

NUTRITIONAL SIGNIFICANCE OF WAPITI (*CERVUS ELAPHUS*) MIGRATIONS TO ALPINE RANGES IN WESTERN ALBERTA, CANADA

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ABSTRACT

This study was designed to provide a better understanding of the nutritional significance of wapiti (*Cervus elaphus*) migrations from low-elevation winter ranges onto high-elevation alpine summer ranges. The study focused on a population along the east slopes of the Rocky Mountains in western Alberta.

Food habits analysis of the study population shows that diets consisted largely of grasses on winter (90%), spring (71%), and fall (72%) ranges. On alpine summer ranges, willows were the dominant dietary component (89%). The yearly cycle of forage quality on seasonal ranges showed that wapiti face low forage nitrogen concentration for seven months. In winter (December-April), wapiti foraged on grasses that were more digestible than willows (67% vs. 51%), but did not meet maintenance nitrogen requirements. From May to July, by moving first onto spring ranges and then onto summer alpine ranges, wapiti had access to forage sufficient to provide nutrient requirements for maintenance, pregnancy, and lactation. On alpine ranges, by shifting their diet to willow leaves, wapiti selected for forage with high crude protein content (16.8%) despite the apparent lower digestibility. Total fecal nitrogen content was correlated ($r^2 = .90$) with the estimated nitrogen content of the diet. The use of spring and summer ranges coincided with a period of higher forage quality in those areas.

INTRODUCTION

In mountain regions of North America, most wapiti (*Cervus elaphus*) populations undertake long seasonal migrations from winter to summer ranges (Adams, 1982). Along the eastern slopes of the Canadian Rocky Mountains, wapiti summer on high-elevation alpine ranges (Morgantini, 1988). The factors governing the migratory behavior of wapiti are little understood. Several authors have suggested that spring movements are in response to plant phenology (Ward et al., 1973). It is known that plants from alpine tundra have a high nutrient content due to their rapid growth and compressed phenological stages (Bliss, 1962; Klein, 1965; Chapin et al., 1975, 1980; Johnston et al., 1968). Klein (1970) estimated a delay of

3 to 4 d in the onset of plant growth in spring for each 100 to 130 m increase in elevation. The nutritional advantage for bighorn sheep and deer to forage on high-elevation ranges has been suggested by several authors (Klein, 1965, 1970; Hebert, 1973; Oosenbrug and Theberge, 1980; Hamr, 1984). In red deer, migratory females gained more weight than sedentary animals of the same population (Langvatn and Albon, 1986). Geist (1982) hypothesized that wapiti, as a northern species adapted to exploit areas of high vegetational productivity, should follow shifting lines of plant growth and migrate to alpine habitats to maximize energy intake and, hence, reproductive fitness.

This study examined seasonal food habits of wapiti in relation to changes in forage quality of three distinct seasonal ranges.

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STUDY AREA

The study was conducted in the Banff National Park–Ya Ha Tinda Ranch region of western Alberta. It focused on a wapiti population of approximately 1000 animals that migrates from low-elevation winter ranges outside Banff National Park to alpine summer ranges in the park (Morgantini and Hudson, 1988).

Summer ranges consist of open alpine meadows dispersed over some 1600 km² of mountain terrain. They are situated at the headwaters of several drainages; elevations range between 2100 and 2400 m. Plant communities are those characteristic of alpine tundra, e.g., mountain avens (*Dryas octopetala*)–snow willow (*Salix nivalis*)–moss campion (*Silene acaulis*) and heather (*Phyllodoce glanduliflora*, *Cassiope mertensiana*)–everlasting (*Antennaria lanata*). In snow accumulation areas, grasses, sedges, and forbs are common within a dominant mat of low-growing willows (*Salix arctica* and *S. nivalis*). Depending on winter severity, summer ranges are snow-covered from late October until May. The growing season is restricted to less than 60 d. The linear distance between winter and summer ranges varies from 31 to 69 km.

