Diet selection in sheep: the role of the rumen environment in the selection of a diet from two feeds that differ in their energy density

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The effect of the energy density (ED) of feeds offered as a choice on the diet selection of sheep, and the relationship between the rumen environment and the diet selected from feeds of different ED were investigated in two experiments. In the first experiment two feeds, L and H, and their mixture M (3:1 w/w) were formulated. All feeds had similar calculated metabolizable protein:metabolizable energy (ME) ratios, but differed in ED (7·4, 8·1 and 10·1 MJ ME/kg fresh feed for L, M and H respectively). The feeds were offered *ad lib.* either singly or in paired choices (L/M, L/H and M/H; *n* 6 per treatment) to growing sheep. Although the rate of live-weight (Lwt) gain on feed H was higher than on feeds L or M, and the daily rate of feed intake lower, the sheep on feed choices did not consume only feed H. Instead they selected a mixture of both feeds offered, such that the total amount of H consumed per kg fresh feed was similar on choices L/H and M/H. The rate of Lwt gain of sheep on choices L/H and M/H was not different from that achieved on feed H alone. In the second experiment the choice L/H was offered to fistulated sheep (10 months of age, mean Lwt 57·5 kg) in an 8 × 8 Latin square, with 7 d periods. Treatments were infusions into the rumen (total volume 1 litre) over 4 h on days 1–4 of each period of acid (HCl; Acid 1, 400; Acid 2, 300 and Acid 3, 200 mmol/l), alkali (NaOH; Alk 1, 316; Alk 2, 212 and Alk 3, 109 mmol/l) and control (NaCl; Con 1, 315 and Con 2, 209 mmol/l). Infusate osmolalities (mOs/kg) were 795 (Acid 1), 585 (Acid 2, Alk 1 and Con 1), 390 (Acid 3, Alk 2 and Con 2) and 200 (Alk 3). Infusion treatment significantly affected the diet selection of the sheep ($P < 0·05$) according to the osmolality of infusate, but not according to rumen pH. During infusions intake of feed H tended to decline with increasing treatment osmolality, whereas intake of L remained constant. The effects on diet selection and feed intake were of a short duration with no carry-over effects. These results show that sheep given a choice between two feeds of different ED select a substantial quantity of the low-ED feed; this diet selection is affected by short-term manipulations of their rumen environment, in a manner that is consistent with the maintenance of effective rumen conditions.

Diet selection: Energy density: Rumen: Feed intake: Sheep

It is a precept of diet selection that animals aim to optimize the advantages to be gained by eating a feed, such as rapid growth and production of viable offspring, whilst minimizing any disadvantages which may be incurred (Emmans, 1991). This assumption has been the underlying hypothesis of most diet selection work and it is implied in optimal foraging theory (Krebs & McCleery, 1984). Research into the diet selection of animals in a

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controlled environment has concentrated on their ability to select, from a choice of feeds differing only in the concentration of one nutrient (such as protein), a diet which meets their requirements for that nutrient (chickens: Shariadmadari & Forbes, 1993; pigs: Kyriazakis *et al.* 1990; sheep: Cropper, 1987; Kyriazakis & Oldham, 1993). The diets selected by the animals in those experiments have enabled them to grow rapidly, and yet avoid an excessive intake of the nutrient in question, since this could present a metabolic burden (e.g. protein: Kyriazakis & Oldham, 1993).

It is predicted from optimal foraging theory (Krebs & McCleery, 1984) that the diet selected by ruminants offered a choice between feeds of different digestibility, would consist almost exclusively of the feed which enables them to maximize their rate of intake (Westoby, 1974; Kenney & Black, 1984). However, evidence from the grazing experiments of Newman *et al.* (1992) and Parsons *et al.* (1994) do not support this hypothesis. In their experiments the sheep selected a mixture of the feeds available to them (monocultures of grass and clover), although they had the opportunity to select a diet composed of clover alone which, from conventional expectations, would have allowed them to maximize their rate of feed intake (Kenney & Black, 1984). In addition Cropper (1987) has found that sheep in a controlled environment, offered a free choice of a pair of feeds which differ in digestibility, do not completely avoid the less digestible feed; instead they choose to eat a mixture of both feeds. However, the feed choices offered by Cropper (1987) did not provide as wide a range of 'bulk densities' as had been intended, and the number of animals allocated to each treatment was small; it is felt that this may have had a bearing on the results obtained (Cropper, 1987). The objective of the first experiment reported here was therefore to give further consideration to the effects of energy density on the diet selections made by sheep.

Both Cropper (1987) and Parsons *et al.* (1994) have suggested that ruminants appear to select from two feeds that differ in nutrient density or digestibility, a diet that enables their rumens to remain in a fit and adaptive state. This strategy would require certain aspects of the rumen environment to remain at optimal levels or at least within an acceptable range of conditions. Microbial activity within the rumen is greatly affected by changes in the rumen environment (Russel & Strobel, 1993). This is of significance to the sheep as the supply of energy and protein to the small intestine depends principally upon the activity of these micro-organisms. Thus if a strategy of maintaining optimal rumen conditions were to influence the diet selection of ruminants, this would assist the animal in achieving its goal of meeting its requirements for energy and nutrients.

One can hypothesize that the rumen conditions that may have a significant effect on the diet selection of ruminants would be those that are related to the consequences of fermentation of rapidly fermentable materials (such as increased acidity and increased osmolality) and the hydrolysis of rapidly degradable protein (high concentrations of NH_3). We have some evidence for the latter, since one of the criteria that influences the diet selection of sheep appears to be the 'desire' to minimize an excessive intake of rapidly degradable protein (Kyriazakis & Oldham, 1993; Cooper *et al.* 1995). It is known that the intake of a single feed is affected by both rumen pH (Battacharya & Warner, 1967) and osmolality (Carter & Grovum, 1990*a*). The objective of the second experiment reported here was to investigate the effects of the latter aspects of the rumen environment (pH and osmolality) on the diet selection of sheep given a choice between two feeds that differ in their energy density.

