Catch-up growth of yearling wapiti stags (*Cervus elaphus*)

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Wairimu, S., Hudson, R. J. and Price, M. A. 1992. **Catch-up growth of yearling wapiti stags (*Cervus elaphus*).** Can. J. Anim. Sci. **72**: 619–631. Ten yearling wapiti stags were used to investigate effects of winter nutrition on subsequent growth on summer pasture. One group of five (LOW) was wintered on medium-quality hay, and the other group of five (HIGH) was wintered on hay and alfalfa-barley pellets (16% crude protein). By the time they grazed spring pasture in mid-April, HIGH wapiti had larger frame dimensions and were 20 kg heavier than those wintered on hay alone, despite their lower pre-winter weights. However, subsequent catch-up growth rapidly narrowed these differences, and both groups attained similar weights and frame measurements by late July. Liveweight gains on summer pasture were 0.30 and 0.15 kg d^{-1} for LOW and HIGH wapiti, respectively. Although LOW wapiti tended to have higher gut fill (3.3 vs. 2.5 kg dry matter), the difference (corrected for assumed dry-matter content) was insufficient to explain compensatory weight gain. Digestibilities and mean retention times did not differ consistently between the treatment groups but were reciprocally related to one another. Forage intakes rose as pastures flushed but declined sharply in July with overgrazing and resumption of supplemental feeding. LOW wapiti consumed more pasture dry matter than HIGH wapiti in May and June. Efficiencies of forage utilization were unrelated to nutritional history. Using data pooled for the two treatment groups from April to June gave estimates of 878 kJ $W^{-0.75}$ for maintenance and 33.4 kJ g^{-1} for liveweight gain. The main factor contributing to compensatory gain on summer pasture was higher forage intakes, particularly in relation to metabolic weight.

Key words: Game farming, elk, compensatory growth, forage intake, passage rate, energy requirements

Wairimu, S., Hudson, R. J. et Price, M. A. 1992. **Croissance compensatrice des cerfs wapitis d'un an (*Cervus elaphus*).** Can. J. Anim. Sci. **72**: 619–631. Dix cerfs (wapitis) mâles d'un an ont été utilisés pour étudier les effets de l'alimentation hivernale sur la croissance subséquente en pâturage d'été. Un groupe de 5 (B) a été hiverné avec un foin de qualité moyenne et les 5 autres recevaient en plus des agglomérés de luzerne (16% PB). À leur mise à l'herbe à la mi-avril, les cerfs (H) avaient un plus grand développement corporel et pesaient 20 kg de plus que les autres, malgré leur poids moindre avant l'hiver. Cependant la croissance compensatrice n'a pas tardé à rétrécir les différences, de sorte qu'en fin de juillet les deux groupes avaient atteint le même poids et les mêmes dimensions. Le gain de poids au pâturage était de 0,30 et de 0,15 kg j^{-1}, respectivement pour les animaux B et H. Bien que les cerfs au régime B avaient un contenu intestinal plus abondant (3,3 contre 2,5 kg m.s.), la différence corrigée en fonction de la teneur théorique en matière sèche ne suffisait pas pour expliquer le gain de poids compensatoire. La digestibilité et la durée moyenne du transit gastro-intestinal ne différaient pas de façon régulière entre les deux groupes de traitement, mais les deux valeurs étaient inversement corrélées l'une à l'autre. L'ingestion de fourrage augmentait avec la flambée de croissance des pâturages au printemps pour ensuite retomber brutalement en juillet sous l'effet du sous-pâturage et de la reprise de la distribution de compléments. En mai et juin, les cerfs au régime B consommaient plus de m.s. que ceux au régime H. Le degré de valorisation du fourrage était sans rapport avec les antécédents nutritionnels des animaux. À partir des données réunies des deux groupes de traitements d'avril à juin, on a obtenu une valeur de 878 $kg^{P-0.75}$ pour l'entretien, et de 33,4 kJ g^{-1} pour le gain de poids vif. Les principaux facteurs responsables du gain compensatoire en pâturage étaient la plus forte ingestion de fourrage, surtout par rapport au poids métabolique.

Mots clés: Élevage de gibier, wapiti (cerf), croissance compensatoire, ingestion de fourrage, transit gastro-intestinal, besoins en énergie

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Weaned red deer (*Cervus elaphus*) exhibit catch-up growth on summer pastures (Suttie et al. 1983; Adam and Moir 1985; Milne et al. 1987). However, they seldom fully compensate by 15 mo of age, when they enter their first rut. Consequently, depending on pasture quality, they may not reach market weights (stags) or pubertal weights (hinds), and pre-rut weight may influence their ultimate mature size (Suttie et al. 1983). Little is known about the nature of this compensatory gain, although it involves skeletal dimensions as well as weight (Suttie et al. 1984). Body composition after compensation is similar to that of stags with uninterrupted growth (Suttie et al. 1984; Adam and Moir 1985; Milne et al. 1987).

