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Foraging Behaviour and Intake in Wapiti Hinds (*Cervus elaphus canadensis*)

by

Jay V. Gedir

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 Ecology and Management

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Foraging Behaviour and Intake in Wapiti Hinds (*Cervus elaphus canadensis*)** submitted by **Jay V. Gedir** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Wildlife Ecology and Management**.

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ABSTRACT

There is an urgent need for feeding standards for farmed deer and knowledge of seasonal intake is essential in achieving this. Use of n-alkane markers for estimating dry matter digestibility and intake (DMI) of wapiti hinds (n=8), administered via intra-ruminal controlled release device, were evaluated in pen trials. Foraging behaviour and DMI of hinds (n=10) on two planes of nutrition (heavily (H) and lightly (L) grazed pasture) were studied during gestation and lactation. Seasonal consistency of natural C_{31} and C_{33} n-alkane recoveries made them dependable compounds to pair with dosed C_{32}. DMI estimates using C_{33}:C_{32} were slightly more accurate, while those using C_{31}:C_{32} were more precise. The bite count method provided field validation of marker technique.

Spring weight loss (-2.9±0.8 g/kg$^{0.75}$/day) reflected the inability of hinds to meet nutritional requirements of late gestation, even though herbage quality was at its seasonal peak. Augmented bite rates (47.7±1.0 bites/min) and grazing time (10.85±1.23 h/day) did not afford sufficient compensation. Although metabolizable energy requirements peaked during early lactation, hinds were able to consume enough high quality forage (5.38±0.25 kg DM/day) to achieve compensatory growth (12.5±1.4 g/kg$^{0.75}$/day). This was accomplished by increasing bite size (280±28 mg). Continued elevated intakes through late summer (5.32±0.41 kg DM/day) and autumn (4.41±0.24 kg DM/day), ensured hinds regained adequate condition in time for the oncoming breeding season and winter, respectively. In autumn, reduced bite rates (37.2±1.5 bites/min) and feeding bouts of shorter duration (59.9±11.1 min), reflected diminishing forage quality.

Maternal care disrupted normal patterns of foraging and bedding in June/July. This occurred, most notably, through reductions in length of foraging bouts (H: 83.3±7.9 min, L: 50.2±2.1 min) and hinds spending less active time foraging (78.8±9.8%). To achieve satisfactory nutrient intake, hinds attempted to compensate by increasing frequency of grazing sessions (H: 8.4±0.8 bouts/day, L: 12.0±0.6 bouts/day). Lactating hinds were able to reduce daily foraging in lightly grazed pasture without comprising intake levels.

This study presented evidence that the double n-alkane ratio technique can provide accurate and precise assessment of DMI in wapiti, at least on known diets. Contributions of empirical information on activity and intake of reproductive female wapiti improved the predictive capabilities of an existing computer simulation model linking wapiti bioenergetics with behaviour.

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CHAPTER ONE

INTRODUCTION

Worldwide, over 4 million cervids are reared on farms, including nearly 100,000 in Canada. This industry has grown into an important, highly profitable form of livestock diversification which taps new markets (velvet, venison) and pasture resources. Throughout North America, more public attention has been directed towards commercialization of wildlife than almost any other aspect of ungulate management (Hawley 1993). Improved economic performance of deer over conventional livestock emanates from exploitation of wildlife adapted to local environs, diversified foraging strategies, high market value of deer products, and reduced veterinary requirements (Stelfox 1993).

Wapiti (*Cervus elaphus canadensis*) offer the advantage of being able to obtain their primary seasonal requirements from pasture, although sufficient supply of nutrients still depends on forage quality and availability. Added benefits are their preferences for cover and diverse diets, which encourage farmers to maintain more natural vegetation than would be expected for beef cattle.

North Americans are still exploring the optimal intensity of management that best capitalizes on adaptations of deer, characteristics of the natural environment, and economic conditions (Haigh and Hudson 1993). As a result, there is an urgent need for research into the development of feeding standards for farmed deer. This thesis is part of the broader 'Digital Deer' initiative to provide a computer-based feeding standard <http://www.deer.rr.ualberta.ca>.

Cervids inhabiting high latitudes demonstrate marked seasonal intake, and hence, weight fluctuations, even when provided an *ad libitum* food source (Fennessy *et al.* 1991). This pattern is presumably an evolutionary selective response to the seasonal nature of food supply, although there is some debate whether the adaptation is to winter scarcity or the brief flush of summer growth.

Most nutritional research on *Cervus elaphus* (which includes red deer (*C. elaphus elaphus*)) has been conducted in New Zealand and the United Kingdom, in penned or indoor settings. Ungulates of these regions do not experience the same seasonal climatic extremes with which Canadian animals must contend. In addition, thermoregulation in extreme environments and activity can have substantial effects on forage intake. Management regimes based on figures derived in other areas would likely be inappropriate in Canada, necessitating local calibration.

Dry Matter Intake

Although extensive work has been done on food intake in reproductive domestic ruminants (*e.g.* Arnold and Dudzinsky 1967; Peart 1967; Forbes 1970, 1971; Flatt and Moe 1971; Arnold 1975; Robinson 1980; Symonds *et al.* 1988, 1990; Penning *et al.* 1991; Parker 1992), little published information is available for cervids (Ullrey *et al.* 1969, 1970; Arman *et al.* 1974; Sadlier 1982; Heydon *et al.* 1992). Until recently, nutrient requirements of farmed game had to be extrapolated from domestic ruminants, using the factorial approach (Oftedal 1985). Some attention was given to free-ranging red deer while addressing other problems (Niezen *et al.* 1993).

Many studies have estimated daily intake of red deer (Brockway and Maloiy 1968; Simpson *et al.* 1978; Fennessy *et al.* 1981, 1991; Suttie *et al.* 1987; Heydon *et al.* 1992; Sibbald 1994; Semiadi *et al.* 1995; Kusmartono *et al.* 1996; Fraser and Gordon 1997) and wapiti (Watkins *et al.*1991; Jiang and Hudson 1992, 1994). However, with the exception of Kusmartono *et al.* (1996), Jiang and Hudson (1992, 1994), Heydon *et al.* (1992), and Watkins *et al.* (1991), all involved stags or non-breeding hinds (adult females).

Kusmartono *et al.* (1996) studied intake of lactating red deer on pasture. Watkins *et al.* (1991) estimated intake of lactating wapiti, but only during June. Heydon *et al.* (1992) investigated performance of lactating red deer on high and low quality pasture from July to October. Some of Jiang and Hudson's (1992, 1994) wapiti intake trials involved pregnant hinds, however, these were pen-fed individuals.

The extent to which gestating and lactating wapiti hinds are able to satisfy their nutritional requirements is likely one of the most important factors affecting productivity of the population (Sadlier 1969). As a result, a crucial information gap exists for managing this species. Therefore, an objective of this study was to extend Jiang and Hudson's (1992, 1994) work (which estimated year-round intake of wapiti on pasture in Alberta) to include breeding females.

n-Alkane Marker

Indicator techniques have been used in nutritional studies since the turn of the century, when Elliot and Barclay-Smith (1904) employed coloured glass beads to examine the distribution of food along the rabbit digestive tract. Since this pioneering study, a plethora of reference substances have been employed to estimate herbage intake on pasture, with varying degrees of success. These markers are described in reviews by Kotb and Luckey (1972), Galyean *et al.* (1986), Cochran *et al.* (1987), Pond *et al.* (1987), Owens and Hanson (1992), and Titgemeyer (1997).

Markers are internal (indigestible components of forage) or external (indigestible foreign compounds introduced into an animal's diet), and all methods require faecal sampling. Marker methods are based on faecal output in association with digestibility of herbage consumed.

The widely used chromic oxide (Cr_2O_3) technique for estimating food intake of free-ranging herbivores presents several problems. These emanate from applying a single digestibility value to all animals in a group, regardless of their intake level (Dove *et al.* 1989a, 1990; Dove and Mayes 1991). Additional problems result from internal markers with variable digestibilities that produce erroneous estimates of DM digestibility coefficients, and therefore, dry matter intake (DMI) (Langlands 1975). All marker methods exhibit biases and losses of accuracy and precision of different magnitudes. Theoretical estimates of intake, based on tabulated feed requirements, have shown similar problems in a pasture setting (Vulich *et al.* 1991).

My study on forage intake of wapiti evaluates a new marker method based on the double n-alkane ratio technique. Long-chain n-alkanes, a component of plant cuticular wax (Tulloch 1976), have demonstrated minimal absorbability in ruminants (Oro *et al.* 1965) and are relatively easy to analyze. Naturally occurring n-alkanes of herbage species are predominantly odd-chain length in the range C_{25} to C_{35} (Hawke 1973). Dotriacontane (C_{32}) and hexatriacontane (C_{36}) would make ideal internal markers, as they can be obtained in pure form, easily and inexpensively, and are present in very low concentrations in herbage.

Use of these indigestible plant components offer several advantages over other methods, as markers for herbage digestibility and intake determination in grazing ruminants (Mayes *et al.* 1986). Dosing with known quantities of n-alkanes of a chain length adjacent to those naturally occurring in high concentrations in herbage provides excellent opportunities for estimating nutritional intake of individual wapiti. That is, errors in digestibility and intake estimation due to between-animal variations in faecal n-alkane recovery, could be eliminated if such faecal recoveries were concurrently estimated in the same animal.

n-Alkane markers have provided accurate results in domestic ruminants (sheep: Mayes *et al.* 1986, Dove *et al.* 1989a, 1989b, 1990, Vulich *et al.* 1991; dairy cows: Dillon and Stakelum 1989, Stakelum and Dillon 1990; goats: Duncan 1986). Therefore, they are increasingly used in domestic animals (cows: Wright *et al.* 1990, Rook *et al.* 1994, Cazcarra and Petit 1995, Cazcarra *et al.* 1995, Fisher and Dowdeswell 1995, Fisher *et al.* 1995; sheep: Milne *et al.* 1986, Salt *et al.* 1992, 1994, Champion *et al.* 1995, Friend *et al.* 1995; goats: Merchant and Riach 1994, Fraser and Gordon 1997) and, in some cases, red deer (Heydon *et al.* 1993; Fraser and Gordon 1997).

Although this paired-marker technique shows considerable promise, it must be thoroughly tested before it can be confidently applied to other herbivores and pastures. For example, studies have revealed significant variation in n-alkane concentrations attributable to effects of cultivar, plant part, seed provenance, stage of development, and environment (Dyson and Herbin 1968, 1970; Herbin and Robins 1968, 1969; Tulloch

1973; Baker 1980; Tulloch *et al.* 1980; Tulloch 1981; Laredo *et al.* 1991), however, interspecies variation is most significant.

n-Alkane Administration

Reliable application of marker to animals is paramount to their success. In early work, Ellis and Huston (1968) used a pipette to apply ^{144}Ce solution to hay. This procedure led to problems of marker adherence and non-uniform distribution in feed. Later work, in which Cr_2O_3 was incorporated into shredded paper or cellulose, reduced these errors. The Cr-mordanting procedure, developed by Uden *et al.* (1980), uses a reagent to fix the marker to the material to be consumed. At high Cr concentrations, density of feed is increased and passage of marked feed may be different than that of unmarked (Ehle *et al.* 1984). Alternatively, low marker level can lead to analytical inaccuracies when determining marker concentrations.

The most widely utilized method of dosing n-alkanes is via n-alkane impregnated paper, shredded and formed into pellets or packed into capsules (Duncan 1986; Mayes *et al.* 1986, 1988; Dillon and Stakelum 1988, 1990; Dove *et al.* 1989a, b; Wright *et al.* 1990; Stakelum and Dillon 1990; Salt *et al.* 1992, 1994; Heydon *et al.* 1993; Merchant and Riach 1994). Others have used n-alkane impregnated powdered cellulose in gelatin capsules (Dove *et al.* 1988, 1989a, b; Vulich *et al.* 1990, 1991; Merchant and Riach 1994), grass coated with xanthan gum containing n-alkanes (Marais *et al.* 1996), and direct marker application through ruminal or duodenal cannulae (Ohajaruka and Palmquist 1991; Marais *et al.* 1996).

All of the above techniques require single or twice daily dosing, which is labour intensive and can result in diurnal variation of n-alkane release and disruption of animal grazing patterns. Although some modifications of these procedures have led to improvements in faecal recovery and reduction of diurnal variation in confinement trials (Nelson and Green 1969), benefits have not always been observed on pasture (Kiesling *et al.* 1969).

A uniform daily release of marker is essential for dependable calculation of forage intake. An intra-ruminal controlled-release device (CRD) eliminates problems associated with daily dosing (Laby 1981; Ellis *et al.* 1981), a particularly important issue with wild ruminants.

Although earlier CRD investigations with chromic oxide demonstrated limited success (Momont *et al.* 1989;, Parker *et al.* 1990; Buntinx *et al.* 1992), recent work has shown more promise (Momont *et al.* 1994). However, with the exception of studies by Kelly *et al.* (1985) on fallow deer (*Dama dama*) and Parker and Ataja (1990) on young red deer stags, testing has largely been restricted to sheep and cattle, and only preliminary evaluation of CRD have been conducted using n-alkanes (K. J. Ellis, Pers. Comm.).

Foraging Behaviour

Northern ranges are characterized by marked seasonal changes in forage quality and availability (Trudell and White 1981). An adaptation (*i.e.* long-term response) of northern ungulates, is to synchronize their annual reproductive cycle with these oscillations in range forage characteristics, which are timed so energy requirements are matched with forage quality and quantity. However, within each season (and even from day to day) forage conditions can vary, and herbivores must have a proximate response to these changes.

Although over the long-term energy balance must control intake, on a short-term basis, intake probably is governed by a combination of plant structural factors that influence rate of ingestion, effect of masticated forage on gut fill, and social behaviour and environmental factors affecting the appetite-satiety complex (Forbes 1989).

Ungulates typically devote 40-60% of each day to finding and consuming food (Craighead *et al.* 1973; White *et al.* 1975; Schwartz 1977; Belovsky and Jordan 1978; Collins *et al.* 1978; Owen-Smith 1979, 1982; Gates 1980; Hanley 1982). Therefore, the time devoted to grazing each day can exert a strong influence on the amount of forage consumed.

Daily feeding activity involves several feeding bouts consisting of a series of events at different hierarchical levels (feeding patch, feeding station, bite) (Gates and Hudson

1983, Jiang and Hudson 1993). Modifications of daily foraging may occur with changes in pattern of feeding bouts and dynamic characteristics of each feeding bout. Jiang and Hudson (1993) suggested that wapiti optimally forage according to Charnov's (1976) 'marginal value theorem'. They found evidence that wapiti gave up foraging when cropping rates at one or two feeding stations dropped below the seasonal expectation.

Intake of grazed herbage can be described as the product of bite size, bite rate, and grazing time (Spedding *et al.* 1966; Allden and Whittaker 1970). Bite size has the greatest influence on short-term intake, while bite rate and grazing time are compensatory variables (Forbes 1989), and all are sensitive to sward conditions (Hodgson 1985). For example, when forage is difficult to harvest (*e.g.* cropped beyond efficient prehension), animals compensate for small bite size by extending time spent grazing (Stobbs 1970), and thus, number of bites increases (Stobbs 1974). However, increased grazing is constrained by limits to daily intake imposed by rumen capacity (forage quality) and feeding logistics (forage availability) (Hudson and Watkins 1986). The ruminant, therefore, must attempt to reach an optimal balance between forage quality and quantity.

For over fifty years, rate of biting has been used to evaluate sward conditions (Johnstone-Wallace and Kennedy 1944). Only recently has it been utilized in conjunction with bite size and grazing time for both determination and explanation of herbage intake. Associations between wapiti feeding rates and phytomass and structure have previously been examined (Collins *et al.* 1978; Collins and Urness 1983; Wickstrom *et al.* 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1986).

Use of instantaneous bite rates can lead to extreme overestimations of intake when extrapolated to a diel period. Therefore, Forbes and Hodgson (1985) modified the 20-bite technique to include time taken for herbage selection and mastication of large mouthfuls. Rate of biting can also decline with time, within an individual grazing period (Hancock 1950; Stobbs 1974). Thus, it is important to measure bite rate on several occasions throughout the day and over several days, to minimize biases resulting from between- and within-day variation.

Objectives

In Chapter Three, I examined a new marker technique (double n-alkane ratio) for estimating dry matter intake and feed digestibility in wapiti. I also evaluated the use of an intra-ruminal controlled-release device for administering n-alkane marker. This calibration trial investigated behaviour of dosed n-alkanes in faecal samples and assessed accuracy of this marker method based on the following hypotheses:

H_1: Double n-alkane ratio estimates of DMI do not differ from actual intakes.

H_2: Intra-ruminal controlled-release devices provide uniform daily release of n-alkane.

Previous studies using the n-alkane double ratio technique have demonstrated that adjacent pairing C_{33}:C_{32} is a better predictor of intake than C_{31}:C_{32} (Mayes *et al.* 1986; Dove *et al.* 1989; Dillon and Stakelum 1989, 1990; Stakelum and Dillon 1990). This theory was tested based on the null hypothesis:

H_0: $DMI_{31:32} = DMI_{33:32}$

In Chapter Four, I utilized the double n-alkane ratio technique to estimate intake of wapiti grazing aspen parkland. I examined seasonal intake of reproductive wapiti hinds on two nutritional environments, from early to late gestation, and from peak to late lactation. The following hypothesis was tested:

H_3: Wapiti hinds regulate DMI based on reproductive condition and forage availability.

Forage intake of gestating and lactating wapiti hinds was compared to determinations made on non-breeding individuals in recent work at the same research station (Jiang 1993).

n-Alkane intake estimates were compared to predictions made from an established behavioural observation method (bite count technique) according to the following null hypothesis:

H_0: $DMI_{n\text{-Alkane}} = DMI_{\text{Bite Count}}$

In Chapter Five, activity and foraging parameters were tested in relation to forage availability and reproductive season, to interpret wapiti behavioural response to meet changing nutritional requirements. The following hypotheses were tested:

H_4: Wapiti alter activity budgets in response to seasonal nutritional demands, reproductive condition, and changing forage availability.

H_5: Pattern of wapiti feeding bouts and characteristics of each bout vary with forage availability and reproductive season.

Expected Contribution

Exploring feeding behaviour of wapiti hinds will further our understanding of their response to seasonal variation in forage availability and nutritional demands. A new marker technique will provide improved means of predicting seasonal intakes in wapiti on pasture, thereby contributing to the development of feeding standards for farmed deer. The goal is to obviate inaccuracies that arise from the extrapolation approach currently used. This study is expected to provide valuable information to facilitate improved animal production in the rapidly growing area of livestock diversification.

With development of this new approach to feeding standards, deer farming may cease to be viewed simply as an extension of traditional domestic livestock husbandry, but as an independent industry posing a unique set of conditions and associated problems.

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CHAPTER TWO

MATERIALS AND METHODS

Study Area

This study was conducted at Ministik Wildlife Research Station, located 48 km southeast of Edmonton, Alberta on the Cooking Lake glacial moraine. Vegetation is classified as lower boreal mixedwood (Strong 1992), consisting of an overstory of balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*), and understory being dominated by beaked hazel (*Corylus cornuta*) and willow (*Salix* spp.). Grasslands are primarily composed of Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), Dutch white clover (*Trifolium repens*), dandelion (*Taraxacum officinale*), and Canada thistle (*Cirsium arvense*).

The climate is continental, typical of northern boreal forest regions. Ambient temperatures are characterized by seasonal extremes, ranging from a minimum of -49°C in winter to temperatures exceeding 32°C in summer (Olson 1985). Permanent snow-cover is usually established in late November, however, in the first year of this study snow arrived at the beginning of November. Snow normally remains into April and growing season typically extends from May until September. Grasses become senescent in October and by the end of the month deciduous trees have shed their leaves.

Study Animals

From June 1996 to April 1998, 13 adult female wapiti were used. Animals ranged from 3 to 12 years of age when the study began (mean: 8±2.6 years). Mean weights of wapiti groups at the commencement of each trial are listed in Table 2-1.

Hinds were free-ranging and supplemented with concentrate alfalfa-barley pellets (year-round) and hay (winter), except during pasture trials, when all supplemental feed was withdrawn. Ten hinds were used in each of seven grazing trials and nine in one pen trial. Animals were selected based on past reproductive success to maximize probability of pregnancy and divided into two groups with similar age distribution. All hinds calved

Table 2-1 - Mean weights of wapiti hinds and calves at trial commencement at Ministik Research Station, AB. Calf gender represents proportion of females (F) to males (M).

