

## Rumen development in the calf

### 2.\* The effect of diets containing different proportions of concentrates to hay on digestive efficiency

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1. Twenty-four Ayrshire bull calves were reared on either high-concentrate or high-roughage diets to study the effect of diet on the subsequent ability of the calf to digest either concentrates or hay when given alone. The rearing diets were known to produce different types of rumen development. 2. Although there were significant differences between the apparent digestibility coefficients of the high-concentrate and high-roughage rearing diets and between concentrates and hay when given alone, the subsequent ability of the calf to digest either concentrates or hay was unaffected by the type of diet given during the rearing period to 13 weeks of age. 3. The amount of nitrogen retained was significantly greater in calves reared on the high-concentrate diet than in those given the high-roughage diet, but similar amounts of N were retained/100 g gain in body-weight in both groups. After the change in diet, the amount of N retained was significantly greater in calves given concentrates after a rearing diet high in concentrates than in those given concentrates after a rearing diet high in roughage, although in both groups 32% of the N intake was retained. Four of the six calves given hay after a rearing diet high in concentrates were in negative N balance, but only one calf lost weight. Only 19% of the N intake was retained in calves given hay after being reared on a high-roughage diet. 4. The concentration of total volatile fatty acids (VFA) in the rumen contents rose to reach peak levels at about 3 h after food was offered; the concentration then declined. VFA concentrations tended to be higher in calves given the rearing diet high in concentrates than in those given the one high in roughage, and differences reached significance when the diet was changed to one of all concentrates or all hay, with no obvious carry-over effect of the rearing diet. The proportion of propionic, butyric and higher acids tended to be greater in calves given high levels of concentrates than in those given high levels of hay and also tended to rise, irrespective of diet, as the concentration of total VFA rose. 5. A change of diet at 14 weeks from one high in concentrates to one consisting entirely of hay resulted in a significant decline in the viable counts of streptococci, lactobacilli and coliform organisms in the rumen liquor at 16 weeks. The numbers of bacteria were unaffected by the other dietary changes. 6. The concentration of total VFA in plasma of peripheral blood tended to be higher in calves given the high-roughage or all-hay diets. A fall in the concentration of plasma VFA occurred when calves were changed from a high-roughage diet to an all-concentrate diet and a rise in concentration was observed when an all-hay diet replaced one containing a high proportion of concentrates. 7. During the initial rearing period the mean blood plasma glucose concentration was 92.8 mg/100 ml in calves given the high-concentrate diet, a value significantly higher than the mean value of 64.5 mg/100 ml found in calves given the high-roughage diet. The concentration of plasma glucose rose to 89.8 mg/100 ml in calves changed from the high-roughage diet to concentrates and declined to 81.7 mg/100 ml in calves that were given hay in place of the high-concentrate diet. 8. The weight of contents of the reticulo-rumen and omasum and the volume displacement of these organs were significantly greater in calves given hay as the sole diet during the last 3 weeks of life than in those given concentrates during this period. The weight of tissue forming the reticulo-rumen was significantly greater in calves given the all-concentrate diet during the last 3 weeks of life than in those given only hay during this period. It was apparent that the rumen papillae developed rapidly in those calves given concentrates as the sole diet for a period of 3 weeks after a rearing diet high in roughage, whereas there was a marked retrogression of papillae when concentrates were withdrawn from the diet. 9. It is concluded that the ruminant calf adapts readily to marked dietary changes, with the result that differences in the size and structure of the ruminant stomach, which have been shown to occur when different types of diet are given, have no permanent effect on the ability of the calf to digest diets of concentrates or hay.

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The view has been widely held by farmers and advisory workers that, in order to be able to utilize efficiently diets containing a fairly high proportion of roughage, cattle must receive a liberal supply of roughage during the rearing period. Although several workers (e.g. Filmer, 1952; Crichton & Aitken, 1954; Reid, Loosli, Turk, Asdell & Smith, 1957) have studied the effect of different planes of nutrition during the rearing period on such factors as age at calving, milk yield and longevity, they did not examine the effect on digestive efficiency. Hansson, Brännäng & Claesson (1953), in an experiment using monozygous twins, found that, although the most efficient utilization of food for growth occurred in heifers reared on a low plane of nutrition from 1 month of age, there was no difference in digestive efficiency between animals on different planes of nutrition at 2 years of age. However, since the diet for both high and low planes of nutrition consisted of the same mixture of concentrates and chopped roughage given at two different levels, the effect of diets high or low in roughage on subsequent ability to utilize foodstuffs was not examined in the investigation.

The effect of giving diets of either high or low roughage content to monozygous twin heifers during the rearing period from 4 months to 2 years of age was studied at this Institute by Balch, Campling, Johnson & Roy (1960). They found that the method of rearing had no effect on the subsequent ability to digest hay or mixed rations of hay and concentrates, but were unable to examine the anatomy of the rumen.

In a recent experiment Stobo, Roy & Gaston (1966) found that, in calves weaned at 5 weeks of age, diets containing a high proportion of concentrates stimulated rapid weight gains and marked development of the mucosal layer of the reticulo-rumen, whereas diets consisting mainly of hay resulted in poorer growth and increased the capacity of the reticulo-rumen without causing extensive papillary development. A similar association, between large weight gains and advanced stages of rumen papillary development, has been reported in the young lamb (Sinclair & Künkel, 1959). It seemed pertinent, therefore, to examine the relationship between rumen development and digestive efficiency in the early-weaned calf.

In the previous experiment (Stobo *et al.* 1966), the two extreme types of rumen development were obtained in calves given concentrates to a maximum of 2.27 kg/day or 0.45 kg/day; the proportions of concentrates to hay at 12 weeks of age were 9:1 and 1:3 respectively. The same two basic treatments were used in the experiment reported here, first, to investigate the ability of the early-weaned calf to digest diets of concentrates and hay in proportions known to produce different types of rumen development, and secondly, to study the effect of diet during the rearing period to 12 weeks of age on the subsequent ability of calves to digest either concentrates or hay.

## METHODS

### *Plan of experiment*

The experiment was made between September 1959 and June 1961, using twenty-four Ayrshire bull calves from 3 weeks of age, in a randomized block design consisting of six blocks, each containing four treatments. The composition of the concentrate mixture and management of the calves during the first 12 weeks of life were as de-

scribed by Stobo *et al.* (1966). The calves were weaned at 5 weeks of age and given hay and water *ad lib.*, together with a maximum daily allowance of concentrates of either 2.27 kg (treatments 1 and 2) or 0.45 kg (treatments 3 and 4). After 12 weeks of age the calves were kept on slatted floors and given daily a constant amount of food, consisting of either 9 parts concentrates to 1 part hay (treatments 1 and 2) or 1 part concentrates to 3 parts hay (treatments 3 and 4). After a preliminary period of 7 days, digestibility and nitrogen-balance trials were made over a 7-day period commencing on the 91st day of life.

At the end of the first digestibility trial (period 1), calves were given either concentrates (treatments 1 and 3) or hay (treatments 2 and 4) together with water, the changeover being made gradually where necessary. After 7 days of *ad lib.* feeding with these diets, constant amounts of diet were given daily for a further 14 days, the last 7 of which constituted a second digestibility and N-balance trial (period 2).

