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UNIVERSITY OF ALBERTA

Compensatory growth of young wapiti stags (*Cervus elaphus*)

by

Saphida Wairimu

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN

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DEPARTMENT OF ANIMAL SCIENCE

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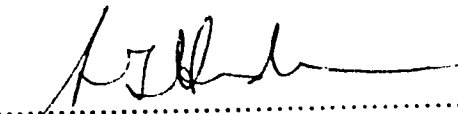
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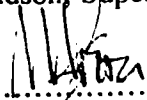
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SIGNED ..Wairimu.....Saphida..

Permanent address

      P.O Box 112

      Kigumo, Kenya

Date...October...9...1991

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Compensatory growth of young wapiti stags (*Cervus elaphus*) submitted by Saphida Wairimu in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Productivity and Management.

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R. J. Hudson, Supervisor

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M. A. Price

....

W. M. Samuel

Date..October..9...1991

DEDICATED TO

my parents, Benson and Esther Mwangi who have provided opportunity, guidance, faith and encouragement for my several and varied endeavors.

ABSTRACT

Ten yearling wapiti stags were used to study the effects of winter nutrition on subsequent performance and behavior on spring/summer pasture. During winter, five wapiti (high quality winter diet, HW) received alfalfa-brome hay and alfalfa-barley pellets. The other five (low quality winter diet, LW) were wintered on native pasture and alfalfa-brome hay. All animals were given access to feed *ad libitum*. On April 4 both groups were merged and released on to a 1.5 ha pasture.

Supplementation with alfalfa-barley pellets during winter improved the growth of calves and the HW group entered spring with a 20 kg advantage (P=0.05). LW wapiti weighed less by late winter but compensatory growth narrowed these differences and both groups attained similar weights by July. Animals that were light in early spring due to winter nutrition grew faster than heavier animals. Live weight gains during spring were 0.30 kg/d and 0.15 kg/d for LW and HW wapiti, respectively (P=0.003).

Weight differences were not explained by gut fill, although wapiti in LW group had significantly higher total gut fill in April and June. Gut fill difference corrected for dry matter were neither significant nor large enough to account for weight differences. Measurements of body water by urea dilution suggested that HW animals had lower fat levels at the end of winter than LW wapiti. Weight gain during compensatory growth contained less fat but there was no significant difference in body composition between the two groups in August. Blood urea nitrogen differed significantly after the winter feeding period in April (P< 0.001) but not in August.

LW wapiti had smaller frame dimensions at start of spring in April (P=0.004). However, compensation was complete by July and linear measurements did not differ significantly between the groups (P=0.83). Hip width (r^2 =0.812) had better recuperative powers than body length and chest girth.

Compensatory growth was achieved mainly by higher intake (overall, 4.3 and 3.6 kg dry matter per day for LW and HW wapiti, respectively). The effect was most striking when intake was expressed on a metabolic weight basis (88.3 kg /BW$^{0.75}$ vs 62.8 kg/BW$^{0.75}$ for LW and HW, respectively). Intake differed between nutritional treatments in April (P= 0.027) and May (P= 0.04). However, digestibility and rate of passage did not differ overall(P> 0.1) but digestibility differed in April

(P=0.05) and rate of passage differed in June marginally (P=0.08). Feed conversion efficiency was unrelated to nutritional history. Using pooled data, energy requirement for maintenance and live weight gain, were calculated to be 877 kJ/BW $^{0.75}$ and 34 kJ/g, respectively.

Higher intakes by compensating wapiti were achieved primarily by foraging longer (12.7 vs 10.6 h per day), and biting faster (43.9 vs 40.4 bites/min) for LW and HW wapiti, respectively. LW wapiti consumed significantly (P< 0.001) more forage per minute (13.8 g/min) than HW wapiti (12.7 g/min). They also spent less time in more energy consuming activities such as walking. Habitat and diet selectivity were unaffected by nutritional history.

I concluded that compensatory growth in wapiti is a adaptation that enables them to exploit seasonally harsh environments and to anticipate and prepare for predictably changing conditions.

Acknowledgements

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I. INTRODUCTION

Compensatory growth, sometimes referred to as 'catch-up growth', is the acceleration in growth that occurs when a period of growth inhibition ends and favourable conditions are restored (Ashworth and Millward 1986). Compensatory growth is essentially a self-correcting response which restores the individual to its original weight trajectory. Compensatory growth has been studied in cattle (Coleman and Evans 1986; Lofgreen and Kresling 1985; Park et al. 1987), sheep (Thompson et al. 1982; Ferrell et al. 1986), pigs (Mersman et al. 1987; Pond and Mersman 1990), poultry (Pokniak and Cornejo 1982; Calvert et al. 1987), and man (Ashworth and Millward 1986).

Few wild herbivores grow to maturity along classical sigmoid growth curves. Instead, live weight follows a saw-tooth pattern over time with troughs corresponding to the timing and severity of feed shortages (Price and White 1985). Forage seasonality influences both the amount and the quality of feed available to wild ruminants and these have separate as well as combined influences on growth. During winter, free-ranging wild ruminants 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. The impact in both absolute and relative terms is greatest for large individuals (Hudson and White 1985). Over-winter weight loss of up to 30% is common in wild red deer *(Cervus elaphus)* (Mitchell 1972; Moore and Brown 1977), white-tailed deer *(Odocoileus virginianus)* (French et al. 1956) and black-tailed deer *(Odocoileus hemionus columbianus)* (Bandy et al. 1970). During spring/summer, forage quality and quantity is high, animals gain weight and light animals are able to narrow the contrast in weight with heavier animals (Hudson et al. 1985). This seasonal growth pulse is particularly marked in northern cervids.

Compensatory growth probably represents a survival mechanism and a normal physiological response in both wild and domestic animals. Therefore, when feed supplies are scarce or expensive as they are in winter, temporary feed restriction may be practised without long-term deleterious effects and it may be economically advantageous to capitalize on compensatory growth the following summer. The theory of compensatory growth predicts that underfeeding animals for a particular

period will not necessarily result in stunting. But, the risk of permanent stunting is real if feed restriction in young animals interferes with cell division.

Accretion of body weight results from both an enlargement of the cells (hypertrophy) and an increase in number of cells (hyperplasia). Severe and prolonged undernutrition at an early age may result in permanent stunting (Maynard et al. 1979). At this early age, hyperplasia is still in progress and any interference with it can result in reduced total number of cells. This would certainly lead to stuntedness because cells have maximum capacity to hypertrophy (Staun 1972).

The nature and physiological basis of compensatory growth is not well understood (Wilson and Osbourn 1960; Allden 1970; Reid and White 1977; O'Donovan 1984). Compensation has been attributed to a number of biological mechanisms; namely, alteration of the composition of tissue gains (Thompson et al. 1982; Baker et al. 1985), reduced maintenance requirements (Saubidet and Verde 1976), increased feed intakes (Meyer et al. 1965), high voluntary intake in relation to maintenance requirements, and increased efficiency of feed conversion (O'Donovan 1984).

The contribution of each of these mechanisms remains unclear due to the divergence in experimental designs, the interdependency of these mechanisms, and the fact that few experiments have examined these mechanisms simultaneously. Conflicting conclusions undoubtedly have resulted from differences in: (a) species of animals and their physiological peculiarities; (b) maturity of the animals at the times of deprivation and rehabilitation; (c) the nature, severity and the duration of the period of undernutrition; (d) physiological requirements of the various tissue groups when undernutrition and refeeding were imposed; and (e) the breed or sex of animals.

Wapiti have a well-developed capacity for compensatory growth on summer pastures following winter nutritional restrictions (Watkins et al. 1991). Weight gains from spring in April until the rut in September are inversely related to the body weights at the end of winter (Hudson et al. 1985). This characteristic is shared by the wapiti's European counterpart, the red deer (Suttie et al. 1983, 1984; Adam and Moir 1985; Milne et al. 1987). This effect is expected to be most marked in young, growing animals (Blaxter et al. 1974; Mitchell et al. 1976). However, work with red deer suggests that the ability of young animals to recover fully weight by the following rut is incomplete.

Previous work at the Ministik Wildlife Research Station has explored compensatory mechanisms in wapiti (Watkins et al. 1991). In that study, restricted wapiti attained similar weights by late June but weight gain was not explained by any one factor. However, interpretation was complicated by the mix of sexes and ages, pregnancy and small sample sizes. To avoid these complications, I used a group of nonbreeding weaned male wapiti calves born in May-June 1989 at the Ministik Wildlife Research Station. I created differences in body condition by offering medium and high quality diets during winter. I then recorded the performance of these animals on spring/summer pasture.

Objectives

This study attempts to compare the performance and behavior on summer pasture of young wapiti stags maintained on either native range and alfalfa-brome hay, or stags maintained on alfalfa-barley pellets and alfalfa-brome hay.

The objectives were to determine whether:

1) Young wapiti stags have the capacity for compensatory growth on spring pastures and whether this is due to relative changes in frame size, gut fill weight, or body composition (Chapter III),

2) Compensation among nonbreeding wapiti might be due to their propensity to:

   a) improve feed conversion efficiency by changing digestive parameters (Chapter IV and V),

   b) increase nutrient intake by feeding longer, more rapidly and/or more selectively within habitats, or by selecting habitats offering superior foraging opportunities (Chapter V).

Literature cited

Adam, C.L. and Moir, C.E. 1985. Effects of winter nutrition of young farmed red deer on their subsequent growth at pasture. Anim. Prod. 40: 135-142.

Ashworth, A. and Millward, D.J. 1986. Catch-up growth in children. Nutr. Rev. 44: 157-163.

Allden, W.G. 1970. The effects of nutritional deprivation on the subsequent productivity of sheep and cattle. Nutr. Abstr. Rev. 40: 1167-1184.

Baker, R.D., Young, N.E. and Laws, J.A. 1985. Changes in the body composition of cattle exhibiting compensatory growth and the modifying effects of grazing management. Anim. Prod. 41: 309-321.

Bandy, P.J., Cowan, I. McT. and Wood, A.J. 1970. Comparative growth in four races of black-tailed deer *(Odocoileus hemionus)*. Part I. Growth in body weight. Can. J. Zool. 48: 1401-1410.

Blaxter, K.L., Kay, R.N.B., Sharman, G.A.M., Cunningham, J.M.M. and Hamilton, W.J. 1974. *Farming the Red Deer*. Her Majesty's Stationery Office, Edinburgh.

Calvert, C.C., McMurty, J.P., Rosebrough, R.W. and Campbell, R.G. 1987. Effect of energy level on the compensatory growth response of broilers following early feed restriction. Poult. Sci. (suppl.1) 66: 75.

Coleman, S.W. and Evans, B.C. 1986. Effects of nutrition, age and size on compensatory growth in two breeds of steers. J. Anim. Sci. 63: 1968-1982.

Ferrell, C.L., Kong, L.J. and Nienaber, J.A. 1986. Effects of previous nutrition on body composition and maintenance energy costs of growing lambs. Br. J. Nutr. 56: 595-605.

French, C.E., McEwen, L.C., Macgruder, N.D., Ingram, R.H. and Swift, R.W. 1956. Nutrient requirements for the growth and antler development in the white-tailed deer. J. Wildl. Manage. 20: 221-232.

Hudson, R.J. and White, R. G. 1985. Computer simulation of energy budgets. pp 261-290. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, FL.

Hudson, R.J., Watkins, W.G. and Pauls, R.W. 1985. Seasonal bioenergetics of wapiti in western Canada. In: P.F. Fennessy and K.R. Drew, eds. *Biology of Deer Production*. Royal Soc. New Zealand Bull. 22: 447-452.

Lofgreen, C.P. and Kresling, H.E. 1985. Effects of receiving and growing diets on compensatory gains of stressed calves. J. Anim. Sci. 61: 320-328.

Maynard, L.A., Loosli, J.K., Hintz, H.F. and Warner, R.G. 1979. Retardation of growth. pp 422-424. In: *Animal Nutrition* . Tata McGraw-Hill, New Delhi.

Mersman, H.J., MacNeil, M.D., Seideman, S.C. and Pond, W.G. 1987. Compensatory growth in finishing pigs after feed restriction. J. Anim. Sci. 64: 752-764.

Meyer, J.H., Hull, J.L., Weitkamp, W.H. and Bonilla, S. 1965. Compensatory growth responses of fattening steers following various low energy intake regimes on hay or irrigated pasture. J. Anim. Sci. 24: 29-37.

Milne, J.A., Sibbald, A.M., McCormack, H.A. and Loudon, A.S.I. 1987. The influence of nutrition and management on the growth of red deer calves from weaning to 16 months of age. Anim. Prod. 43: 511-522.

Mitchell, B. 1972. Annual cycle of condition and body composition of red deer on the island of Rhum. Deer 2: 904-907.

Mitchell, B., McCowan, D. and Nicholson, I.A. 1976. Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. J. Zool. 180: 107-127.

Moore, G.H. and Brown, C.G. 1977. Growth performance in the red deer. New Zealand J. Agric. Sci. 11: 175.

O'Donovan, P.B. 1984. Compensatory gain in sheep and cattle. Nutr. Abstr. Rev. 54b: 389-410.

Park, C.S., Erickson, G.M., Choi, Y.J. and Marx, C.D. 1987. Effects of compensatory growth on regulation of growth and lactation: Response of dairy heifers to a stair-step growth pattern. J. Anim. Sci. 64: 1751-1758.

Pond, W.G. and Mersman, H.J. 1990. Differential compensatory growth in swine following control of feed intake by a high-alfalfa diet *ad libitum* or by limited feed. J. Anim. Sci. 68: 352-362.

Pokniak, J.A. and Cornejo, S.B. 1982. Effects of energy and protein undernutrition on productive performance and carcass, liver and digestive tract composition of broiler males. Nutr. Rep. Int. 26: 319-327.

Price, M.A. and White, R.G. 1985. Growth and development. pp 183-214. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, FL.

Reid, J.T. and White, O.D. 1977. The phenomenon of compensatory growth. Proc. Cornell Nutr. Conf. Feed Manufactures. Cornell Univ., Ithaca, NY.

Saubidet, C.L and Verde, L.S. 1976. Relationship between live weight, age and dry-matter intake for beef cattle after different levels of food restriction. Anim. Prod. 22: 61-69.

Staun, H. 1972. The nutritional and genetic influence on number and size of muscle fibers and their response to carcass quality in pigs. World Rev. Anim. Prod. 8: 18-26.

Suttie, J.M., Goodall, E.D., Pennie, K. and R.N.B. Kay. 1983. Winter feed restriction and summer compensation in the red deer stags *(Cervus elaphus)*. Br. J. Nutr. 50:737-747.

Suttie, J.M., Wenham, G. and Kay, R.N.B. 1984. Influence of winter feed restriction and summer compensation on skeletal development in the red deer stags *(Cervus elaphus)*. Res. Vet. Sci. 36: 183-186.

Thompson, E.F., Bickel, H. and Schurch, A. 1982. Growth performance and metabolic changes in lambs and steers after mild nutritional restriction. J. Agric. Sci. (Camb.) 98: 183-194.

Watkins, W.G., Hudson, R.J. and Fargey, P. 1991. Compensatory growth of wapiti *(Cervus elaphus)* on spring ranges. Can. J. Zool, in press.

Wilson, P.N. and Osbourn, D.F. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35: 324-363.

II. STUDY AREA AND EXPERIMENTAL DESIGN

Study Area

The study was conducted at the Ministik Wildlife Research Station (Sec 26 TP 50 R 21 W4) located approximately 50 km SE of Edmonton, Alberta in the Cooking Lake Moraine. The station is approximately 265 ha enclosed by a game fence 2 m high.

Ministik is underlain by the Edmonton Formation, an upper Cretaceous bedrock of shale, sandstone, clay and coal interbedding (Bayrock and Hughes 1962). The Cooking Lake Moraine overlies the Edmonton Formation and is composed of glacial debris formed during the retreat of the Wisconsin ice sheet. The area is characterized by gently rolling to rolling hills and shallow depressions, typical of hummocky dead-ice moraine. Numerous seasonal and permanent shallow water bodies are found in the area.

Luvisolic soils, derived from calcareous fine-grained till (Bowser et al. 1962; Crown 1977), predominate in the Ministik area. The forest soils are fairly well-drained orthic grey soils developed on glacial till of the Edmonton formation. Poorly-drained mineral soils, humic luvic gleysols, sandy loams, are present in low proportion.

The area is subject to a cool continental climate with short warm summers and long cold winters (Wonders 1969). Temperature extremes range from -50 to 30 degree Celsius (Olson 1985). The frost-free period averages 100 days, although considerable yearly variations occur. Annual precipitation averages 500 mm with 25% as snowfall (Anonymous 1980). The average wind velocity is less than 26 kph. Generally, snow begins to accumulate in November and persists until April.

Rowe (1972) classified the vegetation as boreal forest, although homesteading in the early 1900's gives the area the general characteristic of aspen parkland. Gates (1980) classified the vegetation cover of the Ministik Research Station into five habitat types; poplar forest, upland and lowland grassland, sedge meadow and willow.

Habitat distributions in the 1.5 ha paddock used for this study were 62% poplar forest, 8% lowland and 30% upland grasslands. Balsam poplar *(Populus balsamifera)* and trembling aspen *(P. tremuloides)* dominated the poplar forest. Bluegrass *(Poa* spp.*)* and brome grass *(Bromus pupellianus)* were dominant species

in the upland grassland whereas, bluegrass, brome, and wheatgrass *(Agropyron spp.)* and reedgrass *(Calamagrostis canadensis)* dominated the lowland grassland.

Spring green-up started in April, with the lowland grassland greening-up first and the upland grassland last. Snow fell soon after the April green-up and the trial pasture remained in ℸ ℸor condition until June. In April and May, the forest floor was covered by volunteer grass but, in June, forbs assumed dominance.

Study animals and experimental design

To create body condition differences, ten weaned male wapiti calves born to resident females at the Ministik Wildlife Research Station in May and June 1989 were assigned to two nutritional treatments (Table II.1). During the winter of 1989-90, five calves (low quality winter diet, LW) were ru ℸon native range but were offered alfalfa-brome hay due to the harsh winter conditions. Five others (high quality winter diet, HW) were offered pelleted alfalfa-barley ration and hay. Both groups received the feeds *ad libitum* (Table. II.2). To facilitate close observation, I spent several days each week habituating the calves.

Winter-feeding treatments were started on Dec 7 1989, when significant amounts of snow had fallen, and terminated on April 4 1990, at the beginning of the spring green-up period. However, significant amounts of snow fell after the termination of the treatments and animals were returned to holding pens for two weeks and given hay *ad libitum*.

The animals were placed on the same pasture one week before data collection to accommodate to their new environment. Blood samples and linear measurements were taken at the beginning and end of the experiment. Parameters used to monitor performance and behavior of wapiti are described in Chapters III, IV and V. Throughout the study, the calves were free to forage and were only supplemented with alfalfa-barley pellets in July when the pastures greatly deteriorated. Animal #8923 escaped from the trial paddock and was substituted with #8901 after the first trial period in April.

Statistical design

Data on weight gains, linear measurements, percent urea space, blood urea nitrogen, digestive parameters, forage intake, feeding rates, and habitat selection were subjected to analysis of variance and (in several analyses) linear regression. Due to missing observations and substitution of animals, repeated measure design was used only to compare monthly effects and not treatment effects. Main effects were winter feeding, trial dates and (in several comparisons) habitat type. Student's t-test was used to compare the nutrition treatments on specific trial dates.

Table II.1 Allocation of wapiti calves to winter feeding groups at the Ministik Wildlife Research Station, 7 Dec 1989- 4 April 1990.

Name	Tag#	Initial wt(kg)	Name	Tag#	Initial wt(kg)
Edwin	8901a	174	Elliot	8905	137
Edgar	8903	168	Elvis	8907	142
Eldorado	8911	157	Eric	8909	149
Echo	8913	135	Elmo	8915	140
Emie	8919	143	Euclid	8917	123
Egbert	8923b	129			

a Replaced 8923 in 2rd, 3rd and 4th trials

b Used for April 26-28 trial only

Table II.2. Chemical composition (%) and gross energy of winter feeds. (100% dry-matter basis).

	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)	18.8	18.5

Literature cited

Anonymous. 1980. *Canadian Climate normals. 1951-1980. Temperature and precipitation.* Publ. Can. Climate Program. Environ. Canada. 429 pp.

Bayrock, L.A. and Hughes, G.M. 1962. *Surficial geology of the Edmonton district, Alberta.* Res. Counc. Alta. Prelim. Rep. 62-6, Edmonton. 40 pp.

Bowser, W.E., Kjearscaard, A.A., Peters, T.W. and Wells, R.F. 1962. *Soil survey of Edmonton.* Sheet (83-4). Univ. Alberta. Bull. 55-4. Edmonton. 66 pp.

Crown, P.H. 1977. *Soil survey of Elk Island National Park, Alberta.* Alberta Inst. Pedology S-77-38, Edmonton. 128 pp.

Gates, C.C. 1980. Patterns of behavior and performance of wapiti *(Cervus elaphus nelsoni)* in the boreal mixed-wood forest. Ph.D. Thesis, Univ. Alberta, Edmonton. 240 pp.