		Mean Weight (kg)*		
Trial	n	Hind	Calf	Calf Gender
June/July 1996	10	289±18	40±3	7F, 3M
August 1996	10	303±15	83±7	7F, 3M
November 1996	10	282±13		
May 1997	10	291±18		
June/July 1997	10	275±19	39±3	5F, 5M
August 1997	10	301±20	79±7	5F, 5M
November 1997	10	280±20		
April 1998	9	295±18		

* Mean ± SE

successfully in each year of study and calves were present during all trials between parturition and weaning.

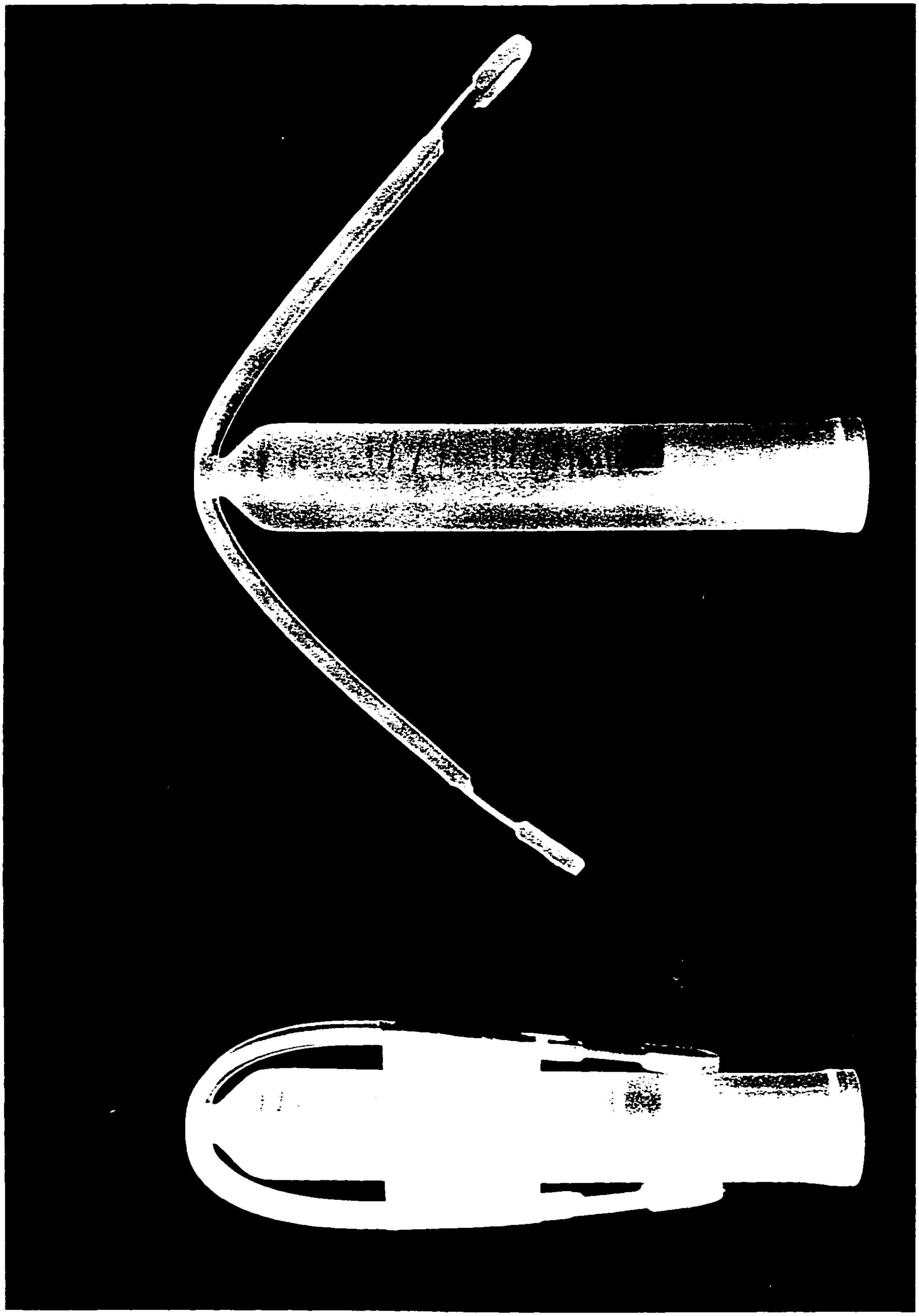
n-Alkane Calibration

A pen trial was conducted in April 1998 using nine wapiti hinds in their last trimester of gestation. Animals were confined to a 50 m x 15 m enclosure void of all vegetation. Hinds were fed an *ad libitum* diet of alfalfa-based (*Medicago sativa*) total ration deer cubes ("El-Kube", Moore's Auctioneering Ltd., Alder Flats, AB) in a Pinpointer 4000B automatic feed monitoring system (Microcomputer Controls Inc., Nashville, TN). This system individually identifies hinds upon entering the chute and tallies the amount of feed taken each visit, for a total daily feed intake per animal.

Following a one week adjustment, a controlled-release device (CRD) (Captec NZ Ltd., Auckland, New Zealand) (Plate 2-1) was administered *per os* into the rumen of each animal, releasing 58.5 mg/day each of dotriacontane (C_{32}) and hexatriacontane (C_{36}) for approximately 15 days. Each CRD is constructed of a plastic barrel (10.5 cm long x 2.0 cm diameter) into which a matrix of C_{32}, C_{36}, and inert surfactant (20:20:60) is inserted as a series of tablets. At one end of the barrel, a 1.0 cm diameter orifice exposes the matrix to the rumen contents, forming a gel. Pressure from a compressed steel spring against a plastic plunger, causes the gel to be extruded into the rumen. Attached to the other end, are two 9.0 cm x 1.5 cm plastic strips (wings), which are folded against the barrel and held in place with cellulose tape. Upon entering the rumen, tape adhesive is dissolved by rumen fluid, releasing wings to form a 'T' configuration, which holds the CRD in place (*i.e.* prevents regurgitation). Capsules used in this study are standard cattle CRD, modified with longer wings to facilitate retention in a wapiti rumen.

The trial lasted 2 weeks following dosing and the initial n-alkane dosing day is referred to as day 0, with trial days being labelled in reference to this day. For example, day 1 would refer to the day after dosing, while day -1 refers to the day before. Rumen n-alkane equilibrium is achieved within 5 days of dosing. Commencing on day 5, a small sample of freshly voided faeces was collected from each animal, daily. Hinds were weighed on day -4, 3, and every 2 days from day 7 to day 15. Faecal samples were

Plate 2-1 - Photograph of intra-ruminal controlled-release device (Captec (NZ) Ltd., Auckland, New Zealand), showing secured wings (left) (pre-dosing) and open wings (right) (post-dosing). CRD specifications found in n-Alkane Calibration.



freeze-dried for 72 h at -60°C, ground through a 20-mesh screen in a Wiley mill, and n-alkanes extracted.

n-Alkane Analysis

Freeze-dried, ground duplicate faecal (0.30 g) and herbage (1.0 g) samples were weighed into 50 ml Pyrex tubes fitted with Teflon-lined screw caps. Two hundred µl of tetratriacontane (C_{34}) internal standard (100 mg C_{34}/100 ml hexane), 10 ml methanol, and 1 ml KOH (45%) were added to each tube and the samples were placed in a water bath for 4.5 h at 90°C.

n-Alkanes were extracted by adding 10 ml hexane (HPLC grade) and 5 ml distilled water, transferring separated hexane layer to a 20 ml scintillation vial, then repeating the extraction with another 8 ml hexane. Pooled hexane layers were evaporated to approximately 500 µl and passed through a silica gel column (70-230 mesh) to separate lipids from n-alkanes. Scintillation vials were rinsed twice with 2 ml hexane, which was also added to the silica gel column. One ml of remaining solution was transferred to a 1 ml glass gas chromatography (GC) vial.

n-Alkane analysis was conducted on a Varian 3400 Capillary GC equipped with a Varian 8100 Autosampler (Varian Associates Inc., Walnut Creek, CA) and Shimadzu EZ Chrom Chromatography Data System (Version 3.1) (Shimadzu Scientific Instruments, Inc., Columbia, MD). Capillary column was an Rt_x-1, 30 m x 0.25 mm Inner Diameter x 0.25 µ film thickness (Restek Corporation, Bellefonte, PA) and the carrier gas was helium. Initial column temperature was set at 80°C, which was held for 0.04 min, then programmed to rise 20°C/min to a maximum of 280°C for a 4 minute holding time. Septum programmable injector temperature commenced at 90°C and increased to 280°C at a rate of 150°C/min, at which point it was held for 12 minutes. The flame ionization detector temperature was 280°C. A volume of 0.5 µl n-alkane-hexane solution was injected into the GC for analysis.

Individual n-alkanes were identified from their retention times on the column, and peak areas on the printout converted to concentrations of n-alkanes (in ppm) by reference to the internal standard (Dove 1992). Resulting chromatograms identified n-alkane peaks ranging from C_{29} to C_{36}.

Grazing Trials

Seven grazing trials lasting 16 days (*i.e.* except November 1996 trial (11 days); see below) were conducted between June 1996 and November 1997. Four periods were selected based on importance in the annual reproductive cycle (early gestation (EG), late gestation (LG), peak lactation (PL), and late lactation (LL)). Two enclosures with similar plant species composition were established on heavily (H) (10.6 ha) and lightly (L) (9.0 ha) grazed pastures. With the exception of LG, pasture phytomass between enclosures differed by at least 30%. Each pasture was randomly assigned 5 reproductive wapiti hinds of similar age distribution. This stocking rate and trial length were chosen to minimize complications arising from pasture growth.

The first trial was in late June/early July 1996 (PL96). H was stocked with at least ten adults for 2 weeks prior to trial commencement to provide sufficient defoliation, while L had been free of grazing for at least two months. Five lactating hinds (with calves) were confined to the enclosures without supplemental feed for the duration of the trial. An adjustment period was not considered necessary, as the animals grazed areas surrounding enclosures prior to the trial. The second trial was conducted during late August of the same year (LL96). Between trials, H was always stocked (except during snowcover periods) to ensure continuous defoliation, while L remained empty.

Commencing November 1996 (EG96), smaller enclosures were employed (H: 5.0 ha, L: 7.8 ha) to enable more rapid defoliation in H. EG96 was terminated after 11 days, as two heavy snowfalls greatly reduced forage availability and supplemental feeding became necessary. Five days (EG97 - 3 days) were added to the beginning of remaining trials, as hinds required 2 to 3 days to adjust to the marked difference in phytomass between study enclosures and pre-trial grazing areas. In 1997, experiments were conducted in early May (LG97), late June/early July (peak lactation, PL97), late August (late lactation, LL97), and early November (EG97). Hinds and calves (during lactation) were weighed four to five times in each trial and liveweight gain (g/kg$^{0.75}$/day) calculated using simple linear regression.

DMI Estimation

The double n-alkane ratio method estimated wapiti dry matter intake. At the commencement of each trial (*i.e.* after adjustment period for 1997 trials), a controlled-release device was administered *per os* into the rumen of each hind. In 1996 trials, these capsules contained equal amounts of dotriacontane (C_{32}) and hexatriacontane (C_{36}), releasing 68 mg of each per day. To increase daily n-alkane dose, thereby improving accuracy of concentration estimations, capsules used in 1997 trials contained only C_{32}, which was released at 101 mg per day.

Sward Measurement

On days 4 and 9 of each trial, 10 cm x 20 cm plots paired with each grazing observation were hand-plucked to ground level to emulate maximum possible removal by grazing wapiti. Samples were freeze-dried for 72 h at -60°C and feeding patch phytomass (FPP) calculated (g DM/m^2). In addition, at the beginning, middle, and end of every trial in 1997, five 0.25 m x 0.25 m phytomass plots were sampled from randomly chosen locations on grassland in each enclosure. These samples were oven-dried for 5 days at 60°C and pasture phytomass estimated (kg DM/ha). These measurements were collected during a concurrent study at Ministik (N. Donkor, unpublished data).

Faecal Collection

Small samples of freshly voided faeces were collected from each hind on days 4 and 9 in 1996 trials. In 1997, collection was changed to days 5 and 10 to create a more accurate association with sampled vegetation, based on a compromise between digesta passage rate in wapiti and trial length. Faecal samples were also collected on day -1 to utilize as a faecal n-alkane reference in non-dosed wapiti. In LL96, four calf faecal samples were obtained (two from each pasture) to compare n-alkane concentrations with those found in non-dosed hind faecals. Samples were freeze-dried for 72 h at -60°C, ground through 20-mesh screen in a Wiley mill, and n-alkanes extracted.

Foraging Behaviour

In EG96 to EG97, foraging parameters were observed during normal feeding bouts on 2 to 7 days, in morning (0800-1130) and afternoon (1400-1700). Cropping bite rates were determined in 4 to 15 minute sessions and corrected for nonforaging activities exceeding 30 seconds. Observation began by selecting a group member and continued sequentially until all animals were observed.

Attempts were made to acquire 10 minutes per individual to correspond with the time interval selected for scan sampling. Bite rates observed during sessions less than 2 minutes duration were discarded. Cropping rates were not collected while animals were in aspen forest, as disproportionate time was spent in activities such as tree rubbing, chewing bark, and eating twigs.

In June to August 1996, instantaneous cropping bite rates were recorded for a total of 1 to 4 minutes per hind, in each morning and afternoon session. Recording began when an animal commenced intensive grazing and when foraging was interrupted, observation was terminated until the animal returned to feeding. Therefore, correction for non-foraging activities was not necessary.

Following each session, mean bite size was estimated by hand-plucking 20 to 40 emulated "bites", to duplicate as closely as possible, amount and species composition of bites ingested by wapiti (Hudson and Nietfeld 1985). Variations in wapiti incisor bar width and observer bias were corrected with the following equation:

$$\text{Corrected Bite Size (BS)} = \text{BS} \times I / O \qquad [1]$$

where I is wapiti incisor bar width (mm) and O is width on observer hand that prehends vegetation (mm). Incisor bar width represents tooth surface available for forage prehension. O accounts for between-observer variation in hand-plucking techniques.

Activity Budgets

Activity budgets were determined using the predominant activity sampling method (Hutt and Hutt 1970). A behaviour was assigned if it occurred more than half of the given interval (10-min), irrespective of its distribution within the interval. Although this method has a degree of subjectivity, it has the advantage of combining simplicity of instantaneous sampling with increased accuracy of continuous sampling estimations. For each group, behaviours were recorded at 10-minute intervals over a 24-hour period (diurnal period only during PL96 and LL96), once per trial. Wapiti were fitted with patterned reflective neck collars, facilitating nocturnal observation and individual identification.

Activities were categorized as foraging, bedded, standing, and other. These represent the only behaviours that these captive wapiti routinely demonstrated for at least 5 consecutive minutes. Activities in the "other" category included movement (running, walking), self-grooming, rubbing (against fence post or tree), cow-calf interaction (nursing, grooming), and cow-cow interaction (agonistic, grooming). However, times when such activities exceeded 5 minutes were rare.

Time budgets and activity patterns (foraging bout distribution, frequency, and duration) were calculated. Short periods of activity associated with disturbance or comfort movements were infrequent, and were not included as part of the total time budget.

Calculations

Dry matter intake was calculated using two pairings of adjacent n-alkanes (C_{31}:C_{32}, C_{33}:C_{32}):

$$\text{Herbage intake (DMI)(kg DM/day)} = \frac{(D_{32} \times F_n/F_{32})}{H_n - (F_n/F_{32}) \times H_{32}} \qquad [2]$$

where D_{32} is release rate (mg/day) of dosed n-alkane (C_{32}), F_{32} and H_{32} are respective concentrations (mg/kg DM) of C_{32} in faeces and herbage, and F_n and H_n are concentrations (mg/kg DM) of natural (*i.e.* non-dosed) n-alkanes (either C_{31} or C_{33}) in faeces and herbage, respectively.

Faecal recovery of n-alkanes increases with increasing carbon-chain length (Dove and Mayes 1991). Therefore, C_{36} was used to determine herbage digestibility (%), since it was dosed and the most indigestible n-alkane. The digestibility equation is based on that used in Heydon *et al.* (1993) and is as follows:

$$\text{Digestibility of DM (\%)} = 1 - \left[\frac{(0.96 \times D_{36}) / F_{36}}{\text{DMI}}\right] \times 100\% \qquad [3]$$

where D_{36} is excretion rate (mg/day) of dosed C_{36}, F_{36} is faecal concentration (mg/kg DM) of C_{36}, and 0.96 represents a correction factor to account for partial digestibility of C_{36} (Heydon *et al.* 1993). DMI represents actual intake (kg) electronically recorded by the automatic feed monitoring system.

Natural (*i.e.* non-dosed) faecal n-alkane recovery (%) was calculated using the following equation:

$$\text{Recovery (natural) (\%)} = \left[\frac{\text{FO} \times F_n}{H_n \times \text{DMI} \times \text{Dig.}}\right] \times 100\% \qquad [4]$$

where FO is faecal output (kg/day), F_n and H_n are concentrations (mg/kg DM) of natural (*i.e.* non-dosed) n-alkanes in faeces and herbage, repectively, and DMI is actual intake (kg/day). Dig. refers to feed digestibility estimated individually in each hind using equation 3.

Dosed faecal n-alkane recovery (%) was calculated and corrected for daily marker excretion as follows:

$$\text{Recovery (dosed) (\%)} = \left[\frac{\text{FO} \times F_d}{(H_d \times \text{DMI} + D_d) \times \text{Dig.}}\right] \times 100\% \qquad [5]$$

where D_d is the expected daily excretion of dosed n-alkane.

The bite count method was used both to estimate herbage intake (kg DM/day) (1997 trials only) and to explore the adaptive responses of wapiti to changing pasture phytomass and structure. The technique is based on behavioural observation according to the following equation:

$$\text{Herbage Intake (DMI) (kg DM/day)} = BR \times BS \times FT \qquad [6]$$

where BR is bite rate (bites/min), BS is bite size (kg DM). and FT represents absolute feeding time (min) over 24 h.

Statistical Analysis

Probabilities of $\alpha<0.05$ were accepted as significant. All statistical computations were performed using SPSS Base 8.0 (1998). Means are reported with standard errors.

Calibration

The preferred technique for assessing the accuracy of the double n-alkane ratio method was to regress estimated against actual intake, and ascertain whether predicted slope differed from unity and intercept differed from zero. Further comparisons were made using nonparametric Mann-Whitney tests (Conover 1980), to confirm findings.

One-way analysis of variance (ANOVA) and Bonferroni's pairwise multiple comparisons (SPSS 1998) were used to compare herbage and faecal n-alkane concentrations and n-alkane faecal recovery. Simple linear regression analysis examined uniformity of marker excretion in faeces, and tested effects of intake level on recovery and excretion of n-alkanes in faeces, and feed digestibility.

Maintenance requirements of pen-fed wapiti hinds in their last trimester of gestation were estimated by regression analysis of metabolizable energy intake (MEI) (kJ/kg$^{0.75}$/day) against net hind liveweight gain (MDG) (g/kg$^{0.75}$/day) and conceptus MDG (g/kg$^{0.75}$/day). DMI was converted to MEI using energy values for alfalfa pellets calculated in Jiang (1993) and an approximated metabolizable portion of 82% (Jiang and Hudson 1992). Conceptus MDG was estimated using Adam *et al.*'s (1988) regression equations for red deer, allometrically adjusted for the size difference between species.

Dry Matter Intake

Seasonal variation in herbage n-alkane concentrations and liveweight gain were compared using factorial ANOVA, with main effects being season (May, June/July, August, November) and pasture (H, L). Bonferroni's pairwise multiple comparisons for n-alkane concentration and Tukey's HSD test (SPSS 1998) for liveweight gain were applied when significant differences were detected.

Factorial ANOVA was used to compare seasonal DMI, with main effects being season and method (n-alkane ($C_{31:32}$, $C_{33:32}$), bite count). Scheffé's test (SPSS 1998) identified which means differed. Regression analysis examined the relationship between intake estimation techniques, and DMI and forage availability.

Maintenance requirements of grazing wapiti hinds during early gestation and late lactation were estimated by simple linear regression of MEI ((kJ/kg$^{0.75}$/day) against MDG (g/kg$^{0.75}$/day). DMI was converted to MEI using seasonal forage energy and digestibility values from Jiang (1993) measured in hinds grazing Ministik pastures. The metabolizable portion of intake was approximated at 82% (Jiang and Hudson 1992). At peak lactation, inclusion of calf MDG (g/kg$^{0.75}$/day) into the regression analysis corrected for calf growth and hence milk production. During late gestation, maintenance was predicted by regressing MEI (g/kg$^{0.75}$/day) against net hind MDG (g/kg$^{0.75}$/day) and conceptus MDG (g/kg$^{0.75}$/day).