Although the wapiti, the red deer's larger Asian and North American conspecific, expresses well-developed catch-up growth (Hudson et al. 1985), its nature and basis have not been fully explored. Red deer stags during catch-up growth have higher dry-matter (DM) intakes (Suttie et al. 1983; Adam and Moir 1985) but no apparent difference in feed-conversion efficiencies (Suttie et al. 1983). Previous studies at the Ministik Wildlife Research Station showed that forage intakes of wapiti were inversely related to weight, and wapiti wintered on a low-quality diet (hay) had higher forage intakes than those wintered on high-quality feed (alfalfa–barley pellets) (Watkins et al. 1991). However, interpretation of the latter study was complicated by pregnancy and the mix of sex-age classes.

We report studies on young wapiti stags that allow comparison with red deer and explore the scope, nature and mechanism of catch-up growth in this larger genotype. Our aim was to establish whether compensatory weight gain is due to increased frame size, soft-tissue growth, or simply gut fill. We also explored whether compensatory growth is achieved by higher DM intake or better feed-conversion efficiencies and if this is associated with changes in digestive kinetics.

METHODS

Experimental Setting and Design

The study was conducted at the Ministik Wildlife Research Station, located 50 km southeast of Edmonton, Alberta. The native vegetation of the surrounding Cooking Lake Moraine is boreal mixed-wood forest, although homesteading in the early 1900s lends the general characteristic of aspen parkland. The 1.5-ha paddock used for this study comprised 62% poplar forest, 8% lowland and 30% upland grasslands. Balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*) dominate the poplar forest. Brome grass (*Bromus pumpellianus*) and volunteer Kentucky bluegrass (*Poa pratensis*) are dominant species in the upland, whereas bluegrass, brome, wheatgrass (*Agropyron* spp.) and reedgrass (*Calamagrostis canadensis*) dominate the lowland.

Ten wapiti stag calves born in May and June were assigned to two winter feeding treatments on 7 December 1989. Five wapiti (low-quality winter diet, LOW) were run on native range but were supplemented with medium-quality hay because of the harsh winter conditions. Five others (high-quality winter diet, HIGH) were offered alfalfa–barley pellets and hay. Both feed sources were offered ad libitum (Table 1).

On 4 April 1990, at the beginning of the spring flush of pasture forage, the groups were merged and placed in the 1.5-ha pasture. Although the winter feeding program was to have ended at this time, a snowfall on 9 April meant that supplementation with hay was required for an additional 2 wk. As pastures were depleted by July, alfalfa–barley pellets were offered as a range supplement from 10 July onward.

Body Weights and Measurements

Wapiti were weighed to the nearest kilogram with an electronic platform scale. No attempt was made to withhold feed and water overnight, so weights reflected differences in rumen fill. The contribution of gastrointestinal fill (GIT) was estimated using a single oral dose of chromic oxide (Cr_2O_3) as described below.

At the beginning and end of the summer grazing trials (24 April and 2 August), frame measurements

Table 1. Chemical composition and gross energy of winter feeds on a dry-matter basis

	Alfalfa–brome hay	Pellets
Dry matter (%)	93.7	90.9
Neutral detergent fiber (%)	62.2	30.2
Acid detergent fiber (%)	32.8	15.3
Lignin (%)	4.07	3.71
Crude protein (%)	12.9	16.7
Gross energy (kJ g^{-1})	18.8	18.5

were taken with a steel tape. Total body length (nose to last sacral vertebra), chest girth (immediately behind the axilla) and hip width (between the ischial processes) were chosen for safety and ease of measurement.

Digestive Parameters

Comparative GIT and rates of passage were estimated using a single dose of Cr_2O_3 administered on 24 April, 13 May, 26 June and 22 July. Approximately 200 g of alfalfa–barley pellets containing 4.04 g kg^{-1} Cr_2O_3 was given to each wapiti during the first trial; 250 g was given for the remaining trials. Individually penned animals usually consumed measured amounts of Cr_2O_3 within several hours. Fecal samples were collected in these individual pens immediately before and on pasture every 3–4 h after dosing for 48 h and at 6–12 h intervals for an additional 3–4 d.

Fecal samples were oven-dried at 110°C for 24 h and ground in a Wiley mill with a 30-mesh screen. The Cr_2O_3 concentrations were determined by atomic spectrophotometry with an air-acetylene flame (Fenton and Fenton 1979). Fecal concentrations through time (C_t, g kg^{-1}) were determined by the Stewart–Hamilton or occupancy principle (Steele 1971; Shipley and Clarke 1972). Mean retention time (MRT, d), fecal output (F, g d^{-1}), indigestible DM fill (VN, g) and gut fill (GIT, g) were estimated as outlined by Holleman and White (1987) and tested in wapiti by Jiang and Hudson (1992). The following calculations were used:

$$F = D / \int_0^\infty C_t \cdot dt$$

$$\mathrm{MRT} = \int_0^\infty t \cdot C_t \cdot dt / \int_0^\infty C_t \cdot dt$$

$$\mathrm{VN} = F \cdot \mathrm{MRT}$$

$$\mathrm{GIT} = \mathrm{VN} + \mathrm{VN} \cdot A/2\ (1 - A)$$

where D is the marker dose administered, C_t is the fecal marker concentration determined at time t; $\int_0^\infty C_t \cdot dt$ is the marker excreted in interval dt estimated by the area under the marker concentration versus time curve for the feces, $\int_0^\infty t \cdot C_t \cdot dt$ is the area under the curve obtained by multiplying the marker concentration in the feces by its respective time since dosing; and A is the fractional digestibility of the diet (described below).