Olson, R. 1985. *The climate of Edmonton.* Climatology studies No. 37. The climate of Canadian Cities. No.2, Environ. Canada, Ottawa, 54 pp.

Rowe, J. 1972. *Forest regions of Canada.* Dept. Envir. Can. For. Serv. Publ. No. 1300. 172 pp.

Wonders, W.C. 1969. *Atlas of Alberta.* Govt. Alberta and Univ. Alberta, Edmonton. 158 pp.

III. NATURE OF COMPENSATORY GROWTH

Introduction

Little is known about the nature of the compensatory weight gain of weaned red deer on summer pasture. Factors involved are not well known but appear to involve the skeleton as well as soft tissues (Suttie et al. 1984). The capacity for compensatory gain in red deer stags is remarkable but not unlimited (Suttie et al. 1983, 1984; Suttie and Kay 1985; Adam and Moir 1985; Milne et al. 1987). Twelve months old red deer stags on low quality winter diets grow faster on good summer pasture than better-fed controls, but they do not fully compensate by their first rut at 15 months of age (Suttie et al. 1983). Consequently, they may not reach pubertal weights and there is a suggestion that pre-rut weight and frame size have an important bearing on their ultimate mature size (Suttie et al. 1984).

One result of compensatory gain in red deer is clear: body composition after compensation is similar to that of continuously growing animals (Suttie et al. 1984; Milne et al. 1987). In studies on other livestock, animals on restricted feed are leaner after compensation than those which received adequate feed supplies (McManus et al. 1972; Drew and Reid 1975).

Although wapiti seem to express well-developed compensatory gain (Hudson et al. 1985; Watkins et al. 1991), neither the magnitude nor the nature of compensatory gain has been fully explored. Previous studies have been based on mixed sex/age groups, so comparisons of wapiti with the red deer literature was not possible. The objective of this study was to assess compensatory growth in young wapiti stags.

Live weight gain has been used as a measure of compensatory growth. This has serious limitations because of the varying weights of gastrointestinal contents (gut fill). Live weights do not necessarily reflect body composition and variable energy content. Therefore, an attempt was made to distinguish whether compensation in live weight is partly due to an increase in frame size, body water, or gut fill.

Materials and methods

Nutritional treatments

Ten wapiti stags, born in May and June 1989 at the Ministik Wildlife Research Station, were assigned to two winter feeding groups. Five wapiti calves (LW, low quality winter diet) were wintered on native range and also received alfalfa-brome hay. The other five (HW, high quality winter diet) received both alfalfa-brome hay and alfalfa-barley pellets as described in Chapter II. Winter feeding programs were terminated and groups merged on April 4 1990, when stags were released together on to pasture for comparisons of changes in live weight, frame size and body composition. Throughout the study, the stags were free to forage in a 1.5 ha paddock and were only supplemented with alfalfa-barley pellets in July when pastures greatly deteriorated. One animal in the LW group escaped to an adjacent paddock and was substituted by another with the same nutritional history after the first trial at the end of April.

Body weights

Wapiti were weighed weekly, to the nearest kg with an electronic platform scale (Western model no. DF-1000 Accurate Scale Industries, Edmonton, Alberta). Feed and water were not withheld prior to weighing so weights included differences in rumen fill.

Gut fill

Dry matter gastrointestinal fill (GIT) was estimated by administering a single oral dose of chromic oxide (Cr_2O_3) on April 24, May 13, June 26 and July 22. Wapiti were placed in individual stalls and offered 200 g of chromic oxide labelled alfalfa-barley pellets (containing 4.04 mg/g chromic oxide) during the first trial and 250 g in subsequent trials. Freshly voided fecal samples from each individual were collected before dosing and at 3-4 h intervals post-dosing for 48 hours and 6-12 h intervals for an additional 3-4 days. The samples were ovendried at 110°C for 24 hours and ground in a Wiley mill using a 30-mesh screen (1 mm). Analysis of chromic oxide was made using an atomic absorption spectrophotometer (Model 4000, Perkin-Elmer) with an air- acetylene flame as described by Fenton and Fenton (1979).

Concentration of chromium in feces with time (Ct) was determined by application of Stewart-Hamilton or Occupancy Principle (Steele 1971; Shipley and Clarke 1972). Total mean retention time (MRT), fecal output (F), indigestible dry matter fill (VN) and GIT were estimated as outlined by Holleman and White (1987). Parameters and calculations were as follows:

$$F = D / {_0}\!\int^{\infty} Ct.dt$$

$$MRT = {_0}\!\int^{\infty} t.\, Ct.dt / {_0}\!\int^{\infty} Ct.dt$$

$$VN = F.MRT$$

$$GIT = VN + VN.A/2(1-A)$$

where,

D is the marker dose,

${_0}\!\int^{\infty} Ct.dt$ is amount of marker excreted in time interval (dt) and estimated by the area under the marker concentration versus time curve for the feces,

${_0}\!\int^{\infty} t.Ct.dt$ is area under a 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.

Gut fill (g DM) was converted to approximate wet fills, assuming that gut contents of wapiti are approximately 17 % dry matter, irrespective of season and diet (Renecker and Hudson 1990).

Frame size

Measurements of frame size were taken to the nearest centimeter using a steel tape on May 1 and August 2, 1990. Animals were measured while standing in a squeeze. Total body length was measured from tip of nose to last sacral vertebra. Chest girth was measured immediately posterior to the axilla. Hip width was measured between the ischial processes on the right hind leg.

Body composition

Body composition was estimated by urea dilution on May 1 and August 2, 1990. Approximately 132 mg of urea-N/kg live weight was infused as 50% urea (Jones et al. 1982) dissolved in 0.9% saline solution in the jugular vein over a period of 2 minutes. Samples of blood were drawn before and 12 minutes after infusion with vacuum containers (SST Gel and clot activator Becton Dickinson Vacutainer systems L42401). Post-infusion blood samples were taken from the contralateral jugular vein, or in several cases, from the saphenous or recurrent tarsal veins. Animals were immobilized using xylazine hydrochloride (Rompun) at approximately 1 mg/kg. Immobilization was reversed with yohimbine hydrochloride (Antagonil).

Urea space (ul /kg) as a percentage of live weight was calculated from the following formula:

$$\text{Urea space} = (\text{vol} \times \text{conc} / \text{diff})/\text{wt.}$$

where,

vol is volume of urea infused (ml),

conc is concentration of urea solution infused (mg urea-N/100 ml),

diff is difference in blood urea nitrogen taken from the blood before and after urea infusion (mg urea-N/100 ml), and

wt is live weight (kg).

Due to hemolysis (3 samples) and substitution of an animal, only 2 observations were available for LW group and 4 for the HW group.

Statistical analysis

Weight gains, frame measurements, blood urea nitrogen and percent urea space (as % live weight) were subjected to analysis of variance and contrasted over time by repeated measures design. The main effect was winter feeding and the "within effect" was trial date. Comparison between nutritional treatments on specific trial dates was made using Student's t-test. Changes in measurements between the beginning and end of the summer grazing trial were related to beginning measurements by

regression analysis. All relationships were computed and evaluated using General Linear Model procedures (SAS 1989).

Results

Body weights

The monthly patterns of live weight of young wapiti stags on LW and HW diets are shown in Fig. III.1. At the start of the experiment in December, live weights did not differ significantly between nutritional groups (P> 0.1). From December to April, LW wapiti lost 13 kg (8.9% of their December weight) while HW group gained 18 kg (13% of December weight). Despite their lower initial weights, HW wapiti entered spring weighing 20 kg more than the LW counterparts (t=6.4, P= 0.05). Both groups subsequently lost weight two weeks following release on to pasture as they adapted to their new environment. During spring/summer, LW wapiti (then yearlings) gained weight rapidly completely closing differences by July (t = 6.4, P= 0.003). Between April 4 and July 28, the LW wapiti gained 34.6 kg (0.30 kg/d) whereas the HW wapiti gained only 15.4 kg (0.15 kg/d).

Gut fill

Overall, LW wapiti tended to have greater gut fill averaging 3.0 kg dry matter, but the treatment by trial date interaction was not significant (P>0.1) (Fig. III.2). Greatest gut fills were recorded on June 26 and least on July 22. LW wapiti showed greatest variation throughout the spring/summer trial.

Frame size

Measurements of frame size were limited to the beginning and end of spring/summer grazing trials. By May 1, HW wapiti were larger framed (P=0.004) than LW wapiti (Fig. III.3). Both groups increased in frame size during the study period but differences disappeared by August (P> 0.1). Regressions of growth increments between May and August on absolute measurements in May showed strong correlation with hip width (r^2 = 0.81) but other regressions were not very strong, although significant (Fig. III.4).

Body composition

Urea space (an estimate of body water) decreased from May (70.8 ± 8.07 %) to August (46.7± 1.61 %) for both groups (Fig. III.V). Neither May nor August values differed significantly between nutritional treatments (P> 0.1). Blood urea nitrogen was significantly higher in LW wapiti in May (P< 0.001) but not in August.

Discussion

Weight dynamics

During winter, free-ranging wild ruminants 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. Spring forage growth comes abruptly and body weights, particularly for the lighter animals, increase rapidly. Over the summer, light animals are able to narrow the contrast in weight with heavier animals.

My study and that of Dean et al. (1976) indicate that wapiti can either maintain or gain weight in winter, given the nutritional opportunity. This may seem obvious but other members of the cervidae such as white-tailed deer (Odocoileus virginianus) (French et al. 1956), black-tailed deer (O. hemionus columbianus) (Bandy et al. 1970) and captive mule deer (O.h. hemionus)(Renecker and Samuel 1991) lose weight during winter months regardless of the amount or quality of feed offered.

Cervidae in temperate climates show cyclic patterns of growth with large investment in body weight during summer and slow growth or weight loss during winter. One possible explanation for winter weight loss in LW wapiti is reduced feed intake. Although, feed intake was not measured in my experiment over winter, results from other studies show that wapiti reduce feed intake to conserve energy (Kozak 1988). In my study, winter weight loss in LW wapiti began in January. This weight loss has been attributed to seasonal inappetance rather than higher winter maintenance requirements. Seasonal declines in feed intake and growth rate are associated with lower metabolic rates in white-tailed deer (Silver et al. 1969) and moose (Schwartz et al. 1988; Renecker and Hudson 1989). Such rhythms may be entrained by photoperiod as a preparatory measure for seasonal change in forage quality and availability. In winter, as the daylength shortens, animals lose weight and feeding times are concentrated in the warmest part of the day.

In my study, lighter animals (LW wapiti) manifested greater weight gains than their heavier counterparts (HW wapiti) during the short growing period. However, both groups of wapiti lost weight in the 2 weeks following turn out. This rapid temporary loss probably was due to changes in gut fill and did not involve any real changes in empty body weight (Taylor et al. 1957; Wright and Russel 1986). HW wapiti may have lost more weight because they still anticipated supplemental feeding to resume. Wapiti took 46 days to attain their pre-turn out live weight. Cattle take between 15 and 50 days to attain their pre-turn out live weight (Wright 1985).

Wapiti stags appear to grow in relation to autumn target weights or set points (Hudson et al. 1985). Price and White (1985) suggested that because northern wild ungulates are seasonal breeders and display annual patterns of weight change, evolutionary pressure must favor a particular target condition or set-point. In my study, the inverse relationship between level of winter feeding and weight gain at pasture reveals the capacity of wapiti for compensatory growth. Probably, they were growing towards their target weight for their chronological age. Verme and Ozaga (1980) concluded that weight gains during late spring and summer in white-tailed deer represent changes in tissue weight and that lipogenesis occurs in autumn in response to photoperiod.

This work supports the theory that lighter animals, as a result of restricted intake, have greater weight gains during recovery than heavier animals (Suttie et al. 1983; Adam and Moir 1985; Milne et al. 1987; Thompson et al. 1987). Compensatory weight gain during a short growth period ensures early maturity and reproductive success (Renecker and Samuel 1991). O'Donovan (1984) suggests that compensatory weight change represents a natural survival mechanism. This adaptation permits wapiti to exploit seasonally harsh environments and to capitalize on grazing opportunities during short summers.

Gut fill

Interpretation of live weight is complicated by differential weights of gastrointestinal contents (gut fill). In this study, the contribution of gut fill was estimated by a digestive marker (Cr_2O_3) rather than holding animals overnight before weighing. In the April trial, higher estimated gut fill in LW wapiti that received a winter diet high in fiber could be attributed to an enlarged rumen. The high rumen fill at the start of the grazing period suggests that absolute quantity of feed was not limiting in winter.

Gut fill has been shown to vary in response to changes in diet composition and energy demands in ruminants (Milne et al. 1978; Staaland et al. 1979). Large rumen fill has been found in red deer (Milne 1980) and cattle (*Bos indicus*) (Mould et al. 1982) receiving fibrous diets in an attempt to eat more to meet their energy requirements.

The highest gut fill in June for both groups was associated with increased intakes (Chapter V), particularly among LW wapiti. Low gut fill in April and July were partly due to poor pasture conditions as plant biomass was low (Chapter V). Overall, there was no significant treatment effect on gut fill suggesting that live weight gain may have been due to lean muscle deposition. Wilson and Osbourn (1960) concluded that increase in weight in animals recovering from weight loss is partly due to increased gut contents, however, in this study, weight changes in wapiti stags did not involve increases in gut fill.

Frame size

In many studies, skeletal dimensions show better ability to recover after undernutrition than body weight. In this study, body weight and the skeleton recovered fully from winter undernutrition. Differences that existed at the beginning of spring disappeared suggesting that compensatory growth included skeletal growth. In similar-aged red deer stags, Suttie et al. (1984) observed that compensation was not complete and winter nutrition had an important early effect on skeletal growth of red deer. This lack of compensation in skeletal growth limits the amount of catch up gain possible in red deer (Suttie et al. 1984).

Low quality feed offered during winter did not distort the animal's form. Undernutrition caused a more or less uniform retardation (the restricted animals conformed in size to their 'normal' counterpart of similar weight at end of compensation period). These results agree with the theory of allometric growth proposed by Huxley (1932). Skogland (1983) and Clutton-Brock et al. (1982) have shown that mature size of reindeer and red deer, respectively, is most vulnerable to stunting during the late fetal-neonatal stage. Retardation of growth has the greatest effect upon late maturing tissues and regions of the body, and may alter the proportions of the body permanently (Wilson and Osbourn 1960).

The theory of compensatory growth predicts that temporary underfeeding will not necessarily result in stunting. However, the risk of permanent stunting is real if feed restriction interferes with cell division. Severe and prolonged undernutrition at an early age may cause permanent stunting (Maynard et al. 1979). The reason for this is that at this pre-natal age, hyperplasia is still in progress in the muscle and bone and any interference with it can result in reduced total number of cells. This would certainly lead to stuntedness because cells have limited capacity to hypertrophy (Staun 1972).

Chronologically, the various tissues achieve their maximum growth and mature in the following order: nervous tissue, skeletal tissue, muscular tissue and adipose tissue (Huxley 1932). Consequently, skeletal measurements should be unaffected by all but extreme nutrition restriction (Price 1976, 1977). However, in my experiment, significant skeletal differences occured and Price's suggestion may hold only in older animals. McCay et al. (1939) showed that body length of undernourished rats, recovered better than body weight. This suggests that skeletal dimensions have higher growth impetus than other parameters of body size and mass.

Skeletal hip width recovered better than both girth and body length. This may be explained in terms of the waves of high growth intensity commencing in the body extremities and converging along the back line as described by Huxley (1932) and Palsson (1955). Since one of the growth waves starts from the metatarsal and metacarpal regions (Palsson 1955) and upwards along the limbs and trunk to the lumbar region, it may be speculated that such a wave takes priority. Unfortunately, no comparative literature is available for hip width measurements.

Girth provides an indication of the bulk of an animal and relates closely to body weight, although, in this experiment it included both fat as well as rib cage. Chest girth measurements are close 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 does not have deleterious effects on final size.

Body composition

Urea dilution has been used to estimate body composition in cattle (Kock and Preston 1979; Bartle et al. 1983), lambs (Bartle et al. 1985), water buffalo (*Bubalus bubalis*) (Johri and Ranjhan 1983), Norwegian reindeer (*Rangifer tarandus tarandus*) (Larsen and Arnoldus 1985) and mule deer (Torbit et al. 1985). Urea meets the requirements of a satisfactory marker, such as even and rapid distribution, non toxic, not foreign to the body, causes no physiological disturbances and is easily measured (Kock and Preston 1979). Urea space is defined as the volume of water with which urea equilibrates and it is assumed that urea space is related to empty body water (Kock and Preston 1979), and inversely, body fatness.

Urea space values (as a % of body weight) were high in May, reflecting lower fat levels assuming that the inverse relationship between empty body fat (%) and urea space (live weight) in domestic ruminants (Reid et al. 1968) holds for wapiti. However, HW wapiti had higher values than LW wapiti at the start of spring grazing trial. This is contrary to my expectations as the HW wapiti receiving high quality diet above maintenance were expected to deposit fat. Although, this differences could be attributed to the small number of samples for the LW group (2). Energy retained in pellet-fed animals may have been directed to lean tissue growth thus minimizing differences in fat content. Evidence comes from measured differences in frame size.

Urea space (as a percentage of body weight) decreased in late summer and was accompanied by an increase in body weight. The higher percent urea space in August in LW wapiti is likely the result of increased energy demands due to growth and deposition of more muscle and less fat. In sheep, restricted and control animals had similar amounts of body fat during restriction. But during weight gain, the former had less fat and more protein and water (O'Donovan 1984). McManus et al. (1972) and Drew and Reid (1975) reported that animals were leaner than those continually grown. Adam and Moir's (1985) study on young red deer stags indicated that periods of restriction followed by realimentation had no significant effect on body composition. My study suggests the same for wapiti stags. However, body composition depends on how different the animals are at the start, and how long they compensate.

In white-tailed deer, compensatory gain in spring resulted in a greater propensity to deposit protein (Verme and Ozaga 1980). Under a prolonged period of negative

energy balance, fat is lost much faster than it is gained after refeeding (Tulloh 1963).
More water is associated with protein than fat (Agricultural Research Council 1980)
and therefore rapid spring weight change may reflect more protein deposition and
hydration of muscle tissue than fat synthesis.

Blood urea nitrogen decreased over spring and summer. High BUN values in May
were interpreted as an adaptation in protein and urea metabolism which compensated
for the low and high protein intakes for the LW and HW wapiti respectively. In
August, considerably higher BUN in the LW wapiti suggested they either were
mobilizing more body tissue or were grazing more so had higher protein intakes
(Chapter V). The two groups may have adapted differently by either reducing (LW)
or increasing (HW) renal clearance of urea to maintain a more nearly 'optimal' or
'normal' blood level. Lower levels of BUN for steers on high energy diets were
attributed to a more efficient utilization of protein by rumen microbes when digestible
energy intake is high, resulting in reduction in ammonia production and subsequent
urea formation (Preston et al. 1961).

Low BUN values in July reflect a decline in nutritional quality of the pasture. BUN
has been used as a realistic predictor of nitrogen utilization and nitrogen intake.
Preston et al. (1961) found a close relationship between protein intake and BUN
levels but indicated that this relationship can be modified by several other factors.
Certainly, starvation or low nitrogen diets can increase BUN levels as body protein is
catabolized (Leibholz 1970).

Conclusion

Young wapiti stags have a capacity for compensatory growth on summer pasture.
Supplementation with alfalfa-barley pellets during winter improved the growth of
calves and created significant differences in spring weights. Compensatory growth
expressed itself as an enhanced rate of gain in LW wapiti compared to that of HW
wapiti and was complete by July.

Skeletal measurements showed a considerable capacity to compensate. There was
complete recovery in both body weight and frame size unlike in red deer, and this
suggests that the winter feeding regimes did not lead to permanent stunting. Weight
gain did not involve increases in gut fill nor changes in body composition.

