills.
3) For the metabolic objective:
    - to determine seasonal 48 h fasting metabolic rates.
    - to determine seasonal maintenance requirements of pen-fed and free-ranging wapiti.
    - to assess metabolizable energy requirements for gain.

My final chapter summarizes the results of 1), 2) and 3) and analyzes the foraging ecological and digestive constraints on the foraging of wapiti in the seasonal environment.

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# CHAPTER II STUDY AREA, ANIMALS AND FACILITIES

This research was conducted at the Ministik Wildlife Research Station in central Alberta, Canada (53° 18'N, 114° 35' W). The station is situated in the Cooking Lake moraine within the southern fringe of the boreal mixed-wood forest (Rowe, 1972). The landscape is dead-ice moraine characterized by gently sloping hills with scattered lakes and ponds. Gates (1980), Nietfeld (1983) and Renecker (1987) have given detailed environmental and vegetation information about the area.

## Geology and Soil

The Cooking lake moraine is underlain by Upper Cretaceous shales, shale-sandstone and sandstones (Bayrock and Hughes, 1962). Surface till deposited by the most recent glacial advance of the Pleistocene has formed an undulating complex of hills and closed depressions. There are numerous seasonal and permanent water bodies. The wetlands form incomplete drainage systems throughout the area.

The Ministik Lake area is located on Luvisolic soils derived from calcareous, fine-grained till (Bowser *et al.*, 1962; Crown, 1977). The forest soils of the Cooking Lake area are classified as Orthic Gray Luvisols, whereas the poorly drained mineral soils are classed as Humic Luvic Gleysols. Organic soils are often found in depressions.

## Climate

The study area has a cool, continental climate. Winters are typically cold and dry with ambient temperature ranging from -49 °C to 10 °C (Olsen, 1985). Summers are usually warm with ambient temperature occasionally reaching 32°C. The frost-free period is about 100 days. Usually, permanent snow cover is established in late November. By late March, most of the grassland is snow free. Annual precipitation is about 500 mm, of which about a quarter is snow. Rain mainly falls in May, June and July.

## Vegetation and Phenology

The major vegetation types are poplar forests, brome-bluegrass grasslands, sedge wetlands and willow margins. Poplar forest is the dominant vegetation. Trembling aspen (*Populus tremuloides*) dominates the drier area whereas balsam poplar (*P. balsamifera*) occupies the mesic sites. Willow (*Salix* spp.) forms a band around the water bodies. Sedge (*Carex atheroides*) and reedgrass (*Calamagrostis canadensis*) are the main understory species. Sedge meadows occurred in wetlands with sedge as principal species. Upland grasslands are dominated by bluegrass (*Poa pratensis*) and brome (*Bromus pumpellianus*). Forbs include clover (*Trifolium* spp.), dandelion (*Taraxacum officinale*), thistle (*Cirsium arvense* ), yarrow (*Achillea millefolium* ), asters (*Aster* spp.) and strawberry (*Fragaria virginiana* spp. *glauca* ). Lowland grasslands are dominated by wheatgrass (*Agropyron cristatum*), bluegrass, brome and reedgrass.

Grasses flush in mid-April. Green graminoid leaves dominate the sward canopy in mid-May. Inflorescences appear in late May and seeds ripen in August. The dominant dicotyledonous plant (dicot), dandelion, emerges in early May, becomes the most visible dicot in early June and persists to autumn. Following dandelion, clovers reach their peak biomass in July, and survive until the end of the frost-free period. Grasses wither in October and leaves of aspen, poplar and birch shed in late October.

## Study Animals

From August 1989 to August 1990, 12 female adult wapiti were used in the study. All wapiti hinds conceived in the fall of 1989 and delivered calves between May and July, 1990. Twelve female calves were used from September, 1990 to September, 1991. In both years, the wapiti were assigned two treatments (pen-fed and free-ranging) of six animals each and were used in pen and pasture energy balance trials, but in late June, 1990, the two groups of lactating hinds merged as one group and free-ranged on pasture. The pen-fed group ate alfalfa-barley pellets throughout the experiment; the free-ranging group in winter had supplementary hay when they were not on harvested pasture herbage trials. Six free-ranging adults were supplemented with brome hay in the winter of 1989 and six free-ranging yearlings were supplemented with alfalfa hay in the winter of 1990. The free-ranging group grazed natural forage from late March till October. For the behavior study in Chapter IV, I observed the free-ranging group; however, my observations were extended to eight 1991 calves (two males and six females), two 1990 males and six female adults. Half of the 1988 cohort and two of the 1990 cohort were hand-reared so they were tame, allowing close observation.

## Facilities

The Ministik Wildlife Research Station is approximately 265 ha in area enclosed by a two m high game fence. Internal fencing divides the area into small enclosures. A central facility consisted of a weighing room, holding pens, isolation pens and alleyways. A main trailer hosts the office and laboratory, two trailers provide shelters for researchers. During 1991, 6 individual pens and 6 metabolic chambers were built. There is a meteorological station at the research station.

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# Part I

# Foraging dynamics

# CHAPTER III DIEL FORAGING BOUTS AND HABITAT SELECTION

For wild ruminants, deciding when and where to forage are important aspects of adapting to natural environments, because to obtain energy with less energy expenditure increases the chance of survival. Foraging orientation may take place at different spatial and temporal scales. For example, some cervids move between widely separated summer and winter ranges (Morgantini and Hudson, 1988; Brown, 1992). Others have more local seasonal movements (Bowyer, 1981; Mann and Putman, 1989; Gillingham and Klein, 1992).

Diel activity patterns may reflect an underlying rumen repletion-depletion cycle (Gates and Hudson, 1981; Renecker and Hudson, 1992). Presumably, distention of the rumen signals satiety and coarse food particles stimulate rumination. However, thermal and social environments modulate the timing and duration of feeding and rumination (Gates and Hudson, 1983; Renecker and Hudson, 1990; Gillingham and Klein, 1992).

This chapter explores the seasonal influences of food quality and availability as well as ambient temperatures on the timing and duration of foraging bouts. I tested the following hypotheses: H1: Durations of rumination bouts are determined by forage quality and intake. H2: Durations of foraging bouts depend on feeding rate. H3: Ambient temperature affects the timing of foraging bouts. H4: Habitat selection is guided by thermal environment and foraging opportunity.

Time and space orientations of birds and small mammals can be studied in the laboratory (Falk and Krebs, 1992). It is more difficult to manipulate the environment of large ungulates. To study the activity pattern and habitat selection of a large herbivore like wapiti, I employed direct observation. Special attention was directed to underlying interactions among foraging duration itself, rumination and foraging, thermal environment and foraging with time series techniques.

## Materials and Methods

I observed six two-year-old free-ranging female wapiti in 1990. During winter (January, February and March), they were offered alfalfa hay but they depended solely on range forage for the rest of the year.

During the trial, a vibracorder (Kienzle Apparate G. M. b. h., Villingen, Schwarzwald, Germany), a currently accepted device for recording activity of grazing animals (Mosley *et al.*, 1987), was suspended from a loosely fitted neck collar. The vibracorder obtained data form January 24-30 (winter), May 8-25 (spring) and July 20-24 (summer). Four dawn to dusk scans were conducted on January 6, April 4, May 16 and August 18. An active/inactive time series was summarized for 30 min intervals. Since most of the active time involved feeding and most bedding time was devoted to rumination, I considered active/inactive bouts as synonyms of foraging/ruminating bouts (see below). I also organized time series of the durations of feeding and rumination bouts.

To determine the proportion of active time feeding and proportion of bedding time spent ruminating, I conducted dawn to dusk behavior scans using a scan interval of 10 minutes. Grazing time was calculated as the product of active time (vibracorder) multiplied by the proportion of the observed active time spent feeding. Rumination time was calculated similarly from the observed resting time and the proportion of resting time spent ruminating. Behavioral synchronization was expressed with the following index (SI):

$$SI(t) = \frac{\underset{i=1,n}{\text{Max}}\ (\text{Occurrence of behavior i at t})}{m} \qquad [III.1]$$

where, n is the number of behavior occurrences at time t, m is the number of animals observed. SI equals 1 indicates all animals engaged in the same activity whereas SI equals 1/m indicates each animal engaged in a different activity.

I recorded habitat selection and behavior of focal wapiti with a pocket computer (TRS-80 PC, Tandy, TX, USA) programmed for field ethological studies (Jiang and Hudson, 1993). Habitats were categorized as forests, upland grasslands, lowland grasslands, willow margin lands, sedge wetlands and winter supplementary feeding site. Rumination was recorded as chews or seconds per bolus. After recording about 20 bolii from a wapiti, I moved to another animal, until all wapiti had been studied. Using results for dry matter (DM) intake from Chapter XI, I calculated mean intake rate (MIR, g/min). Following grazing wapiti, I clipped the pasture forages to simulate the diet of wapiti and determined the neutral detergent fiber (NDF, A.O.A.C., 1984) of the clipped forage samples. Rumination times were expressed as min/kg DM or min/kg cell wall (CW, considered equivalent to NDF).

To check the periodicity of seasonal foraging bouts, I calculated time-series auto-correlations. I also calculated cross-correlations of ambient temperature and foraging time series, as well as of rumination and foraging time series (SYSTAT, 1992). ANOVA of the number and duration of foraging or rumination bouts, of chews or seconds per bolus were conducted with SuperANOVA (Abacus Concepts, 1989). The Tukey-Kramer method (Sokal and Rohlf, 1981) compared differences among seasonal means.

## Results

### Seasonal activity budgets

Although I used a single vibracorder, wapiti synchronized their activities so focal animals generally reflected group activity (Table III.1). Wapiti devoted most of their time to feeding and rumination. Grazing time was the longest in April. Compared with April, grazing time decreased in late May. Wapiti grazed longer in July, than in late May (Fig. III.1). Rumination time declined from January to May before increasing again in July. In April and July, little time was available for activities other than feeding and resting.

Rumination times were related to seasonal forage fiber content and intake (Table III.1). Wapiti masticated each bolus more times ($p < 0.05$) and longer ($p < 0.05$) when fed winter forages (January -April) than green forages (May). Wapiti ruminated less on spring pasture in early April than they did in January and least in late May among all study seasons. As the summer progressed, both ruminating time per kg DM and chews per bolus increased ($p < 0.05$).

According to cross-correlation, the duration of foraging bouts was related to season ($p < 0.05$) but not ambient temperature ($p > 0.05$). MIR declined to its lowest value in April, then increased significantly in May and declined significantly again in July. The number of feeding bouts increased from winter to early spring when wapiti started grazing on pasture. When intake rate peaked in May, foraging pattern was characterized by shorter bouts.

### Active and resting bouts

Activity patterns changed among seasons (Fig. III.2). Active bouts were most regular in early and late spring. Night feeding bouts were short in winter whereas feeding bouts were commonly absent at midday in summer. In late spring, the foraging pattern was typically polyphasic.

Autocorrelation analyses indicated weak 24 h periodicity in January and March. In March there was two and six h periodicity within 24 h. In April, there was revealed one h periodicity within 24 h cycle. In May, 24 h periodicity was weak but there was significant two h cycles. In July, besides the significant 24 h periodicity, there were also 12 h and two h periodicities.

Only in early and mid-summer were feeding and rumination cross-correlated. In May, durations of the last grazing bout had a significant influence on the duration of subsequent rumination ($p < 0.05$). In July, the duration of the last grazing bout influenced the duration of the subsequent rumination bout ($p < 0.05$).

**III.1** Rumination and feeding parameters of wapiti in relation to season and forage quality.

| | **January** | **April** | **May** | **July** |
|---|---|---|---|---|
| **Synchronization index** | 0.87 ± 0.02 (54)$^{a*}$ | 0.98 ± 0.06(69)$^{ab}$ | 0.86 ± 0.02 (72)$^{a}$ | 0.96 ± 0.02 (94)$^{b}$ |
| **Forage** | | | | |
| DM (%) | 88 ± 1 (2)$^{a}$ | 29 ± 1 (2)$^{b}$ | 23 ± 1 (2)$^{c}$ | 32 ± 1 (2)$^{b}$ |
| Cell wall (%) | 68 ± 1 (2)$^{a}$ | 70 ± 2 (2)$^{b}$ | 36 ± 1 (2)$^{c}$ | 48 ± 1 (2)$^{d}$ |
| **Rumination** | | | | |
| Min/bout | 153 ± 15 (39)$^{a}$ | 85 ± 8 (49)$^{ab}$ | 82 ± 5 (55)$^{b}$ | 129 ± 9 (28)$^{a}$ |
| Bouts/d | 5.6 ± 0.4 (7)$^{a}$ | 7.0 ± 0.5 (7)$^{a}$ | 9.2 ± 0.4 (6)$^{b}$ | 5.6 ± 0.4 (5)$^{a}$ |
| Min/kg DM | 219 ± 1 (7)$^{a}$ | 220 ± 1 (7)$^{a}$ | 66 ± 1 (6)$^{b}$ | 96 ± 1 (5)$^{c}$ |
| Min/kg CW | 322 ± 1 (7)$^{a}$ | 314 ± 1 (7)$^{a}$ | 183 ± 1 (6)$^{b}$ | 199 ± 1 (5)$^{c}$ |
| Chews/bolus | 59 ± 2 (40)$^{a}$ | 51 ± 2 (40)$^{bc}$ | 35 ± 3 (40)$^{bd}$ | 48 ± 2 (40)$^{b}$ |
| Sec/bolus | 60 ± 2 (40)$^{a}$ | 52 ± 2 (40)$^{bc}$ | 42 ± 3 (40)$^{bd}$ | 56 ± 3 (40)$^{ac}$ |
| **Feeding** | | | | |
| Mean intake rate (g/min) | 5.5 ± 0.2 (7)$^{a}$ | 2.9 ± 0.3 (7)$^{b}$ | 12.4 ± 0.4 (6)$^{c}$ | 9.8 ± 0.4 (5)$^{d}$ |
| Cell wall intake (kg/d) | 2.1± 0.1 (7)$^{a}$ | 1.7± 0.1 (7)$^{a}$ | 2.6 + 0.1 (6)$^{b}$ | 3.6 + 0.1 (5)$^{c}$ |
| Min/bout | 115 ± 10 (39)$^{a}$ | 118 ± 9 (49)$^{a}$ | 70 ± 2 (55)$^{b}$ | 149 ± 10 (24)$^{a}$ |
| Bouts/d | 5.6 ± 0.3 (7)$^{a}$ | 7.3 ± 0.6(7)$^{b}$ | 9.2 ± 0.5(6)$^{d}$ | 4.8 ± 0.2 (5)$^{a}$ |

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* Data presented as mean ± standard error (sample size). No significant differences between the data that have the same superscripts in the same row ($p > 0.05$).

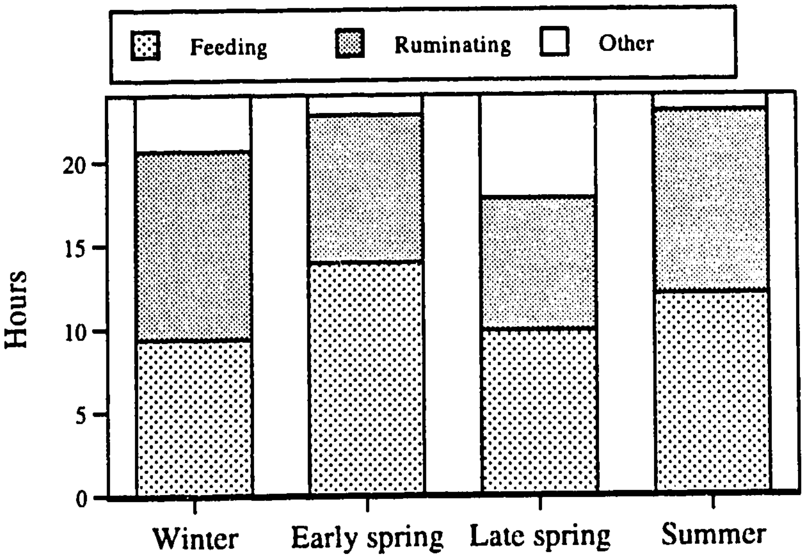

**Fig. III.1** Time budgets of wapiti in winter, early spring, late spring and summer. "Other" includes inactive and active time not related to either rumination or feeding.

### Mean intake rate

Mean intake rate (MIR) was maintained near five g/min in winter but declined to about three g/min in April. MIR significantly increased in May ($p < 0.05$) and declined again in July ($p < 0.05$, Table III.1). Besides feeding time, number of feeding bouts per day increased from winter to early spring ($p < 0.05$) when wapiti started grazing on pasture. When intake rate peaked in May, foraging bouts were further slipped into shorter bouts ($p < 0.05$) and durations of foraging bouts further decreased ($p < 0.05$, Table III.1). Thus, in spring, duration of a foraging bout may be determined by intake rate.

### Thermal environment and foraging

Ambient temperature had more profound impacts on the timing of foraging in summer than in winter. In January, foraging activities of supplementary-fed wapiti were not correlated with ambient temperature ($p > 0.05$). In April, grazing was significantly correlated to the ambient temperature that lagged two-three h ($p < 0.05$), but ambient temperature in May had no effect on grazing ($p > 0.05$). In late July, grazing was significantly correlated with the ambient temperature that lagged about two h ($p < 0.05$).

Wapiti #8806 initially suspended foraging in chronic cold but subsequently compensated for lost foraging time. From January 23 to 31, ambient temperature decreased from -5°C to about -35°C. In response, daily feeding time first decreased consecutively for three days as the temperature dropped, then increased as the cold persisted in the fourth and fifth day, and declined again in the sixth day before finally increasing on the seventh day (Fig. III.3).

The greater contrast between day/night temperature in summer elicited a different response. In late July, when temperature increased above 24°C in late afternoon, wapiti #8811 postponed evening bout for 2 h (Fig. III.4), thus reducing the proportional feeding time from 51% (July 22) and 58% (July 23) to 43% (July 23). The reduced foraging time was compensated in the evening so daily feeding time increased to 51% on July 24.

### Habitat selection

During cold winter days in January, wapiti restricted most of their activities to the supplementary feeding site (Fig. III.5). Most of the time, they bedded and ruminated with their hair coats raised, standing only briefly to feed or ingest snow. However, wapiti made short trips to crater for forage in the upland grasslands even at average daytime temperatures of -29°C, although they took little forage but ingested snow during these bouts.

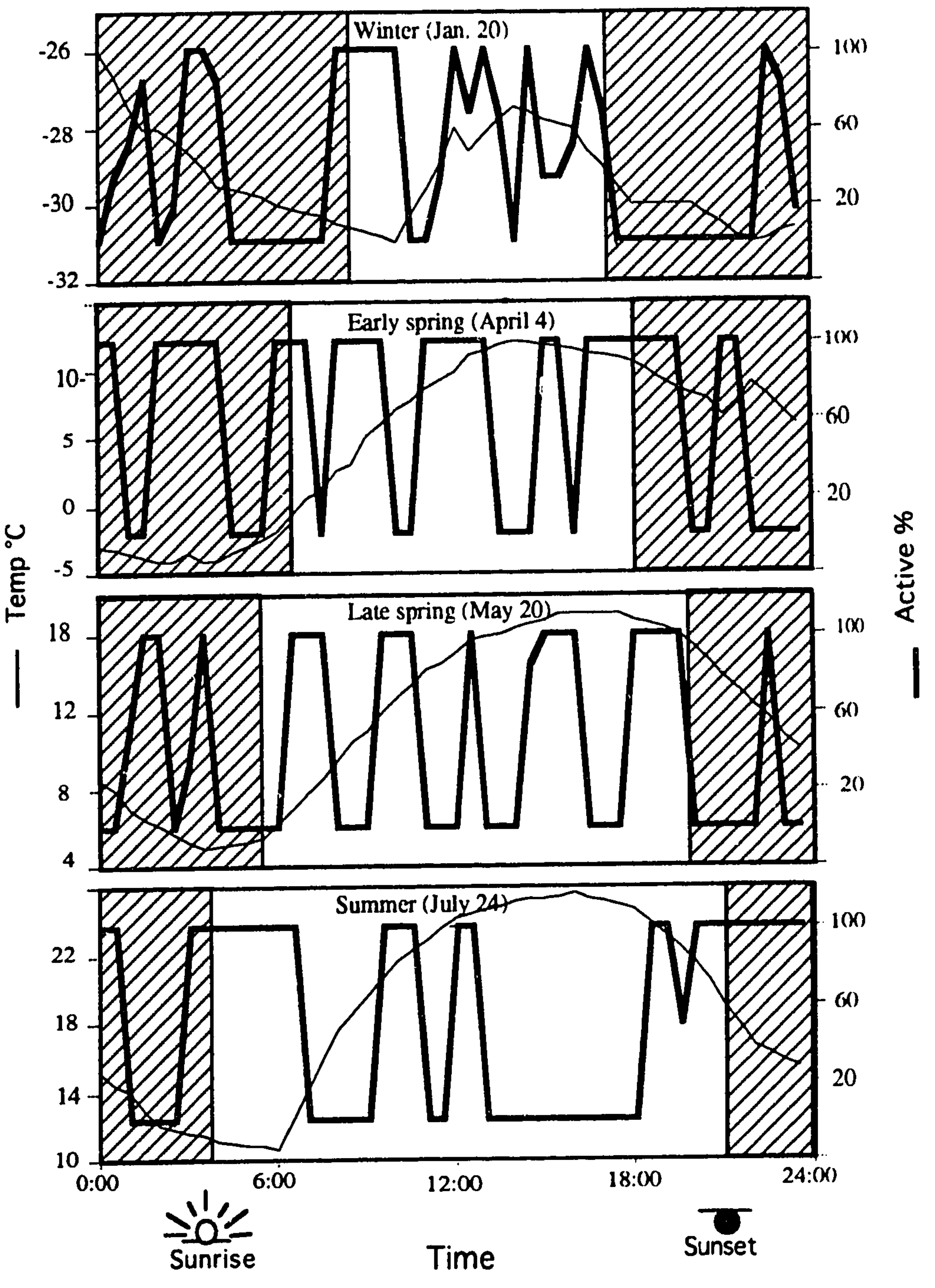

**Fig III.2** Representative activity patterns based on viberacorder in winter, early spring, late spring and summer. Crosshatched areas indicate night times.

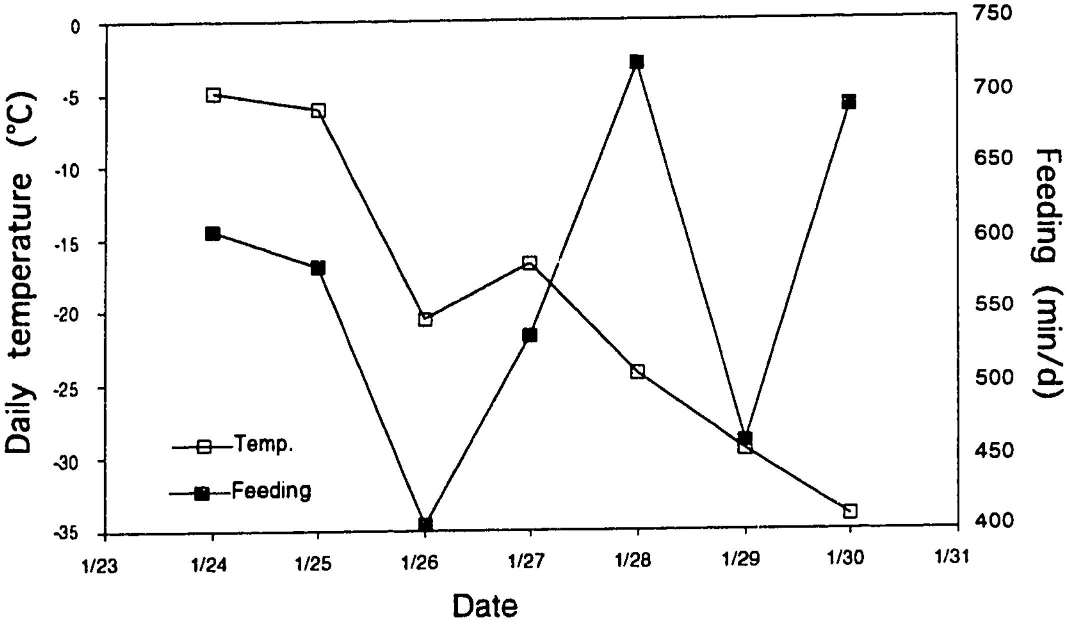

**Fig. III.3** Daily feeding time of wapiti #8806 during a chronic cold period

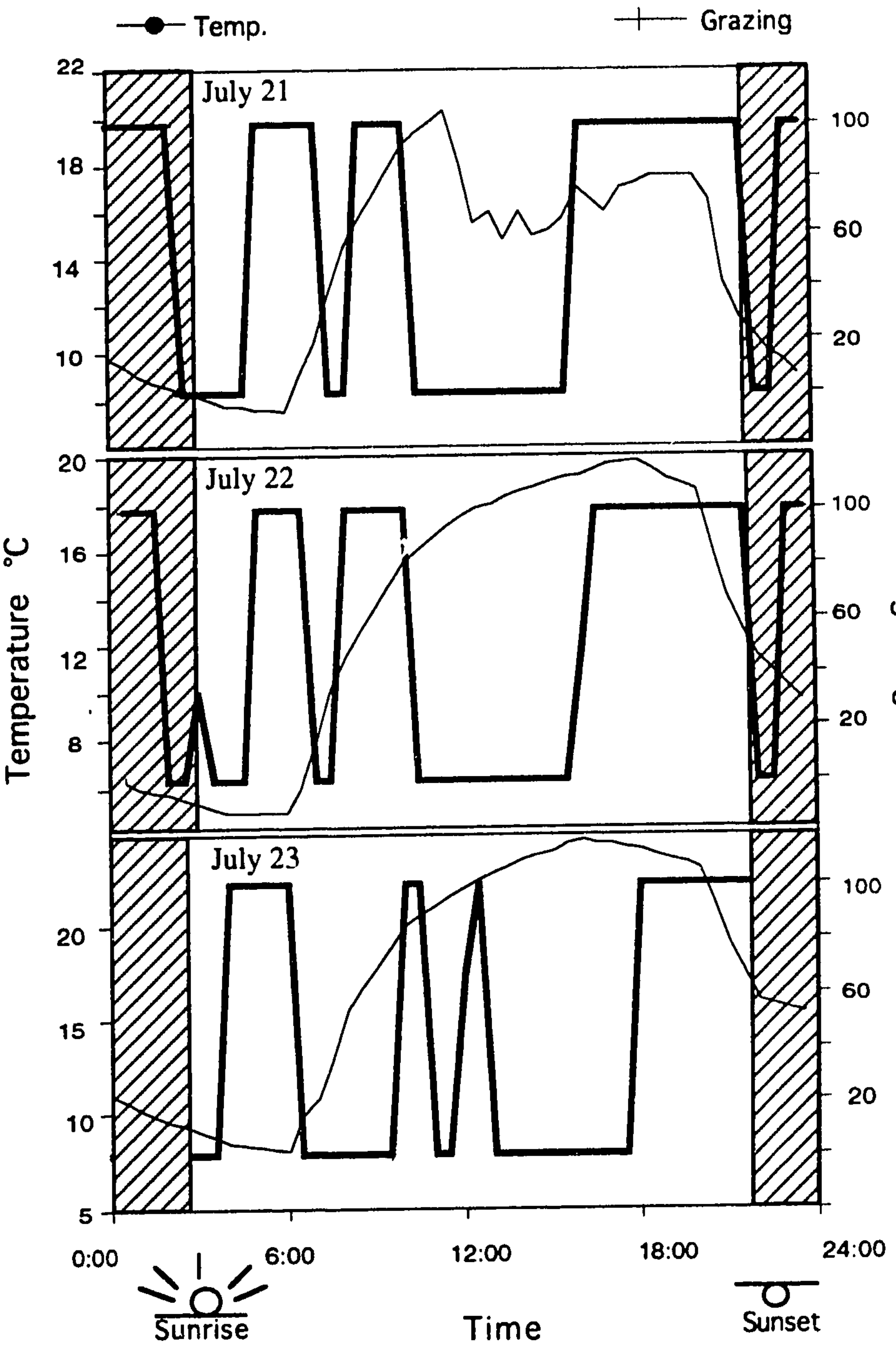

Fig. III.4 In late July, wapiti #8811 postponed late afternoon bouts to avoid heat. Crosshatched areas indicate night times.