Gut fill (g DM) was converted to approximate wet fills by assuming that gut contents of wapiti are approximately 17% DM, irrespective of season and diet, as suggested by pen trials with wapiti by Renecker and Hudson (1990).

Dry-Matter Digestibility and Daily Intakes

We selected representative diet samples by observing and mimicking the selections of grazing animals. Lignin, measured as the ash-free residue after 72% sulfuric acid treatment of acid detergent fibre (Goering and Van Soest 1970), was used as an internal indicator of digestibility (Fahey and Jung 1983). Assuming steady-state kinetics, we obtained dry-matter intake (DMI, g) from daily fecal DM excretion (F) and fractional digestibility of the diet (A) from the following equation:

$$\mathrm{DMI} = F/(1 - A)$$

Statistical Analysis

Weight gains, linear measurements and digestive parameters were subjected to univariate repeated-measures analysis of variance, with winter feeding as the main "between" effect and trial date as the "within" effect. Our primary interest was in the significance of the interaction term (treatment × trial date) because we expected compensation to slow as differences in size narrowed. Differences between groups on specific trial dates were tested by a priori single-degree of freedom contrasts.

Changes in measurements between the beginning and end of the summer grazing trial were related to beginning measurements by regression analysis. We estimated feed-conversion efficiency by regressing metabolizable-energy (ME) intake ($\mathrm{DMI} \cdot \mathrm{digestibility} \cdot 0.82 \cdot 18.4$ kJ $W^{-0.75}$) on gain (g $W^{-0.75}$). The intercept estimated maintenance requirements and the slope gave the energy requirement for liveweight gain. Data from July were excluded because alfalfa–barley pellets were offered as a range supplement. The escape of one animal from the HIGH group reduced the effective treatment group size to four individuals.

RESULTS

From December to April, LOW animals lost 10.2 ± 2.4 kg, whereas the HIGH group gained 22.4 ± 1.2 kg (Fig. 1). Despite their lower initial weights ($P < 0.01$), HIGH animals entered spring weighing at least 20 kg more than their LOW counterparts ($P < 0.01$).

On pasture, following transient weight loss between April and May, the LOW animals rapidly closed weight differences. Between 4 April and 28 July, LOW animals gained

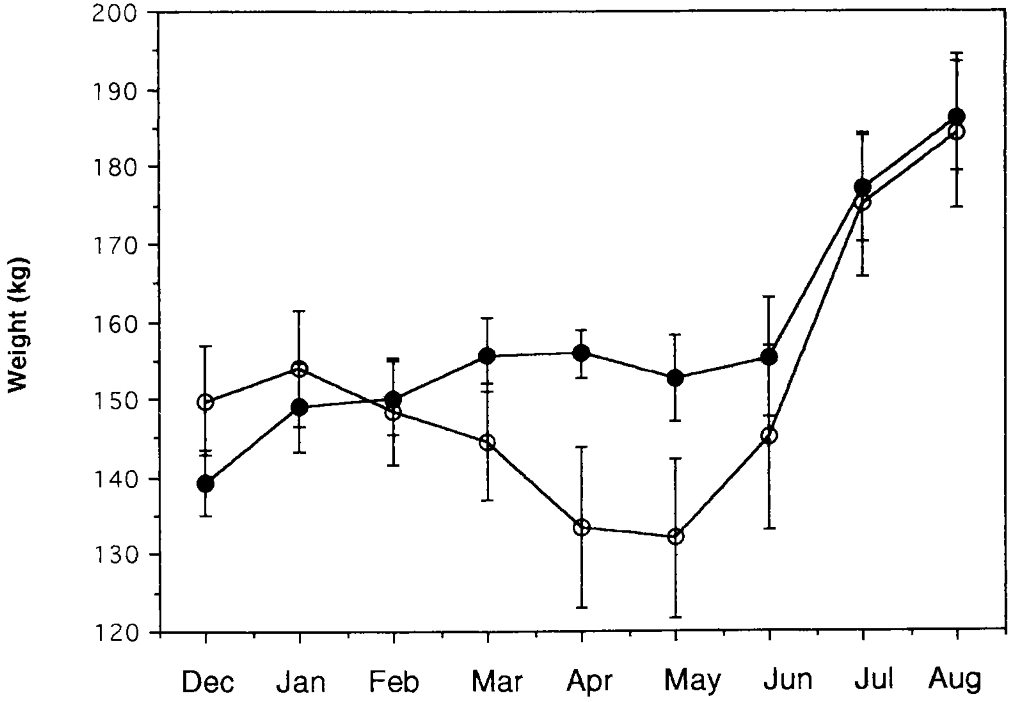

Fig. 1. Seasonal weight dynamics of wapiti stags on low-quality (open symbols) or high-quality (closed symbols) winter diets. Means ± standard errors.

36.0 ± 1.9 kg, whereas the HIGH animals gained only 25.6 ± 5.7 kg ($P = 0.04$).