MATERIALS AND METHODS

Expt 1

Animals and housing. Forty-two Suffolk × Greyface entire male lambs were used. They weighed 21·2 (SD 5·53) kg live weight (Lwt) when they were weaned at approximately 8

Table 1. *Expts 1 and 2. Ingredients and chemical composition of the experimental feeds*

	Feeds		
	L	M	H
Ingredients (g/kg)			
Oatfeed	642·6	557·0	300·0
Barley	—	21·7	86·6
Molassed beet pulp	102·9	153·9	306·8
High-protein soya	180·2	194·2	236·2
CMS 20*	50·0	50·0	50·0
Salt	4·9	4·6	3·6
Dicalphos	7·3	6·7	4·9
Limestone flour	8·1	8·4	9·3
Calcined magnesite	1·9	1·6	0·7
Mineral and vitamin mix†	2·0	2·0	2·0
Chemical analyses (g/kg fresh matter unless otherwise stated)			
Dry matter	891·0	888·0	875·0
Metabolizable energy (ME; MJ/kg)‡	7·4	8·1	10·1
Fermentable ME (fME; MJ/kg)§	6·6	7·4	9·9
Crude protein	124·0	138·0	178·0
Ether extract	22·4	23·6	26·3
Effective rumen-degradable protein (eRDP)	78·7	87·8	114·9
eRDP/fME	12·0	11·9	11·6
Neutral-detergent fibre	440·0	402·0	286·0
Acid-detergent fibre	214·0	192·0	125·0
Crude fibre	170·1	157·2	107·6
Ash	66·0	67·0	70·0
Calcium	8·2	8·9	10·9
Phosphorus	3·5	3·7	4·2
Estimated production (g/kg)§			
Microbial protein	41·9	52·7	63·5
Metabolizable protein (MP)	73·9	83·4	111·8
Estimated ME: MP (g/MJ)	10·0	10·2	11·0

L, low-energy-density diet; H, high-energy-density diet; M, mixture of L and H (3:1).

* Condensed molasses solubles, blended with 200 g cane molasses/kg (Intermol, Cobham, Surrey).

† Scotmin ewe/lamb mixture (Scotmin Nutrition Ltd, Ayr, Scotland).

‡ Calculated using the equation ME = 0·14 (neutral cellulase gaminase digestibility) + 0·25 (acid-hydrolysed ether extract) (Thomas *et al.* 1988).

§ Values calculated using the metabolizable protein system (Agricultural and Food Research Council, 1992) assuming a rumen outflow rate of 0·05/h, and standard values for degradability coefficients.

weeks of age. The lambs were drawn from sets of twins from which one was taken. The lambs were given a creep feed (158 g crude protein/kg fresh feed; 10·1 MJ metabolizable energy (ME)/kg) at a rate of 35 g/kg Lwt per d. It was estimated that this feeding level, which was very close to their *ad lib.* intake, would ensure that all the sheep reached the experimental weight with a similar gut fill. They were kept in individual pens (1·29 × 1·53 m) which contained one water bucket and one or two feed troughs (according to the experimental treatment). The shed in which they were housed has been described previously by Kyriazakis & Oldham (1993). Natural lighting and ventilation were used throughout the experiment (May–September 1992).

Feeds. Two feeds, L and H, were formulated and made into pellets (Table 1); they differed mainly in their energy density (low (L) and high (H)). Both feeds had estimated metabolizable protein:metabolizable energy (MP:ME) ratios that were made as similar as

possible within the constraint of ensuring that the effective rumen degradable protein (eRDP): fermentable ME (fME) ratio was kept constant. The MP content of the feeds was estimated using the system proposed by the Agricultural and Food Research Council (1992), and the method of Thomas *et al.* (1988) was used to calculate the ME content of the feeds. Feed L was formulated to have inadequate concentrations of ME and MP to support potential growth when offered *ad lib.* to sheep (Agricultural and Food Research Council, 1992). Both feeds were non-limiting in minerals and vitamins but in feed H the concentration of macro-minerals was higher to maintain suitable ratios to ME (Agricultural Research Council, 1980). A mixture of feeds L and H was also made, M (L:H 3:1 w/w).

Design. On reaching 30 kg Lwt each sheep was allocated to one of three groups: initial slaughter (*n* 6), free and continuous access to a single feed (L, M and H; *n* 6 per treatment; single fed), or free and continuous access to a choice between two feeds (feed pairs L with M (L/M), L with H (L/H) and M with H (M/H); *n* 6 per treatment; choice-fed). The sheep were allocated randomly to the treatments after taking into account their age at the start weight. The experiment ended at 50 kg Lwt for all the single-fed sheep and those offered choices between feeds L and M or feeds M and H. The sheep allocated to the L/H choice continued to be offered these two feeds until they reached 60 kg Lwt; this was to consider whether their feed intake and diet selections changed with time, and more specifically with natural daylight.

Management and slaughter procedure. The choice-fed sheep were given a training period of 10 d in which the feeds were offered alone on alternate days. The regimen used was a modification of that developed by Kyriazakis & Oldham (1993). The quantity of feed offered to all sheep was increased from 35 g/kg Lwt to *ad lib.* over this period. The sheep were weighed weekly during the afternoon up to 47 kg Lwt (or 57 kg Lwt; L/H choice) and then daily (during the morning, before feeding) until they reached 50 kg Lwt (or 60 kg Lwt; L/H choice). They were offered fresh feed twice daily (morning and afternoon) to minimize spillage; feed refusals were collected daily, weighed and then discarded.

Each of the single-fed sheep was slaughtered on the morning that it reached 50 kg Lwt. Before slaughter the sheep was sheared closely, the wool was collected, cleared of any obvious dirt and then weighed to give the greasy fleece weight. The sheep were killed by an intravenous injection of Pentobarbital sodium (Euthatal-RMB). The dead weight of each sheep was recorded before the gastrointestinal tract was removed and weighed. The rumen – reticulum, omasum, and abomasum were removed together from the rest of the tract; this set of organs is subsequently described as the 'stomachs'. Any omental fat was removed from the 'stomachs' before they were weighed, stripped of their contents and then reweighed. The small and large intestines were stripped of their contents and weighed empty, after the mesenteric fat had been removed. The weights of the contents of the 'stomachs' and the rest of the gastrointestinal tract were then calculated by difference.