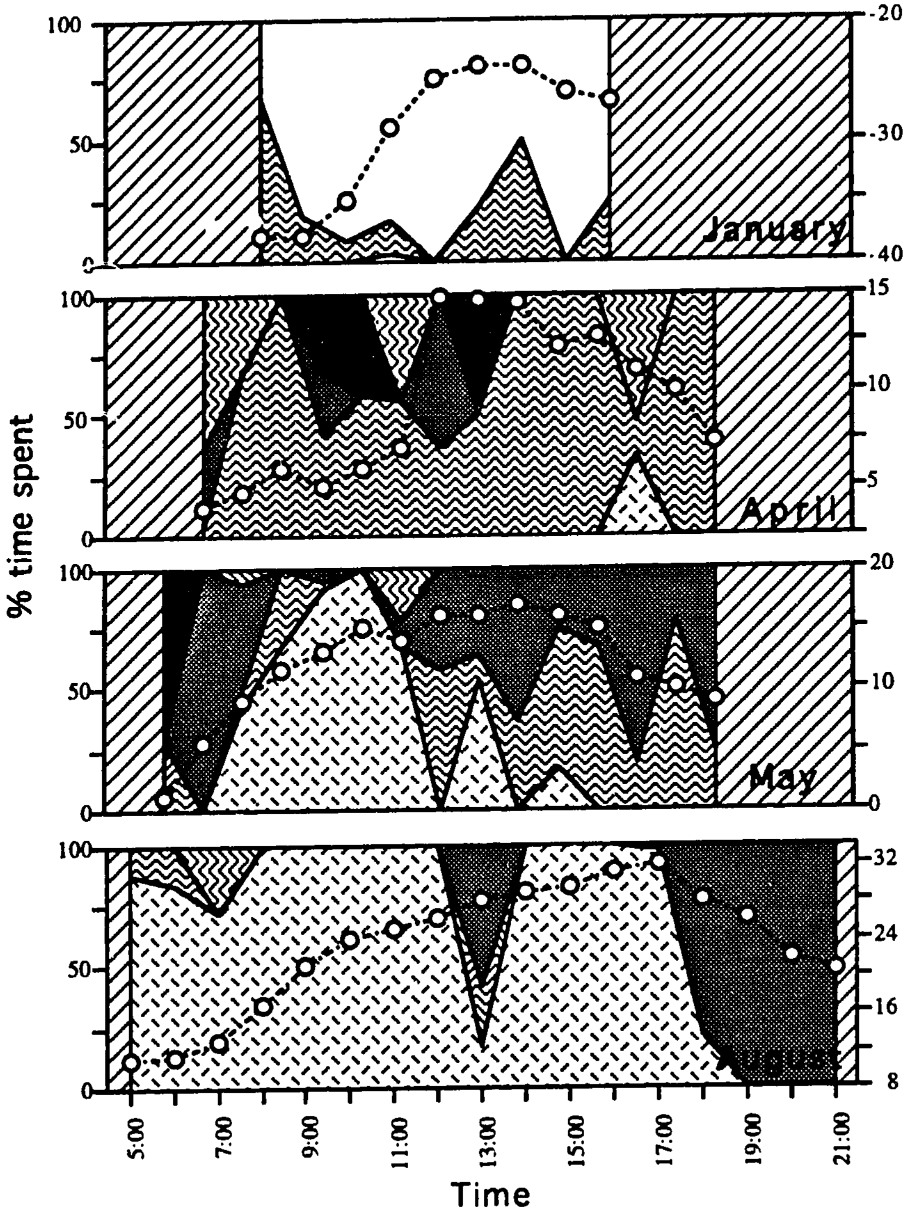

**Fig III.5** Habitat selection of wapiti during dawn to dusk scans in January, April, May and August. Crosshatched areas indicate night times.

-○- Temp °C ▨ Forest ▨ Upland ■ Lowland

▨ Willow ■ Wetland ☐ Feeding site

In April, wapiti browsed willow margins around water bodies in early morning and evening, grazed sedge wetlands in morning and evening and ate tall grass culms and seed heads in lowlands during the day, and bedded/ruminated on the sunny south slopes. In May, wapiti grazed sedge wetlands and lowlands in early morning. Then they rested and ruminated in forests. In late afternoon, wapiti grazed lowland and upland grasslands. In July, wapiti sought shade. They grazed forest floors and upland grasslands in the morning, then rested and ruminated in forests. When insect annoyance increased in forests in late afternoon and dawn, wapiti moved out of forests and grazed lowland grasslands.

## Discussion

Circadian activity patterns of most animals result from interactions between endogenous and environmental influences (Gates and Hudson, 1983). Among ruminants, the underlying diel cycle is polyphasic reflecting the rumen repletion-depletion cycle. However, food quality and availability, and ambient temperature modulate daily foraging cycles.

### Ruminating time constraint

Rumination is an important nutritional adaptation of ruminants (Foose, 1982). But it introduces a constraint on food intake because rumen contents must be mechanically broken down before particles can pass through the meshwork in the omasum (Faichney, 1984). Thus time spent ruminating is affected by food quality and the amount of ingesta.

Rumination time is related to dietary fiber. Scaled on a unit dry weight basis, wapiti spent more time ruminating in winter and early spring, and the least time in late spring. Green forage was less lignified; thus wapiti masticated green forage less than winter forage (min/kg CWI). In moose, chews per bolus increased with maturation of browse species (Renecker, 1987), but moose masticated each bolus longer than wapiti.

### Foraging time constraints

Intake rate is influenced by forage availability (Wickstrom *et al.*, 1984; Nietfeld and Hudson, 1985) and hence the rate of ruminal repletion. Mean intake rates are similar to those from other studies at the Ministik Wildlife Research Station (Wairimu and Hudson, 1993; Nietfeld, 1983). Higher intake rates and shorter feeding bout in May compared with the lower intake rate and longer foraging bouts in April indicated intake rate is the major factor influencing duration of foraging bout.

Gates and Hudson (1983) found that free-ranging wapiti spent considerably more time (52-54%) feeding than wapiti offered supplemental food (39%) in winter. However, free-ranging wapiti spent 38% of their daily time ruminating whereas supplementary fed wapiti spent 47%. Longer foraging time may be due to the lower intake rate and the difference of rumination times may be due to the difference in intakes.

### Diel cycles

In each season, there was evidence of 24 h activity periodicity, although only in April and July, was the periodicity significant. Within a day, there were several feeding cycles that may reflect the rumen repletion-depletion cycle. The 12 h periodicity in July implied that wapiti shifted foraging to crepuscular periods (morning/evening) during hot days.

### Thermal environment

The lower critical temperature of wapiti in winter coat is -20°C (Parker and Robbins, 1983). Wapiti had a smaller activity range and only stood up during feeding when temperature dropped below the critical temperature. Reducing feeding shortened the time standing and thus reduced energy expenditure (Gates and Hudson, 1979). In winter, wapiti coincided their feeding activity with the high ambient temperature during the daytime and adjusted body surface exposed to sunshine in winter. However, the correlation between ambient temperature and activity was not significant in winter. The reasons may be (1) there is no clear diurnal pattern of ambient temperature during a chronic cold period, (2) wapiti may lie down and eat when possible (Jiang and Hudson, 1993), and, (3) ambient temperatures in winter normally remain in the thermal neutral zone of wapiti. Foraging was positively correlated to daily temperature in warm days during spring. Presumably the ambient temperatures in spring were within the thermal neutral zone.

In summer, high heat loads depressed grazing. Parker and Robbins (1983) reported that wapiti in summer coat had an upper critical temperature of 26.5°C. High temperature induced panting. Wapiti took a long rest in the cool forest and shifted their feedings to the evenings. Thus, daily feeding time may be depressed by hot weather. In summer, high ambient temperature affected the timing of foraging. Once a foraging bout began, foraging was positively correlated to high ambient temperature.

### Habitat selection

Habitat selection is guided by thermal environment and forage availability. Free-ranging wapiti mostly browsed in forests and cratered on upland meadows in winter (Gates and Hudson, 1981). In April, free-ranging wapiti grazed in sedge wetland in early morning where intake rate was high and green sedge shoots of high protein were available (Nietfeld, 1983). When biomass of green grasses increased in late spring, wapiti shifted grazing from sedge wetlands and willow margins to southern slope of upland grassland then to upland grassland. In summer, wapiti grazed the forest floor in the morning and open grassland in the evening, and they ruminated and rested in shade. Gates and Hudson (1981) found that shade-seeking behavior of wapiti was directly related to insulation in fall but inversely related to insulation in winter. Renecker and Hudson (1990) found that although generally moose were inactive when it was hot, insect harassment often increased the heart rate of resting moose.

Organizing foraging activities into grazing and ruminating bouts is an adaptation of large herbivores (Foose, 1982). The flexibility of timing and duration of these bouts reflect the adaptation of wapiti to short term thermal environment, food availability and quality. As a northern ungulate, wapiti can tolerate cold but not heat. Different habitats in different seasons have different forage availabilities. Foraging orientations in time and space enhance the adaptability of wapiti in different habitats.

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## CHAPTER IV FORAGING POSTURES[1]

Wapiti encounter diverse seasonal food resources in the aspen boreal forests of western Canada. In the snow-free period, they graze herbaceous vegetation, whereas in winter they consume a considerable portion of browse and bark (Gates and Hudson, 1983).

The three-dimensional distribution of seasonal foods varies with habitat and topography, presenting different foraging opportunities and requiring different feeding tactics. Wapiti orient to potential seasonal foods by adopting different foraging postures. Presumably, foraging behavior develops by trial and error during ontogeny, so wapiti should adopt postures that enhance foraging efficiency in specific habitats. Calves and adults have different body proportions which may affect their foraging postures.

Foraging postures influence the size of feeding stations, defined as the area ungulates feed without moving their forelegs (Novellie, 1978). Adopting postures that cover large feeding stations could improve foraging efficiency by reducing average traveling costs per bite. The objectives of this study were to describe the main foraging postures of wapiti, to determine the frequency and time engaged in each foraging posture in relation to habitat, and to quantify the area of feeding stations associated with the most common postures. I show that calves and adults have different foraging postures and corresponding feeding station areas and that wapiti in different habitats use different postures.

### Methods

#### Animals

I observed six females of the 1988 cohort from August 1988 to August 1990 and another six female animals of the 1990 cohort from September 1990 to August 1991. In the summer of 1991, my observations were extended to eight 1991 calves (two males and six females), two 1990 males and six female adults. Half of the 1988 cohort and two of the 1990 cohort were hand-reared so they were tame and allowed close observation. Data from

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[1] A version of this chapter has been published . Jiang, Z. and Hudson, R. J. 1993. Foraging postures of wapiti (*Cervus elaphus*). Applied Animal Behavior Science 36: 275-287.

the 1988 and 1990 cohorts were pooled.

### Foraging postures

I distinguished ten foraging postures (Fig. IV.1): (P1) grazing with the legs and back straight, which I simplified as grazing while standing, (P2) grazing while walking, (P3) grazing with forelegs apart, (P4) grazing with back arched, (P5) grazing while lying, (P6) grazing with head turned aside, forelegs crossed or one foreleg diagonal, (P7) searching, (P8) grazing while kneeling, (P9) browsing while standing, and (P10) browsing while rearing.

I recorded foraging behavior with a pocket computer (TRS-80 PC, Tandy, TX, USA). I assigned each behavior and habitat a code and developed a program that recorded the date, habitat, animal's identity, behavior, duration and calculated their respective frequencies.

The similarity of the foraging postures between habitats was measured by percentage difference index (Goodall, 1978).

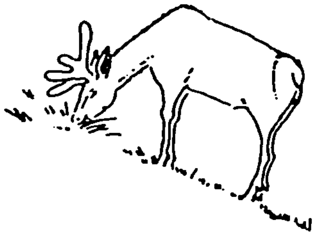
$$PDjk = \frac{\sum_{i=1}^{p} |x_{ij} - x_{ik}|}{\sum_{i=1}^{p} x_{ij} + x_{ik}} \qquad [IV.1]$$

Where: $x_{ij}$ , $x_{ik}$ were the percentage of postures i in habitats j and k. The results were plotted with the percentage similarity as the vertical axis and habitats as the horizontal axis.

### Body measurements

On 24 standing but restrained wapiti, I recorded head length (HL), wither height (WH), and hip height (HH). Head length was measured from the tip of the nose to the posterior edge of the occipital. Neck length was measured from the occipital along the vertebral column to the last cervical vertebra (in front of the scapula) rather than along the nuchal ligament which varies with head position. Withers and hip heights were measured as the vertical heights from the ground. To standardize analysis, I used HL as a standard length to express relative body proportions. An advantage was that such ratios normalized differences in frame size.

**Fig. IV.1** Foraging postures of wapiti: (P1) grazing while standing, (P2) grazing while walking, (P3) grazing with back arched, (P4) grazing with forelegs apart, (P5) grazing while lying, (P6) grazing with head turned aside, forelegs crossed or one foreleg diagonal, (P7) searching, (P8) grazing while kneeling, (P9) browsing while standing, and (P10) browsing while rearing.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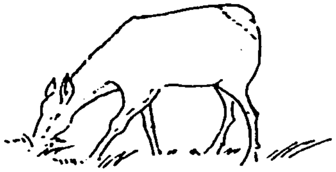
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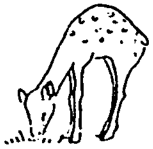
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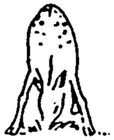
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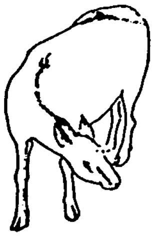
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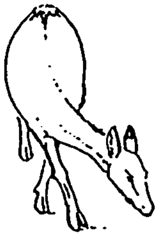
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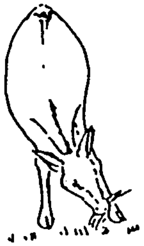
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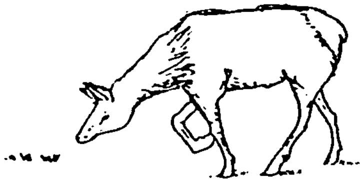
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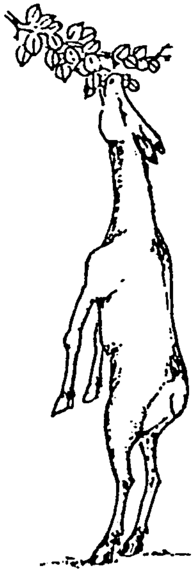
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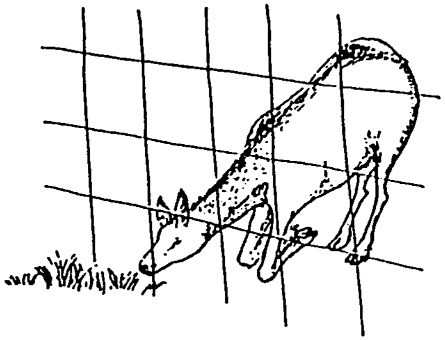
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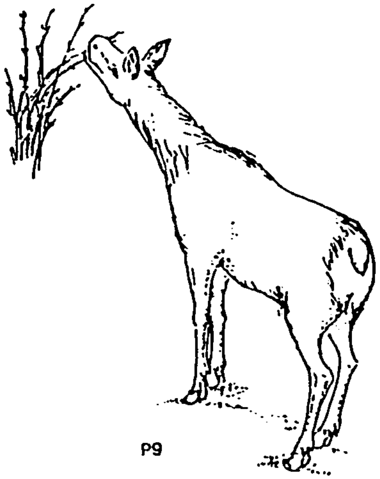

P9

With a compass protractor, I measured the angles formed by the neck and back in relation to a hypothetical horizontal plane above the animal (Fig. IV.2). When wapiti grazed at a feeding station, the smallest angle measured in front of the wapiti was called the vertical neck angle (VNA) and the one measured laterally was called the lateral neck angle (LNA). I calculated the area wapiti can reach when $VNA > 60°$ as the intensive feeding station and the area wapiti can reach at a feeding station as the extensive feeding station (Fig. IV.3).

### Feeding station area

On dew or frost-covered pasture or newly-grazed swards, I measured the pace length from hoof prints, and studied feeding station shapes and dimensions from grazing traces of wapiti at feeding stations.

In Fig. IV.3, the area of intensive feeding station of $P1 = OL \cdot OJ \cdot PI$, where $OL = 2HL \cdot \cos< VNA = 1\ HL$, $OJ = (2HL \cdot \cos< LNA)/2$. The area of intensive feeding station of $P2 = GE \cdot GD \cdot PI$, where $GE = (2HL \cdot \cos< VNA \cdot \cos< C\ E\ B)/2$, $< C\ h1\ B = < FDE = \arctan(h2\ H/2DE) = 37.4°$, $GD = DE \cdot \cos< FDE$. The calculations the areas of extensive feeding station are the same except where $< VNA$ and $< LNA$ are different.

### Statistics

I tested the null hypothesis of no differences among body measurements and ratios with MANOVA (Multivariate Analysis of Variance) and the Tukey-Kramer test (SuperANOVA™, Abacus Software). I also tested the following null hypotheses with univariate ANOVA: 1) wapiti calves and adults used the same foraging postures, 2) wapiti employed the same postures in different habitats, 3) wapiti consumed the same number of bites and spent the same amount of time per feeding station in different habitats. I considered differences significant when the probability of Type I error did not exceed 0.05. Data are presented as the mean ± 1 SE (number of observations).

## **Results**

### Body proportions

Differences among the head lengths, neck lengths, wither heights, hip heights and chest widths of calves, yearlings and adults were all significant (Table IV.1, $p < 0.05$). Despite contrasting body size, the relative neck length (NL/HL) remained equal to 1 across all age groups ($p > 0.05$). The relative leg length (WH/HL) decreased ($p < 0.05$) and chest

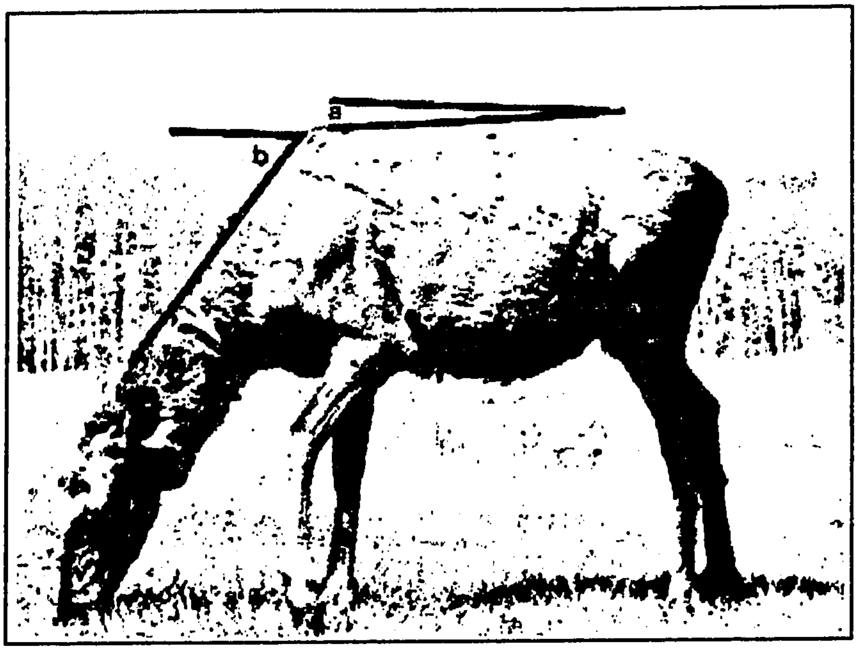
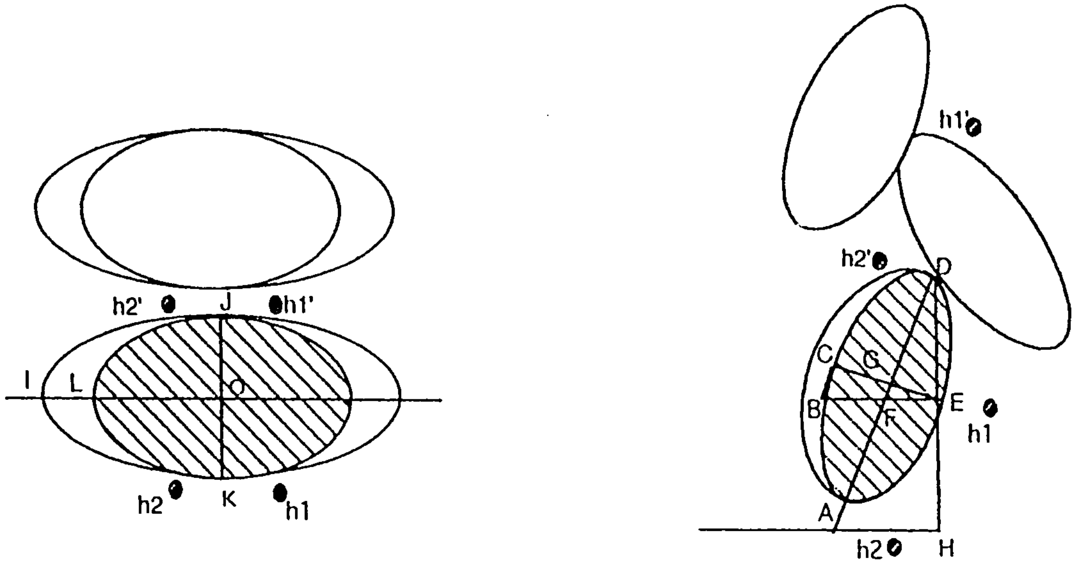


Fig. IV.2 A wapiti grazing on pasture. **a** and **b** show the back and lateral neck angles.



Posture 1

Posture 2

**Fig. IV.3** Feeding station area of posture P1 and P2. h1 and h2 represent the left and right fore-hooves, h1', h2', h1", h" are the consequent positions of the left and right fore-hooves of wapiti. When wapiti forage with P2, the feeding station is the ellipse on the side of wapiti. The shaded areas are the intensive feeding stations. OJ, GE and GD, OL are the short and long radii of intensive feeding stations of P1 and P2.

width increased as wapiti matured ($p < 0.05$, Table IV.2).

Foraging postures

Calves adopted different foraging postures in forest and open level grassland than did adult wapiti ($p < 0.05$, Table IV.3). When calves foraged by postures P3 or P4, I recorded back angles of 24.3° ± 1.6° (16), in contrast to 9.7° ± 0.8° (15) in adult wapiti feeding in the same habitat ($p < 0.01$). Wapiti calves fed 12.8 ±1.0 (81) seconds and consumed 4.9 ± 0.3 (81) bites per feeding station. By weaning in September, the 1990 cohort used P1 and P2 to graze in grasslands.

**Table IV.1** Body measurements (cm) of wapiti

| | Calves | | Yearlings | | Adults |
|---|---|---|---|---|---|
| | Female | Male | Female | Male | Female |
| Head length (HL) | 26.8 ± 1.0(6)$^{a*}$ | 26.5 ± 2.4(2)$^{a}$ | 39.3 ± 0.8(6)$^{b}$ | 42.5 ± 0.5(2)$^{b}$ | 46.6 ± 0.7(6)$^{c}$ |
| Neck length (NL) | 27.2 ± 1.0(6)$^{a}$ | 26.5 ± 8.5(2)$^{a}$ | 39.3 ± 1.0(6)$^{b}$ | 41.8 ± 0.3(2)$^{b}$ | 46.5 ± 0.5(6)$^{c}$ |
| Wither height (WH) | 81.2 ± 3.2(6)$^{a}$ | 81.5 ± 8.5(2)$^{a}$ | 116.0 ± 0.9(6)$^{b}$ | 129.5 ± 0.5(2)$^{c}$ | 129.3 ± 2.4(6)$^{c}$ |
| Hip height (HH) | 85.8 ± 3.6(6)$^{a}$ | 84.5 ± 8.5(2)$^{a}$ | 123.0 ± 2.0(6)$^{b}$ | 127.5± 0.5(2)$^{bc}$ | 136.0 ± 2.9(6)$^{c}$ |
| Chest width (CW) | 14.2 ± 0.5(6)$^{a}$ | 14.5 ± 0.5(2)$^{a}$ | 28.0 ± 0.4(6)$^{b}$ | 30.0 ± 0.6(2)$^{c}$ | 35.7 ± 1.2(6)$^{d}$ |

* Data presented as mean ± standard error (sample size). Data in the same row with the same superscript letters denote no difference at $p > 0.05$. Sample size in parenthesis.

Adult wapiti had different feeding posture profile in different habitats ($p < 0.05$, Table IV.3). To graze single layer habitats such as grasslands, forest floor and sedge meadows, adult wapiti adopted P1, P2 and P6, whereas in the multiple layer habitats such as willow margins and forests, they used P9 and P10 to get browse, bark and foliage. Particularly in late winter and early spring, wapiti kept their heads low and searched between feeding stations (P7). Wapiti also adopted opportunistic postures like lying-grazing (P5) in summer and kneeling to reach food under obstacles such as a fence (P8).

Before green plants appeared on the grasslands in early spring, wapiti foraged by P1 (61%) on green sedge shoots and rhizomes in sedge meadows. There was no difference between posture profiles in sedge swamp and those on sloped and level grasslands ($p > 0.05$). However, postures in sedge meadow were different from those in forest and willow margins ($p < 0.05$ and $p < 0.05$). When foraging with P1 and P2, wapiti spent 28.7 ± 4.1 and 17.5 ± 2.9 seconds per feeding station and extracted 8.4 ± 1.3 and 5.7 ± 1.2 bites per feeding station in sedge meadow, which were not different from those of P1 and P2 on level pasture ($p > 0.05$). However, wapiti ate significantly slower (more seconds per bite) in sedge meadows than on level grassland ($p < 0.05$).

**Table IV.2** Relative body proportions of wapiti

| | Calves | | Yearlings | | Adults |
|---|---|---|---|---|---|
| | Female | Male | Female | Male | Female |
| NL / HL | $1.01 \pm 0.04^{a*}$ | $1.00 \pm 0.00^{a}$ | $1.00 \pm 0.02^{a}$ | $0.99 \pm 0.02^{a}$ | $1.00 \pm 0.03^{a}$ |
| WH / HL | $3.03 \pm 0.23^{a}$ | $3.07 \pm 0.04^{a}$ | $2.95 \pm 0.12^{b}$ | $3.05 \pm 0.07^{a}$ | $2.79 \pm 0.08^{c}$ |
| CW / HL | $0.53 \pm 0.07^{a}$ | $0.55 \pm 0.05^{a}$ | $0.71 \pm 0.03^{b}$ | $0.72 \pm 0.01^{b}$ | $0.77 \pm 0.03^{c}$ |
| WH / HH | $0.95 \pm 0.02^{a}$ | $0.96 \pm 0.01^{a}$ | $0.94 \pm 0.03^{a}$ | $1.02 \pm 0.00^{b}$ | $0.96 \pm 0.01^{a}$ |

* Data presented as mean ± standard error. Data in the same row with the same superscript letters denote no difference at $p > 0.05$.