#### *Digestibility trials*

Calves were kept in individual metabolism crates for a collection period lasting 7 days. Urine was collected into 3.5 l. bottles containing 25 ml glacial acetic acid. The weight of urine was recorded twice daily and a 10% sample was stored at 4°. Faeces were collected in Polythene bags which were changed once or twice daily as necessary and, after thorough mixing, a 10% sample of the faeces was stored at -25°. At the end of the collection period the accumulated sample of faeces was thawed out and mixed, and a 50 g sample was acidified with 100 ml 15% (v/v) sulphuric acid for N determination. The remainder of the faeces was dried to constant weight at 100° and the dry-matter content calculated.

#### *Sampling of blood and rumen contents*

Two days before the beginning of digestibility periods 1 and 2, i.e. at 89 and 110 days of age, samples of blood and rumen liquor were taken from each calf 15 min before and at 1, 2, 3, 4 and 6 h after feeding. The blood sample was removed through a Polythene catheter, having an internal bore of 1 mm and a wall 0.25 mm thick. The catheter was inserted into the jugular vein and stitched in place 2 h before the first sample was taken. To prevent coagulation of blood, the catheter was filled after each sampling with a dilute solution of heparin, consisting of 4 ml heparin solution containing 5000 i.u. heparin/ml (Evans Medical Supplies Ltd, Liverpool) per l. of 0.9% (w/v) saline, and the end was sealed with a clip. Samples of 40 ml of blood were removed by syringe, after constricting the jugular vein and allowing the first 2 ml to go to waste. The contents of the syringe were transferred immediately to a tube containing four drops of the undiluted heparin solution and centrifuged at 2240 g for 20 min. The plasma was drawn off and stored at -25°.

Samples of rumen liquor, consisting of approximately 10 ml, were collected by stomach tube at the stated time intervals for determination of pH and volatile fatty acid (VFA) concentrations. A further 150 ml of rumen liquor were removed 3 h after feeding, for determination of bacterial population: a similar sample had been taken 2½ h after feeding when the calves were 56 days old.

### *Analytical methods*

The chemical composition of the dried samples of food and faeces and the N content of the acid faeces and urine were determined by the methods normally adopted: N was determined by the Kjeldahl method; crude fibre by digestion for 30 min in dilute sulphuric acid (5%, w/v) followed by dilute sodium hydroxide solution (5%, w/v) for a further 30 min; ether extract by extraction in petroleum spirit (b.p. 40–60°) in a Soxhlet extraction apparatus, and ash by incineration in a muffle furnace at 560°. N-free extract was determined by difference.

Concentrations of blood plasma glucose (reducing sugar) were determined by the method of Nelson (1944) using the copper reagent of Somogyi (1952), blood plasma total VFA concentrations by the method of Scarisbrick (1952), and total VFA concentration in rumen liquor by the method described by Annison (1954). The proportions of individual VFA in the samples of rumen liquor were determined by paper chromatography, using the technique described by Reid & Lederer (1951) and Duncan & Porteus (1953).

### *Rumen bacteria*

The viable counts of streptococci, lactobacilli and coliform organisms were determined by the dilution techniques described by Davey, Cheeseman & Briggs (1960) on samples of rumen liquor taken at 2½ h (56 days) or 3 h (89 and 110 days) after feeding.

### *Post-mortem examination*

Each calf was slaughtered at the end of the second digestibility trial and examined *post mortem*. The techniques adopted previously (Stobo *et al.* 1966) were used to determine the weight of contents of the alimentary tract, volume displacement of the stomachs, weight of tissue forming the organs of the alimentary tract and rumen papillary development.

## RESULTS

### *Performance of the calves*

The results for the performance of the calves from 3 to 12 weeks of age and from 15 to 17 weeks, together with information on food intake, are given in Table 1 and Fig. 1. As expected, calves given a maximum of 2.27 kg concentrates daily gained weight significantly faster during the period 3–12 weeks of age than calves restricted to 0.45 kg/day of the same concentrate mixture. The majority of calves were eating 0.45 kg concentrates daily by the time they were weaned at 5 weeks; those restricted to this level of concentrates (treatments 3 and 4) consumed hay at a steadily increasing rate; those given a maximum allowance of 2.27 kg concentrates/day (treatments 1 and 2) reached this level at 11 weeks of age, hay intake being correspondingly lower.

During the period 15–17 weeks, calves on treatments 1 and 3 that received only concentrates, gained weight at a significantly faster rate than those on treatments 2 and 4 that were given hay as the sole diet. As shown in Table 1, calves on treatment 1 gained weight significantly faster than those on treatment 3 (0.71 kg/day compared

Table 1. Performance (mean values with their standard errors) to 17 weeks of age in calves weaned at 5 weeks of age and given a concentrate mixture containing 20% crude protein and hay in the ratio of either 9:1 or 1:3 at 12 weeks of age, followed at 14 weeks by a diet consisting solely of concentrates or hay

	No. of calves	Ratio of concentrates to hay or sole diet	Live weight (kg)		Intake of diet (kg)				Live-weight gain (kg/day)
			At 3 weeks	At 12 weeks	Milk	Concentrates	Hay	Water	
3-12 weeks									
Treatment no. $\left. \begin{matrix} 1+2 \\ 3+4 \end{matrix} \right\}$	12	9:1	39.4	77.6	43.3	89.2	13.7	246	0.63
Standard error of a treatment mean	12	1:3	38.0	57.1	41.1	26.1	39.7	170	0.31
	—	—	±1.8	±2.8	±1.8	±2.7	±5.3	±14	±0.03
Significance of difference between treatments	—	—	—	***	—	***	***	***	***
15-17 weeks									
Treatment no. $\left. \begin{matrix} 1 \\ 2 \\ 3 \\ 4 \end{matrix} \right\}$	6	Concentrates	At 15 weeks 94.0	At 17 weeks 103.9	—	41.5	—	120	0.71
Standard error of a treatment mean	6	Hay	87.6	89.8	—	—	27.6	95	0.16
Significance of difference between diets, 1+3 v. 2+4	6	Concentrates	59.5	66.7	—	26.9	—	76	0.52
Significance of difference within concentrates, 1 v. 3	6	Hay	65.8	68.4	—	—	26.9	77	0.19
Significance of difference within hay, 2 v. 4	—	—	±2.6	±2.8	—	±1.3	±1.3	±7.9	±0.04
	—	—	—	—	—	—	—	—	***
Significance of difference between diets, 1+3 v. 2+4	—	—	***	***	—	***	—	***	**
Significance of difference within concentrates, 1 v. 3	—	—	***	***	—	—	—	—	—
Significance of difference within hay, 2 v. 4	—	—	***	***	—	—	—	—	—

\*\* Significant at  $P < 0.01$ . \*\*\* Significant at  $P < 0.001$ .

with 0.52 kg/day respectively) but consumed a greater amount of concentrates. This may have been because those on treatment 1 were already accustomed to a high-concentrate diet, but since concentrate consumption/unit body-weight was almost identical with both treatments, it may be that the maximum intake of concentrates had been achieved by all calves. Since hay consumption/unit body-weight was lower in treatment 2 than in treatment 4, it is possible that the reticulo-rumen, or the cavity enclosed by the abdominal walls, did not increase in capacity at a sufficiently rapid rate to accommodate the increased volume of contents when the diet was changed from one high in concentrates to one of hay only.

