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DIGESTIVE KINETICS OF MOOSE (*ALCES ALCES*), WAPITI (*CERVUS ELAPHUS*) AND CATTLE

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ABSTRACT

Intake, rumen digesta pool sizes, ruminal digestion rates, passage rates of liquid and particle pools and faecal particle-size distrubutions of grass, browse and lucerne diets were compared in ruminally fistulated moose, wapiti and cattle. For each diet, ruminal digestion rates (nylon bag technique) were similar for the three ruminants. Intakes, rumen digesta pool sizes and passage rates varied among species and higher rates were associated with passage of larger faecal particles. However, it was not possible to simply rank the three ruminants as representative grazers (cattle), browsers (moose) and mixed feeders (wapiti) since intakes, passage rates and rumen pool sizes interacted with diet and season. Contrary to expectation, digestible dry matter intakes of each species were not greatest for their respective typical diets.

KEYWORDS: *Alces alces*, cattle, *Cervus elaphus*, intake, rumen digestion.

INTRODUCTION

HOFMANN (1973) classified African ruminants, and more recently, European and North American *Cervidae* (Hofmann, 1984 and 1985) into three categories: (1) browsers (concentrate selectors); (2) grazers (grass or roughage eaters); and (3) intermediate (mixed) feeders. Rumens of browsers are generally small with few physical barriers, but well papillated for utilizing diets rich in rapidly fermenting cell solubles. In contrast, grazers have highly developed and capacious rumens with numerous pillars and narrow ostia. Mixed feeders have rumens of intermediate size and show marked seasonal adaptation.

Although anatomical differences have been thoroughly documented and functional inferences made (Hofmann, 1988; Kay, Englehart and White, 1980; Langer, 1984 and 1987), definitive tests have received attention only recently (Baker and Hansen, 1985; Huston, Rector, Ellis and Allen, 1986; Spalinger, Robbins and Hanley, 1986; Baker and Hobbs, 1987; Kay, 1987). Consistent with anatomical design, concentrate selectors seem to propel digesta rapidly through the digestive tract, fermenting mainly soluble carbohydrates. Grazers retain food particles in the rumino-reticulum allowing time for more complete digestion of fibre. However, this picture is complicated by differential responses to diet and by seasonal adaptation which may be a direct consequence of photoperiod or physiological events such as lactation (Kay, 1985). Although these phenomena have been studied in several species (White, Holleman, Hubbert and Staaland, 1987), interactions between forage characteristics and season have not been fully evaluated.

This study explores these interactions in moose, wapiti and cattle as representative large browsers, mixed feeders and grazers, respectively. We compared voluntary intake, rumen digesta pools, ruminal fermentation rates and passage rates of grass (timothy-brome hay), forbs (lucerne) and browse (aspen foliage or twigs) during winter and summer.

MATERIAL AND METHODS

Animals and diets

Trials using one adult moose cow, two castrated adult male wapiti and two castrated adult Charolais × Hereford males fitted with ruminal cannulae (Renecker, Hudson and Berzins, 1982) were conducted during winter (January to April) and summer (July to September, 1982). Throughout, they were maintained in outdoor pens cleared of vegetation and were fed *ad libitum* twice daily for 21 days to determine voluntary intake. During this period there was evidence that animals would attempt to select certain plant parts (leaves *v.* stems), however, chemical composition of food residues was not compared. Feeding levels were adjusted to proportionately 0·90 of daily voluntary dry-matter (DM) intake during the 12-day trials conducted in each season.

Diets were selected to represent major forage classes: grasses [timothy (*Phleum pratense*)-brome (*Bromus inermis*)]; forbs [lucerne (*Medicago sativa*)]; and browse [aspen (*Populus tremuloides*)]. However, since moose are unable to subsist on pure diets of grass and cattle are unable to subsist on browse for long periods, each of these forage sources was mixed with an equal quantity of lucerne. The three diets were given each season in the order of timothy-brome hay/lucerne, lucerne and either aspen twigs or foliage/lucerne. The chemical composition of these mixed diets is given in Table 1.