Wapiti adopted posture P1 on sloped grassland but P2 and P6 on level grassland ($p < 0.05$, Table IV.3). On slopes (< 30°), 56% of the 131 recorded postures were P1, whereas on level grassland, 70% of 604 recorded postures were P2 and P6, (P1 was observed only in 23% of the cases). When wapiti adopted P1 on slopes, they consumed more bites per station (11.4 ± 0.9) compared with the same posture on level ground (9.5 ± 0.6, $p < 0.01$). Between P2 and P6 observed on level grassland, wapiti moved directly forward by P2 in 90% and laterally by P6 in 10% of the cases. Often when diagonal movement occurred, wapiti were attracted to what another herd member was eating (P6b). Wapiti sometimes grazed from a bedded position (P5, 2%) before ruminating when grasses were lush, they consumed 44.7 ± 7.9 (10) bites per feeding station from this posture, however they ate slower (2.34 ± .5 sec./bite) than they did with P1 and P2 (1.5 ± 0.03 sec./bite, $p < 0.01$). There were no differences between bites harvested with P1 and P2 on sloped ($p > 0.05$) or level pastures ($p = 0.06$). However, wapiti foraging by P1 on

**Table IV.3** Percentage of foraging postures of calves and adults in different habitats.

| Habitats | Calves | | Adults | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P3 | P4 | P1 | P2 | P3 | P4 | P5 | P6 | P7 | P8 | P9 | P10 |
| **Later winter-early spring** | | | | | | | | | | | | |
| Willow margins | --- | --- | 34 | 15 | 0 | 0 | 0 | 8 | 16 | 1 | 25 | 0 |
| Sedge medow | --- | --- | 61 | 27 | 0 | 0 | 0 | 5 | 7 | 0 | 0 | 0 |
| Poplar forest | --- | --- | 16 | 72 | 0 | 4 | 0 | 5 | 3 | 0 | trace | trace |
| **Later spring-summer** | | | | | | | | | | | | |
| Flat grassland | 68 | 32 | 23 | 63 | 0 | 1 | 2 | 7 | 4 | 0 | 0 | 0 |
| Sloped grassland | --- | --- | 56 | 31 | 0 | 0 | 0 | 0 | 11 | 2 | 0 | 0 |
| Poplar Forest | 65 | 35 | 21 | 65 | 0 | 0 | 0 | 3 | 8 | 0 | trace | 2 |

sloped pasture took more bites and stayed longer at each feeding station than they did with P2 in the same habitat ($p < 0.05$).

Wapiti had shorter paces on sloped pasture during grazing (Table IV.4). Foraging wapiti moved 2.0 m per minute on level pasture but 1.2 m per minute on slopes. There was no difference between foraging postures used in winter and summer in forest habitats ($p > 0.05$, Table IV.3). In summer, P1 and P2 were also the dominant postures (21% and 65%) in the forest. Wapiti also reared to get foliage (2%). Wapiti adopted mobile feeding posture P2 in the forest when there were dense insects in summer. When foraging with P1 in forest, the bites consumed per feeding station did not differ from that on level pasture ($p > 0.05$), but there was significant difference between bites consumed with P2 in the two habitats ($p < 0.05$). Wapiti grazed the herbage layer in late winter forests by the same postures adopted on level grassland in summer ($p > 0.05$). Wapiti used P2 (72%) and P1 (16%) to graze herbage on the forest floor. Occasionally, wapiti reared on their hind legs (P10) to get balsam poplar twigs in winter (< 1%) or debarked trees with P9. Bites per feeding station were different than those of P2 in the two habitats ($p < 0.05$). However, bites per feeding station for posture P1 in late winter forest and summer forest were not different ($p > 0.05$).

**Table IV.4** Neck angles and feeding station areas

| | Yearlings | Adults |
|---|---|---|
| Pace length on level pasture (cm) | 54.7 ± 0.8 (27)$^{a}$ | 76.8 ± 0.6 (68)$^{b}$ |
| Pace length on slopes (cm) | 42.9 ± 1.5 (11)$^{a}$ | 58.2 ± 3.1 (7)$^{b}$ |
| Front neck angle | 54.3° ± 1.0° (341)$^{a}$ | 53.0° ± 0.9°(267)$^{a}$ |
| Lateral neck angle | 47.1° ± 0.6° (118)$^{a}$ | 46.3° ± 0.7° (41)$^{a}$ |
| **Intensive feeding station area** | | |
| P1 ($m^2$) | 0.28 ± 0.02 (6)$^{a}$ | 0.41 ± 0.01 (6)$^{b}$ |
| P2 ($m^2$) | 0.19 ± 0.01 (6)$^{a}$ | 0.26 ± 0.02 (6)$^{b}$ |
| **Extensive feeding station area** | | |
| P1 ($m^2$) | 0.39 ± 0.02 (6)$^{a}$ | 0.56 ± 0.02 (6)$^{b}$ |
| P2 ($m^2$) | 0.21 ± 0.02 (6)$^{a}$ | 0.30 ± 0.01 (6)$^{b}$ |

* Data presented as mean ± standard error (sample size). Data in the same row with the same superscript letters denote no difference at $p > 0.05$.

Wapiti foraged by different postures in the willow habitat ($p < 0.05$, Table IV.3). Besides using P1 (34%) and P2 (15%) to graze the withered grass, wapiti also raised their heads (P9) to browse twigs (25%) in winter and early spring. When using P1 and P2, they consumed 6.6 ± 0.9 and 4.9 ± 1.4 bites per feeding station; less than they did in summer pastures ($p < 0.01$). From P9, they browsed 3.3 ± 0.6 (18) bites and spent 21.2 ± 2.9 seconds per feeding station.

Foraging postures in the six habitats formed two main groups according to the percentage difference index (Fig IV.4). In summer and winter in poplar forests and level grassland, wapiti adopted similar postures. In sloped grassland, sedge meadow and willow, posture formed an identifiable cluster. Foraging postures in willow margins were most dissimilar.

### *Feeding station area*

Of the measured vertical neck angles, 81% were greater than 60° (Fig. IV.5). On level grassland, calves could reach a circular area of 0.06 ± 0.01 $m^2$. For yearlings and adults adopting P1, the extensive feeding station areas were 0.39 ± 0.02 $m^2$ and 0.56 ± 0.02 $m^2$. The corresponding intensive feeding stations were 0.28 ± 0.02 $m^2$ and 0.41 ± 0.01 $m^2$. On sloped pasture, the short axis of feeding station increased with slope. For a yearling wapiti with a head length of 39.3 cm on a 30° slope, the short axis of the feeding station increased to 2 HL, the feeding station was circular, and the area almost doubled (0.49 $m^2$). When yearlings and adults foraged by P2 on level pasture, extensive and an intensive feeding stations were 0.21 ± 0.01 $m^2$ and 0.19 ± 0.01 $m^2$, respectively. Corresponding values for adults were 0.30 ± 0.01$m^2$ and 0.26± 0.02 $m^2$. Feeding station areas of posture P2 were smaller than those of P1. The assessment of feeding station area of P1 and P2 in specific age-sex groups can be applied to the herbage layer in all the habitats, because the area depended only on topography.

## Discussion

Wapiti were opportunistic foragers. They ate fallen leaves on forest floor in autumn, browsed shrubs and twigs and stripped tree bark in winter, consumed sedges in sedge meadows in early spring, and grazed open grasslands or browsed foliage in summer. Even though wapiti mainly fed on the herbage layer, they adopted different postures for each seasonal forage resource. However, the choice and apparent advantage of postures differed among age classes.

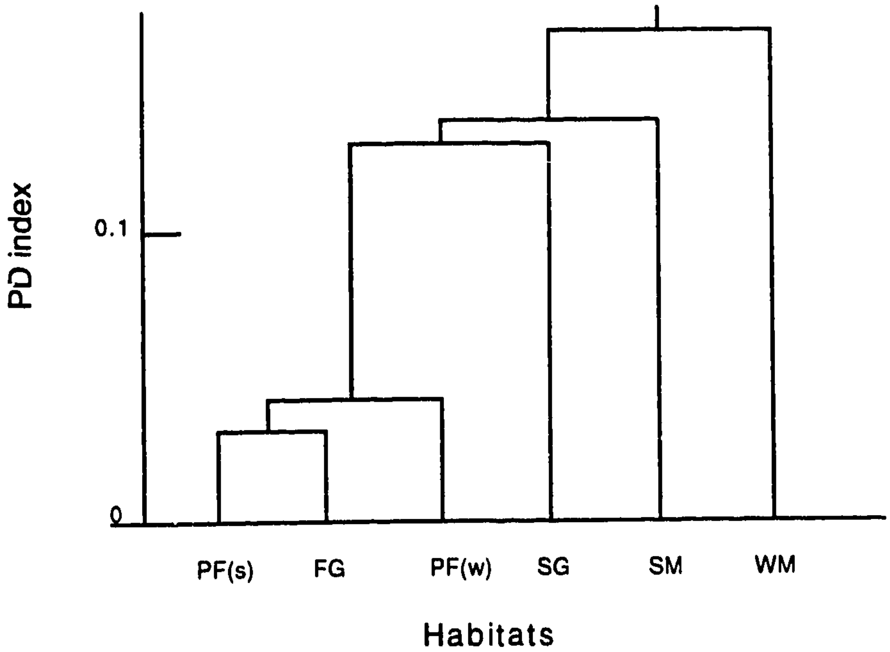


**Fig. IV.4** Dendrogram based Percentage Similarity Index of foraging postures in summer and winter poplar forest (PF(s) and PF(w)), level grassland (FG), and sedge meadow (SG) and willow margin (WM).

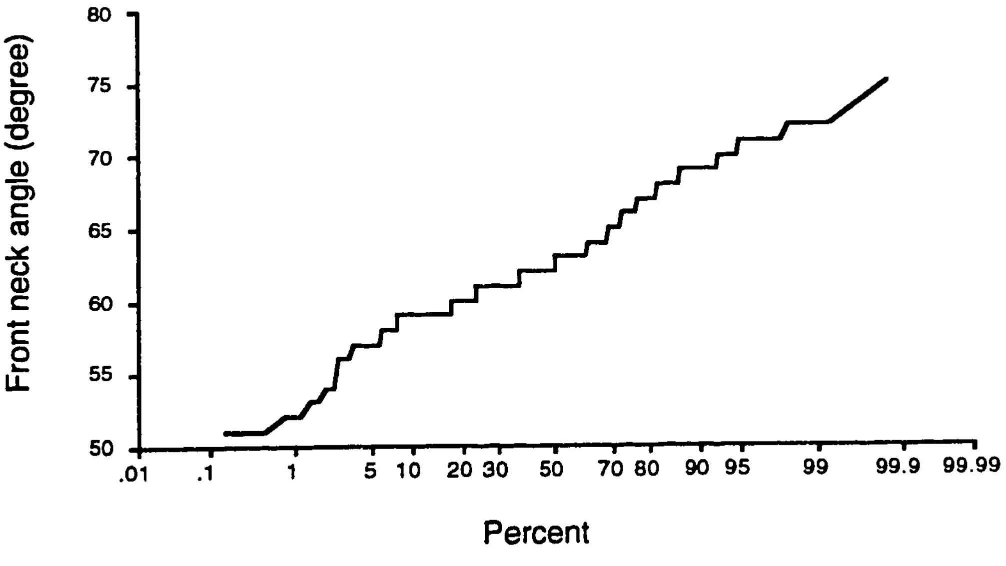


**Fig. IV.5** Probability density of the front neck angles. About 81% of observations were less than 60° range when foraging with postures P1 and P2.

P1 and P2 made up more than 50% of all foraging postures of adults in the 5 habitats, because herbage was the major food in all seasons. On level grassland, wapiti grazed by P2 because they could shift the center of gravity forward to advance to the next feeding station. On slopes where stability presumably outweighs mobility, wapiti adopted P1 to maintain balance. They consumed more bites per feeding station on sloped than level pasture, perhaps because: (1) it was energetically expensive to move on slopes so wapiti stayed at feeding stations on sloped pasture longer and ate more bites, and (2) the area of the feeding station on sloped pasture was larger than that on level pasture. P1 predominated when wapiti grazed sedge meadows. Presumably, this posture offered them maximum standing height and distributed weight to minimize sinking in the soft substrate.

As they began the process of weaning in mid summer (Hudson and Adamczewski, 1990), calves grazed awkwardly in forests and then in open grassland. They adopted mainly P3 and P4, probably due to less foraging experience, their long legs relative to head and neck lengths, and instability. However, adults also grazed by P4 when the grass was short in the late winter and early spring.

Wapiti fed from a bedded position (P5) in cold winter days to eat supplementary hay or in late spring and summer when lush grasses were available. This posture required the least amount of energy, but of course the animal had to use more energy to advance to the next feeding station.

P6 was the most variable and flexible posture. The posture employed in foraging determined the direction of movement. The feeding station areas shown in Fig. IV.3 were simplified situations. Sometimes feeding stations overlapped such as occurred when wapiti took short steps on sloped or lush pasture or when they foraged by P6b or P6c.

Postures P7, P8, P9 and P10 were specialized for specific circumstances, typically low forage availability. P7 offered a close look at the ground and mobility. Wapiti foraged by P8 only when they tried to reach forages outside fence or other obstacle. P9 and P10 were means to reach foods in shrub and canopy layers. I did not observe P9 and P10 very often, perhaps because most foliage within reach in the forest habitat had been consumed, associated energetic costs were high, feeding area was limited, or mobility was impaired.

The occurrence of postures in each habitat was the consequence of foraging opportunities and forage selection. There are multiple layers of forages in forests and willow margins in contrast to a single layer in grasslands and meadows. Although there was a foliage layer in the poplar forest, it was too high for the wapiti to reach. Therefore, wapiti in forests used the same postures as on grasslands. Willow margins were the only habitat where wapiti could reach each layer, and wapiti responded with a wider repertoire of postures. Stability is important in sedge meadow and sloped grassland; the foraging processes in those habitats were dominated by the sedentary posture, P1 instead of the mobile posture, P2.

Besides adopting different postures, wapiti spent different times at each feeding station and changed walking speeds between stations. It is energetically costly to walk on slopes (Robbins *et al*, 1979). Animals may regulate energy expenditure per unit time by moving slowly on slopes.

In conclusion, I documented foraging postures of wapiti and occurrence of each posture in seasonal habitats in this chapter. The main determinants were the vertical structure of food resources in different habitats, topography, substrate and age-specific body proportions. Foraging efficiency and mobility seemed to be two underlying considerations for choosing foraging postures.

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# CHAPTER V OPTIMAL GRAZING IN PATCHES AND FEEDING STATIONS[1]

Charnov (1976) introduced the Marginal Value Theorem to address the question of when a forager should leave a patch. McNair (1982) predicted longer giving-up times for better quality patches. Iwasa *et al.* (1981), testing departure strategies for a patchy environment with a stochastic model, concluded that the choice of foraging strategies depended on prey distribution. Leaving patches at fixed giving-up times was the best when the variance of prey distribution among patches was high, whereas leaving patches after consuming a fixed number of prey tended to be best when variance of prey distribution was low. I was interested in how these strategies applied to the foraging of a large ruminant herbivore, the wapiti.

The departure decision foragers make is a problem of optimal allocation of foraging time, which has stimulated experiments in both laboratory and field. Cowie (1977) reported that great tit adjusted foraging time in artificial patches according to traveling time. Hodges (1981) discovered that bumblebee maximized energy intake by departing from individual *Delphinium* plants when nectar intake rate fell. By computer simulation, Pleasants (1989) tested the fixed and stochastic giving up thresholds of nectarivores with field data of Hodges. He found that the threshold predicted by the Marginal Value Theorem was optimal. Kadmon and Shmida (1992) carried out a field test of whether departure decisions of nectar-collecting bees were based on simple threshold or probabilistic rule. In their study, bees exhibited two distinctive departure decisions: using probabilistic rule at the individual plant level and adjusting inter flower flight distance according to the reward received at the current flower. However, these ideas have seldom been applied to grazing ruminant herbivores.

Whereas predators seek scattered prey of high nutritional quality, large herbivores confront widely dispersed, low quality food (Senft *et al.*, 1987). Foraging of large herbivores is characterized by relative short searching time, and prolonged grazing time. Also, ruminants reprocess ingested food, dividing nutritional activities between grazing and ruminating. However, like predators, herbivores face a patchy environment even on a grassland where heterogeneity is created by micro-environmental factors such as soil,

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[1] A version of this chapter has been published. Jiang, Z. and Hudson, R. J. 1993. Optimal foraging of wapiti on grassland: patch and feeding station departure rules. Evolutionary Ecology 7: 488-498.

moisture, slope and neighboring plant species. Wapiti face two hierarchical levels of patchiness on grassland; namely, patches and feeding stations. I defined a patch as an area on which wapiti initiate and terminate a foraging sequence before starting another feeding station sequence. A series of such sequences make up a foraging bout which is terminated by resting/ruminating (Gates and Hudson, 1983). A feeding station, defined as the area an ungulate can feed without moving its forelegs (Novellie, 1978), is considered a cluster of potential bites. Thus, a patch is a cluster of feeding stations. According to the Marginal Value Theorem, wapiti should give up a patch when the rates of net gain drop to the expected net gain rate.

I addressed departure rules for both hierarchical levels of resource heterogeneity. For grassland patches, I asked whether wapiti depart after grazing a fixed number of feeding stations, after consuming a fixed number of bites, after a fixed time or after cropping rate dropped below the seasonal expectation. For feeding stations within patches I asked whether wapiti leave feeding stations after consuming a fixed number of bites, after a fixed time, or after cropping rate dropped below the seasonal expectation or other threshold. I provide evidence that wapiti terminated foraging after the cropping rate dropped below the seasonal expectation in the patch. Neither foraging time, bites consumed nor cropping rate seemed to serve as departure rules at feeding stations. However, the neck angle of grazing wapiti seemed constant when leaving feeding stations suggesting that biokinetic factors played a role.

## Methods

### Animals and trials

I carried out the study with six tame female wapiti at three points in the snow-free season of 1991: March 2[illegible] to April 3 (spring, snow melt and grass emergence), May 22 to 30 (summer, grass leafed ) and August 15 to 22 (early autumn, grass seeds ripened) at Ministik Wildlife Research Station. I recorded foraging behavior with a pocket computer (TRS-80 PC, Tandy, TX, USA) programmed to recorded each animal's identity, behavior and occurrence of the behavior (Jiang and Hudson, 1993). The duration of a behavior state was determined by the built-in timer and its frequency was calculated instantaneously. I used the computer to record bites, number of feeding stations, steps and cropping rates. I began an observation by selecting a group member at random and continued sequentially until all animals were observed, the that process took up to three h. During March-April trial, I recorded 39 foraging sequences and 711 feeding stations, 23 foraging sequences and 782 feeding stations in May and 73 foraging sequences and 1025 feeding stations in August. Cropping rate was calculated as the bites taken from a feeding station divided by the time elapsed between steps. The seasonal expectation of cropping rate was calculated as the average of the cropping rates at all feeding stations in the season.

### Herbage biomass and qualities

I measured the above-ground grassland biomass by clipping 10 random 0.5 X 0.5 m samples and determined plant height at 22 random points during each seasonal trial in the area where grazing was observed. I sorted the samples into green and withered material and dried them at 60 °C. Sub-samples were dried at 110 °C to determine dry matter (DM). Gross energy content of grass samples was determined with a bomb calorimeter (PARR Instrument Company, IL, USA). Crude protein content was calculated with total nitrogen determined by the macro-Kjeldahl method (A. O. A. C., 1984). Neutral detergent fiber (NDF) was determined according to Goering and Van Soest (1970).

### Geometry of grazing wapiti

To define feeding station dimensions, I measured angles of the trunk (trunk angle) and lateral neck (neck angle) in relation to a hypothetical horizontal plane above the animal (Jiang and Hudson, 1993). Trunk angle is fixed in most situations because wapiti normally move their hind legs at the same time as the forelegs. Neck angle is dynamic because wapiti orient to potential bites by moving their necks. I recorded 20 trunk and neck angles of each wapiti with protractors in May and August.

### Statistics

The cropping rate at feeding stations within a patch is a time series. In each season, I pooled the cropping rates at the last 5 feeding stations before departing patches and calculated the autocorrelation of cropping rates. I tested the hypotheses that the number of feeding stations, number of bites, or foraging time were the same in patches of March-April, May and August with ANOVA. I also tested the hypotheses that cropping rates at the last 1 to 5 feeding stations before leaving a patch were the same as the seasonal expectation. I studied bites per feeding station with foraging time at feeding stations as a covariate and tested the hypotheses that wapiti consumed the same number of bites or grazed the same duration at each feeding station. The data were transformed to their square roots to achieve normality (Sokal and Rohlf, 1989). I also tested the hypothesis that the neck angles of wapiti leaving feeding stations were the same for individual wapiti and were independent of the number of bites consumed at the feeding stations. I analyzed forage characteristics (biomass, height, gross energy, protein and NDF) with MANOVA (multivariate analysis of variance) and conducted multiple comparison among means with Tukey-Kramer method. Data were summarized as mean ± 1 se (number of observations), except where specified otherwise and differences were considered significant where the probability of a type I error did not exceed 0.05.

## Results

### Departure from grassland patches

The behavior of wapiti was most distinctive in May and was characterized by large number of feeding stations per patch, bites per patch and greater grazing time per patch ( Fig V.1). Compared with May, wapiti grazed fewer feeding stations, bites per patch and had short grazing time per patch in March-April and August.

### *Number of feeding stations*

The average number of feeding stations comprising a foraging sequence in a grassland patch varied significantly by season ($p < 0.05$). In March-April as snow melted and grass shoots emerged, wapiti grazed 17.4 ± 1.9 (39) feeding stations per patch. In May when pastures achieved their rapid phase of growth, this increased to 31.3 ± 0.9 (23). In August as seed ripened and pasture quality declined, the number of feeding stations per foraging sequence declined to 12.4 ± 1.1 (76). Within seasons, feeding stations grazed per patch ranged from 1 to 74 feeding stations. Thus, wapiti did not leave a patch after grazing a fixed number of feeding stations.

### *Number of bites*

Wapiti consumed significantly different number of bites from patches in each season ($p < 0.05$). From each patch, wapiti took 139 ± 20.0 (39) bites per patch in March/ April, 247.5 ± 8.2 (23) bites in May, and 108.1 ± 11.9 (79) bites in August. Within season, bites per patch ranged from 1 bite to 634 bites. Hence, wapiti did not leave a patch after a fixed number of bites.

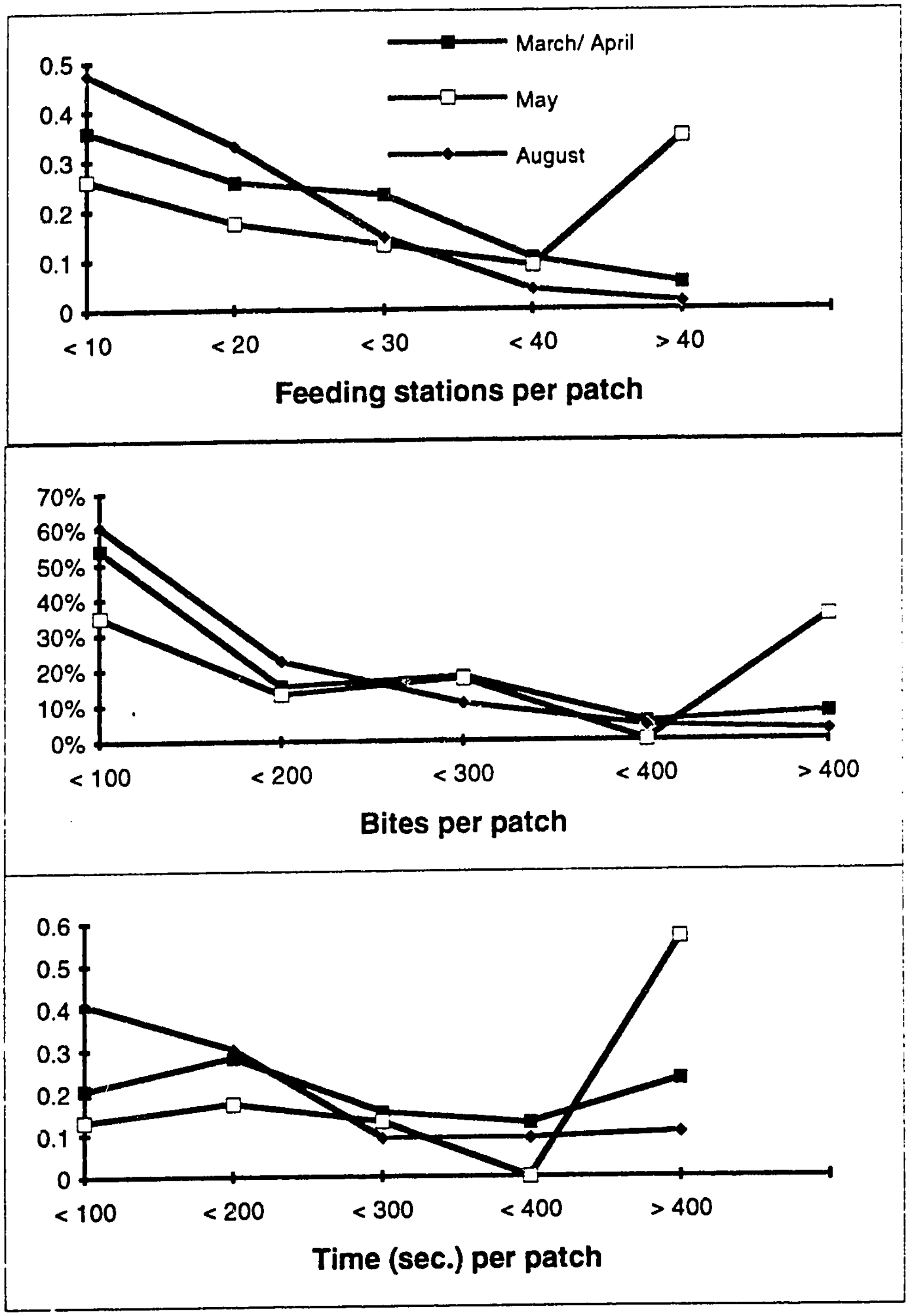

Fig. V.1 Frequency distribution of feeding stations, bites and foraging time per patch.

### *Foraging time*

Wapiti foraged in patches significantly longer during May than during March-April or August ($p < 0.05$). Wapiti stayed in patches for 318.9 ± 20.0 (39) seconds in March-April, for 637. 4 ± 49.6 (23) seconds in May and 108.1 ± 11.7 (79) seconds in August. In the same season, the foraging time in patches ranged from 2 seconds to 1310 seconds. Wapiti did not use foraging time as a departure rule.

### *Average cropping rate at feeding stations*

Cropping rates dropped before wapiti gave up patches in each season (Fig V.2). The serial autocorrelation coefficients of the means at the last 5 feeding stations before giving-up were 0.18 in March-April, 0.12 in May and 0.17 in August. In March-April and August, the average cropping rate at the last feeding station was significantly lower than the second last feeding station ($p < 0.05$). However, the cropping rates at the 2nd, 3rd, 4th and 5th last feeding stations were not significantly different ($p > 0.05$). In May, the average cropping rates at both the last and the second last feeding stations were significantly different from each other ($p < 0.05$) and from those at the 3rd, 4th and 5th last feeding stations ($p < 0.05$). However, the cropping rates at the 3rd, 4th and 5th last feeding stations were not significantly different ($p > 0.05$). In conclusion, wapiti gave up foraging when the cropping rates at one or two feeding stations dropped below the seasonal expectation.

### Departure from feeding stations

Throughout the snow-free grazing season, wapiti took only slightly different numbers of bites and spent different times before advancing to the next feeding station (Fig. V.3).