Measurements of frame size were limited to the beginning (24 April) and end (2 August) of the summer grazing trials. By April, HIGH wapiti were larger framed than LOW wapiti, as reflected in significantly greater body lengths, hip widths and chest girths ($P < 0.01$). By August, these measures had fully compensated from previous undernutrition. Regressions of growth increments between April and August on absolute measurements in April were significant for body length and hip width (Fig. 2).

Gut fill complicates the interpretation of liveweight gain. Overall, LOW wapiti tended to have higher estimated GIT_2 averaging 3.2 vs. 2.5 kg DM but differences were not significant (Fig. 3). Gut fill dropped in July, when alfalfa–barley pellets were offered as a range supplement.

LOW wapiti compensated for lower winter nutrition by higher daily DMI ($P = 0.07$), particularly in relation to metabolic weights ($P = 0.03$). Monthly contrasts (Fig. 4) were significant in May ($P < 0.01$) and June ($P = 0.01$) but not in April, when little forage was available, or July, when weight differences had disappeared.

Dry-matter digestibility differed significantly by month ($P < 0.01$) and was significantly higher in LOW wapiti in April ($P < 0.01$) (Fig. 5). Digestibility rose rapidly with pasture flush between April and May and subsequently declined with forage maturation.

Monthly MRT mirrored digestibilities. The interaction of nutritional history and trial date was marginally significant ($P = 0.07$), and MRTs in June were shorter in LOW wapiti ($P = 0.01$). Mean retention time was highest in April (34.9 h) and lowest in June (21.8 h), when differences between the two groups were greatest.

Feed-conversion efficiency, obtained by regressing ME intake on gain, did not differ

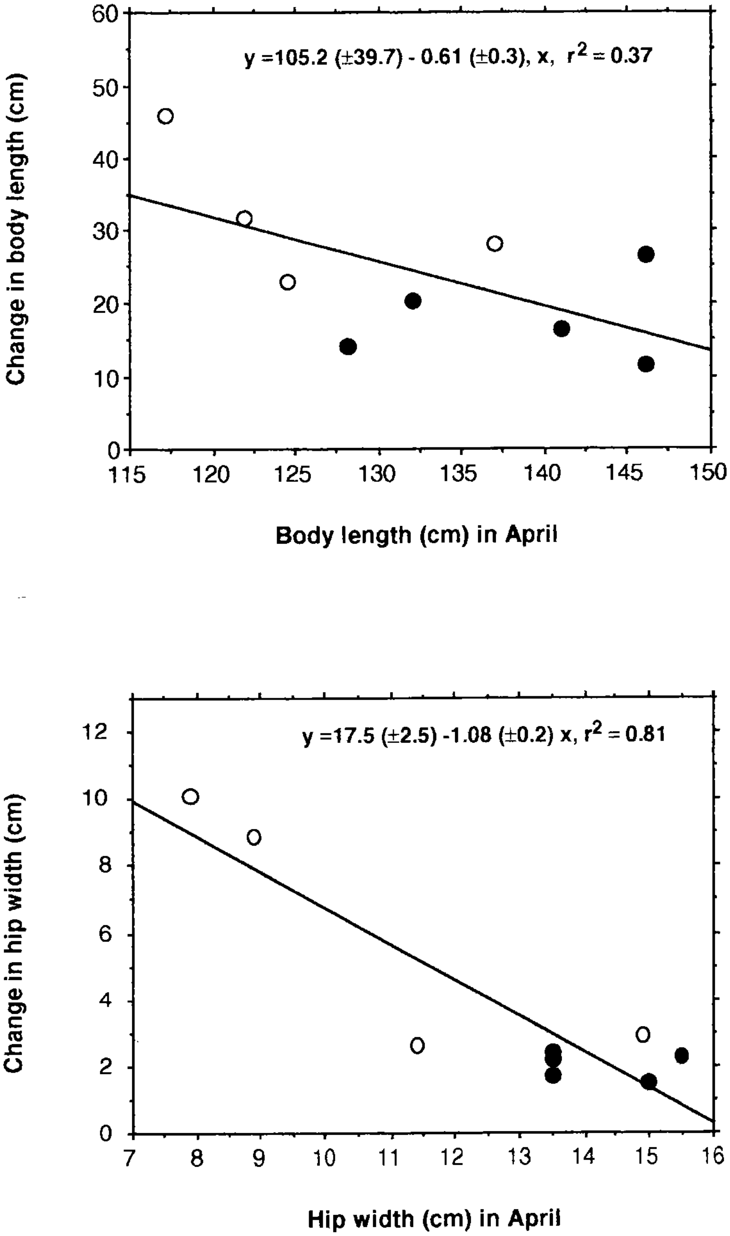

Fig. 2. Growth in body length and hip width in relation to spring measurements of wapiti stags previously kept on low-quality (open symbols) or high-quality (closed symbols) winter diets.

between nutritional treatments (Fig. 6). Therefore, data were pooled to estimate ME requirements of 878 kJ $W^{-0.75}$ d^{-1} for maintenance and 33.4 kJ g^{-1} d^{-1} for liveweight gain.