Lucerne and grass hays were chopped with a tub grinder to stem lengths of about 10 cm to avoid selection of plant parts. Aspen twigs given during winter consisted of the current annual growth from saplings cut in late winter. Aspen foliage offered during summer was stripped by hand from mature trees during early July.

Apparent digestibilities

Apparent digestibility was estimated using lignin as an internal marker (Van Soest, 1982). Digestibilities estimated from the ratio of lignin concentrations in food and faeces were used to calculate digestible DM intakes.

Ruminal digestion

The potential rate and completeness of ruminal fermentation was determined by the *in situ* nylon bag technique (Playne, Khumnualthong and Echevarria, 1978; Ørskov, Hovell and Mould, 1980). Approximately 3 g dried forages (timothy-brome hay, lucerne or aspen twigs or foliage), ground through a 3-mm screen of a Christie-Norris laboratory mill, were weighed with monofilament nylon bags (10 × 15 cm, porosity 10 μm) tied to a weight and placed in the ventral sac of the rumen. Diets offered during the rumen degradability study are listed above. Following incubation in duplicate for 0, 3, 6, 12, 24, 36, 48 and 72 h, the bags were washed and oven-dried at 60°C to constant weight.

Potential digestibilities and disappearance rates of DM were calculated by iterative least squares regression (Jennrich, 1981) using the model: $Y = A - Be^{(-kt)}$ where, Y is food digestibility at time t, A is the asymptotic (potential) digestibility, B is the soluble DM, k is the relative disappearance rate (l/h) of the slowly degradable fraction and t is the

TABLE 1
Chemical composition (g/kg DM) of mixed diets used in winter and summer trials

Foodstuff	Dry matter (g/kg DM)	Crude protein (g/kg DM)	Neutral-detergent fibre (g/kg DM)	Acid-detergent fibre (g/kg DM)	Acid-detergent lignin (g/kg DM)	Ash (g/kg DM)
Timothy-brome hay	975	93	588	329	52	5
Lucerne (winter)	944	162	496	356	118	4
Lucerne (summer)	945	166	478	345	81	5
Trembling aspen twigs	550	65	432	310	155	5
Trembling aspen foliage	444	139	370	240	152	6

time (h) food samples in nylon bags were incubated in the rumen.

Rumen pools and retention times

Passage of particulate digesta was estimated by administering dysprosium (Dy)-labelled and chromium-mordanted grass, lucerne, aspen twigs or aspen foliage. The fluid phase was marked with cobalt ethylene diamine tetra-acetic acid (EDTA). A pulse dose of each marker was administered through the ruminal cannula on the 1st day of each trial. Grab samples of rumen solids were collected every 3 h for the first 36 h, every 6 h for 1 day and then once each day until 120 h. Rumen fluid (20 ml) was collected every 3 h for the first 24 h and then every 6 h until 72 h.

Dysprosium label. Forages (675 g) were immersed in distilled water containing 10·1 g (28 mmol/l) of Dy chloride crystal ($DyCl_3.6H_2O$) for 24 h. Labelled food was rinsed with distilled water for 6 h and oven-dried at 60°C (Ellis, Lascano, Teeter and Owens, 1982). The bound label ranged from 5·3 to 8·4 mg Dy per g DM. Dy concentrations of food and faecal samples were analysed in the University of Alberta SLOWPOKE reactor facility using the Dy INAA scheme (Kennelly, Apps, Turner and Aherne 1980).

Chromium-mordanted fibre. The 1 to 2 mm food fraction separated by wet sieving (Kennedy, 1985) was mordanted with chromium (Cr) as described by Udén, Colucci and Van Soest (1980). Samples (11·2 g) of the Cr-mordanted fibre were placed in a paper bag and then introduced into the rumen through the rumen cannula. Oven-dried rumen subsamples were ground through a 20-mesh screen of a Wiley mill, dry-ashed, digested in concentrated HNO_3, redissolved in HNO_3 (1 mol/l) and centrifuged (Murthy, Rhea and Peeler, 1971). Concentration of Cr in the supernatant was measured by atomic absorption spectrophotometry (Perkin Elmer model 4000).