Foraging Behaviour

Variables were subjected to one-way ANOVA and Bonferroni's pairwise multiple comparisons, and if no significant difference occurred between respective seasons among years, data were pooled. Interrelationships among activity and foraging parameters were tested by non-linear regression. Treatment (H, L) and seasonal differences in activity and foraging parameters, were examined using factorial ANOVA. Tukey's HSD identified those means that differed significantly.

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CHAPTER THREE

CALIBRATION of the DOUBLE n-ALKANE RATIO TECHNIQUE

This chapter contains results of a preliminary evaluation of the double n-alkane ratio technique for estimating dry matter intake (DMI) and digestibility. This initial step includes assessment of the efficacy of n-alkane marker in wapiti hinds according to the following hypothesis:

H_1: Double n-alkane ratio estimates of DMI do not differ from actual intakes

I ascertain which adjacent n-alkane pairing provides better predictions of intake in wapiti, according to the following null hypothesis:

H_0: $DMI_{31:32} = DMI_{33:32}$

Furthermore, reliable application of markers is paramount to their success. Therefore, I also evaluate the use of intra-ruminal controlled-release devices (CRD) for administering n-alkane marker to the wapiti, based on the following hypothesis:

H_2: Intra-ruminal controlled-release devices provide uniform daily release of n-alkane.

To achieve this, pen trials were conducted in which daily feed intake of each hind was measured electronically. When n-alkane estimates of DMI were compared to actual consumption through linear regression, a perfect agreement would result in an intercept of 0 and a slope of 1. Upon validation of this technique in pen-fed wapiti, the n-alkane marker can then be applied to animals grazing pasture.

n-Alkanes

Herbage and faecal n-alkane concentrations (mg/kg DM) are shown in Table 3-1. C_{31} was the most abundant n-alkane found in the pelleted feed offered to wapiti, followed by C_{29}. C_{36} occurred in very low quantities in feed, while only traces of C_{35} could be

Table 3-1 - n-Alkane concentrations (mg/kg DM) in cubed feed offered to wapiti hinds, in faeces, and faecal recovery (%), at Ministik Research Station, AB.

		n-Alkanes						
	n*	C_{29}	C_{31}	C_{32}	C_{33}	C_{34}	C_{35}	C_{36}
Herbage (mg/kg DM)	8	157.9 ± 2.4^{a}	216.3 ± 2.3^{b}	6.6 ± 0.2^{c}	14.6 ± 0.2^{d}	IS**	Trace	1.9 ± 0.4^{c}
Faeces (mg/kg DM)	64	226.1 ± 4.4^{a}	348.0 ± 7.2^{b}	$^{\dagger}21.3\pm2.0^{c}$	23.0 ± 0.8^{c}	IS**	Trace	$^{\dagger}16.1\pm3.5^{c}$
Recovery (%)	64	83.8 ± 14.5^{a}	94.5 ± 15.7^{ab}	95.3 ± 13.7^{ab}	92.9 ± 16.0^{ab}	-	-	113.2 ± 10.9^{b}

* number of samples.

** IS = Internal Standard

† Dosed n-alkanes (58.5 mg/day) for both C_{32} and C_{36}.

a,b,c,d mean ± SE. Row means that do not share superscripts differ ($p<0.01$).

detected. Herbage concentrations of C_{32} were similar to C_{36} (p=0.34). Faecal concentrations of C_{32} were similar to C_{33} (p=1.0) and C_{36} (p=1.0).

n-Alkane concentrations and pattern with increasing carbon chain length are in agreement with other extractions of *Medicago sativa* (Casson *et al.* 1990; Malossini *et al.* 1990). The pattern of n-alkanes in feed was also very similar to that found in pasture herbage in this study (see Table 4-1) and, with the exception of C_{33}, n-alkane concentrations were similar between feed and pasture herbage.

Quantity of C_{33} in the cubed feed was 14.6±0.2 mg/kg DM. Casson *et al.* (1990) suggested that, to make accurate DMI predictions using n-alkanes as markers, natural (*i.e.* odd-chain) n-alkanes should exceed 50 mg/kg DM, although this critical threshold will depend on the accuracy of laboratory analysis. Improved analytical procedures adopted in this study enabled precise n-alkane concentration estimations for values as low as 10 mg/kg DM. Furthermore, similarity in magnitude between C_{32} and C_{33}, likely generated similar precision in quantity estimates, and therefore, reliable intake determinations.

Significant differences of recovery rates were not detected in n-alkanes used to determine DMI and digestibility (Table 3-1, p>0.05). However, faecal recovery of C_{29} (83.8±14.5%) differed from C_{36} (113.2±10.9%) (p=0.01).

With the exception of C_{33}, faecal recovery increased with carbon chain length within the range examined in this study. Recovery (%) of C_{32} (95.3±13.7) more closely resembled that of C_{31} (94.5±15.7), than C_{33} (92.9±16.0), although this was not significant (p>0.05). Each n-alkane was tested for the effects of intake level on faecal recovery using simple linear regression, and no significant effects were found (p>0.05).

Recoveries of C_{31} in faeces have ranged from 63% in sheep (Dillon and Stakelum 1990), to as much as 99% in goats (Duncan 1986). Although quantitative marker recovery is not a requisite of this technique, paired dosed (even-chain) and natural (odd-chain) n-alkanes used in DMI estimation must have the same faecal recovery (Vulich *et al.* 1991). A general trend of increasing recovery with increasing carbon chain length does exist, however, disparity between adjacent n-alkanes is variable, although not significantly ($p>0.05$).

Mayes *et al.* (1986) postulated that relative faecal recoveries of n-alkanes may vary with age, physiological state and animal species, due to differences in conditions within the digestive tract. This highlights the importance of local calibration to examine n-alkane patterns and quantities in pasture species, as well as characterizing behaviour of n-alkanes in the animal under study.

Low quantities of C_{36} found in feed (1.9±0.4 mg/kg DM) and pasture herbage (1.6±0.1 mg/kg DM) (see Table 4-1) in this study, may lead to problems when determining faecal recovery. Inaccuracies that occur when analyzing such minute amounts can bias results. Presumably, this explains C_{36} recovery values exceeding 100% (*i.e.* 113.2%, CI (95%): ±11.8).

Evidence supporting this is found in Duncan (1986) where goats were fed diets containing only two plant species in various prescribed proportions. *Juncus effusus* (rush) had undetectable quantities of C_{35}, while *Lolium perenne* (perennial ryegrass) contained 12.2±0.2 mg C_{35}/kg DM. As the proportion of rush:grass increased, and C_{35} concentration decreased, estimated faecal recovery rose well beyond 100% (*e.g.* at a feeding level of 900 g DM/day and 60:40 rush:grass ratio, estimated C_{35} recovery was 123%). Perhaps, augmenting dosed quantities of C_{36} could minimize these errors, by increasing the difference between herbage and faecal recovery levels.

Another consideration when exploring variability in faecal recoveries among studies, is the treatment of herbage and faecal samples following collection. Samples are most commonly freeze-dried, however, some have oven-dried them at 100°C (Duncan 1986), while others have even used a different drying process for herbage than for faecal samples (Vulich *et al.* 1991). For reasons of precision, identical treatments should be applied to all samples. Both faecal and herbage samples in this study were freeze-dried at -60°C.

Herbage n-alkanes are distributed in the thin film of wax on the plant surface. Exposure to excessive heat could precipitate this delicate layer, either degrading n-alkanes present or leaving behind quantities of n-alkanes as residues in the drying container. Underestimations of herbage concentrations will produce overestimations of faecal recovery. This may be the reason for Duncan's (1986) inordinately high faecal n-alkane recovery estimates.

n-Alkane Administration

Most investigations of intra-ruminal controlled-release devices have used chromic oxide (Cr_2O_3) (Ellis *et al.* 1981, 1982; Costigan and Ellis 1987; Ellis and Rodden 1987; Barlow *et al.* 1988; Hatfield *et al.* 1990; Buntinx *et al.* 1992). Only recently, have researchers explored the use of CRD containing n-alkane markers (Dove *et al.* 1991; Champion *et al.* 1995; Friend *et al.* 1995).

Ideally, CRD should be calibrated locally to determine their behaviour in the animal species under study and on the specific pasture conditions. This would not be critical for situations in which only relative (not absolute) comparisons of DMI are necessary. The most accurate method is measurement of daily rate of plunger travel, however, slaughter and oesophageally-fistulated animals are expensive and impractical. An economical alternative is endpoint determination (Ellis *et al.* 1988) whereby release rate is estimated by monitoring marker disappearance in faeces.

Manufacturer validation tests on the CRD used in this study indicate a daily marker excretion rate of 68.3 mg of both C_{32} and C_{36} over a period of 13 days (K.J. Ellis, unpublished data). Field and pen calibration tests at Ministik using the endpoint determination method established that CRD expiry took longer in wapiti hinds offered cubed feed (15 days), than in those grazing pasture (13 days).

This likely emanates from differences in digesta flow rates often found between animals on pelleted feed and pasture herbage. That is, longer retention of digesta in the rumen (*i.e.* pasture herbage) will increase mixing with gelled n-alkane tablets, thereby causing more rapid CRD expiry. This results in a predicted daily excretion rate of 58.5 mg of both C_{32} and C_{36} from CRD in hinds on cubed feed. Mean excretion rate (mg/day) of dosed n-alkanes, C_{32} and C_{36}, based on faecal output determinations were 51.8±4.4 and 50.4±6.2, respectively (Fig. 3-1).

Simple linear regression revealed that predicted marker excretion (mg/day) in individual wapiti (across days) was closely associated with actual release for C_{32} (p=0.003, R^2=0.80), but not for C_{36} (p=0.35, R^2=0.15). Averaging animals by day had the same effect for C_{36} (p=0.35, R^2=0.15) but exhibited a much weaker relationship for C_{32} (p=0.29, R^2=0.18). Results indicate that there was more variation among days than among animals in excretion rates of C_{32}, but not for C_{36}.

Comparison of DMI (kg) and daily n-alkane excretion rate (mg/day) using simple linear regression demonstrated no significant relationship (C_{32}: p=0.06; C_{36}: p=0.92). Others have also found that level of herbage intake did not affect CRD excretion rates (sheep: Parker *et al.* 1989, 1990; cattle: Barlow *et al.* 1988). This offers the advantage of utilizing the same CRD for concurrent estimation of intake in animals on varying planes of nutrition, and of different age, sex, breed, and physiological status.

Problems with bolus regurgitation and failure of CRD to release marker have been reported (Ellis *et al.* 1981; Parker *et al.* 1990; Momont *et al.* 1993). Capsule failure can be readily identified by an irregular pattern or low faecal recovery of dosed n-alkanes. Researchers at the Ministik Research Station have experienced numerous problems with capsule loss in earlier versions of this CRD. In both calibration and grazing trials (see Chapter 4), 75 of 81 (93%) CRD remained functional in the wapiti rumens for the duration of trials and exhibited reasonable faecal marker concentrations. Superior capsule retention and function in the present study indicates that the current CRD design is well suited for use in mature wapiti.

Dry Matter Intake

DMI was estimated in eight mature gestating wapiti, as one animal regurgitated its CRD early in the trial. Intake calculations were based on the mean of eight consecutive days from day 5 to day 12, to ensure that n-alkane release was in equilibrium. Mean measured

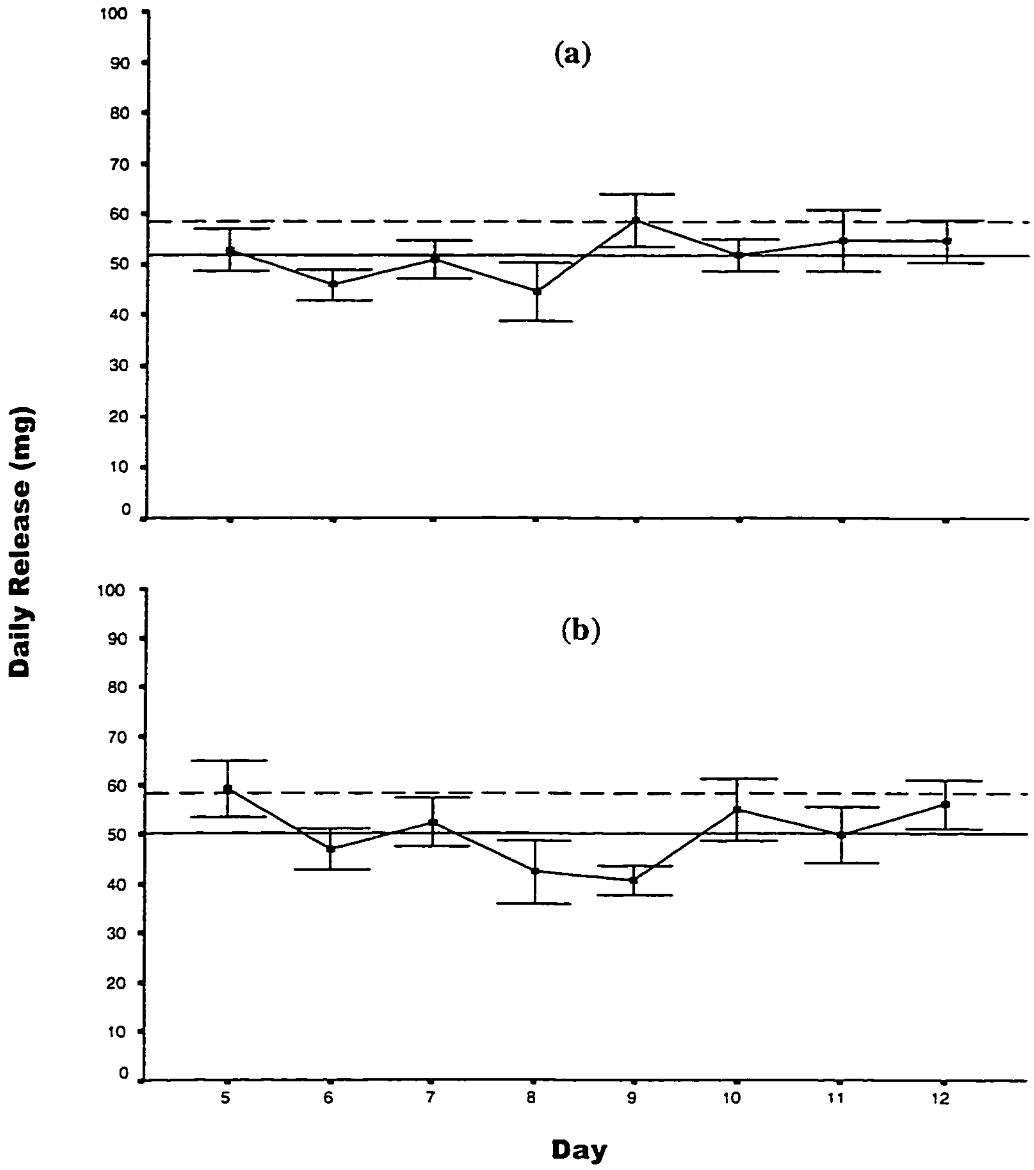

Fig. 3-1 - Mean daily release (mg) of (a) C_{32} and (b) C_{36} dosed n-alkanes in wapiti hinds (n=8) at Ministik Research Station, AB. Horizontal dashed line represents expected release rate (58.5 mg/day). Horizontal solid line represents overall calculated mean. Vertical bars represent one standard error.

intake was 9.18±1.56 kg DM/day (range: 6.99-12.53 kg DM/day). Biases of DMI (difference between estimated and actual intake, expressed as a percentage of actual intake) based on C_{31}:C_{32} and C_{33}:C_{32} estimates were 6.6% and 2.2%, respectively. Both n-alkane pairings overestimated actual intake, albeit by a small extent.

Results were analyzed with a nonparametric Mann-Whitney test, which implied no difference between estimates using n-alkanes, and actual intake for both adjacent pairs (C_{31}: $z = 0.63$, C_{33}: $z = 0.32$, $Z_{0.025} = 1.96$, $p > 0.05$). A Mann-Whitney test also showed that C_{31}:C_{32} and C_{33}:C_{32} estimates of intake were not significantly different ($z = 0.42$, $Z_{0.025} = 1.96$, $p > 0.05$). Actual intake was plotted against estimated DMI using simple linear regression (Fig. 3-2). The C_{31}:C_{32} pairing demonstrated a better fit (slope = 1.09, p=0.001; x-intercept = -0.20, p=0.91; R^2=0.84) than C_{33}:C_{32} (slope = 0.84, p=0.009; x-intercept = 1.71, p=0.44; R^2=0.71).

Most studies that have compared actual intake to n-alkane estimates have found the C_{33}:C_{32} pairing to be a more accurate predictor of DMI, than C_{31}:C_{32} (sheep: Mayes *et al.* 1986, Vulich *et al.* 1991; dairy cows: Dillon and Stakelum 1988, 1990, Dillon 1993). The only exception is Duncan's (1986) work with goats, which demonstrated slightly better accuracy from C_{31}:C_{32} estimates. In the present study, the C_{33}:C_{32} n-alkane pairing produced slightly more accurate herbage intake predictions than C_{31}:C_{32}, however, simple linear regression revealed a strong relationship between them ($y = 0.76x + 1.95$, p=0.002, R^2=0.82).

Dove and Mayes (1991) indicated that, as carbon chain-length increases, differences in faecal recovery between adjacent n-alkanes decrease. Therefore, if the longer chain-length n-alkane is used (*i.e.* C_{33} in this study), lower disparity between recoveries will lead to more accurate predictions of intake. Results in the present study are in agreement.

Furthermore, Mayes *et al.* (1986) suggested that pairing the dosed (even-chain) n-alkane with the adjacent shorter carbon chain-length n-alkane, should produce a slight underestimate of herbage intake, whereas, if coupled with the longer chain n-alkane, DMI should be slightly above measured intake. In the present study, both n-alkane pairings

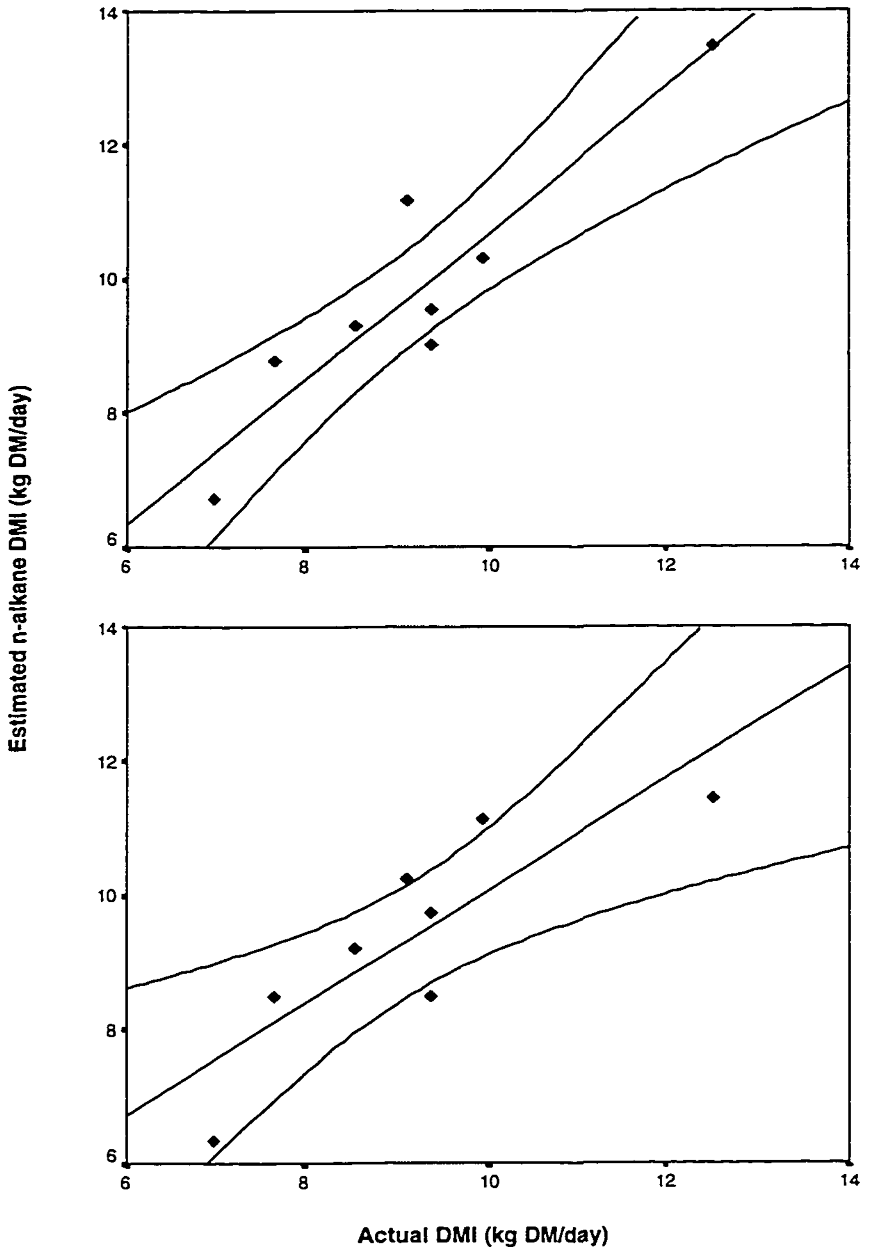

Fig. 3-2 - Relationship between actual dry matter intake (DMI) of wapiti hinds (n=8) and that estimated using (a) C_{31}:C_{32} and (b) C_{33}:C_{32} adjacent n-alkane pairings, at Ministik Research Station, AB. Straight lines represent the least-squares regressions ((a) C_{31}:C_{32} - $y = 1.09x - 0.20$, p=0.001, R^2=0.84; (b) C_{33}:C_{32} - $y = 0.84x + 1.71$, p=0.008, R^2=0.71). Curved lines on either side of regression lines represent 95% confidence limits.

resulted in overestimates of herbage intake. This likely emanates from the fact that the difference in faecal recovery between C_{31} and C_{32} (0.8%), was less than that between C_{33} and C_{32} (2.4%), although, all three n-alkane recovery values were not significantly different ($p>0.05$).