Winter ranges consist of rolling rough fescue (*Festuca scabrella*) grasslands surrounded by aspen (*Populus*

tremuloides) and pine (*Pinus contorta*) forests. Willows (*Salix* spp.) and dwarf birch (*Betula glandulosa*) are abundant in the grassland-forest ecotone. Elevation ranges between 1600 and 1700 m. Due to sheltering by the surrounding mountains, winter ranges are subject to mild winter weather with westerly winds keeping grasslands largely snow free.

During their migration, wapiti make extensive use of intermediate ranges located along the major river valleys. Elevation varies from 1700 to 1900 m. Intermediate ranges consist of mostly small grasslands and alluvial meadows within spruce (*Picea glauca* and *P. mariana*) and pine forests. Rough fescue, wild rye (*Elymus innotatus*), and bluegrass (*Poa pratensis*) are the dominant grass species. In winter, westerly winds keep these meadows largely snow free but result in extensive snowdrifts that persist throughout the season.

Wapiti are found on alpine ranges in July and August, on intermediate ranges from September through November and in June, and on winter ranges from December through May. Calving occurs in late May and early June on winter and intermediate ranges.

METHODS

Diet composition was determined through identification of plant cuticular fragments in composite fecal samples (Hansen et al., 1973; Todd and Hansen, 1973). Every month, 20 samples of fresh wapiti pellets were randomly collected, oven-dried at 55°C for 48 h, and pooled in one composite monthly sample. Plant fragments were identified and enumerated by the Composition Analysis Laboratory, Colorado State University.

The fecal fragment analysis technique has several limitations (Putman, 1984). Differential digestion of forage types may result in fecal fragment compositions where more digestible species (e.g., forbs in summer) are under-represented. However, the cuticle is considered indigestible although fragments may become more difficult to discern. In this study, the diet composition of wapiti, as estimated through fecal analysis, is consistent with habitat utilization patterns, forage availability, and with direct observation of animals feeding (Morgantini, 1988). This suggests that the results represent a reliable estimate of the food habits of wapiti in the region.

Range quality was assessed by collecting composite forage samples from seasonal ranges. Samples were obtained by clipping standing forage 2 cm above the ground from 10 randomly distributed 20×50 cm plots. Composite range collections were considered adequate for this study, as an efficient technique to assess overall range quality in areas with homogeneous plant composition

when no prior information on food habits is available (Morgantini and Hudson, 1985). Willow samples consisted of current annual growth. Collections on alpine summer ranges were restricted to snow-free months, July–September. The samples were dried and crude protein content (Kjeldahl N×6.25) was determined using the macro-Kjeldahl technique (A.O.A.C., 1965). *In vitro* digestible dry matter (IVDDM) determination followed Tilley and Terry (1963) and Minson and McLeod (1972), as modified by Morgantini and Hudson (1985). Rumen inoculum was obtained in winter from a fistulated wapiti steer maintained on a diet of pelleted aspen-barley concentrate, chopped alfalfa, and browse (willow). The animal had *ad libitum* access to a tame grass pasture.

Fecal protein content was adopted as a crude index of diet quality (Lambourne and Reardon, 1963; Cordova, 1977; Mould and Robbins, 1981; Renecker and Hudson, 1985). Fecal lignin was used as a supplementary measure because it reflects the amount of woody material in the diet (Van Soest, 1982). Every month, 20 fresh fecal samples were collected and frozen before they were oven-dried at 55°C for 48 h. For analysis, composite samples were prepared by taking approximately 5 g of material from each of five original samples. Fecal crude protein was determined using the macro-Kjeldahl method (A.O.A.C., 1965). Permanganate lignin was determined according to Van Soest (1976).

RESULTS

DIETS

The contribution of major plant groups to the diet of wapiti on seasonal ranges is summarized in Table 1.

On winter ranges, grasses made up 89.9% of the diet. Rough fescue (*Festuca scabrella*) was the dominant grass species. On intermediate ranges, the contribution of grasses decreased to 70.6%, and browsing increased from 3.7 to 19.4%. On summer ranges, wapiti diet shifted from grasses to shrubs. The contribution of willow increased from 10.5 to 88.6%, whereas grasses and forbs accounted for only 8.7% of the diet. Since animals were largely observed feeding on alpine tundra, it must be assumed that they were "browsing" on low-growing species, such as arctic and snow willow, that were very abundant in

the region.

