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The role of gut tissue in the energy metabolism of growing lambs fed forage or concentrate diets

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The role of the gastrointestinal tract (GIT) in explaining the less efficient utilization of metabolizable energy (ME) in growing lambs fed forage rather than concentrate-based diets was investigated by feeding forage (legume–grass silage) and concentrate (whole shelled maize) diets, at isoenergetic intakes (ME basis), using five groups of lambs. One group of seven lambs was an initial slaughter group and of the two groups (eight lambs per group) fed each diet, one group was fed for 8 weeks, whereas the other group was fed for 16 weeks. All lambs were slaughtered between 18·5 and 20 h following their last meal. Retained energy (as a percentage of ME intake) was higher (concentrate-fed 28, forage-fed 17; $P<0·001$) for the concentrate-fed animals. Weight-specific mucosal O_2 uptake (ml/g DM per h), measured *in vitro*, was 37 % higher for the forestomach (reticulum, rumen and omasum) and small intestine (jejunum) than for the abomasum and large intestine (caecum and colon), but there was no evidence for a diet effect (except colon; forage-fed 5·3, concentrate-fed 4·2; $P=0·036$). Total GIT heat loss was estimated as 14 (forage-fed) and 18 (concentrate-fed) % of the whole-body heat loss. Although the GIT did not contribute to increased thermogenesis in the forage-fed lambs in the present study, greater relative contribution of GIT tissue to whole-body mass, i.e. GIT as a percentage of empty-body weight(forage 7·6, concentrate 6·6; $P<0·001$) in the forage-fed animals supports a role for the GIT in contributing to higher thermogenesis observed in ruminants fed forage as opposed to concentrate diets.

Gut energy metabolism: Forage: Concentrate

When growing ruminants are fed the same amount of metabolizable energy (ME) as either forage or concentrate, the ME is used less efficiently, with more energy being lost as heat, on the forage diet (Orskov & MacLeod, 1990). Initially, it was suggested (McClymont, 1952; Armstrong & Blaxter, 1957) that inefficient utilization of acetate, a rumen fermentation end product produced in higher molar proportions by forage- than by concentrate-fed animals, might explain the higher heat increment associated with forage feeding. Subsequent respiration calorimetry (Orskov *et al.* 1969, 1979, 1991; Johnson, 1972; Orskov & MacLeod, 1993) and comparative slaughter trials (Bull *et al.* 1970) have not supported this theory. More recently, enhanced metabolic activity of gut tissue in forage-fed animals has been considered as a potential contributor to high thermogenesis (Reynolds *et al.* 1991). As there are no currently published data that describe the comparative metabolic activity of all seven major gastrointestinal tract (GIT) components in ruminants fed forage or concentrate diets, the objective of the present study was to investigate the metabolic activity (weight-specific O_2 consumption) of mucosal tissue from each of these GIT components.

Methods

Experimental design

This comparative slaughter trial was designed as a randomized complete block experiment, using two diets (forage and concentrate) and two feeding durations (8 and 16 weeks) in a 2×2 factorial treatment design. Each of the four treatments was replicated with eight animals, and an initial slaughter group was replicated with seven animals. The trial was carried out as two blocks, with the two groups of lambs born 3 months apart.

Animals

After weaning, the Rideau Arcott (Ainsworth *et al.* 1990) wether lambs were allowed to adjust to the change in

Abbreviations: GIT, gastrointestinal tract; ME, metabolizable energy.

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environment, for 3–4 weeks before introduction of the experimental diets. Animals were housed in pairs, with one forage- and one concentrate-fed lamb in each pen. Each animal was weighed weekly throughout the trial, and on each of the 2 d preceding slaughter, with weights being recorded at 14.00 hours.