### *Number of bites*

Average bites per feeding station did not change significantly ($p > 0.05$) although plant heights and biomass changed considerably from May to August (Fig. V.4, $p < 0.05$). Wapiti took 7.7 ± 0.3 (711) bites per feeding station on March-April grassland, 8.0 ± 0.2 (782) bites on May grassland and 8.6 ± 0.3 (1025) bites on August grassland. Within seasons, the bites per feeding station was not constant. Wapiti did not depart feeding stations after consuming certain number of bites.

### *Foraging time*

Grazing time of wapiti at feeding stations differed significantly among seasons ($p < 0.05$). Wapiti grazed 15.4 ± 0.5 (711), 14.4 ± 0.4 (782) and 13.6 ± 0.3 (1025) seconds on feeding stations in March-April, May and August, respectively. Wapiti foraged less time at feeding stations in August than in March-April ($p < 0.05$) despite improved forage

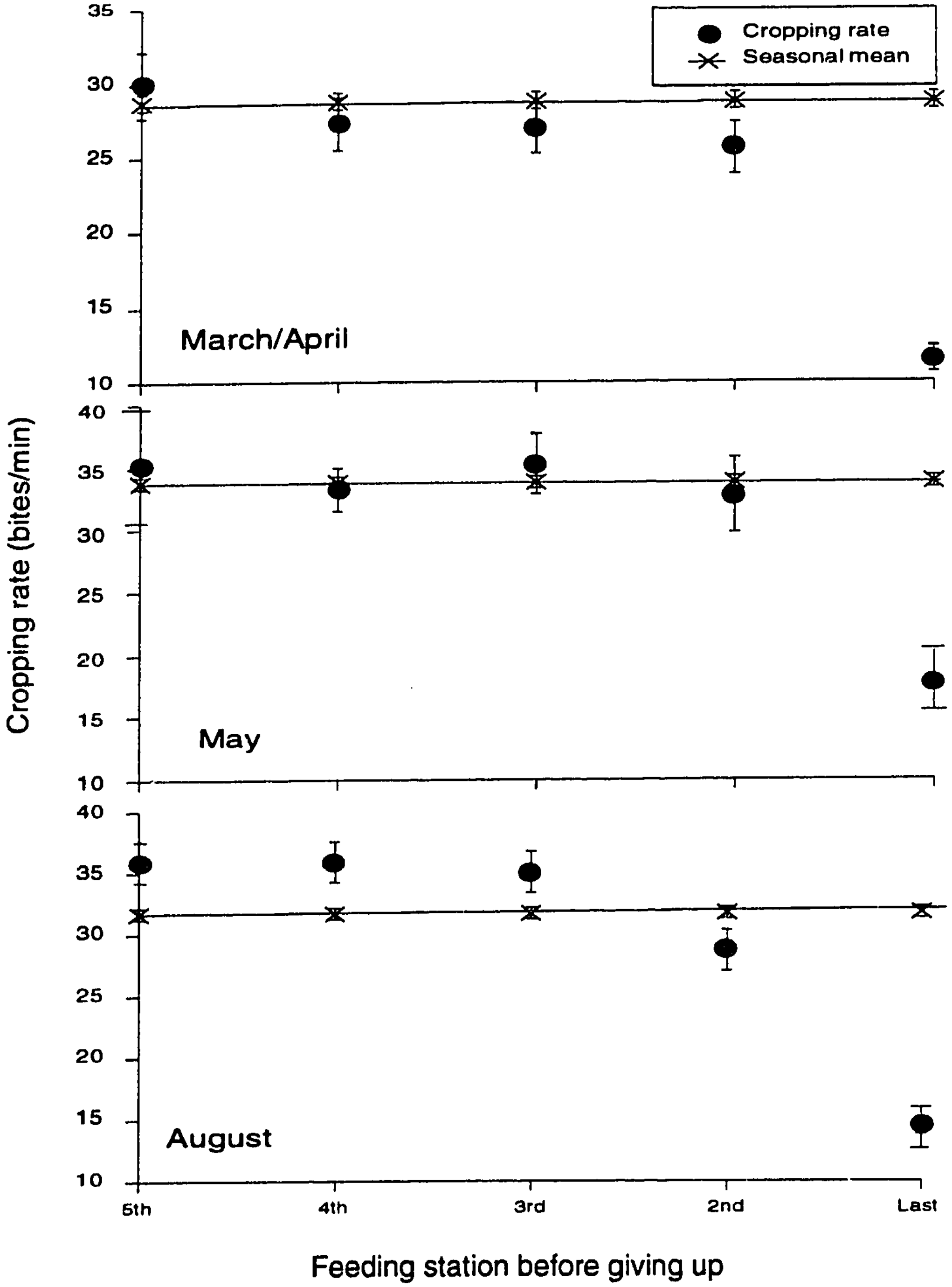

**Fig. V.2** Cropping rates at the last five feeding stations before giving up a patch. In all seasons, wapiti terminated foraging when cropping rate dropped below the seasonal expectation.

quality (compare protein contents, $p < 0.05$, Table V.1), forage biomass ($p < 0.05$) and forage heights ($p < 0.05$). However, the difference between grazing time in March-April and May was not significant ($p > 0.05$). Among the feeding stations, which was classified by the number of bites harvested, grazing time per feeding station in the same season was significantly different ($p < 0.05$, Fig V.3); wapiti did not leave feeding stations after a fixed foraging time.

**Table V.1.** Seasonal forage characteristics at the Ministik Wildlife Research Station

| | March-April | May | August |
|---|---|---|---|
| Biomass (g DM/m$^2$) | 103 ± 43 (10)$^{a*}$ | 188 ± 63 (10)$^a$ | 371 ± 171 (10)$^b$ |
| Sward height (cm) | 3.3 ± 1.1 (22)$^a$ | 13.9 ± 3.8 (22)$^b$ | 24.0 ± 6.3 (22)$^c$ |
| Energy (kJ/g) | 17.4 ± 0.2 (2)$^a$ | 18.0 ± 0.3 (2)$^b$ | 17.6 ± 0.3 (2)$^b$ |
| Protein (%) | 12.6 ± 0.0 (2)$^a$ | 16.6 ± 0.1 (2)$^b$ | 16.3 ± 0.2 (2)$^b$ |
| NDF (%) | 68 ± 3 (2)$^a$ | 64 ± 0.2 (2)$^b$ | 67 ± 0.5 (2)$^a$ |

*Data presented as mean ± standard error (sample size). Data in the same row with one different superscript letter indicate a significant difference at $p < 0.05$.

### *Cropping rate in relation to bites taken*

Among seasons, average cropping rates differed significantly ($p < 0.05$, Fig V.4 ). Cropping rate was 28.8 ± 0.5 (695) bites per min. in March-April, whereas cropping rate was 33.8 ± 0.5 (775) bites per min. in May and 31.6 ± 0.5 (988) bites per min. in August. Within seasons, cropping rate increased asymptotically with bites consumed at feeding station and varied significantly among feeding stations ($p < 0.05$, Fig V.4). As the grazing season progressed, both asymptotic cropping rates and "saturation coefficients" increased. Wapiti did not leave feeding stations at a constant cropping rate or as cropping rate decreased.

### *Neck angles*

Lateral neck angles of specific individuals in May and August did not vary with season (Table V.2 ; $p > 0.05$) nor the interaction between focal animals and seasons ($p > 0.05$). Threshold neck angle at departure was independent of bites consumed at the feeding stations ($p > 0.05$). Although I did not measure neck angles in March-April, wapiti

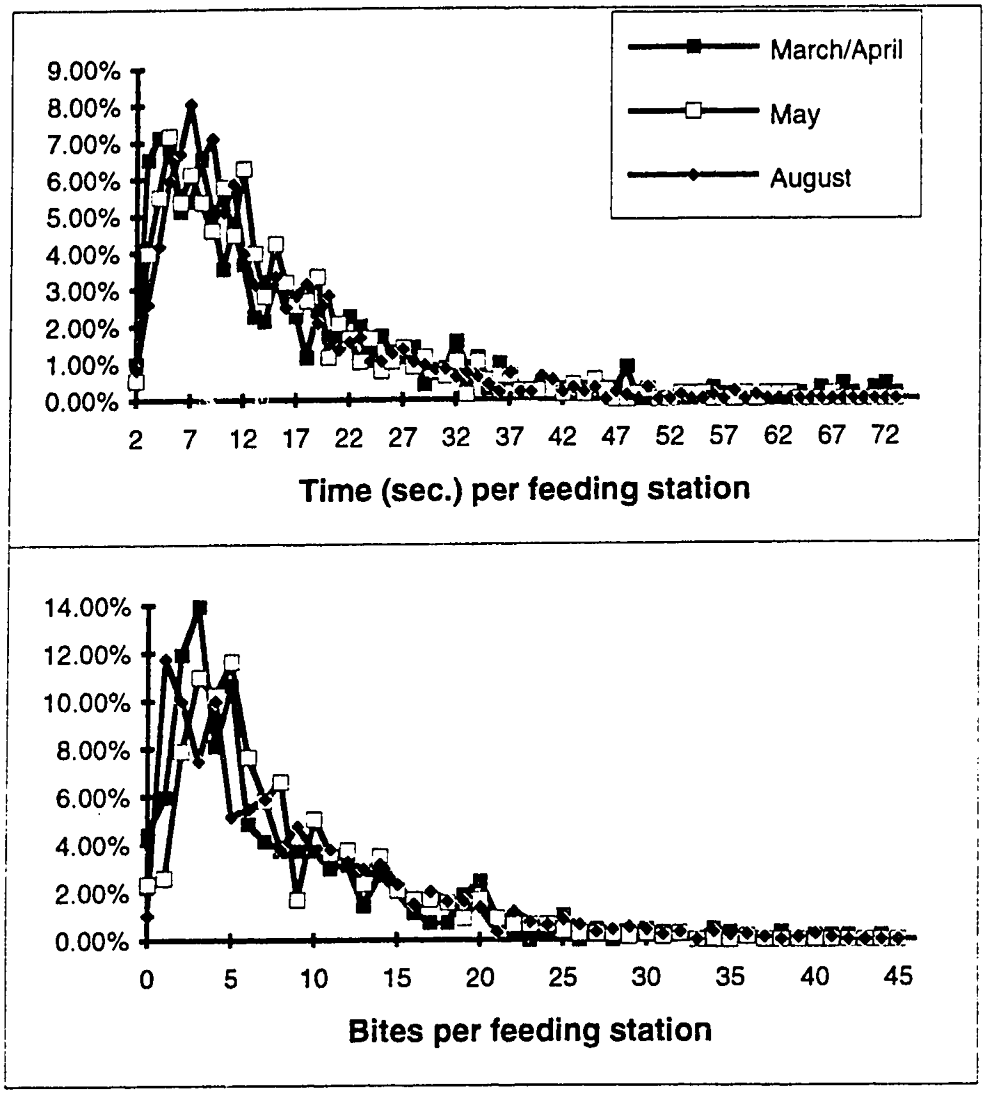

Fig. V.3 Frequency distributions of bites consumed and grazing time at feeding station.

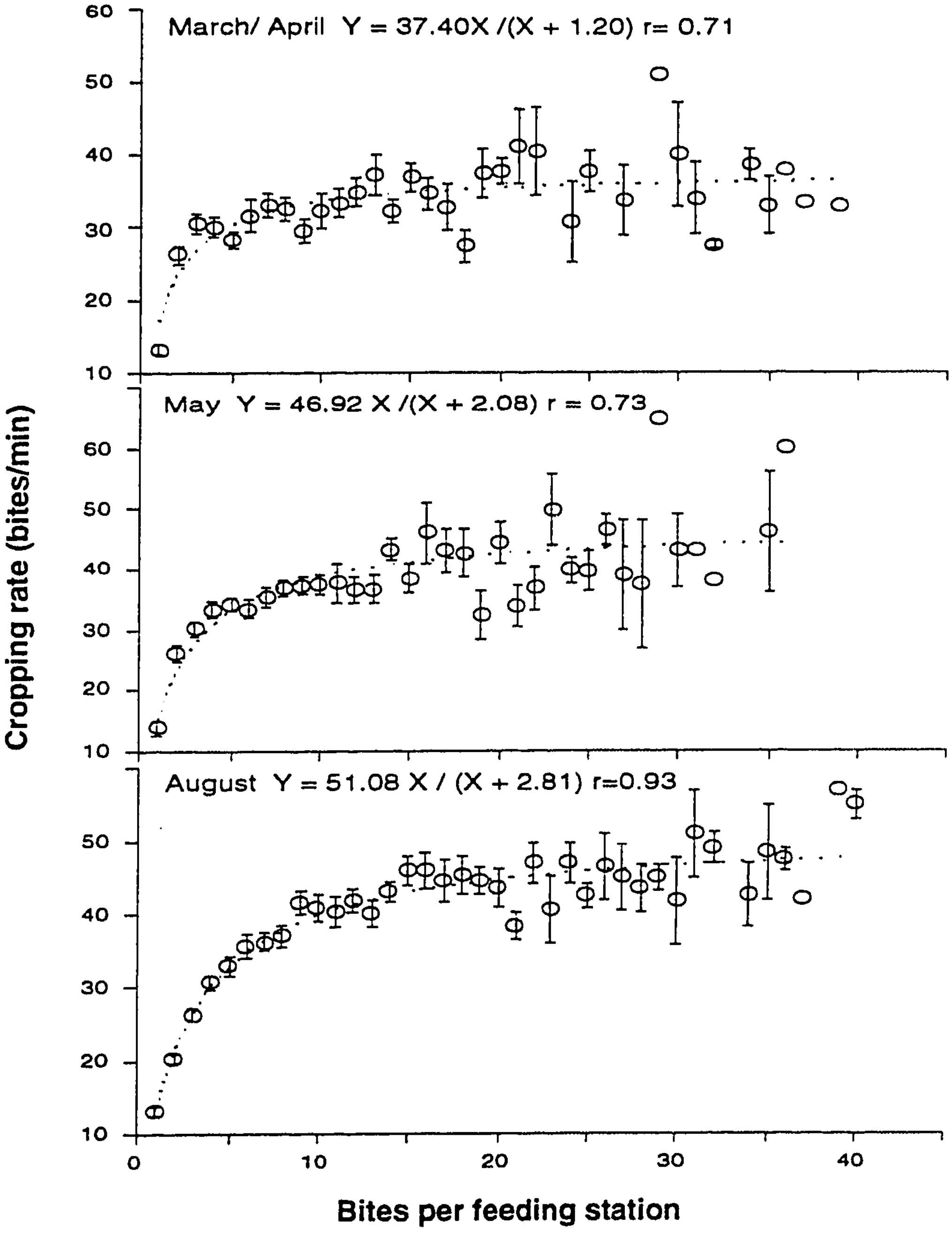

Fig. V.4 Cropping rates at feeding stations. The data were fitted with the Michaelis-Menton equation Y = ( m1 * X) / (X + m2), where Y represents the cropping rate, X represents bites consumed, m1 is the asymptotic cropping rate and m2 is the "saturation coefficient".

**Table V.2.** Critical angles when wapiti left feeding stations, 20 measurements for each animal.

| Wapiti | May | | August | |
|---|---|---|---|---|
| | Mean | SD | Mean | SD |
| No. 9015 | 54.6° | 4.5° | 54.7° | 3.2° |
| No. 9026 | 55.3° | 3.7° | 55.3° | 3.6° |
| No. 9029 | 51.4° | 2.9° | 50.5° | 3.9° |
| No. 9036 | 53.5° | 3.0° | 54.0° | 2.6° |
| No. 9037 | 57.5° | 2.6° | 57.2° | 2.4° |
| No. 9039 | 54.3° | 4.6° | 54.2° | 4.1° |
| Mean ± SE | 54.4° | ± 2.0° | 54.2° | ± 2.2° |

behaved similarly to those in Ma [illegible] grazing from the area near the fore-hooves to the distal end of the feeding st [illegible]

## Discussion

### Patch definition

Krebs *et al.* (1981) pointed out the difficulty in defining a patch when testing the Marginal Value Theorem. I attempted to express the size of grassland patches in terms of animal behavior as a sequence of feeding stations. The smallest unit is a feeding station which has its boundary set by the reach of wapiti. A grassland patch is a cluster of feeding stations separated from others by a break in the foraging sequence when the animal starts a new feeding sequence. I found evidence that wapiti used different rules at each level and these changed subtly as the grazing season progressed.

Broadly similar hierarchical patch departure rules have been found in nectar-foraging bees. Kamon and Shmida (1992) reported that bees adopted different departure strategies at different patch levels: leaving an individual plant according to a probabilistic rule and moving a distance to next flower according to the nectar reward at the current flower.

### Patches

To forage efficiently, a forager must keep track of changes that occur in its environment by learning. The state of their environment affects the subsequent foraging decision (Krebs and Inmant, 1992). Because of the positive autocorrelation of the cropping rates before leaving patches, wapiti might already decide to give-up at the second last feeding station by learning. The most striking indication that wapiti would progress to the next patch was a dramatic drop in cropping rate below the seasonal expectation. This seems to be a definitive test of the Marginal Value Theorem. However, it is difficult to distinguish whether the animal interrupted a foraging sequence because foraging returns declined or whether feeding slowed because the animal had decided to move to a new patch. If I accept the former (conventional) explanation, I might wonder how cropping rates are compared. Perhaps the expected cropping rate is memorized as the frequency of head movement in grazing, a rhythm which may be easily timed with other inner physiological rhythms such as heart and respiration rate.

Seasonal changes in average patch size may be related to both animal condition and grassland quality and heterogeneity. After a long winter, grazing and other factors such as wind and snow created considerable grassland heterogeneity. Wapiti mainly lived on weathered grass left over from last year. Under such an energetic stress, wapiti seemed reluctant to give up a patch. Wapiti grazed each feeding station longer and foraged for two consecutive feeding stations of low intake rates before interrupting a foraging sequence to move to another patch. In May, patch size was the greatest, fresh green grass was in surplus so wapiti could easily satisfy their growth impetus (Jiang and Hudson, 1992). Under such circumstances wapiti left a patch as soon as the cropping rate dropped below the seasonal average. Wapiti grazed patches in May about two times longer as in spring and about six times longer as in autumn. In August, the grassland was again fragmented with small patches of matured sward, which offered foraging opportunities reminiscent of spring and departure rules appeared similar.

### Feeding stations

Wapiti develop a rhythm of cropping bites and steps during grazing which determines their rate of advance. They seldom took all possible bites within reach before moving on. Presumably, foraging selectivity, reach and balance are the main factors determining behavior at this level. When a wapiti moves its head to search the next bite, the gravity of the head produces a vector which acts on its shoulder. The smaller the neck angle, the greater the pulling force. Foraging seemed to be interrupted whenever the neck angle reaches a threshold such that the shifting center of gravity necessitates movement of the foreleg to maintain balance.

### Optimal grazing of wapiti

Wapiti terminated foraging sequences in patches as the intake rates dropped, even though they may tolerate low intake rate longer when energetically stressed. The results provided a critical test of the Marginal Value Theorem, suggesting that wapiti foraged optimally. At feeding stations, cropping rate accelerated as bites consumed increased. The distance between bites decreases as the number of bites consumed at a feeding station increases, a situation thoroughly explored by Holling (1959). Unless bite size declines, wapiti should graze a feeding station as long as possible. Therefore, both giving-up strategies seem to be optimal.

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# CHAPTER VI BITE CHARACTERISTICS[1]

Gates and Hudson (1983) explored the foraging behavior of wapiti with a focus on the habitat selection. Hudson and Nietfeld (1985) and Hudson and Watkins (1986) studied feeding rate of wapiti in relation to forage biomass. Both studies indicated that sward structure is an important determinant of foraging behavior of wapiti.

Sward structure influences the foraging behavior of other herbivores as well (Milne *et al.*, 1982; Barthram and Grant, 1984). Grazing sheep adjust their bite stratum according to sward structure (Burlison *et al.*, 1991). Sward height in homogeneous hand-constructed swards is the most influential parameter influencing bite depth (Ungar *et al.*, 1991). Tiller length is correlated with herbage availability which in turn is correlated with bite size and forage intake (Allen and Whittaker, 1970; Forbes, 1989; Ungar *et al.*, 1991).

Hodgson (1981) noted the importance of sward structure on the foraging selectivity of domestic grazers and adopted a point quadrat to study the vertical sward profile. On Serengeti grasslands, Coughenour *et al.* (1984) studied the effects of grazing on grass canopy structure by measuring leaf angle, biomass concentration, and tiller heights. On grassland in the boreal forests, because of the dense tillers and leaves in the swards, leaf angle measurement was inappropriate. Other technique needs to be developed.

A bite is the basic unit of diet selectivity by herbivores and it forms the basis of several grazing models (Demment and Greenwood, 1988; Ungar and Noy-Meir, 1988). Unfortunately, bite size and food intake are difficult to quantify. Stobbs (1973a) and Milne *et al.* (1982) used esophageal fistulation and Allden and Whittaker (1970) employed short-term weight gain during grazing. Other approaches include hand-plucked samples (Hudson and Nietfeld, 1985), artificial swards (Demment and Greenwood, 1988; Spalinger *et al.*, 1988; Ungar and Noy-Meir, 1988), and marker methods (Holleman and White, 1989; Jiang and Hudson, 1992).

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[1] A version of this chapter has accepted for publication. Jiang, Z. and Hudson, R. J. 1994. Bite characterisucs of wapiti (*Cervus elaphus*) in seasonal *Bromus-Poa* swards. Journal of Range Management 47 (1).

In this study, I assessed bite size and diet quality of wapiti in relation to bite depth in seasonal *Bromus-Poa* swards with different vertical biomass and quality profiles. Specific questions guiding the study were (1) how does stratification of sward biomass and forage quality change seasonally? (2) how do wapiti adjust bite characteristics in relation to these changes in sward structure? From this, I inferred how bite depth affected bite size and diet quality.

## Methods

### Animals

I studied 12 female wapiti, six born in 1988 for the 1990 grazing season and another six born in 1990 for the 1991 grazing season (denoted adults and yearlings, respectively). Half of the adults and two of the yearlings were hand-reared, facilitating close observation. In May 1990, the adults weighted 230 ± 7 kg. In May 1991, the yearlings weighed 138 ± 7 kg.

### Sward structure and bite characteristics

I studied sward structure with a cubic sampling quadrat. The quadrat had three stacked 0.5 X 0.5 m quadrats welded with four steel wires (one m long and five mm in diameter) at the four corners. Between the top and the bottom quadrats, a movable quadrat was adjusted to specific heights and fixed by wing-nuts. Two one m rulers were welded at opposing sides to measure the height of the movable quadrat. With this device, I randomly sampled nine quadrats per season from the area where wapiti grazed in late May (fully leafed stage, late spring), late June and early July (full bloom stage, summer) and August (seed ripened stage, autumn), respectively in 1990. In spring, I cut the swards into three layers of equal height, whereas in summer and autumn I cut seven and six layers, respectively. I separated the sample into graminoid stems, graminoid leaves, dicots and unidentified portions. In spring, I also sorted the sample into withered and green matter. I clipped another ten 0.5 x 0.5 m samples (without distinguishing layers) in each season to increase the sample size for studying the relationship of sward height and biomass. For the additional samples, I averaged the sward height at the four corners of the quadrat. From mid-May until mid-October, 1990, I measured 22 randomly selected plant heights every ten days.

I observed the wapiti and subsequently assessed bite depth and bite area. On dew, frost and newly grazed swards, I measured bite imprints to calculate bite areas (Jiang and Hudson, 1993). The bite imprints were measured in two dimensions: the long axis and short axis. The bite area was calculated as an ellipse. In each season, I assumed that bite areas of the same age group were similar. I opportunistically measured the stubble heights of 50 bites and 50 adjacent ungrazed plants in the bites site and calculated the difference as bite depth. Vertical diet selection in spring was determined in May 1990. Wapiti were released into a previously ungrazed paddock. I measured the height of dried plants, green grass and bite stubble. Horizontal diet selection in summer and autumn was taken from research conducted at the same site (Nietfeld, 1983).

### Forage quality

Samples were pooled by layer and season, then oven-dried at 60°C for laboratory analysis. Sub-samples were taken for dry matter determination at 110°C. I determined the gross energy, crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF) and 72% sulfuric acid lignin. Gross energy was determined with a bomb calorimeter (PARR Instrument Company, IL, USA). Crude protein (N x 6.25) was determined by the macro-Kjeldahl method (A.O.A.C., 1984). NDF, ADF and lignin were determined according to Goering and Van Soest (1970).

### Calculating bite size and diet quality

I calculated relative height (RHi) or relative biomass (RBi) of layer i in relation to the total height or biomass (Jiang and Xia, 1987). I also calculated the median RHi and RBi in each layer, MRHi and MRBi:

$$MRH_i = \frac{RH_i + RH_{i-1}}{2} \qquad (i=1,\dots, L) \qquad [VI.1]$$

$$MRB_i = \frac{RB_i}{RH_i - RH_{i-1}} \qquad (i=1,\dots, L) \qquad [VI.2]$$

Where: L is the number of layers cut in the season.

Exponential regression between $MRH_i$ and $MRB_i$ in each season gave a dimensionless biomass density-distribution function along the vertical axis. Bite depth was calculated as an empirical function of sward height. Bite volume is a cylinder with the bite area as the bottom and bite depth as the height of the cylinder (Ungar and Noy-Meir, 1988). Finally, I quantified bite size in relation to bite volume and biomass distribution:

$$BS_{(SH,\,SN)} = BM_{(SH,\,SN)}\, BA \int_{BD\%_{(SH,\,SN)}}^{100} a\, e^{-b\,RH} dRH \qquad [VI.3]$$

Where: a and b are the exponential regression coefficients, BS is bite size (g), BM is biomass (g/cm$^2$), BA is bite area (cm$^2$), and SN is season. $BM_{(SH, SN)}$ is biomass distribution calculated by logarithmic regression of herbage biomass on sward height in each season. $BD\%_{(SH, SN)}$ is the relative bite depth calculated by linear regression of bite depth on sward height in each season.

In Equation (3), the driving variables are sward height and season. Sward height increased at 10 cm intervals from 10 cm to 30 cm in spring, to 50 cm for adults and 40 cm for yearlings in summer, and to 40 cm in autumn. The 95% confidence limits of the bite size was calculated using 95 % confidence limits of the bite depth at specific sward height.

I calculated expected dietary quality as the percentage of protein and NDF. For progressive bite depth, dietary protein and NDF were calculated according to the proportions of green, dead matter, leaf, stem and their respective protein and NDF contents in each season.

$$DC_{(k)} = \sum_{i=1}^{k}\sum_{j=1}^{n} sc_{ij}\, p_j \qquad (k=1,\ldots, L) \qquad [VI.4]$$

Where: $DC_{(k)}$ is the dietary component such as protein or NDF when bite depth reached the kth layer of the sward. L is the number of layers cut in the season as defined in Eq. VI.1. $sc_{ij}$ is the proportion of sward component j such as cured leaves, cured culms, green leaves, green culms or forbs in the kth layer. n is the number of sward components found in the layer. $p_j$ is the percentage of protein or NDF in the sward component j. The unidentified portion of the sward sample was pooled with cured stems.

### Sod experiment

I refined our estimates of bite characteristics using six pieces of 0.5 x 0.5 m sods removed with about 5 cm of soil layer from the study pasture. I measured the sward heights and placed one piece of sod in a pen with two hand-reared sub-adult wapiti. When wapiti started to eat, I took bites from its mouths to determine bite weight by placing a finger on the diastema, causing the animal to egest the bite as he attempted to remove the finger with his tongue. Then I measured the corresponding bite heights.