In fall, after moving to lower elevation intermediate ranges, wapiti returned to a grass-dominated diet. Browsing decreased to 19.7% and mostly occurred on wolf-willow (*Eleagnus commutata*).

FORAGE QUALITY

From October until May, crude protein and IVDDM of herbaceous plants (Table 2) from winter and intermediate ranges were not significantly ($P > 0.05$) different. In June, however, when wapiti were on intermediate ranges, forage from these ranges had a significantly higher protein content ($P < 0.0003$) and dry matter digestibility ($P < 0.005$) than that found at the same time

TABLE 1
Percent diet composition of wapiti on seasonal ranges in west-central Alberta, based on fragment analysis, January 1977–December 1978

	Winter range (Dec.–May) <i>n</i> = 12 ^a		Interm. range (June) <i>n</i> = 2 ^a		Summer range (July–August) <i>n</i> = 4 ^a		Interm. range (Sept.–Nov.) <i>n</i> = 4 ^a	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Grasses								
Fescue	88.2	0.61	56.7	11.9	0.4	0.05	64.7	10.2
Wild rye	0.6	0.08	7.8	4.7	1.7	0.36	3.6	0.77
Bluegrass	0.5	0.10	5.7	2.6	1.3	0.19	3.9	1.5
Other	0.6	0.06	0.4	0.3	0.5	0.17	0.1	0.07
Total	89.9	0.47	70.6	4.5	3.9	0.55	72.3	7.9
Sedges								
Total	4.2	0.13	6.4	1.4	2.4	0.71	3.5	0.58
Browse								
Willow	1.5	0.16	10.5	3.4	88.6	1.51	1.0	0.18
Other	2.2	0.22	8.9	0.6	0.3	.06	18.7	8.48
Total	3.7	0.27	19.4	4.0	88.9	1.57	19.7	8.30
Forbs								
Total	2.2	0.45	3.6	1.0	4.8	0.64	4.5	0.92

^aEach monthly sample represents a composite sample of twenty pellet groups.

TABLE 2
Percent crude protein (CP) content and in vitro digestible dry matter (IVDDM) of composite range samples from seasonal ranges

	Winter range				Intermediate range				Summer range			
	CP		IVDDM		CP		IVDDM		CP		IVDDM	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
December–April	3.6	0.06	67.4	0.22	3.7	0.10	67.9	2.16	— ^a		—	
May	7.5	0.28	71.1	0.85	6.8	0.32	72.8	0.88	—		—	
June	10.5a ^b	0.48	78.2a	1.45	13.5b	0.42	81.6b	1.70	—		—	
July–August	8.2a	0.37	72.6a	1.66	10.2b	0.33	76.9b	1.15	13.8c	0.63	71.4a	4.81
September–November	4.3a	0.59	65.1a	0.91	5.2b	0.36	69.4b	1.46	7.8c	0.72	66.2a	1.31

^aRanges not accessible due to deep snow.

^bValues for a parameter within a row followed by different letters are significantly different at $P < 0.05$.

TABLE 3
Percent crude protein content (CP) and *in vitro* digestible dry matter (IVDDM) of willow leaves and twigs from seasonal ranges

	Winter range				Intermediate range				Summer range			
	CP		IVDDM		CP		IVDDM		CP		IVDDM	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
December–April ^a	8.8	0.08	51.1	1.13	8.0	0.30	49.1	0.36	— ^e		—	
May ^b	9.6 ^d	0.03	52.9 ^a	0.93	8.6 ^b	0.20	48.7 ^b	1.03	—		—	
June ^b	19.4 ^a	0.70	61.5	2.06	17.9 ^b	0.04	57.7	1.99	—		—	
July–August ^c	13.1 ^a	1.00	61.9	1.43	15.8 ^b	0.10	60.1	0.35	16.8 ^b	0.80	61.8	1.17
September–November ^a	9.9 ^a	3.90	55.4	4.35	7.8 ^b	0.60	55.1	2.02	9.6 ^a	0.45	57.5	0.38

^aTwigs only.

^bLeaves and twigs.

^cLeaves only.