Expt 2

Animals and foods. Eight Texel × Scottish Blackface female sheep (aged 10 months) and weighing 57·5 (SD 6·92) kg Lwt were used. Each animal was fitted with a rumen cannula under surgical anaesthesia (O_2/halothane general anaesthesia), 3 months before the start of the experiment. During the experiment the sheep were kept in metabolism cages, placed in a naturally ventilated room, and given a minimum of 12 h light. The sheep had been given prior experience of the cages, the procedures to be used and the experimental routine during a 23 d pilot study.

The sheep were introduced to the experimental feeds in an alternating pattern 3 weeks before they were fitted with a rumen cannula. They were given free and continuous access to the feeds at all times until the end of the experiment. The feed choice offered consisted

Table 2. *Expt 2. The concentrations and osmolalities of solutions infused into sheep given access to two feeds that differed in energy density**

Infusate	Treatment	Concentration (mmol/l)	Osmolality (mOs/kg)
HCl	Acid 1	400	795
	Acid 2	300	585
	Acid 3	200	390
NaOH	Alkali 1	316	585
	Alkali 2	212	390
	Alkali 3	109	200
NaCl	Control 1	315	585
	Control 2	209	390

* For details of procedures, see pp. 42–44.

of the high-energy-density feed H, and the low-energy-density feed L, used in Expt 1. The feeds were given in two identical feed troughs; water was available at all times, but its intake was not monitored. Fresh feed and water were given each day.

Design. The experiment was an 8 × 8 Latin square design (eight treatments, each block was 1 week in length), there was a 1-week interval dividing the experiment into two 4-week sections to allow the animals a period of rest so that they were not held in metabolism cages for more than 4 weeks, in accordance with Home Office regulations. The treatments were rumen infusions of 1 litre and were administered to the sheep over a 4 h period (10.00–14.00 hours) on four consecutive days (1–4) of each of the 8 weeks of the experiment. There was an interval of 3 d between successive treatments (days 5–7) to avoid carry-over effects. The treatments were three concentrations of HCl (Acid 1–3 treatments), three of NaOH (Alkali 1–3 treatments) and two concentrations of NaCl (Control 1 and 2 treatments). HCl was chosen for the acid treatments in preference to an organic acid as it would have an effect on pH without acting as a source of energy. NaCl was chosen as the control as it would not cause rumen pH to be altered and its osmotic effects at specified concentrations could be easily predicted (Schiller *et al.* 1988). The molarity and osmolality of the solutions are given in Table 2. An *in vitro* study of the buffering capacity of rumen contents taken from the sheep during the pilot study indicated that infusions of the acid treatment of highest concentration (Acid 1) or the alkali of highest concentration (Alkali 1) would cause equal but opposite changes in the pH of the rumen contents. Acid 2, Alkali 1 and Control 2 had the same high osmolality, Acid 3, Alkali 2 and Control 2 were of a lower osmolality.

Management and measurement. Feed refusals were removed at 08.00 hours each day, weighed and discarded. Feed consumption was recorded at 10.00 and 16.00 hours each day. On days 1–4 feed intake was measured every 2 h between 08.00 and 16.00 hours, by removing the troughs, weighing and returning them to the pens. The Lwt of the ewes was measured on day 7 of each week before feeding. The rumen infusates were administered via a piece of semi-rigid PVC tubing (i.d. 3 mm) inserted through a rumen cannula bung. On the fourth day of rumen infusion in each block (day 4), samples of about 80 ml rumen contents were withdrawn at 08.00, 10.00, 12.00, 14.00 and 16.00 hours. To take rumen samples, a stiff piece of tubing (polypropylene; i.d. 9 mm) was inserted through the rumen cannula bung, which was adjacent to the infusion tubing but did not touch it. The rumen contents samples were withdrawn using a hand-held pump, and collected into glass containers. Efforts were made to collect the samples from the same parts of the

rumen–reticulum (different sampling sites) at each sampling time. Small rubber plugs were used to seal the rumen cannula bung when infusion and sampling procedures were not being conducted. In addition, on day 2, blood samples were collected into evacuated heparinized tubes by jugular venepuncture, at 09.00, 12.00 and 15.00 hours.

Sample processing and analysis. The pH of each rumen contents sample was measured immediately after sampling, using a glass electrode. The rumen contents were then strained through double thickness muslin. Strained rumen contents samples were stored at −20° and were subsequently analysed to determine ruminal concentrations of volatile fatty acids (VFA) and ammonia-N (NH_3-N). Separate samples for VFA and NH_3-N analyses were treated with 250 μl saturated mercuric chloride or three drops of concentrated H_2SO_4 respectively before freezing. The rumen contents were analysed to determine the concentrations of individual VFA using a gas–liquid chromatograph (GLC, Model 304, Pye Unicam Ltd, Cambridge, Cambs) and for NH_3-N on an autoanalyser (Kjeltec 1030 Autoanalyser, Perstop Analytical Ltd, Maidenhead, Berks). Repeated attempts were made to measure the osmolality of the rumen contents samples that had been filtered through 0·45 μm microbial filters (Whatman Ltd, Maidstone, Kent) but these were not successful as the contents were too viscous for reliable measurements to be taken.

Blood samples were centrifuged (1500 ***g***; 20 min), 1 ml portions of plasma were mixed with 6 μl 750 mM-LiCl solution and stored at −20°. These samples were analysed for Na, Cl and total CO_2 (tCO_2) with commercially available kits, using a micro centrifugal auto analyser (Monarch 2000, Instrument Laboratory, Warrington, Ches.).

Statistical analyses

Expt 1. All statistical analyses were performed using GENSTAT version 5.3 (Lawes Agricultural Trust, 1988). Treatment effects for the single- and choice-fed sheep in Expt 1 were analysed by ANOVA. Comparisons between treatments were made using orthogonal contrasts. The rate of Lwt gain and feed conversion efficiency were analysed by including data from the 10 d training period in the first instance (whole period) and then by excluding data from the training period (experimental period). The rate of Lwt gain over the whole period was calculated as the quotient of Lwt gained over this period and the time taken. For each animal a simple linear regression was used to calculate the rate of Lwt gain over the experimental period. The rate of empty-body-weight gain (single-fed sheep only; Lwt excluding the weight of the contents of the gastrointestinal tract) was calculated over the whole period.