Cobalt EDTA. Cobalt EDTA (CoEDTA) (15 g) was prepared as a sodium salt as described by Udén *et al.* (1980). Samples of rumen fluid were centrifuged at 20 000 **g** for 15 min and 1 to 5 ml of the supernatant was diluted to a volume of 50 ml with HCl (0·3 mol/l). Cobalt was analysed by atomic absorption spectroscopy.

Rumen outflow and volume. Outflow was determined by least-squares regression of the natural logarithm of marker concentration in rumen contents against time post administration. The first sample was taken 3 h post dosing. The resulting slope was the rate constant (k_1) and its intercept estimated marker dilution at time zero. Rumen volume was calculated from the estimated initial marker concentration in the rumen and the zero-time dose of water soluble marker of Dy-labelled particles. Rumen turn-over time (RTT) was calculated as the reciprocal of k_1 (Hungate, 1966).

Faecal particle size

Distributions of food particle sizes in faecal grab samples (collected concurrently with rumen samples) were obtained by wet-sieving (Dixon and Milligan, 1985; Kennedy, 1985) using a series of screens (mesh size openings were 7·4, 4·0, 3·35, 2·0, 1·0, 0·71, 0·50 and 0·25 mm). Material retained on each sieve was oven-dried to constant weight. Particulate material which passed through the smallest screen was collected by centrifugation at 20 000 **g**, washed and oven-dried at 60°C to constant weight.

The log-normal distribution was fitted to cumulative weights of particles of decreasing sizes (Waldo, Smith, Cox, Weinland and Lucas, 1971) and distributions were expressed as $\log_{10}$ mean (± s.d.) particle size (MPS) in µm. Also, the cumulative percentage of DM retained on screens was reported as large particle size (LPS) (> 3·35 mm), medium particle size (1 to 3·35 mm) and small particle size (< 1·0 mm). Proportion of particles in each fraction were expressed as ratio of uniformity (American Society of Agricultural Engineers (ASAE), 1967).

Statistical comparisons

Because two different aspen diets were used (foliage and twigs), comparisons were made between seasons and rations (grass hay and lucerne) using orthogonal sets of comparisons (Steel and Torrie, 1980) and the CONTRAST subcommand in one-way procedures of SPSS (Anonymous, 1983). Asymptotes, rate constants and intercepts were compared by analysis of variance (Anonymous, 1983) and Duncan's Multiple Range Test (Steel and Torrie, 1980). Analysis of variance (Steel and Torrie, 1980) and orthogonal comparisons (Anonymous, 1983) were applied to particle size data.

RESULTS

Voluntary intake

Intakes by the three ruminants were proportionately about 0·02 body weight during summer but because of their larger size, intakes by cattle on a metabolic weight basis were generally highest (Table 2). In winter, forage consumption by moose and wapiti was lower than cattle ($P < 0·05$) which maintained relatively constant intakes of grass/lucerne and lucerne hays but low DM consumption of aspen.

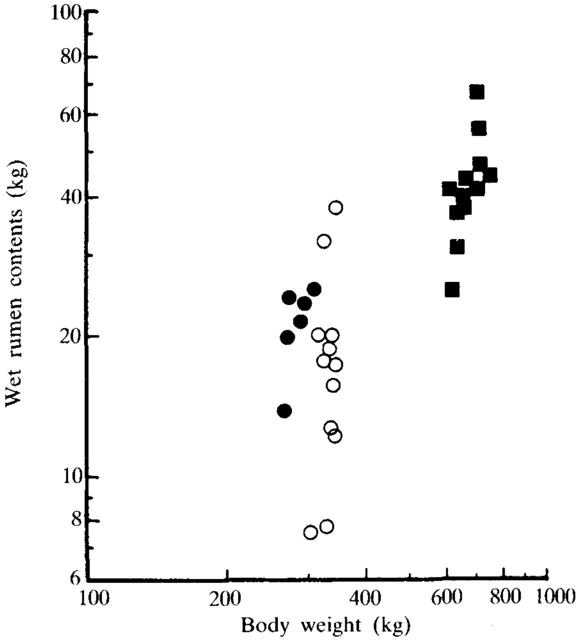

FIG. 1. Relationship between live body weight and rumen capacity in three ruminant species: ● moose; ○ wapiti; ■ cattle.

