

Weight Dynamics of Wapiti in the Boreal Forest

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Seasonal weight changes in wapiti *Cervus elaphus nelsoni* (V. Bailey, 1935) were correlated with certain environmental parameters. Diet quality, a function of forage availability, appeared to be the dominant factor. The apparent duration of negative energy balance during winter was 131 days. Weight gain began in spring with the emergence of new forage. Growth patterns differed among age/sex cohorts. The effect of insect harassment on summer growth was assessed.

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1. INTRODUCTION

Changes in body weight are expressions of energy and matter balances and reflect attempts by animals to use resources to best advantage. Optimal patterns of resource use are particularly important in seasonal stochastic environments in which availability of nutrients and energy costs vary widely.

In temperate regions wild ruminants must capitalize on temporally concentrated food supplies. Mature males must deposit adequate tissue reserves to subsidize energetically costly breeding activities leaving sufficient reserves for winter when maintenance costs cannot be met. Mature females must attain a level of condition which will enable them to survive submaintenance nutrient consumption and produce viable offspring (Thorne *et al.*, 1976). Lactation constrains the ability of the female to rapidly achieve adequate tissue reserves during periods of nutritional abundance.

The wapiti *Cervus elaphus nelsoni* (V. Bailey, 1935) is a generalist herbivore which exhibits diverse food habits and habitat preferences and is highly opportunistic in its resource use behavior. Opportunism is expressed in seasonal migrations (Knight, 1970), in taking advantage of locally abundant and temporal food resources and in diverse food habits (Kufeld, 1973). Its opportunistic nature should enable this species to shorten the annual period of negative energy balance more than is possible by specialist herbivores like the moose (*Alces alces*) (Stewart *et al.*, 1977).

This study examines weight dynamics of wapiti in relation to age, reproductive status, and certain seasonal factors in the environment.

2. METHODS

Study Area and Animals

The study was conducted at the Ministik Wildlife Research Area, a 60 ha enclosure in an outlying area of boreal mixed wood vegetation (Rowe, 1972) near Edmonton, Alberta. The vegetation mosaic was characterized by a complex interspersed of aspen (*Populus tremuloides*) forests, shrublands, grasslands and wet meadows. These habitats and prevailing environmental conditions are described by Telfer and Scotter (1975). Seasonal patterns of resource use behavior by wapiti in the boreal forest have been described by Gates & Hudson (1980).

The animals were obtained as calves and hand-reared on milk replacers (Gates, 1980). They were released into the enclosure in September 1977. The initial herd consisted of 2 bulls, 3 cows and 3 calves.

Weight Measurement

The wapiti were assembled periodically in a handling facility designed to minimize stress and risk of injury to either the animals or the handler. Body weight was measured using an electronic platform scale. Feed and water were not withheld so that body weights also included rumen fill.

Weights of pregnant cows were adjusted for weight of the gravid uterus using data reported for singly-conceived cattle (Eley *et al.*, 1978), domestic sheep (Rattray *et al.*, 1974) and white-tailed deer (Robbins & Moen, 1975). For these species the weight of the fetus at term represents an average of 57% of the weight of the total gravid uterus. For a wapiti calf weighing 18.2 kg at birth the weight of the gravid uterus would be 31.89 kg.

Using data for sheep and white-tailed deer an equation was developed for relating percent of maximum uterus weight to the percent stage of gestation. The percent weight of the gravid uterus was estimated from the equation:

$$\text{Log } Y = .0499X - .0189 \quad (r^2 = .955)$$

Where Y = percent maximum uterus weight and X = % days of gestation. This weight was subtracted from total body weight to give the corrected body weight.

Fecal Analysis

To gain an impression of seasonal changes in forage quality consumed by wapiti, five to nine feces samples were collected for 1–2 days during 2–4 week intervals. They were frozen until analysis. Crude protein ($N \times 6.25$) content was determined using the macro-kjeldahl procedure (A.O.A.C., 1965).

Statistical Methods

Differences in weight gain or loss between age and sex cohorts were analysed using Student's t -test (Sokal & Rohlf, 1969) after logarithmic transformation. Linear regression was used to derive relationships between feces crude protein content and rate of gain for calves and bulls.

3. RESULTS

Growth of Calves

After introduction into the enclosure in early September, the wapiti calves gained weight until late December (Fig. 1). The male calf experienced an 89.2% increase in weight at an average rate of 0.44 kg per day. Similarly, female calves gained 91.5% over their initial weight at an average rate of 0.37 kg per day. The percentage increase in body weight was significantly greater than for cows or bulls (Table 1). The calf reared naturally the following year achieved a peak weight of 134 kg which was 29 kg above that of the hand reared male calf.