Expt 2. Data from this experiment were analysed according to an 8×8 Latin square design. Daily feed intake and the proportion of H selected were analysed with day and treatment as factors. Secondly the effects of day and treatment on the feed intake and diet selection during the 4 d of the infusion were tested. The data were divided into three time intervals (08.00–10.00 hours, 10.00–16.00 hours and 16.00–08.00 h) which were analysed separately. The feed intakes and diet selections during these intervals were then analysed using day and osmolality within treatment (treatment/osmolality) as factors. The pH, NH_3-N and VFA data (collected on day 4 of each week), and the plasma concentrations of Na, Cl and tCO_2 were analysed in two ways. First, data from the five sampling times (three times for blood sampling) were analysed separately; data from the 08.00 hours sampling (for pH, NH_3-N and VFA) and 09.00 hours sampling (for plasma concentrations) were used as a covariate respectively. Subsequently, mean data from the infusion period were treated in a similar manner to the feed intake and diet selection data, using treatment as a factor. To ensure that the data distribution met the assumption of normality, the following variates were transformed: total VFA (X^3), molar proportion of isobutyrate ($\log_{10}$), and isovalerate (sqrt); the terms within the parentheses indicate the transformation

used. The diet selection data from both Expts 1 and 2 were not transformed by any means, since in both cases they met the criteria for normal distribution.

RESULTS

Expt 1

Single-fed sheep. The rates of daily feed intake, Lwt gain, feed conversion efficiency, empty-body-weight gain and daily ME intake of the sheep given free and continuous access to a single feed are given in Table 3. Two values are quoted for both rate of Lwt gain and feed conversion efficiency. The former includes the 10 d training period (whole period) and the latter excludes it (experimental period). Both feed intake and feed conversion efficiency increased significantly ($P < 0{\cdot}001$) as the energy density of the feed decreased. This effect of energy density on feed conversion efficiency was apparent over the whole period and the experimental period. The sheep fed on H alone had significantly higher rates of Lwt gain ($P < 0{\cdot}05$) over the experimental period; however, this difference was not present when the whole period was considered. The rate of empty-body-weight gain (Lwt excluding gut fill) on feed H was significantly higher than on feeds L or M alone.

The weights of the contents of the rumen, reticulum, omasum and abomasum ('stomachs') and the remaining sections of the gastrointestinal tract are given in Table 3. The 'stomachs' contents of the sheep on H weighed significantly less than those of the sheep on feeds L or M. There was no effect of energy density on either the contents of the remaining sections of the gastrointestinal tract or the cleaned tissue weights of the entire gastrointestinal tract or the 'stomachs' which were: 2030, 1949 and 2050 (SED 152·2) g for feeds L, M and H respectively.

Choice-fed sheep. The performance and diet selection of the sheep given access to two feeds as one of three choices during the experimental period (which excludes the training period) are given in Table 4. The sheep showed a preference for the feed of high energy density in each feed choice offered: 830, 680 and 590 (SED 83) g/kg total feed intake (TFI) for choices L/M, L/H and M/H respectively. Since feed M was a mixture of feeds L and H (L:H 3:1), it is possible to express the diet selections of all the choice-fed sheep as a selection between feeds L and H. The proportion of H selected was not significantly different when the other feed offered was either L or M (680 *v.* 695 g H/kg TFI, SED 54·2). The average proportion of the higher density feed selected by the sheep on feed choices L/M, L/H and M/H is plotted against time in Fig. 1; no systematic changes in the pattern of diet selection of the L/H sheep were observed. The diet selections of the L/M choice-fed sheep showed less daily variation than the choices made by the sheep offered the feed choices L/H or M/H. The L/H choice-fed sheep continued to be offered this choice as they grew from 50 to 60 kg Lwt; the mean length of this period was 29 (SEM 4·5) d. The proportion of H selected by the L/H choice-fed sheep as they grew from 50 to 60 kg Lwt was 663 (SEM 83·3) g H/kg TFI; this was not significantly different from the proportion of H selected by the same animals over the lower Lwt range (30–50 kg).

There was no effect of feed choice on either the rate of Lwt gain or feed conversion efficiency. Over the experimental period the choice-fed sheep had higher rates of Lwt gain ($P < 0{\cdot}05$) than the single-fed sheep on L or M alone and their performance was not significantly different from that of the sheep on H alone.

Expt 2

Rumen pH. There was a significant effect of sheep and week on rumen pH and all other measurements analysed. There was a significant effect of treatment at all sampling times during the 4 h period of the infusion. The changes of rumen pH with time (08·00–16·00

Table 3. *Expt 1. The performance of sheep given access to feeds with different calculated energy densities (ED; MJ ME/kg fresh feed) but similar protein:energy ratios, from 30 to 50 kg live weight*†

Feed...	L	M	H	SED	Statistical significance of effects of		
						Orthogonal contrasts	
Calculated ED...	7·4	8·1	10·1	(14 df)	Feed	H *v.* others	L *v.* M
Feed intake (g/d)	2802	2769	2107	110·0	***	***	NS
ME intake (MJ/d)	22·9	24·9	24·2	0·98	NS	NS	NS
Live-wt gain (g/d)‡							
Whole period§	463	471	512	23·2	NS	NS	NS
Experimental period	421	443	503	31·1	NS	*	NS
Feed conversion efficiency (g gain/g feed)							
Whole period§	0·187	0·193	0·268	0·0154	***	***	NS
Experimental period	0·151	0·160	0·244	0·0122	***	***	NS
EB-wt gain (g/d)§	341	361	423	37·6	NS	*	NS
'Stomachs' contents (g)	7230	6197	5306	727·6	NS	*	NS
Remaining gastrointestinal tract contents (g)	5345	4852	3392	795·7	NS	*	NS

L, low-energy-density diet; H, high-energy-density diet; M, mixture of L and H (3:1); SED, standard error of the difference between means; ME, metabolizable energy; EB, empty body.

* $P < 0·05$, *** $P < 0·001$.

† For details of diets and procedures, see Table 1 and pp. 40–42.

‡ Calculated by regression.