^dValues for a parameter within a row followed by different letters are significantly different at $P < 0.05$.

^eRanges not accessible due to deep snow.

on winter ranges. At the time, summer ranges were largely unavailable due to extensive snowdrifts and late snow melt.

In July, while forage crude protein from both winter and intermediate ranges decreased with advancing maturity, the vegetation on summer ranges was in full seasonal growth. Crude protein content of herbaceous plants was higher than on intermediate and winter ranges. However, no significant change in digestibility values between intermediate and summer ranges was recorded.

From August to October, protein content of alpine forages decreased but remained higher than that on intermediate ranges. In autumn, crude protein content and

digestibility of herbaceous plants on intermediate ranges was higher than that on winter ranges.

Throughout the year, crude protein of willow species (Table 3) was consistently higher than that of herbaceous plants. In contrast, *in vitro* digestibility was consistently lower, ranging from a winter low of 47.7% on winter ranges to 63.4% in July on summer ranges.

FECAL INDICES

Fecal crude protein followed a seasonal cycle parallel to that observed in forage protein from seasonal ranges (Figure 1). During both years of study, fecal protein from October to May ranged between 8.06 and 10.94%. In

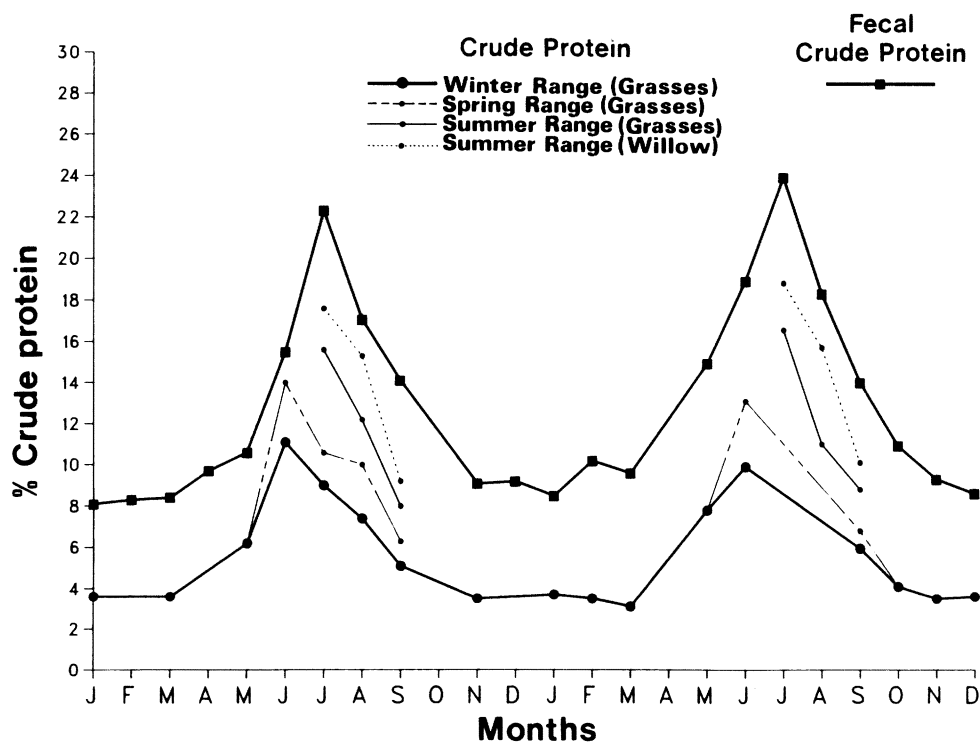


FIGURE 1. Crude protein in forage and feces from different seasonal ranges in the Red Deer-Panther-Clearwater region along the east slopes of the Rocky Mountains in western Alberta (1977-1978).

summer, when wapiti were on alpine ranges, it rose to over 22%, sharply decreasing afterwards. Total nitrogen content of wapiti feces was correlated ($r^2=0.90$; $P<0.001$) with the estimated nitrogen content of their diet (Figure 2).