Digestible DM intakes of grass hay were high in all three ruminants. Although

TABLE 2

Body weights (BW), dry-matter intake (DMI) and digestible dry-matter intakes (DDMI) of moose, wapiti and cattle given four diets ad libitum

	Winter					Summer				
	Moose†	Wapiti‡		Cattle‡		Moose†	Wapiti‡		Cattle‡	
Grass hay/lucerne										
BW (kg)	265	302	329	631	612	303	326	346	738	694
DMI (g/kg BW)	15·7	11·4	13·2	22·0	22·8	22·4	21·6	21·0	20·2	24·2
DMI (g/kg $\mathrm{BW}^{0·75}$)	63·3	47·6	56·0	110·2	113·2	93·3	91·8	90·7	105·4	124·3
DDMI (g/kg BW)	5·0	3·3	3·9	8·6	8·7	15·5	15·2	15·0	15·1	16·1
Lucerne										
BW (kg)	271	331	340	650	633	294	327	347	698	702
DMI (g/kg BW)	16·0	12·0	14·2	22·0	22·5	19·7	20·3	19·5	21·7	21·1
DMI (g/kg $\mathrm{BW}^{0·75}$)	64·7	51·2	60·8	111·3	112·6	92·7	86·1	84·1	111·4	108·5
DDMI (g/kg BW)	5·6	3·8	4·8	7·9	8·1	7·9	7·8	7·0	7·4	7·2
Aspen twigs/lucerne										
BW (kg)	271	331	340	641	611					
DMI (g/kg BW)	14·5	11·3	11·7	9·3	7·6					
DMI (g/kg $\mathrm{BW}^{0·75}$)	58·8	48·2	50·4	46·9	45·8					
DDMI (g/kg BW)	4·8	3·0	3·2	2·2	1·2					
Aspen foliage/lucerne										
BW (kg)						288	317	339	711	686
DMI (g/kg BW)						20·1	19·1	18·5	17·7	18·5
DMI (g/kg $\mathrm{BW}^{0·75}$)						82·9	80·6	79·3	91·4	94·7
DDMI (g/kg BW)						10·7	9·9	8·5	9·5	9·7

† Values indicate observations from a single animal.
‡ Data from each of two animals.

digestible DM intakes of cattle were low when given aspen twigs and high when given grass hay, moose and wapiti did not show clear superiority on browse and intermediate diets, respectively.

Whole gut digestibilities using lignin as a marker (0·30 to 0·39 in winter and 0·34 to 0·71 in summer) were lower than 50-h rumen degradabilities (0·45 to 0·52 in winter and 0·48 to 0·54 in summer). This divergence, especially during winter, may reflect a partially digestible lignin marker.

Rumen capacity

Inter-specific differences in wet rumen contents (rumen liquid volumes and DM) were partly related to body weights (Figure 1). As a proportion of body weight, ruminal liquid volumes were generally greatest for moose particularly in winter and on grass diets whereas wapiti had the lowest volumes (Table 3). During winter, ruminal DM contents of all three ruminants were greatest for the aspen twig diet. In summer, lucerne diets were associated with the highest rumen DM. Irrespective of diet, cattle had the driest and moose the most fluid rumen contents.

Ruminal digestion

Ruminal DM disappearance conformed to first-order kinetics and could be adequately described by the asymptote, intercept and rate constant of asymptotic regression (Table 4).

Potential digestibility. Asymptotic digestibilities representing the potentially digestible fraction did not vary significantly among ruminant species. However, diets were ordered in terms of increasing potential digestibility as follows: aspen twigs, lucerne, grass hay and aspen foliage. No difference between seasons nor ration × season interactions occurred for grass hay or lucerne. Potential digestibility of neutral-detergent fibre was inversely related to lignin content ($Y = 76{\cdot}6 - 3{\cdot}6X$, $\text{s.e.}_b = 0{\cdot}66$, $r^2 = 0{\cdot}88$, $P < 0{\cdot}001$), a relationship which differed little among ruminant species.