Other studies have established equal precision between C_{31}:C_{32} and C_{33}:C_{32} DMI estimates. For example, when Vulich *et al.* (1991) tested the relationship of actual intake in sheep versus predicted using C_{31}: C_{32} and C_{33}:C_{32}, coefficients of determination (R^2) were 0.84 and 0.85, respectively. Results in this study suggest that C_{31}:C_{32} (R^2=0.84) provides slightly more precise estimations of DMI than C_{33}:C_{32} (R^2=0.71). Therefore, the n-alkane pair that one chooses for determination of herbage intake, will depend on the accuracy and precision desired.

During laboratory analysis of n-alkanes, C_{34} (tetratriacontane) was selected as an internal standard, as its concentration in herbage is generally very low. It is sometimes assumed to be negligible and even absent in some plant species (Mayes *et al.* 1986, 1988; Dove *et al.* 1989). Assumption of insignificant C_{34} quantities would have to be validated and confirmed for each case, as it can lead to loss of accuracy and precision if it is not accounted for when present.

For example, within the range of herbage n-alkane concentrations observed in this study, the presence of 2 mg C_{34}/kg DM would induce a bias of 0.75% in DMI estimation. A way to circumvent this error would be to run a duplicate set of samples using an alternative internal standard. For instance, results revealed only trace amounts of C_{35} (pentatriacontane) in the feed offered to wapiti, and therefore, it would make an ideal internal standard to test for the presence of herbage C_{34}. If quantities of C_{34} were detected, then herbage n-alkane concentrations could be corrected accordingly.

Digestibility

C_{36} (due to its high recovery) was used to estimate individual feed digestibilities in wapiti. Overall mean digestibility of alfalfa-based cubes offered wapiti (63.0±4.0%) was similar to *Medicago sativa* digestibility in dairy cows (65.6%) (Ohajuruka and Palmquist

1991), but much lower than in sheep (75.5%) (Casson *et al.* 1990). Other studies have demonstrated higher digestibilities in sheep compared to red deer, when fed identical herbage (Maloiy and Kay 1971; Milne *et al.* 1978). Simple linear regression was used to test for effect of feeding level on digestibility, and no significant effect was found (p=0.38, R^2=0.13).

Unlike herbage intake calculations using n-alkanes (where use of adjacent pairs obviates problems of unknown faecal recovery), estimations of digestibility require correction for incomplete recovery. In the present study, a faecal recovery of 96% for C_{36} was assumed. Based on the faecal recoveries of n-alkanes C_{29} to C_{33}, and the logarithmic response displayed in other work (*i.e.* n-alkane recovery against carbon chain-length) (Duncan 1986; Dove and Mayes 1991), this value seems a reasonable conjecture.

Total faecal collection offers an unbiased estimate of digestibility, however, this approach requires extensive physical effort and poses problems of variation between days and animals (Smith and Reid 1955). Dosing with a chromic oxide (Cr_2O_3) external marker provides reliable results due to its virtual indigestibility, however, a separate, tedious analytical procedure is necessary for Cr_2O_3 extraction.

Inclusion of more than one n-alkane in a CRD offers the advantage of concurrent herbage intake and digestibility estimation, while using only one laboratory analytical procedure. It should be kept in mind, however, that predicting both DMI and digestibility with a single analysis can cause compounding errors.

For example, any error in procedure (*e.g.* sample contamination, minor GC malfunctions, *etc.*) will lead to erroneous estimations of both intake and digestibility. It is recommended that, in addition to use of an n-alkane (C_{35} or C_{36}) to predict digestibility, an alternative method (*e.g.* marker, total collection) should also be employed. This would provide values calculated independently of the n-alkanes, and therefore, furnish reference as to the accuracy of estimations using the double n-alkane ratio technique.

Maintenance Requirements

Maintenance requirement refers to the energy equilibrium of an animal (*i.e.* amount of energy necessary to maintain body weight). DMI was converted to liveweight digestible energy intake (kJ/kg$^{0.75}$/day), using digestibilities calculated in this study and an energy value of 17.5 kJ/g for alfalfa-based (*Medicago sativa*) pellets (Jiang 1993). The proportion of digestible energy considered to be metabolizable by wapiti was approximated at 82% (Jiang and Hudson 1992). Hind weights (kg) (n=7) were plotted against day and the least-squares regression line fitted. The slope provided an estimate of hind liveweight mean daily gain (MDG) (g/kg$^{0.75}$) over the length of the trial.

In an attempt to estimate wapiti maintenance requirement, metabolizable energy intake (MEI) (kJ/kg$^{0.75}$/day) was regressed against liveweight MDG (g/kg$^{0.75}$). From this regression equation, maintenance (kJ/kg$^{0.75}$/day) (intercept) and energy cost of gain (kJ/g) (slope) can be predicted. No significant relationship was revealed (p=0.19).

Precise predictions of energy requirements (*i.e.* R^2>0.7, when MEI was regressed against MDG) were made in previous studies on non-reproductive *C. elaphus* (*e.g.* Fenessey *et al.* 1981; Jiang and Hudson 1992; Semiadi *et al.* 1995). However, maintenance requirements of gestating mammals are difficult to determine, as energy for the mother and growing foetus is obtained from both exogenous (nutrient intake) and endogenous (mobilization of body tissue) sources. In this case, maintenance of the gestating hind would actually be a function of increased weight of the developing conceptus.

In non-reproductive individuals, hinds may be treated as a single unit, and therefore, the correlation between energy intake and liveweight gain is much more obvious. Gestating animals present a more complex situation. Energy conversion abilities (*i.e.* energy required for deposition of tissue) can vary between foetal and maternal growth. As well, digestive efficiencies can change slightly through gestation (Mattingly and McClure 1982; Oftedal 1985).

For these reasons, it would be more appropriate to consider MDG of the hind and products of conception as separate entities. Therefore, multiple regression was used to examine daily MEI (kJ/kg$^{0.75}$) against hind net MDG (total MDG - conceptus MDG) and conceptus MDG (g/kg$^{0.75}$). MDG allocated to products of conception (*i.e.* foetus, placenta, uterus, amniotic and allantoic fluid, and mammary tissue) at specific stage of gestation were estimated with regression equations for red deer (Adam *et al.* 1988) (Table 3-2). Gestation day was estimated by calculating the number of days from trial midpoint to parturition, and subtracting that from 255 (*i.e.* wapiti gestation length). To account for size difference between species, a factorial conversion was applied (*i.e.* ratio of individual wapiti neonatal mass to mean red deer neonatal mass (from Adam *et al.* 1988)).

Again, there was no significant association between these variables (hind net MDG: p=0.34; conceptus MDG: p=0.82). In contrast to expectations, the best-fit line had a negative slope, and therefore, maintenance requirement could not be determined. Presumably, energy requirements of wapiti hinds during this trial would have been approaching their gestational maximum. However, attempts to differentiate between conceptus and maternal tissues were unsuccessful.

There are limitations to use of energy intake and weight change for maintenance predictions. Gittleman and Thompson (1988) suggest that a combination of caloric consumption, respirometry, and activity budgets (which account for both energy uptake and expenditure), is needed for assessment of energy allocation to maintenance and net production during gestation.

Likewise, daily weight gain can also lead to errors. Weight change is an expression of a number of interacting factors, including nutrient intake, energy expenditure, physiological status, and body composition (Gates and Hudson 1981). As well, total energy investment of a gestating animal involves many additional components, including net production of foetal, uterine, placental, and mammary tissue, and increased maintenance costs associated with these new tissues (Gittleman and Thompson 1988).

For example, studies conducted on wapiti at the same research station showed that, although total hind weight remained constant from March to May, there was a loss of

Table 3-2 - Regression equations relating mean daily gain (MDG) (g/day) of foetus and associated tissues, to proportion of gestation (p = day of gestation/gestation length). Equations were derived from values for red deer in Adam *et al.* (1988). Estimated MDG of conceptus components represents mean of values (n=8) obtained when proportion of gestation for wapiti was substituted into equations and the difference in species size accounted for (*i.e.* factoring by ratio of individual wapiti neonatal mass to mean red deer neonatal mass (from Adam *et al.* 1988)).

Dependent Variable	Regression Function	Estimated MDG of Conceptus Components
Foetus	$77.021 \text{ Ln}(p) + 85.054$	206
Placenta	$4.562 \text{ Ln}(p) + 7.099$	18
Amniotic Fluid	$333.54p^2 - 400.09p + 118.77$	44
Allantoic Fluid	$1.578 \text{ e}^{2.855p}$	48
Empty Uterus	$-43.687p^2 + 54.848p - 4.776$	32
Mammary Tissue	$0.0051 \text{ e}^{8.623p}$	18

13.3% in maternal tissue mass (Gates and Hudson 1981). Therefore, without the ability to distinguish allocation of resources to products of conception from deposition to the maternal unit, efforts to predict maintenance requirements would be unreliable.

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CHAPTER FOUR

DRY MATTER INTAKE OF WAPITI HINDS

Pen trial validation of n-alkane marker in Chapter 3 facilitated application of this technique in wapiti on pasture. In this chapter, I employed the double n-alkane ratio technique to estimate seasonal intake of reproductive wapiti hinds grazing aspen parkland. Results provided empirical information of wapiti intake in response to phase of reproduction and available phytomass, according to the following hypothesis:

H_3: Wapiti hinds regulate DMI based on reproductive condition and forage availability.

Comparison to a direct method of estimating forage intake (bite count) afforded field validation of the marker technique according to the null hypothesis:

H_0: $DMI_{\text{n-Alkane}} = DMI_{\text{Bite Count}}$

Comparison with figures derived on non-reproductive hinds at the same research station (Jiang 1993) gave insight into the incremental demands of reproduction.

n-Alkanes

Table 4-1 shows seasonal herbage n-alkane concentrations (mg/kg DM) as growth period progresses. n-Alkane content of feeding patch phytomass (FPP) did not differ significantly from emulated bites ($p>0.05$), therefore samples were pooled. Concentrations of C_{29}, C_{32}, and C_{35} declined considerably through the growing season, and increased markedly in autumn ($p<0.001$). C_{36} exhibited an identical trend although changes were not significant ($p>0.05$). Quantities of C_{31} and C_{33} n-alkanes remained relatively constant across all seasons ($p>0.05$).

Little published information is available on n-alkane concentrations in temperate pasture species, however, others have reported similar seasonal trends in other plant systems (Laredo *et al.* 1991; Vulich and Hanrahan 1990). Greater autumn concentrations are a

Table 4-1 - Seasonal herbage n-alkane concentrations (mg/kg DM) from *Poa-Bromus* grasslands at Ministik Research Station, AB.

	n*	C_{29}	C_{31}	C_{32}	C_{33}	C_{35}	C_{36}
May	16	162^{a}	151^{a}	5.0^{a}	47^{a}	5.5^{a}	3.7^{a}
June/July	16	123^{bc}	192^{a}	3.8^{b}	47^{a}	3.6^{b}	1.6^{a}
August	20	116^{c}	175^{a}	2.6^{c}	43^{a}	1.7^{c}	0.2^{a}
November	26	154^{ab}	155^{a}	5.6^{a}	44^{a}	4.4^{a}	1.9^{a}
SE		5	6	0.2	2	0.2	0.2

*Number of samples.

a,b,c Column means that do not share superscripts differ ($p<0.001$).

consequence of rapidly increasing cell wall content in senescing vegetation. Because n-alkanes are found in the cuticular wax of plants, increased quantities would be expected.

Species n-alkane concentrations of the commonly encountered pasture plants in this study are detailed in Table 4-2. Concentrations are in the same range as those reported by other authors for some of the same species (Malossini *et al.* 1990; Dove and Mayes 1991). Plant parts that were analyzed separately (*i.e. Taraxacum officinale, Trifolium repens*), demonstrated much higher concentrations in flowers than in stems and leaves, for C_{29} to C_{33} n-alkanes. This high variation suggests that care should be taken to achieve accuracy when obtaining emulated bite samples for pasture intake determinations.

For example, wapiti displayed an exuberant preference for *Taraxacum officinale* flowers, and were often observed moving quickly from one plant to another, ingesting only flowers. When plants are in bloom in early summer, inaccuracies of this magnitude during collection of representative bites, could create heavily biased DMI estimations.

The dominant tree in the study enclosures was *Populus tremuloides.* This species had inordinately high concentrations of C_{29} in its leaves (1351 mg/kg), while n-alkane quantities in twigs were negligible.

Although trees in the enclosures were browsed beyond the reach of wapiti, deciduous trees shed their leaves in autumn, providing a formerly inaccessible forage. Hinds were frequently observed exclusively selecting *Populus tremuloides* leaves from the ground. They either find these leaves highly palatable, or simply easily consumed. Whatever the reason, the result is presumably diminished foraging energy expenditure and incisor wear (or both). Fortunately, consumption of these leaves should not have biased intake estimations, as C_{29} was the only n-alkane present in *Populus tremuloides* in such extreme quantities.

n-Alkanes utilized in this study for calculating intake (C_{31} to C_{33}) exhibited normal levels in *Populus tremuloides*, however, some species from other regions contain excessive amounts of C_{31} to C_{33} (*e.g. Acacia aneura*, *Dedonea attenuata*, *Duboisia hopwoodii*) (H. Dove and S. Muir, unpublished data, *In* Dove and Mayes 1991). Analysis of *Duboisia*

Table 4-2 - Mean summer n-alkane concentrations (mg/kg DM) (n=8) of common pasture species at Ministik Research Station, AB.

	C_{29}	C_{31}	C_{32}	C_{33}	C_{35}	C_{36}
Poa pratensis	225	388	6	125	12	2
Bromus inermis	106	103	2	6	0	2
Taraxacum officinale - flower	526	169	10	34	10	3
- leaf/stem	63	35	4	4	9	0
Senecio spp.	304	139	6	9	1	2
Descurainia sophia	109	283	17	33	0	2
Agropyrow repens	83	132	3	37	2	5
Urtica spp.	175	277	5	9	0	2
Trifolium repens - flower	464	560	20	47	1	2
- leaf/stem	75	76	5	8	1	2
Glyceria grandis	202	150	7	25	1	2
Phleum pratense	82	131	3	36	1	1
Polemonium spp.	163	269	5	10	0	1
Cirsium arvense	79	75	5	7	0	0
Populus tremuloides - leaf	1351	189	3	14	3	2
- twig	7	4	0	0	0	0

hopwoodii revealed more than twenty-five times the average amount of C_{31} found in this study. Before undertaking investigations using n-alkane markers, it is imperative to appraise the common plant species in the study area available for consumption, to ensure these problems do not exist, avoiding unreliable results.

In captive studies, pretrial grazing would obviate errors by rapidly clearing pasture of plant species with higher palatability (reducing selectivity biases) and disproportionate n-alkane concentrations. Other studies have encountered difficulties when attempting to collect representative samples of consumed herbage (Friend *et al.* 1995). Similarity of n-alkane content in phytomass and bite samples, implies that the vegetation pattern occurring here enables accurate representation of consumed forage and may have little importance when using n-alkane markers. That is, feeding patch phytomass collection paired with grazing observations may suffice, if bite size estimation is not necessary.

Vulich *et al.* (1993) investigated sward sampling techniques for determining DMI with the n-alkane method. On mixed pasture containing 40% *Lolium perenne*, they found limited variation between oesophageally-fistulated sheep and non-animal techniques (*i.e.* clipping and plucking). In this study, patterns of n-alkanes in bite samples were compared to those in faeces, to assess the accuracy of collecting herbage truly representative of that selected by wapiti. The procedure involved examination of individual odd- and even-chain n-alkanes, as a proportion of total odd- and even-chain n-alkanes, respectively.

Strong agreement in relative proportions of n-alkanes between herbage and faeces suggest that forage sampled compared well with that consumed by wapiti. Hand-plucking as a reliable method of sampling vegetation is supported in the present study. Although further research is necessary exploring alternative techniques to circumvent errors encountered with wild herbivores.

Commencing in the early gestation trial in 1996 (EG96) (*i.e.* new enclosures), vegetation in the heavily (H) grazed pasture had significantly lower C_{31} and C_{33} n-alkane concentrations than in the lightly (L) grazed pasture ($p<0.001$). These differences may emanate from changing relative proportions of pasture plant species through progressive defoliation. Heavy grazing in H has left many tall patches of *Cirsium arvense* and exposed a predominance of *Trifolium repens*. Both of these species (*i.e.* stems and leaves of *T. repens*) contain very low concentrations of C_{31} and C_{33} (see Table 4-2).

Dry Matter Intake

Seasonal dry matter intake (DMI) estimates in wapiti hinds are summarized in Table 4-3. Intakes based on the n-alkane method increased significantly in early summer (p=0.001), remained constant as weaning approached (p=1.0), then dropped off again in autumn (p=0.15). In August, n-alkane DMI (kg DM/day) estimated from C_{31}:C_{32} was higher in H (7.51±1.49) than in L (4.38±0.17) (p=0.04). n-Alkane intakes based on C_{33}:C_{32}, were similar, with August also being the only season with a significant difference between pastures (H: 7.71±1.07 kg DM/day; L: 4.84±0.27 kg DM/day; p=0.04).

Seasonal intake estimates using the bite count method are also reported in Table 4-3. Estimates were only calculated for EG96 and subsequent trials, due to unavailability of 24 h activity budgets in prior trials. Seasonal bite count intake predictions paralleled n-alkane determinations, but were generally higher (p>0.05) (Table 4-4). In all seasons, bite count DMI (kg DM/day) estimations were greater in L. Even though this difference between pastures was considerable in some seasons (*e.g.* August - L: 6.08±3.39, H: 3.30±1.18), high variation among hinds within pastures precluded statistical significance (p>0.05).

DMI estimation methods are compared in Table 4-4. For purposes of comparison, 1996 trials were excluded due to unavailability of 24 hour scan samples (PL96, LL96) or snow cover (EG96), preventing accurate intake estimates using the bite count method. Mean seasonal intakes based on bite counts were higher than those calculated using n-alkanes (p>0.05), ranging from 7.8% in autumn, to 48.3% in early summer.

Simple linear regression tested the relationship between n-alkane and bite count intake estimates (Fig. 4-1). When C_{31}:C_{32} n-alkane predictions were compared, they produced an x-intercept that was significantly greater than zero (2.27±1.72, p=0.23), and a slope

Table 4-3 - Seasonal dry matter intake (DMI) (kg DM/day) of wapiti hinds on heavily (H) and lightly (L) grazed pasture at Ministik Research Station, AB. n-Alkane estimates are based on seasons pooled over two years, whereas, bite count estimates are based on one year.

DMI	May	n^{*}	June/July	n^{*}	August	n^{*}	November	n^{*}	SE
n-Alkane - C_{31}:C_{32} (H/L Pooled)	3.46^{a}	10	5.44^{b}	15	4.90^{b}	12	4.46^{ab}	18	0.16
H	3.67^{a}	5	4.87^{a}	10	$^{\dagger}7.51^{b}$	2	4.39^{a}	9	0.30
L	3.25^{a}	5	5.72^{b}	10	$^{\dagger}4.38^{ab}$	10	4.52^{ab}	9	0.19
n-Alkane - C_{33}:C_{32} (H/L Pooled)	3.44^{a}	10	5.38^{b}	15	5.32^{b}	12	4.41^{ab}	18	0.17
H	3.57^{a}	5	4.91^{a}	5	$^{\dagger}7.71^{b}$	2	4.27^{a}	9	0.31
L	3.30^{a}	5	5.61^{b}	10	$^{\dagger}4.84^{ab}$	10	4.55^{ab}	9	0.19
Bite Count (H/L Pooled)	3.97^{a}	10	7.65^{b}	10	7.19^{bc}	10	4.69^{ac}	10	0.42
H	3.31^{a}	5	7.27^{a}	5	6.12^{a}	5	3.30^{a}	5	0.59
L	4.62^{a}	5	8.03^{a}	5	8.27^{a}	5	6.08^{a}	5	0.54

[*] Number of wapiti.