Wapiti exhibited compensatory growth at pasture in spring/summer after a winter period of restriction. Therefore, lack of winter feed or even a severe drought can impose a period of little or no growth. A plentiful supply of feed following this deprivation gives rapid growth. Since the nutritional deprivation, did not adversely affect the quality of the final product (body composition) after realimentation, it therefore, might be feasible to exploit and extend this natural pattern by maintaining low planes of nutrition until the start of the grazing period. This will lower feeding costs in winter and animals are able to exploit the compensatory growth phenomenon fully.
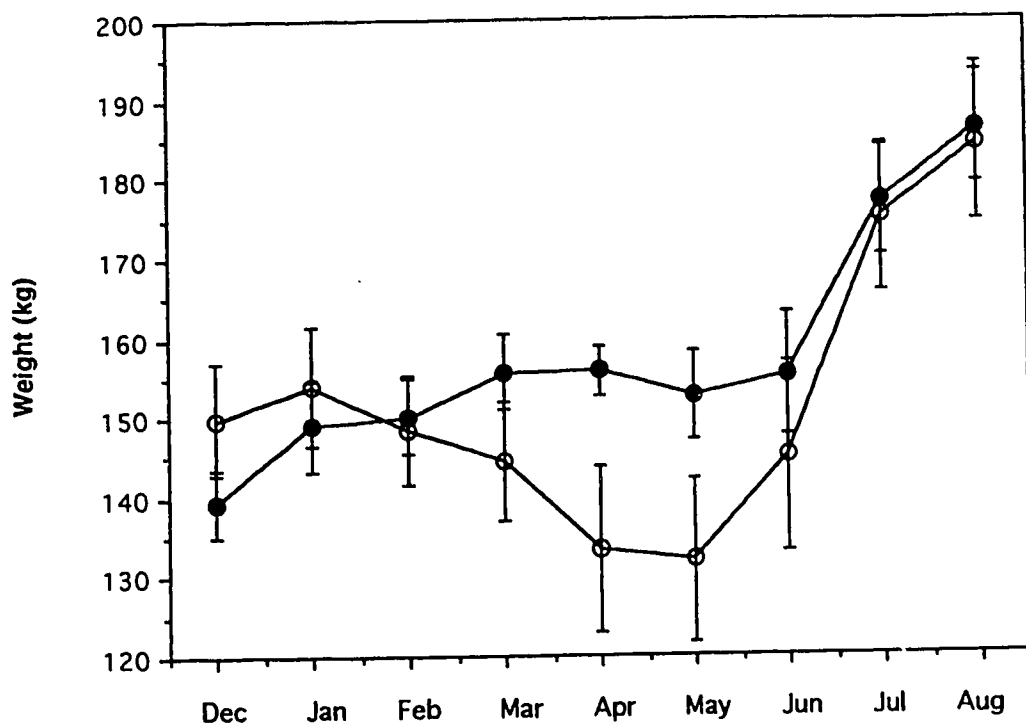
Fig. III.1. Seasonal weight dynamics of young wapiti stags that were hay-fed (LW, open symbols) or pellet-fed (HW, closed symbols). Each observation is the monthly mean of weights collected weekly.
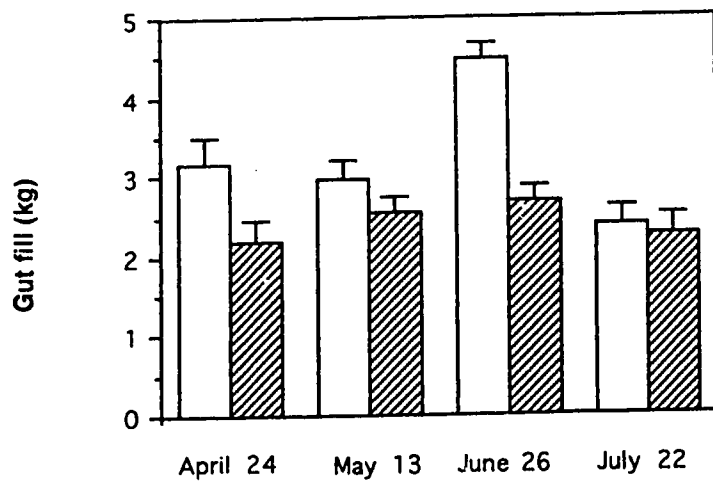
Fig. III.2. Dry matter gut fill (kg) estimate of LW (open bars) and HW (hatched bars) wapiti. Treatment by trial date interaction not significant between the groups (P>0.1).
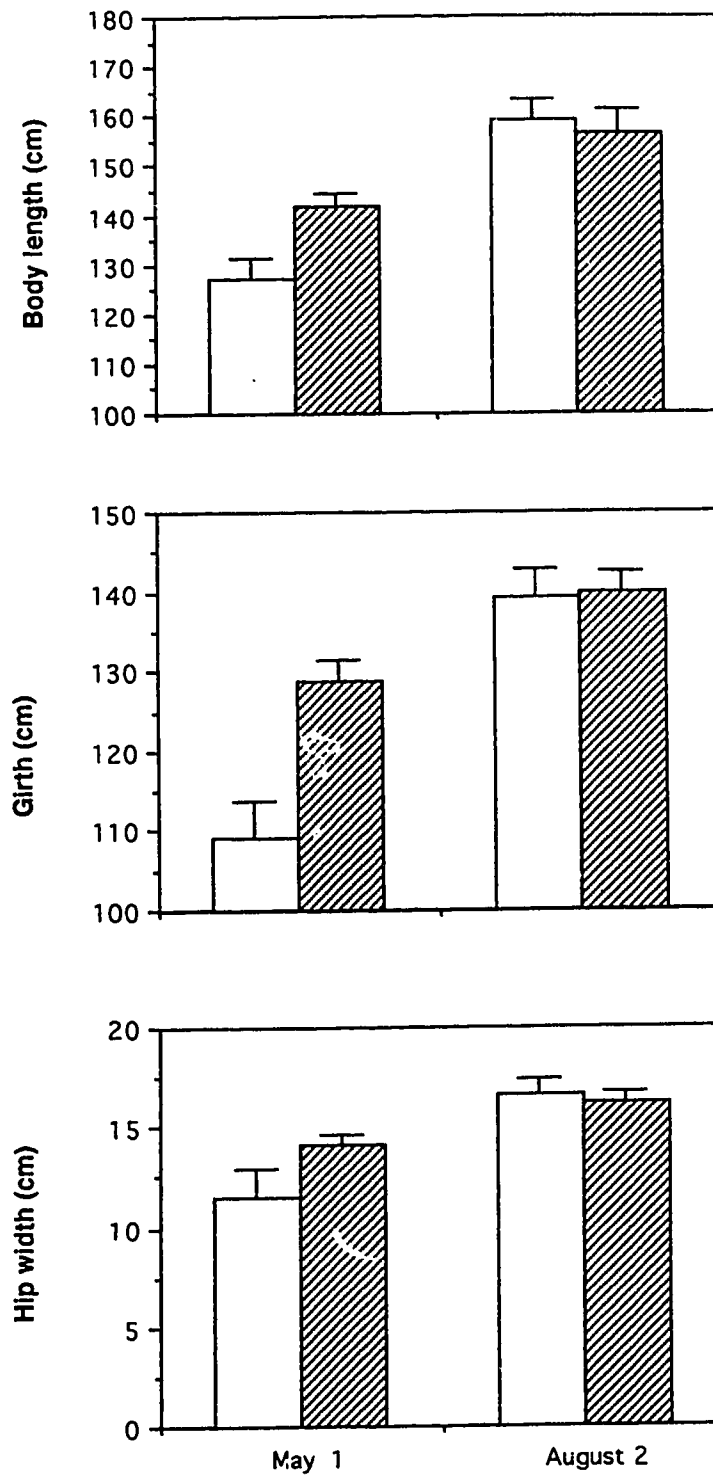
Fig. III.3. Linear measurements (body length, girth and hip width) of LW (open bars) and HW (hatched bars) wapiti. Significant in May (length P=0.03, girth P< 0.001) and not in August (length P=0.89, girth P=0.584. hip P=0.785).

$y = 104.31 - 0.60x \quad R^2 = 0.37$

Change in body length (cm)

May body length (cm)

$y = 73.34 - 0.39x \quad R^2 = 0.03$

Change in girth (cm)

May girth (cm)

$y = 17.25 - 1.06x \quad R^2 = 0.81$

Change in hip width (cm)

May Hip width (cm)
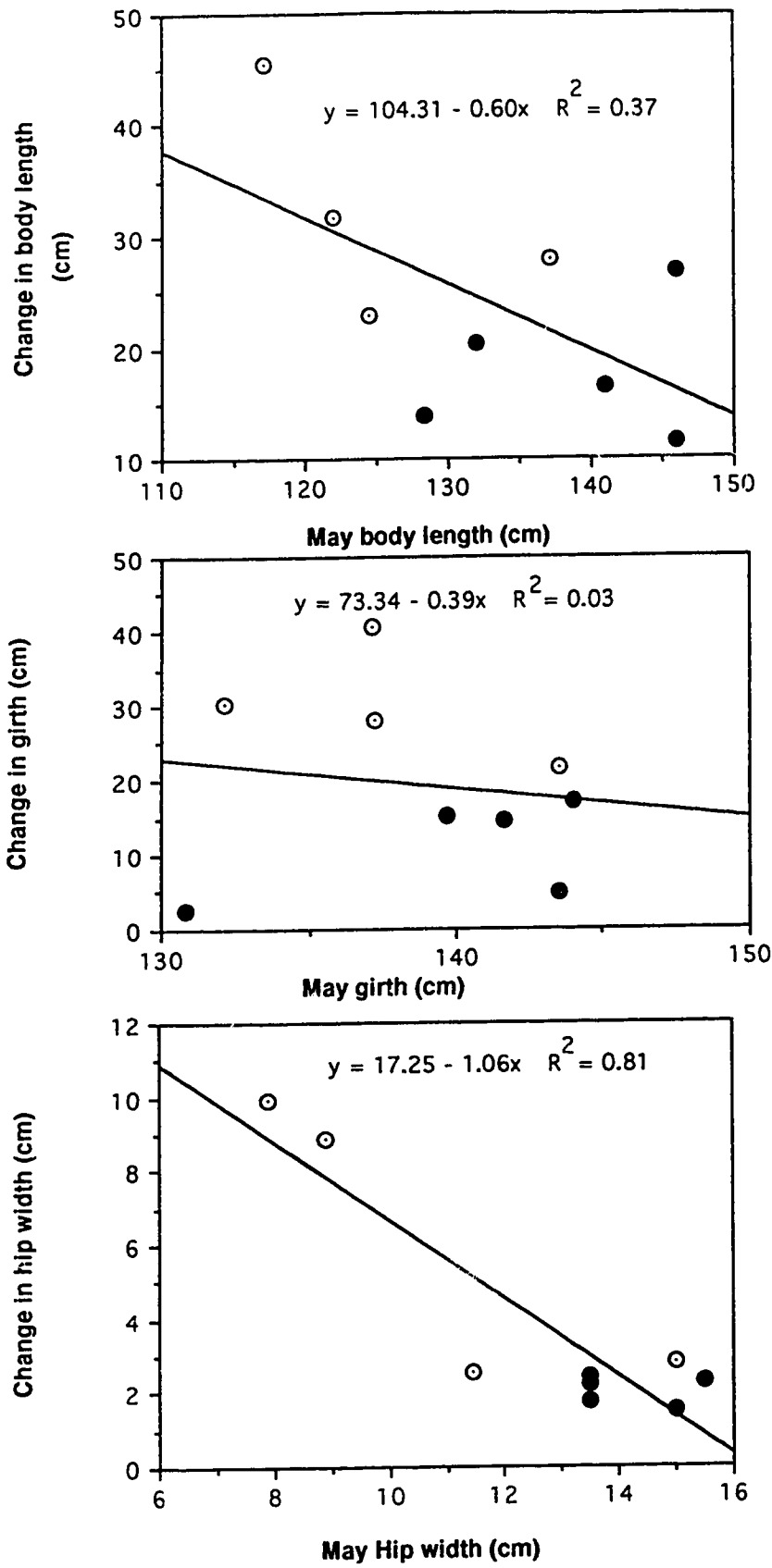
Fig. III.4. Linear growth (body length, girth and hip width) in relation to May 1 measurements of LW (open symbols) and HW (closed symbols) wapiti.
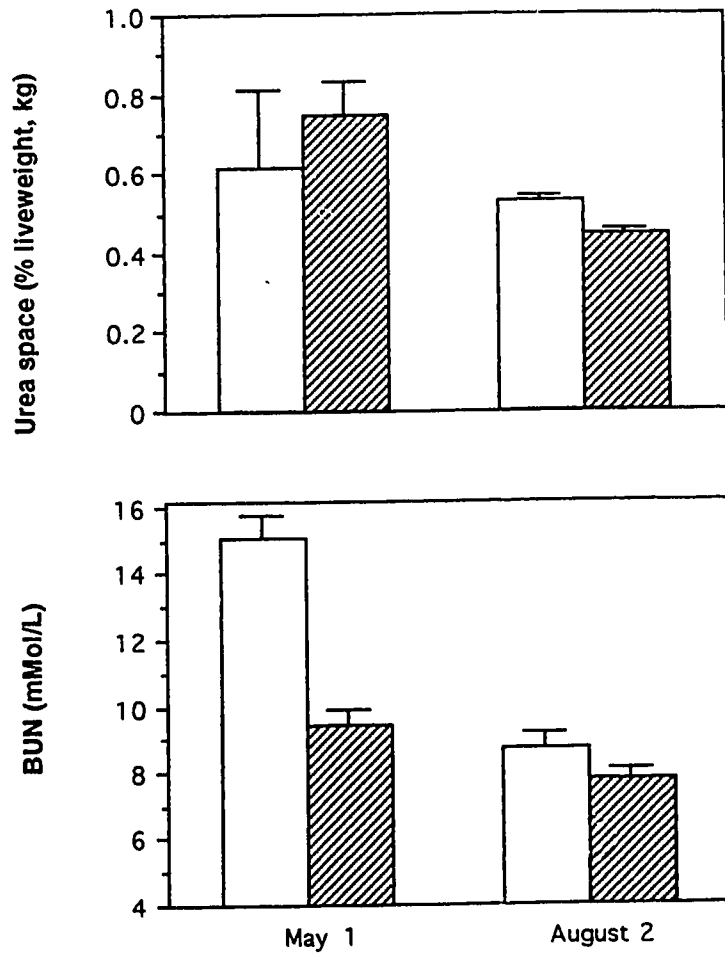
Fig. III.5. Urea space and blood urea nitrogen for LW (open bars) and HW (hatched bars) wapiti. BUN values were significant different between treatments in May (P<0.001).

Literature cited

Adam, C.L. and Moir, C.E. 1985. Effects of winter nutrition of young farmed red deer on their subsequent growth at pasture. Anim. Prod. 40: 135-142.

Agricultural Research Council. 1980. *The Nutrient Requirements of Ruminants Livestock.* Agricultural Research Council, London.

Bandy, P.J., Cowan, I. McT. and Wood, J.A. 1970. Comparative growth in four races of black-tailed deer *(Odocoileus hemionus)*. Part I. Growth in body weight. Can. J. Zool. 48: 1401-1410.

Baker, R.D., Young, N.E. and Laws, J.A. 1985. Changes in the body composition of cattle exhibiting compensatory growth and the modifying effects of grazing managements. Anim. Prod. 41: 309-321.

Bartle, S.J., Males, J.R. and Preston, R.L. 1983. Evaluation of urea dilution as an estimator of body composition in mature cows. J. Anim. Sci. 56: 410.

Bartle, S.J., Preston R.L., McCann, M.A. and Craddock, F.B. 1985. Evaluation of urea dilution as an estimator of body composition in finishing lambs. J. Anim. Sci. 61 (Suppl.1): 265.

Clutton-Brock, T.H., Guiness, F.E. and Albon, S.D. 1982. *Red deer: Behavior and Ecology of Two Sexes.* University of Chicago Press, Chicago.

Dean, R.E., Thorne, E.T. and Yorgason, I.J. 1976. Weights of Rocky Mountain elk. J. Mammal. 57: 186-189.

Drew, K.R. and Reid, J.T. 1975. Compensatory growth in immature sheep. I. The effects of weight loss and realimentation on the whole body composition. J. Agric. Sci. (Camb.) 85: 193-204.

Fenton, T.W. and Fenton, M. 1979. An improved procedure for the determination of chromic oxide in feed and feces. Can. J. Anim. Sci. 59: 631-634.

Flook, D.R. 1970. *A Study of Sex Differential in Survival of Wapiti.* Canadian Wildlife Service Report Series 11, Indian Affairs and Northern development, Ottawa, Ont.

French, C.E., McEwen, L.C., Macgruder, N.D., Ingram, R.H. and Swift, R.W. 1956. Nutrient requirements for growth and antler development in the white-tailed deer J. Wildl. Manage. 20: 221-232.

Hudson, R.J. and White, R.J. 1985. Computer simulation of energy budgets. pp 261-290. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, FL.

Hudson, R.J., Watkins, W.G. and Pauls, R.W. 1985. Seasonal bioenergetics of wapiti in western Canada. In: P.F. Fennessy and K.R. Drew, eds. *Biology of Deer Production*. Royal Soc. New Zealand Bull. 22: 447-452.

Holleman, D.F. and White, R.G. 1987. Determination of digesta fill and passage from nonabsorbed particulate phase markers using the singe dosing method. Can. J. Zool. 67: 488-494.

Huxley, J.S. 1932. *Problems of Relative Growth*. Methuen. London.

Johri, C.B. and S.K. Ranjhan. 1983. Use of C^{14}-urea for body water determination in young buffalo calves *(Bubalus bubalis)*. Indian J. Nutr. 113: 2280.

Jones, S.D.M., Walton, J.S., Wilton, W.J. and Szkotnicki, J.E. 1982. The use of urea dilution and ultrasonic thickness to predict the carcass composition of live lambs and cattle. Can. J. Anim. Sci. 62: 371-379.

Kock, S.W. and Preston, R.L. 1979. Estimation of bovine carcass composition by urea dilution technique. J. Anim. Sci. 48: 319-329.

Kozak, H.M. 1988. Effects of winter feeding programs on weight changes, calving and lactation of wapiti (*Cervus elaphus nelsoni*) on farms. Msc. Thesis, Univ. of Alberta, Edmonton, Alta.

Larsen, T.S. and Arnoldus, S.B. 1985. Seasonal changes in total body water: Body composition and water turnover in Reindeer. Rangifer 5: 2-9.

Leibholz, J. 1970. The effects of starvation and low nitrogen intakes on the concentration of free amino acids in the blood plasma and on the nitrogen metabolism in sheep. Aust. J. Agric. 21: 723-734.

Maynard, L.A., Loosli, J.K., Hintz, H.F. and Warner, R.G. 1979. Retardation of growth. pp 422-424. In: *Animal Nutrition.*. Tata McGraw-Hill, New Delhi.

McCay, C.M., Maynard, G.A., Sperling, G. and Barnes, L.L. 1939. Retarded growth, life span, ultimate body size and age changes in the albino rat after feeding diets restricted in calories. J. Nutr. 18: 1-15

McManus, W.R., Reid, J.T. and Donaldson, L.E. 1972. Studies of compensatory growth in sheep. J. Agric. Sci. (Camb.). 79: 1-12.

Milne, J.A, MacRae, J.C., Spence, A.M. and Wilson, S. 1978. A comparison of the voluntarily intake and digestion of a range of forages at different times of the year by the sheep and red deer *(Cervus elaphus)*. Br. J. Nutr. 40: 347-357.

Milne, J.A. 1980. Comparative digestive physiology and metabolism of the red deer and the sheep. Proc. N. Z. Soc. Anim. Prod. 40: 151-157.

Milne, J.A., Sibbald, A.M., McCormack, H.A. and Loudon, A.S.I. 1987. The influence of nutrition and management on the growth of red deer calves from weaning to 16 months of age. Anim. Prod. 43: 511-522.

Mould, F.L., Saadullah, M., Haque, M., Davies, D., Dolberg, F. and Ørskov, E.R. 1982. Investigation of some of the physiological factors influencing intake and digestion of rice by native cattle in Bangladesh. Trop. Anim. Prod. 7: 174-181.

O'Donovan, P.B. 1984. Compensatory gain in cattle and sheep. Nutr. Abstr. Rev. Series B. 54: 389-410.

Palsson, H. 1955. Conformation and body composition. pp 430-542. In: J. Hammond, eds. *Progress in the Physiology of the Farm Animals*. Vol.2. Butterworths, London.

Preston., R.L. Bresser; L.H. and Thompson, G.B. 1961. Blood urea in cattle as affected by energy, protein and stilbestrol. J. Anim. Sci. 20: 977. (Abstr).

Price, M.A. 1976. Changes in body composition associated with weight loss in early- and later-maturing types of steers. Aust. J. Agric. Res. 27: 729-738.

Price, M.A. 1977. The effects of severe feed restriction on bulls and steers. II. Carcass composition. Aust. J. Agric. Res. 28: 529-541.

Price, M.A. and White, R.G. 1985. Growth and development. pp 183-214. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores.* CRC Press, Boca Raton, FL.

Renecker, L.A. and Hudson, R.J. 1989. Ecological metabolism of moose in aspen-dominated boreal forests, Central Alberta. Can. J. Zool. 67: 1923-1928.

Renecker, L.A. and Hudson, R.J. 1990. Digestive kinetics of moose *(Alces alces),* wapiti *(Cervus elaphus)* and cattle. Anim. Prod. 50: 51-61.

Renecker, L.A. and Samuel, W.M. 1991. Growth and seasonal weight changes as they relate to spring and autumn set points in mule deer. Can. J. Zool. 69: 744-747.

Reid, J.T., Wellington, G.H. and Dunn, H.O 1968. Some peculiarities in the body composition of animals. Body composition in animals and man. Natl. Acad. Sci. Publ. 1598: 19-44.

SAS. 1989. *SAS User's Guide: Statistics.* SAS Inst., Inc. Cary, NC.

Schwartz, C.C., Hubert, M.E. and Franzmann, A.W. 1988. Energy requirements of adult moose for winter maintenance. J. Wildl. Manage. 52: 26-33.

Shipley, R.A. and Clark, R.E. 1972. *Tracer Methods for in Vivo Kinetics.* Academic press, New York.