Soluble dry matter. The intercept (B of the asymptotic regression) estimates the proportion of forage DM which is rapidly solubilized in the rumen. Ruminant species were not different but grasses and lucerne were different ($P \leqslant 0{\cdot}01$) as was their

TABLE 3

Rumen liquid volumes (Vol) and dry matter (DM) pool of food particles in moose, wapiti and cattle given four diets

	Winter					Summer				
	Moose†	Wapiti‡		Cattle‡		Moose†	Wapiti‡		Cattle‡	
Grass hay/lucerne										
Vol (l/100 kg BW)	21·0	11·0	7·6	13·7	14·5	10·9	75	6·9	13·8	11·8
DM (kg/100 kg BW)	0·79	0·39	0·37	1·06	0·71	1·18	0·95	0·87	1·04	1·07
DM	0·15	0·16	0·16	0·17	0·18	0·14	0·17	0·18	0·17	0·18
Lucerne										
Vol (l/100 kg BW)	18·4	9·2	7·8	16·7	18·9	16·3	17·2	15·0	14·1	13·9
DM (kg/100 kg BW)	1·11	0·58	0·56	1·18	0·91	1·31	1·63	1·81	1·77	1·46
DM	0·15	0·15	0·16	0·18	0·19	0·16	0·16	0·17	0·18	0·19
Aspen twigs/lucerne										
Vol (l/100 kg BW)	14·9	7·8	6·0	17·9	16·1					
DM (kg/100 kg BW)	1·36	0·93	0·76	1·03	1·13					
DM	0·15	0·17	0·17	0·16	0·18					
Aspen foliage/lucerne										
Vol (l/100 kg BW)						17·6	9·8	10·8	12·8	14·0
DM (kg/100 kg BW)						1·12	1·07	0·99	1·15	1·10
DM						0·15	0·17	0·17	0·17	0·18

† Values indicate observations from a single animal.
‡ Data from each of two animals.

TABLE 4

Regression† of dry-matter loss of food from nylon bags on the time that bags were incubated in the rumen of moose, wapiti and cattle

	Asymptotic digestibility (A)	Soluble dry matter (B)	Relative digestion rate		
			k, % per hr	s.e.	Significance
Winter					
Timothy-brome hay					
Moose	55·0	4·9	4·46	0·96	***
Wapiti	64·2	7·9	3·86	0·80	***
Cattle	62·1	3·8	3·31	1·60	***
Lucerne					
Moose	51·9	4·3	7·79	0·90	***
Wapiti	51·5	5·1	8·81	1·10	***
Cattle	53·9	4·6	4·76	2·42	***
Aspen twigs					
Moose	48·1	13·6	5·90	1·10	***
Wapiti	46·2	12·1	8·03	1·49	***
Cattle	45·3	9·8	7·47	1·94	***
Summer					
Timothy-brome hay					
Moose	67·9	5·3	2·26	1·68	***
Wapiti	58·8	2·0	3·27	0·91	***
Cattle	60·8	6·3	3·13	2·06	***
Lucerne					
Moose	52·4	8·4	4·08	2·81	***
Wapiti	57·7	9·1	4·33	1·54	***
Cattle	55·1	8·4	4·70	0·17	***
Aspen foliage					
Moose	57·7	6·9	7·98	2·23	***
Wapiti	54·7	11·8	7·24	1·14	***
Cattle	52·9	14·1	4·63	1·04	***

† Variables fit an equation where $Y = A - Be^{-kt}$.

interaction with season ($P < 0{\cdot}01$). Intercepts of asymptotic regressions were correlated with cell solubles determined by detergent fibre methods (Goering and Van Soest, 1970) ($P < 0{\cdot}001$, $r = 0{\cdot}74$).

Fermentation rate. DM disappearance rates for the slowly degraded fraction did not differ significantly among ruminants. However, differences in rate of disappearance were evident between grass hay and lucerne ($P \leqslant 0{\cdot}05$) and the diet × season interaction ($P \leqslant 0{\cdot}05$). Aspen twigs and lucerne were digested more rapidly than winter grasses ($P < 0{\cdot}01$). In summer, foliage was digested more rapidly.