### Statistics

Two way multivariate analysis of variance (MANOVA) evaluated seasonal and botanical composition effects and their first order interaction on energy, protein, NDF, ADF and lignin. A multiple comparison among the means was carried out with Tukey-Kramer test

(Sokal and Rohlf, 1981). Because of the different initial sward heights in each season, the impacts of season and cohort on bite depth and their first and second order interactions were explored by 2-way ANCOVA with sward height as a covariate. Data were transformed into their square-roots to achieve homogeneity of variance. Multiple comparisons among the means of sward heights and bite depth were carried out by Fisher's protect LSD method (Sokal and Rohlf, 1981). Differences were considered significant where the probability of a type I error did not exceed 0.05. All data are presented as the mean ± 1 se.

## Results

### Sward characteristics

Biomass in swards was pyramidal, with the greatest bulk density at the base of the sward (Fig. VI.1). Spring swards had more biomass at the bottom ($p < 0.05$). Biomass and height of layers expressed in relative scale were related exponentially ($p < 0.05$). The slope (b) of the exponential regression in spring was significantly different from those in summer and autumn ($p < 0.05$). However, summer swards were no different in vertical biomass distribution from autumn ones ($p > 0.05$).

Protein, NDF, ADF and lignin differed significantly among seasons ($p < 0.05$) and forages ($p < 0.05$) and the interactions between season and forages were significant ($p < 0.05$). Green matter had more protein and less fiber than cured plant material ($p < 0.05$; Table VI.1). Dicots had more protein and less fiber than graminoids ($p < 0.05$; Table VI.1). Gross energy content differed significantly among forages ($p < 0.05$) but not among seasons ($p > 0.05$).

### Bite characteristics

Bite depth was affected by season ($p < 0.05$), sward height ($p < 0.05$) and their interaction ($p < 0.05$, Fig. VI.2). Relative to sward height, wapiti grazed deeper in spring swards than in summer and autumn ones ($p < 0.05$). Bite area was related to the age of wapiti. The bite area of adults was 38 ± 0.1 $cm^2$ in spring, and 49 ± 0.1 $cm^2$ in summer and autumn of 1990. Bite area of yearlings was 27 ± 0.03 $cm^2$ in spring and 38 ± 0.1 $cm^2$ in summer and autumn of 1991.

In early spring, wapiti selected the green leaves above the previous year's growth, which set a constraint on diet selection. In the first time grazed paddock, the heights of green grasses were about double that of dried grasses, whereas grazed stubble height was about the same as that of dried grasses. The regressions of bite height (BH), green grass height (GH) and dried grass height were as follows: (DGH) GH = 3.31(±0.29)

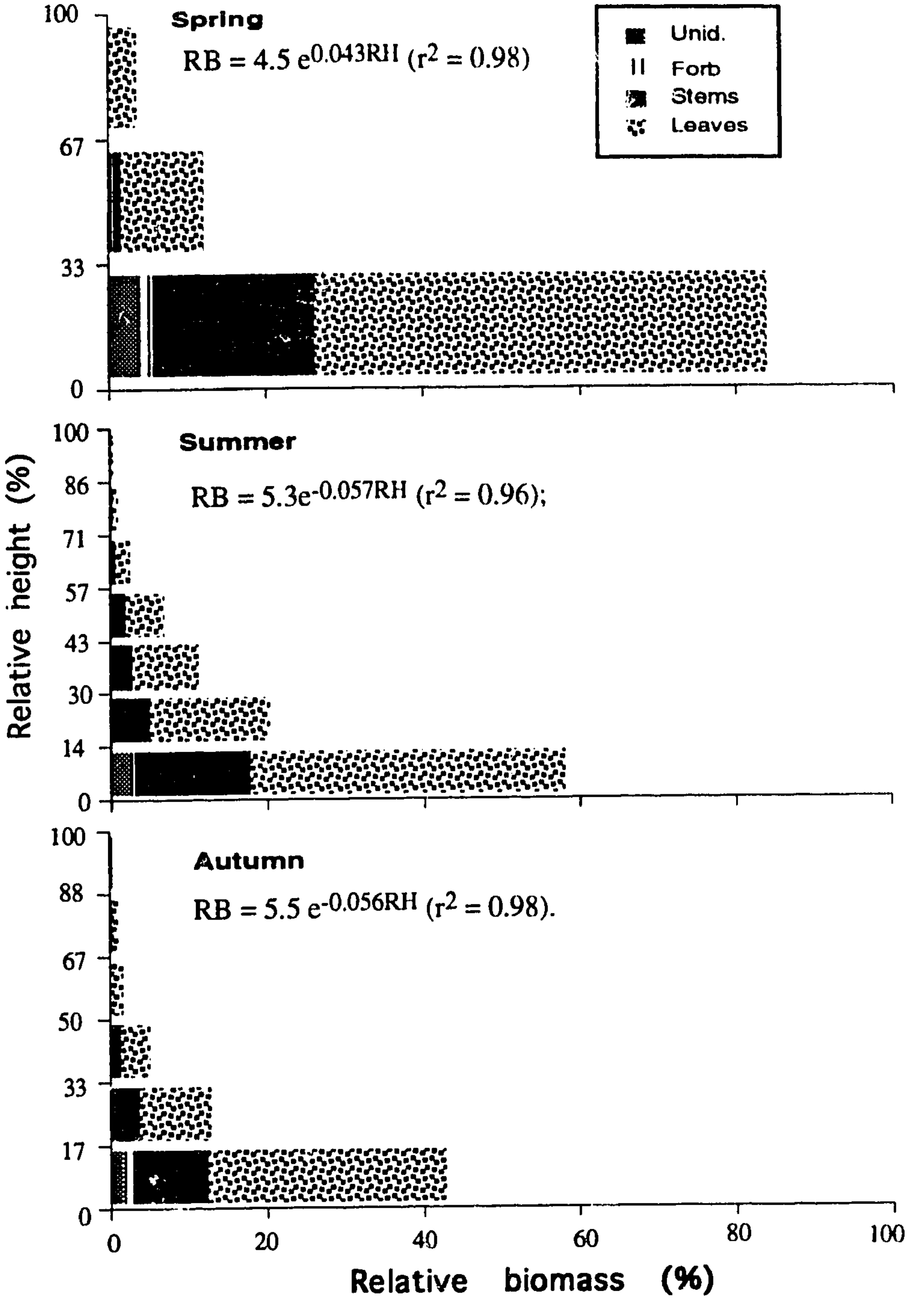

**Fig. VI.1** Seasonal sward structure and composition. In the equations, RB is relative biomass and RH is relative height.

+1.95(±0.07)DRH ($r^2 = 0.86$) and BH = 0.081(±0.14) +1.18(±0.04)DRH ($r^2 = 0.92$). In summer, wapiti shifted from a solely grass diet to a mixed grass and dicot diet. Nietfeld (1983) reported that dandelions accounted for 18% of the diet of wapiti in late May and 36% in June.

**Table VI.1** Energy, protein, NDF, ADF, and lignin in graminoids and dicots

| | Energy (kJ/g) | Protein (%) | NDF (%) | ADF (%) | Lignin (%) |
|---|---|---|---|---|---|
| **Spring** | | | | | |
| C$^1$. Leaves | 15.8 ± 0.4 | 13 ± 0.2 | 67 ± 1 | 35 ± 1 | 8 ± 0.1 |
| C. Culms | 16.3 ± 0.3 | 9.± 0.5 | 76 ± 1 | 42 ± 1 | 6 ± 0.1 |
| G.Gr$^2$. Leaves | 17.2 ± 0.0 | 17 ± 0.0 | 36 ± 2 | 18 ± 1 | 4± 1.0 |
| G. Gr.Culms | 16.6 ± 0.2 | 14 ± 0.4 | 63 ± 3 | 35 ± 3 | 6 ±0.4 |
| G. Dicots | 17.2 ± 0.0 | 25 ± 0.4 | 51 ± 1 | 26 ± 1 | 3 ±0.1 |
| **Summer** | | | | | |
| G. Gr. Leaves | 16.9 ± 0.0 | 16 ± 0.1 | 65 ± 2 | 32 ± 1 | 6 ± 0.2 |
| G. Gr. Culms$^3$ | 16.6 ± 0.2 | 9± 0.4 | 75 ± 1 | 44 ± 1 | 7 ± 0.1 |
| G. Dicots | 16.7 ± 0.0 | 22 ± 0.1 | 33 ± 1 | 17 ± 1 | 4 ±0.0 |
| **Autumn** | | | | | |
| G. Gr Leaves | 16.9 ± 0.1 | 16 ± 0.2 | 68 ± 0.9 | 34 ± 1 | 6 ± 0.1 |
| G. Gr. Culms$^3$ | 17.1 ± 0.1 | 10 ± 0.8 | 75 ± 0.9 | 42 ± 1 | 7 ± 0.2 |
| G. Dicots | 17.0 ± 0.1 | 16 ±0.1 | 49 ± 1.0 | 29 ± 1 | 6 ±0.1 |

1: C: cured.
2: G: green; Gr: grass.
3: Including heads.

Yearlings and adults had different bite sizes in seasonal swards (Fig. VI.3). In spring, yearling and sub-adult animals had larger bites in 30 cm tall swards than in 10 cm tall swards ($p < 0.05$), whereas in summer they took smaller bites in 30 cm tall swards than in 10 cm tall swards ($p < 0.05$). In autumn, yearlings had smaller bites in swards > 20 cm high than in 10 cm tall swards ($p < 0.05$), whereas adults had bites of 0.25 g in 10 cm tall swards and bites of about 0.1 g across all swards taller than 20 cm ($p > 0.05$). In autumn, the bite size of yearlings decreased as sward height increased. Bite size for adults was 0.15 g in 10 cm tall swards, 0.12 g in 20-30 cm tall swards and 0.13 g in 40 cm tall swards.

In 6 experiments using cut sod pieces, one tame wapiti ate 0.28 ± 0.06 g (3 bites) and another ate 0.18 ± 0.03 g (3 bites) on sod pieces with plant heights of 11.2 ± 1.2 cm. The predicted bite size for this sward was 0.25 g with 0.13 g and 0.51 g as the 95%

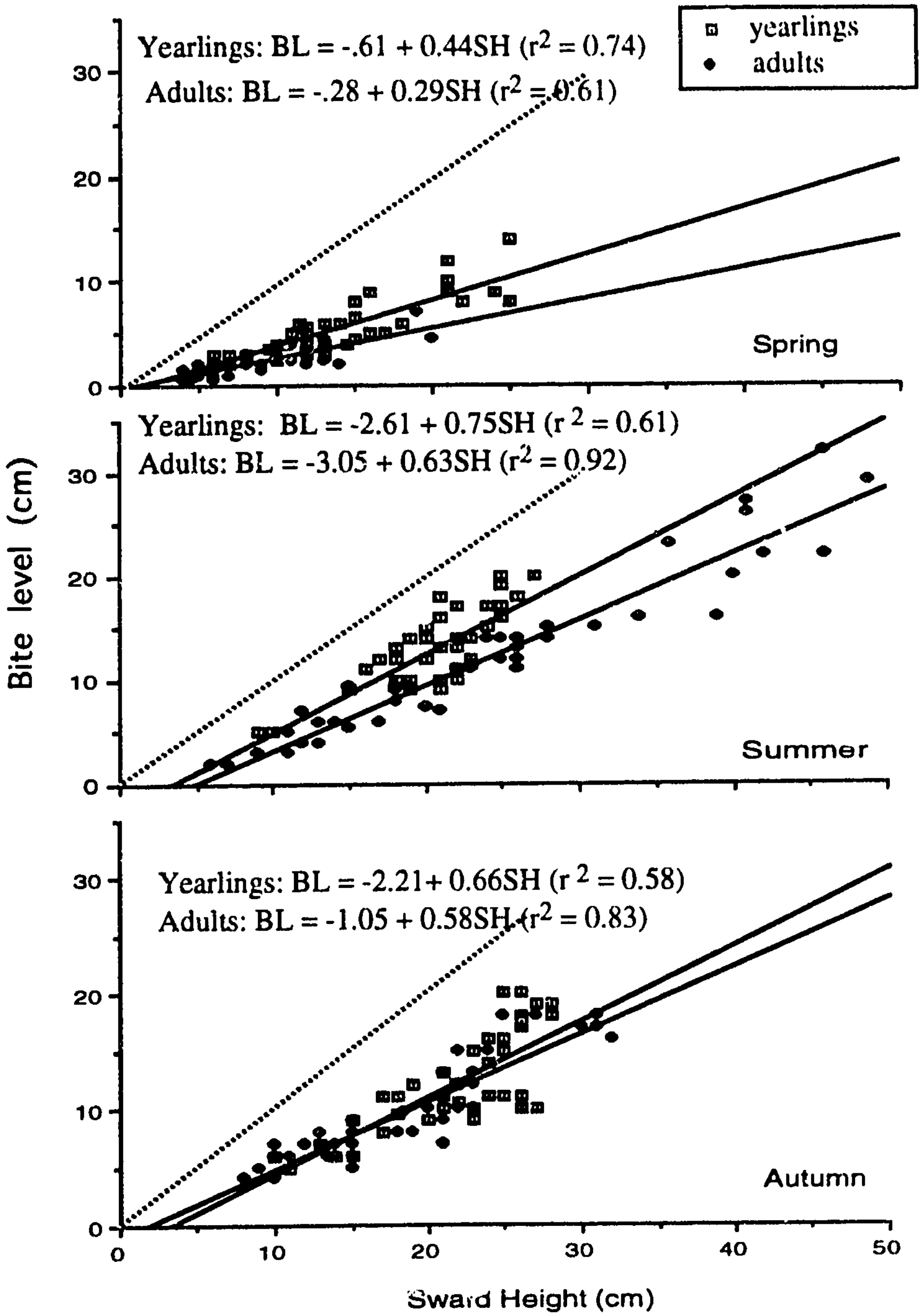

**Fig. VI.2** Bite depths of adults in 1990 and of yearlings in 1991 in seasonal swards. Dotted lines represent sward heights. In the equations, BL is the bite level, SH is sward height.

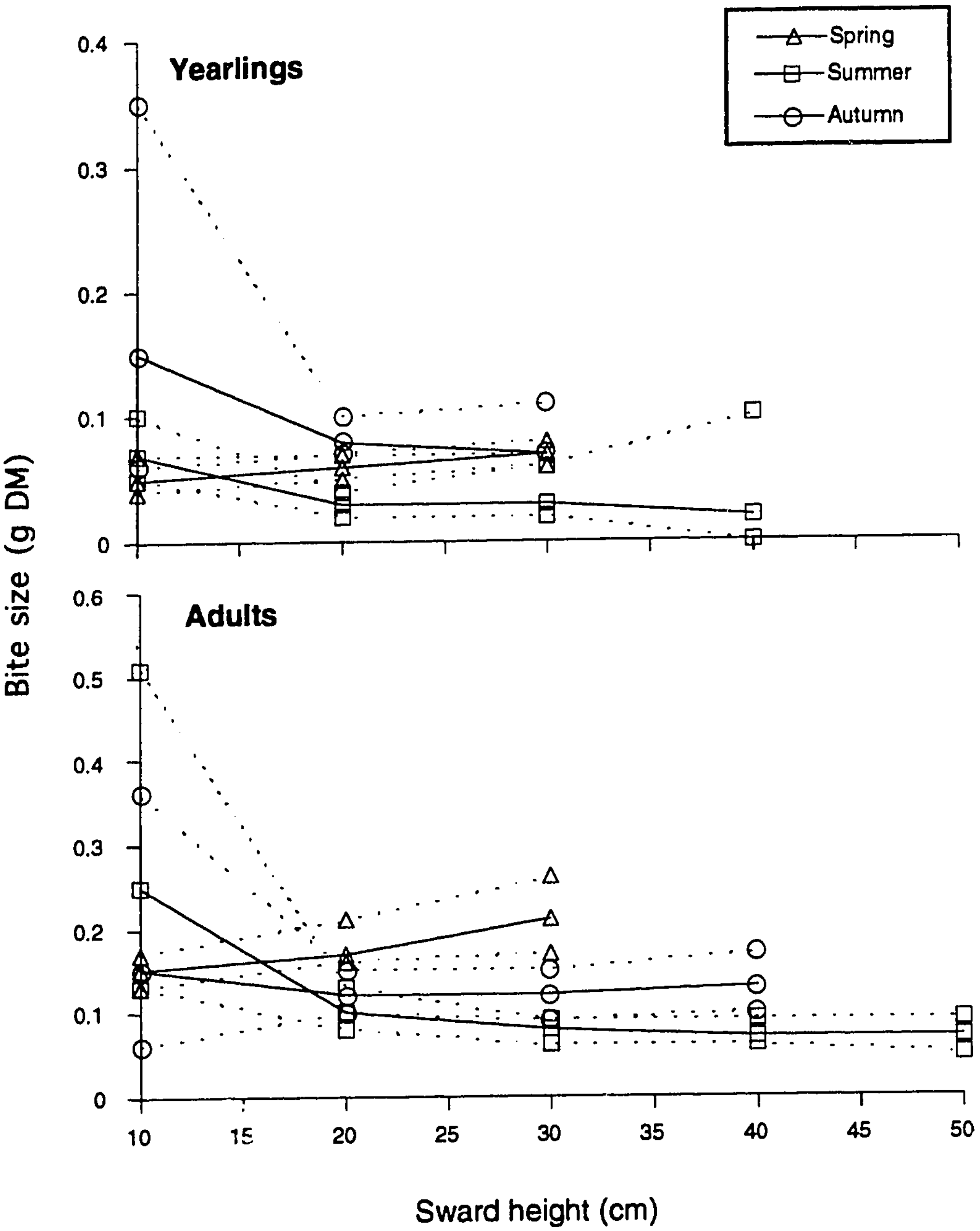

**Fig. VI.3** Simulated bite size of yearlings and adults in seasonal swards. Dashed lines are the 95% confidence limits.

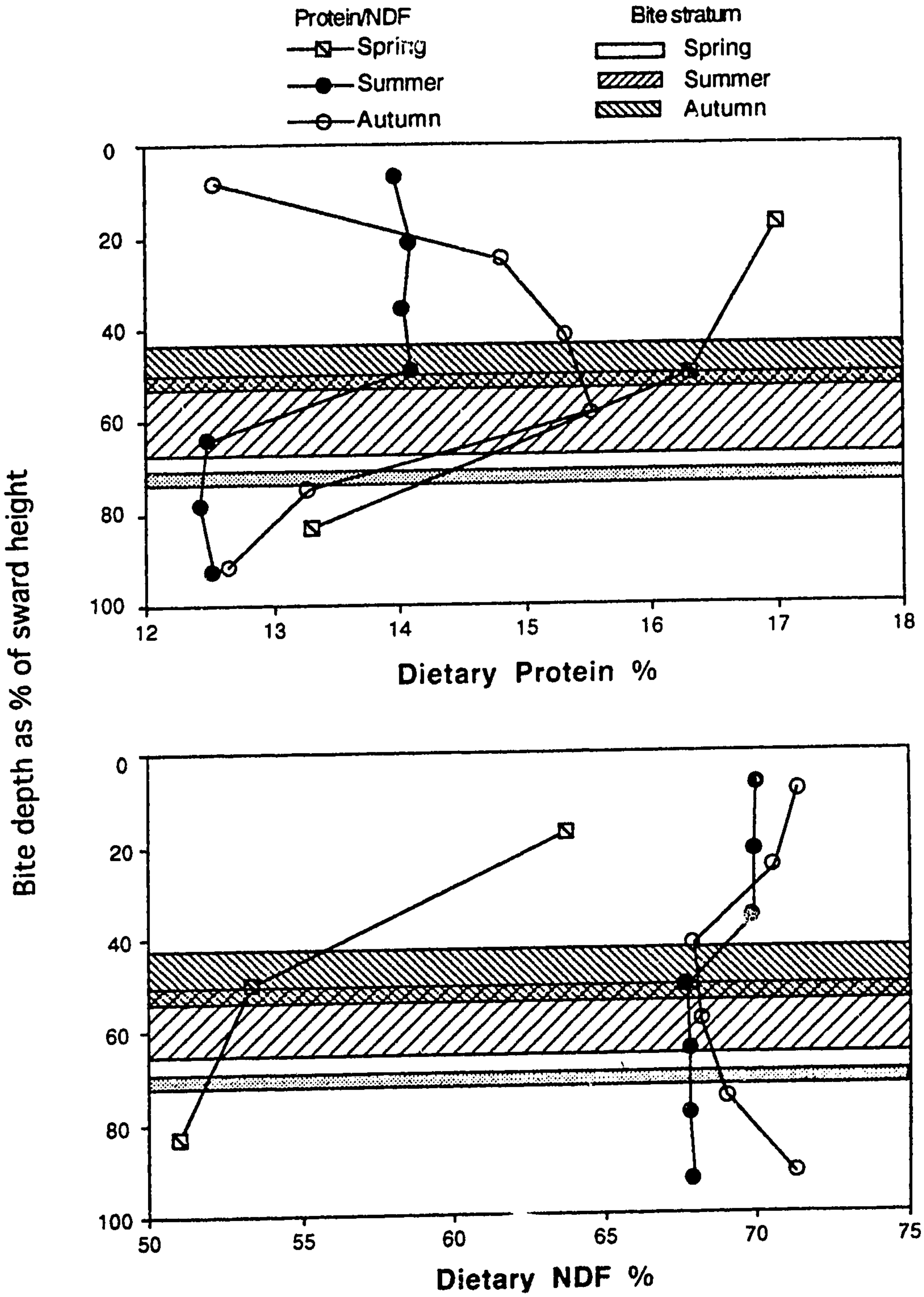

**Fig. VI.4** Bite strata in each season (range of mean bite depth corresponding to different sward height) and corresponding nutritional quality (protein above; neutral detergent fiber, below) of bites taken at various sward depth (% of the maximum sward height).

confidence limits. These results were within the range of predicted bite sizes.

### Bite level and diet quality

The expected dietary protein and NDF are summarized in Fig. VI.4. In spring, as the bite level increased from the surface to the bottom of sward, calculated dietary protein in diet decreased and NDF increased. In summer, dietary protein increased as bite level increased to 60% of the sward height. Beyond this point, dietary protein decreased, but NDF only increased slightly. In autumn, dietary protein remained relatively constant until wapiti cropped about half of the sward height. I noted a decrease in dietary protein when wapiti cropped more than 60% of the sward height. Dietary NDF increased in spring as bite level decreased because of short forbs in the swards in summer and autumn.

The average bite depth stratum of wapiti shifted upward in swards from spring to autumn (Fig XI.4). Adults, for example, grazed deeper in spring swards and they elevated their bite strata in summer and autumn swards. However the actual bite strata covered highest dietary protein than other cropping heights in summer and autumn.

## Discussion

### Sward structure

I developed the cubic sampling quadrat to quantify sward structure of pastures. Except in swards less than 5 cm tall, the cubic quadrat sampling appeared suitable. The profile I obtained was similar to the triangle shape obtained by Hodgson (1981) using a point quadrat and that by Stobbs (1973b) with a hedge trimmer mounted on an adjustable frame. Biomass and height expressed in relative scales facilitated the calculation of bite size and the comparisons among seasons.

Milne *et al.* (1982) noted the linear relationship between depth of grazed horizon and sward height would allow the prediction of forage intake. Bite depth of wapiti in seasonal swards was very similar to those of sheep and cattle (Milne *et al.*, 1982; Barthram and Grant, 1984). Grazers tend to bite a fairly constant proportion of total sward height, because they select tillers with greater leaf length and younger laminae. Barthram and Grant (1984) noticed that reduction of bite depth in tall swards may limit intake per bite and consequently total intake. Our calculated bite sizes depicted that in tall matured swards wapiti had smaller bites than in short swards during summer and autumn.

### Foraging modes

Wapiti had two foraging modes on pasture: horizontal selection and vertical selection. Bite depth represents food selection along the vertical dimension of swards. In spring, wapiti completely relied on grasses. When green leaves dominated the sward canopy, dried grasses in bottom of swards set a constraint on bite depth. Domestic grazers also consume more green than cured matter and more leaves than stems (Arnold, 1987; Black and Kenney, 1984; Dudzinski and Arnold, 1973). In summer and autumn, wapiti preferred short swards with new leaves to tall mature ones (unpublished data). Grass leaves appear more slowly in tall swards and take longer to complete their expansion (Parsons *et al.*, 1991), so grazing can improve pasture quality.

Wapiti horizontally selected individual forbs. In early summer, dandelion accounted for 20% of the total pasture biomass (Nietfeld, 1983) and wapiti shifted their diet from solely grasses to both dandelion and grasses. Pasture became heterogeneous as seed ripened in autumn, wapiti normally nibbled the leaves, avoided tall reproductive culms and selected feeding stations with short grasses. The horizontal selection in autumn differed from that in summer; the former was a selection of feeding stations whereas the latter was a selection of individual plants.

### Bite size

Bite sizes of adults calculated in this study were in the range of bite sizes measured by other methods with the same wapiti. Jiang and Hudson (1992) reported wapiti had average bites of 0.35 ± 0.08 to 0.41 ± 0.10 g in later spring , compared to 0.13 to 0.51 g in this study. Wilmshurst (1992) measured bite sizes of yearling wapiti as 0.05 to 0.4 g with a sod experiment at same research site.

Bite size is determined by bite dimensions and sward bulk density. Laca *et al.* (1992) found that bite area increased with sward height and decreased with bulk density in homogeneous swards. Whether this is true for wapiti needs to be tested, because wapiti and cattle differ in foraging mechanism. Wapiti graze by using their lips, dental pad and lower incisors to grasp and break the forage instead of using their tongues to sweep and hold forage. Furthermore, tiller density did not vary greatly in our study area, so I assumed that bite area was constant in the same season.

The relationship between bite size and sward height varies with pasture maturity, plant species composition and grazing system. On homogeneous pastures, animals grazed deeper (Milne, 1991) and took larger bites from tall swards than short swards (Burlison *et al. 1991*), whereas on heterogeneous natural grassland, grazing animals take smaller bites in mature swards than in young swards (Van Soest, 1982; Stobbs, 1973a). In our study, adult wapiti grazed larger bites in tall swards in spring than in summer, since the green material in spring swards was homogeneous and highly digestible (Jiang and Hudson, 1992). As swards matured, wapiti spent more time in short swards, perhaps due to larger bites and high quality of the newly generated leaves. In summer and autumn, wapiti did not crop as deep as they did in tall spring swards, but their bite depth covered the maximum possible dietary protein. Vertical selection is a balance of the tradeoff between dietary protein and bite size. Sacrifice of bite size in summer and autumn might be compensated by the higher diet quality.

There are limitations in the methodology I employed. First, the method of calculating bite size probably is more suitable for swards of intermediate heights. In swards less than 5 cm tall, wapiti may break the grasses at ground level; bite depth may be difficult to measure. Bite depth is only an indicator of average length of tiller removed (Laca *et al.*, 1992). In such a case, it may be a proper way to treat bite volume as a cylinder plus a hemisphere. Another shortcoming may arise from Equation VI.3 when wapiti adjust the angle of mouth to select the leaf stratum in matured swards, but I did not observe this foraging posture frequently. However, the equations of the method provide a theoretical frame work. In application, the relationship between bite size and sward height may differ from the results reported here due to different swards structure and foraging response of grazer.

This approach integrated bite depth, sward height and biomass density to predict bite sizes and diet quality of wapiti in different seasons, depicted the foraging responses of wapiti to sward structure and provided another avenue to study bite sizes and diet selection of grazing herbivores. As a functional response to sward structure, wapiti may select bite depth and bite site according to the distribution of food items, forage quality and sward configuration. Consequently, bite size of wapiti may change to a relatively large extent in response to seasonal changes in sward structure and forage quality.