Silver, H., Colovos, N.F., Holter, J.B. and Hayes, H.H. 1969. Fasting metabolism of white-tailed deer. J. Wildl. Manage. 33: 490

Skogland, T. 1983. The effects of density-dependent resource limitation on size of wild reindeer. Oecologia, 60: 156-168.

Staaland, H., Jacobsen, E. and White, R.G. 1979. Comparisons of the digestive tract in Svalbard and Norwegian reindeer. Arct. Alp. Res. 11: 457-466.

Staun, H. 1972. The nutritional and genetic influence on number and size of muscle fibers and their response to carcass quality in pigs. World Rev. Anim. Prod. 8: 18-26.

Steele, R. 1971. *Tracer Probes in Steady State Systems.* Charles C. Thomas Publisher, Springfield, IL.

Suttie, J.M., Goodall, E.D., Pennie, K. and Kay, R.N.B. 1983. Winter food restriction and summer compensation in the red deer stags *(Cervus elaphus).* Br. J. Nutr. 50: 737-747.

Suttie, J.M., Wenham, G. and Kay, R.N.B. 1984. Influence of winter feed restriction and summer compensation on skeletal development in the red deer stags *(Cervus elaphus).* Res. Vet. Sci. 36: 183-186.

Suttie, J.M. and Kay, R.N.B. 1985. Influence of plane of winter nutrition on plasma concentrations of prolactin and testosterone and their association with voluntary food intake in red deer stags *(Cervus elaphus).* Anim. Prod. Sci. 8: 247-258.

Taylor, J.C., Alder, F.E. and Rudman, J.E. 1957. Fill and carcass changes of yard-fed and outwintered beef cattle turned on to spring pasture. Nature. London. 179: 197-198.

Thompson, K.F., Sykes, A.R. and Greenly, K. 1987. Effects of body condition on feed intake and live weight regain in grazing ewes. pp. 235-236. In: M. Rose, ed. *Herbivore Nutrition Research.* Occasional Publication of the Australian Society of Animal Production.

Torbit, S., Carpenter, L.H., Swift, D.M. and Alldredge, A.W. 1985. Differential loss of fat and protein by mule deer during winter. J. Wildl. Manage. 49: 80-85.

Tulloh, N.M. 1963. The carcass composition of sheep, cattle, and pigs as functions of body weight. pp. 5-1 to 5-15. In: *Carcass Composition and Appraisal of Meat Animals,* CSIRO, Melbourne.

Verme, L.J. and Ozaga, J.J. 1980. Effect of diet on growth and lipogenesis in deer fawns. J. Wildl. Manage. 44: 315-324.

Watkins, W.G., Hudson, R.J. and Fargey, P. 1991. Compensatory growth of wapiti *(Cervus elaphus)* on spring ranges. Can. J. Zool, in press.

Wilson, P.N. and Osbourn, D.F. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35: 324-363.

Wright, I.A. 1985. Compensatory growth in beef cattle. pp 195-201. In: F.H. Baker and
M.E. Miller, eds. *Emerging Technology and Management for Ruminants.*
Livestock Seminars, International Stockmen's School. Winrock International.

Wright, I.A. and Russels, A.J.F. 1986. The effects of winter food levels on compensatory
growth of weaned, suckled calves grazed at two sward heights. Anim. Prod. 43:
211-223.

IV. DAILY FORAGE INTAKE AND DIGESTION

Introduction

Wapiti stags wintered on a low quality diet (alfalfa-brome hay) showed compensatory growth on summer pasture (Chapter III). Compared with stags wintered on a high quality diet (alfalfa-barley pellets and alfalfa-brome hay), they showed greater growth in live weight and frame size. This live-weight gain was explained by neither gut fill nor change in body composition. Unlike similar-aged red deer stags (Suttie et al. 1983; Adam and Moir 1985; Milne et al. 1987), young wapiti stags compensated fully for the previous undernutrition by 15 months of age.

Higher feed intakes are a common but variable feature of compensatory growth (Allden 1968; Wilson and Osbourn 1960). Increased dry matter intakes occur in red deer stags (Suttie et al. 1983; Adam and Moir 1985) but no differences 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 wapiti wintered on high quality feed (alfalfa-barley pellets) (Watkins et al. 1991). However, interpretation of the latter study was complicated by the mix of sex/age and pregnancy.

The objective of this experiment was to evaluate potential compensatory mechanisms in wapiti. Is compensatory growth achieved by higher dry matter intake, and/or better feed conversion efficiencies, and is this associated with changes in digestive kinetics?

Materials and Methods

Nutrition treatments

Ten wapiti stags, born May and June 1989 at the Ministik Wildlife Research Station, were assigned to two winter feeding groups. Five wapiti calves (LW, low quality winter diet) were wintered on native range and also received alfalfa-brome hay. The other five (HW, high quality winter diet) received both alfalfa-brome hay and alfalfa-barley pellets as described in Chapter II. Winter feeding programs were terminated and groups merged in on April 4 1990, they were then released together in a 1.5 ha

pasture for comparisons of changes in live weight, frame size and body composition. Throughout the study, the stags were free to forage and were only supplemented with alfalfa-barley pellets in July when pastures greatly deteriorated. One animal in the LW group escaped to an adjacent paddock and was substituted by another with the same nutritional history after the first trial at the end of April.

Rate of passage

Comparative rates of passage were studied in trials starting on April 24, May 13, June 26 and July 22. Passage rate of digesta was estimated by orally administering a single dose of chromium oxide (Cr_2O_3). Approximately 200 grams of chromium oxide labelled alfalfa-barley pellets (containing 4.04 mg/g chromic oxide) were given to each wapiti during the first trial and 250 grams in subsequent trials. At the time of dosing, wapiti were offered the marked pellets in individual stalls. HW wapiti ate their marked pellets within three minutes while the LW wapiti took up to three hours. Both groups were later released to pasture together. Freshly voided fecal samples from each individual were collected before dosing and every 3-4 hours post-dosing for 48 hours and at 6-12 hours intervals for an additional 3-4 days.

Fecal samples were ovendried at 110°C for 24 hours and ground in a Wiley mill using a 30-mesh (1 mm) screen. Chromic oxide was analyzed using an atomic absorption spectrophotometer (Model 4000, Perkin-Elmer) with an air-acetylene flame as described by Fenton and Fenton (1979).

Concentration of chromium in feces with time (Ct) was determined by application of Stewart-Hamilton or Occupancy Principle (Steele 1971; Shipley and Clarke 1972). Digestive parameters were estimated following Holleman and White (1987). Mean retention time (MRT) was calculated as:

$$MRT = {}_0\int^\infty t.\ Ct.dt / {}_0\int^\infty Ct.dt$$

and, fecal output as:

$$F = D/{}_0\int^\infty Ct.dt$$

where;

D is marker dose administered,

C_t is the fecal marker concentration determined at time (t),

$_0\int^\infty C_t.dt$ is amount of marker excreted in time interval (dt) and estimated by the area under the marker concentration versus time curve for the feces,

$_0\int^\infty t.C_t.dt$ is the area under a curve obtained by multiplying the marker concentration in the feces by its respective time since dosing.

Dry matter digestibility and daily intakes

Lignin was used as an internal indicator of digestibility. Fractional digestibility of the diet was calculated as % forage lignin / % fecal lignin. Lignin as the ash-free residue was determined after 72% sulphuric acid treatment of ADF by the method of Goering and Van Soest (1970). Fecal samples obtained during the middle of each trial were used to estimate lignin. Forage samples were obtained at the same time to estimate lignin.

Dry matter intake (DMI) was obtained from daily fecal dry matter excretion (F) and fractional digestibility of the diet (A) by:

$$DMI\ (g) = F/(1 - A)$$

Feed conversion efficiency

Feed conversion efficiency was estimated by regressing daily gain (g/BW $^{0.75}$) against metabolizable energy (ME) intake (DMI x digestibility x 0.82 x 18.4 kJ/BW $^{0.75}$). The intercept estimated maintenance requirements and the slope gave energy requirements for live weight gain. Data from July was excluded because alfalfa-barley pellets were offered as a range supplement.

Statistical analysis

Data were analyzed using repeated measures analysis of variance (SAS 1989). The main 'between factor' was winter nutrition. The 'within factor' was trial date. Comparison between nutritional treatments on specific trial dates was made using Student's t-test. Feed conversion efficiency was analyzed by regression analysis.

Results

Daily forage intake

LW wapiti had higher dry matter intake in April (P= 0.027) and in May (P= 0.041) but intake did not differ in June and July (P>0.1) (Fig. IV.I). Intake varied among months (P < 0.001) with a peak in June. Contrasts were even greater (P= 0.05) for all months when intakes were expressed relative to metabolic body weight (g/kg BW 0.75).

Dry matter digestibility and rates of passage

Overall, LW wapiti showed slightly higher digestibility values (59.7%) than HW wapiti (57.1%). Dry matter digestibility differed significantly by month (P< 0.001) and between treatments during the first trial in April (P= 0.05) (Fig.IV.2). Treatment by month interaction was significant (P< 0.001). Digestibility rose rapidly with pasture growth between April and May and subsequently declined in July as pasture matured and alfalfa-barley pellets were offered as a range supplement.

Despite higher intakes and digestibility, LW wapiti had a shorter mean retention time overall (25.6 vs 26.9 h) (Fig. IV.2). Treatment by month interaction was marginally significant (P= 0.074). Mean retention time varied by month (P< 0.001). 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 (P= 0.082).

Feed conversion efficiency

Feed conversion efficiency did not differ significantly between nutritional treatments and among trial dates (P>0.1). Therefore, estimates were pooled and ME intake (kJ/BW $^{0.75}$) was regressed against gain (g/BW $^{0.75}$) to provide estimates of metabolizable energy requirements of 877 kJ/BW $^{0.75}$ for maintenance and 33.5 kJ/g for live weight gain (Fig.IV.3).

Discussion

Forage intake

Animals recovering from winter weight loss should attempt to increase daily dry matter intakes to meet their higher nutritional requirements (Wilson and Osbourn 1960; Allden 1970; Graham and Searle 1975; Wright 1985). As in a previous study (Watkins et al. 1991), this was generally supported because daily forage intake on pasture were higher in LW wapiti than in HW wapiti. This seems to be the main factor accounting for compensatory growth in red deer (Suttie et al. 1983; Adam and Moir 1985; Milne et al. 1987) and in cattle (Wright et al. 1989; Baker et al. 1985). However, there are exceptions to this general pattern: Fox et al. (1972), Hironaka and Kozub (1973), and Saubidet and Verde (1976) found no changes in intakes, and reduced feed consumption were reported during compensation by Foote and Tulloh (1977) and Murray (1980).

Estimates of intake expressed relative to metabolic weight in this study fell within the range of 40-90 g/kg BW $^{0.75}$, typical among livestock (Cordova et al. 1978). However, several reports show that wild ungulates can have intakes greatly exceeding 90 g/kg BW $^{0.75}$, particularly in summer with diet exceeding approximately 65% dry matter digestibility. In mule deer grazing on sagebrush (*Artemisia* spp), daily intake estimated by the chromic method are 102 and 96 g/kg BW $^{0.75}$ in early and late winter (Fulgham 1978). The highest intake by penned wapiti calves from October through June is 112 g/kg BW $^{0.75}$ (Westra and Hudson 1981). Estimated intakes for reindeer are 99-137 g/kg BW $^{0.75}$ (White and Trudell 1980). These high intakes may indicate that some wild ungulates are better adapted to capitalize on high feed available than domestic species.

Feed intake is determined by a range factors related to the animal's physiological state, diet and environment. Theoretically, herbivores recovering from winter weight loss should have high energy requirements for growth. When the feed restriction is removed, such animals whose energy stores were depleted gain weight at a faster rate than their better fed counterparts (Wilson and Osbourn 1960). The initial increase in feed intake for the LW wapiti could be explained in terms of increased energy demand for growth to reach body weight 'targets'. There is a strong tendency for animals to reach a certain target weight appropriate for a given age. Price and White (1985) suggested that northern wild ungulates are seasonal breeders and display annual

patterns of weight change, therefore, evolutionary pressure dictates that a particular condition or set-point weight must be achieved for an animal to survive and reproduce.

Monthly variation in forage intake could be attributed to changes in pasture availability and quality. Physical and chemical composition of the diet influence feed intake, the former by affecting the rate at which particles can be broken down by mastication and microbial digestion, and the latter by affecting nutrient supply to the microbial populations involved in fiber digestion (Arnold 1985). In April, low forage biomass and high fiber levels could have limited intake. At low nutritive values, limited gastrointestinal capacities and passage rates prevent an animal from meeting its energy requirements. As nutritive value increases, the animal is ultimately able to ingest enough dry matter to meet requirements. The initial rise in daily consumption during April preceded spring growth. Forage intake increased with pasture biomass and crude protein (Chapter V). Subsequently, intake declined as forage matured and pasture biomass declined in late July. The major drop in intake in July coincided with supplementary feeding of alfalfa-barley pellets.

Appetance in many species of wild herbivores responds to photoperiod and this effect is mediated through hormonal status. The ultimate regulatory centres lie in the brain which plays the dominant role in balancing and integrating signals from various parts of the body. White-tailed deer (Arman et al. 1974), red deer and sheep (Kay 1979) reduce their voluntary feed intake to maintenance levels in mid-autumn and increase it again with the approach of spring. This annual cycle of voluntarily feed intake is clearly an adaptation to the availability of forage. In spring/summer, when good quality forage is abundant, wild ruminants eat well above maintenance requirements. In winter when forage is poor and scarce, appetite declines.

It has been suggested that feed intake could be regulated by changes in the function of endrocrine glands (Ryg and Jacobsen 1981). Annual levels of various hormones have been reported, including thyroid and growth hormones (Ringberg et al. 1978; Seal et al. 1972), both of which influence growth rate in mammals. However, the reports are somewhat conflicting as to the exact patterns of the variations. This could be possibly be due to differences in nutritional status and may be involved in appetence in LW and HW wapiti.

Dry matter digestibility and rates of passage

Animals recovering from weight loss may improve forage digestible by increasing passage rates to increase intake. However in this study, forage digestibility was not related to nutritional history; both LW and HW wapiti digested forage in a similar manner. This has been the conclusion of most other studies on compensatory growth (Wilson and Osbourn 1960; Drew and Reid 1975). However, monthly effects existed and, as expected, highly digestible feeds traversed the alimentary tract faster than less digestible forages in April (due to litter) and July as the forage matured. However, LW wapiti had significantly l. er digestibility in April suggesting that they were selecting highly digestible diets.

Completeness of digestion is closely linked to the competitive rates of digestion and passage. Increasing rates of passage will reduce digestibility if sufficient time is not available for complete fermentation. This implies that, if diet digestibility is high and the rate of passage fairly low, the animal will have a better chance to utilize a greater mass of feed to acquire enough energy for daily maintenance. Although such a strategy was observed only in the first trial period, it would have been the best for wapiti recovering from winter undernutrition.

Digestibility decreases as intake increases due to decreased retention time. The amount of dietary fiber lignin will depress digestibility as fiber increases. Retention time will also be relatively shorter because fiber cannot be utilized completely. For domestic ruminants at a constant rate of feed intake, passage rate is inversely related to feed digestibility (Hungate 1966). In my study, digestibility, mean retention time and intake were not strongly related and differences could not be traced to nutritional history.

Rate of passage determines how long individual portions of ingesta are subjected to various processes including mixing, digestion, microbial fermentation, and absorption. The faster flow compensates for incomplete digestibility and improves energy supply by a larger intake. The components of the diet given during the experiment, the species of plant eaten and particle size taken influence the rate of passage. In this study, rate of passage was unrelated to nutritional history suggesting that particles moved at the same rate. Low forage digestibility in April in both groups was compensated by longer retention times. High fibrous material (in April due to

litter) remained longer in the gut. This causes the digesta to remain in the rumen until the particles are small enough to pass the rest of the gut.

Increased intake during compensatory growth is associated with increased rumen digesta and enhanced rates of passage (Wilson and Osbourn 1960). Intake can be increased by accelerating ruminal emptying via absorption or escape, or by increased rumen fill (Van Soest 1982; Grovum 1984). The rate of passage through the gut is related to voluntary intake through its effect on frequency of recurring appetite. The more quickly ingesta moves out of the gut, the sooner the animal desires more food.

Rates of passage reported in this study are similar to rates of 23.6 h in deer (Mautz and Petrides 1971) and 22.5 h in white-tailed deer (as reviewed by Van Hoven and Boomker 1985) on pasture. In April, less digestible forage was retained for a longer period. An increase in gut fill in June (Chapter III) allowed LW wapiti to increase intake, although, the rate of passage decreased. This suggests that wapiti improved energy supply for growth and extracted more nutrients by retaining less digestible forage for longer time in April. High feed intakes in June were accompanied by accelerated passage rate.

Variations among individuals in parameters describing the rate of passage are typically large (Westra and Hudson 1981; Mautz and Petrides 1971). In my study, such variations could be attributed to difficulties in administering the marker. Time to eat the marked pellets differed and was related to nutrition history. HW wapiti ate their pellets within three minutes whereas the LW wapiti took up to three hours. Generally, tamer animals ate their pellets faster.

Measuring the digestibility of herbage eaten presents a special problem. In theory, natural herbage constituents like lignin can be employed as indicators. In practise, this application is complicated by the fact that lignin in new growth may not be completely indigestible (Wallace and Van Dyne 1970; Fahey and Jung 1983). Another difficulty with any internal indicator is that of obtaining feed samples which are truly representative of the diet.

Feed conversion efficiency

In general, increased feed intake is accompanied by increased efficiency although conflicting results have been reported, probably due to various factors prevailing under the experimental conditions. Improved feed efficiency is evident particularly

in the early stages of realimentation (O'Donovan 1984). Suttie et al. (1983) who restricted young red deer stags, observed increased feed conversion efficiency. However, in this study, feed conversion efficiency during compensation was not related to nutritional history.

The underlying factor for increased efficiencies is that the basal metabolism of an animal declines as energy intake is reduced (Wilson and Osbourn 1960). Since maintenance requirements are proportional to live weight (NRC 1984), it may be assumed that animals subjected to undernutrition become more economical in their use of feed. Such animals, when given access to good quality feed, only slowly raise their basal metabolic rate to the normal rate. This would result in a greater proportion of food available for productive purposes, especially growth, and would result in an increased growth rate compared with that shown by control animal receiving similar diets. Such, improved efficiency however, would only be temporary, and would be gradually reduced throughout the period of refeeding. Resting metabolic rates include tissue and feed-related components so a positive association between metabolic rate and feed intake is expected. Studies on white-tailed deer (Silver et al. 1969) indicates that fasting metabolic rate declines with feed intake during winter, compensating to some extent for the reduced energy intake.

Energy expenditures of animals represent the sum of expenditures of individual tissues, each of which may have different metabolic rates. Generally, lean body mass is considered to be more metabolically active than fat because of the relative high cost of protein turnover. High maintenance requirements in wapiti would be influenced by body composition. The daily maintenance requirements of penned red deer are 520 kJ/BW $^{0.75}$ for hinds and 570 kJ/BW $^{0.75}$ for stags (Fennessy et al. 1981; Suttie et al. 1987). Red deer stags wintered outdoors have requirements approaching 850 kJ/BW $^{0.75}$. Grazing presumably increases costs further. Estimates for wapiti range from 572 kJ/BW $^{0.75}$ for hinds held in pens during winter and 936 kJ/BW $^{0.75}$ for hinds on spring pasture (Jiang and Hudson 1991). The latter figure is close to my estimate of 877 kJ/BW $^{0.75}$ obtained for wapiti stags.

Energy requirements for growth are determined by the energy content content of gain as well as the growth rate. Because metabolizable energy is used with an efficiency of about 50%, energy requirements for live weight gain vary from 16-55 kJ/g (Hudson and Christopherson 1985). Energy requirements of red deer for live weight gain range from 37 kJ/g for stags to 55 kJ/g for hinds (Fennessy et al. 1981; Suttie et

al. 1987). Young wapiti hinds on spring pasture required 38.5 kJ/g for live weight gain, a value that is similar to 33.5 kJ/g 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 one year of age.