DISCUSSION

Young wapiti stags had a well-developed capacity for compensatory growth on aspen-parkland ranges in western Canada. Despite

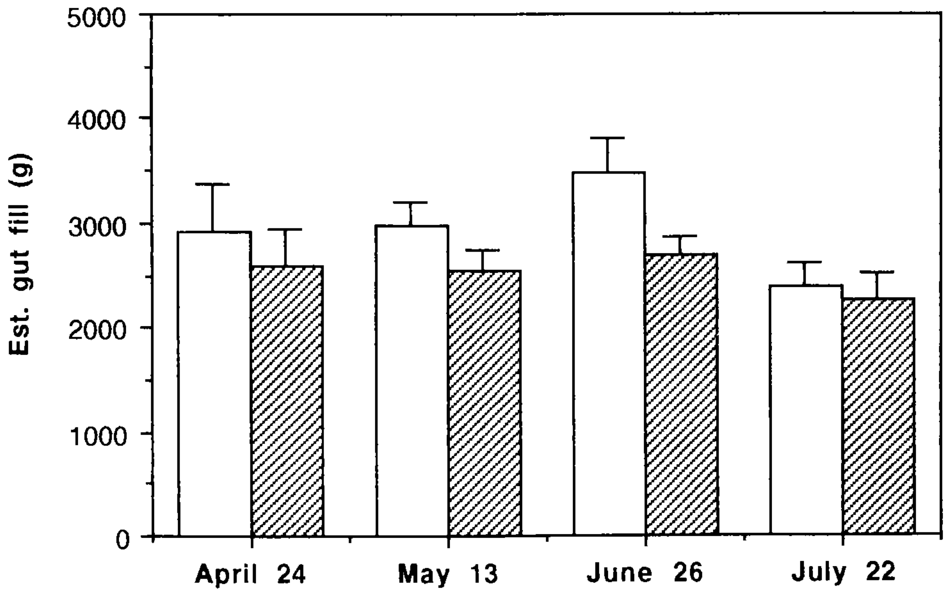

Fig. 3. Estimated dry-matter gut fill of wapiti stags previously kept on low-quality (open bars) or high-quality (hatched bars) winter diets. Means ± standard errors.

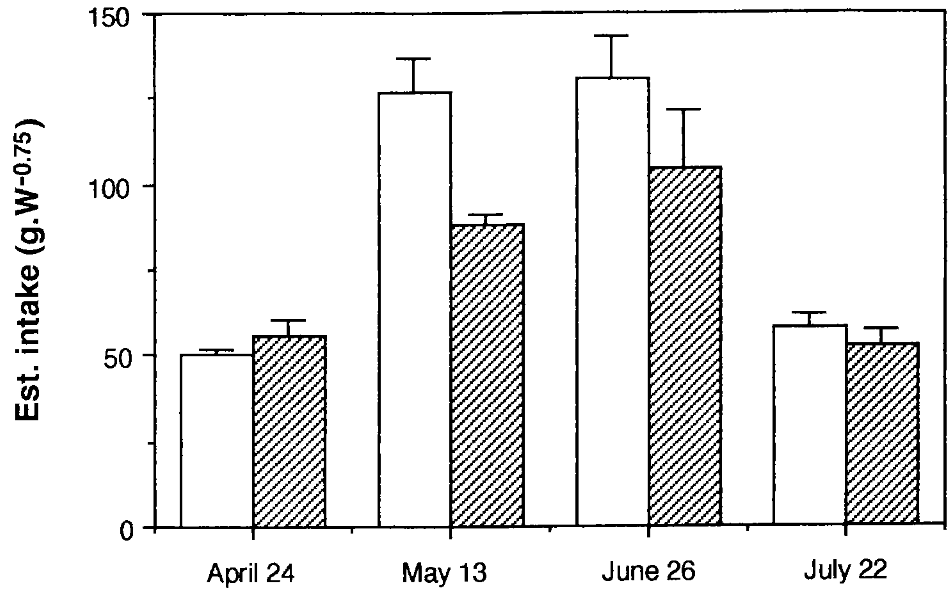

Fig. 4. Estimated dry-matter intake of wapiti stags previously kept on low-quality (open bars) or high-quality (hatched bars) winter diets. Means ± standard errors.