Fecal lignin content was found to be highly correlated with the amount of browse in the diet (Figure 3). During

the first year, fecal lignin ranged from an average of 13.5% (± 1.1) in winter to 21.5% (± 0.20) in summer, and, during the second year, from 14.5% (± 0.40) to 24.5% (± 0.3).

Seasonal fluctuations in fecal lignin content paralleled changes in dietary browse content and were opposite to changes in fecal ash content (Figure 4).

DISCUSSION

DIET QUALITY

The seasonal cycle of forage quality on seasonal ranges reflects the natural cycle of plant phenology, i.e., a sharp decline in protein and digestibility after the early growth stages (Moen, 1973). Crude protein content of forage species in the study region are consistent with data presented by Johnston and Bezeau (1962), Johnston et al. (1968), and Hebert (1973).

Within the study region, the timing of wapiti use of intermediate (June) and summer (July) ranges coincided with a period of higher forage quality in those areas.

In winter, rough fescue made up a large portion of the diet. However, despite its high digestibility, rough fescue is a poor source of nitrogen. Crude protein content at a weathered stage ranges from 2.6% (Morgantini and Hudson, 1985) to 4.2% (Johnston and Bezeau, 1962). Dietary protein requirements for wapiti in winter are believed to range between 5 and 7% (Hobbs et al., 1981; Nelson and Leege, 1982). Crude protein content of composite range samples collected during this study were below maintenance requirements. Nitrogen requirements may be partially met by nitrogen recycling, by selective foraging for plant parts with a higher nitrogen content, or by an increase in dry matter intake (Nelson and Leege, 1982). Nonetheless, this study indicates that wapiti inhabiting mountain regions of west-central Alberta likely face low forage nitrogen for 7 mo of the year.

Nelson and Leege (1982) estimated that forage crude protein concentrations required by an adult wapiti cow in spring and summer for maintenance and lactation would increase from 5% in May to 11% in August. During this study, wapiti, by grazing first on intermediate ranges and then on alpine ranges, had access for three months to forage containing over 13% crude protein.

The importance of shrubs in the summer diet of wapiti has been reported by Hash (1973) in Idaho and Bohne (1974) in Montana. During this study, wapiti on alpine ranges shifted to a browse-dominated diet. Fecal analysis might have overestimated willow due to its low digestibility (Pulliam and Nelson, 1979). However, a major increase in browsing is also indicated by the increase of fecal lignin content and decrease in fecal ash residue. Higher fecal lignin in summer indicates higher dietary lignin content and, hence, lower diet digestibility (Van Soest, 1982). However, through the early stages of plant growth, lignin only partially reduces the digestibility of cell wall constituents (Choo et al., 1981). Further, dietary lignin may increase the rate of forage passage through the diges-

tive tract by enhancing particle breakdown and stimulating rumination (Mertens, 1973; Ulyatt et al., 1986; Renecker, 1987).

There is limited information on the nutritional quality of alpine willows. In arctic environments, the cell solubles of some willow species (*Salix arctica*, *S. lanata*, *S. pulcra*) are comparable to those of forbs and grass-like plants (70 to 80%) (Person et al., 1980). In this study, while alpine willows had a significantly higher crude protein content than grasses, they were less digestible. The low *in vitro* digestibility could reflect the lack of adaptation of the rumen inoculum as shown by Person et al. (1980). The concentration of secondary metabolites, which varies among plant species, may also affect *in vitro* digestibility by limiting microbial fermentation (Trudell et al., 1980).

Wapiti, as mixed feeders, can adjust to changes in forage quality depending on local environmental conditions (Hofmann, 1985). On alpine ranges, by shifting their diet to willow leaves and current-year twigs, wapiti appear to select for a diet of high crude protein content. The eventual decrease in digestibility may be compensated by increased intake and rate of passage.