Diets and feeding

The forage diet was based on mixed (legume–grass) silage, and the concentrate diet was based on whole shelled maize (*Zea mays indentata*). The silage, which was made from first-growth wilted forage, cut in the early bloom stage of development, consisted mainly of lucerne (*Medicago sativa*) with a small amount of grass, mostly timothy (*Phleum pratense*). The silage contained 393 g DM/kg and the composition (g/kg DM) was: organic matter 923, crude protein ($N_{total} \times 6{\cdot}25$) 183 (g/kg total N; NH_3-N 126, non-protein N 580, soluble N 601), lactic acid 63, acetic acid 11·3, propionic acid 0·1, butyric acid 0·2, neutral-detergent fibre 475, acid-detergent fibre 366, acid-detergent-fibre lignin 60, with pH 4·5. The silage was supplemented with pellets containing maize-gluten meal, blood meal and a vitamin–mineral mix, and the maize was supplemented with pellets containing soyabean meal, maize-gluten meal, blood meal, urea and a vitamin–mineral mix (Table 1). The supplementary pellets were formulated so that lambs on the forage diet would be provided with equivalent amounts of rumen-undegradable crude protein to those of animals fed concentrate. The crude protein content of both diets was decreased by 3 % after the first 8 weeks, to reflect modified protein requirements with increasing animal live weight (National Research Council, 1985).

Each animal was fed individually isoenergetic (ME basis) amounts of the diets with half their daily allotment given between 08.00 and 10.00 hours and the remainder between 14.00 and 16.00 hours. Diets were introduced gradually within the first 3 weeks of the trial, by replacing 25, 50, 75 and finally 100 % of the creep feed to which the lambs were adapted during the pre-trial period. At the start of the trial, the lambs were grouped by 5 kg body-weight intervals. Intake limitations were reached first by those lambs fed the forage diet. To establish equivalent intakes of ME between diets, forage-fed animals were fed *ad libitum*, whereas concentrate-fed animals were restricted to a ME intake equivalent to that of forage-fed lambs in the same weight group. Water was available to all lambs at all times.

Total faeces were collected daily for a 7 d period, during week 12 of the 16 week feeding trial, using faecal collection bags. ME was calculated as digestible energy $\times 0{\cdot}82$ for the forage-fed animals (National Research Council, 1985), and as digestible energy $\times 0{\cdot}90$ for those fed concentrate, using the higher ratio reported by Johnson (1972) for growing lambs fed a whole-maize diet.

Slaughter procedures and carcass sampling

Initial-slaughter-group animals, which had been fed only the creep feed used during the pre-trial period, were slaughtered during week 1 of the feeding trial. Animals fed either the forage or concentrate diet for 8 weeks were slaughtered during week 9 and animals fed for 16 weeks were

Table 1. Diet composition for four groups of eight growing lambs

Diet…	Forage		Concentrate	
Feeding period…	Weeks 1–8	Weeks 9–16	Weeks 1–8	Weeks 9–16
Ingredients (g/kg DM)				
Lucerne silage	882	938	–	–
Whole shelled maize	–	–	500	500
Supplementary pellets	118	62	500	500
Ground maize	–	–	226	290
Maize-gluten meal	59	25	77	36
Blood meal	39	17	51	24
Soyabean meal	–	–	69	70
Urea	–	–	5	5
Limestone	–	–	34	38
Dicalcium phosphate	–	–	8	9
Vitamin–mineral mix*	17	18	24	24
Fat	3	2	6	4
Composition				
DM (g/kg fresh weight)	419	408	886	885
Organic matter (g/kg DM)	918	914	942	928
Crude protein†	234	205	223	193
Gross energy (MJ/kg DM)	18·92	18·67	19·09	18·51
Ca (g/kg DM)	14	15	19	24
P (g/kg DM)	7	7	7	9

* Vitamin–mineral mix contained (g/kg DM): MV700 (Masterfeeds, Maple Leaf Mills Limited, London, Ontario, Canada) 904, $CaSO_4.2H_2O$ 95, $Na_2MoO_4.2H_2O$ 1: MV700 contained (g/kg DM): Ca 150, P 100, NaCl 310, Na 120, Fe 6·5, S 6, Fl 1·4, Mn 0·6, Zn 0·6, I 20 mg, Se 8 mg, Co 5 mg, vitamin A 30 mg, vitamin D 250 μg, vitamin E 200 mg.