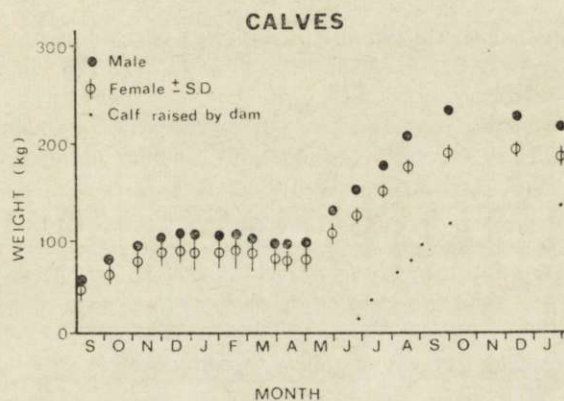


Fig. 1. Seasonal weight dynamics of male and female hand raised wapiti calves and a naturally raised wapiti calf. The mean weight of three female calves is shown and plus or minus one standard deviation is indicated.

After late December 1977, the calves ceased growing until early May when spring forage first appeared. In the intervening period they lost an average of 9.9% of their peak weight (Table 1).

During the spring and summer the calves, (then yearlings), gained rapidly. Between May 2 and August 20 females grew at an average of 0.85 kg per day, and achieved weight gains averaging 118.6%. During the same period, the male experienced a weight gain of 114.4% (1.01 kg/day). Gain of female yearling was significantly greater than for cows or bulls. The maximum weights recorded for the yearlings occurred in October 1978. By December and January winter weight loss commenced (Fig. 1).

The calf raised by its dam achieved a remarkable growth rate of 1.08 kg per day between birth (June 25) and August 20. Its birth

weight was 18.2 kg and by August 20 had reached 78.6 kg, a weight gain of 331.9%. This calf continued to grow, though at a reduced rate until January 31, 1980, when last weights were obtained.

Growth of Cows

Peak weights (212 kg) were recorded on December 21. This represented an average gain of 9.4% since the time of introduction. Over the winter (December 21 to May 2) the cows lost an average of 21.3% of their peak body weight (corrected for weight of the conceptus). This did not differ significantly ($P < .40$) from the weight loss of bulls (Table 1).

Table 1
Weight changes of wapiti in different periods of the year.

Period	Calves		Age-sex Cohort Cows*		Bulls	
	% Change	Rate (kg/day)	% Change	Rate (kg/day)	% Change	Rate (kg/day)
Fall-Early Winter (Sept. 1—Dec. 21, 1977)	93.9	0.39	9.4	0.16	5.8	0.11
Winter-Early Spring (Dec. 21, 1977—May 2, 1978)	-9.9	-0.06	-21.3	-0.35	-16.9	-0.28
Spring-Summer (May 2—Aug. 20, 1978)	118.6**	0.85	37.0	0.57	48.0	0.86

* Weights corrected for gravid uterus weight. ** Male calf not included.

By the end of March, the weight of the gravid uterus made an important contribution to actual body weight (Fig. 2). Although the actual weight of the cow remained relatively constant between the beginning of March and the start of May, there was a loss in weight of maternal tissues (-13.3%). Over the same period the bulls lost an average of only 7.0%. Presumably the difference was a result of loss of maternal tissue as a consequence of the accelerated demands of the rapidly growing fetus.

Calves were born on June 15, 20, and 25, 1978 to each of the cows. Between June 25 and August 20, the cows gained an average of 14.4% at a rate of 0.51 kg/day while the bulls gained 23.4% at a rate of 0.99 kg/day. The difference could have been due to the cost of lactation.

After the end of August the cows experienced little growth (Fig. 2). The mean weight on August 20 was 229.0 and increased to only 233.9 kg (0.11 kg/day) by October 3, which was their peak weight for that year. During the period August 20 to October 3 the female yearlings gained more (9.5%) than the cows (2.18%). This may have been due to the

additional cost of lactation. However the performance of these two cohorts may not be strictly comparable due to possible effects of age. Weight increments of female yearlings in 1978 and 1977 were similar during the fall to early winter period.

Growth of Bulls

Similar to the yearling cows, the two yearling bulls gained weight until December (Fig. 3). The peak weight of the dominant bull was considerably greater than that of the subordinate bull.

Over winter (December 21 to May 2) bulls lost an average of 16.9% of their peak fall weight. During the spring and summer (May 2 to August 20) the bulls gained 0.86 kg/day and achieved an increase of 48% over their initial spring weight.