FECAL NITROGEN

The relationship between fecal nitrogen content and dietary nitrogen content and its value for evaluating diet quality of free-ranging ungulates, has been reviewed by

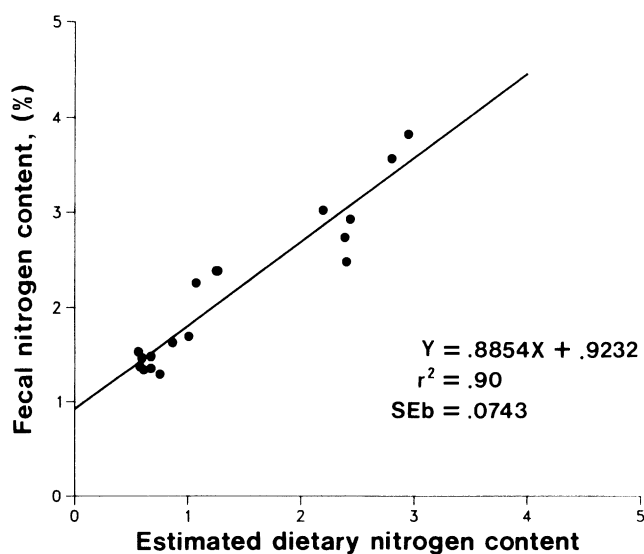


FIGURE 2. Relationship between fecal crude protein and crude protein content of estimated diet.

Robbins (1983). In this study, the regression coefficient between fecal nitrogen and estimated diet nitrogen (browse and herbaceous plant components) differed markedly from that reported by Mould and Robbins (1981) for wapiti. The prediction of dietary nitrogen from fecal nitrogen by using the Mould and Robbins (1981)

equation yields unrealistic values of diet crude protein content ($N \times 6.25$) of 35.3% and 39.5% in July 1977 and 1978, respectively. The regression coefficient obtained in this study was closer to that reported by Renecker and Hudson (1985) for moose, and it may indicate, as suggested by these authors, a high level of total fecal nitrogen

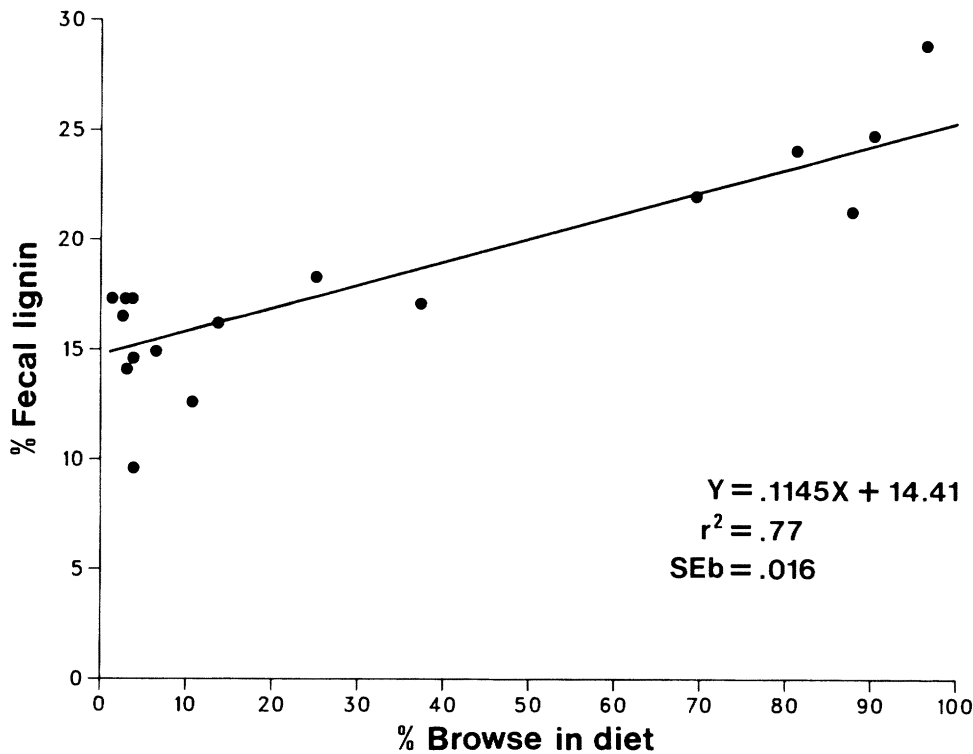


FIGURE 3. Relationship between fecal lignin and browse content of diet of wapiti.