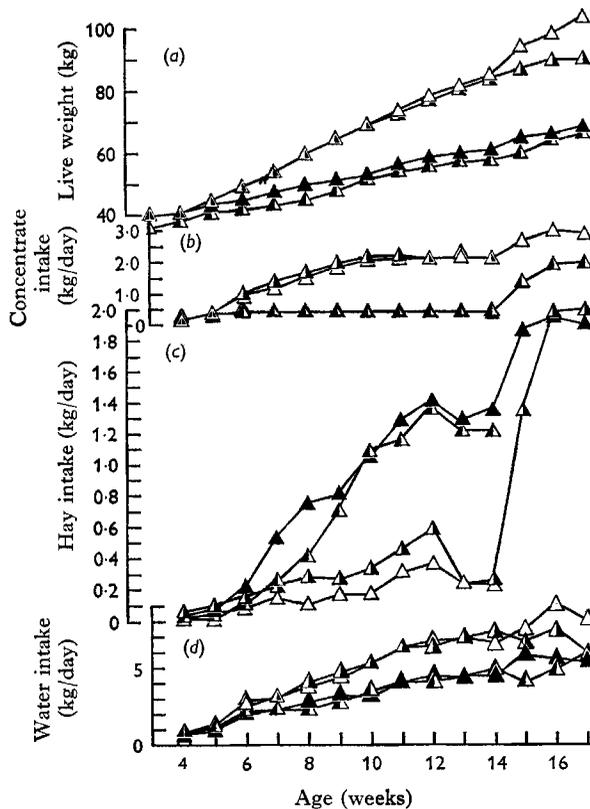


Fig. 1. Mean live weight (a) and daily intake of concentrates (b), hay (c) and water (d) of calves given diets consisting of concentrates and hay in different proportions.  $\Delta$ — $\Delta$ , high-concentrate diet to 14 weeks followed by an all-concentrate diet;  $\triangle$ — $\triangle$ , high-concentrate diet to 14 weeks followed by an all-hay diet;  $\triangle$ — $\triangle$ , high-roughage diet to 14 weeks followed by an all-concentrate diet;  $\blacktriangle$ — $\blacktriangle$ , high-roughage diet to 14 weeks followed by an all-hay diet.

Table 2. Chemical composition (%) of the foods used in the digestibility trials

Food	Dry matter	Crude protein	Crude fibre	Ether extract	Ash	Nitrogen-free extract
Concentrates	85.1	20.1	3.6	1.9	4.7	54.8
Hay	84.9	7.0	24.3	1.2	5.7	46.7

### Digestibility

The chemical composition of the diets used in the digestibility trials is given in Table 2 and the mean apparent digestibility coefficients are presented in Table 3. The results show that when diets containing a high proportion of concentrates were given in period 1 the dry matter, crude protein, ether extract and N-free extract fractions were digested more efficiently, and the crude fibre fraction digested less efficiently than when the diet consisted mainly of hay (differences significant at  $P < 0.001$ ).

Table 3. *Apparent digestibility coefficients (mean values with their standard errors) of the diet of calves given concentrates and hay in different proportions*

	No. of calves	Ratio of concentrates to hay or sole diet	Dry-matter intake (kg/day)	Apparent digestibility (%)				
				Dry matter	Crude protein	Crude fibre	Ether extract	N-free extract
Period 1 (13-14 weeks)								
Treatment no.	12	9:1	2.1	75.1	73.0	18.4	69.8	82.3
	12	1:3	1.5	62.5	54.9	57.3	31.6	68.6
Standard error of a treatment mean	—	—	±0.04	±1.0	±1.8	±3.7	±4.8	±1.1
Significance of difference between treatments	—	—	***	***	***	***	***	***
Period 2 (16-17 weeks)								
Treatment no.	6	Concentrates	2.5	80.8	80.2	2.2	68.9	87.2
	6	Hay	1.7	57.3	39.5	53.5	22.6	62.2
	6	Concentrates	1.7	78.7	75.7	16.8	61.0	85.9
	6	Hay	1.6	57.9	43.4	54.4	25.0	62.5
Standard error of a treatment mean	—	—	±0.08	±1.1	±2.2	±7.0	±4.4	±1.5
Significance of difference between diets, 1+3 v. 2+4	—	—	***	***	***	***	***	***
Significance of difference within concentrates, 1 v. 3	—	—	***	—	—	—	—	—
Significance of difference within hay, 2 v. 4	—	—	—	—	—	—	—	—

\*\*\* Significant at  $P < 0.001$ .

In period 2, when the diet consisted entirely of concentrates or of hay, the differences in apparent digestibility coefficients between the diets were even more pronounced. The apparent digestibility of dry matter, crude protein, ether extract and N-free extract was slightly greater in treatment 1 than in treatment 3, although these differences were not significant. The low value of 75.7% for apparent digestibility of crude protein, found with treatment 3 in period 2, was the lowest value obtained by us for this high-protein concentrate; it was accompanied by the relatively high level of faecal N excretion of 0.86 g/100 g dry-matter intake.

### Nitrogen balance

Mean values for the N-balance trials are presented in Table 4. In period 1 calves given the high-concentrate diet (treatments 1 and 2) retained very much more N than those given the high-roughage diet (treatments 3 and 4). Those given the high-

Table 4. *Body-weight changes and nitrogen balance results (mean values with their standard errors) in calves given concentrates and hay in different proportions*

Period 1 (13-14 weeks)		No. of calves	Ratio of concentrates to hay or sole diet	Live weight (kg)	Live-weight gain (kg/day)†	N intake (g/day)	Faecal N (g/day)	Apparently digested N (g/day)	Urinary N (g/day)	N balance (g/day)	N balance (% of N intake)
Treatment no.	{ 1+2 3+4	12	9:1	82.9	0.50	72.9	19.5	53.4	33.3	20.2	27.7
Standard error of a treatment mean		12	1:3	58.8	0.17	29.4	13.2	16.2	8.9	7.4	24.4
Significance of difference between treatments		—	—	±2.4	±0.06	±2.0	±0.56	±2.1	±2.1	±1.6	±3.0
		—	—	***	***	***	***	***	***	***	—
Period 2 (16-17 weeks)											
Treatment no.	{ 1 2 3 4	6	Concentrates	102.6	0.65	97.5	19.3	78.2	47.2	31.1	32.5
		6	Hay	89.8	0.20	22.1	13.1	8.9	11.0	-2.1	-10.7
		6	Concentrates	65.1	0.45	59.0	14.3	44.7	25.3	19.3	32.2
		6	Hay	67.7	0.19	21.7	12.1	9.6	5.3	4.4	18.8
Standard error of a treatment mean		—	—	±2.7	±0.06	±3.4	±0.85	±2.8	±2.8	±1.6	±3.5
Significance of difference between diets, 1+3 v. 2+4		—	—	—	***	***	***	***	***	***	***
Significance of difference within concentrates, 1 v. 3		—	—	***	*	***	***	***	***	***	—
Significance of difference within hay, 2 v. 4		—	—	***	—	—	—	—	—	*	***

\* Significant at  $P < 0.05$ .      \*\*\* Significant at  $P < 0.001$ .  
 † Live-weight gain/day calculated over a fortnightly period (see p. 197).

concentrate diet also excreted considerably more N in the urine and therefore made less efficient use of a greater intake of apparently digested N (ADN) than those given the high-roughage diet. The amount of N retained was 4.13% of the mean live-weight gain, determined over the 14-day period commencing 7 days before the beginning of the digestibility trial. Live-weight gain measured over the 14-day period was more closely related to N retention than was live-weight gain measured over a 7-day period, since the longer period partly eliminated the effect of marked day-to-day fluctuations in live weight of calves while on digestibility trials; these fluctuations were thought to be caused by a combination of such factors as the strange environment of the digestibility crate, the effect of the harness and the frequent day-to-day irregularity in water consumption.