Conclusion

Young wapiti stags wintered on low quality diet showed a pronounced increase in voluntarily feed intake on spring/summer pastures. LW wapiti increased forage intake on pasture during compensation and this seems to be the main factor accounting for compensatory gain. No consistent differences were observed in mean retention time, digestibility and feed conversion efficiency and therefore higher intakes and consequently, higher gains of LW wapiti were not explained. As feed intake increased mean rentention time decreased. Diet digestibility, and therefore digestive efficiency were not important effects of nutritional history. However, compensating wapiti had higher intakes relative to maintenance requirements. I concluded that a high level of feed consumption provided a large margin above maitenance needs, thus allowing a high proportion of energy to be used for compensatory growth.
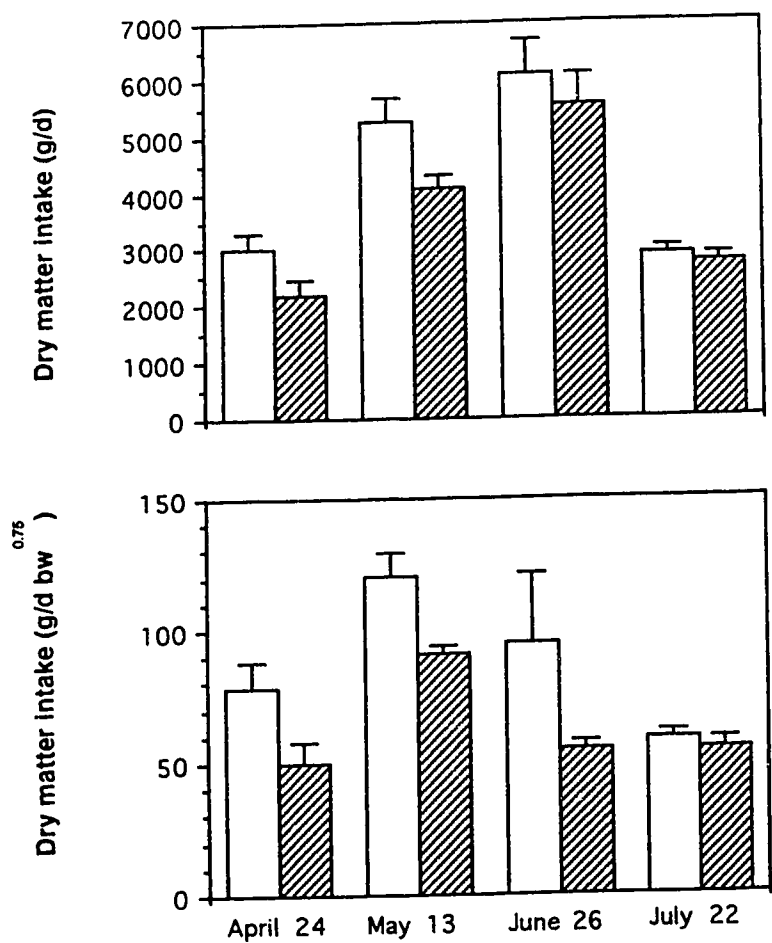
Fig. IV.1. Dry matter intake (g.d, g/kg bw$^{0.75}$) of LW (open bars) and HW (hatched bars) wapiti. Significant differences in forage intake between treatments in April (P=0.027) and May (P=0.041).
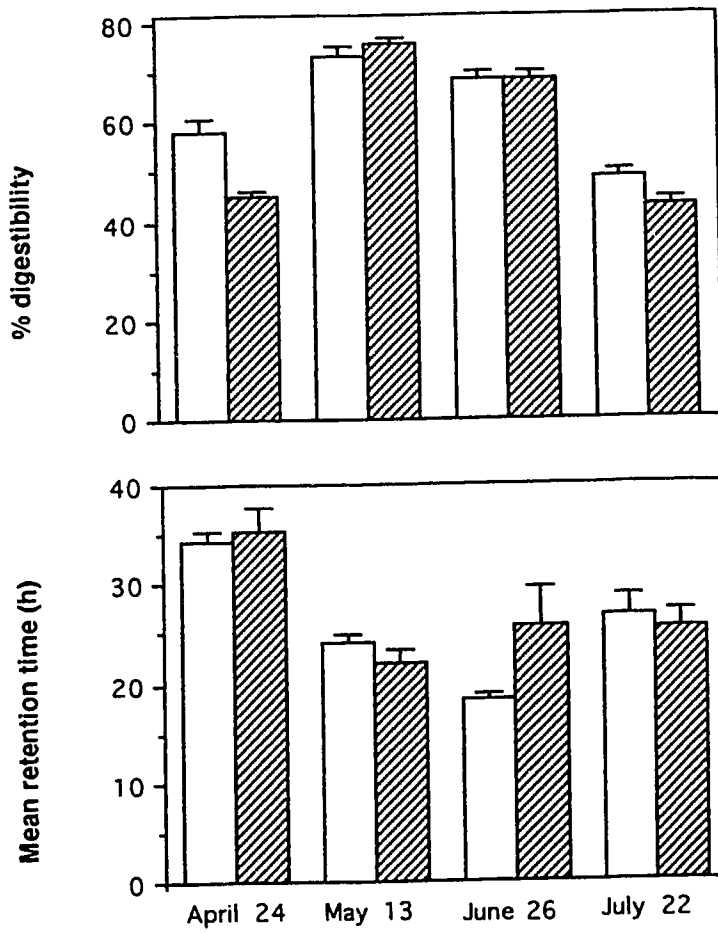
Fig. IV.2. Digestive parameters (digestibility, mean retention time) of LW (open bars) and HW (hatched bars) wapiti. Significant differences between treatments in dry matter digestibility in April (P=0.05) and mean retention time marginally significant in June (P=0.08).
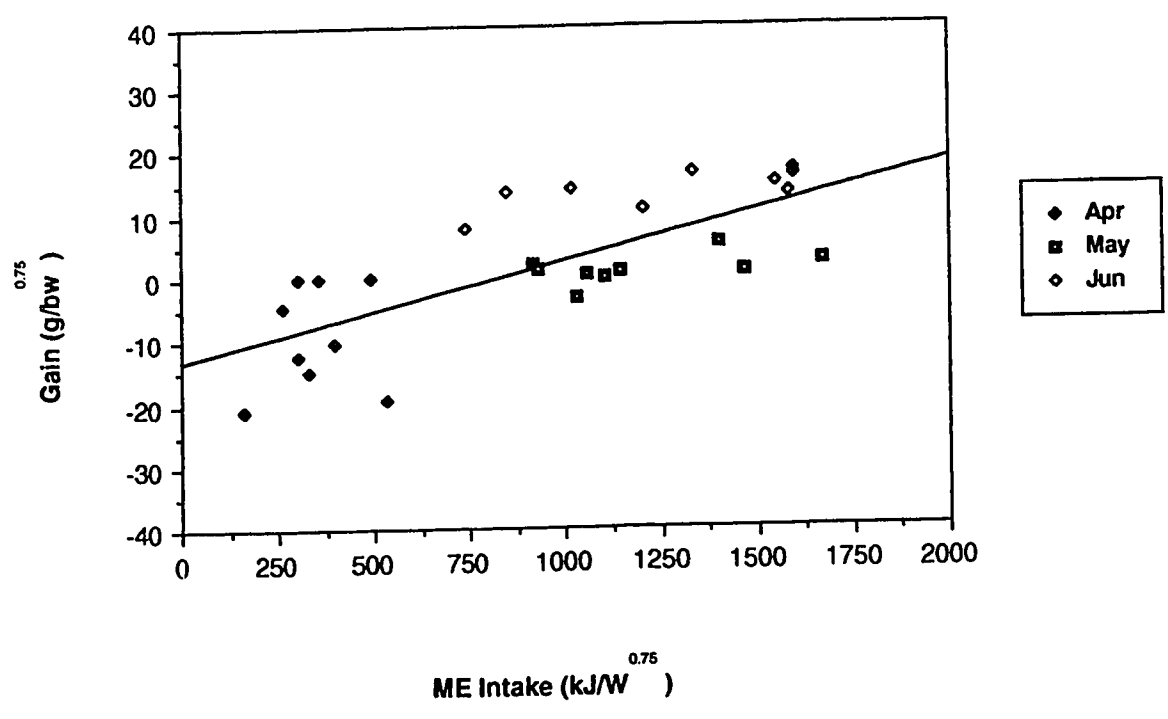
Fig. IV.3. Efficiency of use (g/W$^{0.75}$) of metabolizable energy (kJ/W$^{0.75}$) of wapiti (y = - 13.040 + 0.016x, r^2 =0.53).

Literature cited

Adam, C.L. and Moir, C.E. 1985. Effects of winter nutrition of young farmed red deer on their subsequent growth at pasture. Anim. Prod. 40: 135-142.

Allden, W.G. 1968. Undernutrition of the merino sheep and its sequelae 1. The growth and development of lambs following prolonged periods of nutritional stress. Aust. J. Agric. Res. 19: 621-638.

Allden, W.G. 1970. The effects of nutritional deprivation on the subsequent productivity of sheep and cattle. Nutr. Abstr. Rev. 40: 1167-1184.

Arman, P., Kay, R.N.B., Goodall, E.D. and Sharman, G.A.M. 1974. The composition and yield of milk from captive red deer (Cervus elaphus). J. Reprod. Fert. 37: 67-72

Arnold, G.W. 1985. Regulation of food intake. pp 81-101. In. R.J. Hudson and R.G. White, eds. Bioenergectics of Wild Herbivores. CRC Press, Boca Raton, FL.

Baker, R.D., Young, N.E. and Laws, J.A. 1985. Changes in the body composition of cattle exhibiting compensatory growth and the modifying effects of grazing management. Anim. Prod. 41: 309-321.

Cordova, F.G., Wallace, J.G. and Pieper, R.D. 1978. Forage intake by grazing livestock: a review J. Range. Manage 31: 430:438.

Drew, K.R. and Reid, J.T. 1975. Compensatory growth in immature sheep. III. Feed utilization by sheep subjected to feed deprivation followed by realimentation. J. Agric. Sci. (Camb.) 85: 215-220.

Fahey, G.C. Jr. and Jung, H.G. 1983. Lignin as a marker in digestion studies: A review. J. Anim. Sci. 57: 220-225.

Fennessy, P.F., Moore, G.H. and Corson, I.D. 1981. Energy requirements of red deer. Proc. N.Z. Soc. Anim. Prod. 41: 167-173.

Fenton, T.W. and Fenton, M. 1979. An improved procedure for the determination of chromic oxide in feed and feces. Can. J. Anim. Sci. 59: 631-634.

Foote, J.Z. and Tulloh, N.M. 1977. Effects of two paths of live-weight change on the efficiency of feed use and on body composition of Angus steers. J. Agric. Sci. (Camb.) 88: 135-142.

Fox, D.C., Johnson, R.R., Preston, R.L., Dockery, T.R. and Klosterman, E.W. 1972. Protein and energy utilization during compensatory growth in beef cattle. J. Anim. Sci. 34: 310-318.

Fulgham, K.O. 1978. Influence of spring sheep grazing on the forage intake and quality of diets considered by reared mule deer under winter-range condition. Ph.D. Diss., Utah State Univ., Logan 159 pp.

Goering, H.K. and Van Soest, P.J. 1970. *Forage Fiber Analyses (Apparatus, Reagents, Procedures and some Applications)*. USDA Agric. Handbook, No. 379.

Grovum, W.L. 1984. Integration of digestion and digesta kinetics with control of feed intake-a physiological framework for a model of rumen function. pp. 244-268. In: F.M.C. Gilchrist and R.I. Mackie, eds. *Herbivore Nutrition in the Tropics and Subtropics* The Science Press, Pretoria.

Holleman, D.F. and White, R.G. 1987. Determination of digesta fill and passage from nonabsorbed particulate phase markers using the singe dosing method. Can. J. Zool. 67: 488-494.

Hironaka, R. and Kozub, G.C. 1973. Compensatory growth of beef cattle restricted at two energy levels for two periods. Can. J. Anim. Sci. 53: 709-715.

Hudson, R.J. and Christopherson, R.J. 1985. Maintenance metabolism. pp 121-142. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, FL.

Hungate, R.E. 1966. *The Rumen and its Microbes*. Academic press, NY and London. pp 533.

Jiang, Z. and Hudson, R.J. 1991. Estimating feed intake of wapiti (*Cervus elaphus*) with a single-dose of chromic oxide. Can. J. Zool. in press.

Kay, R.N.B. 1979. Seasonal changes of appetite in deer and sheep. Agricultural Research Council Research Review 5: 13-15.

Mautz, W.W. and Petrides, A.G. 1971. Food passage rate in the white-tailed deer. J. Wildl. Manage. 35: 723-731.

Milne, J.A., Sibbald, A.M., McCormack, H.A. and Loudon, A.S.I. 1987. The influence of nutrition and management on the growth of red deer calves from weaning to 16 months of age. Anim. Prod. 43: 511-522.

Murray, D.M. 1980. The effect of three different growth rates on feed utilization of cattle. Aust. J. Agric. Res. 31: 1139-1145.

National Research Council (NRC). 1984. *Nutrient Requirements of Beef Cattle*. 6th ed. National Academy press, Washington D.C.

O'Donovan, P.B. 1984. Compensatory gain in cattle and sheep. Nutr. Abstr. Rev. Series B. 54: 389-410.

Price, M.A. and White, R.G. 1985. Growth and development. pp 183-214. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton FL.

Ringberg, T.E., Jacobsen, E., Ryg, M. and Kro, J. 1978. Seasonal changes in levels of growth hormone, somatomedin and thyroxine in free ranging, semidomesticated Norwegian reindeer (*Rangifer tarandus tarandus* L.). Comp. Biochem. Physiol. 60A: 123-126.

Ryg, M. and Jacobsen, E. 1981. Seasonal changes in groth, feed intake, growth hormone, and thyroid hormones in young male reindeer (*Rangifer tarandus tarandus*). Can. J. Zool. 60: 15-23.

Saubidet, C.L and Verde, L.S. 1976. Relationship between live weight, age and dry-matter intake for beef cattle after different levels of food restriction. Anim. Prod. 22: 61-69.

SAS 1989. *SAS User's Guide:Statistics*. SAS Institute Inc., Cary, NC.

Seal, U.S., Verme, L.J., Ozanga, J.J. and Ericson, A.W. 1972. Nutritional effects on thyroid activity and blood of white-tailed deer. J. Wildl. Manage. 36: 1041-1052.

Shipley, R.A. and Clark, R.E. 1972. *Tracer Methods for in vivo Kinetics*. Academic press, New York.

Silver, H., Colovos, N.F., Holter, J.B. and Hayes, H.H. 1969. Fasting metabolism of white-tailed deer. J. Wildl. Manage. 33: 490-498.

Steele, R. 1971. *Tracer Probes in Steady State Systems*. Charles C. Thomas Publisher, Springfield, IL.

Suttie, J.M., Goodall, E.D., Pennie, K. and Kay, R.N.B. 1983. Winter food restriction and summer compensation in the red deer stags *(Cervus elaphus)*. Br. J. Nutr. 50: 737-747.

Suttie, J.M., Fenne   eenVliet, B.A., Littlejohn, R.P., Fisher, M.W., Corson,
I.D. and Lab.   .. . Energy nutrition of young red deer (*Cervus elaphus*)
hinds an.' ..   .vith young stags. Proc. NZ Soc. Anim. Prod. 47: 111-
114.

Van Hoven, W. and Boomker, E.A. 1985. pp 81-101. In: R.J. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, FL.

Van Soest, P.J. 1982. Rate of passage of digesta through the gut of mammals and birds. Nutr. Abstr. Rev. Ser. B. Livest. Feeds. 51: 789-820.

Wallace, J.G. and Van Dyne, G.M. 1970. Precision of indirect methods for estimating digestibility of forage consumed by grazing cattle. J. Range Manage. 23: 424-430.

Watkins, W.G., Hudson, R.J. and Fargey, P. 1991. Compensatory growth of wapiti *(Cervus elaphus)* on spring ranges. Can. J. Zool. in press.

Westra, R. and Hudson, R.J. 1981. Digestive function of wapiti calves. J. Wildl. Manage. 45: 148-155.

White, R.G. and Trudell, J. 1980. Habitat perference and forage consumption by reindeer and caribou near Atkasook, Alaska, J. Arctic and Alpine Res. 12: 511-529.

Wright, I.A. 1985. Compensatory growth in beef cattle. pp 195-201. In: F.H. Baker and M.E. Miller, eds. *Emerging Technology and Management for Ruminants*. Livestock Seminars, International Stockmen's School. Winrock International.

Wright, I.A., Russel, A.J.F. and Hunter, A.E. 1989. Compensatory growth in cattle grazing different vegetation types. Anim. Prod. 48: 43-50.

Wilson, P.N. and Osbourn, D.F. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35: 324-363.

V. FORAGING ECOLOGY

Introduction

Compensatory gain among young wapiti stags (Chapter III) appears to be achieved largely by increasing voluntarily feed intake, particularly in relation to metabolic weight (Chapter IV). Differences between the treatment groups in digestibility, feed conversion efficiency and rate of passage were slight. Therefore, the question turns to how this compensatory intake is achieved. Compensating wapiti might attempt to maximize energy intake by grazing longer, foraging faster, and/or feeding more selectively.

Assuming that increased energy intake increases survival and reproduction (fitness) (Schoener 1971; Belovsky 1984), feeding times should increase when requirements for energy and nutrients are high or forage supplies are sparse (Renecker and Hudson 1989). But, requirements for other activities may place an upper limit on time spent grazing.

Herbivores also can increase daily feed intake by feeding faster, which they could achieve with higher biting rates or larger bite sizes. Effects of forage biomass and structure on feeding rates of wapiti have received some attention (Collins and Urness 1983; Hudson and Nietfeld 1985). Bite size and cropping rate are greatly influenced by habitat type.

Nutrient intake could be increased at the same dry matter intake by feeding selectively. Diet selection, a process that governs the amounts and varieties of feed consumed (Ellis et al. 1976), is a means by which herbivores can attenuate fluctuations in forage quality. Diet selection is influenced by quality and quantity of available feeds, which are influenced by location and time of feeding (Hobbs 1979).

Feeding selectively improves diet quality but often at the expense of feeding rate (Westoby 1974). If the animal selected only relatively abundant low quality forages, intake may be limited by gut fill. On the other hand, if it selected rare high quality feeds it likely would be limited by its ability to ingest an amount which would meet it requirements. If the animal chose a combination of forages, total consumption could increase both for physiological reasons (associative effects of feeds) and for logistic

reasons (in searching for one type of plant, another would be discovered fortuitously).

This chapter examines how compensatory intake can be achieved. Is it achieved by feeding longer, more rapidly and/or more selectively within habitats or selecting habitats offering superior foraging opportunities?

Materials and Methods

Nutritional treatments and grazing trials

Ten weaned wapiti calves born at the Ministik Wildlife Research Station were assigned to two winter feeding treatments on Dec 7 1989. Five calves (low quality winter diet, LW) were run on native range and supplemented with alfalfa-brome hay. Five others (high quality winter diet, HW) were offered alfalfa-barley pellets as well as hay. Winter feeding programs were terminated and groups merged in April 4 1990 at the beginning of spring growth of pasture. Because the pastures deteriorated under heavy cumulative grazing pressure, alfalfa-barley pellets were offered as a range supplement in the July grazing trial.

Grazing trials were conducted on April 28, May 11, June 19, and July 25. During each trial, the following data on vegetation, activity budgets, foraging behavior, diet selectivity and habitat selection were collected. Due to rapid changes in vegetation, biomass, forage quality and bite sizes was also sampled on May 30.

Vegetation biomass and quality

Vegetation was sampled each month in poplar forest, upland grassland and lowland grassland habitats. Ten 0.25 m^2 clip plots were randomly sampled in each habitat during the 24 h scans. In each plot, vegetation was clipped to a height of 1 cm and samples were stored in plastic bags at -20°C. Samples were later oven-dried at 60°C for 48 hours then ground through a Wiley mill with a 30 mesh screen (1 mm) and stored at 5°C until analyzed.

Materials obtained for biomass estimates were used for nutritional analyses. Crude protein (N X 6.25) was determined using the macro-Kjeldahl method (A.O.A.C 1990). Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined using procedures of Goering and Van Soest (1970).

Foraging behavior

Foraging parameters were assessed by direct observation (bite-count method) from within 5-10 m of an animal using methods described by Hudson and Watkins (1986), Hudson and Nietfeld (1985) and Nietfeld (1983). Daily dry matter intake (g/day) of each individual was calculated as the product of cropping rate, bite size and foraging time. Feeding rate was calculated as the product of cropping rate (bites/min) and bite size (g/min).

Cropping rates (bites/min) of individual wapiti were determined from the number of bites taken for several 3-10 minute scans during the feeding period in each habitat. Each distinct removal of a plant, plant part, or a number of plants was considered a bite (Nietfeld 1983). Cropping rates were recorded only when animals grazed at a single feeding station.

Bite sizes (g/min) of each forage category were estimated from 20 'mimicked bites' taken in close proximity to each wapiti during the 24-h scans. Since these bites were mimicked, they did not provide information on variability among individuals so the results were pooled to provide estimates for individual habitats. These samples were then ovendried at 60°C for 48 h or to constant weight.

Movements while feeding (steps/min) were noted. An animal was considered to make a step when the right leg was moved, as the animal moved to a new feeding station (defined as the area an animal feeds on without moving) and recording for cropping rate stopped.

Indices of diet quality and selectivity

Fecal crude protein (N X 6.25) provided an index of diet quality (Gates 1980). Feces were collected at the time of defecation to avoid exposure to the environment. Feces were frozen until ovendried at 60°C for 3-5 days and ground through a 30 mesh screen (1 mm) in a Wiley mill. A further sample (2 g) was ovendried at 110°C overnight for dry matter (DM) determination. Nitrogen was determined using the macro-Kjeldahl method (A.O.A.C 1990). Fecal ADF and NDF were determined using the same procedures as for forage.