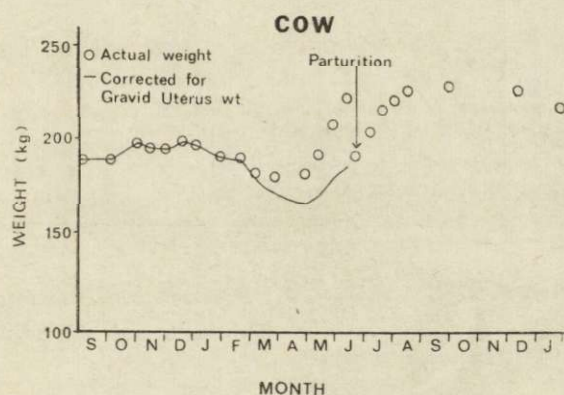


Fig. 2. Seasonal weight dynamics of a cow wapiti. Change in nonpregnant body weight is indicated by a solid line.

While there was a considerable difference between weights of the dominant and subordinate bull in the fall of 1977 and subsequent winter, their spring and summer weights were similar. However, this did not alter the dominance hierarchy. In mid-August the bulls stripped velvet and polished antlers. While both bulls were aggressive and dangerous during the following 40-day period, the dominant bull was notably more so than the subordinate.

Growth ceased in both bulls during the rutting season. The subordinate bull remained at a relatively constant weight between August 20 and October 3, but the dominant bull lost 16.8 kg at a rate of -0.38 kg/day. After the rut both bulls gained weight until December 17. The

subordinate's weight increased to 301.4 kg. The dominant bull recovered the loss it experienced during the rut, increasing its weight to 294 kg.

Influence of Environmental Factors

Many environmental factors affect the energetic status and hence weight dynamics of free-ranging wapiti. Forage quality and availability as affected by range and snow conditions, thermal stress, and disturbance are generally considered the most important influences. Among these it was possible only to investigate the effects of forage quality and biting insects.

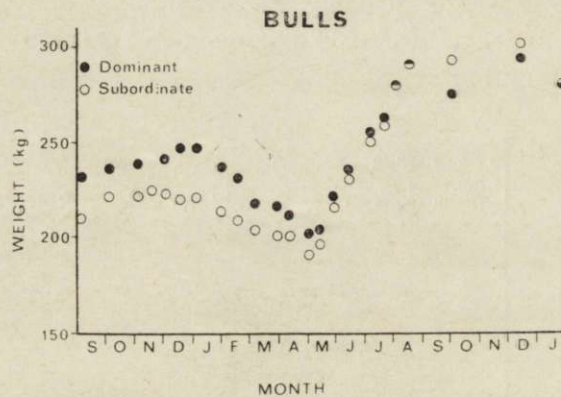


Fig. 3. Seasonal weight dynamics of the dominant and subordinate bull wapiti.

Forage Quality

The quality of herbage available to the wapiti varied seasonally with plant phenology and snow conditions. The consequent pattern of diet quality was reflected in the crude protein content of feces (Fig 4). Diet quality declined steadily throughout the fall and winter but began to rise with the disappearance of snow cover in late March. By April 25 the wapiti began to feed on fresh forage, primarily in sedge wetlands. However, they continued to lose weight until after May 2 when fresh herbage became abundant. Diet quality and growth rates of the wapiti remained high until late August.

The relationship between average daily gain and diet quality (feces crude protein) was investigated for female calves born in 1977 and bulls (Fig. 5) excluding data from the rutting period. Due to the additional energetic costs of pregnancy and lactation, cows were excluded from

this analysis. A strong relationship between average feces crude protein (%) and rate of gain was determined for bulls ($r^2=.85$) and for the wapiti calves ($r^2=.89$).

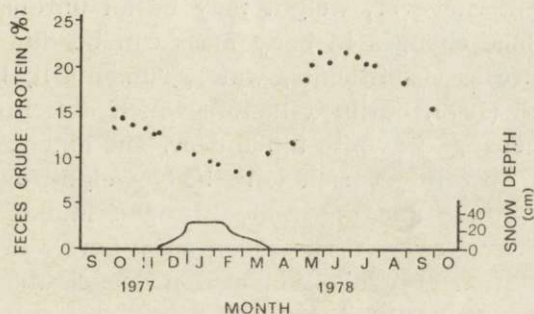


Fig. 4. Seasonal variations in crude protein content (%) of wapiti feces.