In period 2, the intake of ADN, excretion of urinary N and the amount of N retained were all significantly greater in calves given concentrates (treatments 1 and 3) than in those given hay (treatments 2 and 4). Four of the six calves on treatment 2 were in negative N balance, although only one calf lost weight, and it appears that the increase in weight of contents of the alimentary tract, that occurred when calves were changed from a high-concentrate to an all-hay diet, exceeded the loss in body tissue that occurred as the result of a lower level of nutrient intake. Calves on treatment 1 retained 31.1 g N/day, which was 61% greater than the amount retained by calves on treatment 3, despite a higher level of urinary N excretion by the former group. Since the greater N balance was accompanied by a faster rate of growth, the amounts of N stored were 4.78 and 4.29 g/100 g live-weight gain in treatments 1 and 3 respectively.

The efficiency of utilization of dietary N (N balance expressed as a percentage of N intake) is also shown in Table 4. In period 1 the amount of N retained varied between 1.4 and 38.5% of the total N intake, but there was no significant difference between treatments, the mean value being 26.0%. In period 2, on the other hand, 32.4% of the N intake was retained in calves given the all-concentrate diet, with no difference between treatments 1 and 3, compared with 18.8% on treatment 4, in which calves were given the all-hay diet (differences significant at  $P < 0.05$ ). Since calves given hay after a high-concentrate rearing diet were in negative N balance, the efficiency of utilization of dietary N averaged -10.7% in treatment 2, which was significantly different ( $P < 0.001$ ) from all the other mean values.

#### *Rumen VFA and pH*

The mean total VFA concentration and pH of samples of rumen liquor taken 15 min before feeding and 1, 2, 3, 4 and 6 h after feeding are shown in Figs. 2 and 3 for periods 1 and 2 respectively. Although there was considerable within-treatment variation at any one sampling time, rumen total VFA concentration tended to increase with time after feeding to reach a peak at about 3 h, accompanied by a steady decline in the pH of rumen contents. The mean values for total VFA concentration and rumen pH before, and 3 h after, feeding are presented in Table 5. At these times, although the concentration of total VFA in period 1 tended to be higher in calves given high-concentrate diets (treatments 1 and 2) than in those given high-roughage diets (treat-

ments 3 and 4), the differences were not significant. However, as can be seen from Fig. 2, the decline in concentration of total VFA that began 3 h after feeding was more rapid in calves given the high-roughage diet, so that an obvious difference was apparent at 4 and 6 h after feeding, mean values at these times being 8.69 and 7.71 m-equiv./100 ml for high-concentrate diets, compared with 6.27 and 6.06 m-equiv./100 ml for high-roughage diets. The decline in pH of rumen contents from before to 3 h after feeding was much greater with the high-concentrate than with the high-roughage diet.

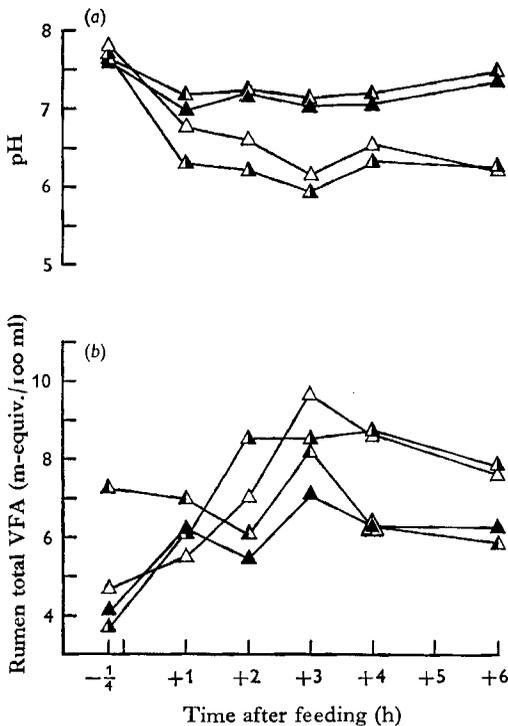


Fig. 2

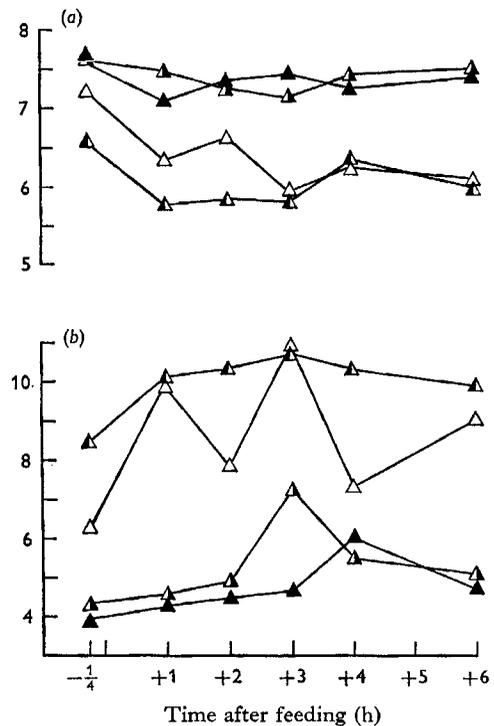


Fig. 3

Fig. 2. Period 1. Mean pH (a) and total VFA concentration (b) in the rumen liquor at intervals after feeding in 13-week-old calves given a high-concentrate ( $\Delta$  and  $\blacktriangle$ ) or a high-roughage ( $\triangle$  and  $\blacktriangle$ ) diet.

Fig. 3. Period 2. Mean pH (a) and total VFA concentration (b) in the rumen liquor at intervals after feeding in 16-week-old calves given a diet consisting entirely of concentrates or of hay from 14 weeks of age.  $\Delta$ — $\Delta$ , high-concentrate diet to 14 weeks followed by an all-concentrate diet;  $\triangle$ — $\triangle$ , high-concentrate diet to 14 weeks followed by an all-hay diet;  $\blacktriangle$ — $\blacktriangle$ , high-roughage diet to 14 weeks followed by an all-concentrate diet;  $\blacktriangle$ — $\blacktriangle$ , high-roughage diet to 14 weeks followed by an all-hay diet.