† Rumen undegradability (g/kg crude protein) estimated from National Research Council (1989) as 371, 297, 513 and 432 for forage (1–8 weeks), forage (9–16 weeks), concentrate (1–8 weeks) and concentrate (9–16 weeks) diets respectively.

slaughtered during week 17. For slaughter, animals were stunned by captive bolt, followed by exsanguination. Two animals, from the same pen, transported together with a third companion sheep, were slaughtered daily (two initial-slaughter animals, or one fed forage for 8 weeks and one fed concentrate for 8 weeks, or one fed forage for 16 weeks and one fed concentrate for 16 weeks), with last feeding the previous afternoon (14.00–16.00 hours), and water available up to time of transport (08.30 hours, transport duration 20 min). The times of slaughter (09.30 and 11.00 hours) were staggered by 1·5 h, with half the forage-fed animals being randomly selected for slaughter at the earlier time (09.30 hours). Immediately following slaughter and exsanguination, carcasses were dressed, with the complete GIT being removed to facilitate immediate excision of samples for measurement of metabolic activity. All empty-body component samples were stored sealed and frozen until prepared for analysis by autoclaving of the frozen samples directly from the freezer, followed by homogenization, lyophilization and final grinding of the lyophilate, to provide dry ground homogenates from bony and soft, carcass and non-carcass components.

Gastrointestinal tract tissue metabolic activity

Samples (36 cm^2) from each GIT component (reticulum, rumen (ventral sac), omasum (laminal free-edge sections, away from the omasal pillar), abomasum, small intestine (jejunum), caecum and colon) were removed from the carcass immediately following slaughter. These samples were washed with, and placed in fresh, ice-cold Krebs–Henseleit buffer, for transport to the laboratory, where measurement of metabolic activity started within 30 min of slaughter. Mucosal tissue samples from each GIT component (reticulum (from outer edges of primary mucosal crests), rumen (one or more papillae), omasum (double-sided, from thin outer edges of laminae), abomasum, jejunum (representative of the small intestine), caecum and colon, as well as muscularis tissue samples (rumen only), 15–30 mg fresh weight (two replicates from each GIT component)) were dissected under × 10 magnification, then blotted dry and weighed, before being placed in M199 medium (Sigma Chemical, St Louis, MO, USA) before O_2 uptake analysis. *In vitro* O_2 uptake was measured polarographically using a YSI (Yellow Springs Instruments Inc., Yellow Springs, OH, USA) Clark-style O_2 electrode. The tissues were maintained in 4 ml M199 medium at pH 7·4 and 37°C during measurement of O_2 uptake for 10 min. Larger fresh-weight samples of reticulum (600–800 mg), rumen (300–800 mg), jejunum (15–70 mg) and colon (30–80 mg) were dissected into mucosa and muscularis under × 10 magnification to determine the DM proportion of mucosa and muscularis in the GIT components sampled.

Chemical analyses

DM was determined by oven drying (Association of Official Analytical Chemists, 1990). Silage DM was determined by oven drying (Association of Official Analytical Chemists, 1990) and corrected for loss of volatile compounds (Dulphy & Demarquilly, 1981; Galletti & Piccaglia, 1988). Samples were analysed for ash using a muffle furnace, for crude protein by automatic Kjeldahl N analysis, for energy content by bomb calorimetry, for total fats by diethyl ether extraction, for Ca by atomic absorption spectrophotometry, and for P by autoanalyser (Association of Official Analytical Chemists, 1990). Analyses for neutral-detergent fibre, acid-detergent fibre and acid-detergent-fibre-lignin involved methods described by Robertson & Van Soest (1981). Characterization of silage samples was carried out to determine pH and soluble N (Buchanan-Smith & Yao, 1981), non-protein N (Buchanan-Smith & Yao, 1978), lactic acid (Barker & Summerson, 1941; Hadzija, 1974) and NH_3-N (Novozamsky *et al.* 1974). Volatile fatty acid analysis for silage samples was by GC (Okeke *et al.* 1983).

Statistical analyses

Data were analysed using a general linear model procedure, with diet, duration and block specified in the CLASS statement as discrete, independent variables (SAS Institute Inc., 1989).