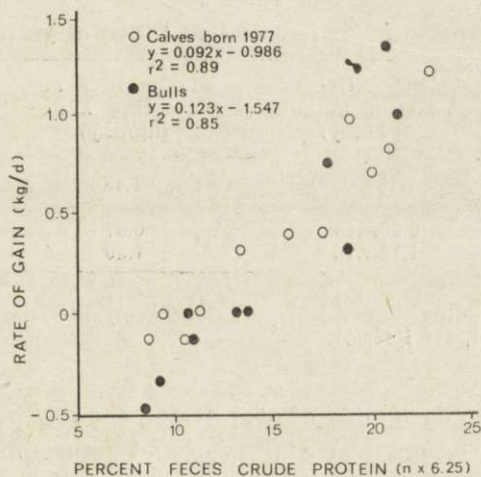


Fig. 5. Relationship between average daily rate of gain and feces crude protein (forage quality indicator) for wapiti calves and non-rutting bulls.

Insect Harassment

During the month of June the wapiti were frequently subjected to intense insect annoyance. The animals responded by altering feeding patterns and habitat use. The effect on growth is evident in Table 2. In both yearling females and bulls, rates of gain were significantly less during the period of insect harassment. The effect on the yearling male was obvious as well, for all of these age/sex cohorts, rate of gain dropped by an average of 54% during the month of June compared with the immediately preceding two-week period.

4. DISCUSSION

Weight change is an expression of a number of interacting factors including nutrient intake, energy expenditures, physiological status, and body composition. However, weight may be an unreliable indicator of energy status since changes in body mass can be due to variations in a number of carcass constituents, water, rumen fill, bone, protein or fat. Holter *et al.* (1979) outlined factors which determined the composition of weight change in white-tailed deer. The extent of fat or protein deposition or mobilization varied with body weight, age or season, digestible energy intake and digestible nitrogen intake. Nutritional demands for growth of other tissues such as antlers and pelage and the demands of gestation and lactation also influence the magnitude and form of energy storage or mobilization.

Table 2

Influence of insect harassment on rate of gain (ADG) of yearling and bull wapiti.

Time periods	Mean ADG of Yearling Females (kg/day)	Mean ADG of Yearling Male (kg/day)	Mean ADG of Bulls (kg/day)
2 weeks before	1.18±.03 **	1.49	1.38±.07 ***
Period of Insect Harassment	0.68±.15	0.87	0.62±.02
2 weeks after	1.16±.13 *	1.20	1.03±.06 ***

Significant differences between the period of intense insect harassment and the preceding and succeeding two-week periods (*t*-test) are indicated by asterisks.

* $P < .02$, ** $P < .01$, *** $P < .001$.

Seasonal weight dynamics of wapiti followed a pattern which was correlated with variations in certain seasonal environmental parameters. Diet quality, a function of forage availability, appeared to be a major determinant. This parameter was influenced by plant phenology and snow cover, and probably by weathering of forage in late winter and early spring.

Diet quality declined in the fall and rates of gain were correspondingly lower. Continuation of weight gain in the fall enhances energy reserves for the ensuing period of negative energy balance. In this study the wapiti began to lose weight after arrival of heavy snow cover in late December. This period coincided with fecal protein levels of about 10%. Although snow cover receded in late winter and early spring, loss of weight and body condition continued until the initiation of herbage growth in early May. On this basis the apparent duration of negative energy balance was about 131 days. In comparison the average estimated

annual duration of negative energy balance over an 18-year period for moose was 225 days (Stewart *et al.*, 1977).

Seasonal changes in energy expenditure were not quantified. The energy costs of locomotion and thermoregulation likely increased in the winter as a result of snow cover and low temperatures. Voluntary restrictions in feed intake also may have influenced winter weight loss. This phenomenon has been demonstrated in captive caribou (*Rangifer tarandus groenlandicus*) (McEwan & Whitehead, 1970) and in white-tailed deer and mule deer (*Odocoileus hemionus*) (Silver *et al.*, 1969; Wood *et al.*, 1962), despite availability of adequate feed. However this has not yet been demonstrated in wapiti. On the contrary, it appears that wapiti are able to maintain or increase weight over winter if supplied with adequate feed (Dean *et al.*, 1976).

Physiological status also appeared important. Body composition at peak fall weight may play a role in determining over winter weight loss. While older animals accumulated extensive fat stores, moose and caribou calves entered winter with smaller reserves (Dauphine, 1976; Stewart *et al.*, 1977). Catabolism of a unit weight of tissue in a calf would consequently yield less energy than one unit in an older animal. It is possible that calves attempt to minimize weight loss to a greater extent than older animals by foraging more effectively and by supplementing forage intake as long as possible with milk. Weight loss in wapiti calves was significantly less than that experienced by yearling bulls and pregnant cows in this study.