[a,b,c] Row means that do not share superscripts differ ($p<0.05$).

[†] H differs from L ($p<0.05$) within season, within method.

Table 4-4 - Comparison of techniques (1997 only) for estimating dry matter intake (DMI) (kg DM/day) in wapiti hinds at Ministik Research Station, AB. Differences between seasonal means within method were not significant (*p*>0.05).

DMI	May (n=10)	June/July (n=10)	August (n=7)	November (n=8)	SE
n-Alkane - C_{31}:C_{32}	3.46	5.43	5.16	4.29	0.22
n-Alkane - C_{33}:C_{32}	3.44	5.16	5.43	4.35	0.22
Bite Count	3.97	7.65	7.22	5.23	0.43

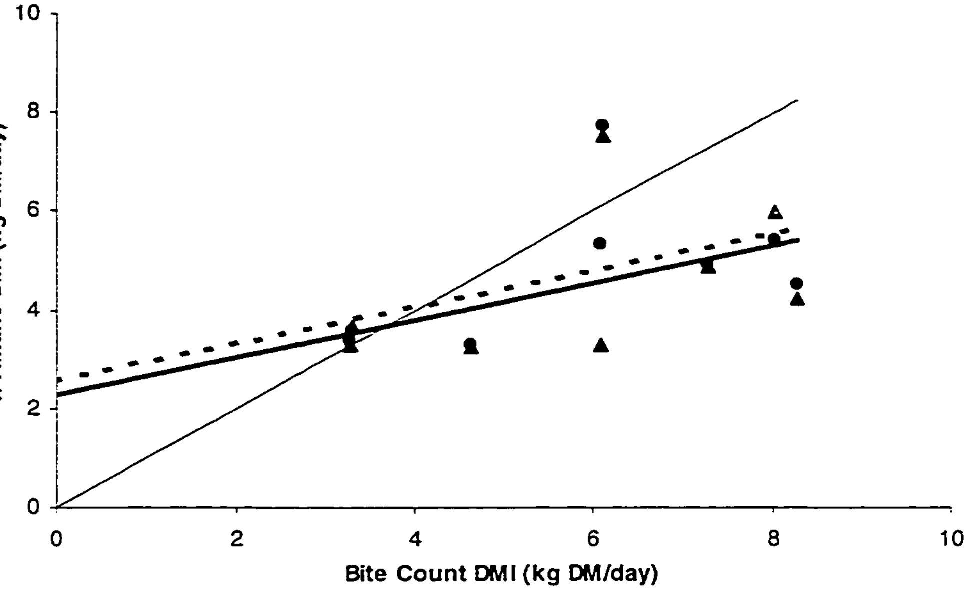

Fig. 4-1 - Estimate of seasonal dry matter intake (DMI) (kg DM/day) of wapiti hinds using the n-alkane method (1997 only), in relation to the bite count method, at Ministik Research Station, AB. Heavy solid line represents C_{31}:C_{32} n-alkane estimates (▲) ($y = 2.27 + 0.38x$, R^2=0.24, p=0.22). Dashed line represents C_{33}:C_{32} n-alkane estimates (●) ($y = 2.54 + 0.38x$, R^2=0.26, p=0.20). Light solid line represents perfect agreement ($y = x$).

that was less than unity (0.38±0.28, $p=0.22$). Predictions from C_{33}:C_{32} n-alkane comparisons had similar x-intercept (2.54±1.60, $p=0.16$) and slope (0.38±0.26, $p=0.20$).

For purposes of brevity and because C_{33}:C_{32} n-alkane estimates of herbage intake appeared to be slightly more accurate than C_{31}:C_{32} (see Chapter 3), discussion of intakes will be those predicted using C_{33}:C_{32}, unless otherwise stated.

Similar seasonal trends of intake have been reported for red deer (Clutton-Brock *et al.* 1982; Heydon *et al.* 1993). There was a marked increase in early summer and decline as lactation progressed. This was likely due to either higher energy requirements during peak lactation (which decrease towards weaning) or greater herbage availability in early summer, followed by a slight decrease when plants mature (or a combination of both).

The former is supported by Heydon *et al.* (1993) in their comparison of red deer milk (reproductive) and yeld (non-reproductive) hinds on pasture with similar forage availability. Both exhibited the same trend from July to October, with lactating hinds having significantly higher intakes, and the difference decreasing as weaning approached. Results of Clutton-Brock *et al.* (1982) agree with the latter premise, in that their lactating and non-lactating wild hinds adhered to the same intake pattern (*i.e.* based on gut contents as a percentage of liveweight) from spring to late summer, yet a difference between groups was not evident. Regression of bite count liveweight DMI (g DM/$kg^{0.75}$/day) against forage availability (kg DM/ha) suggests that phytomass has a strong influence on intake ($p<0.001$, $R^2=0.88$) (Fig. 4-2).

Disparity between intakes of Jiang's (1993) barren hinds and gestating/lactating hinds in the present study, were contrary to expectations. Reproductive animals in this study had considerably lower spring forage consumption than Jiang's barren 2 year old hinds (Jiang: 122; this study: 49±8), when one might expect augmented intakes in animals attempting to meet the needs of a rapidly developing conceptus. However, gut capacity of gestating hinds may have been reduced through physical displacement by products of conception, thereby restricting intake. This has been demonstrated in other species (Forbes 1986).

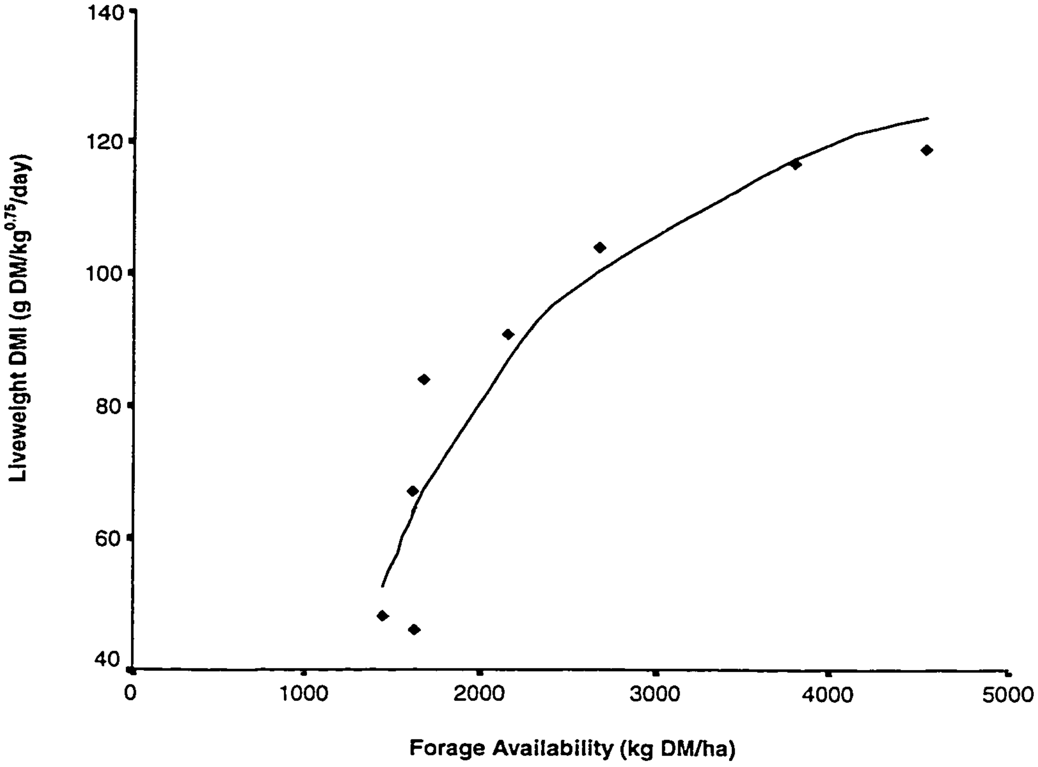

Fig. 4-2 - Bite count estimates of seasonal liveweight dry matter intake (DMI) (g DM/kg$^{0.75}$/day) of wapiti hinds (n=5) on heavily and lightly grazed pasture in relation to forage availability (kg DM/ha), at Ministik Research Station, AB (y = 157.4 - 151605/x, p<0.001, R^2=0.88).

Forage intakes during early summer were similar to those previously determined in lactating (Niezen *et al.* 1993) and non-lactating (Heydon *et al.* 1992) red deer. Jiang (1993) did not present estimates in this season. Forage intakes of ruminants tend to be around two or three percent of bodyweight, approximately 6 kg in wapiti. This level may be very difficult to surpass, due to digestive constraints, and may act as an upper limit, regardless of an animal's energy requirements. While this quantity may be suitable for maintenance in non-lactating females, lactating hinds would experience condition loss, which would have to be re-gained prior to the breeding season.

As weaning approaches, nutrient requirements for lactating wapiti should decrease, as calves rely more heavily on grazing than nursing for nutritional needs. In late summer, Jiang's hinds maintained higher intakes, although the difference was much less pronounced (Jiang: 103 g DM/kg$^{0.75}$; this study: 75±20 g DM/kg$^{0.75}$). Given that Jiang's hinds were yearlings, some of this disparity may be a result of growth impetus. Other non-reproductive wapiti on pasture at the same research station also had higher August intakes (9.5 kg DM/day (Hudson and Nietfeld 1985); this study: 5.32±0.41 kg DM/day). However, this group also contained 2 yearlings (1 stag, 1 hind), as well as 2 adult hinds.

Perhaps hinds are forced to maintain augmented intake levels, capitalizing on persisting abundant forage to increase weight in preparation for the ensuing rut and winter. Rumen capacity may be another explanation, as Remond (1988) established in dairy cows, that rumen volume increases by 40% in the first two months of lactation. Other studies on *C. elaphus* reported similar late summer intakes [*e.g.* Hudson and Watkins (1985) (wapiti): 6.1 kg/day; Niezen *et al.* (1993) (red deer): 88 g DM/kg$^{0.75}$/day; Semiadi *et al.* (1995) (red deer): 86 g DM/kg$^{0.75}$/day].

The autumn decline in DMI may have been due to the predominance of senescent vegetation, thereby increasing rumination requirement and decreasing passage rates. One would expect minimal difference between reproductive and non-reproductive wapiti, a consequence of calf weaning and negligible incremental energy requirements of early gestation. Autumn intakes reported by Jiang (1993) (yeld hinds (yearlings): 60 g DM/kg$^{0.75}$), Heydon *et al.* (1993) (milk hinds: 63 g DM/kg$^{0.75}$), and Semiadi *et al.* (1995)

(milk hinds: 67 g DM/kg$^{0.75}$) are in agreement with the results of this study (64±16 g DM/kg$^{0.75}$).

The bite count method often overestimates DMI, when compared with predictions using markers (*e.g.* Jiang and Hudson 1992). When measuring bite rate, Jamieson and Hodgson (1979) suggest that instantaneous (short-term) records may overestimate long-term means by at least 16%. In this study, bite count estimates consistently exceeded n-alkane predictions. Although slight in May and November, overestimations were more pronounced in summer. This likely reflects the increased difficulty in accurately emulating bite size during periods of peak phytomass.

Seasonal liveweight gain (MDG) (g/kg$^{0.75}$/day) of wapiti hinds are shown in Fig. 4-3. There was no significant difference between H and L (p>0.05), therefore, data were pooled. Gains peaked in early summer at 12.5±1.4 g/kg$^{0.75}$ (p<0.001), while differences among other seasons were not significant (p>0.05). Spring was the only season where hinds exhibited a negative MDG (-2.9±0.8 g/kg$^{0.75}$).

Maximum MDG in early summer is interesting, as peak lactation should be a hind's most energetically expensive season. Considering this time of year demonstrates a coincidence of peak pasture phytomass (see Table 5-2) and quality, combined with maximum wapiti intake, these results seem logical. Pre-parturition weight loss was likely a result of greatly depressed DMI, and this suggests a major source of energy for foetal growth was from mobilization of body tissue.

Calculated DMI (g DM/kg$^{0.75}$/day) using the bite count method increased as an inverse function of forage availability (kg DM/ha) ($y = 157.4 - 151605/x$, p<0.001, R^2=0.88) (Fig. 4-2). When n-alkane estimates were regressed against pasture phytomass, a very weak association was exhibited (p>0.05).

Intake and forage availability are strongly correlated (Trudell and White (1981) (reindeer); Sheath *et al.* (1987) (sheep); Forbes and Coleman (1987) (cattle)). Closer association of bite count estimates compared to n-alkane estimates may be due to bite count DMI computation utilizing behavioural foraging parameters (*i.e.* DMI = bite rate x

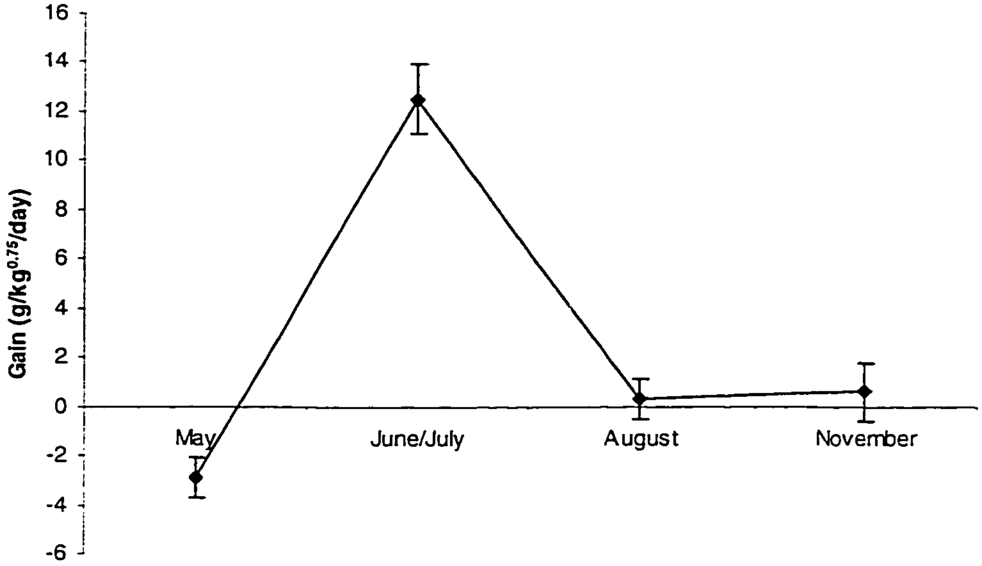

Fig. 4-3 - Seasonal liveweight gain (g/kg$^{0.75}$/day) of wapiti hinds (n=10) at Ministik Research Station, AB. The vertical bars represent 1 standard error.

bite size x grazing time), which are strongly influenced by forage availability (see Figs. 5-7 and 5-8).

Maintenance Requirements

An attempt was made to predict seasonal maintenance requirements of wapiti hinds using regression analysis. In the resulting equations, *x*-intercepts provide an estimate of maintenance requirement (kJ/kg$^{0.75}$/day), while slopes represent the energy cost of gain (kJ/g).

Multiple regression was used to estimate hind maintenance during late gestation. Metabolizable energy intake (MEI) (kJ/kg$^{0.75}$/day) was regressed against hind net MDG (total MDG - conceptus MDG) and conceptus MDG (g/kg$^{0.75}$). DMI was converted to digestible energy intake using seasonal forage energy and digestibility values from Jiang (1993). The metabolizable portion of consumed energy was approximated at 82% (Jiang and Hudson 1992). MDG allocated to products of conception at specific stage of gestation were estimated by substituting proportion of gestation (*i.e.* gestation day/gestation length) into Adam *et al.*'s (1988) regression equations for red deer (see Table 3-3). Differences in species size were then accounted for by factoring the ratio of individual wapiti neonatal mass to mean red deer neonatal mass (from Adam *et al.* 1988). MDG (g/kg$^{0.75}$) of separate parts of conceptus (mean of ten hinds) were estimated as 218 (foetus), 19 (placenta), 88 (amniotic fluid), 60 (allantoic fluid), 25 (empty uterus), and 38 (mammary tissue).

During early gestation, hind MEI (kJ/kg$^{0.75}$/day) was regressed against MDG (g/kg$^{0.75}$). The incremental energy cost of the developing blastocyst was considered to be negligible, and therefore, was not included in the regression analysis.

Multiple regression was used in estimations during peak lactation with the inclusion of calf liveweight gain (g/kg$^{0.75}$/day). This corrects for growth of the calf and hence, milk production. Although calves continue to nurse in August, increased presence of n-alkanes in calf faeces indicated that a substantial portion of their nutrition is acquired from grazing. Therefore, calves were not factored into the regression analysis for late lactation.

Relationships between MEI and liveweight MDG were not significant ($p>0.05$). However, standard errors of the x-intercepts (*i.e.* maintenance requirement) were small, and predictions seem logical, therefore, these values are included in the discussion. Alternatively, standard errors of the slopes (*i.e.* energy cost of gain) were very large, likely partly arising from the fact that the hinds had achieved their full mature weight, resulting in a small range of liveweight changes. Therefore, these values were unreliable and have not been addressed.

Hind energy requirements (kJ/kg$^{0.75}$/day), predicted from the n-alkane method, peaked in early summer at 1229±215, nearly double spring demands (641±51). By late summer, maintenance was reduced to 802±74 kJ/kg$^{0.75}$/day and reached an annual low in autumn (502±28 kJ/kg$^{0.75}$/day). Bite count estimates for hind maintenance (kJ/kg$^{0.75}$/day) were considerably greater than n-alkane determinations. Annual minimum was 1201±177 in May, slightly lower than in November (1304±211), and peaked during summer (June/July: 3514±1017, August: 1780±200).

Bite count maintenance predictions for reproductive wapiti hinds were closer to expectations than estimates from the n-alkane method. Summer maintenance peaks are similar to values of 1500 kJ/kg$^{0.75}$/day estimated for wapiti yearlings by Hudson *et al.* (1994). This suggests lactational energy expense may match that of a rapidly growing yearling. Higher values than Jiang and Hudson's (1992) non-reproductive hinds in spring (Jiang and Hudson: 936 kJ/kg$^{0.75}$/day; this study: 1201±177 kJ/kg$^{0.75}$/day) reflect the incremental energy requirements of late gestation. Trends for both methods seem reasonable, if one assumes maternal energy reserves supply much of the energy required for exponential foetal growth during late gestation.

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CHAPTER FIVE

BEHAVIOURAL RESPONSE TO MEET NUTRIENT REQUIREMENTS

Having determined the annual pattern of nutrient requirements for reproductive wapiti (Chapter 4), the next task was to explore how they altered foraging behaviour to meet these demands. This chapter investigated behavioural compensation by examining seasonal interrelationships between activity, foraging parameters, and forage availability. These associations were tested according to the following hypotheses:

H_4: Wapiti alter activity budgets in response to seasonal nutritional demands, reproductive condition, and forage availability.

H_5: Pattern of wapiti feeding bouts and characteristics of each bout vary with forage availability and reproductive season.

Activity

Wapiti exhibited polyphasic patterns of foraging activity throughout the year, with peaks at dawn and dusk (Fig. 5-1). These peaks demonstrated seasonal and photoperiodic shifts. In all seasons they had long foraging bouts (*i.e.* relative to seasonal mean) late in the day, terminating at sunset in summer, but continuing for approximately one hour after sunset in spring and autumn. Feeding patterns were similar between heavily (H) and lightly (L) grazed pasture in all seasons.

Cervids are well known for their crepuscular habits, however, other studies have also found polyphasic activity patterns in wapiti (Gates and Hudson 1983; Jiang and Hudson 1996), red deer (Semiadi *et al.* 1993), roe deer (*Capreolus capreolus*) (Cederlund 1989), sambar deer (*Cervus unicolor*) (Semiadi *et al.* 1993), moose (*Alces alces*) (Cederlund 1989; Renecker and Hudson 1985; Gillingham and Klein 1991), and reindeer (*Rangifer tarandus*) (Erriksson *et al.* 1981).