The model is given as:

$$Y_{ijk} = \mu + D_i + L_j + (DL)_{ij} + B_k + \varepsilon_{ijk},$$

where D is diet, L is duration, B is block, (DL) is D × L interaction and i is 1–2, j is 1–2 and k is 1–2. ε is error, where $\varepsilon_{ijk} \sim N(0, \sigma^2)$; that is, ε is random, normally (N) distributed, with mean of zero (0), and constant variance (σ^2). Results are presented as the arithmetic means with their standard errors, for each of the four treatments. Results were considered significant when the probability of a significant difference was $P \leq 0{\cdot}05$.

Results

Performance and final body composition of the four groups of lambs and their feed utilization are shown in Table 2. As designed, DM intake of the forage-fed lambs was higher than that of the concentrate-fed lambs, in order to equalize ME intakes. However, ME intakes of the forage-fed lambs were higher than those of the concentrate-fed lambs, which was a result of a lower than expected digestibility (DM digestibility: forage 0·55, concentrate 0·58), hence calculated metabolizability, for the concentrate diet. Although live-weight gains achieved by lambs on both diets were similar, rates of empty body energy gains (empty-body gain (MJ/d): forage-fed 1·01, concentrate-fed 1·59, $P<0{\cdot}001$) were greater for the lambs fed concentrate compared with those for lambs fed forage. Hence, lambs on the concentrate diet retained 0·28 of their ME intake in their empty-body gain compared with only 0·17 of the ME intake for lambs fed forage. The GIT accounted for 0·076 of the final empty-body weight in forage-fed lambs compared with a corresponding value of only 0·066 ($P<0{\cdot}001$) in lambs fed concentrate. Lambs fed concentrate consumed less crude protein than those fed forage, and this finding reflected the fact that the forage-fed diet was based on lucerne silage, which was high in total protein and rumen-degradable protein. Lambs fed both diets for 16 weeks ate more DM and energy per d during the trial, compared with

Table 2. Performance of growing lambs fed forage or concentrate diets for 8 or 16 weeks*
(Mean values with their standard errors for eight lambs per treatment group)

Diet (D)…	Forage		Concentrate		Statistical significance (*P*) of effect of:		
Feeding period (L)…	Weeks 1–8	Weeks 1–16	Weeks 1–8	Weeks 1–16	D	L	D × L
Initial live wt (kg fresh wt): Mean	26·86	25·80	26·46	25·17	0·75	0·471	0·945
SE	2·11	1·48	1·12	1·51			
Initial EB wt (kg fresh wt): Mean	21·59	20·74	21·29	20·22	0·75	0·463	0·931
SE	1·51	1·20	0·96	1·16			
Feed intake							
DM (g/d per kg $W^{0·75}$): Mean	54·90	59·53	44·62	47·22	<0·001	0·007	0·414
SE	1·35	1·83	0·79	1·22			
ME (kJ/d per kg $W^{0·75}$): Mean	452·84	486·05	431·49	456·70	0·025	0·011	0·711
SE	11·18	14·95	7·66	11·81			
CP (g/d per kg $W^{0·75}$): Mean	12·50	12·96	9·67	9·84	<0·001	0·226	0·566
SE	0·32	0·39	0·17	0·18			
Wt gain							
Live wt gain (g fresh wt/d): Mean	161·1	144·2	161·1	157·2	0·557	0·349	0·555
SE	14·2	13·1	9·0	9·5			
EB gain (g fresh wt/d): Mean	101·2	94·6	126·0	127·6	0·001	0·748	0·597
SE	6·9	9·9	8·1	6·0			
Final empty body composition							
Energy (kJ/kg EB fresh wt): Mean	9034·7	9202·6	10808·2	11468·5†	<0·001	0·399	0·632
SE	481·1	538·4	396·9	481·1			
GIT (% EB fresh wt): Mean	7·48	7·69	6·81	6·37	<0·001	0·659	0·215
SE	0·25	0·32	0·22	0·20			

EB, empty body; ME, metabolizable energy; CP, crude protein ($N_{total} \times 6·25$); $W^{0·75}$, metabolic body weight (live $weight^{0·75}$); GIT, gastrointestinal tract (mesenteric and omental fat excluded).
* For details of diets and procedures, see Table 1 and p. 258.
† *n* 7.

those fed for only 8 weeks, but demonstrated very little difference in rates of live or empty-body gain.