In period 2, the concentration of total VFA in the rumen was significantly greater in calves receiving the all-concentrate diet (treatments 1 and 3) than in calves given only hay (treatments 2 and 4) both before and 3 h after feeding. At both of these times rumen pH was significantly higher in the hay-fed calves. Although differences within diets in period 2 did not reach significant levels, some were of sufficient magnitude to merit attention. For instance, the concentration of total VFA before feeding was

Table 5. Comparison of the levels of rumen total volatile fatty acids and pH, blood plasma total VFA and reducing sugar (mean values with their standard errors) in calves before feeding and at 3 h after offering concentrates and hay in different proportions

Time relative to feeding (h) ...	Ratio of concentrates to hay or sole diet	Rumen total VFA (m-equiv./100 ml)		pH of rumen contents		Plasma total VFA (mg/100 ml)		Plasma glucose (mg/100 ml)		Food consumption (kg)				
		-½	+3	-½	+3	-½	+3	-½	+3	Previous 24 h		0 to +3 h		
										Concentrates	Hay	Concentrates	Hay	
<b>Period 1 (89 days)</b>														
No. of samples	—	10	10	12	12	10	10	12	12	10	10	10	10	
Treatment no. {	1+2	4.20	9.14	7.7	6.1	0.53	1.45	96.2	88.6	2.2	0.3	1.1	0.1	
Standard error of a treatment mean†	3+4	5.73	7.69	7.6	7.1	1.17	2.12	62.3	66.0	0.45	1.4	0.45	0.3	
Significance of difference between treatments	—	±1.3	±1.2	±0.08	±0.26	±0.18	±0.54	±4.9	±5.6	—	—	—	—	
<b>Period 2 (110 days)</b>														
No. of samples	—	5	5	6	6	5	5	6	6	6	6	6	6	
Treatment no. {	1	6.24	10.96	7.2	5.9	1.11	0.92	99.2	93.3	3.1	—	0.9	—	
Standard error of a treatment mean†	2	4.32	7.28†	7.6	7.1	1.58	1.58	77.5§	73.1§	—	2.1	—	0.8	
Significance of difference between diets, 1+3 v. 2+4	3	8.24	10.71	6.6	5.8	1.27	1.00†	91.0§	87.8§	1.9	—	0.45	—	
Significance of difference within concentrates, 1 v. 3	4	3.88	4.68	7.7	7.4	1.70	1.25	62.4	56.1	—	1.9	—	0.3	
Significance of difference within hay, 2 v. 4	—	±1.3	±0.85	±0.21	±0.23	±0.22	±0.22	±4.5	±5.0	—	—	—	—	
Significance of difference between diets, 1+3 v. 2+4	—	*	***	**	***	—	—	***	***	—	—	—	—	
Significance of difference within concentrates, 1 v. 3	—	—	—	—	—	—	—	—	—	—	—	—	—	
Significance of difference within hay, 2 v. 4	—	—	—	—	—	—	—	*	*	—	—	—	—	

\* Significant at  $P < 0.05$ . \*\* Significant at  $P < 0.01$ . \*\*\* Significant at  $P < 0.001$ .  
 † In calculating the standard errors, the arrangement in blocks has been ignored.  
 ‡ Mean of only four samples. § Mean of only five samples

Table 6. Mean values for the molar percentages of volatile fatty acids and lactic acid in samples of rumen liquor from calves given diets containing different proportions of concentrates to hay

Treatment no. ... Diet*	Period 1 (89 days)				Period 2 (110 days)							
	1+2		3+4		1		2		3		4	
	High concentrates	After	High roughage	After	Concentrates	After	Concentrates	After	Concentrates	After	Concentrates	After
Time relative to feeding†	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
Total VFA:	10	49	10	50	5	25	5	24	5	25	5	23
No of samples	4.20	7.82	5.73	6.48	6.24	9.04	4.32	5.40	8.42	10.29	3.88	4.74
Concentration (m-equiv./100 ml)												
Individual acids (molar %):												
Acetic	59.2	44	9	48	4	19	5	22	4	23	5	22
Propionic	24.5	49.2	69.4	65.3	60.2	46.2	74.9	70.1	42.1	47.5	75.5	76.3
Butyric	9.8	27.1	20.3	17.1	21.2	27.7	18.5	19.5	29.5	29.6	15.6	16.7
Valeric	3.5	13.6	7.8	12.8	7.9	13.5	4.4	7.6	14.6	12.3	7.2	6.0
Hexoic	—	5.5	0.4	1.5	3.4	7.0	—	0.5	8.1	6.6	—	—
Heptoic	—	1.1	—	0.4	3.0	1.6	—	—	4.1	1.7	—	—
Lactic	3.0	1.0	—	—	—	0.8	—	—	—	0.5	—	—
		2.6	2.2	2.9	4.3	3.2	2.2	2.3	1.7	1.7	1.7	1.1

\* In period 1 the ratio of concentrates to hay was 9:1 (high-concentrate diet) or 1:3 (high-roughage diet). In period 2 the diet consisted solely of concentrates or hay.

† Values of samples taken after feeding are the mean values for samples taken at 1, 2, 3, 4 and 6 h after feeding.

35% higher in treatment 3 than in treatment 1, and this higher value was accompanied by a slightly lower pH, whereas at 3 h after feeding the concentration of total VFA was 56% higher in treatment 2 than in treatment 4, and again accompanied by a slightly lower pH value. The wide fluctuations in concentration of rumen total VFA in treatment 1 were found in three of the five calves used for the determination. Since no relationship could be found between VFA concentration in the rumen and the level of food intake, the results may reflect the difficulty of obtaining representative samples by stomach tube, especially from calves given an all-concentrate diet at a fairly high level of intake.

The proportions of individual VFA present in the rumen liquor, expressed as molar percentages, are shown in Table 6. It is clear that when the diet consisted of 9 parts concentrates to 1 part hay, there was proportionately less acetic acid and more propionic, butyric, valeric and higher acids in the rumen liquor than when the diet contained only 1 part concentrates to 3 parts hay. These differences became even more marked in period 2, for on all-concentrate diets the molar percentages were: acetic 47.5%, propionic 28.4%, butyric 12.8%, valeric and higher acids 9.0%, compared with corresponding values of 73.4, 18.0, 6.8 and 0.2% on all-hay diets. Lactic acid was present even on all-hay diets, but the proportion was slightly higher with calves reared on a high-concentrate diet. There was no marked carry-over effect of the rearing diet on the proportion of individual acids found in the rumen.

There was a distinct tendency for the molar percentage of propionic and butyric acids to increase at the expense of acetic acid, with increase in concentration of total VFA until the peak was reached, usually 3 h after feeding. As the total VFA concentration declined, the molar percentages of propionic and butyric acids also fell, suggesting that appreciable quantities of these acids are removed from the rumen, probably by absorption.