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# Part II

# Digestive constraint and metabolic requirement

## CHAPTER VII DIGESTIVE KINETICS

Understanding seasonal digestive kinetics of free-ranging wild ruminants extends our knowledge of their foraging ecology (Spalinger and Robbins, 1992; Verlinden and Wiley, 1989). Because of microbial fermentation in the forestomach, longer retention times allow ruminants to extract sufficient energy from fibrous food. On the other hand, faster passage may relieve the digestive constraint of gut fill on intake. Although ruminants appear to exert most control over digestion by regulating passage rate and gut fill (Renecker and Hudson, 1990), the rumen environment also may change in response to diet and host factors.

Interrelationships among digestive parameters in *Ruminantia* and *Tylopoda* have received some attention (Renecker and Hudson, 1990; Lechner-Doll *et al.*, 1991; Warner, 1981). However, logistic and technical constraints have largely limited work to controlled laboratory conditions. Little is known about the seasonal passage and digestion of natural forage, especially for free-ranging animals.

Here, I explore how seasonal forages affect digestibility, passage rate and gut fill in wapiti grazing *Poa-Bromus* pastures in western Canada. The specific objectives were: 1) to explore whether seasonal differences in digestive parameters were due to diet or morphophysiological adaptation, 2) to assess relative importance of reticulorumen and hindgut in digesta retention and gut fill.

### Methods

The study was conducted at the Ministik Wildlife Research Station, Alberta, Canada (53° 18'N, 114° 35' W). The research station is located on dead ice moraine characterized by low hills covered with *Populus* forests interspersed with scattered lakes and ponds in depressions. *Carex* spp. dominated the wetlands whereas *Bromus pumpellianus, Poa pratensis* and *Taraxacum officinale* dominated the grasslands. In both years of the study, snow covered the ground from November to April.

I determined digestibility (Dig), mean retention time (MRT) and dry matter intake (DMI) and calculated digestion rate and gut fill of 12 adult hinds (2 years old) in 1989-1990 (Experiment 1) and 12 yearling hinds in 1990-1991 (Experiment 2). In both experiments, half of the wapiti were fed pellets and the rest were pastured throughout the year but were offered supplementary hay during late winter. In Experiment 1, only one trial with pellets was conducted in winter. In all trials, the wapiti were fed *ad lib.*, except the grazing trials.

The control groups were offered alfalfa-barley pellets, a standard ration allowing nutrient requirements to be easily met throughout the year. When on trial, animals were placed in individual digestion crates for a week to quantify intakes. They were then administered a single dose of labeled pellets as described below and returned to a group pen with access only to pellets and water. Group intakes and individual body weights were recorded at least once a week.

The control group was contrasted with a group fed harvested herbage in winter and grazed in spring and summer (to distinguish, the term *herbage* applies to hand-fed material and *forage* refers to grazed material). Herbage was harvested in the study area in October just before snow covered the pasture. When on herbage trials in winter, the group was allowed to adjust to the diet for two weeks, followed by one week group feeding, and one week in individual digestion stalls. Herbage rejected was removed, weighed and corrected for moisture content daily. Feces also were collected quantitatively to determine apparent digestibilities. Passage rate studies with a dose of $Cr_2O_3$ labeled pellets followed the digestion trial (Jiang and Hudson, 1992). When not on trial in winter, wapiti were supplied with brome hay in Experiment 1 and alfalfa hay in Experiment 2 because of the low availability of pasture forage. When pasture flushed in May, the pastured groups in both experiments obtained their diets from grazing until autumn.

### Passage rate

Chromic oxide ($Cr_2O_3$) was used as an indigestible marker with the alfalfa-barley pellet serving as the carrier (Jiang and Hudson, 1992). The concentration of chromic oxide was 0.40%. The wapiti were placed in individual stalls and each was given 250 g labeled pellets (less than 10% and 3% of their daily DMI in winter and spring-summer, respectively). Normally, the wapiti consumed the pellets within 10 minutes without prior fasting. After consuming the marked pellets, they were released to group pens (pellet and herbage trials) or to pasture (free-ranging trials).

From 18 to 22 fecal samples were collected from each wapiti during a six day collection period after marker administration. For the first two days, fecal samples were collected at four-six h intervals, but less frequently in the following days. Fecal samples were collected opportunistically as wapiti grazed. Although fresh feces could be easily collected from snow in winter, feces on bare ground and pasture in spring and summer were sometimes contaminated with soil or litter, so only the top layer of the feces was collected.

Samples were dried at 60°C, ground through 20-mesh screen with a Wiley Mill, and sub-sampled for determining NDF, ADF and lignin. About two g ground sample was weighed before and after drying at 110°C overnight. The procedure for chromium determination was modified from Fenton and Fenton (1979). The sample was ashed at 550°C in a muffle furnace overnight. The ashed sample was digested in a ventilation hood at 250-300°C on a hot plate in a solution of 150 ml distilled water, 150 ml concentrated sulfuric acid, and 200 ml 70% perchloric acid. The digesta was filtered through No. 4 Whatman filter paper and diluted to known volume. The absorbance of the filtrate was determined by atomic absorption spectrophotometry using an air-acetylene flame.

Marker concentrations were fit quantitatively using a two-compartment time-dependent model (Grovum and Williams, 1973b):

$$Y(t) = A(e^{-k_1(t-TT)} - e^{-k_2(t-TT)}) \qquad [VII.1]$$

Where: Y(t) is the fecal marker concentration at time t, $k_1$ is the rate of ruminal emptying and $k_2$ is the rate of emptying a secondary mixing pool in the hindgut, TT is the digesta transit time through the omasum and the small and large intestines (Grovum and Phillips, 1973). A is a fitted parameter representing the theoretical maximum initial marker concentration.

MRT was calculated as the sum of reticulorumen retention time (MRTr), $-1/k_1$, hindgut retention time (MRTh), $-1/k_2$ and transit time (TT):

$$MRT = MRTr + MRTh + TT \qquad [VII.2]$$

Digestibility

Digestibilities of both forage and pellets were determined by total fecal collection or from the ratio of indigestible internal markers in forage and feces. During individual trials, feces were collected quantitatively and sampled for dry matter determination at 110 °C.

The choice of internal marker depended on circumstances. Lignin and acid-insoluble ash (AIA) were accurate in pen studies and satisfactory on winter pasture. However, lignin in spring forage did not appear completely indigestible and was sensitive to diet where animals had access to browse. Soil consumption was a serious limitation of AIA on spring and summer pastures. Under such circumstances, chromogen was the preferred method.

AIA was analyzed according to Van Keulen and Young (1977). Chromogen was extracted from ground dry samples in 85% acetone and determined by spectophotometric absorption at 406 mμ (modified from Reid *et al.*, 1953). Alfalfa pellets, random clipped pasture forage, harvested herbage and fecal samples were analyzed for dry matter (DM), crude protein (N x 6.25), neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin and ash (Association of Official Analytical Chemists, 1984).

I estimated digestion rates (DR) from forage indigestibility and MRT:

$$DR = -\frac{\ln(1 - Dig)}{MRT} \qquad [VII.3]$$

The negative sign in Eq. VII.3 indicates that digestion is a negative exponential process; i.e. the amount of forage which remains undigested decreases with time.

Gut fill was estimated according to Holleman and White (1989).

$$Vn = Dfec \cdot MRT \qquad [VII.4]$$

$$V = \frac{Vn - Vn/(1 - Dig)}{\ln(1 - Dig)} \qquad [VII.5]$$

Where: Dfec (g/hr) is the dry feces output, Vn (g) is indigestible dry matter fill, and V (g) is the dry matter gut fill. DMI and gut fill were scaled to g/kg body weight, because of the linear allometry of alimentary size (Van Soest, 1982).

### Statistics

ANOVA was calculated with Super ANOVA (Abacus Concepts, 1989). Seasonal and dietary differences of MRT, MRTr, MRTh and TT were tested using pooled data on forages which were either harvested or grazed in both Experiment 1 and 2. I also compared differences in MRT, MRTr, MRTh and TT among pellets trials and differences between wapiti on pasture forage or pellets in Experiment 2. Multiple-comparison among means were carried out with the Tukey-Kramer Test. Data were summarized as mean ± se. Differences were considered significant where the probability of Type I error did not exceed 0.05.

## Results

Alfalfa-barley pellets offered wapiti a high protein and low fiber ration (Table VII.1). Spring pasture forage had lowest fiber contents and highest protein among the seasonal pasture forages. Fiber content increased and protein content decreased as pasture matured.

### Passage

Total tract MRT of wapiti on pasture forage changed seasonally in both experiments (Fig. VII.1). The MRTs of cured winter pasture herbage were significantly longer than those from spring and summer pasture forages ($p < 0.05$). In Experiment 1, the pelleted diet was retained for shorter period than winter pasture herbage ($p < 0.05$). In Experiment 2, seasonal differences seemed largely related to diet (Fig. VII.1b). Pellets were retained slightly longer in winter than summer, but the difference was not significant ($p > 0.05$). Pellets were passed faster through the gut than pasture herbage in winter ($p < 0.05$), but pellets were retained about the same duration as spring green forages ($p > 0.05$).

MRTr, MRTh and TT were affected by season (Table VII.2, $p < 0.05$). Retention times in the reticulorumen and hindgut of wapiti fed harvested herbage were different from those of free-ranging wapiti in spring and summer in pastured animals in both experiments. In both experiments, pasture forages were retained longer in the reticulorumen in winter than in spring-summer ($p < 0.05$). In Experiment 2, yearlings on pasture forages had longer transit times in winter than in spring-summer ($p < 0.05$).

### Digestion

Pellets and pasture forage had distinctive digestibilities (Fig. VII.1), which were affected [illegible] type ($p < 0.05$) and season ($p < 0.05$). As expected, digestibility of pasture [illegible] in spring was highest and declined as forage approached maturity in both experiments.

In Experiment 1, digestibility of pasture forage declined 20 percentage points ($p < 0.05$) from spring to autumn. In Experiment 2, digestibilities were significantly affected by diet ($p < 0.05$) and season ($p < 0.05$). However, digestibilities of pellets in winter and summer were not different from each other ($p > 0.05$) and neither were significantly different from the summer forage ($p > 0.05$).

Digestion rates of pellets, calculated from total digestibilities and mean retention times, were significantly higher than those of cured winter herbage ($p < 0.05$) but similar to those of spring and summer forages (Table VII.2). Digestion rates of pasture forages peaked during the period of most rapid growth in May.

### Gut fill

Season had no effect on calculated gut fills of adults and yearlings on pasture forages or on pellets ($p > 0.05$), but gut fills were typically higher for wapiti on pasture forage diets than for those on pellets in winter and early spring ($p < 0.05$, Fig. VII.2). For the adults, the gut fills of wapiti on pasture were relatively constant, between 16.2 ± 1 g per kg body weight in winter to 17.4 ± 2.7 in summer. However, the highest gut fills (28.1± 4.9g/kg body weight) were seen in the yearlings fed harvested herbage in winter. Yearlings on pellets had low gut fill in winter (10.7 ± 0.3g/kg body weight). The gut fill of the yearlings on pellets increased to 13.6 ± 1.8 in April and to 22.2 ± 2.2, which approached that of pastured animals in July.

**Table VII.1** Diet composition (DM basis).

| | Energy (kJ/g) | Protein (%) | ADF (%) | NDF (%) | Lignin (%) | Ash (%) |
|---|---|---|---|---|---|---|
| Pellets (alfalfa/barley) | 17.5 | 17.1 | 14.2 | 29.3 | 3.4 | 6.4 |
| Harvested herbage | 17.1 | 9.6 | 39.0 | 68.5 | 5.4 | 11.0 |
| Spring pasture forage | 18.0 | 16.7 | 18.0 | 35.5 | 2.0 | 6.8 |
| Summer pasture forage | 17.6 | 16.0 | 36.4 | 67.0 | 5.3 | 7.9 |

## Discussion

This study examined digestive dynamics of a wild ruminant on seasonal pastures and, therefore, adopted methods which required minimal intervention. The study offers the advantage of natural context but necessarily lacks tight experimental control. The results are expected to be sensitive to methodology, particularly the choice of analytical models and indigestible markers.

Holleman and White (1989) pointed out that digestive markers have not been used to their analytical potential and offer considerable advantages for studying wild and semi-domestic ruminants (Jiang and Hudson, 1992). Although single-dose markers are widely used for determining passage rates, it is theoretically possible to use them to estimate gut fill and digestion rates if total tract digestibility is also determined.

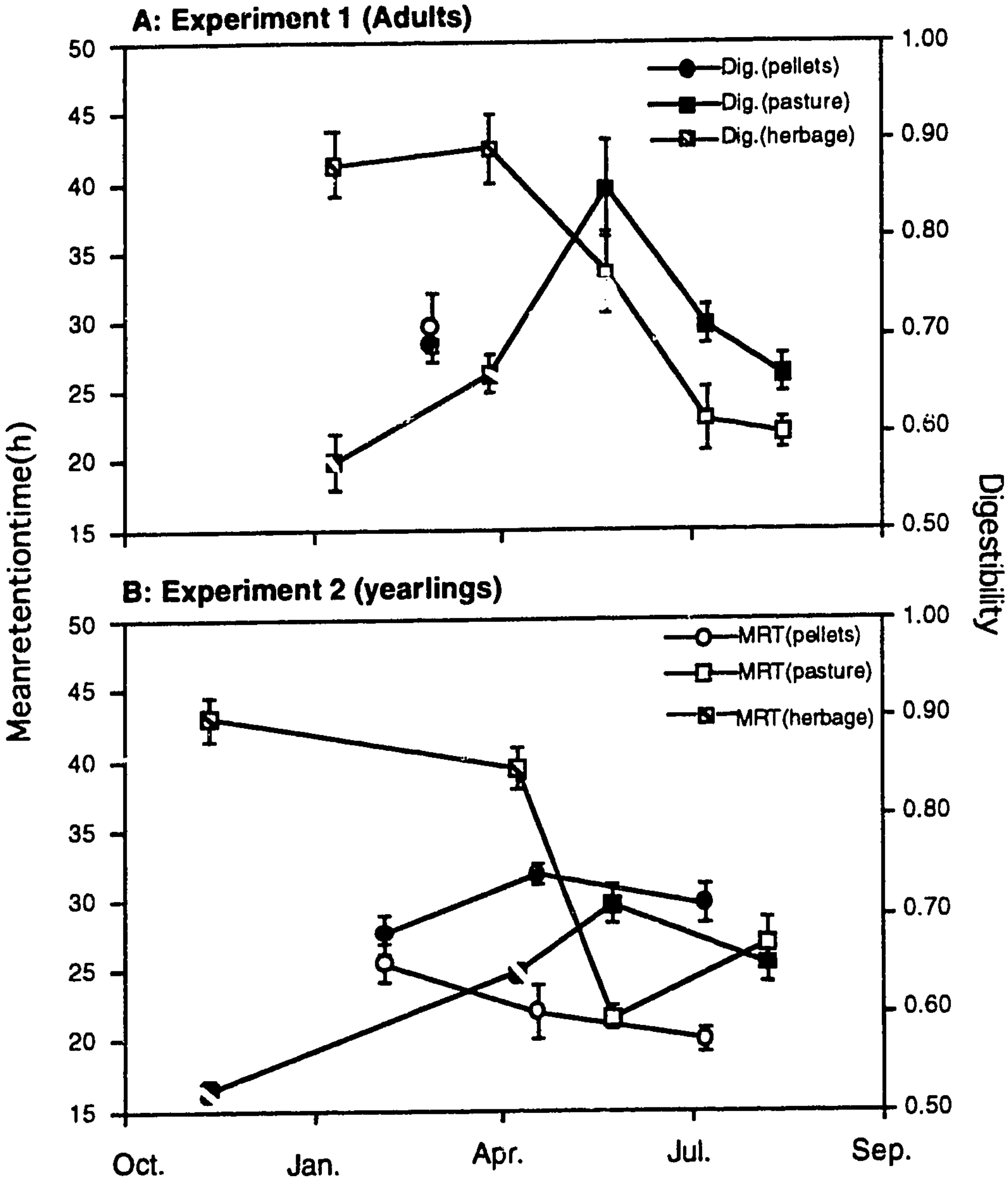

**Fig. VII.1** Seasonal mean retention time (MRT) and digestibility (Dig.) in adults and yearlings.

**Table VII.2** Digestive parameters of wapiti consuming pellets, hand-cut winter herbage or pasture forage.

| Date | Diet | BW[1] (kg) | DMI[1] (g/kg) | Digestion rate (%/h) | MRTr[1] (h) | MRTh[1] (h) | TT[1] (h) |
|---|---|---|---|---|---|---|---|
| **Experiment 1 (adults):** | | | | | | | |
| 1/10/90$^{W2}$ | herbage | 230±6$^{a, 3}$ | 14 ± 1$^{a}$ | 2 ± 0.2$^{a}$ | 13.7 ± .4$^{a}$ | 13.2 ± .7$^{a}$ | 11.5 ± 1.2$^{ab}$ |
| 2/26/90$^{W}$ | pellets | 228±6$^{a}$ | 15 ± 1$^{a}$ | 4 ± 0.4$^{ac}$ | 11.6 ± .8$^{ac}$ | 9.3 ± 1.2$^{ac}$ | 9.5 ± 2.2$^{ab}$ |
| 3/26/90$^{W}$ | herbage | 226±5$^{a}$ | 16 ± 2$^{a}$ | 3 ± 0.2$^{ac}$ | 11.9 ± 1.2$^{a}$ | 8.7 ± 1.7$^{ac}$ | 12.7 ± 0.6$^{a}$ |
| 5/21/90$^{sp}$ | pasture | 230±7$^{ab}$ | 27 ± 5$^{b}$ | 7 ± 1.5$^{b}$ | 9.8 ± 2.3$^{ad}$ | 7.0 ± 1.7$^{bc}$ | 4.3 ± 0.9$^{ac}$ |
| 7/8/90$^{s}$ | pasture | 238±5$^{ab}$ | 44 ± 4$^{b}$ | 6 ± 0.4$^{b}$ | 7.1 ± 1.0$^{b}$ | 4.1 ± 0.9$^{bd}$ | 8.7 ± 0.6$^{a}$ |
| 8/14/90$^{s}$ | pasture | 253±5$^{b}$ | 40 ± 6$^{b}$ | 5 ± 0.3$^{bc}$ | 7.5 ± 0.5$^{bc}$ | 7.0 ± 0.5$^{bcd}$ | 8.5 ± 0.2$^{a}$ |
| **Experiment 2 (yearlings):** | | | | | | | |
| 11/10/90$^{W}$ | herbage | 129±7$^{a}$ | 20 ± 2$^{a}$ | 2 ± 0.1$^{a}$ | 16.4 ± 2.6$^{a}$ | 7.2 ± 1.6$^{a}$ | 20.9 ± 1.0$^{a}$ |
| 2/3/91$^{W}$ | pellets | 131±9$^{a}$ | 17 ± 2$^{a}$ | 4 ± 0.3$^{b}$ | 12.6 ± [illegible].2$^{ab}$ | 7.8 ± 1.4$^{ac}$ | 8.8 ± 0.8$^{bc}$ |
| 4/8/91$^{sp}$ | herbage | 129±7$^{a}$ | 22 ± 2$^{a}$ | 2 ± 0.1$^{a}$ | 16.4± 1.5$^{a}$ | 3.8 ± 1.6$^{a}$ | 20.6 ± 1.6$^{a}$ |
| 4/18/91$^{sp}$ | pellets | 141±6$^{a}$ | 18 ± 3$^{a}$ | 6 ± 0.6$^{c}$ | 8.4± 1.4$^{b}$ | 5.0 ± 1.7$^{a}$ | 10.4 ± 1.4$^{b}$ |
| 5/24/91$^{sp}$ | pasture | 138±7$^{a}$ | 45 ± 3$^{b}$ | 7 ± 0.3$^{c}$ | 5.9 ±0.8$^{b}$ | 1.4 ± 0.6$^{ab}$ | 11.8 ± 0.5$^{b}$ |
| 7/8/91$^{s}$ | pellets | 158±6$^{b}$ | 41 ± 5$^{c}$ | 6 ± 0.4$^{c}$ | 6.6 ± 0.3$^{b}$ | 3.4 ± 1.1$^{a}$ | 9.7 ± 1.7$^{bc}$ |
| 8/7/91$^{s}$ | pasture | 163±7$^{b}$ | 29 ± 3$^{c}$ | 4 ± 0.3$^{b}$ | 9.6 ± 1.3$^{ab}$ | 5.5 ± 1.3$^{a}$ | 7.3 ± 0.3$^{bc}$ |

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1. BW: body weight; DMI: dry matter intake; MRTr, MRTh: reticulorumen, hindgut retention times, TT: transit time.
2. w: winter, sp: spring, s: summer.
3. Values that share the same superscript letter with others in the column within each experiment are not significantly different ($p > 0.05$). Data presented as mean ± standard error.

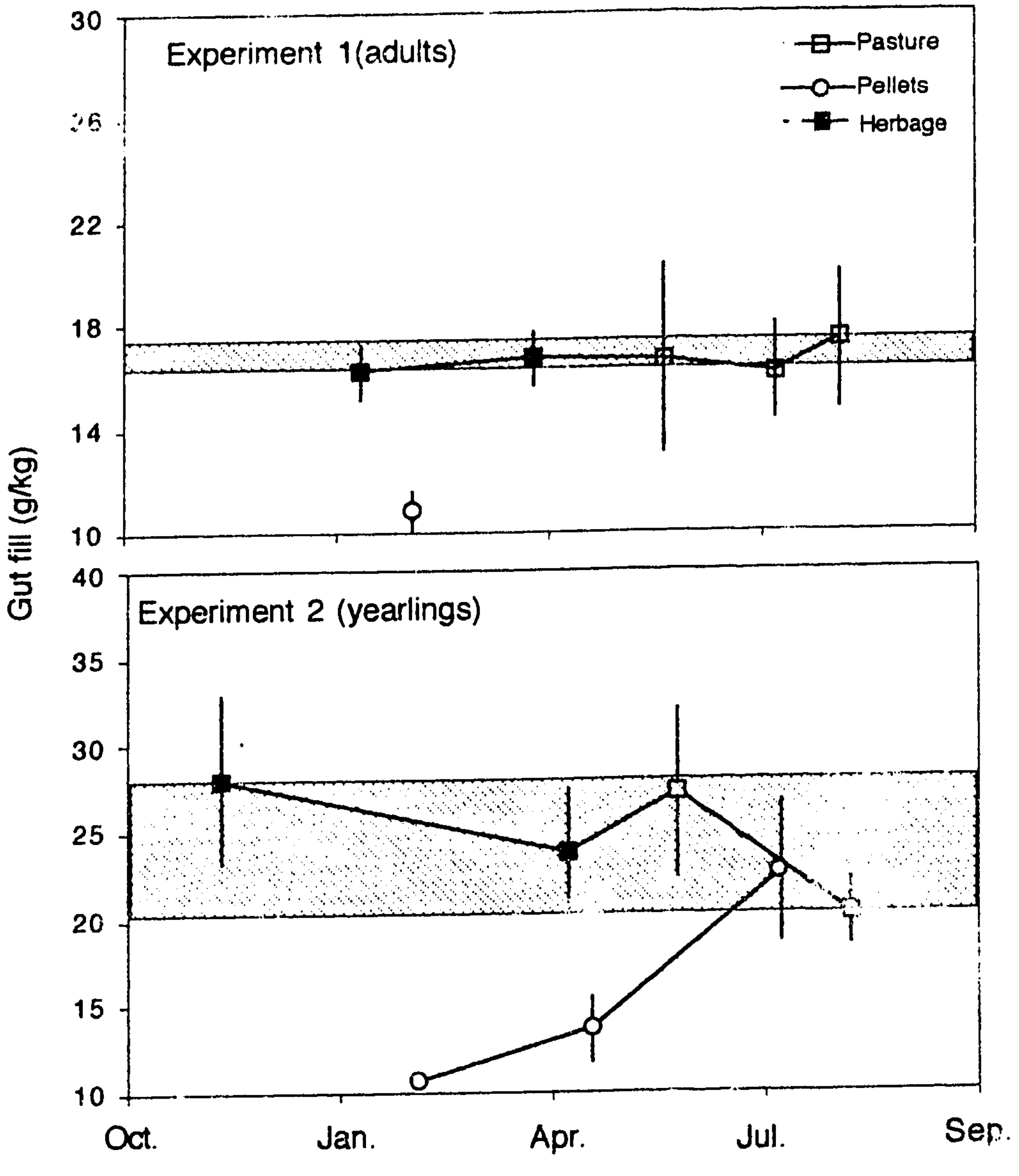

**Fig. VII.2** Seasonal gut fills (g digesta per kg body weight) in adults and yearlings. Crosshatched areas indicate the average maximum and minimum gut fills when wapiti fed on pasture forages.

The basic model used in this study recognizes only two mixing [illegible] which represent the reticulorumen and hindgut. This model is one of many proposed to study kinetics of ruminant digestion (Spalinger and Robbins, 1992; Van Bruchem *et al.*, 1990; Holleman and White, 1989; Baker and Hobbs, 1987; Westra and Hudson, 1981; Van Soest, 1982; Grovum and Williams, 1973b; Blaxter, 1956). The abomasum is another potential mixing pool but Grovum and Williams (1973a) determined abomasum retention time was less than 5% of the reticulorumen retention in sheep, and they (1973b) suggested that the mixing effect of abomasum is incorporated into the effect of hind gut. Additional parameters may improve the fit of the model but the coefficients typically have large standard errors and seldom reveal interesting differences.

No digestive marker is perfect (Warner, 1981). Chromic sesquioxide, used in this study, may migrate separately from forage fibers (Uden *et al.*, 1980). However, in wapiti, liquid and particulate phases tend to move together (Renecker and Hudson, 1990) and this may be typical of mixed feeders and browsers (Kay, 1993). Chromium-mordanted fiber could be an alternative, but mordanting blocks microbial digestion sites (Van Soest, 1982). Longer mordanted fiber will not be broken down like forage particles and forage particles of different size have different migration speeds in the alimentary tract (Spalinger and Robbins, 1992).

Passage rates of the pelleted diet were similar in winter and summer which may imply that the digestive system of wapiti adapts to diet rather than photoperiod. Passage of feed particles through the digestive tract depends on the physical and chemical properties of forage (Blaxter *et al.*, 1956; Van Soest, 1982). Although passage rates generally reflected diet quality, the rapid passage of green forage and pellets in spring and summer may be partially due to seasonally high intake (Warner, 1981; Van Soest *et al.*, 1988). Ruminal retention times were most clearly linked to intake.

Feed particles are subject to competing rates of digestion and passage. In the absence of fistulated animals, I attempted to calculate instantaneous digestion rates from passage rate and total tract digestibility. Because of the indigestible residue after prolonged fermentation (Van Soest, 1982), the method may be more precisely applied only to potentially digestible matter. Nevertheless, I obtained values for winter forages in the same order of magnitude (3.8%/h) determined for ruminally-fistulated wapiti fed timothy-brome hay (Renecker and Hudson, 1990). Fresh aspen foliage had digestion rates of over 7%/h (*op. cit.*) similar to our values for summer pasture. Fractional digestion rates reflected neutral and acid-detergent fiber contents.

Gut fill is the outcome of interacting rates of digestion, passage and intake. Gut fill is increased by either increasing intake rate or decreasing digestion and passage rates.

Wapiti on harvested herbage maintained the same gut fill as those on spring-summer pastures. In both experiments, wapiti were offered *ad lib* harvested herbage during winter trials and thus were spared the cost of foraging in snow-covered pastures. Despite physiological inappetance in winter (Jiang and Hudson, 1992), the animals ate to maintain gut fill.

Spring forage was highly digestible and passed rapidly, so gut fill in spring did not increase significantly with increased intake. Pasture biomass was high in 1990, so the adults had no difficulty grazing enough to satisfy their requirements into the summer. But pasture biomass was lower in August 1991 than in 1990 and the gut fill of grazing yearlings decreased while the gut fill of pellet-fed animals increased. This suggests that intake was constrained by other factors such as the logistics of foraging (Jiang and Hudson, 1993a and b; 1994 in press). Because pellets had similar digestion and passage rates in winter and summer, seasonal increased intake was reflected in the elevated gut fill.