The contribution of component segments of the gut to the total GIT indicated no differences between concentrate- and forage-fed animals or between those fed the diets for only 8 weeks as opposed to 16 weeks (Table 3). Thus, increased proportional GIT weight in lambs as a result of feeding forage appears to have reflected itself in all components of the GIT.

The GIT is made up of layers of smooth muscle (muscularis) lined with mucosal tissue (mucosa). Metabolic activity, as *in vitro* O_2 uptake of the inner mucosal layer, was measured immediately after slaughter for each component of the GIT (Table 4). The colon was the only

Table 3. Gastrointestinal tract (GIT) composition at slaughter for growing lambs fed forage or concentrate diets for 8 or 16 weeks*
(Mean values with their standard errors for eight lambs per treatment group)

Diet (D)…	Forage		Concentrate		Statistical significance (*P*=) of effect of:		
Feeding period (L)…	Weeks 1–8	Weeks 1–16	Weeks 1–8	Weeks 1–16	D	L	D × L
GIT gross anatomical composition (g fresh wt/kg GIT fresh wt)							
Reticulum: Mean	62·3	60·9	63·4	65·5	0·332	0·915	0·541
SE	2·7	2·5	4·3	3·5			
Rumen: Mean	352·7	348·1	334·1	346·2	0·221	0·65	0·32
SE	9·5	9·3	5·7	13·3			
Omasum: Mean	60·0	55·3	51·2	54·4	0·175	0·831	0·269
SE	2·6	2·2	4·3	3·5			
Abomasum: Mean	72·2	74·2	82·2	75·4	0·23	0·602	0·342
SE	2·2	3·3	7·5	1·7			
Small intestine: Mean	266·5	274·1	290·5	277·4	0·128	0·755	0·246
SE	7·1	8·5	13·1	14·3			
Caecum: Mean	67·8	63·5	67·2	58·1	0·47	0·115	0·562
SE	3·5	4·1	4·2	4·2			
Colon: Mean	118·4	123·9	111·4	122·9	0·61	0·285	0·695
SE	10·2	9·0	4·5	7·4			

* For details of diets and procedures, see Table 1 and p. 258.

Table 4. Oxygen uptake by gastrointestinal mucosal tissue (ml oxygen/g DM per h) for growing lambs fed forage or concentrate diets for 8 or 16 weeks*

(Mean values with their standard errors for eight lambs per treatment group, except the group fed concentrates for 8 weeks where values are for seven lambs)

Diet (D)…	Forage		Concentrate			Statistical significance (*P*=) of effect of:		
Feeding period (L)…	Weeks 1–8	Weeks 1–16	Weeks 1–8	Weeks 1–16	Mean	D	L	D × L
Reticulum: Mean	7·54	5·30	4·38	5·14	5·59	0·135	0·457	0·177
SE	1·96	0·34	0·25	0·28				
Rumen: Mean	6·33	6·86	5·61	6·49	6·32	0·189	0·086	0·696
SE	0·52	0·55	0·29	0·60				
Omasum: Mean	7·56	5·66	6·88	5·82	6·48	0·74	0·039	0·58
SE	0·90	0·41	0·47	0·76				
Abomasum: Mean	4·14	4·78	4·88	4·55	4·59	0·568	0·679	0·261
SE	0·44	0·25	0·39	0·47				
Jejunum: Mean	7·56	6·00	6·47	6·55	6·65	0·758	0·206	0·244
SE	0·57	0·81	0·50	0·77				
Caecum: Mean	4·79	4·86	4·74	4·08	4·62	0·385	0·406	0·316
SE	0·51	0·46	0·41	0·40				
Colon: Mean	5·77	4·85	3·66	4·63	4·73	0·036	0·983	0·085
SE	0·69	0·54	0·31	0·27				
Rumen (muscularis): Mean	2·32	2·56	2·28	2·57	2·43	0·972	0·236	0·925
SE	0·18	0·26	0·21	0·22				

* For details of diets and procedures, see Table 1 and p. 258.