#### *Rumen bacteria*

The viable counts, expressed logarithmically, of streptococci, lactobacilli and coliform-type organisms are shown graphically in Fig. 4. It is clear that normal rumen bacteria had become well established even at 8 weeks of age. There was a significant reduction in the viable count between 13 and 16 weeks of age, following a change from a high-concentrate diet to one of all hay (treatment 2), streptococci falling from  $10^{8.3}$  to  $10^{6.2}$ /ml (significant at  $P < 0.001$ ), lactobacilli from  $10^{8.7}$  to  $10^{6.3}$ /ml (significant at  $P < 0.05$ ) and coliforms from  $10^{5.7}$  to  $10^{4.3}$ /ml (significant at  $P < 0.01$ ), but there was no other significant difference in viable count.

#### *Blood plasma VFA and reducing sugar*

The mean concentrations of total VFA and reducing sugars present in the plasma of blood drawn from the jugular vein at 15 min before and 1, 2, 3, 4 and 6 h after feeding are shown in Fig. 5 for period 1 and in Fig. 6 for period 2, and the mean initial and 3 h values are given in Table 5.

Plasma VFA concentrations showed considerable variation within the range 0.24–4.80 mg/100 ml, but tended to be higher in hay-fed calves than in calves given diets containing mainly concentrates. In period 1 the mean plasma VFA concentra-

tions rose to peak levels at the same time after feeding as those of rumen total VFA, but in period 2 there was a decline in plasma VFA concentration immediately after feeding, followed by a gradual rise in most instances. Whereas in period 1 the mean concentration was 1.14 mg/100 ml plasma on high-concentrate diets and 1.72 mg/100 ml on high-hay diets, the concentrations had fallen to 1.09 and 1.41 mg/100 ml,

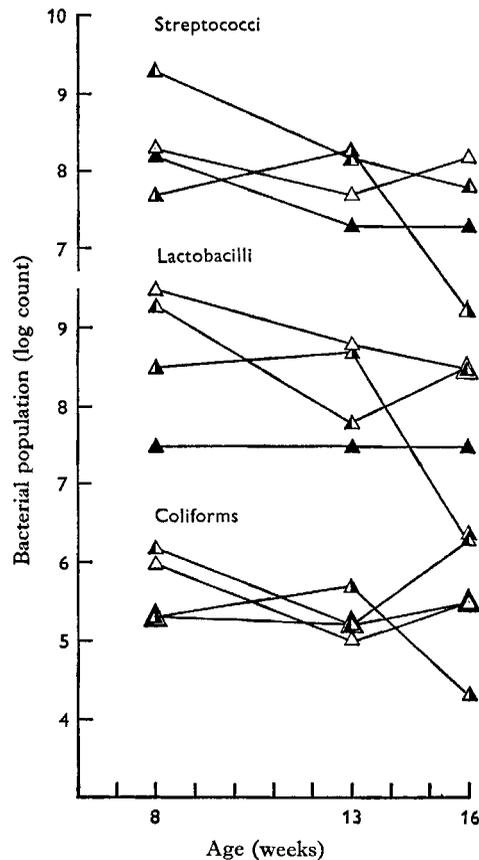


Fig. 4. Viable count of streptococci, lactobacilli and coliform-type organisms in the rumen liquor at 8, 13 and 16 weeks of age in calves given diets containing concentrates and hay in different proportions.  $\Delta$ — $\Delta$ , high-concentrate diet to 14 weeks followed by an all-concentrate diet;  $\triangle$ — $\triangle$ , high-concentrate diet to 14 weeks followed by an all-hay diet;  $\triangle$ — $\triangle$ , high-roughage diet to 14 weeks followed by an all-concentrate diet;  $\triangle$ — $\triangle$ , high-roughage diet to 14 weeks followed by an all-hay diet.

respectively, in period 2. The biggest fall in plasma total VFA concentration occurred when, in treatment 3, the high-hay diet was changed to all concentrates (from 1.80 to 1.11 mg/100 ml), but there was a rise from 1.12 to 1.52 mg/100 ml in treatment 2 when an all-hay diet replaced one consisting mainly of concentrates. Changes in treatment 1 were from 1.17 to 1.07 mg/100 ml and in treatment 4 from 1.65 to 1.30 mg/100 ml.

The concentration of plasma glucose (reducing sugars) in period 1 was 44% higher

in calves reared on the high-concentrate diet (treatments 1 and 2) than in calves reared on the high-roughage diet (treatments 3 and 4), the overall mean values being 92.8 mg/100 ml and 64.5 mg/100 ml respectively. As shown in Table 5, there were significant differences in glucose level between diets, both before and 3 h after feeding.

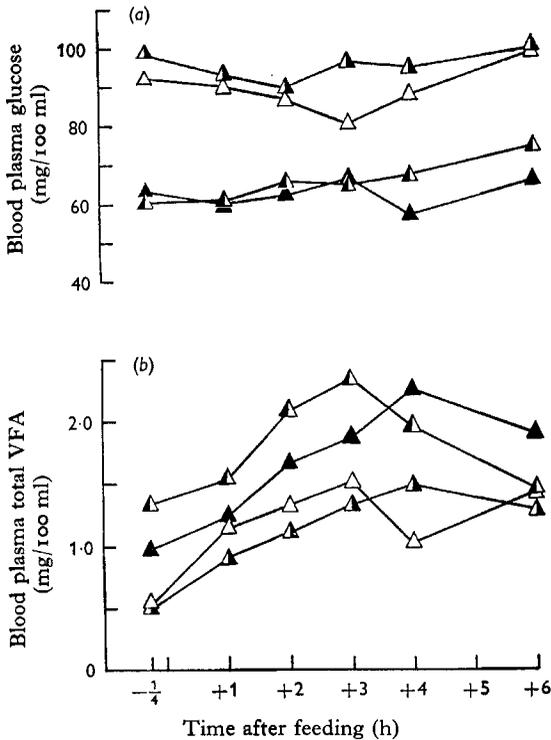


Fig. 5

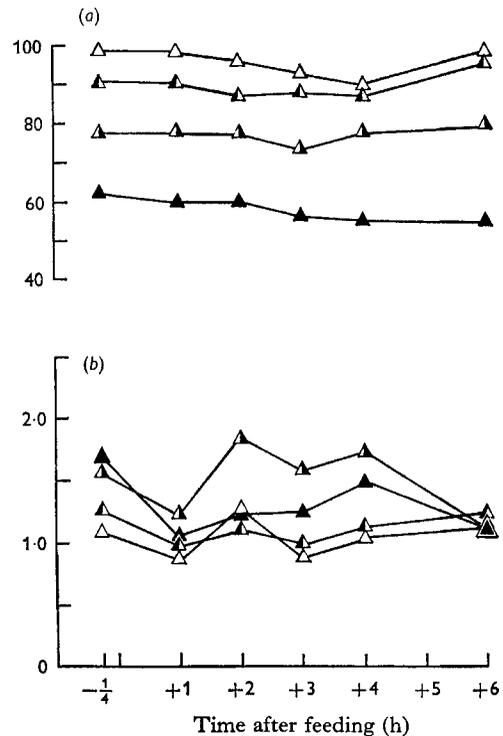


Fig. 6

Fig. 5. Period 1. Mean concentrations of glucose (a) and total VFA (b) in blood plasma at intervals after feeding in 13-week-old calves given a high-concentrate ( $\Delta$  and  $\blacktriangle$ ) or high-roughage ( $\triangle$  and  $\blacktriangle$ ) diet.