Baker and Hobbs (1987) reported that the calculated gut fill of wapiti remained unchanged whereas that of mule deer increased and that of mountain sheep decreased as the proportion of grass/browse increased. Renecker and Hudson (1990) also found considerable differences in rumen fill associated with diet and season.

I conclude that seasonal digestive adaptation in wapiti appears to be largely related to diet and seasonal appetance rather than to endogenous morphophysiological changes which might anticipate seasonal changes in resources.

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# CHAPTER VIII ESTIMATING FORAGE INTAKE[1]

Forage intake is a central variable in grazing ecology and management. Unfortunately, its importance is matched with its difficulty of measurement under field conditions. Although progress has been made in determining feeding rates of wild ruminants, measuring daily intake under field conditions remains a challenge (Wickstrom, *et al.* 1984; Hudson and Watkins, 1986; Renecker and Hudson, 1985; Spalinger *et al.*, 1988).

Estimates of forage intake usually are based on: (1) pasture biomass depletion, (2) direct estimates of ingestion using esophageal or ruminal fistulae, (3) bite rates, bite sizes and grazing times, and (4) fecal output (by total collection or inert marker) and a measure of digestibility. For wild ruminants, the latter two methods apparently offer the greatest prospects.

Direct observation of bite rates, bite sizes, and grazing times (bite-count method) has been widely applied to wild ruminants because it imposes the least manipulation and disturbance (Wickstrom *et al.*, 1983; Hudson and Nietfeld, 1985; Renecker and Hudson, 1985; Spalinger *et al.*, 1988). Its greatest limitation is the long period of continuous observation required and the subjectivity of estimating bite sizes.

If digestibility is known, forage intake can be determined from fecal output. Although fecal output is most precisely measured by total collection (Galyean *et al.*, 1986), the method is expensive, labor intensive, and may alter grazing behavior (Hatfield *et al.*, 1990), particularly of less tractable wild ruminants. Therefore, digestive markers are an attractive alternative, although their precision varies. Hatfield *et al.* (1990) reported that a once-daily dose with ytterbium was more precise and accurate than either a pulse-dose or intraruminal bolus. Holleman and White (1989) found that measured and calculated feces output differed by less than 2% in pen-fed sheep administered a single-dose of radioactive marker (cerium$^{141}$ chloride).

In this study, I evaluated use of a single-dose of chromic oxide to determine fecal output and, in conjunction with digestibility coefficients, forage intake of wapiti. We then

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[1] A version of this chapter has been published. Jiang, Z. and Hudson, R. J. 1992. Estimating forage intake and energy requirement of free-ranging wapiti (*Cervus elaphus*). Can. J. Zool. 70:675-679.

applied the method to estimate the metabolizable energy requirements of wapiti for maintenance and live weight gain.

### Materials and Methods

Twelve adult non-lactating female wapiti averaging 234 kg at the beginning of the study were assigned to two groups of six animals. One group was kept in a 0.1 ha enclosure before and between pen trials whereas the other group grazed 65 ha of aspen parkland vegetation.

Feed intakes determined by the marker method were compared with those determined directly in pen-feeding trials using herbage (January) and alfalfa-barley pellets (February). For free-ranging animals on spring pasture (May), the single-dose method was compared with the bite-count method. To corroborate the results, I pooled estimates of metabolizable energy intake from pen and field studies and compared them with rates of body weight gain.

#### Digestion marker and digestibility

The single-dose marker method, fecal sampling and marker determination process are described in Chapter VII. The determination of digestibilities of herbage, alfalfa-barley pellets and pasture forage are as described in Chapter VII.

#### Calculation of food intake

The calculation was based on the assumption that the input and output of the alimentary tract of wapiti were in a steady state. First, the mean concentration during the fecal sample collection period was calculated:

$$\mathrm{MC}\ (\mathrm{mg/g}) = \frac{\sum_{1}^{n}((m_{i+1}+m_{i})-M_{0})*(t_{i+1} - ti)}{2(T_{2} - T_{0})} \qquad [\mathrm{VIII.1}]$$

Where, MC is the mean concentration of marker; $m_{i+1}$, $m_i$ are marker concentrations at times $t_{1+1}$ and $t_1$; $M_0$ is the chromium concentration at $T_0$, which is calibrated for the chromium background. $T_2$ is the time of the last sampling.

Then the hourly dry fecal matter output was calculated by a modified Stewart-Hamilton equation (Holleman and White 1989):

$$D_{fec}(\mathrm{g/hr}) = \frac{D}{\mathrm{MC}(T_{2}-T_{0})} \qquad [\mathrm{VIII.2}]$$

where, $D_{fec}$ is the dry feces output ; D is the marker dosage.

Finally, the daily dry matter intake was calculated:

$$\text{DMI (kg/day)} = \frac{2.4\text{Dfec}}{100 - \text{Dig\%}} \qquad [\text{VIII.3}]$$

Digestible energy intake was calculated from digestible dry matter intake and the gross energy of each diet. Metabolizable energy was calculated conventionally as 85% of digestible energy (Blaxter, 1989).

Pen trials

Before each pen trial, the animals was allowed to adapt to their food for at least two weeks. For measuring their daily intake, they were subsequently placed in individual digestion stalls for a week. The foods offered and rejected were removed, weighed and corrected for moisture content daily. Feces also were quantitatively collected to determine apparent digestibilities. During group and individual feeding, feed was offered *ad lib.*

The herbage used in the first trial was harvested at the research station in October, 1989 before a permanent snow cover was established. The dominant forage species were bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis* ), white clover (*Trifolium* spp.) and dandelion (*Taraxacum officinale*). The harvested herbage was naturally dried, then stored under a plastic tarpaulin until the trial. The alfalfa-barley pellets used in the second pen trial were formulated as a complete feed for captive ruminants and contained 17% protein and provided 11 MJ/kg of metabolizable energy.

Bite-count method

Forage intake on pasture was calibrated using the bite-count method based on bite rate, bite size and feeding time (Hudson and Watkins, 1986). Dry matter intake (DMI) was calculated:

$$\text{DMI (kg/day)} = \text{BR} \cdot \text{BS} \cdot \text{AT} \cdot \text{FR} \qquad [\text{VIII.4}]$$

where, BR is the bite rate (bite/min), BS is bite size (g/bite) in dry matter, AT is active time (min/day), and FR is the foraging/active ratio.

A pocket computer program was developed to determine the proportion of active time spent foraging and to tally bite rates of focal animals. Average bite sizes were estimated by hand-picking 50 simulated bites to duplicate as closely as possible the amount and species composition ingested by wapiti (Hudson and Nietfeld, 1985). Activity time was determined with a vibracorder (Kienzle Apparate G. M. b. h., Villingen, Schwarzwald, Germany) suspended from a loosely fitted neck collar. Active and nonactive states were read from 7-10 day charts.

## Results

### Intakes and digestibilities

Dry matter intakes estimated by the single-dose technique compared well with intakes measured directly in pen feeding trials with herbage and alfalfa-barley pellets despite the narrow range of feed intakes (Fig. VIII.1). Diets (herbage, pellets) were not significantly different and there were no interactions with the slope of the covariate (actual intake). However, the intercept (1.46 ± 0.59) was significantly greater than zero and the slope (0.54 ± 0.18) was less than unity.

Bias differed for each diet (Table VIII.1). Differences between calculated and measured DMI ranged from -6.3% to 9.8 % for herbage whereas bias among pellet-fed animals ranged more widely from -9.5 % to 13.9%. Although not directly comparable, intakes on spring pasture estimated by the marker method were overall 6% lower than bite-count estimates and ranged widely from -21 to 5%.

Estimated by the bite-count method, wapiti foraged at 38 bites/min taking individual bites which weighed 0.229 g DM. The daily activity time for a focal animal fitted with a vibracorder was 15 h and of this time, 96% was engaged foraging. The calculate intake, therefore, was 7.6 kg/d. Intakes (Table VIII.1) in the winter pen trials were at or below maintenance. On the herbage diet, wapiti consumed only 32 g/kg$^{0.75}$ of digestible dry matter daily, providing 588 kJ digestible energy. Wapiti on pellets consumed 37 g/kg$^{0.75}$ of digestible dry matter daily. Intakes increased three-fold on spring pasture to 105 g/kg$^{0.75}$ and the animals rapidly gained weight. Pellets (69%) were more digestible than cut-grass (61%) but less digestible than spring forage (85%).

### Metabolizable energy requirements

Liveweight gains were strongly related to intake estimates expressed as metabolizable energy pooled from pen and field trials (Fig. VIII.2). The strong fit was partly due to the 6-fold range of energy intakes. Although the relationship approached linearity, the convention in bioenergetic studies is to reverse the axes and fit separate lines above and below maintenance to obtain estimates of ME requirements for maintenance and liveweight gain. For the winter pen trials, metabolizable energy requirements were 572 kJ/W$^{0.75}$ for

Table VIII.1 Daily intakes of wapiti during pen and field trials

| | Herbage (Jan) | Pellets (Feb) | Pasture (May) |
|---|---|---|---|
| Body weight (kg) | 232 ± 5 | 226 ± 6 | 230 ± 4 |
| Dry feces (g/hr) | 57 ± 4 | 45 ± 4 | 45± 2 |
| Digestibility (%) | 57 ± 3 | 69 ± 1 | 85 ± 1 |
| Calculated DMI (kg/d) | 3 23 ± 0.11 | 3 17± 0.18 | 7.27 ± 0.43 |
| Measured DMI (kg/d) | 3.37 ± 0.17 | 3.05 ± 0.19 | 7.60 ±0.16[a] |
| Bias (%) | 1 ± 3 | 1 ± 4 | -6 ± 5[a] |
| Gain (g/d) | -190 ± 80 | -130 ± 80 | 900± 140 |
| Digestible DMI (g/kg$^{.75}$ d) | 32 ± 3 | 38 ± 3 | 105 ± 7 |
| Energy intake (kJ/kg$^{.75}$d) | 588±53 | 634±39 | 1857±116 |

[a] By bite-count method.

maintenance and mobilized tissues contributed 25.7 kJ/g ($Y = 572 + 25.7X$, $r^2 = 0.84$). On spring pasture, wapiti apparently required 936 kJ/W$^{0.75}$ for maintenance and 38.5 kJ/g for liveweight gain ($Y = 936 + 38.5X$, $r^2 = 0.92$).

## Discussion

Inert markers are widely used in ruminant nutrition. Generally, continuous administration (at least daily doses) is used to determine fecal output and pulse doses are used to determine the kinetics of digesta passage (Grovum and Williams, 1973a,b; Warner, 1981; Hatfield *et al.*, 1990). The potential for using single doses to determine fecal output and indirectly forage intake of free-ranging wild ruminants seems to have been dismissed until Holleman and White's (1989) paper. In this study, I explored this possibility with captive wapiti.

### Marker and protocol

Although not a perfect marker, trivalent chromium is commonly used in animal nutrition

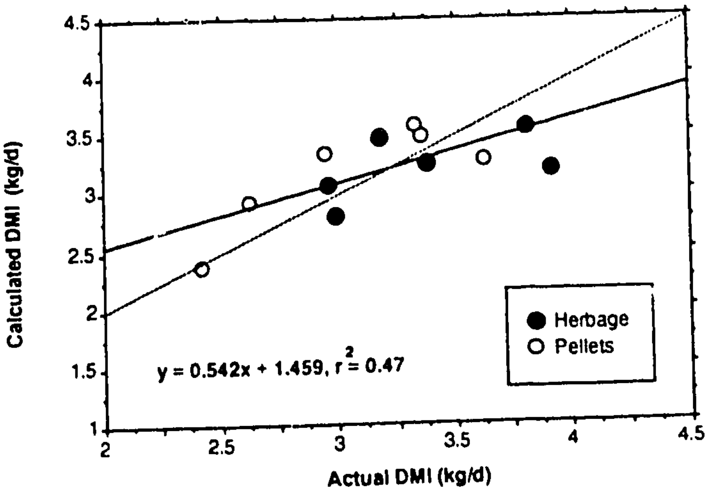

Fig. VIII.1 Dry matter intakes (DMI) of young wapiti hinds estimated by a single dose marker technique compared with actual intake determined in pen trials using herbage or pellets. The solid line is the least-squares regression; the dotted line is the 1:1 slope.

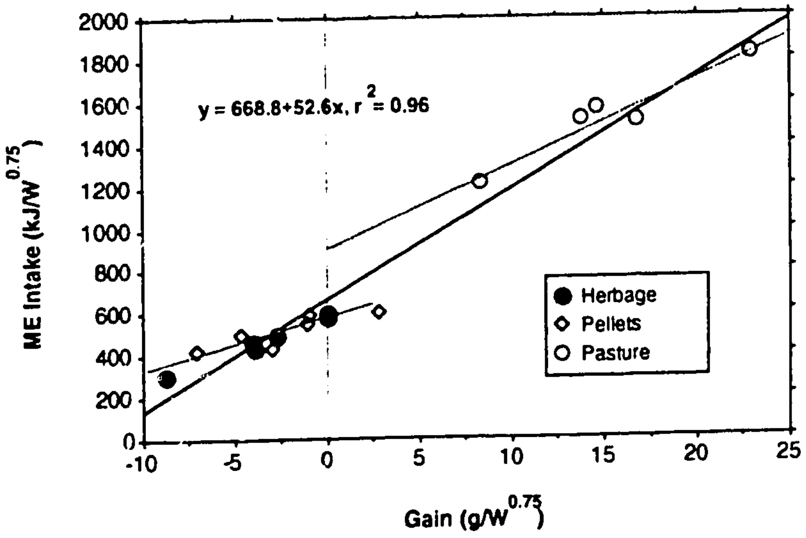

Fig. VIII.2 Estimation of metabolizable energy (ME) requirements for maintenance and liveweight gain in winter pen trials and on spring pasture by regression of intake of ME (kJ/W$^{0.75}$) on liveweight gain (g/W$^{0.75}$). The equation given is that of the pooled regression line (heavy solid line). Parameters of separate regressions for penned (herbage, pellets) and pasture trials are presented in the text.

(Uden *et al.*, 1980; Warner, 1981; Van Soest *et al.*, 1983; Renecker and Hudson, 1990). Chromic oxide is a purified chemical and thus lends itself to accurate dosing (Hatfield *et al.*, 1990) and it forms stable complexes with food ingredients (Martz *et al.*, 1974). Despite its limitations, no practical marker yet described meets all the desired properties, so its use continues (Warner, 1981).

Using chromic oxide-labeled pellets to dose wapiti proved a practical means of administration. The animals voluntarily ate the labeled pellets. The use of atomic absorption rather than chemical methods for determining chromium resolved the problem of sensitivity. The advantage of using marked pellets was that I avoided the stress of using boluses, drenches and fistulae.

The area under the curve describing fecal marker concentrations was calculated by a different method than the empirical differential method of Holleman and White (1989) which involved fitting 2 polynomial equations to the build-up and peak phases and an exponential equation to the terminal phase. Hatfield *et al.* (1990) also fitted their data according to an empirical one-compartment model.

### Precision and bias

Estimates of DMI using the single-dose method compared well with empirically-determined intakes of herbage and pelleted feeds. This spans the wide range of diet quality wapiti might be expected to encounter in the wild although it does not cover all physical forms. For example, pelleted feeds are characterized by high rates of passage which reduces their apparent digestibility without impairing their nutritional value. Browse also is an important component of the seasonal diet and should be included in future calibrations of the method.

Deviation between the single-dose and bite-count methods becomes greater under field conditions. This may be due to the greater day-to-day variability in forage intake by grazing animals and to a variety of problems with both methods. The main bias of the single-dose method probably is related to soil ingestion by grazing animals which inflates the estimate of digestibility derived from acid-insoluble ash. But a greater number of problems plague the bite-count method. Most serious is the subjectivity of visually estimating bite sizes and the assumption that all animals spent the same time grazing. Therefore, the bite-count method is not particularly satisfactory for calibrating the new method.

### Metabolizable energy requirements

The non-linear relationship between gain and metabolizable energy intake suggests that either dry matter intakes on pasture were underestimated, or metabolizable energy is used more efficiently for maintenance than gain. Biased estimates of intake on pasture should not be discounted, particularly when the marker method gave lower estimates than the bite-count method. However, the most likely error is overestimation of digestibility when animals ingest soil while grazing and this should inflate estimates of intake. The last explanation is conventional and is the reason for fitting separate curves above and below maintenance.

Maintenance requirements of 570 kJ/W$^{0.75}$ for penned wapiti during winter are similar to 520 kJ/W$^{0.75}$ determined for penned red deer hinds and 570 kJ/W$^{0.75}$ for stags in New Zealand (Fennessy *et al.*, 1981; Suttie *et al.*, 1987). No comparable estimates are available for maintenance requirements of 936 kJ/W$^{0.75}$ for young wapiti hinds on spring pasture.

Since the animals were of similar body weight during the pen and field trials, the energy content of body weight change should be similar. Because body fat has an energy value of about 39 kJ/g and lean tissue (with associated water) about 5 kJ/g, and protein and fat are deposited and mobilized together, typical energetic values of gain generally range from 8-30 kJ/g. In our study, mobilization of body tissue provided 26 kJ/g during the winter pen trials but required 38.5 kJ to deposit 1 g body tissue on spring pasture. Thus, metabolizable energy was used for gain with an efficiency of 67%, a value consistent with estimates for red deer and domestic livestock on high quality forages (Simpson *et al.*, 1978).

Estimates of requirements for liveweight gain among red deer vary from 37 kJ/g for stags to 55 kJ/g for hinds (Fennessy *et al.*, 1981; Suttie *et al.*, 1987). The similarity of our wapiti to stags rather than hinds may have been due to their young age. Weaned calves, for example, require only about 16 kJ/g (Simpson *et al.*, 1978). However, because these animals were pregnant, growth of the fetus may have been relevant.

## Conclusion

The single-dose method was a convenient and reliable method for measuring forage intake of wapiti in the field. Using highly palatable pelleted feed as a carrier solved the problem of marker administration. Forage intakes calculated with the single-dose method agreed with those measured directly and were strongly related to liveweight gains. With the single-dose method, rates of passage of digesta, digestive tract fill and forage intake all can be studied with the same data set. It opens another avenue for determining energy requirements for maintenance and gain of free-ranging wild herbivores.

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## CHAPTER IX FASTING HEAT PRODUCTION[1]

One of the most striking characteristics of northern ruminants is their seasonal rhythm of appetite, energy expenditures and growth (Bandy *et al.*, 1970). However, recent studies on seasonal fasting metabolic rates measured under carefully standardized conditions question whether metabolic rate and hence requirements change from winter to summer (Tyler and Blix, 1990; Pekins *et al.*, 1992)

### Methods

I determined the seasonal fasting metabolic rate and metabolizable energy requirements for maintenance and live weight gain of yearling wapiti hinds held in pen or on pasture. Six wapiti grazed native pastures supplemented with alfalfa hay when pasture availability declined in winter whereas another six were on alfalfa/barley pellets to maximize growth throughout the year. Body weights of both groups were recorded at least once a week. Energy balance trials were conducted in winter, spring and summer. The penned wapiti were allowed to adjust to the diet for two weeks, followed by one week group feeding, then confined in metabolic crates for the measurements of feed consumption and total feces excretion. Forage consumption of the free-ranging yearlings was determined by the single dose method (Jiang and Hudson, 1992). Finally, both penned and pasture groups were fasted for 48 hours for measuring fasting metabolic rate. Season and diet-specific metabolizable energy requirements for maintenance and gain were determined from regression of ME intake on live weight gain.

### Results and Discussion

Statistically, the 48 hour fasting metabolic rates did not change among seasons ($p > 0.05$) or between penned and pastured wapiti ($p > 0.05$, Table IX.1), even though the maintenance energy requirement of the wapiti was low in winter and high in summer. Presumably, the behavioral adaptations and thermal regulation are the factors influencing the energy expenditure. Daily maintenance requirements of young wapiti held in pens ranged from 473 kJ/kg$^{0.75}$ in winter to 728 kJ/kg$^{0.75}$ in summer. On spring and summer pasture, daily maintenance requirements ranged from 900 to 984 kJ/kg$^{0.75}$, the energetic cost of grazing added 246 kJ/kg$^{0.75}$ to the maintenance requirement of wapiti. Growth of

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[1] This chapter has been reported as a poster paper at VII World Conference on Animal Production. Edmonton, Canada. pp 154-155 in Vol. 3 of *Proceedings of VII World Conference on Animal Production*.

the wapiti slowed in winter and accelerated in spring, a profile matching the availability of natural forage. Energy requirements for gain were the same in pen and field trials but were lower in winter (29 kJ/g) than in spring or summer (40 kJ/g).

## Conclusion

My study supported the finding of Tyler and Blix (1990) and Pekins *et al.* (1992) and provides basic information on the metabolizable energy needs of wapiti.

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Jiang, Z. and Hudson, R. J. 1992. Estimating forage intake and energy requirements of free-ranging wapiti (*Cervus elaphus*). Can. J. Zool. 70: 675-679.

Pekins, P. J. Mautz, W. W. and Kanter, J. J. 1992. Reevaluation of the basal metabolic cycle in white-tailed deer. pp. 418-422. In *The Biology of Deer*. Brown, R. D. (ed). Springer-Verlag, NY.

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**Table IX.1** Intercepts and slopes of regression: MR(w) = a + bT(hr) in winter, spring and summer. where, MR is metabolic rate, T is the fasting time in hour.

| | a, RMR(w)[1] | b | 48 hr FMR[2](w) |
|---|---|---|---|
| **Winter** | | | |
| Penned | 5.30±0.24 | 0.043±0.008 | 2.67±0.22 |
| Pastured | 5.96±0.41 | 0.058±0.016 | 2.37±0.52 |
| **Spring** | | | |
| Penned | 6.52±0.38 | 0.060±0.014 | 2.37±0.42 |
| Ranging | 6.67±0.29 | 0.055±0.011 | 2.48±0.32 |
| **Summer** | | | |
| Penned | 5.67±0.29 | 0.040±0.010 | 2.83±0.29 |
| Ranging | 6.66±0.51 | 0.058±0.016 | 2.41±0.42 |

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1 RMR stands for resting metabolic rate.

2 FMR stands for fasting metabolic rate.

# CHAPTER X MAINTENANCE AND GROWTH REQUIREMENTS[1]

The wapiti farming industry is rapidly growing in western Canada. To control feeding costs, information about seasonal maintenance and growth energy requirement of wapiti is needed. At the present time, owing to lacking of information on wapiti, farmers, veterinarians and extension agents must refer to research on red deer (half the size of wapiti) conducted under quite different conditions in Britain and New Zealand.

Wapiti graze native pasture forages from spring to autumn, and live on local hay and alfalfa-barley products in winter. The unique climatic environment and the seasonal cycles of growth, appetite and energy metabolism of the northern ungulates (Bandy *et al.*, 1970; Hudson and White, 1985; Hudson *et al.*, 1985) characterize the wapiti game industry in western Canada.

One of the problems with previous studies is that researchers measured energy expenditure rather than requirements. Maintenance requirements can be assessed more directly by determining the amount of feed needed to maintain body energy throughout t year (Blaxter, 1989). Energy requirements for seasonal live weight gain can be simultaneously estimated by regression of metabolizable energy intake (MEI) on live weight gain. The objective of this study was to determine whether the energy costs for maintenance and live weight gain change on a seasonal or dietary basis.

## Materials and Methods

### Experimental design

Twelve female calves averaging 108 ± 7 kg when weaned were divided between two treatments (pellets and pasture) and engaged in chamber and field energy balance trials in winter (November 1, 1990 - March 15, 1991), spring (March 15, 1991 - May 31, 1991) and summer (June 1, 1991 - August 31, 1991). The pellet group was offered alfalfa-barley pellets *ad lib.* whereas the pasture group grazed 65 ha of aspen parkland vegetation.

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[1] A version of this chapter has been accepted for publication. Jinag, Z and Hudson, R. J. 1994. Seasonal energy requirements for maintenance and gain by wapiti (Cervus elaphus). Canadian Journal of Animal Science.

During winter, the free-ranging group had access to supplementary alfalfa hay. When snow covered the ground, pastured wapiti mainly fed on alfalfa hay and cratered only when temperatures rose and snow conditions improved.

### Pen trials

Following a 2-week adjustment period, *ad lib*. feed intake was determined on a group basis for a week before each trial. To measure individual daily intake, wapiti were subsequently placed in digestion crates for a week. Because feed intakes in crates were lower than expected from group feedings, data were scaled to seasonal group-fed means. Feeds offered and rejected were removed, weighed and corrected for moisture content daily. Feces were collected quantitatively to determine apparent digestibilities.

### Pasture trials

Intakes of pasture forage by free-ranging wapiti were determined by a single-dose marker method (Jiang and Hudson, 1992).

### Digestibility Estimates

The estimation of digestibility of hay, alfalfa-barley pellets and pasture forages are as described in Chapter VII.

### ME requirements for maintenance and gain

Although a variety of models could have been used (France *et al.* 1989), energy requirements for maintenance and gain were estimated as the intercept and slope of ME intake (kJ/kg$^{0.75}$ d) on gain (kJ/kg$^{0.75}$ d) which transforms to the required form: ME = $aW^{0.75} + b\text{Gain}$. Metabolizable energy was assumed to be 85% of digestible energy (Blaxter, 1989).

### Statistics

The effect of seasons and treatments on dry matter intake (DMI), MEI, digestibility and live weight gain were analyzed by Repeated Measures Design (Abacus Concepts, 1989). Multiple comparisons among means of these variables were determined by the t-test. Comparisons of the intercepts and slopes of regression lines used to estimate requirements for maintenance and gain were conducted according to Sokal and Rohlf (1981). The difference was considered significant where the probability of Type 1 error exceeded 0.05.

## Results

### Body weight dynamics

Both pen-fed and free-ranging wapiti exhibited growth stasis in winter (Fig. X.1). *Ad lib.* supplements of highly digestible pellets did not revoke growth dormancy ($p > 0.05$). Pellet-fed wapiti initiated rapid growth in May, in contrast to the pastured animals which lost body weight ($p < 0.05$). When lush green grasses emerged, pastured wapiti gained weight and caught up with their pellet-fed counterparts. Body weights of pastured and pellet groups were not different in late June ($p > 0.05$). When grass matured in late summer growth of pastured wapiti slowed relative to pellet-fed animals which grew rapidly until autumn ($p < 0.05$).

Dry matter intakes and digestibilities (Table X.1) were all significantly affected by season ($p < 0.05$) and feeding program ($p < 0.05$). In winter, DMIs of pellet-fed and pastured wapiti were not significantly different ($p > 0.05$). The pastured group had the highest intakes during compensatory growth on lush spring forage. Intakes of pellet-fed wapiti increased from spring to summer ($p < 0.05$). Digestibility was not depressed with higher summer intakes. ME intakes were significantly affected by season ($p < 0.05$) and treatment ($p < 0.05$) and their interaction ($p < 0.05$). Growth rates were significantly affected by season ($p < 0.05$), but not by feeding programs ($p > 0.05$). Interaction between season and feeding program was significant ($p < 0.05$).

### Maintenance and growth requirements

Estimates of ME requirements for maintenance based on regression analysis varied by season ($p < 0.05$) but not significantly by treatment ($p > 0.05$, Table X.2). Maintenance requirements of penned wapiti ranged from 473 to 508 $kJ/kg^{0.75}$ d in winter and early spring but rose to 728 $kJ/kg^{0.75}$ d in summer. The energy cost of grazing on spring and summer pasture increased the cost of ecological maintenance to 900-984 $kJ/kg^{0.75}$ d.