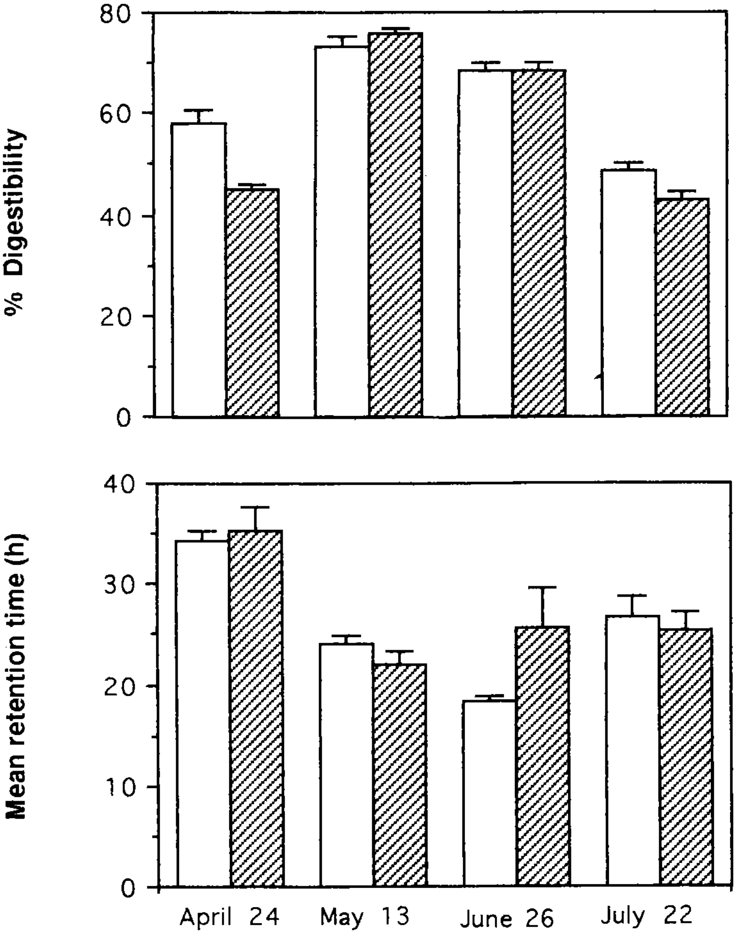

Fig. 5. Estimated digestibility and mean retention time of pasture forage consumed by wapiti stags previously kept on low-quality (open bars) or high-quality (hatched bars) winter diets. Means ± standard errors.

wide differences in spring condition following winter feeding, they compensated well before their first rut. Although the two genotypes have not been compared under the same circumstances, studies on Scottish red deer stags imply a poorer capacity. Weights of red deer had not fully recovered by the end of the grazing season, even when fed to maintain or slowly increase weight during winter (Suttie et al. 1983, 1984; Adam and Moir 1985; Milne et al. 1987).

Explanations for the apparent difference could be environmental or genetic. The simplest explanation would be relative pasture condition. However, Scottish studies have been conducted on improved pasture as well as hill pasture; the parkland range used in our study flushed late and was heavily grazed. If differences have a genetic basis, they may be related to the earlier maturity of wapiti. Red deer calves do not seem to have the same body reserves and are in serious condition if they lose much weight during winter. In contrast, wapiti calves may be better able to use pasture forage during their first summer and sustain growth longer into autumn.

Seasonal Weight Dynamics

During winter, free-ranging wild ruminants typically lose weight in the face of declining quality and availability of native forage. Weight loss occurs mainly in late winter as snow deepens and forage quality declines to critical levels. However, even in stable environments, cervids show cyclic patterns of appetence, energy expenditures and growth that are entrained by photoperiod (Schwartz et al. 1988; Renecker and Hudson 1989). Such rhythms may be preparatory for seasonal change in forage quality and availability.

Metabolic rhythms are modulated by body condition. Weight losses of wapiti on unsupplemented winter pasture are strongly related to autumn weight (Hudson et al. 1985). Small weaned calves typically gain weight, large calves maintain weight, and larger and older animals lose weight. But wintered on medium-quality hay, wapiti maintain weight irrespective of initial weight. In this study, hay-fed stags lost weight, whereas pellet-fed animals gained slowly and continuously. Smaller cervids such as mule deer show the same pattern but seem more sensitive to forage quality (Renecker and Samuel 1991).

During adaptation to spring forage, liveweight losses can be precipitous but transient. This usually is attributed to changes in gut fill rather than empty body weight (Tayler et al. 1957; Wright and Russel 1986). Our wapiti took 46 d to attain their pre-turn out liveweight. This is within the range of 15–50 d reported for cattle (Wright 1985).

On summer pasture, differences in weight at the end of the winter feeding period closed rapidly in this and a previous study on wapiti (Watkins et al. 1991). Such compensatory gain after periods of nutritional restriction is characteristic of many species and is of obvious relevance to domestic livestock production (Wilson and Osbourn 1960; O'Donovan 1984). The existence of compensatory gain suggests that natural selection must favor seasonal targets in weight or perhaps body composition (Price and White 1985).