Kjeldahl nitrogen of forage samples from 10 randomly placed clip plots in each habitat and the mimicked bites described above allowed expression of forage intake

on a protein (N X 6.25) basis as well as an index of diet selectivity (N diet /N clip plot). All samples were analyzed in duplicate.

Activity budgets and habitat selection

The activity and habitat choice of each animal were monitored for 24 hours in each trial. All animals were fitted with wide, bright identification collars to facilitate both day and night observations. Both groups were observed simultaneously at distances of 5-20 m. Instantaneous scan sampling at 10 min intervals (Jacobsen and Wiggins 1982) was used. Activities were categorized as 1) feeding, 2) resting (lying), 3) standing, 4) walking and other minor activities. Each 10 min record was based on the predominant activity of an individual animal. Simultaneously, habitat choice was coded as poplar forest, upland grassland and lowland grassland.

Night observations depended mainly on moonlight, but occasionally a spotlight was used. Scan data were converted to proportion of total observed time engaged in each activity.

Statistical analysis

Data on habitat selection, biting rate, steps/min, forage biomass, forage quality, fecal crude protein, NDF and ADF were analyzed statistically using General Linear Models procedure (ANOVA) (SAS 1989). The main effects in analysis of habitat selection, cropping rates, steps/min, were trial dates and nutritional treatment. For nutritional and forage biomass results, habitats and months were the main effects. Comparison of treatment means was by Student's t-test. Significant specific comparisons of the nutrition treatment by month by habitat interaction were computed using the LSD procedure (Steel and Torrie 1980)

Results

Range availability and quality

Forage biomass differed significantly among habitats and months (P< 0.001). From mid April until late July, forage biomass increased rapidly to a peak in June (1384 kg/ha) (Fig. V. 1). Although pasture growth initiated in April, it was diluted with carry-over so pasture crude protein peaked in May (Table V.1). Pasture crude protein varied significantly among habitats (P= 0.028) and among months (P= 0.033).

Crude protein declined in all three habitats as the plants matured and lowest values were recorded in July (12.7%).

Highest fiber contents (NDF, ADF) were observed during April. Lowest fiber contents were observed in May in the lowland habitat. Forage NDF varied within habitats (P= 0.002) and among months (P< 0.001) (Table V.1). Forage ADF varied within habitats and among months (P< 0.001). Dietary ADF exhibited monthly variations similar to NDF, v. ghest values in April and lowest in May. Highes. values were recorded in the poplar forest. Habitat by month interaction was significant.

Total daily forage intake (g/day)

Estimated total daily dry matter intake (feeding rate x foraging time) differed significantly between treatments (P=0.048) (Fig.V.2) and among months (P< 0.001). Overall, LW wapiti consumed more than HW wapiti. Daily intakes peaked in June when biomass was at its maximum. Lowest intakes were observed in July when pasture condition deteriorated and alfalfa-barley pellets were offered as a range supplement.

Estimates of intake were not significantly different during the May and June trials using the bite count and single dose method described in Chapter II. However, in April, the bite count method overestimated intake by a factor of two. Comparison in July were not possible because supplemental feed was offered.

Activity Budgets

Higher forage intakes could be achieved by grazing longer. Foraging and walking were the predominant activities in all months and differed significantly between the two nutritional treatments (P< 0.01) and among months (P< 0.001) (Fig.V.3). Other activities, resting and standing did not differ significantly between the two groups (P>0.01). LW wapiti expressing compensatory gain spent approximately 50% of their time foraging in April, however, foraging time decreased in May and June. In April (P=0.008) and in May (P= 0.002), LW wapiti spent more time feeding.

Table V.1. Least square means of crude protein, neutral detergent fiber and acid detergent fiber for poplar forest, upland and lowland grasslands at the Ministik Wildlife Research Station.

	April 28	May 11	May 30	June 19	July 25	Probability
Crude protein						
PF	16.74aA	21.97aB	21.67aB	17.22aA	12.94aC	P<0.001
UG	17.12aA	15.40bB	14 59bC	11.47bD	11.76bD	P<0.001
LG	18.23bA	17.33cA	18.21cA	17.19aA	13.99aB	P<0.001
Probability	P=0.041	P<0.001	P<0.001	P<0.001	P=0.027	
Neutral detergent fiber						
PF	67.55aA	50.44aB	54.96aC	53.26aD	59.40aA	P<0.001
UG	65.51aA	55.67aB	57.81aB	53.33aB	58.69aB	P=0.003
LG	59.70bA	43.27aB	57.88aA	49.17aC	56.14aA	P<0.001
Probability	P=0.022	P>0.05	P>0.05	P>0.05	P>0.05	
Acid detergent fiber						
PF	41.74aA	26.56aB	29.84aC	30.58aC	35.61aD	P<0.001
UG	35.61bA	29.03aB	26.82aB	27.99aB	31.54bC	P<0.001
LG	33.91cA	21.61bB	29.38aB	27.51aC	31.40bA	P<0.001
Probability	P<0.001	P<0.001	P>0.05	P>0.05	=0.035	

PF Poplar forest
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abc Similar lower case letters within a column are not significantly different $P \leq 0.05$
ABC Similar upper case letters within a row are not significantly different $P \leq 0.05$

Grazing time dropped to less than 15% in July when supplemental feed was offered and pasture condition deteriorated. During this trial, a relatively large proportion of their time was spent resting and walking. Walking and resting increased from less than 5% to 10-15%, and from 45% to over 55% respectively, in April and July. Differences in all activities except walking disappeared in June and July.

Foraging behavior

As well as grazing longer, daily intake also can be increased by feeding faster (g/min), the product of biting rate (bites/min) and bite size (g/bite).

Feeding rate

Forage intake rates for the two groups differed significantly (P= 0.002) (Fig. V.4) between months and among habitats (P< 0.001) (Table V.2). Treatment by month interaction was significant (P=0.004). LW wapiti consumed more forage per minute (13.8 g/min) than HW wapiti (12.7 g/min). Feeding rates increased from 8.8 g/min in April to a plateau of about 17 g/min in June and July. Except in April, feeding rates were highest in the upland grassland and lowest in poplar forest.

From pooled observations, intake rates were inversely related to body weight. Lighter animals tended to consume more than their heavier counterparts. However, when treatment effects were evaluated using trial weight as a covariate, trial weight was not related to consumption rate (P> 0.1).

Cropping rates

Cropping rates (bites/min) differed significantly between nutritional treatments (P= 0.007), among habitats and months (P< 0.001)(Fig.V.5). Month by habitat interaction was significant (P<0.001). Overall, LW wapiti recorded higher bites/min (43.9 vs 40.4 bites/min) than HW wapiti. Generally, the highest cropping rates were observed immediately after release to pasture, with maximum cropping rates of 54.1 bites/min for LW wapiti in April compared to 49.2 bites/min for HW wapiti (P= 0.039). Bite size was inversely related to cropping rate (Fig.V.6).

Cropping rates varied significantly within habitats (P < 0.001) with highest values in the upland grassland (Table V.3). Highest bites rates for both LW and HW wapiti were observed in the lowland grassland and the lowest in the poplar forest. In May, cropping rate still varied significantly between the two treatments (P= 0.01) and between habitats (P< 0.001). In June and July, average cropping rates were 34.7 and 31.8 bites/min for LW and HW wapiti, respectively. Cropping rate decreased for both groups over the experimental period.

Table V.2. Least square means of dry matter intake (g DM/min) of LW and HW wapiti at the Ministik Wildlife Research Station.

	April 28	May 11	June 19	July 25	Probability
LW wapiti					
PF	5.2[aA]	8.6[aB]	16.3[aC]	13.8[aC]	P<0.001
UG	10.6[bA]	16.2[bB]	21.6[bC]	21.3[bC]	P<0.001
LG	11.5[bA]	10.8[cA]	15.5[aB]	14.6[aC]	P<0.001
Probability	P<0.001	P<0.001	P<0.001	P<0.001	
HW wapiti					
PG	4.6[aA]	7.7[aB]	14.2[aC]	12.5[aC]	P<0.001
UG	10.4[bA]	13.0[bA]	19.0[bB]	20.9[bC]	P<0.001
LG	10.6[bA]	9.6[aA]	16.0[aB]	13.9[aA]	P=0.034
Probability	P<0.001	P<0.001	P<0.001	P<0.001	

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Bite size

Bite sizes (g/min) were mimicked and therefore could not be used to test differences between nutritional treatments. Bite size varied significantly by month (P= 0.002) and by habitat (P= 0.006) (Table V.4). Bite size increased with plant biomass and the highest bite sizes were recorded in upland grassland and the smallest in lowland grassland (Fig. V.7). Bite sizes were correlated with forage biomass (r^2=0.89 poplar forest, r^2=0.60 upland and r^2=0.52 lowland grasslands).

Table V.3. Least square means of cropping rate (bites/min) in habitats selected by LW and HW wapiti at the Ministik Wildlife Research Station.

	April 28	May 11	June 19	July 25	Probability
LW wapiti					
PF	48.9^{aA}	47.4^{aA}	29.4^{aB}	21.7^{aC}	P<0.001
UG	53.8^{aA}	58.2^{bA}	40.8^{bB}	41.3^{bB}	P<0.001
LG	59.6^{bA}	54.3^{bB}	38.1^{bC}	35.1^{bC}	P<0.001
Probability	P=0.038	P<0.001	P=0.002	P<0.001	
HW wapiti					
PF	42.7^{aA}	42.1^{aA}	25.5^{aC}	19.8^{aA}	P<0.001
UG	52.3^{bA}	50.9^{bA}	35.9^{bB}	40.6^{bB}	P<0.001
LG	54.8^{bA}	47.5^{bA}	39.4^{bB}	33.4^{bB}	P<0.001
Probability	P<0.001	P<0.001	P<0.001	P<0.001	

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ABC Similar upper case letters within a row are not significantly different $P \leq 0.05$

Rate of movement

The rate of movement (steps/min) during grazing did not differ significantly between treatments (P> 0.1) (Table V.5), although it differed significantly among months (P< 0.001) and among habitats (P= 0.047). Treatment by month by habitat interaction was significant (P< 0.001). However, in April, movement rates differed significantly (P=0.01) between the LW and HW wapiti. Wapiti moved most rapidly in the poplar forest where rates were 3.0 and 3.8 steps/min for the LW and HW wapiti, respectively. In May, June and July, the rate of movement did not differ significantly between the groups (P > 0.1).

Table V.4. Least square means of bite size(g) in poplar forest, upland and lowland grasslands at the Ministik Wildlife Research Station.

	April 28	May 11	May 30	June 19	July 25	Probability
PF	0.08^{aA}	0.17^{aB}	0.25^{aC}	0.52^{aD}	0.59^{aE}	P<0.001
UG	0.18^{bA}	0.23^{aA}	0.36^{bB}	0.49^{aC}	0.48^{bC}	P≤0.001
LG	0.19^{bA}	0.26^{aA}	0.24^{aA}	0.38^{bB}	0.39^{cB}	P<0.001
Probability	P=0.025	P>0.05	P=0.003	P<0.001	P=0.009	

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Diet quality and selectivity

Available protein (crude protein in mimicked bites) exhibited monthly variations similar to the clip crude protein but values were generally two percentage points higher in each month (Fig. V.8). For both, month by habitat interaction was significant (P< 0.001). Crude protein varied greatly among habitats during May. In all months except April, the upland grassland recorded the lowest values.

Overall, there were no significant differences in fecal crude protein between the two nutritional treatments, although it varied significantly by month (P< 0.001) (Fig.V.9). However, treatment by month interaction was significant (P< 0.001). Fecal crude protein peaked in June following the same monthly trend as dietary crude protein although values were lower except in June and July. LW wapiti wintered on alfalfa-brome hay had significantly lower fecal crude protein in May (P<0.01)

Fecal NDF and ADF varied significantly among months (P< 0.001) but not between treatment groups (P> 0.1). Low NDF and ADF values corresponded to high fecal crude protein values in June. Crude fiber decreased as the forage matured in July.

Table V.5. Least square means of the number of steps per minute of LW and HW wapiti at the Ministik Wildlife Research Station.

	April 28	May 11	June 19	July 25	Probability
LW wapiti					
PF	3.0^{aA}	1.9^{aA}	2.6^{aA}	2.6^{aA}	P>0.05
UG	3.0^{aA}	1.7^{aB}	2.4^{aB}	1.8^{bB}	P=0.004
LG	2.0^{bA}	1.6^{aA}	2.5^{aA}	1.7^{bB}	P=0.025
Probability	P=0.01	P>0.05	P>0.05	P=0.04	
HW wapiti					
PF	3.8^{aA}	1.9^{aB}	2.1^{aB}	2.3^{aB}	P<0.001
UG	2.5^{bA}	1.9^{aA}	2.6^{aA}	1.9^{aA}	P>0.05
LG	4.4^{aA}	1.7^{aB}	2.1^{aB}	1.7^{aB}	P<0.001
Probability	P=0.001	P>0.05	P>0.05	P>0.05	

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Resource selection

Wapiti used all habitats in a pattern that was independent of nutritional history (Fig. V.10). Although habitats were used differently by month (P< 0.001), the only difference traced to nutritional history was higher use of lowland grassland by compensating wapiti during the spring forage growth in May (P=0.007).

Generally, more time was spent in all three habitats in April and May, as the cropping rates peaked and decreased in June when intake rates peaked in all habitats. Least amount of time was spent in July when alfalfa-barley pellets were offered as a range supplement.

Discussion

Total daily forage intake

At the start of the grazing period at 11 months of age, the two groups of wapiti differed widely in both weight and nutritional history. Animals that were light in early spring due to nutritional hardship grew much faster on pasture than their counterparts (Chapter III). Compensatory gain appeared to be achieved largely through increasing forage intake particularly in relation to metabolic weight and hence maintenance requirements (Chapter IV, Watkins et al. 1991). One explanation for compensatory growth is increased feed intake as reported for red deer stags (Suttie et al. 1984) and cattle (Meyer et al. 1965).

Amount of feed consumed by temperate Cervidae is a function of several criteria: a) metabolic demand which is strongly seasonal, b) forage quality and abundance can limit intake, c) the physical constraint of digestive anatomy and size limits gut fill, d) available biomass and structure of feed items can influence the amount of time required to capture a meal, and e) the amount of time available for feeding can be influenced by search time for new feed patches.

Feed intake is influenced by time devoted to foraging each day, the time spent in search during foraging, the cropping rate and the size of the bite (Allden and Whittaker 1970). Of these variables, the animal has most control over foraging time and biting rate. This suggests that as energy demands increase, an animal can increase both total time foraging and biting rate to produce a greater intake of forage. Allden (1962) proposed that increasing forage availability increased consumption while decreasing grazing time and the number of bites required.

Estimates of daily intake from grazing behavior in this study were consistent with simultaneous estimates based on single-dose method. The single-dose method is a convenient and reliable method for measuring forage intake of wapiti on pasture (Jiang and Hudson 1991). Chromic oxide is a purified chemical and thus lends itself to accurate dosing (Hatfield et al. 1990) and it forms stable complexes with feed ingredients (Martz et al. 1974). Therefore, separation of chromic oxide from the feed with which it was given is not likely to occur. Also, in moose and wapiti, both the liquid and the particulate matter flow together unlike in cattle and presumably other large grazers in which rumen contents are stratified (Renecker and Hudson 1990).

Wide variations between the two method par ... rly in April may have been due to a variety of problems with both methods. The main bias of the single dose method is related to lignin digestibility. Lignin in new growth may not be completely indigestible (Wallace and Van Dyne 1970; Fahey and Jung 1983) and this underestimates digestibility. Another problem is that chromic oxide was administered in pellets. Pelleted feeds are characterized by high rates of passage and this may have overestimated intake rates. However, although the single dose method is laborious, it is still better method to estimate intake in wapiti provided low chromium concentrations are used.

The subjectivity of visually estimating bite sizes and the assumption that all animals had similar bite sizes may have underestimated intake. Direct observation (bite-count method) greatest limitation is the long period of continous observation required and subjectivity of estimating bite sizes and therefore, less subjective method like the single-dose method should be used.

Because LW wapiti had higher intake rates, the question of how this was achieved is considered. Was it achieved by grazing longer, faster or more selectively within a habitat or simply by selecting habitats that offered superior foraging opportunities?

Activity Ludgets

Wild ruminants presumably engage in exclusive activities in a way that maximizes fitness (McFarland 1977). They spend a disproportionate part of each day feeding or resting or ruminating; other behavior (e.g grooming, travel, security and social interaction) comprise a small part of the daily activity (Hudson 1985). Time invested in these activities (particularly feeding and rumination) shows marked diel and seasonal variations and can be viewed as an adaptive response. The fundamental decision made by large herbivores is when and how much to forage. Although grazing animals generally respond to declining forage availability by increasing foraging effort (cropping rate and search effort) (Arnold 1964), there is a point where the marginal benefit of feeding will be overshadowed by the marginal cost of obtaining feed.

Feeding times should increase when requirements for energy and nutrients are high or forage supplies are sparse (Renecker and Hudson 1989). Both factors seemed to contribute to the observed pattern in this study. Early spring can be a particularly

critical time for wapiti recovering from winter weight loss because of increased energy and crude protein requirements for growth. One way wapiti might increase nutrient intake and energy is by foraging longer. My study confirmed this expectation, as LW wapiti foraged for a longer period of time than their counterparts, in April, May and June trials.

Ecological theory has emphasized the state of the animal as a determinant of behavior (Mangel and Clark 1986). LW wapiti undergoing compensatory growth grazed longer particularly during the first two months when weight differences were being narrowed. They also spent less time engaged in energetically expensive activities complying with the law of "least effort" (Geist 1982) to conserve energy. The ultimate factor for the increase in foraging time by LW wapiti may have been energy requirements. However, low forage quality and rumen fill may limit forage intake short of metabolic demands.

Limitations of gut distention, requirements for other activities (particularly rumination) and preemption by heat stress or insect annoyance may impose an upper limit on grazing times of ruminants (Belovsky 1984). The longest grazing times of 12.7 h/day by compensating wapiti during the first grazing trial may have approached this limit. This value exceeded 11 hour feeding times reported by Collins and Urness (1983), and 10.6 hours reported by Craighead et al. (1973) (10.6). However, Gates and Hudson (1983) on similar pastures reported wapiti spent 13 hours foraging in early spring.

Time spent foraging declined over the experimental period and could be attributed to changes in diet quality and quantity. More time was spent when the diet had high fiber content in April (due to litter), and declined as fiber decreased in May and June. Rumination increases at the expense of feeding if forages are of low quality (Foose 1983). Rumination is determined largely by cell wall intake (Deswysen et al. 1986) because feed particles must be reduced in size before they can pass from the rumen (Foose 1983). As forage quality improves, ruminating declines and foraging increases. Decline in fiber in May and June was accompanied by an increase in plant biomass and crude protein. The very short feeding times in July may be attributed to heat stress and insect annoyance but more likely were due to the availability of palatable supplemental feed.

Foraging rate

The ability of free-ranging animals to meet their nutritional requirements often is constrained by the logistics of foraging. Compensating wapiti increased forage intake by grazing more rapidly. This difference was not detected by Watkins et al. (1991) in a mixed group of wapiti during compensatory growth on spring pasture. Although motivational state may have some effect, the most important determinants of feeding rate of wapiti are forage biomass and structure (Collins et al. 1978; Collins and Urness 1983; Wickstrom et al. 1984; Hudson and Nietfield 1985; Hudson and Watkins 1986). Maximum rates approaching 18 g/min were generally above asymptotic rates of 11-15 g/min from the above studies.

Foraging rate is the product of cropping rate and bite size. Bite size is most strongly influenced by structural attributes such as leaf area, plant configuration and, for grasslands, tiller length and density. This relationship has a mechanical basis and is assumed to scale to the width of the incisor. On the basis of incisor bar width, Gordon and Illius (1988) predicted that bite sizes (and presumably feeding rates) should scale to $8.96 \, BW^{0.35}$ and $7.17 \, BW^{0.35}$ for grazers and intermediate feeders, respectively. However, I had no opportunity to directly evaluate differences in bite size and assumed that bite size were the same for all animals. Therefore, variations in feeding rate was entirely due to observed cropping rates. Maximum bite sizes of 0.47 g/bite and maximum cropping rates of 50-55 bites/min compare favourably with estimates of Hudson and Watkins (1986) on the same pastures. When animals are grazing, the bite size increases and the cropping rate decreases with increasing biomass (Allden 1962; Allden and Whittaker 1970).

Cropping rates are influenced by bite size, with large mouthfuls of feed requiring more time to be chewed and swallowed than smaller ones. The main limit on cropping rates is time required to handle, wet masticate, and swallow feed items. Except in very sparse plant communities, cropping rates are inversely related to bite size and perhaps dietary fiber because of handling (mastication) time. Cropping rates in my study, declined with increasing bite sizes to slightly over 30 bites/min. The strength of this relationship suggests that handling time rather than search time is the most important determinant of cropping rates on aspen parkland ranges. The significant relationship between cropping rate to forage biomass may be secondary to the relationship between bite size and forage biomass.