Apparent ME requirements for live weight gain ranged from 25-33 kJ /g in winter to 40-43 kJ/g in spring and summer but these figures were not significantly different ($p > 0.05$, Table X.2). Requirements for live weight gain were not affected by feeding program ($p > 0.05$).

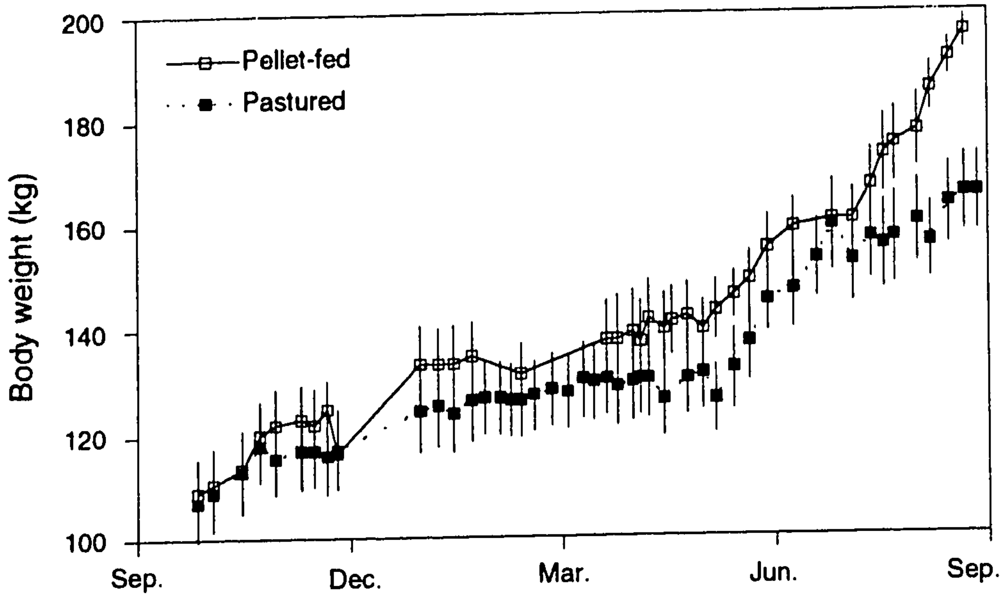

**Fig. X.1** Body weight dynamics of pellet-fed and free-ranging yearlings. The vertical bars represent 1 standard error.

**Table X.1** Dry matter intake (DMI), digestibility (DIG), metabolizable energy intake (MEI) and daily gain

| | Date | Temperature (°C) | | DMI | DIG | MEI | Daily gain[1] |
|---|---|---|---|---|---|---|---|
| | | Max. | Min. | (g/ kg$^{0.75}$ d) | (%) | (kJ/kg$^{0.75}$ d) | (g /kg$^{0.75}$ d) |
| **Winter** | | | | | | | |
| Pellets | Feb. 91 | -0.8 ± 1.0$^{a2}$ | - 9.8 ± 1.3$^{a}$ | 56 ± 4$^{a}$ | 68 ± 2$^{ac}$ | 676 ± 90$^{a}$ | 2.6 ± 0.9$^{a}$ |
| Pasture[3] | Nov. 90 | -2.7 ± 1.4$^{a}$ | -13.4± 1.4$^{b}$ | 60 ± 4$^{a}$ | 65 ± 0$^{a}$ | 558 ± 36$^{a}$ | 2.4 ± 1.3$^{a}$ |
| **Spring** | | | | | | | |
| Pellets | Apr. 91 | 12.0 ± 0.9$^{b}$ | -0.7 ± 0.5$^{c}$ | 62 ± 9$^{a}$ | 74 ± 1$^{b}$ | 685 ± 102$^{a}$ | 4.1 ± 2.2$^{a}$ |
| Pasture | May 91 | 17.5 ± 1.7$^{c}$ | 5.0 ± 0.7$^{d}$ | 154 ± 10$^{b}$ | 77± 2$^{b}$ | 1686 ± 95$^{b}$ | 18.3 ± 2.0$^{a}$ |
| **Summer** | | | | | | | |
| Pellets | Jul. 91 | 23.8 ± 1.2$^{d}$ | 12.8± 1.0$^{e}$ | 103 ± 5$^{c}$ | 71 ± 1$^{bc}$ | 957 ± 123$^{c}$ | 8.5 ± 0.9$^{b}$ |
| Pasture | Aug. 91 | 21.6 ± 1.1$^{d}$ | 11.2± 0.8$^{e}$ | 103 ± 10$^{c}$ | 65 ± 2$^{a}$ | 958 ± 123$^{c}$ | -0.7 ± 3.0$^{a}$ |

1 Daily gain during the trial period.

2 Data are presented as mean ± se. Different superscript letter indicate difference at $p < 0.05$.

3 With supplementary alfalfa hay.

**Table X.2** ME requirements for maintenance and gain

| | ME for maintenance (kJ/kg$^{0.75}$ d) | ME for gain (kJ/g) | Correlation coefficient |
|---|---|---|---|
| **Winter** | | | |
| pellets | 473 ± 35$^{a1}$ | 33 ± 5$^{a}$ | 0.92 |
| pasture | 497 ± 22$^{a}$ | 25 ± 6$^{a}$ | 0.94 |
| **Spring** | | | |
| pellets | 508 ± 57$^{a}$ | 43 ± 9$^{a}$ | 0.92 |
| pasture | 900± 26$^{b}$ | 43 ± 12$^{a}$ | 0.88 |
| **Summer** | | | |
| pellets | 728 ± 78$^{ab}$ | 41 ± 11$^{a}$ | 0.90 |
| pasture | 984 ± 37$^{b}$ | 40 ± 6$^{a}$ | 0.90 |

1. Values that share the same superscript letter with others in the column are not significantly different ($p > 0.05$). Data presented as mean ± standard error.

## Discussion

### Seasonal weight dynamics

During late winter, free-ranging wild ruminants typically lose weight in the face of declining quality and availability of native forage. Weight loss occurs mainly in late winter as snow deepens and forage quality declines to critical levels or in early spring when new growth of forage is not available. Winter weight losses of wapiti on unsupplemented winter pasture are strongly positively related to autumn weight (Hudson *et al.*, 1985). Smaller cervids such as mule deer show the same pattern but seem more sensitive to forage quality (Renecker and Samuel, 1991). During adaptation to spring forage, liveweight losses can be precipitous but transient. This usually is attributed to changes in gut fill rather than empty body weight ( Tayler *et al.*, 1957; Wright and Russel 1986).

On summer pasture, differences in weight of pellets and pastured groups at the end of the winter feeding period closed rapidly in this and previous studies on wapiti (Watkins *et al.*, 1991; Wairimu and Hudson, 1993). The catch-up growth of young wapiti stags on spring and summer pasture is achieved largely by increased forage intakes on lush pasture (Wairimu *et al.*, 1992).

### DMI and digestibility

No difference between the DMI of pellet-fed and supplemented-pasture groups in winter indicate that low intake in winter is not due to diet quality. Even though the fasting metabolic rate dose not change among seasons (Jiang and Hudson, 1993), voluntary DMI of the yearlings increased from winter to spring, matching the availability of natural pasture forages. Presumably such a seasonal appetite cycle is shaped by natural selection. The decline of forage intake in late summer probably is due to a foraging logistic constraint instead of appetite (Jiang and Hudson, 1994 in press).

Digestibilities of both pellets and natural pasture forage peaked in spring. High digestibility and intake of spring pasture forage contributed to the highest live-weight gain rate in spring. Surprisingly, increased levels of intake did not depress digestibility of the standard pelleted diet.

### Maintenance requirements

Maintenance energy requirements of wapiti changed seasonally. Maintenance requirements determined for penned wapiti calves during their first winter (493 kJ/kg$^{0.75}$ d) is comparable to 520 kJ·kJ/kg$^{0.75}$ d for penned red deer hinds (Suttie *et al.* 1987) and 570 kJ/kg$^{0.75}$ d for stags in New Zealand (Fennessy *et al.* 1981). At our research site, Cool (1992) estimated a winter maintenance requirement of 570 kJ/kg$^{0.75}$ d for penned wapiti calves.

The difference between pellet fed and pastured animals is a measure of the energy cost of free-existence. The narrow difference in winter was because wapiti minimized movement on snow covered pasture and mainly fed on hay (Chapter III). Summer maintenance costs of penned yearling hinds increased to 728 kJ/kg$^{0.75}$ d. Our estimated ecological maintenance requirements of about 900 kJ/kg$^{0.75}$ d for young wapiti hinds grazing spring pasture is similar to 870 kJ/kg$^{0.75}$ d of New Zealand red deer stags wintered in outdoor paddocks (Fennessy *et al.*, 1981). The data is comparable to the result of yearling stags (878 kJ/kg$^{0.75}$ d, Wairimu *et al.*, 1992) and wapiti hinds (936 kJ/kg$^{0.75}$ d, Jiang and Hudson, 1992) on spring pasture at same research site. Ecological maintenance, the cost of living of free-ranging animal (Moen, 1985), is therefore about 1.6 times physiological maintenance in agreement with energy expenditures of free-ranging wapiti estimated by heart rate (Pauls *et al.*, 1981).

### Gain

Energy requirements for live weight gain were different in winter and spring-summer. Yearling wapiti hinds in our study required 27 kJ/g for live weight gain in winter and 40 kJ/g in spring-summer. Cool (1992) estimated the cost of live weight gain of yearling wapiti to be 28 kJ/g in winter, whereas yearling stags required 33 kJ/g on spring pasture (Wairimu *et al.*, 1992).

Energy requirements of red deer for live weight gain range from 16 kJ/kg for weaned red deer calves (Simpson *et al.*, 1978) and 37 kJ/g for stags (Fennessy *et al.*, 1981) to 55 kJ/g for hinds (Suttie *et al.*, 1987). Suttie *et al.* (1987) suggested that the high value obtained for red deer hinds might be related to their relative carcass maturity (fatness).

Because body fat has an energy value of about 39 kJ/g and lean tissue (with associated water) about 5 kJ/g, and protein and fat are deposited and mobilized together, typical energetic values of gain generally range from 8-30 kJ/g. This implies greater efficiency of lean tissue gain. However, net protein deposition is much less efficient than fattening and this tends to cancel the difference (Orskov and Mcdonald, 1970).

Jiang and Hudson (1992) considered seasonal differences in costs of gain to depend on whether energy was supplied by body or feed energy. Mobilization of body tissue provided 26 kJ/g during winter pen trials with pregnant adult hinds but required 39 kJ/g to deposit on spring pasture. However, with new information on yearling hinds, it seems that the difference cannot be explained only by positive or negative weight change. Alternative explanations include tissue hydration or perhaps rate of protein turnover.

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# CHAPTER XI SYNTHESIS

## Hierarchical Constraints

Foraging is comprised of a cluster of hierarchical feeding decisions which balance gains and costs. The controlling mechanism of foraging is complex. Foraging ecology, digestive capacity, and metabolic requirement plus the thermal environment and photoperiod all interact to regulate food intake.

Wapiti orient to forage in time and space. Tactical orientation in time may reduce foraging costs by avoiding hot or cold times of the day. Orientation in space, including seasonal migration between summer and winter ranges (Morgantini and Hudson, 1989) and selection of habitats within seasonal range, offers feeding sites with high food availability, high food quality or a favorable thermal environment (Chapter III).

Patch size and the distribution of foods within patches influence behavior at a different scale. Wapiti adopt different feeding postures in different habitats, this may have consequences for both foraging efficiency and energy expenditure (Chapter IV). The foraging response of wapiti in different patches is reflected in giving-up strategies. Wapiti may leave grassland patches as the marginal gain diminishes but give-up feeding stations according to biokinetic factors such as balance and proprioception (Chapter V).

Food selection in a sward is based on the basic unit - the bite, which determines intake rate in terms of bite size and diet quality. Horizontally, wapiti select feeding locations and choose particular food plants or plant parts. Vertically, wapiti adjust bite depth in response to the sward profile, e.g. to ingest green grass leaves (Chapter VI). Sacrificing bite size is often compensated by improved diet quality.

Once food is ingested, the digestive capacity constraint comes into effect. The interaction of intake, digestion and passage determines gut fill. Although wapiti forage selectively, seasonal diets still differ in chemical composition and have distinctive digestive kinetics (Chapter VII). However, wapiti on harvested pasture forages in winter and on pasture in spring and summer maintained their gut fills from winter to late summer (except yearlings on late summer pasture).

Ultimately, satiation and hence food intake is determined by the animal's seasonal energy requirement. Energy requirement has five components; requirements for physiological maintenance, growth, gestation and lactation, activity and thermoregulation. Fasting heat production represents the minimal metabolic requirement.

Since the minimum requirement does not change by season (Chapter IX), the seasonal metabolic cycle is predominantly determined by seasonal demands for growth, gestation and lactation. Foraging dominates the activities of wapiti. Wapiti walk greater distances and are active longer in spring-summer than in winter. Energetic expenditure of foraging activities is related to thermal environment and food availability. In summer, ambient temperature frequently exceeds the upper critical temperature and thus imposes a thermoregulatory cost. Therefore, although the minimum energy requirement did not change among seasons, the maintenance requirement increased from winter to summer (Chapter X).

In the following sections, I summarize seasonal patterns of intake and live-weight change and then discuss the relative importance and interactions of foraging ecology, digestive capacity and metabolic requirement on foraging of wapiti in a seasonal environment.

## Seasonal Forage Intakes and Weight Dynamics

Food consumption of both yearlings and adults showed a seasonal pattern, their intakes were low in winter but high in summer (Fig. XI.1). In 1989-90 winter, both hay and pellet-fed adult wapiti had similar intakes and low growth rate (Fig. XI.2). In 1990-91 winter, both alfalfa hay and pellet-fed yearlings also had similar low appetite and low growth rate. In April 1990, pregnant adults on pellets initiated rapid growth and dramatically increased food intakes. In May 1991, the pellet-fed yearlings also gained weight. However, during this period, both free-ranging yearlings and adults lost weight. The loss in the pregnant adults was more severe than in yearlings probably because of imbalance of metabolic requirement and intake. In May, while the pellet-fed wapiti showed rapid live weight gain, new growth of pasture forage was available for free-ranging wapiti. The free-ranging wapiti initiated compensatory growth (Chapter X, Fig. X.1; Fig. XI.2). However, both pastured and pellet-fed adults lost weight due to calving in May-June. On late summer pasture, the intakes of free-ranging yearlings declined and their growth slowed. But the pellet-fed yearlings maintained their intake and growth. In summer 1990, the lactating adults regained the weight lost at calving.

## Seasonal Constraints

### Winter (November 1-March 14)

If foraging in winter was constrained by the logistics of foraging, I would expect that both yearlings and adults on *ad lib.* harvested herbage would eat to satiety.

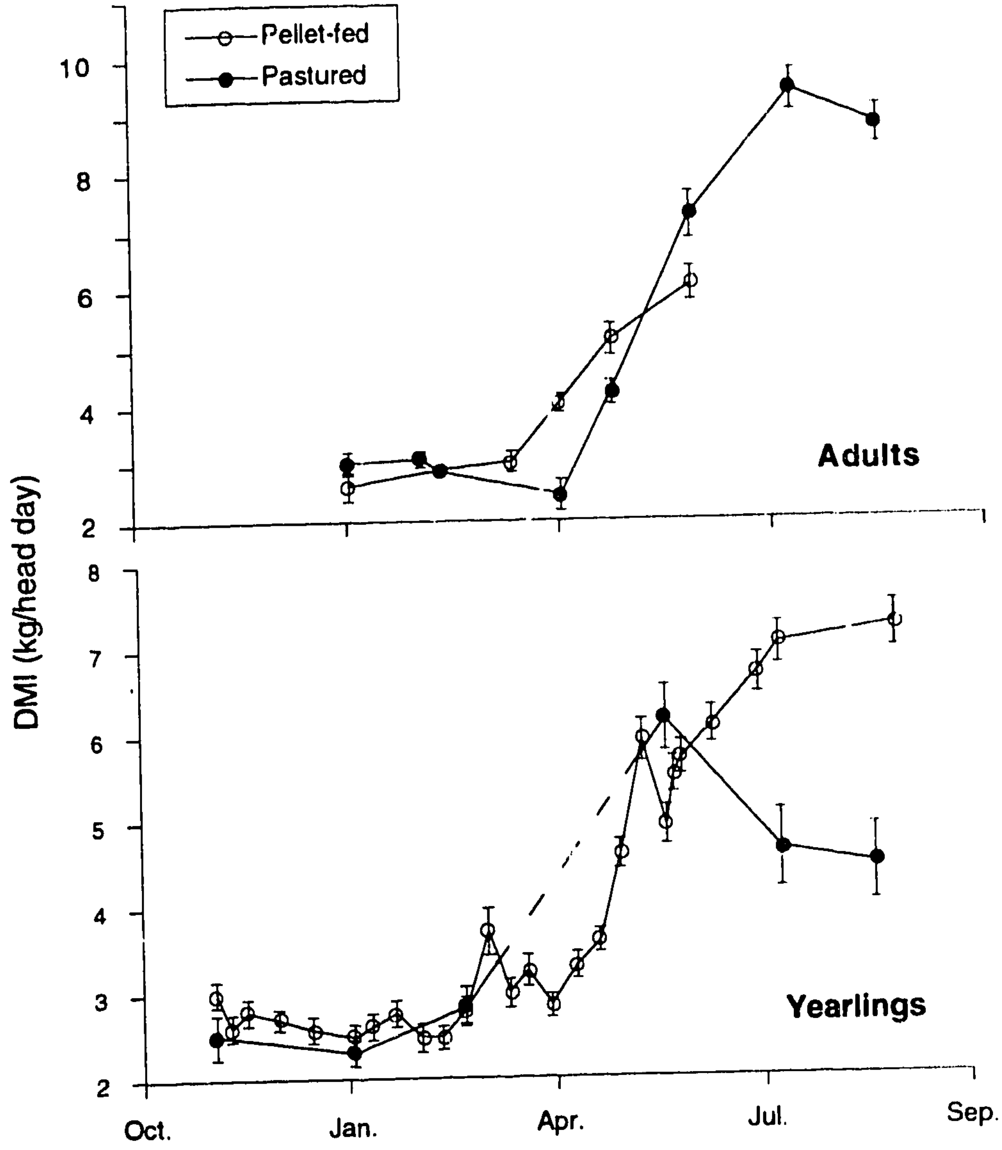

**Fig. XI.1** Dry matter intake (DMI) of 12 adults during October, 1989 to Sept. 1990 and 12 yearlingsduring October, 1990 to Sept. 1991. Both adults and yearlings were assigned to two groups with six wapiti each. During both years, one group fed on pellets while another group had supplementary hay when not on herbage trials in winter and free-ranged from late March till late October. Two adult groups merged in late June, 1990. Vertical bars represent 1 standard error.

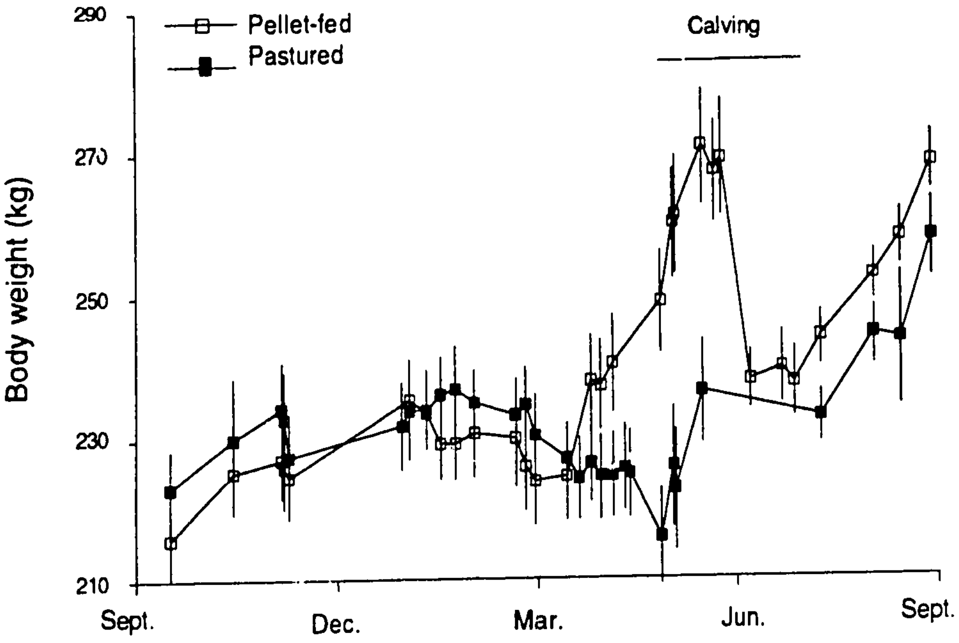

**Fig. XI.2** Body weights of six pastured adults and six pellet-fed adults in 1989-1990. Vertical bars represent 1 standard error. From late June, both groups of lactating adult hinds free-ranged on pasture.

However, both age groups still had low intakes and growth rates. The situations were similar for the hay and pellets trials; wapiti had abundant food supply, but they maintained low intakes. Thus, intakes of yearlings and adults in winter were not constrained by foraging ecology.

If digestive capacity constrained food intake in winter, both yearlings and adults should have consumed more on standard alfalfa-barley pellets, herbage or hay, because the pellets were made of ground feedstuffs with high digestion and passage rates. But yearlings and adults on pellets consumed similar dry matter as those on herbage or alfalfa hay. Although the pelleted diet relieved the digestive capacity constraint, yearlings and adults still had low intakes and slow growth in winter. Therefore, intake in winter was not constrained by digestive capacity.

To achieve the metabolic objective, wapiti should have similar digestible dry matter intakes whatever food they ate. Because yearlings or adults all had similar digestible dry matter intakes and slow growth rates in winter, regardless of forage type, food intake of wapiti in winter seemed to be determined mainly by the low seasonal metabolic requirement.

### Early spring (March 15-May 14)

Onset of growth and increased activity and maintenance requirement in early spring stimulated feeding. Decreased body weights of free-ranging adults in early spring 1990 and free-ranging yearlings in early spring 1991 were probably because free-ranging wapiti cannot satisfy their metabolic demand; thus the foraging of free-ranging wapiti was constrained by digestive capacity or foraging logistics.

I did not measure the digestive function of free-ranging wapiti in early spring, because the season was brief. Yearlings on alfalfa-barley pellets had lower gut fills in March than in summer (Chapter VII). Apparently digestive capacity did not constrain food intake of the free-ranging yearlings in early spring, or the digestive constraint is not as important as the foraging logistic constraint. If it were, wapiti on pellets would have higher gut fills.

Both metabolic energy demand and foraging cost increased in yearlings and adults in early spring. They grazed the cured grasses, browsed willows, and more frequently, they walked in the shallow water of a lake to pull out sedge shoots, the first available green material (Chapter IV). However, they could hardly satisfy their metabolic energy demand. Food intakes of free-ranging adults were lower than those of pellet-fed counterparts. Thus, foraging logistics seemed to be the most important constraint on free-ranging animals in early spring.

Late spring (May 15- June 14)

Ambient temperature in late spring remained in the thermal neutral zone of wapiti. Pasture in late spring offered wapiti forage of the highest protein and the lowest fiber among the seasons. Wapiti had frequent but short foraging bouts which probably reflected the rumen repletion-depletion cycle.

Forage from late spring pasture was highly digestible and passed rapidly. Although dry matter intake increased three fold in free-ranging adults, and two - three fold in yearlings compared with winter, calculated gut fills of free ranging yearlings or adults were not significantly higher than those in winter (Chapter VII). The higher digestion and passage rates relieved the digestive capacity constraint in late spring.

Although the mean intake rate of free-ranging yearlings increased three fold when they grazed late spring pasture compared with winter, they still had the most free time which was not engaged in either feeding or rumination among all seasons (Chapter III). The cropping rate was the highest among early and late springs and summer. Thus, foraging ecology was not the main constraint on food intake in late spring.

Due to compensatory growth and ecological maintenance, the metabolic energy requirement of free-ranging wapiti increased (Chapter X). Whether grazing or fed pellets, wapiti could satisfy their growth demands. Thus, food intake in late spring was not constrained by either digestive or foraging logistic, but was adjusted to the metabolic energy requirement.

Summer (June 15- August 31)

In summer, ambient temperature in mid-day was normally higher than the upper limit of the thermal neutral zone of wapiti, and this altered the diel foraging pattern (Chapter III). As the grazing season progressed, pasture condition changed in terms of patch size (Chapter V) and sward structure (Chapter VI). Summer rain fall was critical for the growth of pasture forages. Because spring-summer rainfall in 1990 was more than in 1991, pasture biomass was greater (unpublished data).

That summer, lactating hinds re-gained weights in preparation for the coming rut season and their ecological maintenance was high due to thermal environment and foraging (unpublished data). Nevertheless, they had the same gut fill as in late spring and maintained growth. The metabolic energy demand of yearlings also was high. But while the yearlings on pellets still grew, the food intake of free-ranging yearlings declined and growth of the yearlings slowed. Thus, whereas the metabolic requirement of adults was met, free-ranging yearlings did not meet their metabolic requirement.

Summer pasture forage was of lower digestibility and slower passage rate than pasture forage in late spring. However, the calculated gut fills of free-ranging yearlings were lower than those in late spring and winter (Chapter VII). Digestive capacity did not constrain food intake of yearlings on summer pasture, because the calculated gut fills decreased. But the free-ranging adults maintained their gut fills (Fig. VII.2).

On late summer pasture, the size of grassland patches declined, yearlings grazed fewer bites from each patch and feeding station and tolerated low bite rates longer than in late spring (Chapter V). On the other hand, the bite size of yearlings declined in tall swards (Chapter VI). Foraging selectivity in the heterogeneous pasture caused the decline of food intake of yearlings in late summer. Thus, the foraging logistics in matured continuously grazed pasture constrained food intake. Adults increased their foraging time (unpublished data) and selectively foraged in grassland patches with short swards, thus ingested enough food to meet their metabolic demand.

## Conclusion and Management Implications

The low food consumption of wapiti in winter was adjusted to the low metabolic energy requirement due to growth dormancy and low activity level. Such growth dormancy was not overcome by high quality food supplementation. In early spring, onset of growth and increasing grazing costs elevated the metabolic energy requirement. However, free-ranging wapiti could not ingest enough food to satisfy their metabolic energy demand. When high quality green pasture forage was available in late spring, foraging logistics were no longer a constraint on intake for free-ranging wapiti. The digestive system of wapiti can process several times more food than in winter due to the higher digestion rate and faster passage rate of spring forages. The metabolizable energy intake of free-ranging wapiti met their demand during this period. Foraging in the heterogeneous pasture with matured swards in late summer was more time consuming and less profitable in terms of energy expenditure and gain. Wapiti had low mean intake rate in mature swards. The foraging logistics on summer pasture prevented yearlings from ingesting enough food to meet their metabolic energy demand.

This information benefits the wapiti game industry in western Canada by contributing information on both voluntary intake and energy requirements. Oskov and Rile (1990) criticized existing livestock feeding standards for failing to consider the amount that animals will voluntarily consume. This study provided information of voluntary intakes of a standard ration and seasonal pasture forage and seasonal gain of wapiti. Thus, the study provides information about the metabolizability of native forages and the productivity of wapiti.

The study also provides basic information on the nutritional needs of wapiti and insights into how their seasonal requirements can be optimally met. Seasonal estimates of metabolizable energy requirements of maintenance and gain provided by this study are a first step in developing feeding standards for the species. This will be increasingly important as the wapiti farming industry matures and farmers turn their attention to controlling feed costs and optimizing use of seasonal pastures.

## Literature Cited

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