GIT component for which a significant diet effect (P=0·036) was observed, with greater activity noted for the forage- compared with the concentrate-fed lambs. There were no effects of length of feeding period on O_2 consumption of GIT tissue with the exception of the omasum, which had significantly less activity (P=0·039) in lambs that had been fed longer and were older than those on the diets for only 8 weeks. Overall, for animals from all treatment groups, four components of the GIT (reticulum, rumen, omasum and jejunum) demonstrated consistently greater O_2 consumption activity than other GIT components (abomasum, caecum, colon). There was no effect of diet or length of feeding period on O_2 consumption in muscularis tissue taken from the rumen.

Total O_2 uptake by GIT tissue was calculated on the basis of the proportions of mucosa and muscularis measured for reticulum, rumen, jejunum and colon (Table 5), and on estimates for the remaining GIT components. There were no significant effects of either diet or feeding period on proportions of mucosa in reticulum, rumen, jejunum and colon (Table 5). To estimate the proportions of mucosa and muscularis in abomasal and caecal tissue, mean values for the jejunum and colon respectively were used. For the omasum, a value of 0·25 was chosen for the proportion of mucosa, since use of this value resulted in the total omasal mucosa having an O_2 uptake of 8·9 % of the total rumen mucosa. Hofmann (1988) had observed that ovine omasal mucosa had only 10 % of the absorptive capacity of rumen mucosa. Values for weight-specific O_2 uptake for mucosal tissues from all GIT components were taken

Table 5. Mucosal tissue (DM) as a proportion of total (mucosa plus muscularis) tissue in some gastrointestinal components following slaughter of growing lambs fed forage or concentrate diets for 8 or 16 weeks*

(Mean values with their standard errors for eight lambs per treatment group)

Diet (D)…	Forage		Concentrate			Statistical significance (*P*=) of effect of:		
Feeding period (L)…	Weeks 1–8	Weeks 1–16	Weeks 1–8	Weeks 1–16	Mean	D	L	D × L
Reticulum: Mean	0·42†	0·41‡	0·45†	0·47§	0·44	0·856	0·512	0·414
SE	0·06	0·03	0·03	0·04				
Rumen: Mean	0·44	0·47	0·48	0·55	0·48	0·112	0·199	0·631
SE	0·04	0·03	0·04	0·04				
Jejunum: Mean	0·68	0·74‡	0·75‖	0·73‖	0·72	0·82	0·671	0·616
SE	0·08	0·04	0·08	0·09				
Colon: Mean	0·59	0·57	0·61	0·55	0·58	0·966	0·413	0·785
SE	0·05	0·04	0·07	0·04				

* For details of diets and procedures, see Table 1 and p. 258.
† *n* 4.
‡ *n* 6.
§ *n* 5.
‖ *n* 7.

from Table 4, with the value measured for rumen muscularis tissue being used as an estimate of activity in muscularis tissue from all other GIT components. Based on these calculations, weight-specific O_2 consumption on a DM basis (ml/g DM per h) was estimated to be GIT 4·2, foregut 4·1 and hindgut 4·3. The weight-specific O_2 uptake (ml/g DM per h) for each GIT component (mucosal + muscularis tissues) was estimated to be reticulum 3·5, rumen 4·3, omasum 3·4, abomasum 3·8, small intestine 4·9, caecum 3·8 and colon 3·7. The estimate of total O_2 uptake by a GIT component, expressed as a proportion of total GIT uptake, was higher for the abomasum in concentrate-fed animals (forage-fed 0·08, concentrate-fed 0·10; $P=0·035$), and higher for the caecum when forage was fed (forage-fed 0·06, concentrate-fed 0·05; $P=0·011$); all other components demonstrated no effect of diet, with values of reticulum 0·05, rumen 0·32, omasum 0·04, small intestine 0·27 and colon 0·17.

Using a value of 17·15 kJ/l as the heat equivalent for O_2 consumption (Blaxter, 1989), it was possible in the present study to estimate the contribution of GIT tissue to total heat production. Total heat production was taken as the difference between ME intake and energy retention. Heat equivalent to O_2 consumption by the GIT was estimated at 0·77 and 0·82 MJ/d in forage- and concentrate-fed animals respectively. Corresponding whole-body heat-loss estimates were 5·5 and 4·6 MJ/d, hence the GIT represented 0·14 and 0·18 of the total for forage- and concentrate-fed animals respectively.