Fig. 6. Period 2. Mean concentrations of glucose (a) and total VFA (b) in blood plasma at intervals after feeding in 16-week-old calves given a diet consisting entirely of concentrates or of hay from 14 weeks of age.  $\Delta$ — $\Delta$ , high-concentrate diet to 14 weeks followed by an all-concentrate diet;  $\blacktriangle$ — $\blacktriangle$ , high-concentrate diet to 14 weeks followed by an all-hay diet;  $\triangle$ — $\triangle$ , high-roughage diet to 14 weeks followed by an all-concentrate diet;  $\blacktriangle$ — $\blacktriangle$ , high-roughage diet to 14 weeks followed by an all-hay diet.

In period 2, the overall mean concentrations of plasma glucose were 92.8 mg/100 ml and 67.5 mg/100 ml for all-concentrate (treatments 1 and 3) and all-hay (treatments 2 and 4) diets respectively. The increase in plasma glucose concentration in calves changed from a high-roughage to an all-concentrate diet (treatment 3) was greater than the decrease that occurred when calves were changed from a high-concentrate to an all-hay diet (treatment 2). The concentration of plasma glucose both before and 3 h after feeding was significantly higher ( $P < 0.05$ ) in calves whose diet was changed

from high-concentrate to all-hay (treatment 2) than in calves that received a high-hay diet throughout (treatment 4).

In both periods 1 and 2 plasma glucose concentration tended to decline, to reach minimum levels at 2-4 h after feeding. If this had corresponded with the rise in plasma VFA concentration it would have suggested an inverse relationship between glucose and VFA levels, but this relationship was not statistically significant, either in periods 1 and 2 separately, or in combination. However, it is of interest to speculate that had blood samples been taken from the portal vein, the concentrations of both glucose and VFA might have differed from those found in peripheral blood, and borne a more distinct inverse relationship to one another.

#### Post-mortem examination

*Contents of the alimentary tract.* The results given in Table 7 show that the weight of contents of the reticulo-rumen of calves that had received hay as the sole diet from 14 to 17 weeks was approximately twice that found in calves given only concentrates.

Table 7. Mean values with their standard errors for the weight of contents of different parts of the alimentary tract, recorded on post-mortem examination at 17 weeks in calves given a diet consisting of concentrates and hay in the ratio of either 9:1 or 1:3 at 12 weeks of age, followed at 14 weeks by a diet consisting solely of concentrates or hay

	Treatment no.				Pooled standard error of means	5% least significant difference between two means
	1	2	3	4		
Ratio of concentrates to hay at 12 weeks ...	9:1	9:1	1:3	1:3	—	—
Diet after 14 weeks	Concentrates	Hay	Concentrates	Hay	—	—
No. of calves	6	6	6	6	—	—
Live weight at slaughter (kg)	105.8	89.8	67.9	69.0	±2.7	8.0
Weight of contents of reticulo-rumen (kg)	7.23	14.29	6.06	14.50	±0.86	2.60
Weight of contents of omasum (g)	119	759	95	647	±79	237
Weight of contents of abomasum (g)	711	752	774	734	±113	340
Weight of contents of intestine (kg)†	3.40	2.87	2.37	2.68	±0.19	0.57
Weight of contents of alimentary tract (kg)	11.46	18.67	9.30	18.56	±0.98	2.94
Empty body weight (kg)	94.3	71.2	58.6	50.4	±2.6	7.7

† Values calculated from an estimated 42.4% of total weight of intestine + contents (see p. 205).

The mean weight of contents of the reticulo-rumen in hay-fed calves was 14.4 kg, equivalent to 16 and 21% of the live weight for treatments 2 and 4 respectively, and 6.7 kg in concentrate-fed animals, equivalent to 7 and 9% of live weight for treatments 1 and 3 respectively.

In the omasum, the mean weight of contents was much greater in the hay-fed calves

than in those given the all-concentrate diet. There were no significant differences within hay or concentrates, but the weight of contents of the reticulo-rumen and omasum tended to be greater for calves on treatment 1 than for those on treatment 3. The weight of reticulo-rumen contents in the calves on these two treatments was not related to live weight or daily intake of concentrates.

There was a wide range in weight of contents of the abomasum, from 352 to 1290 g, but no difference between treatment means. The weight of contents of the intestine, assuming that the weight of contents was 42.4% of the weight of the intact intestinal tract, as suggested by Stobo *et al.* (1966), was significantly greater on treatment 1 than on either treatments 3 or 4.

The total weight of contents of the alimentary tract was significantly greater in calves given the all-hay diet from 14 weeks, than in those given the all-concentrate diet, mainly because of the high proportion of total contents that was contained in the reticulo-rumen (77% for treatments 2 and 4 compared with 64% for treatments 1 and 3). The contents of the alimentary tract accounted for 26.9% of the live weight at slaughter in treatment 4, but only 10.8% in treatment 1.

Table 8. *Partial regression coefficients of the weight of contents of different parts of the alimentary tract on live weight at slaughter and daily concentrate consumption in the week before slaughter in calves given concentrates or hay as the sole diet*

	General mean weight of contents	Partial regression coefficients with their standard errors†		Residual standard deviation	Significance of regression equation
		Live weight (kg)	Concentrate consumption (kg/day)		
General mean ...	—	83.1	1.23	—	—
Reticulo-rumen (kg)	10.52	0.106 ± 0.024***	-3.42 ± 0.33***	1.87	***
Omasum (g)	405	7.68 ± 2.4**	-263 ± 33***	185	***
Abomasum (g)	743	0.378 ± 3.5	-13.7 ± 4.8	272	ns
Intestine (kg)	2.83	0.0179 ± 0.0058**	0.0120 ± 0.0078	0.44	**
Total (g)	14.50	0.132 ± 0.027***	-3.68 ± 0.37***	2.10	***

\*\* Significant at  $P < 0.01$ . \*\*\* Significant at  $P < 0.001$ . ns, non-significant.

† In calculating the partial regression coefficients and their standard errors, arrangement in treatments and blocks has been ignored.

Empty body weight was significantly greater in calves given the high-concentrate diets to 14 weeks of age (treatments 1 and 2) than in those given the high-roughage diets (treatments 3 and 4). At 14 weeks, empty body weight must have been similar for treatments 1 and 2, and also for treatments 3 and 4. The difference in empty body weight at 17 weeks, of 23.1 kg between treatments 1 and 2 and of 8.2 kg between treatments 3 and 4, shows the marked effect of liberal concentrate feeding between 14 and 17 weeks of age.

Multiple covariance analyses of weight of contents of the reticulo-rumen, omasum, abomasum, intestine and total weight of contents were made for each organ separately using the variables: live weight at slaughter, daily concentrate consumption and daily hay consumption in the 7-day period before slaughter. Hay consumption was not

significant in its effect on weight of contents, and the partial regression coefficients were recalculated using live weight and concentrate consumption as the independent variables. The partial regression coefficients are presented in Table 8.