§ Over live-weight range 30–50 kg.

hours; day 4) are presented in Fig. 2(*a*) (acid treatments) and Fig. 2(*b*) (alkali treatments). The control treatments were not significantly different from each other and so these two treatments have been combined for the purpose of presentation. The effect of treatment on rumen pH was still present 2 h after the end of the infusion. Data from this interval (14.00–16.00 hours) have been included in the analyses of all other measurements as a consequence. Rumen pH on Acid 1, Acid 2 and Alkali 1 treatments was altered significantly when compared with the control treatments (Fig. 2(*a*) and (*b*)) over the interval 12.00–16.00 hours. The mean change in pH over the infusion period (10.00–14.00 hours) on these treatments was 0·42 pH units. At the end of the infusion period rumen pH on these treatments began to return to levels comparable with those of controls

Feed intake. The feed intakes over specific time intervals on the days when infusions were administered (days 1–4) are shown in Table 5. There were clear tendencies for the treatment administered ($0·1 < P < 0·05$) to have an effect on feed intake during the 4 h of the infusion and the 2 h after it had ended (10.00–16.00 hours). Feed intake was depressed on the treatments of highest concentration within each treatment type, but this was not statistically significant. Feed intake decreased significantly ($P < 0·05$) with increasing treatment osmolality. There were no differences in the response to treatment osmolality due to treatment type, since there were no interactions between treatment type and osmolality.

The osmolality of the treatment administered (10.00–14.00 hours) had a significant effect on feed intake during the interval 16.00–08.00 hours; it is presumed that this was due to the intake on treatment Alkali 3 being particularly high relative to all the other treatments. Intake on day 2 was 1564 (SEM 56·9) g/d and was significantly depressed ($P < 0·05$) relative

Table 4. *Expt 1. The diet selection and performance of lambs given access to two feeds with different energy densities (MJ ME/kg fresh feed), but similar protein:energy ratios, from 30 to 50 kg live weight*†

Feed pair...	L/M	L/H	M/H	SED (14 df)	Statistical significance of effects of: Choice	Orthogonal contrasts: L/M *v.* others	Orthogonal contrasts: L/H *v.* M/H
Feed intake (FI; g/d)	2654	2483	2326	89·1	*	**	NS
ME intake (MJ/d)	23·6	25·9	24·4	0·90	NS	NS	NS
Proportion of feed of higher energy density selected (g M or H/kg FI)	834	680	592	81·1	NS	*	NS
Proportion of feed H selected‡ (g/kg FI)	208	680	695	54·2	***	NA	NA
Life-weight gain (g/d)							
Whole period§	491	494	482	26·3	NS	NS	NS
Experimental period§	444	451	429	38·5	NS	NS	NS
Feed conversion efficiency (g gain/g feed)							
Whole period‖	0·209	0·226	0·224	0·0139	NS	NS	NS
Experimental period	0·163	0·181	0·187	0·0152	NS	NS	NS

L, low-energy-density diet; H, high-energy-density diet; M, mixture of L and H (3:1); SED, standard error of the difference between means; ME, metabolizable energy; NA, not applicable.

* $P < 0·05$, ** $P < 0·01$; *** $P < 0·001$.

† For details of feeds and procedures, see Table 1 and pp. 40–42.

‡ Because M was a mixture of L and H, the diet selection of all sheep can be expressed as a selection between feeds L and H.

§ Calculated by regression.

‖ Over live-weight range 30–50 kg.

to the other days when infusions were administered; day 2 was the blood sampling day. There were no persisting effects of the infusion treatments on feed intake on the days when no infusates were administered.

Diet selection. The diet selection results are presented as g feed H/kg TFI consumed during each time interval considered (Table 6). There was a significant effect of treatment on the proportion of H selected ($P < 0·05$) during the interval 10.00–16.00 hours, which included the infusion period. The proportion of H selected during the interval 16.00–08.00 hours was not affected by treatment, and neither was the proportion of H selected on the non-infusion days.

There was a clear tendency for the proportion of H selected during the time interval 10.00–16.00 hours to be depressed at high treatment osmolalities ($0·1 < P < 0·05$), irrespective of treatment type. The treatment administered had a significant effect on the intake of H, being 176, 174, 238, 168, 182, 273, 173 and 247 g/4 h (SED 33) for Acid 1, Acid 2, Acid 3, Alkali 1, Alkali 2, Alkali 3, Control 1 and Control 2 respectively. Intake of L during this time interval was not affected by treatment, the mean being 180 (SEM 8·9) g/4 h. The osmolality of the treatment tended to affect the intake of H during the interval 10.00–16.00 hours, but it had no effect on the intake of L, as shown in Fig. 3. Treatment osmolality had no effect on the proportion of H selected outside this time interval.

Ruminal concentration of total VFA, molar proportion of individual VFA, ruminal

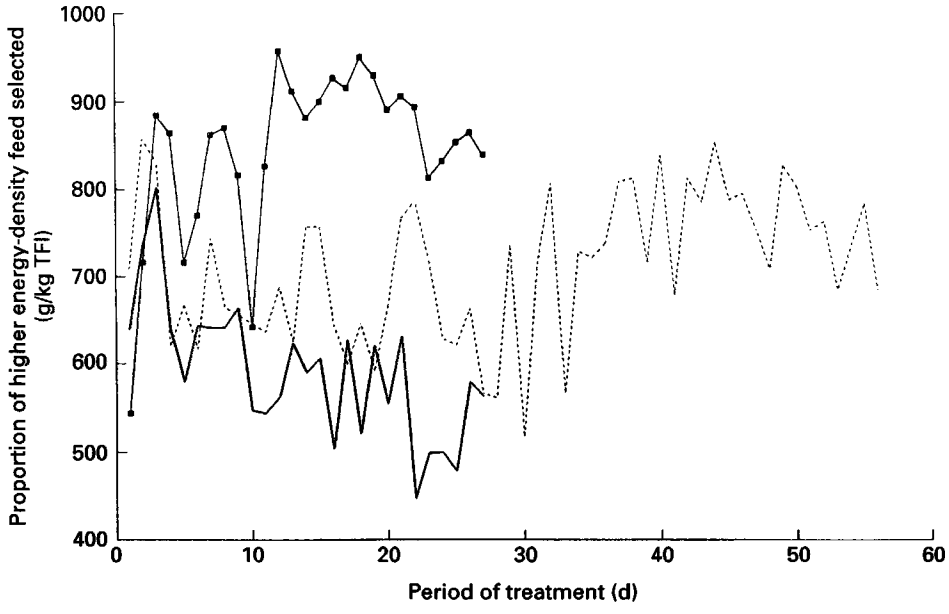

Fig. 1. Expt 1. Mean daily proportion (g/kg total feed intake, TFI) of the higher energy-density feed selected by sheep given access to two feeds of different energy densities: low (L), high (H) or a 3:1 mixture of L and H (M). Feed choices: L/M (■—■), L/H (– – –), M/H (——). For details of feeds and procedures, see Table 1 and pp. 40–42.