Passage rates

Moose generally had the longest retention times of particulate matter and wapiti the shortest (Table 5). Lucerne was retained longest and aspen foliage shortest. In winter, wapiti passed all diets rapidly. Cattle retained food particles longer. Moose showed the greatest responsiveness to diet, propelling aspen twigs rapidly but grass hay and especially lucerne very slowly. In summer, all species and diets were passed more uniformly. The shortest retention times were for moose given aspen foliage and the longest retentions were for cattle given lucerne. Mordanted food particles were retained longer than Dy-labelled particles but showed the same pattern (Table 6).

Moose generally had the longest liquid retention times and wapiti and shortest (Table 7). Liquids passed most rapidly for the aspen foliage diet. Flow rates of Dy-labelled food

TABLE 5

Turn-over times (h) of food particles in moose, wapiti and cattle given Dy-labelled forages during winter and summer

	Winter					Summer						
	Moose†	Wapiti‡		Cattle‡		Moose†	Wapiti‡		Cattle‡		Mean	s.d.
Grass hay/lucerne	28·2	18·7	15·7	20·8	20·6	18·1	16·1	17·5	18·0	17·2	19·1	1·1
Lucerne	32·7	18·8	16·2	21·3	20·9	19·1	20·1	21·7	22·5	20·3	21·4	1·4
Aspen twigs/lucerne	19·3	18·4	16·0	23·3	24·3						20·3	1·6
Aspen foliage/lucerne						12·4	13·8	14·2	14·7	14·5	13·9	0·4

† Values indicate observations from a single animal.
‡ Data from each of two animals.

TABLE 6

Turn-over times (h) of several Cr-mordanted forages given to moose, wapiti and cattle during winter and summer

	Winter					Summer						
	Moose†	Wapiti‡		Cattle‡		Moose†	Wapiti‡		Cattle‡		Mean	s.d.
Grass hay	30·7	18·4	26·1	31·4	23·6						26·0	2·4
Lucerne	36·9	20·0	22·8	28·0	30·1	19·2	23·5	26·6	27·8	24·8	26·0	2·3
Aspen twigs	27·9			35·3	35·9						33·0	2·6
Aspen foliage						16·4	19·8	21·2	20·4	20·8	29·7	0·9

† Values indicate observations from a single animal.
‡ Data from each of two animals.

TABLE 7

Turn-over times (h) of rumen liquids in moose, wapiti and cattle given four diets during winter and summer

	Winter					Summer						
	Moose†	Wapiti‡		Cattle‡		Moose†	Wapiti‡		Cattle‡		Mean	s.d.
Grass hay/lucerne	23·5	11·3	11·9	9·5	8·1	14·4	11·2	10·3	11·3	13·3	12·5	1·4
Lucerne	23·1	11·8	9·4	11·5	11·9	16·8	10·6	10·0	10·4	11·0	12·7	1·3
Aspen twigs/lucerne	18·9	10·0	0·6	15·7	11·3						13·1	1·8
Aspen foliage/lucerne						9·7	9·7	10·3	11·9	11·7	10·7	0·5

† Values indicate observations from a single animal.
‡ Data from each of two animals.

particles were highly correlated with the flow of liquids in moose ($r = 0{\cdot}96$, $P < 0{\cdot}01$) (Figure 2). A similar but weaker relationship was obtained for wapiti ($r = 0{\cdot}62$, $P > 0{\cdot}05$) but not for cattle.