Discussion

Although the same ME intakes across groups were anticipated, actual ME intake of concentrate-fed lambs was lower than expected, owing to correspondingly low metabolizability of the concentrate diet. Further, the bulk of the forage diet and the twice daily feeding schedule restricted ME intakes of all lambs to only approximately twice the estimate of fasting heat production in sheep (Agriculture and Food Research Council, 1993). Thus, the amount of energy available for body-weight gain was limited. Despite these limitations, concentrate-fed lambs gained gross empty-body weight and energy at a greater rate than was observed with the forage-fed animals. Thus, the hypothesis for the present study of greater efficiency of ME utilization by concentrate- compared with forage-fed ruminants was confirmed.

Some of the effects observed for forage-fed lambs in the present study may have reflected their higher intake of crude protein, compared with those of lambs fed concentrate. This difference was caused by planning the diets so that the expected intakes of rumen-undegradable protein, hence amino acid supply through digestion, were similar across diets. Actual intakes of undegradable protein, calculated from the rumen-undegradability values from the National Research Council (1989) were 4·77 and 4·34 g/d per kg live weight$^{0·75}$ for lambs fed forage for 8 and 16 weeks respectively, compared with 5·13 and 4·64 g/d per kg live weight$^{0·75}$ for lambs fed grain for 8 and 16 weeks respectively. Thus, the excess crude protein intake for the forage-fed lambs arose primarily through a higher intake of rumen-degradable protein in these lambs compared with those fed concentrate. Excessive intake of rumen-degradable protein would be expected to have metabolic implications, such as increased synthesis of urea by the liver, and protein metabolism in GIT tissue. However, the only indication of a diet effect on GIT protein metabolism (weight-specific *in vitro* O_2 uptake (ml/g DM per h), mucosal tissue) in the present study was for the colon (forage 5·31, concentrate 4·15; $P=0·036$). Further, excess intakes of rumen-degradable protein are often observed with ruminants consuming high-quality forage diets (Reynolds *et al.* 1991; Kelly *et al.* 1993*a*), and increased liver-driven thermogenesis could be a contributing factor to the higher than expected thermogenesis associated with these diets.

Although feeding a forage diet compared with a concentrate diet in the present study was associated with enhanced growth of the total mass of the GIT, no effects on weights of different GIT components, expressed as a proportion of the total, were observed. Both Bailey (1986), feeding cattle, and McLeod & Baldwin (1998), feeding sheep, offered isoenergetic ME diets based on either forages or concentrates and demonstrated heavier omasa in the forage-fed animals, although the weights of the reticulo-rumen, abomasum and intestine were unaffected by diet.

Although no published data demonstrate the comparative metabolic activity of all seven major GIT components, previous studies have reported on the *in vitro* metabolic activity of bovine (Harmon *et al.* 1991; Kelly *et al.* 1991, 1993*a*, 1995) and ovine (Burrin *et al.* 1990) rumen mucosa, bovine (McBride & Milligan, 1984) and ovine (McBride & Milligan, 1985; Kelly *et al.* 1993*b*) duodenal mucosa, and bovine (McBride *et al.* 1989) and ovine (Burrin *et al.* 1990) jejunum (combined mucosa and muscularis). These studies have demonstrated consistent values for DM weight-specific O_2 uptake by mucosa of 6–9 ml/g DM per h, across species and ages, with the single reported value for muscularis (bovine rumen, 2·8 ml/g DM per h; Kelly *et al.* 1991) being only 36 % of the corresponding mucosal value. The current study reports values of 5·61–7·56 ml O_2/g DM per h (Table 4) for rumen and jejunal mucosa, and values for rumen muscularis which are 39 % of the rumen mucosal values. These values are consistent with those from previous studies.

Harmon *et al.* (1991) have also investigated the effect of feeding either forage or concentrate diets on the *in vitro* O_2 uptake by rumen mucosal tissue. They fed either forage (lucerne hay) or concentrate (rolled wheat and sorghum, 50:50, w/w) at two net energy intake levels (maintenance and twice maintenance), in two daily meals, and reported no effect of diet on weight-specific *in vitro* O_2 uptake. However, Harmon *et al.* (1991) reported significantly greater metabolic activity in the rumen mucosa of animals fed at twice maintenance *v.* maintenance. McLeod & Baldwin (1998) also found no effect of isoenergetic intakes of forage- and concentrate-based diets on *in vitro* O_2 uptake by mucosal cells isolated from the rumen, duodenum, jejunum and ileum. In the present study O_2 consumption was higher in the mucosa from the colon of forage-fed compared with that of concentrate-fed lambs, but other tissues were not significantly affected. This response to diet in the colon mucosa may reflect increased intake of both fibre and protein.