concentration of NH_3-N, and plasma concentrations of Na, Cl, and CO_2. The treatment administered had a significant effect ($P < 0.05$) on the total concentration of VFA (tVFA) at all sampling times of the 4 h infusion period; the mean concentrations during the infusion period were: 108, 112, 125, 122, 138, 137, 120 and 128 (SED 7·8) mM-tVFA for Acid 1, Acid 2, Acid 3, Alkali 1, Alkali 2, Alkali 3, Control 1 and Control 2 respectively. There was no significant effect of treatment on the molar proportions of propionate, butyrate or acetate (for example the mean molar proportions of acetate during the infusion period were: 0·591, 0·596, 0·587, 0·599, 0·594, 0·568, 0·616 and 0·606 (SED 0·0129) mmol/mmol tVFA for Acid 1, Acid 2, Acid 3, Alkali 1, Alkali 2, Alkali 3, Control 1 and Control 2 respectively). There was a significant effect of treatment on the molar proportion of isovalerate, which was markedly higher on Alkali 1 than on the other treatments. During the infusion period the mean concentrations were: 0·013, 0·013, 0·012, 0·018, 0·014, 0·013, 0·013 and 0·013 (SED 0·0015) mmol isovalerate/mmol tVFA for Acid 1, Acid 2, Acid 3, Alkali 1, Alkali 2, Alkali 3, Control 1 and Control 2 respectively. The plasma concentrations of Na, Cl and CO_2 were not affected by treatment, and neither was ruminal concentration of NH_3-N.

DISCUSSION

The objective of the first experiment reported here was to test whether energy density has any effect on the diet selections made by sheep. The results from the single feeding treatments, L, M and H have been used to interpret the diet selections of the choice-fed sheep. It is assumed that the sheep on the single feed H were able to meet their requirements for energy and protein as they maintained very rapid rates of Lwt gain (503 (SEM 28·6) g Lwt/d), although they had low rates of feed intake relative to the other single-feeding treatments, L and M.

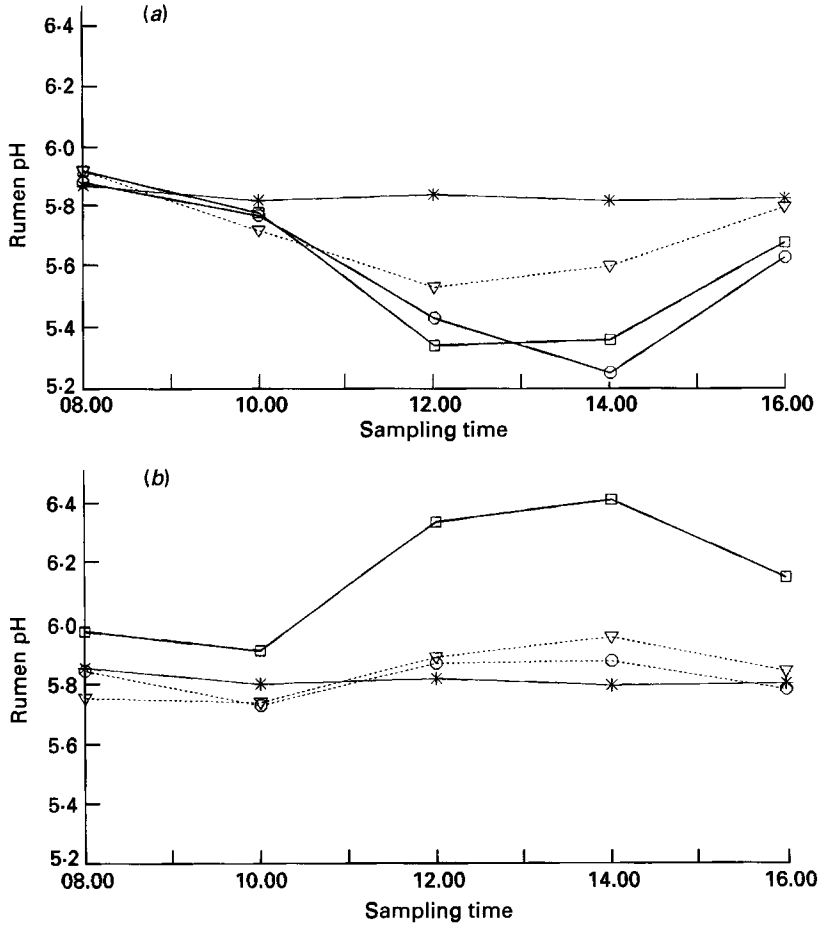

Fig. 2. Expt 2. Mean pH of the rumen contents, measured at 2 h intervals over the period 08.00–16.00 hours, of rumen-fistulated sheep given 1-litre rumen infusions over a 4 h period (10.00–14.00 hours) and offered a choice of two feeds that differed in their energy density. (*a*) Acid treatments: (□), 400 mM-HCl; (○), 300 mM-HCl; (▽), 200 mM-HCl; (*), NaCL control. (*b*) Alkali treatments: (□), 316 mM-NaOH; (○), 212 mM-NaOH; (▽), 109 mM-NaOH; (*), NaCL control. For details of treatments and procedures, see Table 2 and pp. 42–44.