Reproductive status played an obvious role in weight dynamics of mature males. The dominant bull at the age of two and a half years lost considerably more weight during the rut than its subordinate. Social status apparently is correlated with the extent of depletion of tissue energy reserves during the rutting season. Unless recovery following the rut is possible due to favorable foraging conditions, as occurred in this study, depletion of energy reserves during the rut may adversely affect survival in the subsequent winter period. The appropriate behavioral strategy which would maximize reproductive fitness would therefore represent a compromise between participating in one rut and sparing energy reserves to ensure survival to the next.

Reproductive status of cows also had marked effects on weight dynamics. The demands of late pregnancy and lactation depressed body weight gains. Rapid growth of the fetus began about mid March. This meant that the cows had to compensate for an additional demand on energy stores for six to seven weeks until diet quality improved with

emergence of new growth herbage at the beginning of May. Prior *et al.* (1979) suggested that during pregnancy, fetal and maternal tissues compete for available nutrients and that when the supply is limited fetal tissues have a higher priority than maternal tissues. Consequently during this period the cows mobilized tissues rapidly. However, during the remaining four to five weeks of gestation high quality herbage was abundant and the cows apparently were able to recover much of the winter weight loss.

There is an obvious adaptive advantage to timing late gestation with a period of nutritional abundance considering the serious impact that maternal weight loss can have on neonatal birth weight and subsequent survival in wapiti (Thorne *et al.*, 1976). Both weight loss due to the products of gestation and birth weight of the one calf weighed in this study were comparable to the weights in wapiti maintained by Thorne *et al.* (1976) on a high plane of nutrition throughout the winter and spring.

The rate of gain of the maternally raised calf was much higher than predicted by a regression equation relating rate of gain of a calf to average maternal weight (225 kg) for a large number of ungulates and subungulates (Robbins & Robbins, 1979). The growth of the calf was prolonged at least until the end of January 1979 when the last weights were obtained. This was likely only possible as a result of prolonged supplemental milk consumption.

Wapiti are adapted to marginal subsistence during winter as a result of versatility and flexibility in food habits and occupational patterns which permit them to extend the period of positive energy balance late into the fall and to capitalize on the most available and nutritious forage items throughout the year. However they depend on full nutritional recovery during the summer to prepare for demands of body maintenance and reproduction in the following autumn and winter. Short (1975) concluded that winter survival of white-tailed deer depends heavily on good nutrition during late summer and early fall. Any disruptive factor, physical or biotic, which results in a decrease in feeding time or a decreased efficiency in use of that time, or increases energy expenditure is potentially detrimental. This is especially true preceding or following harsh or prolonged winters with early snow cover or late green-up. The presumed influence of insect harassment in this study was expressed in reduced growth rates and if sufficiently intense or prolonged could have resulted in a shortfall on target fall weights. Prolongation of such a disruptive factor could seriously affect reproductive success and/or survival. In light of this possibility wildlife managers should consider the potential disruptive impacts of human activity.

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WAHANIA CIĘŻARU *CERVUS ELAPHUS NELSONI* W LASACH BOREALNYCH

Streszczenie

Badania prowadzono w 60 ha zagrodzie położonej wśród północnych lasów mieszanych, w pobliżu Edmonton, w stanie Alberta w Kanadzie. Stado początkowe stanowiły 2 byki, 3 łanie i 3 cieleta *Cervus elaphus nelsoni* (V. Bailey, 1935). Ciężar ich ciała mierzono przy pomocy urządzenia elektronicznego, aby nie stresować zwierząt. Stwierdzono, że sezonowe zmiany tego ciężaru były skorelowane z niektórymi parametrami środowiska. Głównymi czynnikami były jakość pokarmu i jego dostępność. Zmieniały się one sezonowo w zależności od fenologii i warunków śniegowych (Ryc. 4, 5). Okres trwania ujemnego bilansu energii w ciągu zimy wynosił 131 dni. Ciężar ciała jeleni zaczął się podnosić na wiosnę, w chwili ukazania się nowego pokarmu. Wzorzec wzrostu jest różny w grupach wiekowo-płciowych (Ryc. 1, 2, 3; Tabela 1). Szacowano również wpływ owadów nękających jelenie na ich wzrost letni (Tabela 2). Stwierdzono, że zarówno u byków, jak i u łan poziom przyrostu jest istotnie niższy w tym czasie.