Most work revealing biphasic activity patterns in wapiti involved wild (free-roaming) individuals (Craighead *et al.* 1973; Collins *et al.* 1978; Hanley 1982; McCorquodale *et al.*

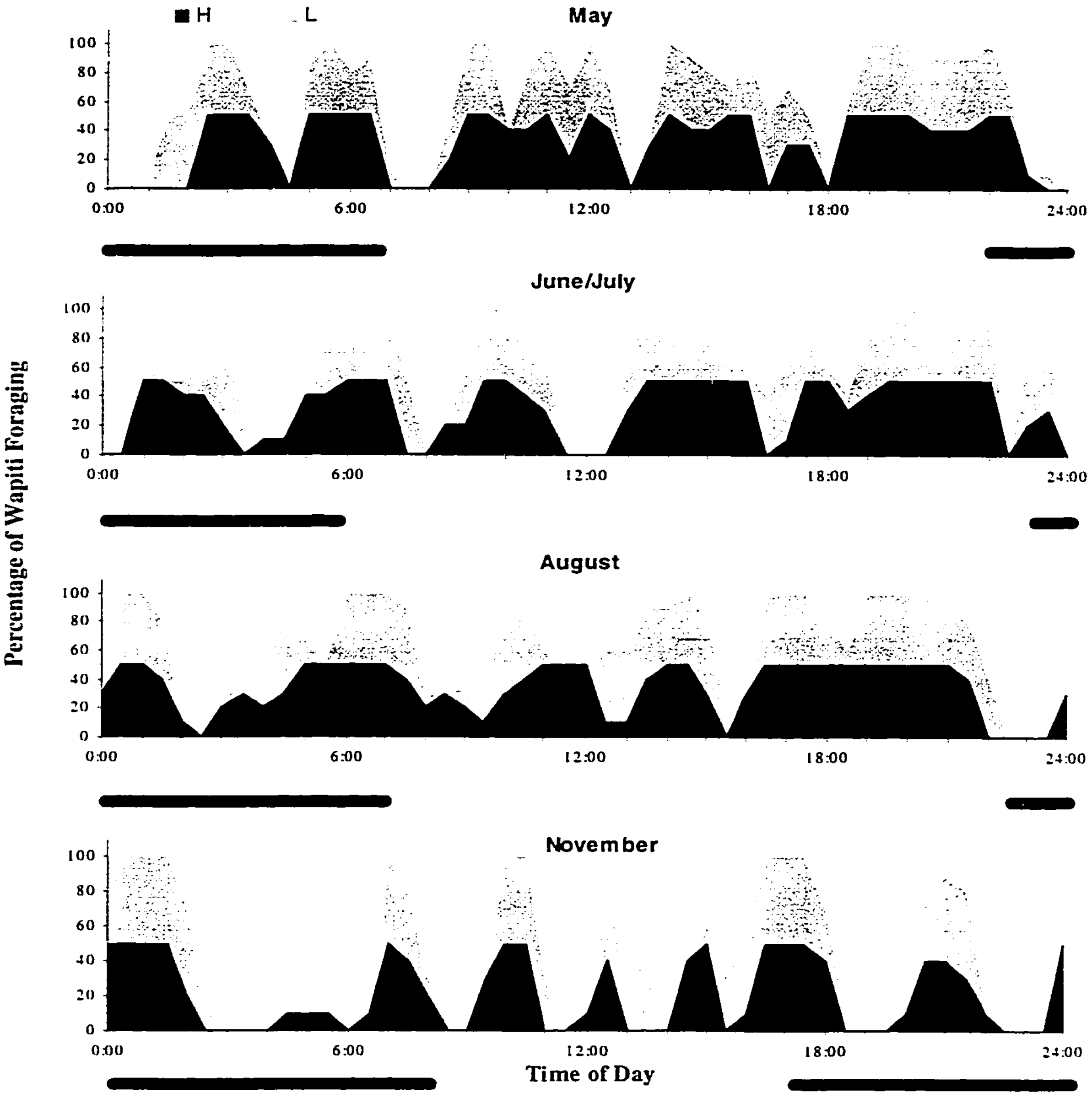

Fig. 5-1 - Seasonal daily foraging patterns of wapiti hinds (n=5) on heavily (H) and lightly (L) grazed pasture expressed as percentage of animals observed foraging in each one-half hour interval. Solid bars below graphs represent hours of darkness.

1986). This indicates that wapiti may alter their daily distribution of activity in captivity. Wild populations must contend with predation risk and human disturbance, while captive groups are habituated to humans and under minimal predatory threat.

Undisturbed wapiti prefer grazing to browsing (Morgantini and Hudson 1985) and in both study pastures, browsing was a very limited foraging option, as trees were defoliated beyond wapiti reach. This, coupled with confinement to enclosures, would greatly reduce forage selectivity (through reduced variety of habitats causing lower plant diversity) and search time (caused by restricted search area), thereby increasing consumption rates. Because grazing ruminants are more restricted by digestive capacity than browsers (*i.e.* due to lower quality forage), perhaps gut fill and the repletion-depletion cycle are primary factors causing polyphasic activity patterns.

The bimodal pattern displayed by Jiang and Hudson's (1996) non-breeding hinds in July, emphasizes the difference in lactating hinds and is probably a consequence of the necessity of frequent nursing bouts. Gates and Hudson (1983) also observed biphasic patterns in spring and summer, however, of the nine animals in their sample, only three were lactating (*i.e.* there were also 2 stags and 4 calves), which may account for the disparity.

Wapiti were largely bedded during the night in all seasons, particularly in the hours immediately after sunset and before sunrise (Fig. 5-2). Peaks of inactivity followed seasonal and photoperiodic shifts. They also remained bedded in the middle of day in spring and early summer, with peaks of inactivity becoming less pronounced in late summer, and absent in autumn. Bedding patterns were similar between H and L in all seasons.

Seasonal activity budgets for wapiti hinds are presented in Fig. 5-3. Wapiti spent a large portion of their active time foraging, however, seasonal variation was marked ($p<0.01$) (Table 5-1). In both pastures, percentage of active time engaged in foraging activities was less in early summer (H: $p=1.0$, L: $p<0.001$), increasing in late summer (H: $p=0.008$, L: $p<0.001$), followed by a notable decline in autumn (H: $p<0.001$, L: $p<0.001$).

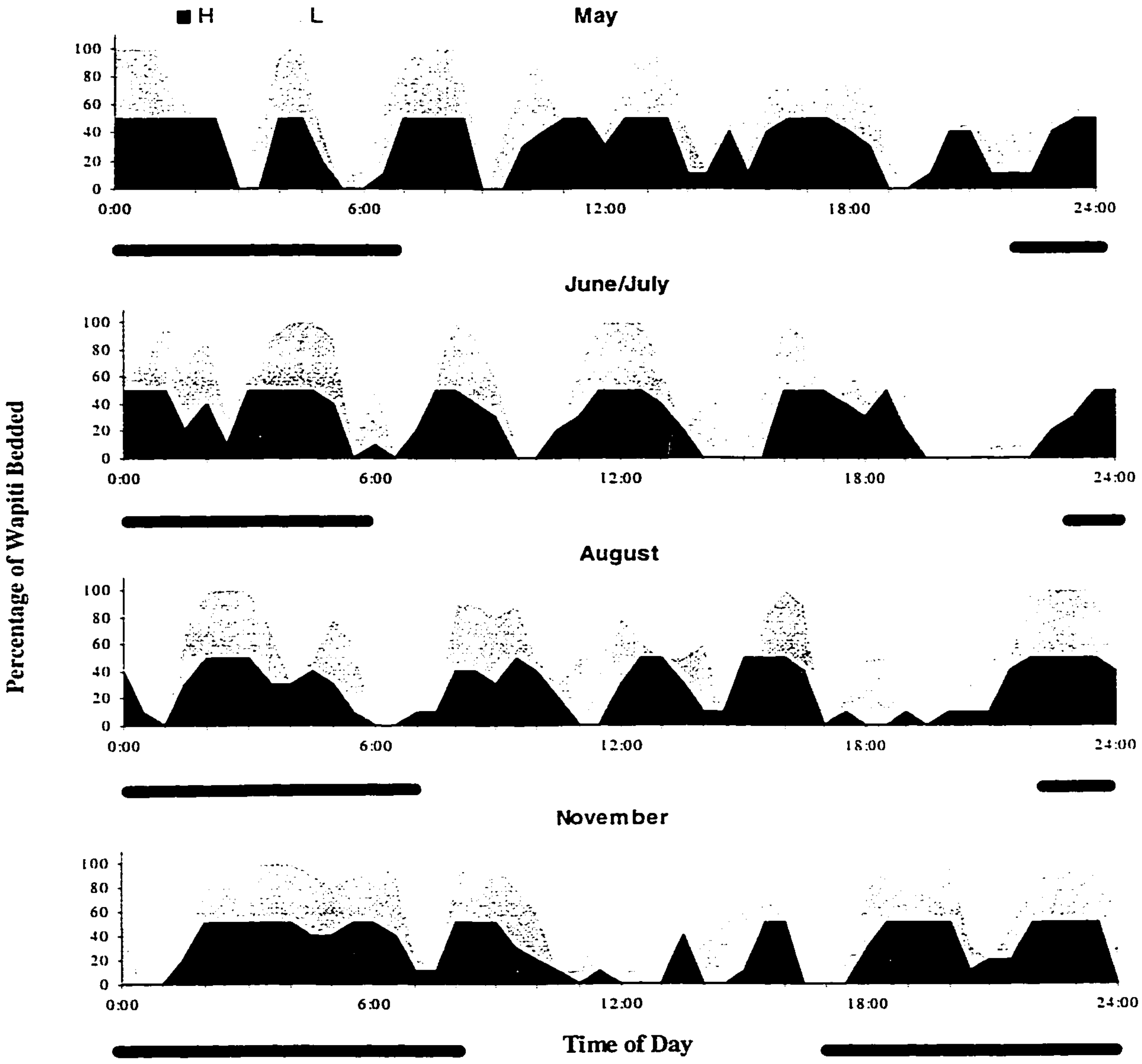

Fig. 5-2 - Seasonal daily bedding patterns of wapiti hinds (n=5) on Heavily (H) and Lightly (L) grazed pasture expressed as percentage of animals observed bedded in each one-half hour interval. Solid bars below graphs represent hours of darkness.

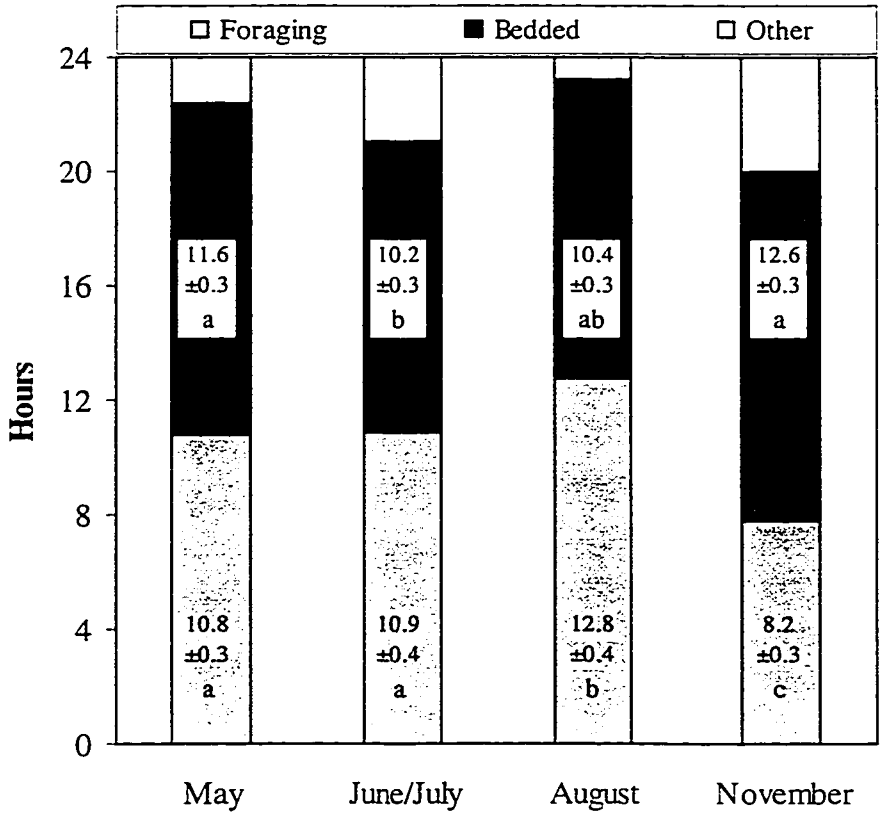

Fig. 5-3 - Seasonal activity budgets of wapiti hinds (n=10) at Ministik Research Station, AB. "Other" refers to any behaviours exhibited when not foraging or bedded (*eg.* standing, social interaction, nursing, movement, *etc.*). Values are mean ± SE. Within foraging and bedding, seasons that do not share letters differ (p<0.05).

Table 5-1 - Seasonal percentage of active time spent foraging for wapiti hinds (n=5) on heavily (H) and lightly (L) grazed pasture at Ministik Research Station, AB.

	1996	1997				
	November	May	June/July**	August*	November**	SE
H	81.9^{a}	89.2^{a}	87.5^{a}	98.8^{b}	59.7^{c}	2.8
L	76.8^{ab}	85.3^{c}	70.2^{a}	89.2^{c}	73.1^{a}	1.7
Total	79.4^{a}	87.2^{ab}	78.8^{a}	94.0^{b}	66.4^{c}	1.6

* H differs from L ($p<0.05$) within season.
** H differs from L ($p<0.01$) within season.
^{a,b,c} Row means that do not share superscripts differ ($p<0.01$).

Differences between H and L were significant ($p<0.05$) in 1997, from early summer through November.

Seasonal daily foraging times (hours) observed in the present study were comparable to those found in other wapiti (Craighead *et al.* 1973; Collins *et al.* 1978; Hanley 1982; Jiang 1993; Florkiewicz 1994) and red deer (Georgii 1981; Clutton-Brock *et al.* 1982; Heydon *et al.* 1992; Kusmartono *et al.* 1996). Frequently, other studies did not differentiate grazing from total active time, therefore, foraging estimates were made by correcting with seasonal values of percent active time foraging found in this study (Table 5-1).

Grazing time of milk hinds in the present study were similar to Jiang's (1993) yeld hinds. This implies that greater nutrient requirements of gestating and lactating wapiti were not satisfied by increasing grazing time, but possibly by augmenting other foraging parameters (*e.g.* bite rate, bite size).

Gates and Hudson (1983) suggest that fatigue and demand of alternate activities (*e.g.* rumination, neonate care) place an upper limit on daily foraging time, and this is commonly cited to be around twelve hours. Presumption that these wapiti may have been constrained by this upper limit is supported by Clutton-Brock *et al.* (1982) and Heydon *et al.* (1992), whereby, increases in daily grazing time from yeld to milk red deer hinds were 9.8 h to 11.8 h and 10.8 h to 12.2 h, respectively.

The pattern of increasing foraging time from spring through late summer, followed by decline in autumn, has also been demonstrated in past work on *C. elaphus* (Georgii 1981; Hanley 1982; Carranza *et al.* 1991; Semiadi *et al.* 1993; Jiang 1993; Florkiewicz 1994). Observations on red deer in Spain (Carranza *et al.* 1991) showed a similar trend, however, animals were active for much longer over 24 hours (winter/spring: 17.5 h, summer: 19.2 h, rut: 14.4 h). This is probably a result of decreased foraging efficiency in the relatively sparse, unproductive Mediterranean scrub habitat. Increase in daily foraging at the end of summer, is likely a result of allowance for hinds to devote more time to feeding and less tending to their calves, as weaning approaches.

When not foraging, wapiti are mostly bedded, however, maternal care disrupts these alternating cycles. This is highlighted by examining wapiti nocturnal activity (Fig. 5-4), as they are essentially a diurnal species. Increase in nocturnal bedding in autumn (post-weaning) corresponds with an almost equal decrease in nocturnal foraging.

These associations do not occur while the hind is lactating. For example, the reduction in nocturnal bedding during peak lactation (June/July), is accompanied by a decrease in nighttime grazing. This suggests that hinds were engaging in alternate activities, such as tending to their calves. Clutton-Brock *et al.* (1982) found the same proportion of diurnal to nocturnal foraging in lactating red deer hinds.

There was no significant difference in diel foraging (p=0.95) and bedding (p=0.53) (hours) between pastures, therefore, data were pooled. Foraging time (h/day) in early summer (10.85±0.41) did not differ from spring (10.82±0.30) (p=1.0), however, there was a significant increase to 12.77±0.43 in late summer (p=0.007), followed by a substantial decrease to 8.23±0.24 in autumn (p<0.001). Time spent bedded (h/day) was greater in spring (11.60±0.30) (p=0.04), consistent through summer (June/July: 10.20±0.27, August: 10.43±0.33) (p=0.97), and peaked at 12.64±0.25 in autumn (p<0.001).

Seasonal foraging and bedding of wapiti hinds during diurnal and nocturnal periods are presented in Fig. 5-4. Due to marked seasonal variation in daylength, diurnal and nocturnal behaviours are expressed as percentage of total hours of daylight and darkness, respectively. There was no significant difference between H and L (p>0.05), therefore, data were pooled. Annual peak of nocturnal bedding in autumn (65.1±7.6%) corresponded with nocturnal feeding minimum (27.8±6.5%). Late summer maximum of 62.3±5.7% diurnal feeding also corresponded with the 35.2±5.0% annual low of diurnal bedding.

In early summer, one would expect animals to seek cover during day to prevent excess thermoregulatory expenditure. Slight increase in diurnal foraging and reduced bedding in

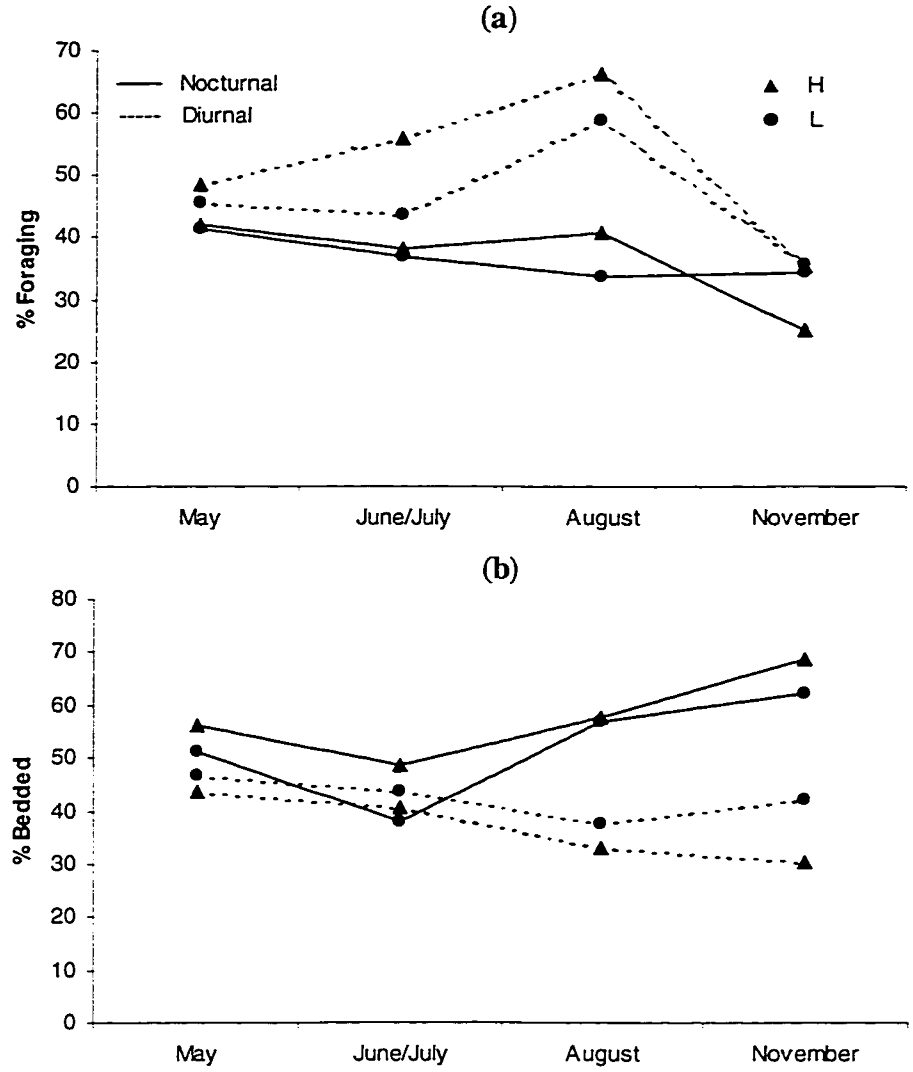

Fig. 5-4 - Seasonal (a) foraging and (b) bedding of wapiti hinds (n=5) on heavily (H) and lightly (L) grazed pastures, in diurnal and nocturnal periods, expressed as percentage of total hours of daylight and darkness, respectively.