Table 5. *Expt 2. The feed intakes (g) of sheep given access to feeds with different energy densities during infusion of different concentrations of acid, alkali or NaCl (control) into the rumen*†

Treatment...	Acid			Alkali			Control		SED	Statistical significance of effects of		
Time period	1	2	3	1	2	3	1	2	(32 df)	Infusate	Osmolality	Interaction
08.00–10.00	237	221	266	215	229	230	217	189	35·3	NS	NS	NS
10.00–16.00	345	342	421	332	390	458	374	409	46·8	$0{\cdot}1 < P < 0{\cdot}05$	*	NS
16.00–08.00	929	924	1135	900	990	1234	1002	980	76·3	NS	*	NS

SED, standard error of difference between means.
* $P < 0{\cdot}05$.
† For details of treatments and procedures, see Table 2 and pp. 42–44.

Table 6. *Expt 2. Diet selections made by sheep given access to feeds with different energy densities (MJ metabolizable energy/kg fresh feed) during infusion of different concentrations of acid, alkali or NaCl (control) in the rumen*†

(Values are proportions of the high-energy-density feed (H; g/kg total feed intake) selected during the interval considered)

Time period	Acid			Alkali			Control		SED (32 df)	Statistical significance of effects of		
	1	2	3	1	2	3	1	2		Infusate	Osmolality	Interaction
08.00–10.00	526	530	516	468	495	533	406	436	68·8	NS	NS	NS
10.00–16.00	511	508	566	507	466	595	462	603	49·7	*	$0{\cdot}1 < P < 0{\cdot}05$	NS
16.00–08.00	548	544	582	556	533	632	470	571	62·8	NS	—	NS

SED, standard error of the difference between means.
* $P < 0{\cdot}05$.
† For details of treatments and procedures, see Table 2 and pp. 42–44.

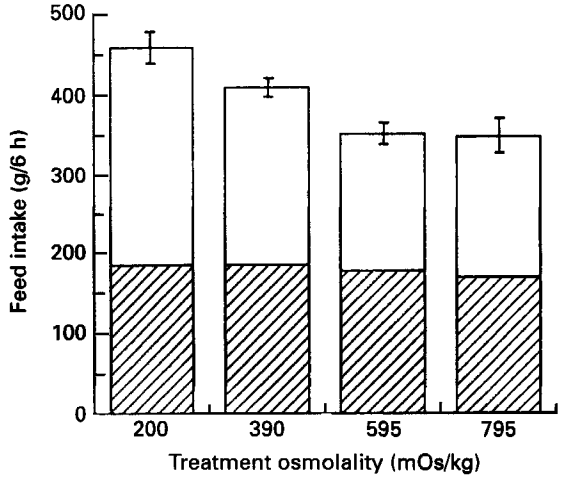

Fig. 3. Expt 2. Mean feed intake over a 6 h period (10.00–16.00 hours) of rumen-fistulated sheep given access to a low-energy-density feed (L, ▨) and a high-energy-density feed (H, □) as a choice. Rumen infusions of different osmolalities were administered over a 4 h period (10.00–14.00 hours). Values are means for eight sheep with their standard errors (for intakes of feeds L and H) indicated by vertical bars. For details of infusates and procedures, see Table 2 and pp. 42–44.

The benefits of eating H must be considered in relation to the possible 'costs' to the animals of eating this feed. It is possible that the consumption of feed H may have had some adverse effects on the rumen environment, the rumen wall and the animal's acid–base balance. For example, the pH of the rumen contents when feed H was offered alone was 5·59 (SEM 0·040); at such a pH cellulolysis would be inhibited (Mould & Ørskov, 1984) and rumen papillae would be clumped (Ørskov, 1973). In addition, feeds such as H which are composed of highly fermentable materials, would be expected to contribute to a high rumen osmolality (Ward *et al.* 1976). A high rumen osmolality is frequently associated with a decrease in time spent ruminating (Carter & Grovum, 1990*a*). However, the sheep fed on feed H alone appear to have adapted to cope with the costs of eating H, at least for the duration of the experiment, given their rapid growth rate on this feed. On the other hand,

the consumption of feed L appeared to limit the rate of Lwt gain as sheep fed on L had significantly lower rates of Lwt gain than the sheep on H, although the sheep on feed L attempted to compensate for the low energy density of the feed by increasing their rate of feed intake. It is also likely that the rumen conditions associated with the consumption of L would be less extreme than those associated with feed H. No measurements of rumen pH of sheep fed on L alone were made, but it can be safely predicted that the rumen pH on feed L would be greater than 6·00 (Kaufman, 1976).

From a simplistic theory point of view, such as optimal foraging (Krebs & McCleery, 1984), one would expect that sheep offered a choice between a pair of feeds of differing digestibility would show an absolute preference for the more digestible feed, since this choice would enable them to maximize their rate of energy intake whilst minimizing their intake of dietary bulk (Belovsky, 1978). The diet selections made by the choice-fed sheep in the present experiment do not appear to support this hypothesis. The sheep offered the feed pairs L/H and M/H did not select feed H alone, which suggests that although the sheep had the potential to cope with the costs of eating H, they chose not to adopt this strategy when feed H was offered in a choice. If the diet selections of these animals are expressed as a choice between feeds L and H (M was a mixture of feeds L and H, 3:1 w/w), then the similarities in their dietary choices become more obvious. Castle *et al.* (1979), Cropper (1987) and Newman *et al.* (1992) amongst others have also found that the diet selections of ruminants do not appear to follow an 'optimal foraging' strategy.

A few explanations are now offered to account for the behaviour of the choice-fed sheep in Expt 1. The inclusion of a less digestible feed in the diet selected by the L/H and M/H choice-fed sheep may be an example of sampling behaviour, whereby the animal maintains current knowledge of all feeds available to it from the environment by eating small quantities of each one at regular intervals (Illius & Gordon, 1990). Herbivores continue to sample feeds, even familiar ones in a familiar environment, as their contents of nutrients and anti-nutritive factors may change with time (Provenza & Balph, 1990). The selection of food L by the L/M choice-fed sheep, which accounted for approximately 10–15% of their total intake, can be seen as sampling behaviour. However the L/H and M/H choice-fed sheep chose to eat at least a third of their total intake as a food of low energy density; it is unlikely that sampling behaviour alone would account for such a high intake of one of the foods offered in a choice.