Faecal particle sizes

Faecal particle-size distributions of the three ruminants did not differ significantly (Table 8). Differences in mean particle size due to diet ($P < 0{\cdot}01$) and diet × season interaction ($P < 0{\cdot}01$) were apparent for grass hay and lucerne. Faecal particles tended to be larger on diets containing aspen leaves or twigs, particularly in moose where some aspen leaf fragments measured 13 × 8 mm. Wapiti passed a relatively constant proportion of particles in the 1 to 3·35 mm fraction on all diets except winter lucerne. Large cylindrical particles measuring 24 × 2 mm, were

TABLE 8

Faecal mean particle size (MPS) distributions from moose, wapiti and cattle given three diets during winter and summer†

	Winter			Summer		
Diets	Moose‡	Wapiti	Cattle	Moose‡	Wapiti	Cattle
Grass/lucerne						
MPS (μm)	668	909	578	630	797	616
Ratio of particle uniformity§	1:4:5	1:5:4	1:3:6	1:4:5	1:5:4	1:4:5
Lucerne						
MPS (μm)	667	398	476	568	746	700
Ratio of particle uniformity	1:3:6	0:3:7	0:3:7	1:3:6	1:4:5	1:4:5
Aspen twigs/lucerne						
MPS (μm)	915	827	876			
Ratio of particle uniformity	1:5:4	1:5:4	1:5:4			
Aspen foliage/lucerne						
MPS (μm)				963	748	627
Ratio of particle uniformity				2:4:4	0:5:5	0:4:6

† All regressions were significant at $P < 0·05$.

‡ Values indicate mean of four samples × two replicates from a single animal.

§ Ratio of particle uniformity = % of particles > 3·35 mm: % of particles 1 − 3·35 mm: % of particles < 1 mm (ASAE, 1967).

collected in the faeces of wapiti given pure lucerne. On grass hay/lucerne diets, cattle passed smaller particles except on the aspen/lucerne diet.

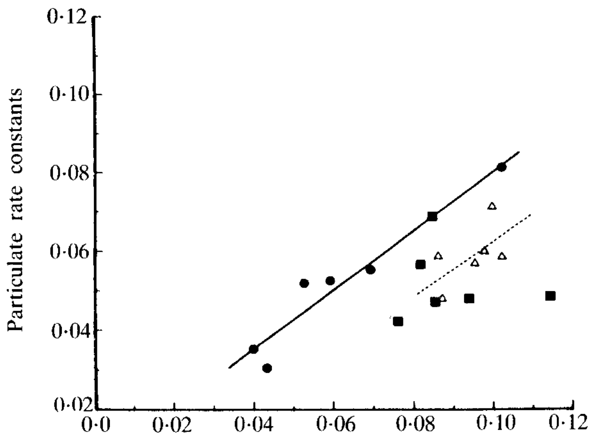

Fig. 2. Relationship between particulate and liquid passage rates for pooled data of moose and wapiti fed on grass, lucerne, aspen foliage and aspen twig diets during summer and winter trials 1982: moose ● —— $Y = 0·004 + 0·761X$, $r^2 = 0·93$; wapiti △ — — — $Y = -0·005 + 0·679X$, $r^2 = 0·38$; cattle ■.

DISCUSSION

To maximize daily digested organic matter intakes, ruminants should optimize the trade-off between passage rate and completeness of digestion (Foose, 1982). Their ability to do so depends on digestive morphology and function. Large browsers (e.g. moose) are expected to propel highly lignified browse residues through the rumino-recticulum but become bulk-limited on more fibrous grass diets. Grazers (e.g. cattle) should detain food in the rumen for extensive digestion, with flow decelerating with diet indigestibility. Our study revealed interactions of species, diets and seasons which suggest a more complex picture.

Dry matter intake

Voluntary intake of fibrous forages is limited by physical distention of the rumino-reticulum (Balch and Campling, 1962; Baumgardt, 1970) and therefore, should scale isometrically to body weight (Poppi, Minson and Ternouth, 1981; Van Soest, 1982; Baker and Hansen, 1985). Expressed in this manner, few differences were found among the three ruminants except that cattle consumed little of the aspen twig diet. Since cattle were considerably larger, intakes were typically higher on a metabolic weight basis ($M^{0.75}$) and this factor may have accounted for their generally higher weight gains during the experiment.

In this experiment moose and wapiti, but not cattle, reduced food intake during winter. Whether this widespread phenomenon reflects trophic adaptation of wild ungulates is not certain (Ozoga and Verme, 1970; Milne MacRae, Spence and Wilson, 1978; Westra and Hudson, 1981; Suttie, Goodall, Pennie and Kay, 1983). Although domestic sheep share this trait (Kay, 1979), large wild bovids such as bison (*Bison bison*) do not appear to have well developed seasonal cycles (Richmond, Hudson and Christopherson, 1977).