June/July, may be an artifact of insect harassment. Infestation was extreme that year, and wapiti were frequently observed avoiding insects. Higher prevalence of nocturnal foraging in spring and summer found in this study, has been reported in other work on wapiti (Gates and Hudson 1983) and Dall's sheep (*Ovis dalli*) (Hoefs and McTaggart Cowan 1979).

Characteristics of foraging bouts showed marked seasonal variation ($p<0.05$) (Table 5-2). Differences between pastures were only significant during summer ($p<0.05$), when wapiti grazing L had more bouts of shorter duration. Across all trials, foraging bouts of less than 20 minutes accounted for only 0.9% of total grazing time, while 20 minute bouts accounted for 5.0%. Therefore, foraging bouts of less than 20 minutes were deleted from analyses of duration and number of foraging bouts. Overall, duration of foraging bouts (min) were longest in August (99.5±20.3) ($p=0.006$), followed by a sharp decline in November (59.9±11.1) ($p=0.001$). Number of bouts per day were highest in spring (9.7±1.2) and early summer (10.2±2.2), and fewest in late summer (7.0±0.8) and autumn (7.3±0.6) ($p<0.01$).

Simple linear regression of foraging bout duration (min) against number of bouts revealed a significant relationship from spring through late summer ($y = 10.8x + 173.6$, $p=0.005$, $R^2=0.88$) (Fig. 5-5). Foraging bouts in autumn did not demonstrate this relationship ($p=0.97$).

The increasing length of foraging bouts, coupled with decreasing frequency in summer, agree with the literature (wapiti: Hanley1982, Florkiewicz 1994, Jiang and Hudson 1996; moose: Cederlund 1989, Van Ballenberghe and Miquelle 1990; black-tailed deer: Hanley 1982), although bout durations were much shorter in this study. This is probably a result of less rapid rumen fill in wild herbivores due to higher incidence of browsing, and hence, greater forage selectivity and search time. Decrease in bout duration from late summer to autumn ($p=0.001$) is probably in response to increased rumination, reflecting declining forage quality.

Table 5-2 - Seasonal foraging parameters and forage availability for wapiti hinds (n=5) on heavily and lightly grazed pasture (1997 only) at Ministik Research Station, AB.

	Spring (May)	Early Summer (June/July)	Late Summer (August)	Autumn (November)	SE
Heavily Grazed					
Grazing Time (h/day)	11.1^{a}	11.8^{ab}	13.7^{b}	7.2^{c}	0.6
No. of Bouts (bouts/day)	9.2^{a}	$^{**}8.4^{ab}$	6.6^{b}	7.2^{b}	0.3
Duration (min/bout)	67.9^{ab}	$^{**}83.3^{b}$	$^{*}114.2^{c}$	54.5^{a}	6.0
Bite Rate (bites/min)	48.9^{a}	49.8^{a}	62.4^{b}	33.8^{c}	2.5
Bite Size (mg)	98^{a}	222^{a}	143^{a}	226^{a}	18
Feeding Patch Phytomass (g DM/m^2)	183^{a}	321^{a}	314^{a}	257^{a}	26
Pasture Phytomass (kg DM/ha)†	1625^{ab}	$^{**}2669^{b}$	$^{**}1680^{ab}$	1449^{a}	88
Lightly Grazed					
Grazing Time (h/day)	10.6^{ab}	9.9^{bc}	11.8^{b}	8.4^{c}	0.3
No. of Bouts (bouts/day)	10.4^{a}	$^{**}12.0^{a}$	7.4^{b}	7.4^{b}	0.5
Duration (min/bout)	59.6^{ab}	$^{**}50.2^{b}$	$^{*}84.7^{a}$	65.4^{ab}	3.3
Bite Rate (bites/min)	44.6^{ab}	45.5^{b}	61.4^{c}	40.6^{a}	1.9
Bite Size (mg)	155^{a}	339^{b}	210^{ab}	281^{ab}	23
Feeding Patch Phytomass (g DM/m^2)	263^{a}	580^{b}	498^{ab}	312^{a}	42
Pasture Phytomass (kg DM/ha)†	1645^{a}	$^{**}4875^{b}$	$^{**}3799^{b}$	2152^{a}	243

^{a,b,c} Row means that do not share superscripts differ (p<0.05).

* Heavily grazed differs from lightly grazed pasture (p<0.05) within season.

** Heavily grazed differs from lightly grazed pasture (p<0.01) within season.

† From N. Donkor (unpublished data)

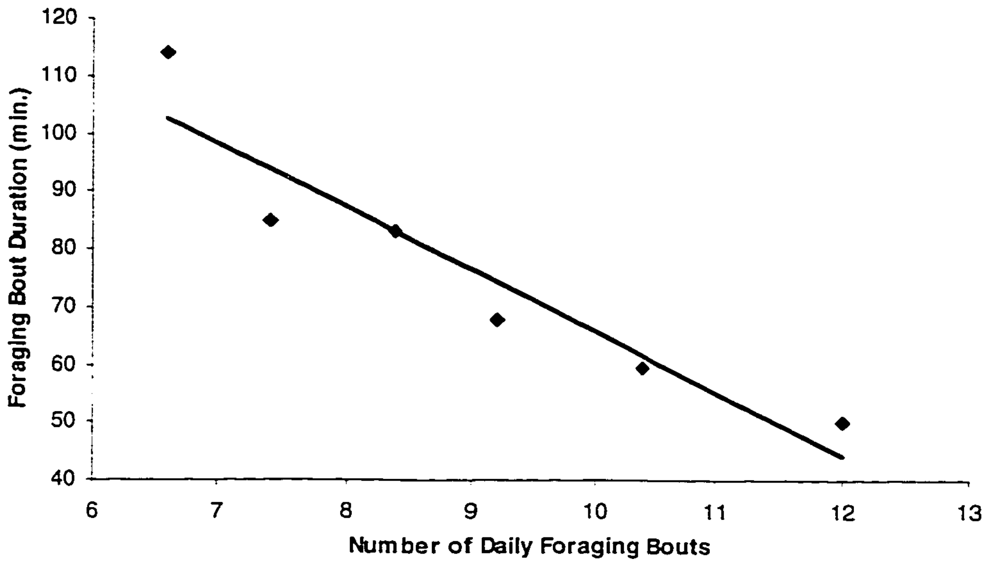

Fig. 5-5 - Seasonal duration of foraging bouts for wapiti (n=5) on heavily and lightly grazed pasture in relation to number of daily bouts, from spring to late summer at Ministik Research Station, AB ($y = 10.8x + 173.6$, p=0.005, $R^2 = 0.88$).

Similarities to Jiang and Hudson's (1996) yeld hind spring foraging bout characteristics (Jiang and Hudson: 70 min./bout, 9.2 bouts/day; this study: 63.8±9.9 min./bout, 9.7±1.2 bouts/day) and differences in early summer (Jiang and Hudson: 149 min./bout, 4.8 bouts/day; this study: 66.8±20.2 min./bout, 10.2±2.2 bouts/day), underscore effects of lactation on foraging activity patterns. Although total daily grazing times are comparable, milk hind foraging is regularly interrupted for nursing and other cow-calf interactions.

Foraging and Pasture Parameters

Wapiti foraging rates followed the same seasonal trend as daily grazing time (Table 5-2). There was no significant variation between H and L in any season ($p>0.05$), therefore, data were pooled. Bite rates (BR) (bites/min) were constant through spring (46.7±1.3) and early summer (47.7±1.0) ($p=1.00$), increasing to 61.9±1.6 ($p<0.001$) in late summer, followed by a sharp decline to 37.2±1.5 in autumn ($p<0.001$).

Wapiti BS (mg) and FPP (g DM/m^2) displayed identical seasonal trends in both pastures (Table 5-2). Although seasonal differences in these variables between H and L were appreciable, none were significant ($p>0.05$), probably a result of high between-animal variation within enclosures. Therefore, data from H and L were pooled. Both parameters were higher in early summer (BS: 280±28 mg, FPP: 451±68 g DM/m^2) compared to spring (BS: 127±14 mg, FPP: 223±21 g DM/m^2) ($p<0.01$), down again to 176±19 mg (BS) ($p=0.001$) and 406±54 g DM/m^2 (FPP) ($p=1.0$) in late summer, and in autumn returned to the early summer level at 254±35 mg (BS) ($p=0.23$) and 285±28 g DM/m^2 (FPP) ($p=0.45$).

On spring pasture of similar phytomass (1880 kg DM/ha), Jiang's (1993) yeld hinds had lower mean BR (34 bites/min) with nearly double the BS (229 mg). In an attempt to maintain intake level, having already approached the theoretical seasonal maximum of daily grazing time (Jiang: 10 h, present study: 10.8±0.3 h), wapiti in this study may have been compensating for smaller BS (127±14 mg) by increasing foraging rate (46.7±1.3 bites/min). Several authors postulate that through interaction of these variables (*i.e.* BR, BS, and grazing time), this inverse relationship allows animals to regulate and maintain intake over a wide range of forage availabilities (Allden and Whittaker 1970; Arnold and Dudzinski 1978; Trudell and White 1981).

When BR was regressed against daily grazing time (hours), a significant exponential relationship was revealed ($y = 17.8e^{0.0931x}$, R^2=0.89, p<0.001) (Fig. 5-6). BR declined exponentially as a function of increasing bite size (BS) ($y = 59.5e^{-0.0011x}$, R^2=0.64, p=0.002) and inversely in relation to increasing feeding patch phytomass ($y = 25.1 + 5548/x$, R^2=0.36, p=0.04) (Fig. 5-7).

Regression of BS against FPP revealed a significant positive association (p<0.001). However, caution should be exercised when referring to this relationship, as the proportion of variation in bite size that can be accounted for by forage availability, was low (R^2=0.21).

In this study, the relationship between BR and BS was normal, however, atypically, peak BR occurred in late summer, a season with high forage availability. Cropping rate may be limited at very low phytomass levels (through difficulty in prehending short, stemmy vegetation) and at very high levels (due to time involved masticating a large mouthful). Therefore, the relationship may assume the shape of a quadratic function (*i.e.* $y = a + bx + cx^2$). In this case, perhaps the range of higher phytomass values encountered in the present study occurred at levels where, on the curve, foraging rate declines with phytomass. Alternatively (or additionally), a combination of greater intake requirements and foraging interruptions associated with lactation, may demand augmented BR from hinds in late summer, regardless of phytomass levels. Similar results were found in reindeer (Trudell and White 1981) and cattle (Forbes and Coleman 1987).

The regression curve of bite rate against feeding patch phytomass, predicts a minimum bite rate of 25 bites/min., slightly higher than a previous prediction of 15 bites/min. for wapiti and mule deer (*Odocoileus hemionus*) (Wickstrom *et al.* 1984). Given that their estimates were based on observations of foraging in both grass and shrub habitats, and

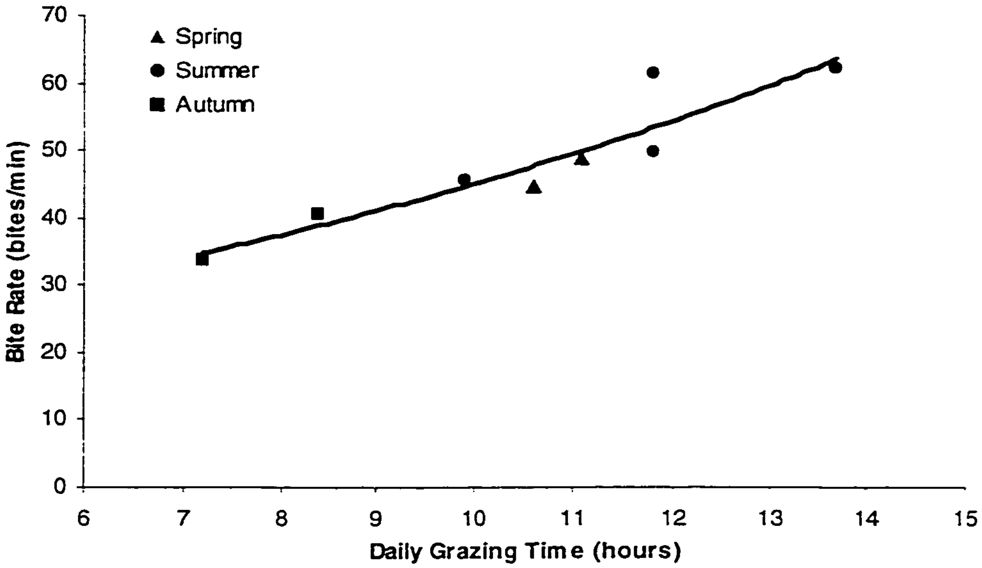

Fig. 5-6 - Seasonal foraging rates (bites/min) of wapiti (n=5) on heavily and lightly grazed pasture in relation to daily grazing time (hours), at Ministik Research Station, AB ($y = 17.8e^{0.0931x}$, $p<0.001$, $R^2 = 0.89$).

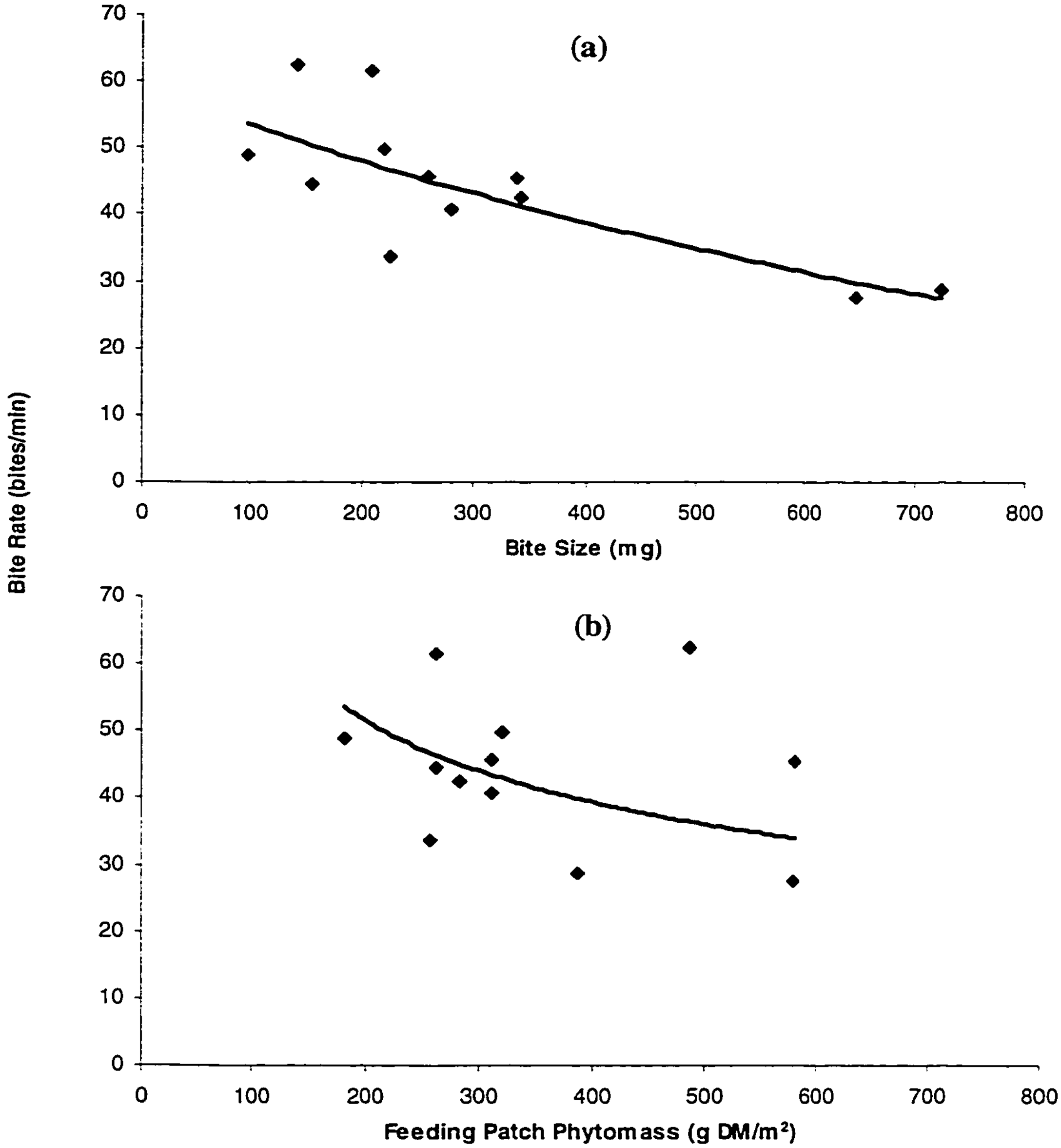

Fig. 5-7 - Seasonal foraging rates (bites/min) of wapiti (n=5) on heavily and lightly grazed pasture in relation to (a) bite size (mg) and (b) feeding patch phytomass (g DM/m^2), at Ministik Research Station, AB ((a) $y = 59.5e^{-0.0011x}$, R^2=0.64, p=0.002; (b) $y = 25.1 + 5548/x$, R^2=0.36, p=0.04).

shrub data comprised nearly all lower values on the graphs, this would explain the difference.

When regressed against forage availability (kg DM/ha), strong linear relationships were observed for BS ($y = 97.7 + 0.05x$, R^2=0.46, p=0.04) and FPP ($y = 74.5 + 0.11x$, R^2=0.91, p<0.001) (Fig. 5-8). A positive correlation between bite size and forage availability has commonly been reported (Allden 1962; Allden and Whittaker 1970; Stobbs 1973, 1974, Hodgson 1975; Chacon and Stobbs 1976; Arnold and Dudzinski 1978; Chacon *et al.* 1978; Hendrickson and Minson 1980; Wickstrom *et al.* 1984; Hudson and Nietfeld 1985; Hudson and Watkins 1985). They have also found decreasing BR as a function of increasing BS, and hence, phytomass.

When pastures were examined separately, BR and BS demonstrated a strong negative exponential association in L (p=0.02, R^2=0.78), whereas it was very weak in H (p=0.29). This may reflect differences in wapiti ingestion efficiencies. When grazing a well cropped pasture, wapiti feed very close to the ground where inedible elements may be encountered (*e.g.* faecal matter, stones, twigs, *etc.*). Excessive variation in BS may occur, due to objects displacing prehended vegetation and/or loss of plant material during manipulation and ejection of inedible portion. Overestimation of BS may also occur on well-grazed pasture, as there is higher incidence of plant matter falling from the corner of their mouths when they consume very short grass. These problems are less likely to occur in L, as long grass stems are not easily lost, and wapiti forage in a higher horizon.