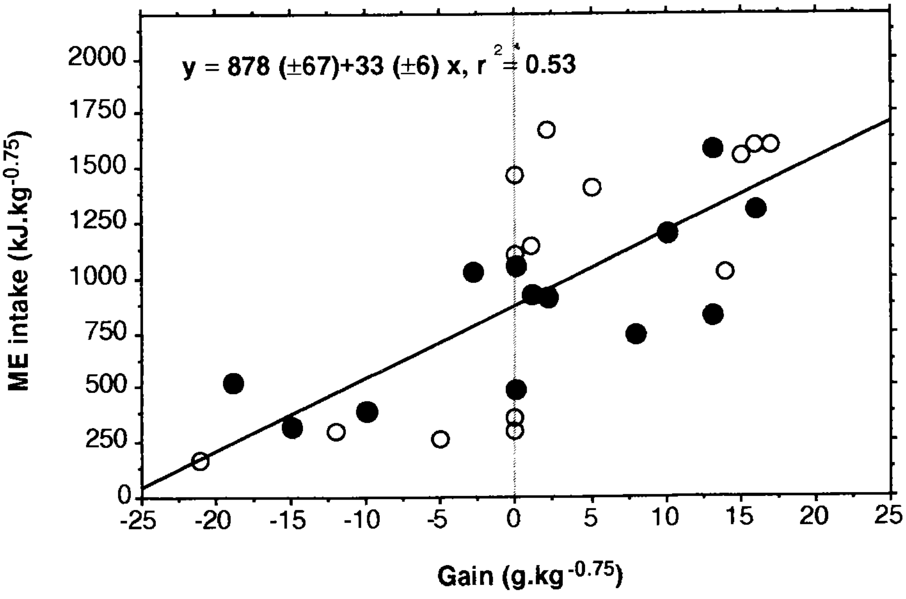

Fig. 6. Conversion efficiency of pasture forage by wapiti stags previously kept on low-quality (open symbols) or high-quality (closed symbols) winter diets. The intercept (877.9 kJ $W^{-0.75}$) estimates maintenance requirements, and the slope (33.4 kJ g^{-1}) estimates the costs of liveweight gain. ME, metabolizable energy.

Gut Fill

Interpretation of liveweight is complicated by gastrointestinal contents (gut fill) (Wilson and Osbourn 1960), which in cervids accounts for about 10% of body weight. We estimated the contribution of GIT with a digestive marker (Cr_2O_3) rather than attempting to control differences by withholding feed and water before weighing. Differences in GIT were marginally significant, but converted to approximate wet fills (using the range of values expected for diet or season from pen trials by Renecker and Hudson 1990), they remained too small to account for compensatory gain. We saw little evidence of the compensatory increases in rumen capacity sometimes seen in ruminants on high-fibre diets (Staaland et al. 1979).

Frame Size

By the end of winter, wapiti stags receiving alfalfa-barley pellets were larger framed than those wintered on hay alone. Three months later, these differences had disappeared, indicating that skeletal growth and soft-tissue deposition were involved in compensatory growth. In similar-aged red deer stags, winter nutrition had an early and lasting effect on skeletal growth (Suttie et al. 1984) but not on carcass composition at slaughter (Adam and Moir 1985).

Interruption of growth has the greatest effect on late-maturing tissues and regions of the body and may alter the proportions of the body permanently (Wilson and Osbourn 1960). Because bone is an early-maturing tissue, skeletal measurements should be unaffected by all but extreme nutritional restriction (Price 1977). However, this seems to hold only in older animals.

The risk of permanent stunting is real if feed restriction interferes with cell division, because cells have limited capacity for hypertrophy (Staun 1972). Severe and prolonged undernutrition at an early age may cause permanent stunting (Maynard et al. 1979). The mature size of reindeer (Skogland 1983) and red deer (Clutton-Brock et al. 1982) is most vulnerable to stunting during the late-fetal–neonatal stage when hyperplasia is still in progress.

Girth provides an indication of the bulk of an animal and relates closely to body weight. Chest girth measurements were similar to those of young wapiti stags reported by Flook (1970), although the latter measurements were taken in winter. Therefore, a period of undernutrition of the type and duration used in this study did not cause permanent stunting of young wapiti stags, and moderate undernutrition during winter did not have deleterious effects on final size.

Forage Intake

Animals recovering from winter weight loss should increase daily DMI (Wilson and Osbourn 1960; Allden 1968, 1970; Wright 1985). As in a previous study (Watkins et al. 1991), this was generally supported, since daily forage intakes were higher in compensating wapiti. In red deer (Suttie et al. 1983; Adam and Moir 1985; Milne et al. 1987) and cattle (Baker et al. 1985; Wright et al. 1989) increased feed intake seems to be the main factor accounting for compensatory gain. However, there are exceptions. Fox et al. (1972), Hironaka and Kozub (1973) and Saubidet and Verde (1976) found no change in intake, and Foote and Tulloh (1977) and Murray (1980) found decreases.

Estimates of intake expressed relative to metabolic weight fell within the range of 40–90 g $W^{-0.75}$ d^{-1}, typical among livestock (Cordova et al. 1978). Monthly variation corresponded to pasture availability and quality. In April, low forage biomass and high fibre levels limited intake despite the high appetite drive. Forage intake increased with pasture biomass and crude protein. Subsequently, intake declined as forage matured and pasture biomass declined in late July. The major drop in July coincided with supplementary feeding of alfalfa–barley pellets.

Appetence in many species of wild herbivores responds to photoperiod. White-tailed deer (Arman et al. 1974), red deer and sheep (Kay 1979) reduce voluntary intakes to maintenance levels in mid-autumn and increase them again with the approach of spring. Although peak appetence may coincide with the summer solstice, it is difficult to evaluate the contribution of such intrinsic effects over the 4-mo duration of the pasture trials.

Digestibility

Forage digestibility was not greatly affected by nutritional history, as concluded by most other studies on compensatory gain (Wilson and Osbourn 1960; Drew and Reid 1975). The one significant difference was the higher digestibility measured in LOW wapiti. Whether this was due to ruminal adaptation because of the winter diet or to greater selectivity of grazing cannot be distinguished.

Digestibility increased in May as pasture growth gained momentum and subsequently declined with forage maturation in June and July. The continuing decline in digestibility despite supplementation with alfalfa-barley pellets (70% digestible in pen trials) indicates pellets did not constitute a large proportion of daily intake.