Rumen capacity

Gut capacity scales allometrically among herbivores (Parra, 1978; Demment, 1982; Demment and Van Soest, 1985) but slightly different relationships are expected for browsers and grazers. Contrary to this expectation, liquid and DM pools as a proportion of body weight of the moose were similar to (summer) or higher (winter) than those of wapiti and cattle.

Rumen fill was related to voluntary intake and fermentation and passage rates. When feeding on forage with a high cell content, browsers seldom use more than 0·60 of the rumino-reticular space (Van Hoven and Boomker, 1985) because this highly nutritious food is digested and propelled rapidly through the gastrointestinal tract (Demment, 1982), whereas slowly digesting grasses occupy greater rumen volume.

Fermentation rate

Fermentative capacities of moose, wapiti and cattle given equal opportunity for digestive adaptation were not detectably different. This corroborates with *in situ* comparisons of domestic sheep and cattle (Prigge, Baker and Varga, 1984) and *in vitro* comparisons of wapiti and mule deer (*Odocoileus hemionus*) (Baker and Hansen, 1985). Other than through diet selection, ruminants seem unable to adjust to the rumen environment sufficiently to select different microbial populations. This suggests that digestive adaptations are primarily related to regulating the flow of food particles and changing absorptive surfaces.

Particle kinetics

Hofmann (1973) generalized that retention times should be lowest in browsers and highest in grazers. Passage rates did vary among ruminants and this seemed to be achieved by passing larger particles. However, it was not possible simply to rank species according to typical passage rates since this varied widely with diet. However, moose were most sensitive to diet; propelling browse diets more rapidly than cattle but retaining grass hay and lucerne longer than wapiti or cattle.

The close association between the flow of solid and liquid phases from the rumen of moose and wapiti but not cattle (this study, Schwartz, Regelin, Franzmann, White and Holleman, 1988) may indicate the kinetic mechanism. Since no stratified layers of solids were found in the rumen of moose, particulates may be flushed through the reticulo-omasal orifice by volumes of liquids.

Based on the critical particle-size theory (Poppi, Norton, Minson and Hendricksen, 1980), threshold range (< 5% of faecal particles oversize) of particles was highest for moose ranging from 4·4 to 6·9 mm with the probability of passage increasing for high lignin rations. In wapiti, the critical size for particle escape from the rumino-reticulum and passage through the lower gastrointestinal tract was lower, ranging between 3·2 and 4·8 mm. In cattle, the critical size of particles generally ranged between 3·0 and 4·2 mm with the exception of aspen twigs which averaged 5·4 mm.

In conclusion, the ability of browsing ruminants (moose) to extract adequate energy from forages of low asymoptotic digestibility depends on their rapid passage rate. This is achieved by propelling larger particles through the rumen. The reticulo-omasal orifice also may be selective for shape and size, restricting passage of long fibrous particles but allowing larger cuboidal browse particles to pass. Similar findings were reported for mule deer (browser) which passed highly lignified *Vaccinium* spp. faster than grass (Milchunas, Dyer, Wallmo and Johnson, 1978).

Grazers (cattle) achieve more complete digestion of diets high in cell walls by retaining forages longer. When grazers are given highly lignified browse, well developed delaying structures cause ruminal accumulation of indigestible material and intake limited by gut fill.

Mixed feeders (wapiti) appear to be more flexible without compromising their ability to use either grass or browse. Despite the similarity in retention times and particle distributions of the 1 to 2 mm fractions of wapiti given different rations, it is probable that their ability to adjust chewing rates may be the controlling factor. Studies with moose indicate that daily rumination times (to a maximum of 11 h) and mastication rates increase with dietary neutral-detergent fibre (Renecker and Hudson, 1989). This suggests that ungulates do have the ability to adjust the duration and intensity of chewing and that further comparative information about chewing behaviour and particle-size reductions in ruminants is required before a comprehensive understanding can be achieved.

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