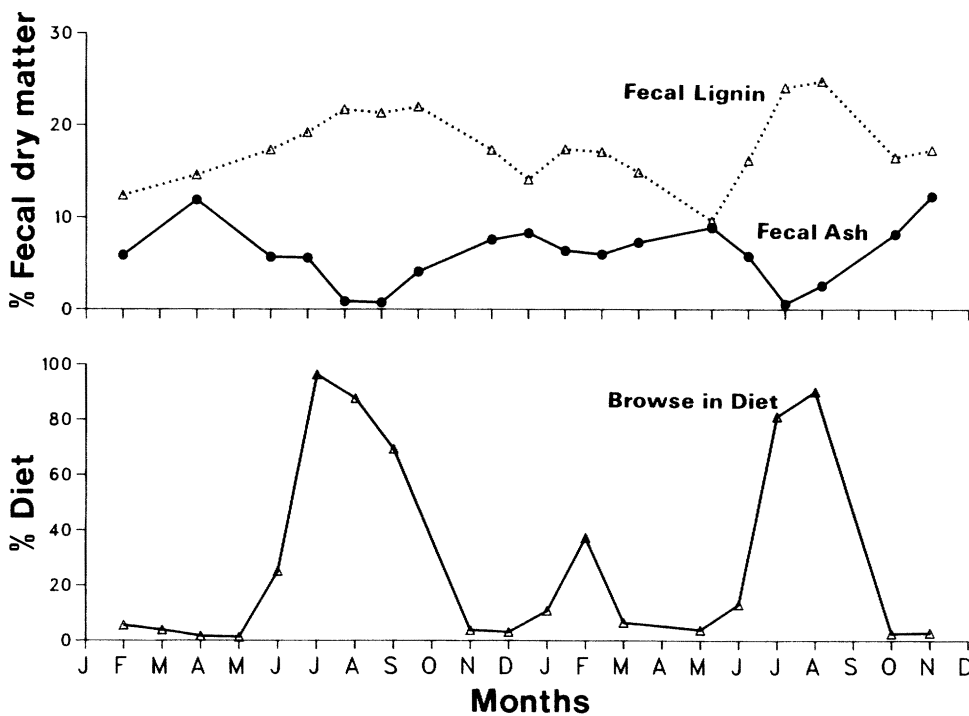


FIGURE 4. Fecal lignin, fecal ash, and browse dietary components of wapiti in study region.

and of metabolic fecal nitrogen (MFN) excretion for browsers. The low nitrogen content of the wapiti diet on winter ranges, and the high level of browsing in the summer, support this suggestion. In winter, a large compo-

nent of total fecal nitrogen may be of metabolic origin, while in the summer MFN may be complemented by undigested dietary nitrogen.

CONCLUSIONS

Ungulates living in northern environments depend on summer forage of high nutritional quality for reproduction and growth and to compensate for nutritionally inadequate winter diet. Weight loss during the winter can ultimately determine survival and reproductive success (Thorne, 1976; White, 1983). Hence, herbivores "should" adopt a feeding "strategy" which will maximize summer growth (Geist, 1982).

In the study region, wapiti likely face low forage protein content for 7 mo of the year. In the remaining 4 to 5 mo, the animals must engage in the following energy-demanding activities: completion of gestation, calving, lactation, replacement of body reserves, weight gain, and breeding. The benefits of following early plant growth and of summering on alpine ranges appear evident. Due to the absence of a significant number of nonmigratory wapiti in the study region, it could not be assessed whether wapiti summering on winter ranges or in their vicinity were on a poorer nutritional diet. However, the use of spring and summer ranges by migratory wapiti did coincide with higher forage quality in those areas. Thus, the

study supports the hypothesis that wapiti undergo seasonal migrations in order to optimize foraging for nutritional quality. On the other hand, it is also possible that the animals move to seasonal ranges for other reasons (such as insect avoidance, interspecific competition, predator avoidance, human disturbance, learned behavior, etc.), and that the apparent nutritional benefits are totally or partially coincidental (Morgantini, 1988). Even assuming that nonmigratory wapiti consumed poorer quality summer forage, they could still be able to meet nutritional requirements through dietary changes, increased intake, higher selectivity, or digestive adjustments.

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