Comparison of BR against BS and FPP in the original (PL96, LL96) and new (1997) enclosures, showed a significant relationship in the original (p<0.001) and very little association in the new (p>0.05). This may be an artifact of methodology. Considering the variable swards in all enclosures, in a ten minute foraging session, a hind may visit several feeding patches, traversing numerous microhabitats. This could create difficulty when emulating bites. Instantaneous cropping rates for one to four minutes were recorded in the original enclosures. This would limit the distance traveled during foraging, thereby increasing accuracy of representative 'bite' and phytomass measurements. Although instantaneous rates would be preferable when assessing

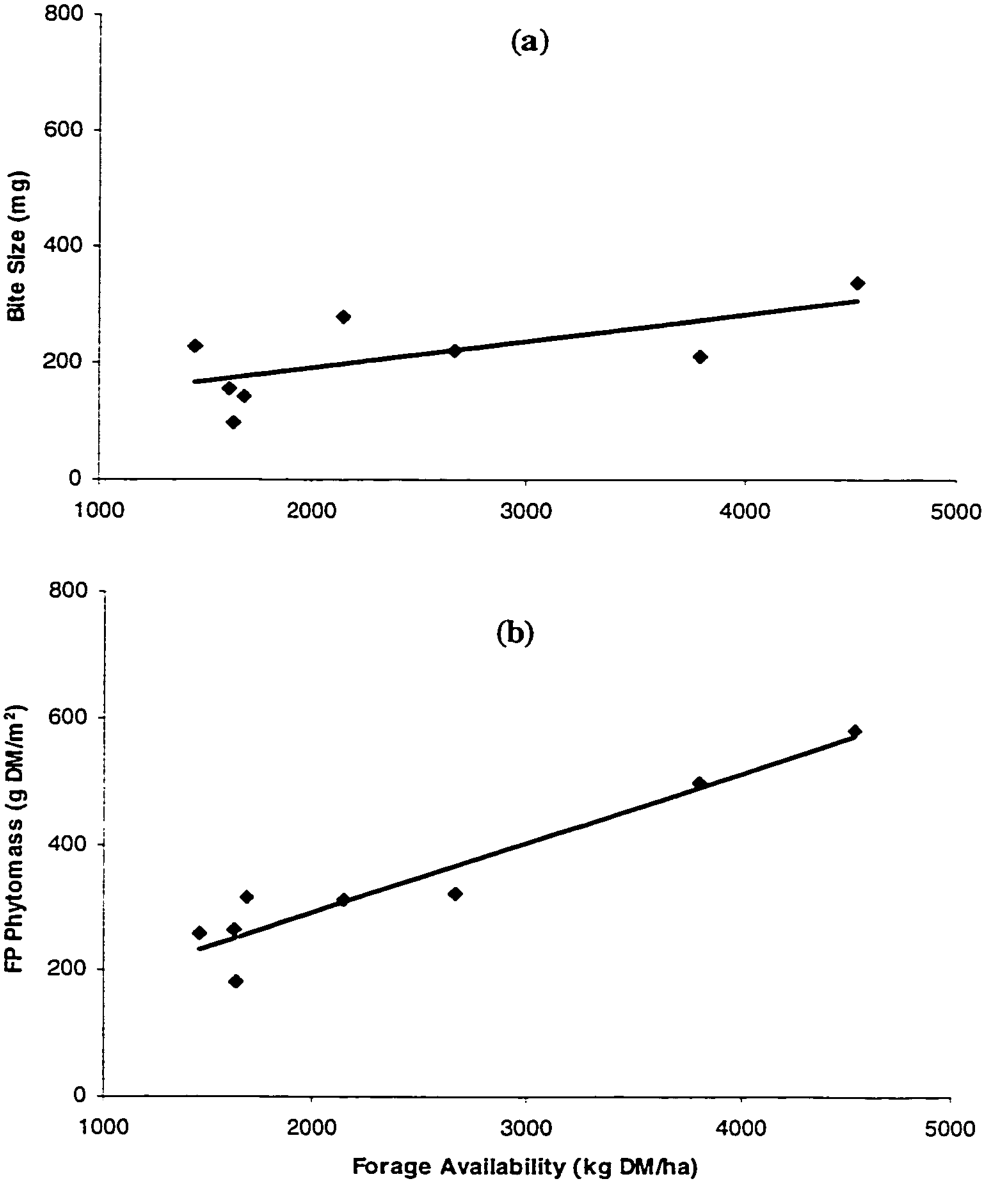

Fig. 5-8 - Seasonal (a) bite size (mg) and (b) feeding patch phytomass (g DM/m^2) for wapiti (n=5) on heavily and lightly grazed pasture, in relation to forage availability (kg DM/ha), at Ministik Research Station, AB ((a) $y = 97.7 + 0.05x$, R^2=0.46, p=0.04; (b) $y = 74.5 + 0.11x$, R^2=0.91, p<0.001).

foraging parameter relationships, it is still recommended to observe ten consecutive minutes of foraging, for intake estimates using the bite count method.

Forage availability increased substantially from spring to early summer (H: $p=0.12$; L: $p<0.001$), decreased as vegetation matured in late summer (H: $p=0.17$; L: $p=0.10$), declining further as vegetation senesced in autumn (H: $p=1.0$; L: $p=0.001$) (Table 5-2). From nearly identical forage quantities in both pastures in May (*i.e.* commencement of the growing season), there was an almost threefold increase in L in July, compared to approximately 60% in H. This reflects the early summer growth potential of unstocked pasture.

When forage availability is expressed in g DM/m^2 (*i.e.* (kg/ha)/10), comparison between whole pasture and feeding patch phytomass indicates that wapiti select foraging locations of higher forage availability than the pasture average. This suggests that wapiti may selectively graze by assessing the average within-pasture forage availability and electing to forage in optimal locations. That is, criterion for selection of foraging location may be based more on vegetation density, rather than plant species. This premise seems logical, considering the low variation in plant species that exist within the study pastures (especially without option for browsing).

In the present study, attempts to maintain marked difference in phytomass between H and L were successful. Unfortunately, between-trial time constraints and fear of animal condition loss resulted in H forage availability being well above that which would normally be regarded as limiting for wapiti (*e.g.* 900 kg DM/ha (Gates and Hudson 1983)). This may explain the general lack of disparity in foraging behaviour between pastures. For example, when Heydon *et al.* (1993) compared lactating red deer hinds on high and low phytomass pastures, they found considerable difference in bite rate (high: 62 bites/min; low: 82 bites/min). The higher phytomass pasture contained 1659 kg DM/ha, while forage availability would likely be considered a limiting factor in the 'low' pasture, with only 466 kg DM/ha.

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CHAPTER SIX

SYNTHESIS

This study provided evidence that the double n-alkane ratio technique can provide accurate and precise assessment of dry matter intake (DMI) in wapiti, at least on known diets. Value on pasture depends on two criteria. Initially, selection of appropriate n-alkanes for dosing should be based on a preliminary survey of common plants in the study area. Secondly, accurate knowledge of animal diet is necessary, through detailed observation of foraging.

Choosing C_{32} and C_{36} for dosing was appropriate for the pasture systems at Ministik. Seasonal consistency of C_{31} and C_{33} herbage concentrations made them dependable compounds to pair with dosed C_{32} for intake determinations. C_{36} provided the requisite reference to estimate forage digestibility due to its high faecal recovery.

DMI predictions using C_{33}:C_{32} n-alkanes did not differ significantly from those using C_{31}:C_{32}. However, C_{33}:C_{32} estimates were slightly more accurate, while those from C_{31}:C_{32} adjacent pairs were more precise. It would still be judicious to verify n-alkane estimations with other methods, to evaluate error associated with assumptions inherent in marker mathematics (Owens and Hanson 1992).

The present study demonstrated that intra-ruminal controlled-release devices (CRD) for n-alkane administration provides uniform daily marker release in wapiti. Capsules offer the advantage of eliminating daily dosing, thus minimizing disturbance to normal grazing patterns. There is also evidence that marker is more uniformly dispersed in the faeces when administered by CRD (Ellis et al. 1981). It would still be prudent to perform a total faecal collection on a representative subsample of animals to substantiate n-alkane excretion rates.

Application of n-alkane markers in CRD to wapiti hinds on pasture enabled reliable seasonal estimations of intake. Comparison to intake estimates from direct observation (bite count method) afforded field validation. Results revealed that n-alkane DMI estimates did not differ significantly from bite count predictions. Findings also demonstrated seasonal (*i.e.* phases of reproduction) relationships between intake and forage availability.

Gittleman and Thompson (1988) posit that behavioural compensation is potentially the most important tactic for minimizing additional energy requirements during reproduction. Results of this study showed how wapiti alter activity and foraging parameters in response to forage availability and reproductive condition.

Reproductive Seasons

Early Gestation (November)

Immediately following conception, one would expect the incremental demand of reproduction to be at an annual minimum. That is, energy required for the developing blastocyst would be negligible. Wapiti voluntary intake during early gestation, did not differ significantly from other seasons.

During lactation and rut, much of the time that hinds normally devoted to foraging is taken up in alternate activities (*i.e.* non-foraging activities). Rut is a very energetically taxing time of year, and occurring immediately after calf weaning, the hind has not been afforded the opportunity to improve condition, in preparation for the ensuing winter. Therefore, hinds maintain higher intake levels.

The post-rut/pre-winter period is extremely important for deposition of body tissue, energy reserves for the upcoming term of prolonged food shortage. Hind feeding is now limited by digestive constraints (rumen fill) due to diminished forage quality. This reduction in quality is evident in decreased wapiti bite rates, presumably a result of increased selectivity while foraging in an effort to optimize quality of ingested herbage (*i.e.* energy intake). Decreased duration of feeding bouts, while frequency of bouts remained the same, reflects increased rumination requirement, which also signifies diminishing forage quality.

Late Gestation (May)

Digestive constraints (rumen fill) continue to limit wapiti foraging into late gestation. However, at this time it is not caused by reduced forage quality, but physical displacement by the rapidly developing foetus. This is reflected in reduced intakes, at a time of year when high quality forage is once again becoming abundant. Further evidence of reduced rumen capacity is demonstrated in hinds maintaining shorter feeding bouts, while frequency of bouts increased markedly. This reflects the rumen repletion-depletion cycle and suggests that rumination requirement ceased to be the primary constraining factor.

In an effort to increase daily DMI and satisfy energy demands of exponential foetal growth, bite rate and grazing time were augmented. However, hinds were unable to achieve intake levels sufficient to meet their nutritional requirements, as reflected in spring weight loss. Given that spring herbage quality is naturally superior, improved pasture would not obviate this response.

Persistence of weight loss in lightly grazed pasture, which feasibly contains the maximum seasonal plane of nutrition, supports this hypothesis. Although, supplemental feeding is commonly extended during pre-parturition, this negative energy balance conforms to their natural pattern of seasonal weight fluctuations. Furthermore, overweight hinds are susceptible to calving problems, and thus, should be avoided.

Peak Lactation (June/July)

Even though nutritional requirements were greatest during peak lactation, hinds were able to ingest enough high quality forage for compensatory growth. Having already reached the theoretical limit of daily grazing time, this was not achieved through extended foraging. Considering bite rates also remained unchanged from spring, this reflects the efficacy of increasing bite size to enhance intake.

It is assumed that high intakes in early summer are a response to increased energy demands associated with peak lactation. Alternatively, calf disruption of bedding hinds for nursing sessions may create a feeding stimulus. Synchronous herd behaviour commonly displayed by wapiti, would essentially enhance this stimulus. If this were the case, we would see an increase in nocturnal feeding during peak lactation, and this does not occur. Furthermore, a marked increase in active time spent foraging in late summer, when disruptions for neonate maintenance would be much less frequent, indicates that increased DMI is presumably a response to higher nutritional requirements.

Late Lactation (August)

High levels of intake are maintained during late lactation, when one might expect a decrease consistent with reduced lactational energy demands. Hinds achieved this through increased bite rates (annual maximum), while capitalizing on the still abundant high quality forage. Increase in rumen capacity over the first two months of lactation (Remond 1988) would also accommodate higher intakes. Other foraging parameters remain unchanged from the previous season.

In this season, hinds are able to focus more attention on foraging and less on tending to their calves, as calves spend more time grazing and less nursing. Evidence supporting this can be found by looking at the percentage of active time spent foraging. In August, hinds spent 94% of their active time foraging, compared to 79% in June/July. This is also an important time of year for regaining condition in preparation for the ensuing rut and winter.

Forage Availability

Attempts were unsuccessful to provide pasture with a limiting nutrient supply. However, considering the superior productivity of aspen parkland, perhaps comparison of 'average' with 'improved' pasture might be more appropriate, as this situation may be more typical of Alberta deer farms.

When available forage is not limited, there was little noticeable difference in intake and foraging behaviour between wapiti hinds on heavily and lightly grazed pastures. In summer, wapiti spent more of their active time foraging, and grazed longer on heavily grazed pasture, while intake and weight gain did not differ from the lightly grazed pasture.

This suggests that foraging efficiency of the lactating hind, and hence performance, is superior on lightly grazed pasture. Perhaps during lactation, it would be advantageous to move wapiti to pastures with higher forage availability. Although short-term dividends are subtle, long-term advantages would be allowance for more time for alternate beneficial activities (*e.g.* grooming, neonate maintenance, social interaction) and delayed advance of toothwear.

Increased grooming would aid in alleviating ectoparasite load. Greater time allocated to neonate maintenance (*e.g.* nursing, grooming, social learning) could essentially improve calf physical condition and social integration. Delay of toothwear allows continuance of efficient forage cropping and particle breakdown, thereby maintaining higher digestibility. As well, Deakin and Rawlings (1997) showed that red deer hinds with good teeth produced calves with heavier birth weights and higher daily liveweight gains than those with poor teeth. All factors combined would ultimately lead to improved sustainability of herd production.

Maintenance Requirements

Most energy requirement studies on cervids have used pen-fed individuals (*e.g.* Jiang and Hudson 1992; Suttie *et al.* 1987; Fennessy *et al.* 1981). Although housed experiments provide reliable estimates, application of these results to deer grazing pasture are of limited use. On pasture, there are many additional sources of variation. For example, defining accuracy of herbage intake estimates, knowledge of plants consumed (*e.g.* energy value, digestibility), and energy expenditure (*e.g.* thermoregulation, activity), just to name a few.

Requirements for reliable maintenance predictions are accurate estimates of both metabolizable energy intake (MEI) and liveweight gain (MDG).

Although seasonal voluntary intake of wapiti on pasture is useful nutritional information for management, it has its constraints. It is only the initial step towards accurate measurement of MEI. DMI only defines quantity of consumed forage, while MEI combines both quantity and quality. In order to achieve accuracy in predicting quality of herbage ingested, one must conduct an extensive and detailed survey of wapiti foraging. Even then, variability of feeding behaviour between individuals (*e.g.* selectivity, ability) can still create biases. Although use of oesophageally-fistulated (OF) animals can help reduce these biases, unnatural grazing behaviour of OF animals may be an introduced source of error.

n-Alkane markers have provided a reliable means of estimating herbage intake of animals on pasture. This technique has also demonstrated success predicting botanical composition of consumed forage in ruminants (Dove 1992; Armstrong *et al.* 1993; Dove and Farrell 1993; Dove *et al.* 1993; Salt *et al.* 1994; Mayes *et al.* 1995; Cuartas and Garcia-Gonzalez 1996). This would improve predictive capabilities when determining energy content of ingested forage. Use of n-alkanes for estimation of botanical composition is limited, however, to plants exhibiting distinct n-alkane patterns, and therefore, may only be effective in specific situations.

Measuring animal weight change over the course of a trial seems a simple procedure, however, there are many factors that can bias results. A few examples are, body composition (*e.g.* mobilization of tissue), variation in rumen fill (and to a lesser extent, bladder and rectum), and coat water retention or molt. Problems may also arise from trial periods that are too short or use of animals that have achieved their full mature weight, as changes in weight are not always readily manifested. Perhaps restricted feed trials would be appropriate when estimating maintenance requirements of animals at their mature weight. This could provide a greater range of weight changes (*i.e.* liveweight loss), thereby improving precision of regression estimates.

Furthermore, Gates and Hudson (1981) suggest that weight may be an unreliable indicator of energy status, because changes can arise from variations in a number of carcass constituents (*e.g.* water, rumen fill, bone, protein, fat). This means that changes in body composition through mobilization of tissues, can cause changes in weight that are independent of energy intake.

Within seasons, the consistent pattern of grazing that wapiti demonstrate among days, would help minimize errors resulting from variation in rumen fill. This is achieved by measuring weights at the same time each day. Standardization of weighing conditions could also be ensured, if animals were exposed to the same routine each time. Hinds in this study were always weighed in late morning and followed the same procedure, during which they generally voided between pasture and handling facility. Also, weighing of hinds was avoided on days of heavy precipitation.

Optimizing frequency of weight measurements during an experiment will increase precision of liveweight gain determinations. That is, maximize the number of weight readings while minimizing grazing disturbance. This will increase the number of points used in regression analysis to define the trend in weight change. Although the goal is to obtain a range of negative and positive liveweight gains, Tyler (1987) suggests that growth stasis and, to an even greater extent, loss of weight, have the effect of reducing an animal's daily energy requirements.

The above difficulties will be realized in all mammals, regardless of age, sex, or physiological status. However, in reproductive females, there are additional confounding variables when attempting to account for energy allocation to products of conception, or energy partitioning between lactating mother and neonate. Furthermore, studies have shown that individuals within a single population can vary considerably in quality and quantity of maternal care, energy utilization, and ability to produce milk, all of which tilt the balance of energy costs (Thompson and Nicoll 1986).

In this study, I sought to account for energy allocation to the conceptus by using foetal growth rates obtained from red deer (Adam *et al.* 1988), with allometric adjustment for the larger wapiti. Although this improved predictions, results were still unreliable. Oftedal (1985) states that estimates of foetal growth rates from birth weight and gestation lengths are a poor substitute for weight data on known-age foetuses over the course of gestation. Perhaps it is necessary to conduct slaughter experiments on gestating wapiti (similar to Adam *et al.*'s (1988) red deer experiments), to derive values specific to this species. Due to the expense of obtaining these data, it likely would not be feasible until the market value of wapiti declined considerably.

Similar to the present study, most work on energetics has treated reproductive events separately. This may be where the problem lies in obtaining accurate maintenance predictions. Gittleman and Thompson (1988) contend that many large mammals store energy for carryover from one reproductive event to another, which may confound the relative cost of each. They say that problems arising from this carryover are particularly evident when gestation and lactation are studied separately.

In future, perhaps a "top-down" approach should be used to determine maintenance during phases of reproduction. That is, focus on the annual cycle as a whole, then attempt to narrow the scope to include individual reproductive stages singly, and adjacent events in unison.

Conclusions and Implications

The present study has taken a multifaceted approach to providing information necessary to develop feeding standards for farmed deer. Knowledge of voluntary intake and behavioural compensation in reproductive wapiti is integral to their management. This study attempted to link wapiti nutrition with foraging behaviour, in an effort to obviate inaccuracies that arise from the extrapolation approach currently used.

Comparison with numerous *Cervus elaphus* studies in Europe and New Zealand afforded an opportunity to assess seasonal response of reproductive wapiti, when foraging on northern temperate grasslands (with a very short growing season), as well as the effects of Canadian climate. Contrasting intake and foraging behaviour of non-reproductive wapiti on identical pastures at the same research station, offered insight into the effects of reproduction on seasonal intake and foraging behaviour in a captive, free-ranging herd.

Reproductive females have markedly different nutritional demands during gestation and lactation. In addition, they are the most important demographic component of a population, in terms of production. This study's focus on these individuals filled a crucial information gap.

Much effort has been devoted to developing systems for estimating intake in grazing animals, and research continues as most systems have sampling, analytical, or accuracy problems (Friend *et al.* 1995). Therefore, results of the n-alkane marker evaluation for estimating intake of wapiti on pasture are encouraging. However, further research is necessary in order to obtain reliable predictions in wild herbivores.

The intra-ruminal controlled-release device for administering marker may bridge this gap. The difficulty still lies in obtaining forage samples that are representative of that actually consumed. Additionally, incorporating visual markers into the CRD (*e.g.* colour, indigestible particles) would facilitate individual identification of faeces. Improvements in analytical procedures for n-alkane extraction, will further enhance applications of this method.

Use of CRD, with a combination of one-time dosing (minimizing disruption of normal grazing patterns and facilitating use in wild herbivores) and uniform dispersion of marker in faeces, allows for more flexible sampling routines to be adopted. This greatly reduces labour requirement normally associated with ungulate studies of this nature. In turn, it would facilitate investigations of longer duration and larger sample size, fostering a better understanding of ungulate nutrition and management.

A carefully designed grazing management system ensures high use in all seasons and a herbage allowance that sustains liveweight maintenance or gain over most of the year (Brougham and Cosgrove 1987). Wapiti should be grazed on pastures maintained in a condition such that they are not restricted by forage availability and are able to feed at their maximum rate. In this study, both heavily and lightly grazed pastures were suitable. However, lactating hinds were able to reduce daily foraging in lightly grazed pasture without compromising intake levels.

Ingested energy by a reproductive wapiti hind is to be utilized by both the mother and the conceptus or calf. It has already been recognized that energy conversion efficiencies differ between maternal growth and foetal or neonatal growth. And so, a fundamental problem exists in accounting for the flow of nutrients and energy directly to the foetus or to the calf through transfer of milk. Although, maintenance refers to the overall weight stasis of an individual animal, in gestating and lactating wapiti, this includes weight gain of a growing foetus and calf, respectively, and hence, incremental cost of reproduction. The difficulty in determining allocation of energy intake is reflected in this study, and therefore, reference to bioenergetic information derived here should be with discretion. Values should be considered approximate, as they are based on much conjecture and extrapolation.

BION (Hudson and White 1985) is a computer simulation model which links wapiti bioenergetics with behaviour. This model incorporates variables such as habitat and diet selection, energy and nitrogen balance, body composition, weight change, and activity of hinds on pasture. It also includes reproductive characteristics like foetal development and milk production. BION facilitates empirical analysis of costs and consequences of supplementing shortfalls of pasture and serves as a preliminary dynamic electronic feeding standard (Hudson and Gedir 1998). The present study offered field validation of model predictions. It provided supplementary data on seasonal intakes and activity of reproductive wapiti hinds, thereby improving the predictive capabilities of BION.

The present study has contributed valuable resources towards enhanced cervid production in this thriving industry. The advent of deer farming, although still in its infancy in North America, has provided the livestock industry with new avenues for sustainable agriculture. It should no longer be treated as a simple branch of domestic livestock farming. This study has facilitated this by providing a platform of baseline information, on which to build.

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