A second possibility is that the sheep were selecting on a continuous 'avoidance' basis, whereby they would eat from one feed only until some signals (metabolic or otherwise) indicated that there were some adverse consequences associated with the consumption of that feed and therefore they would only consume from the other feed in a subsequent meal (a theory based on observations on rats (Rozin & Kalat, 1971) but refuted for domesticated animals (Zahorik & Houpt, 1977)). There was no evidence in the present experiment that the meals eaten by the sheep consisted exclusively of one of the feeds offered or that the composition of the selected diet changed with time. A third explanation of the diet selections made by the L/H and M/H choice-fed sheep is that they were exhibiting a preference for rarity (Newman *et al.* 1992). Given the method of presenting the two feeds and the little variation in diet selection over the entire experiment, it is improbable that the diets selected by both group of animals resulted from this.

A fourth and preferred explanation is that maintenance of rumen conditions conducive to rapid rates of cellulolysis and microbial growth as well as the avoidance of conditions such as acidosis and ruminitis is of importance to sheep, and that they will modify their diet selections to maintain an equilibrium within the rumen (as discussed earlier). Given this suggestion the sheep would be expected to limit their intake of the feed that had greatest potential to change rumen conditions, in this case feed H. This hypothesis could also

account for the small individual variations in the diet selection of the L/H and M/H choice-fed animals, since it is known that animals vary in their ability to cope with the adverse effects of feeds (Kyriazakis & Oldham, 1993). The second experiment was designed to consider the above hypothesis, that is whether the maintenance of rumen conditions (pH and osmolality) has a direct effect on the diet selection of sheep. The objective of this experiment was to manipulate rumen conditions (pH and osmolality) in the short term and to observe the effects on the diet selections of sheep. Although fistulated sheep were used in this experiment it is felt that the conclusions that can be drawn from this experiment can be used to interpret the diet selections made by the sheep in the first experiment.

It is accepted that rumen pH can account for some of the variation in feed intake of ruminants (Williams *et al.* 1987); however, it is likely that the effects of the treatments on feed intake in Expt 2 were mediated by factors other than rumen pH, such as treatment osmolality. Feed intake during the time interval in question (10.00–16.00 hours) declined systematically in response to increasing treatment osmolality. This result is consistent with the work of a number of other groups (for a review see Grovum, 1987) who have also found that infusions of hypertonic solutions into the rumen are associated with a short-term decline in feed intake. There was an apparent effect of the treatment osmolality on feed intake after the infusion had ceased (16.00–08.00 hours). It would be expected that the influence of treatment osmolality would have been such that sheep with low intakes during the preceding interval (10.00–16.00 hours), caused in part by the osmotic effects of treatment, would have compensated during the time interval 16.00–08.00 hours. The observed direction of the effect of the treatment osmolality on feed intake is opposite to this prediction. In addition, the significance of the treatment osmolality on feed intake during the latter time interval appears to have been due to two treatments (Acid 3 and Alkali 3), which were of dissimilar osmolality. This suggests that this effect, though statistically significant, is not of biological relevance, and so we agree with Phillip *et al.* (1981) who have shown that the osmotic effect on feed intake is of a short-term nature only.

There was a significant effect of treatment on the proportion of feed H selected by the sheep in Expt 2 during the time interval from the start of the infusion until 2 h after it had ceased (10.00–16.00 hours). In this experiment the effect of pH on diet selection has not been completely separated from the osmotic effects on diet selection. This is because it is not possible to alter rumen pH without affecting osmolality with the acid and alkali treatments used here. However, it is thought that the effect of the treatment on diet selection was mediated through the changes in rumen osmolality that were induced by the infusion of the treatments. In response to increasing treatment osmolality, the intake of feed H declined significantly whereas the intake of L remained constant irrespective of treatment osmolality. It is proposed that the decline in the consumption of feed H during the infusion period was because this feed was composed of materials that would be fermented rapidly within the rumen causing rumen pH to drop and osmolality to rise (Van Soest, 1982). The sheep in Expt 2 may have been able to associate feed H with adverse changes to the rumen environment such as low pH and high osmolality. Thorhallsdottir *et al.* (1990) have demonstrated that sheep do have the ability to associate feeds with post-ingestive consequences of eating them. In contrast to feed H, feed L was composed of materials which would be fermented more slowly (Van Soest, 1982); the sheep may have maintained their intake of feed L under these conditions as the consumption of this feed would generate only a marginal increase in the osmotic load. Engku Azahan & Forbes (1992) have also found that sheep offered a choice between a slowly fermented feed (hay) and a rapidly fermented feed (barley–dried grass pellets) maintain their intake of hay but reduce their intake of the barley-based food when hypertonic solutions are infused into their rumen. An important finding of our experiment is that although sheep were 'trained'

to associate the consumption of the feeds with their consequences, their subsequent diet selection was not inflexible but able to respond to short-term manipulations of their rumen environment.

It is therefore proposed that sheep in Expt 2 may have responded to the imposed changes in their rumen environment, in particular increased rumen osmolality, by reducing their intake of feed H, and in doing so they minimized further increases in rumen osmolality. The process of altering diet selection patterns in response to changes in rumen osmolality must be a short-term mechanism, since the sheep were capable of switching between the two feeds very rapidly within the 4 h of the infusion period. Hou (1991) has also demonstrated that sheep can make fast changes in their diet selection as a result of manipulation of the rumen environment. Carter & Grovum (1990*b*) have shown that sheep can respond to changes in rumen osmolality very rapidly by reducing their intake within 10 min of the start of rumen infusion of a hypertonic solution. The only receptors that could respond within such a short interval would be those sited in the rumen-reticulum (Carter & Grovum, 1990*b*). At present the evidence remains equivocal that osmoreceptors do exist in the rumen and that they can be stimulated by changes that are within the physiological range (Forbes & Barrio, 1992).

Tactical adjustments of diet selection in the short term could be viewed within the overall feeding strategy of the sheep, which is to enable it to maximize its evolutionary fitness. These results suggest that sheep will make short-term changes in diet selection to promote effective rumen conditions for achieving a feed intake which allows animal needs for nutrients and energy to be met. The effect of these shifts in dietary choice would be of benefit to the sheep in the long term as they would ensure rapid growth and development over the long term.

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