As observations of O_2 consumption were made in the present study for all GIT segments, the results of these observations were integrated to obtain estimates of heat production in the entire GIT. The validity of this process was suggested by the fact that the estimate for the proportional contribution of the GIT to total heat production, of between 14 and 18 %, is comparable with other estimates of 18–28 %, based on *in vivo* measurements of O_2 consumption by the entire portal-drained viscera (in sheep: 19–28 % Burrin *et al.* 1989, 18·5 % Thompson *et al.* 1978; in cattle: 18–25 % Huntington, 1990). Johnson *et al.* (1990), in their review of energy use by ruminant visceral organs, compared daily GIT O_2 consumption determined using *in vitro* and *in vivo* techniques; the estimate of energy use of 1202 J/g per d from *in vitro* studies compared closely with the estimate from *in vivo* studies of 1101 J/g per d. Although heat production in the GIT of forage- and concentrate-fed lambs in the present study could not be compared statistically, the estimates made in each group of animals (forage-fed 5·5 MJ/d, concentrate-fed 4·6 MJ/d) were close.

Reynolds *et al.* (1991) investigated energy expenditure by the entire portal-drained viscera (GIT, pancreas, spleen and mesenteric fat), and reported increased *in vivo* O_2 consumption by the portal-drained viscera (l/h; forage-fed, 26·4, concentrate-fed 20·9; $P<0·05$) when heifers were fed a forage diet (ground lucerne hay–ground maize 0·75:0·25, w/w) as opposed to a concentrate-based diet (ground maize–ground lucerne 0·75:0·25, w/w). Both diets, each fed at two isoenergetic ME intake levels (maintenance and twice maintenance), were ground and fed as pellets, with twelve equal daily meals being offered at 2 h intervals. If GIT mucosal O_2 uptake, on a weight-specific basis, differed for concentrate- and forage-fed animals, such a difference might be more easily demonstrated in animals on a continuous feeding schedule, such as the twelve equal daily meals offered at 2 h intervals reported by Reynolds *et al.* (1991), rather than 18 h after the last meal, as in the current study. Kelly *et al.* (1993*a*) described the 24 h pattern of O_2 consumption by the rumen mucosa in steers fed lucerne hay in a single daily feeding. O_2 uptake increased by more than 20 % during the 3 h meal period, and was still elevated 9 h after the meal ended, returning to premeal levels before the start of the meal on the following day (a pattern paralleled by the rumen concentration of acetate, propionate and butyrate). Harmon *et al.* (1991) found a significant effect of intake level (O_2 uptake (nmol/mg per h) net energy at maintenance 42·3, twice maintenance 53·1; $P<0·01$) on O_2 uptake by rumen mucosa taken from animals slaughtered following an overnight fast, but they did not demonstrate an effect of diet (lucerne hay, or wheat and sorghum) in the same experiment.

No evidence is presented from the present study for significantly higher metabolic activity in the mucosal gut tissues of the forage-fed animals (with the exception of the colon; $P=0·036$), but GIT tissue did represent a significantly higher proportion of total empty-body gain in these animals compared with that of animals fed a concentrate diet ($P<0·01$). As implied earlier, the fact that measurements of weight-specific O_2 uptake were taken at approximately 18 h after the lambs were last fed may have prevented detection of greater effects of diet on metabolic activity that could have existed earlier after the last feeding or over an entire 24 h period. More measurements of O_2 uptake, *in vitro* or *in vivo*, were beyond the scope of the present study. Although no large differences in estimated total energy expenditures of gut tissues from forage- and concentrate-fed lambs were found in the present study, the significant effect of diet on proportional weight of the GIT does not exclude a role for the GIT in the increased thermogenesis of ruminants fed forage diets as opposed to concentrate diets.

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