Passage Rate

Completeness of digestion is closely linked to the competitive rates of digestion and passage. In general, MRTs mirrored monthly changes in digestibility. The MRT of grazing wapiti (25–27 h) were similar to values for wapiti calves on pelleted diets (21–29 h, Westra and Hudson 1981) and adult wapiti on grass, alfalfa and aspen (16–18 h, Renecker and Hudson 1990). Values for red deer (Milne et al. 1978) are 21–23 h for pelleted diets and about 40 h for dried grass and heather. Such rapid passage rates appear typical of cervids.

We assume in these comparisons that Cr_2O_3 reflects the movement of particulate matter. In moose and wapiti, both the liquid and the particulate matter are correlated and flow together, unlike in cattle and presumably other large grazers in which rumen contents are stratified (Renecker and Hudson 1990). Therefore, separation of chromic oxide (if given in low doses) from food particles may be less important than it is in large grazers.

Variations among individuals in passage rates are typically large (Westra and Hudson 1981; Mautz and Petrides 1971). In our study, such variations could be attributed to difficulties in administering the marker. HIGH wapiti ate their pellets within several minutes, whereas the LOW wapiti took up to 3 h. Measuring the digestibility of forage presents another problem. In theory, natural herbage constituents like lignin can be employed as indicators. In practice, this application is complicated by partial digestion of lignin in new growth (Wallace and Van Dyne 1970; Fahey and Jung 1983). Another difficulty with any internal indicator is that of obtaining feed samples that are truly representative of the diet.

Interrelationships of Digestive Parameters

For a fixed diet, rumen contents, passage rate, digestion rate and intake rate usually are predictably related. Rapid passage should depress digestibility but allow higher intakes. However, several exceptions have been reported in studies on red deer. Milne et al. (1978) found that digestibility and MRT did not decrease with seasonal increases in voluntary feed intake. Domingue et al. (1991) found no depression of digestibility but increased rumen pool sizes as intake increased in summer.

In our study, of course, diet changed from mainly coarse carry-over during the April trial to lush growth during May and June and sparse mature pasture in July. This accounts for the inverse relationship between digestibility and MRT. Differences between treatment groups during specific trials could be explained by diet selection as easily as by physiological adaptation.

Requirements for Maintenance and Gain

Differences in diet digestibility and rate of passage were small and did not fully explain higher intakes and higher gains in LOW wapiti. So, the question of feed-conversion efficiency in terms of energy requirements for maintenance and gain invites consideration. Improved feed efficiency is evident particularly in the early stages of realimentation (O'Donovan 1984). Compensating young red deer stags have higher feed-conversion efficiencies (Suttie et al. 1983), perhaps due to either the leaner composition of gain or lower maintenance requirements. Feed-conversion efficiency of our wapiti stags was not influenced by nutritional history.

The daily maintenance requirements of penned red deer are 520 kJ $W^{-0.75}$ for hinds and 570 kJ $W^{-0.75}$ for stags (Fennessy et al. 1981; Suttie et al. 1987). Red deer stags wintered outdoors have requirements approaching 850 kJ $W^{-0.75}$ d^{-1}. Grazing presumably increases these costs. Estimates for wapiti range from 572 kJ $W^{-0.75}$ d^{-1} for hinds held in pens during winter and 936 kJ $W^{-0.75}$ d^{-1} for young hinds on spring pasture (Jiang and Hudson 1992). The latter figure is close to our estimate of 878 kJ $W^{-0.75}$ d^{-1} for these wapiti stags.

Energy requirements of red deer for liveweight gain range from 37 kJ g^{-1} d^{-1} for stags to 55 kJ g^{-1} d^{-1} for hinds (Fennessy et al. 1981; Suttie et al. 1987). Young wapiti hinds on spring pasture required 38.5 kJ g^{-1} d^{-1} for liveweight gain (Jiang and Hudson 1992), a value that is similar to 33.4 kJ g^{-1} d^{-1} for young wapiti stags in this study. Suttie et al. (1987) suggested that the high value obtained for red deer hinds might be related to their relative carcass maturity (fatness). If so, wapiti hinds must mature less rapidly than red deer so that the composition of gain of the sexes is not different by 1 yr of age.

PRACTICAL CONSIDERATIONS

During winter, free-ranging wild ruminants lose weight in the face of declining quality and availability of native forage. The impact in both absolute and relative terms is greatest for large individuals (Hudson and White 1985). Weight loss occurs mainly in late winter as snow deepens and forage quality declines to critical levels. In spring, animals (particularly the lighter ones) increase weight rapidly to deposit body reserves to participate in the autumn rut and survive winter's scarcity. Although environment plays an important part, it is also an expression of an underlying endogenous cycle (Bandy et al. 1970).

This natural rhythm provides an opportunity for game farmers to work with rather than against the seasons, capitalizing on the seasonal adaptations of indigenous ruminants. Although nutritional management of the breeding herd has received study (Kozak 1988), it has generally been accepted that weaned calves should be fed high-quality diets to enable them to grow as rapidly as their appetence allows throughout the winter. However, this study shows that weaned stag calves could be fed to attain spring weights of about 150 kg without impairing their capacity to compensate completely on summer pasture.

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