Foraging rates continued to increase with the accumulation of pasture biomass until June after which pasture consumption exceeded growth and pasture condition deteriorated. Another interacting factor was forage quality which changed the amount of forage needed to meet requirements. Therefore, by increasing forage intake until June, LW wapiti were able to meet their high requirements for growth.

Watkins et al. (1991) were uncertain whether the low intake of previously well-fed wapiti of mixed ages and sexes may be due to the fact that they were simply waiting in anticipation that supplemental feed may resume. However, since both groups in my study were merged and held for 2 weeks before the first grazing trial, this explanation is less likely.

Diet selection

Although wapiti stags were able to increase diet protein by two percentage points in each trial, selective grazing was not part of the adaptive behavior of animals undergoing compensatory growth. No differences were observed in fecal crude protein and mimicked bites suggesting that wapiti of the two groups grazed similarly. High crude protein in feces in May reflects high dietary crude protein associated with initiation of new growth. A decrease in NDF content indicated an increase in the proportion of the dry biomass containing cell contents and a corresponding decrease in cell walls (Stewart et al. 1977).

Grazing ruminants generally face the following dilemma: Feeding selectively improves diet quality but often at the expensive of feeding rate. Therefore, selectively feeding is most adaptive on abundant but low quality forages which limit intake through digestive capacity. On the other hand, intake of digestive energy may be maximized by feeding less selectively where forages are of generally high quality but limited availability. The latter would seem to be the case on spring/summer pastures.

Diet selection could be achieved on a different scale. LW wapiti also could theoretically compensate by selecting habitats that provided better foraging opportunities, to meet their high demands for growth.

Habitat selection

Habitat selection is an important way that ruminants can ameliorate environmental adversity and capitalize on opportunities. An optimal foraging consumer should

include at least the feed type of highest value in the diet (Owen-Smith and Novellie 1982) and should base selection of feeding habitats on foraging effort (Krebs and McCleery 1984). Although this seems to hold for a variety of taxa, studies with wild ruminants have been limited largely to testing whether preferred habitats provide more forage of better quality (Festa-Bianchet 1988; Morgantini and Hudson 1988).

Selection of habitat by wapiti appeared to be strongly influenced by forage availability and associated grazing values and not nutritional history. Studies examining specific forage attributes have shown that dry matter digestibility, crude protein and fiber contents are often significantly correlated to ruminant diet selection (Gesshe and Walton 1981). Interpretation of these relationships is problematic because there is no evidence that animals can detect these components directly. In this study, such a relationship was not established.

The physical structure of forages has also been related to selection. Ruminants select leaves over stems (Arnold 1960), new growth over old brown material (Hamilton et al. 1973) and for plant species higher in moisture content over drier material (Gesshe and Walton 1981). LW wapiti spent a considerable amount of time in lowland grassland. However, in July this relationship was not as obvious. Higher fiber levels and high proportions of dead brown material may have influenced selection of upland habitat.

Conclusion

Wapiti maintained on a low quality diet over winter, spent more time foraging and foraged faster than wapiti wintered on high quality diet. They also spent less time engaged in energetically expensive activities. By foraging longer, LW wapiti were able to ingest more feed and therefore were able to compensate for their condition loss in winter. They also increased their daily forage intake by foraging faster (bites/min).

Bite size and cropping rate were greatly influenced by habitat type. Bite size increased with increasing plant biomass and decreased with an increase in cropping rate. Cropping rates were higher in early spring but decreased as biomass increased in summer when forage was highly digestible.

Although wapiti were able to increase forage intake and diet quality by selecting habitats offering superior opportunities, both HW and LW wapiti used the habitats in

a similar manner. Selecting superior habitats did not appear to be a unique part of the adaptive strategy of wapiti undergoing compensatory growth.
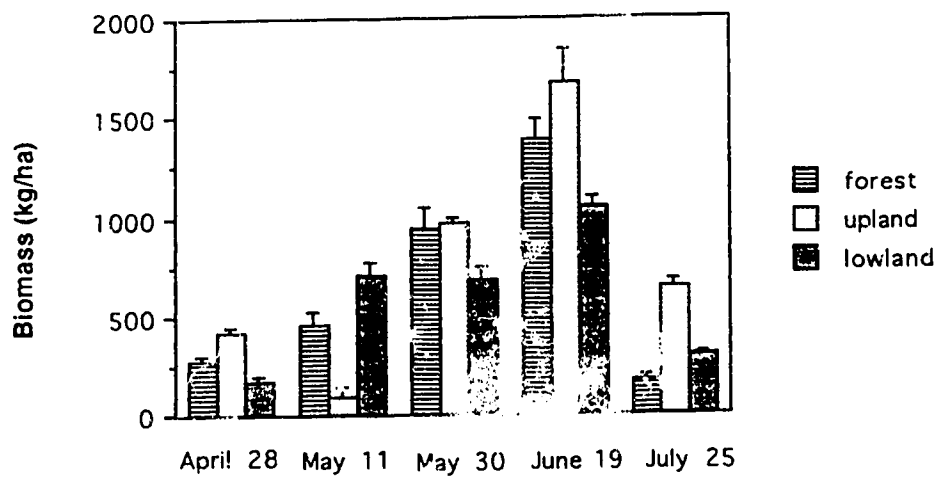
'ig. V.1. Monthly forage biomass (Kg/ha) of 3 habitats in paddock grazed by wapiti.
: gnificant differences between habitats and months (P<0.001).
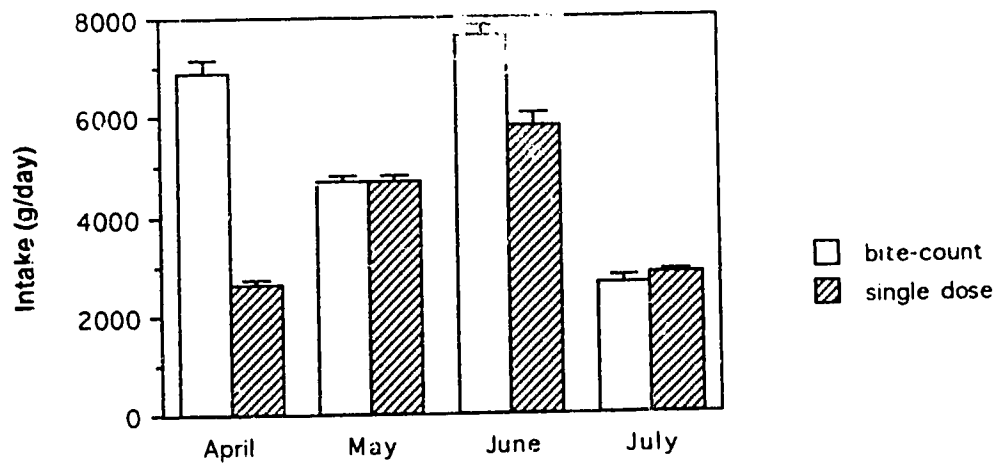
Fig. V.2. Comparison of dry matter intake (g/day) of wapiti stags from April to July based on bite-count and single dose (chromium oxide) methods. Significant differences in April (P<0.001).
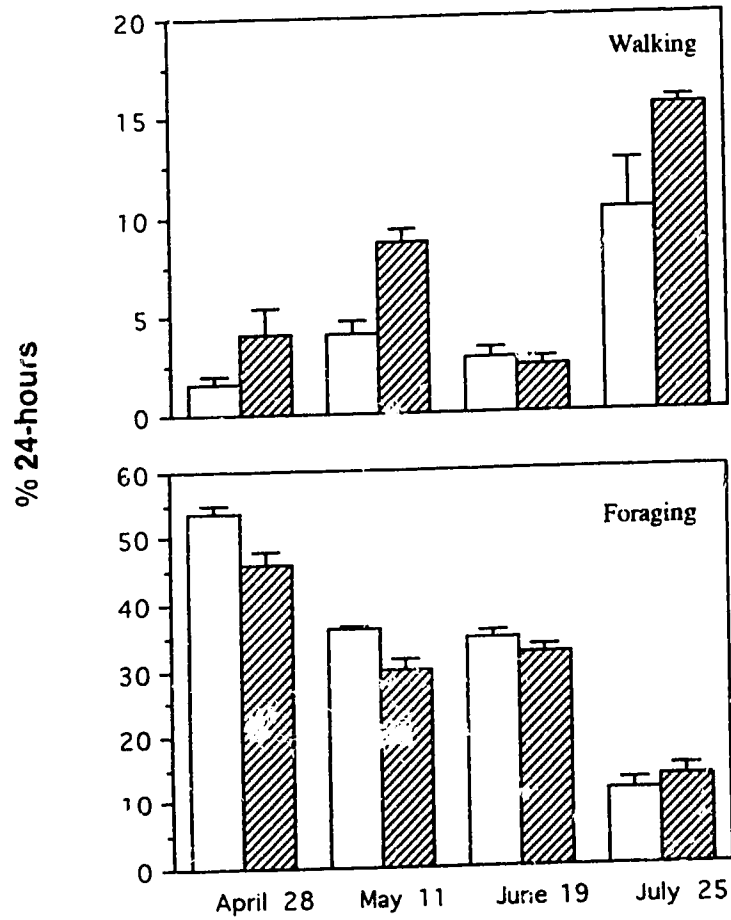
Fig. V.3. Percent time spent walking (top) and foraging (bottom) of LW (open bars) and HW (hatched bars) wapiti. Other activites were not significantly different between treatments (P>0.1).
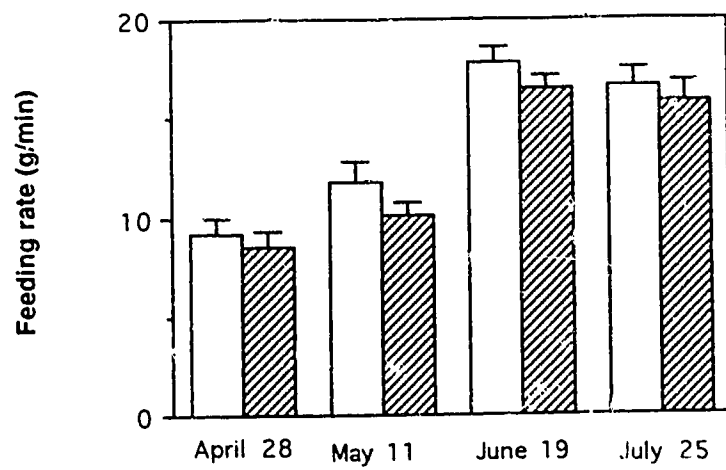
Fig. V. 4. Dry matter intake (g/min) of LW (open bars) and HW (hatched bars) wapiti. Significant differences between treatments (P=0.002).
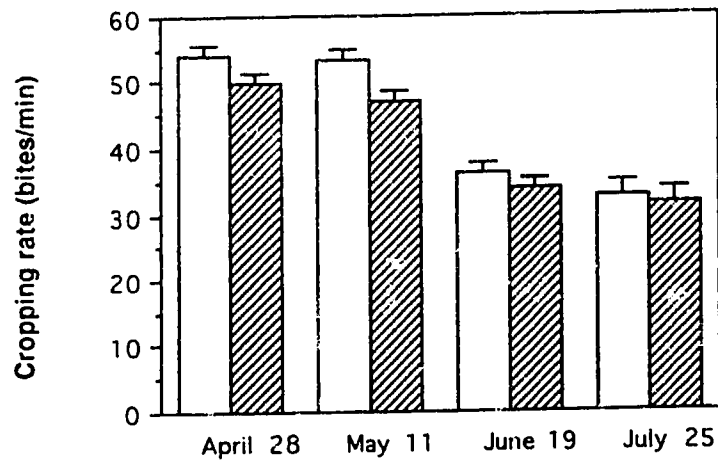
Fig. V. 5. Cropping rates (bites/min) of LW (open bars) and HW (hatched bars) wapiti. Significant differences between treatments (P=0.007).
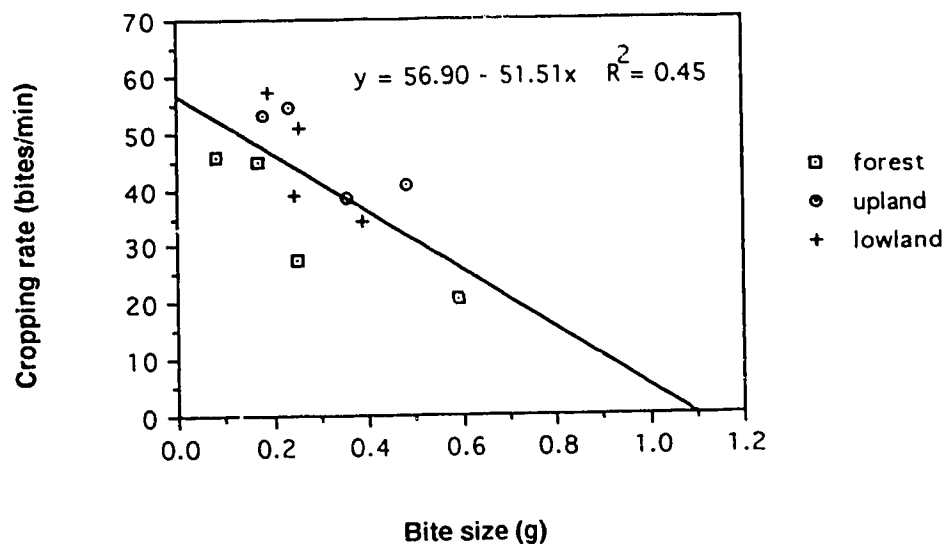
Fig. V. 6. Foraging rate in relation to bite sizes of 3 habitats grazed by young wapiti stags.

$y = 6.37e\text{-}2 + 2.82e\text{-}4x \quad R^2 = 0.76$
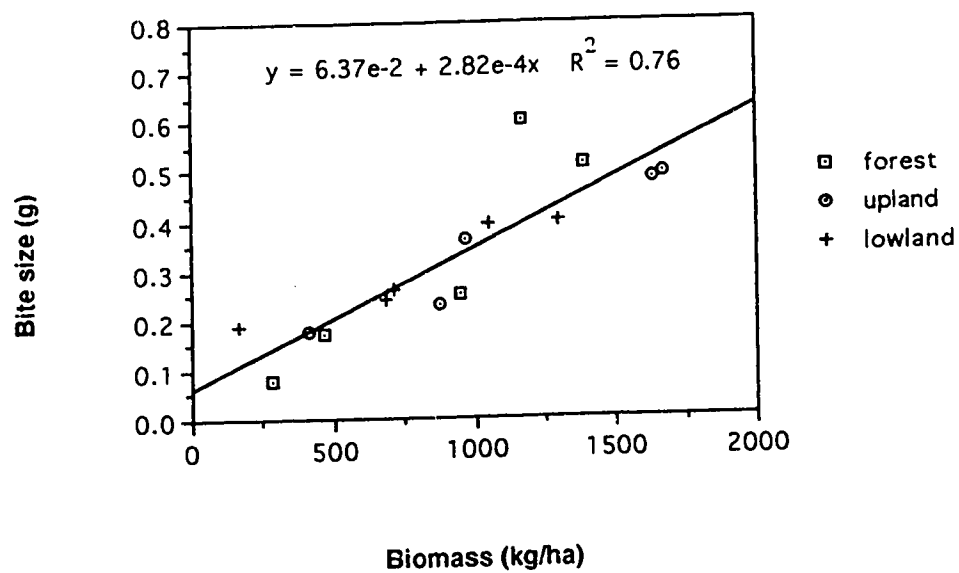
Fig. V.7. Bite size in relation to forage biomass (excluding browse) of 3 habitats grazed by wapiti.
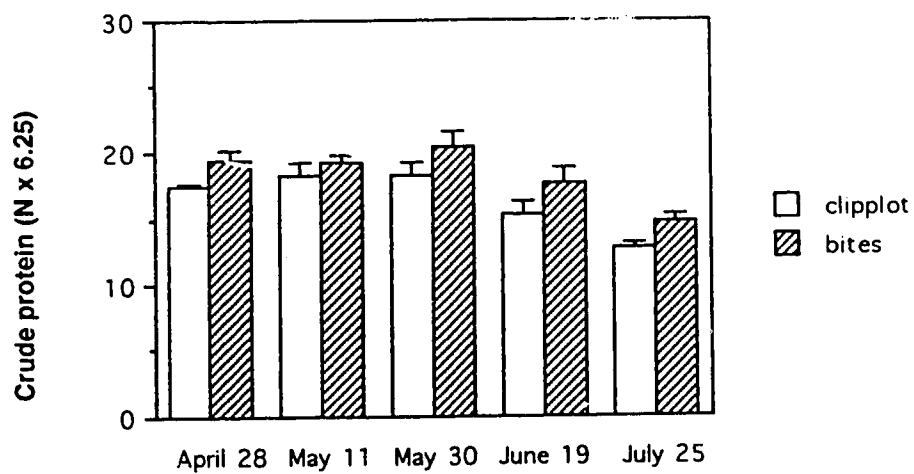
Fig. V. 8. Clip plot (open bars) and dietary crude protein (hatched bars) on spring/summer pasture. No significant differences between clip plots and bites on July 25 (P>0.1).
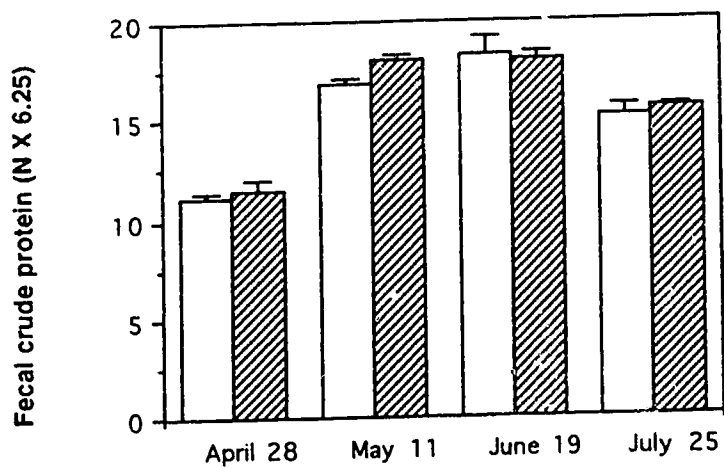
Fig. V.9. Monthly variation in fecal crude protein (N×6.25) of LW (open bars) and HW (hatched bars) on spring/summer pasture. Significant differences between treatments in May (P<0.01).
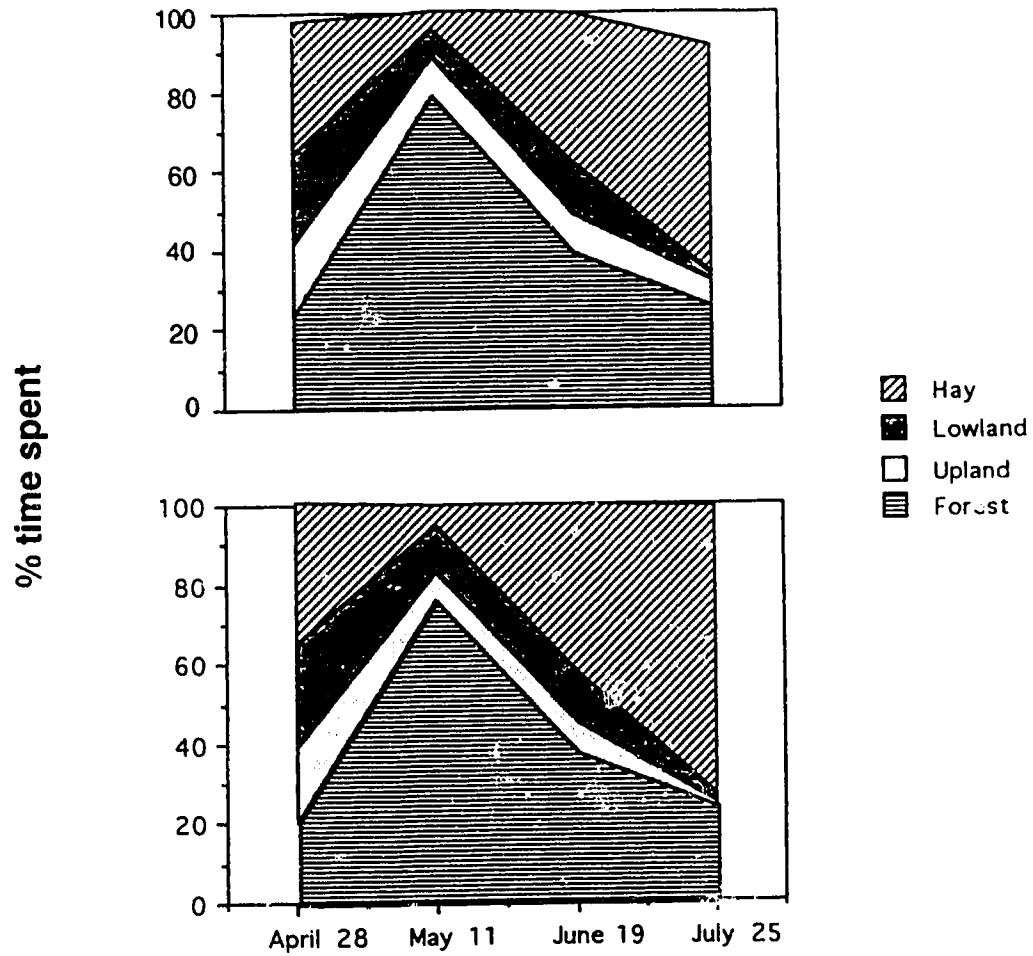
Fig. V.10. Habitat selection by LW (top) and HW (bottom) wapiti on spring/summer pastures. Significant differences between treatments in May on lowland grassland (P=0.037).

Literature cited

A.O.A.C. 1990. *Official Methods of Analysis*. 15th ed. Association of Official Agricultural Chemists, Washington, D.C.

Allden, W.G. 1962. Rate of herbage intake and grazing time in relation to herbage availability. Proc. Aust. Soc. Anim. Prod., IV, 163.

Allden, W.G. and Whittaker, I.A. 1970. The determinants of herbage intake on grazing sheep: the interrelationship of factors influencing herbage intake and availability. Aust. J. Agric. Res. 21: 755-766.

Arnold, G.W. 1960. Selective grzr ; by sheep of two forages species at different stages of growth. Aust. J. Agric. kes. 11: 1026-1033.

Arnold, G.W. 1964. Factors within plant associations affecting the behavior and performance of grazing animals. pp 133-154. In: D.J. Crisp ed. *Grazing in terrestrial and marine environments*. Blackwell Sci. Publ., Oxford, 322 pp.

Belovsky, G.E. 1984. Herbivore optimal foraging: a comparative test of three models. Am. Nat. 124: 97-115.

Cc.ns, W.B. and Urness, P.J. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47: 646-663.

Collins, W.G., Urness, PJ. and Austin, D.D. 1978. Elk diets and activities on different lodge-pole pine habitats segments. J. Wildl. Manage. 42: 799-810.

Craighead, J.J., Craighead, F.C. Jr., Ruff, R.L. and O'Gara, B.W. 1973. Home ranges and activity patterns of non-migratory wapiti on the Madison Drainage herd as determined by bictelemetry. Wildl. Monogr., No.33, pp 50.

Deswysen, A.G., Ellis, W.C. and Pord, K.R. 1986. Inter-relation entree, less activities alimentairies et mery ciques, la digestibilite reticulo-ruminate et le niveau d'ingestion volontaire. Res-prod. Nutr. Dev. 26: 271-272.

Ellis, J.E., Weins, C.F., Rodell, C.F. and Anway, J.C. 1976. A conceptual model of diet selection as an ecosystem process. J. Theriol. Biol. 60: 93-108.

Fahey, G.C. Jr. and Jung, H.G. 1983. Lignin as a marker in digestion studies: A review. J. Anim. Sci. 57: 220-225.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75: 580-586.

Foose, T.L. 1983. Trophic strategies of ruminants versus nonruminants. Ph.D. Thesis, Univ., Chicago, Ill. 337 pp.

Gates, C.C. and Hudson, R.J. 1983. Foraging behavior of wapiti in a boreal forest enclosure. Nat. Can. 110: 197-206.

Geist, V. 1982. Behavioral Adaptive Strategies. pp 219-278. In: J.W. Thomas and D.E. Toweill, eds. Elk of North America. Ecology and Management. Stackpole Books, Harrisburg, Pa. 698 pp.

Gesshe, R.H. and Walton, P.D. 1981. Grazing animal preferences for cultivated forages in Canada. J. Range Manage. 34: 42-45.

Goering, H.K. and Van Soest, P.J. 1970. Forage Fiber Analyses (Apparatus, Reagents, Procedures and Some Applications). USDA Agric. Handbook, No. 379.

Gordon, I.J. and Illius, A.W. 1988. Incisor arcade structure and diet selection in ruminants. Functional Ecology 2: 15-22.

Hamilton, B.A., Hutchinson, K.J., Annis, P.C. and Donnelly, J.B. 1973. Relationship between the diet selected by grazing sheep and the herbage on offer. Aust. J. Agric. Res. 24: 271-277.

Hatfield, P.G., Clanton, D.C., Sanson, D.W. and Eskridge, K.M. 1990. Methods of administering ytterbium for estimation of fecal output. J. Range Manage. 43: 316-320.

Hobbs, N.T. 1979. Winter diet quality and nutritional status of elk in the upper montane zone, Colorado. Ph.D. Dissertation. Colorado State Univ. Fort Collins. pp 131.

Hudson, R.J. 1985. Body size, energetics, and adaptive radiation. pp 1-24. In: R.J. Hudson and R.G. White, eds. Bioenergetics of Wild Herbivores. CRC Press, Boca Raton, FL.

Hudson, R.J. and Watkins, W.G. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64: 1705-1708.

Hudson, R.J. and Nietfeld, M.T. 1985. Effects of forage depletion on the feeding rate of wapiti. J. Range Manage. 38: 80-82.

Jacobsen, N.K. and Wiggins, A.D. 1982. Temporal and procedural influences on activity estimated by time-sampling. J. Wildl. Manage. 46: 313-324.

Jiang, Z. and Hudson, R.J. 1991. Estimating feed intake of wapiti (Cervus elaphus) with a single-dose of chromic oxide. Can. J. Zool. in press.

Krebs, J.R. and McCleery, R.H. 1984. Optimization in behavioral ecology. pp 91-121. In: J.R. Krebs and N.B. Davies, eds. Behavioural Ecology: an Evolutionary Approach. 2nd ed. Blackwell Scientific Pub. Oxford.

Mangel, M. and Clark, C.W. 1986. Towards a unified foraging theory. Ecology 76: 1127-1138.

Martz, F.A., Van Soest, P.J., Vogt, P.R. and Hildebrand, E.S. 1974. Use of elemental tracers and activation analysis in digestion, rate of digesta flow and feed particle tracking studies in cattle. Proc. 6th Symp. Energy Metab., Stuttgart, Germany. 111-114.

McFarland, D.J. 1977. Decision-making in animals. Nature 269: 15-21.

Meyer, J.H., Hull, J.L., Weitkamp, W.H. and Bonilla, S. 1965. Compensatory growth responses of fattening steers following various low energy intake regimes on hay or irrigated pastures. J. Anim. Sci. 24: 29-37.

Morgantini, L.E. and Hudson, R.J. 1988. Migratory patterns of the wapiti, Cervus elaphus, in Banff National Park, Alberta. Can. Field. Nat. 102: 12-19.

Nietfeld, M.T. 1983. Foraging behavior of wapiti in the boreal mixed-wood forest, central Alberta. M.Sc. Thesis, Univ. Alberta, Edmonton. 187 pp.

Owen-Smith, N. and Novellie, P. 1982. What should a clever ungulate eat? Am. Nat. 119: 151-178.

Renecker, L.A. and Hudson, R.J. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forest. J. Wildl. Manage. 53: 296-302.

Renecker, L.A. and Hudson, R.J. 1990. Digestive kinetics of moose (Alces alces), wapiti (Cervus elaphus) and cattle. Anim. Prod. 50: 51-61.

SAS 1989. SAS User's Guide: Statistics. SAS Institute Inc., Cary, NC.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 11: 369-404.

Steel, R.G.D. and Torrie, J.H. 1980. Principles and Procedures of Statistics: a biometrical approach. 2 ed. McGraw-Hill, New York.

Stewart, R.R., MacLeannan, M.M. and Kinnear, J.D. 1977. The relationship of plant phenology to moose. Sask. Dept. Tourism Res. Tech. Bull. No. 3, pp 20.

Suttie, J.M., Wenham, G. and Kay, R.N.B. 1984. Influence of winter feed restriction and summer compensation on skeletal development in the red deer stags (Cervus elaphus). Res. Vet. Sci. 36: 183-1186.

Wallace, J.G. and Van Dyne, G. M. 1970. Precision of indirect methods for estimating digestibility of forage consumed by grazing cattle. J. Range Manage. 23: 424-430.

Watkins, W.G., Hudson, R.J. and Fargey, P. 1991. Compensatory growth of wapiti (Cervus elaphus) on spring ranges. Can. J. Zool. in press.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108: 290-304.

Wickstrom, M.L, Robbins, C.T., Hanley, T.A., Spalinger, D.E. and Parish, S.M. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48: 1285-1301.

VI. INTEGRATING DISCUSSION

Young wapiti stags in my study demonstrated a capacity for compensatory growth after a period of undernutrition in winter. Wapiti stags that received alfalfa-brome hay in winter exploited the compensatory growth phenomenon on pasture. Young wapiti that were lighter at the start of spring due to winter undernutrition showed superior weight gains, and fully compensated their weight on summer pasture. LW wapiti also increased in frame size during the compensation period and attained similar sizes. This indicated that the skeleton as well as soft tissue were involved in compensatory growth in wapiti.

Wilson and Osbourn (1960) and Donnelly et al. (1974) concluded that part of the increased weight gain during compensation reflected increases in gut content. I measured its contribution and concluded that gut fill could not fully account for increase in weight gains. Body composition of wapiti maintained in a low quality diet in winter after compensation was similar to that of HW wapiti. Therefore, undernutrition in winter, did not alter the body composition of young growing wapiti.

Young wapiti stags wintered on low quality diet showed a pronounced increase in voluntarily feed intake on spring/summer pastures. Higher intakes and consequently, higher gains of LW wapiti were not explained. Diet digestibility, and therefore digestive efficiency were not important effects of nutritional history. However, compensating wapiti had higher intakes relative to maintenance requirements. I concluded that a high level of feed consumption provided a large margin above maitenance needs, thus allowing a high proportion of energy to be used for compensatory growth.

A comparison of behavior and performance of the two groups of wapiti during the compensating period, showed that both were influenced by the nutritional history. High daily weight gains were explained by higher feed intakes. Higher intake rates were achieved primarily through foraging longer and foraging much faster. Feeding rates were primarily determined by forage characteristics and appetite. Although wapiti could have increased dry matter intake by selecting habitats offering superior foraging opportunities, both HW and LW wapiti used the habitats in a similar manner. However, in April, LW wapiti preferred lowland grasslands. Selection of this habitat appeared to be strongly influenced by forage availability and quality.

Compensatory growth seems to be a complex multifactorial phenomenon enabling animals to survive in climates involving annually 'difficult' seasons. Despite weight stasis or loss during winter when feed diminishes in supply and quality, such animals eventually achieve normal mature size by increased rates of growth during periods of adequate feed supply. Summer weight gain is strongly related to body weight and condition at the end of winter, and differences in weight are largely made up by the rut (Hudson et al. 1985). During spring/summer, when good quality forage is abundant, wapiti eat above maintenance requirements to optimize growth and replenish depleted body tissue store. Therefore, the animal's ability to demonstrate weight gains during a short growth pulses ensures early maturity, and early reproductive success. This adaptation permits wapiti to exploit seasonally harsh environments and to anticipate and prepare for predictably changing conditions.

Intermittent restrictions in feed intake, whether they are imposed by management or reflect seasonal variability, are characteristic of most animals in production systems, particularly those based on extensive grazing. When the feed restriction is removed, animals show an increased voluntarily intake, and this is largely responsible for compensatory growth. The existence of the phenomenon if often to justify withholding expensive supplements from grazing animals during periods of feed shortage. However, growth compensation is only possible if pasture biomass is sufficient to permit it.

Practical implications

This natural rhythm provides an opportunity for game farmers to work with rather than against nature, capitalizing on the seasonal adaptations of indigenous ruminants. Animals conserve energy during seasons when feed is in diminishing supply and quality, then show marked increase and actually show superior gains over animals maintained on high quality, free-choice feed. During times when feed is in diminishing supplies (particularly in winter or dry season), animals can be fed less without reducing their capacity to recover. Recovery from undernutrition depends on several factors as suggested by Wilson and Osbourn (1960) and Reid and White (1977). This factors include, the nature of undernutrtion, severity of undernutrition, duration of the undernutrition period, stages of development at which undernutrition is imposed, the relative rate at which an animals matures, and its effect upon recovery and pattern of realimentation.

It is however, as a means of reducing the cost of rearing farm animals for meat that compensatory growth has the greatest application. With the increasing prices of cereals and purchased conserved fodders, the costs of maintaining livestock over winter period need careful consideration. However, winter feeding restrictions must not be too severe (i.e not to interfere with hyperplasia or hypertrophy), or else complete compensation may not occur during the following grazing season (Wilson and Osbourn 1960). The decrease in forage quantity and quality in late summer may also limit the extent of compensation during the grazing period (Wright 1985).

For farm animals to exploit fully compensatory growth on summer pastures, any feed restriction must be imposed immediately prior to the spring forage growth. However, whenever a farmer is faced with a problem of temporary scarcity of feed, as when spring is late, he can either ration the feed as a constant daily allowance, or he can give larger quantities of feed at less frequent intervals. There is evidence that the latter system is preferable. This short periods followed by *ad libitum* feeding on pasture, will enable animals to exploit compensatory growth. In this experiment, alfalfa-brome hay is a suitable winter diet and weaned stag calves could be fed to attain spring weights of about 150 kg, without impairing their capacity to compensate completely on summer pasture.

For a number of reasons, wapiti will be raised commercially under more extensive systems. This will demand a deeper understanding of compensatory phenomena and related mechanisms, and this will result in a more judicious application. One of the most pressing questions is that of determining optimal winter weight loss for different classes (age/sex) of wapiti and the appropriate stocking rates. Once we understand how to fully exploit compensatory growth, considerable cost savings and benefits can emerge from restricting animals at strategic times growth and development. Given the often unpredictable feed supply, the question may not be so much one of whether or not to restrict, but rather when and to what extent so as to minimize losses.

Literature cited

Donnelly, J.R., Davidson, J.L. and Freer, M. 1974. Effects of body condition on the intake of food by mature sheep. Aust. J. Agric. Res. 25: 813-823.

Hudson, R.J., Watkins, W.G. and Pauls, R.W. 1985. Seasonal bioenergetics of wapiti in western Canada. pp 447-452. In: P.F. Fennessy and K.R. Drew, eds. *Biology of Deer Production.* Royal Soc. New Zealand Bull. 22.

Reid, J.T. and White, O.D. 1977. The phenomenon of compensatory growth. Proc. Cornell Nutr. Conf. Feed Manufactures. Cornell Univ. Ithaca, NY.

Wilson, P.N. and Osbourn, D.F. 1960. Compensatory growth after undernutrition in mammals and birds. Biol. Rev. 35: 324-363.

Wright, I.A. 1985. Compensatory growth in beef cattle. pp 195-201. In: F.H. Baker and M.E. Miller, ed. *Emerging Technology and Management for Ruminants.* Livestock seminars, International Stockmen's school. Winrock International.

APPENDICES

Appendix 1

Monthly weight dynamics (kg) of LW and HW wapiti at the Ministik Wildlife Research Station.

Month	Dec	Jan	Feb	March	April	May	June	July
LW wapiti								
8901	178	183	176	170	170	181	203	300
8903	172	177	172	167	163	168	188	203
8911	160	164	156	157	155	157	173	185
8913	138	145	137	136	128	128	152	164
8919	146	149	142	136	127	132	159	161
8923	134	135	135	127	117	—	—	—
HW wapiti								
8905	139	163	150	161	161	166	191	191
8907	143	146	150	164	164	169	186	200
8909	152	161	166	176	173	172	184	195
8915	140	142	149	161	161	156	172	180
8917	125	133	136	145	152	139	152	162

Appendix 2

Linear measurements (cm) for LW and HW wapiti on May 1 and August 2 at the Ministik Research Station.

Month	May 1			August 2		
	Length	girth	hip width	Length	girth	hip width
LW wapiti						
8901	—	—	—	—	—	—
8903	137	122	14.9	165.1	143.5	17.8
8911	136.6	116.3	14.5	—	—	—
8913	124.5	109.2	11.4	147.3	137.2	14
8919	121.9	101.6	8.9	153.7	132.1	17.8
8923	117.1	96.5	7.9	—	—	—
HW wapiti						
8905	146.1	127	15.5	172.7	144	17.8
8907	132.1	127	15	152.4	141.6	16.5
8909	146.1	138.6	13.5	157.5	143.5	15.9
8915	144.1	128.3	13.5	142.2	130.8	15.2
8917	141.0	124.5	13.5	157.5	139.7	15.7

Appendix 3

Percent urea space (us/kg), and blood urea nitrogen (mMol/L) of LW and HW wapiti at the Ministik Wildlife Research Station.

Month	Percent urea space		Blood urea nitrogen	
	May 1	August 2	May 1	August 2
LW wapiti				
8901	—	—	—	—
8903	—	43.8	16.1	8.6
8911	39.4	54.6	13.6	7.9
8913	83.1	51.3	15.4	9.6
8919	—	—	15.4	—
8923	—	—	—	—
HW wapiti				
8905	62.4	42.7	10.4	8.6
8907	59	44.2	8.9	7.5
8909	91.8	46.8	8.2	7.9
8915	99.7	41.4	9.3	7.1
8917	60.1	48.5	10.4	7.9

Appendix 4

Monthly mean and standard errors of three habitats biomass (kg/ha), poplar forest upland and lowland grasslands at the Ministik Wildlife Research Station

Month	Poplar forest		Upland grassland		Lowland grassland	
	Mean	Se	Mean	Se	Mean	Se
April 28	278.6	22.9	413.3	32.9	167.8	32.9
May 11	462.5	62.2	880.4	57.8	709.7	61.1
May 30	945.7	102.7	968.8	30.6	682.0	64.6
June 19	1384.2	180.2	1674.4	162.3	1051.7	42.7
July 25	167.9	29.0	639.2	39.4	297.2	22.1

Appendix 5

Percentage of 24-hour day allocated to different activities by LW and HW wapiti at the Ministik Wildlife reasearch Station.   Dates shown are the starting dates for the trials.

Activity	Foraging	Resting	Standing	Walking + others
Animal no.				
APRIL 28				
8901	—	—	—	—
8903	57	34	6	3
8911	50	47	2	3
8913	53	35	9	2
8919	53	39	6	2
8923	56	37	5	1
8905	45	41	7	7
8907	41	43	9	7
8909	43	42	9	4
8915	48	39	10	1
8917	52	36	10	1
MAY 11				
8901	36	54	8	2
8903	35	52	9	4
8911	37	53	7	3
8913	35	50	8	6
8919	37	51	7	5
8905	33	48	9	9
8907	27	52	8	11
8909	31	54	6	8
8915	27	53	12	8
8917	32	55	8	7
JUNE 19				
8901	31	51	14	4
8903	35	49	14	2
8911	34	50	15	1
8913	38	44	14	4
8919	35	54	15	3
8905	30	54	15	2
8907	31	52	14	2
8909	31	55	12	1
8915	30	52	15	4
8917	38	43	17	3
JULY 25				
8901	18	59	8	12
8903	9	68	9	14
8911	10	70	8	12
8913	8	61	17	13
8919	11	65	7	15
8905	17	60	7	15
8907	12	63	8	17
8909	15	59	12	15
8915	7	67	11	15
8917	16	56	12	16

Appendix 6

Digestive parameters of LW and HW wapiti during spring/summer 1990 at the Ministik Wildlife Research Station. Dates shown are the starting dates for the trials.

Month	Digestibility (%)	Gut fill (kg)	Mean retention time (h)	Fecal Output (kg/d)
APRIL 24				
8901	—	—	—	—
8903	38.5	4.61	35.5	1.46
8911	46.1	2.66	36.3	1.23
8913	33.5	2.59	35.0	1.13
8919	39.3	2.87	30.8	1.18
8923	28.2	1.81	33.9	0.99
8905	48.4	1.97	36.2	1.07
8907	50.0	2.42	33.7	1.22
8909	52.7	3.58	30.2	1.51
8915	57.1	2.37	41.3	1.12
MAY 13				
8901	78.5	2.56	25.2	1.00
8903	75.9	2.67	23.6	1.45
8911	76.5	2.59	23.6	1.04
8913	74.9	3.19	22.0	1.42
8919	71.4	3.79	22.7	1.46
8905	75.0	2.0	24.8	0.94
8907	77.0	2.26	20.2	0.99
8909	74.1	2.66	24.6	1.03
8915	73.3	3.14	18.6	1.11
8917	78.4	2.68	21.7	0.90
JUNE 26				
8901	73.1	3.31	17.0	2.11
8903	69.0	8.72	16.9	2.36
8911	69.1	3.19	18.2	1.45
8913	71.6	4.59	18.3	1.83
8919	69.1	2.55	19.6	1.76
8905	66.0	2.54	17.7	1.47
8907	68.0	2.09	29.1	1.17
8909	70.4	2.72	23.4	1.70
8915	71.9	2.93	38.9	1.96
8917	65.0	3.19	19.5	1.91
JULY 22				
8901	56.7	3.20	34.3	1.35
8903	49.2	2.22	24.9	1.48
8911	46.1	2.36	27.3	1.45
8913	56.0	2.11	22.0	1.41
8919	44.1	2.09	25.2	1.43
8905	37.1	1.74	23.0	1.40
8907	46.0	1.82	19.6	1.56
8909	40.0	2.53	29.5	1.54
8915	44.0	3.05	29.5	1.78
8917	46.1	2.21	25.0	1.48