Table 9. Comparison of the volume displacement of the intact organs and weight of tissue forming the organs of the alimentary tract (mean values with their standard errors) recorded on post-mortem examination at 17 weeks in calves given a diet consisting of concentrates and hay in the ratio of either 9:1 or 1:3 at 12 weeks of age, followed at 14 weeks by a diet consisting solely of concentrates or hay

	Treatment no.				Pooled standard error of means	5% least significant difference between two means
	1	2	3	4		
Ratio of concentrates to hay at 12 weeks ...	9:1	9:1	1:3	1:3	—	—
Diet after 14 weeks	Concentrates	Hay	Concentrates	Hay	—	—
No. of calves	6	6	6	6	—	—
Empty body weight (kg)	94.3	71.2	58.6	50.4	±2.6	7.7
Volume displacement of intact organs:						
Reticulo-rumen (l.)	27.8	34.2	22.7	37.2	±1.5	4.4
Omasum (l.)	0.8	1.9	0.6	1.7	±0.1	0.4
Abomasum (l.)	3.4	3.7	3.3	3.7	±0.5	1.4
Weight of fresh organ tissues:						
Reticulo-rumen (kg)	3.07	2.31	2.08	1.84	±0.11	0.33
Adjusted reticulo-rumen tissue (kg)†	2.26	2.23	2.39	2.41	±0.17	0.52
Omasum (g)	608	830	390	722	±70	212
Abomasum (g)	591	459	445	341	±28	85
Adjusted abomasum tissue (g)†	399	440	520	477	±47	141
Intestine (kg)‡	4.62	3.90	3.23	3.64	±0.26	0.77
Total (kg)	8.90	7.50	6.14	6.54	±0.27	0.83
Weight of oven-dried organ tissues:						
Reticulo-rumen (g)	571	312	305	231	±24	71
Adjusted reticulo-rumen dried tissue (g)†	439	299	356	325	±44	133
Omasum (g)	119	129	65	102	±12	35
Adjusted omasum dried tissue (g)†	33	120	98	163	±18	54
Abomasum (g)	160	104	95	56	±10	31

Regression coefficient of weight of fresh tissue of reticulo-rumen on empty body weight =  $0.032 \pm 0.008^{**}$ .

Regression coefficient of weight of fresh tissue of abomasum on empty body weight =  $7.49 \pm 2.2^{**}$ .

Regression coefficient of weight of oven-dried tissue of reticulo-rumen on empty body weight =  $5.15 \pm 2.0^*$ .

Regression coefficient of weight of oven-dried tissue of omasum on empty body weight =  $3.33 \pm 0.82^{**}$ .

\* Significant at  $P < 0.05$ .

\*\* Significant at  $P < 0.01$ .

† Adjusted for differences between treatment groups in mean empty body weight.

‡ Values calculated from an estimated 57.6% of total weight of intestine + contents (see p. 205).

*Volume displacement of the stomach compartments.* The results given in Table 9 show that the volume displacement of the reticulo-rumen and omasum was significantly greater in calves given hay during the last 3 weeks of life than in calves given only

concentrates. The difference between treatments 1 and 3 in volume displacement of the reticulo-rumen was obviously related to the greater intake of concentrates by the former group (2.9 kg/day) than the latter group (2.0 kg/day), since there was a positive relationship between reticulo-rumen volume and total concentrate consumption during the period 14–17 weeks ( $b = 0.250 \pm 0.10$ , significant at  $P < 0.05$ ). The volume displacement of the abomasum did not differ between treatments.

*Weight of tissue forming the organs of the alimentary tract.* As shown in Table 9, the weight of fresh tissue forming the organs of the alimentary tract was greatest, except for the omasum, in treatment 1. However, after treatment means had been adjusted for differences in empty body weight, by use of the regression coefficients given in Table 9, the differences were no longer significant.

The weight of tissue forming the omasum was greater in calves given hay from 14 to 17 weeks of age than in calves given only concentrates during this period. However, since the weight of omasal tissue was significantly greater in treatment 1 than in treatment 3, and in treatment 2 than in treatment 4, it is clear that the weight of omasal tissue was related to empty body weight.

As expected, the weight of oven-dried tissues showed trends similar to those of the weight of fresh tissues, as given in Table 9.

*Development of the rumen.* The musculature of the rumen was well developed in all twenty-four calves. Although the muscular pillars appeared to be slightly thicker in the rumens of calves on treatment 4 than in those on treatment 1, as judged from photographs at the end of the experiment, the greater development of papillas found in the areas adjacent to the pillars in treatment 1 may have obscured the extent of muscular development in the photographs. In consequence little importance is attached to this observation.

The extent of papillary development of the reticulo-rumen is presented photographically in Pls. 1 and 2, to show the anterior dorsal sac near the rumino-reticular fold and the ventral sac of the rumen. There was an obvious difference in the length and density of papillas in the different treatments. Dense clumps of papillas were found in calves on treatment 1, covering most of the internal surface of the rumen except for parts of the dorsal sac and the main parts of the muscular pillars. There was a tendency towards clumping together of papillas in three of the six calves on treatment 3, although the development of the mucosa was not so marked as in treatment 1. In treatments 2 and 4 there were no signs of clumping of papillas, although a larger area of the rumen was lined with papillas in the former of these two treatments.

Photographs of a section through the rumen wall in the region just caudal to the rumino-reticular fold are also shown in Pls. 1 and 2. The mean values for measurements made from these photographs for all twenty-four calves are shown in Table 10. The muscular wall was 1.8 mm thick in treatment 4, compared with 2.6 mm in each of the other three treatments. The average length of papillas for each of the twenty-four calves ranged from 3.3 mm for a calf on treatment 4 to 10.5 mm for a calf on treatment 1, with mean values of 4.9 and 9.1 mm respectively for these two treatments. The mean length of papillas in treatment 3, in which calves had been changed from a high-roughage diet to one of all concentrates, was 6.9 mm, compared with 5.9 mm

in treatment 2, in which the diet was changed from high-concentrates to all-hay. An estimate of the change in mean length of papilla following the change in diet is made in Table 11 by comparing the mean length of papilla found at 17 weeks in these calves after the change in diet with values found at 12 weeks in calves given the corresponding high-concentrate or high-roughage rearing diets (Stobo *et al.* 1966). If the difference in length of papillas is assumed to represent the change in length in response to change in the diet at 14 weeks of age, there is a clear indication that papillary development progressed rapidly in the presence of concentrates (treatments 1 and 3) and retrogressed almost as rapidly when concentrates were withdrawn from the ration and replaced by hay (treatment 2). Similar trends were shown in the weight of the 6 cm square section of rumen tissue, the differences in weight before and after change of diet being +4.4, -9.6, +9.4 and +1.0 g in treatments 1, 2, 3 and 4 respectively.

Table 10. *Mean values with their standard errors for the thickness of muscle and papillas in a 6 cm square section of the rumen wall from the region of the rumino-reticular fold, together with the weight of the section, recorded on post-mortem examination at 17 weeks in calves given concentrates and hay in the ratio of either 9:1 or 1:3 at 12 weeks of age, followed at 14 weeks by a diet consisting solely of concentrates or hay*

	Treatment no.				Pooled standard error of means	5% least significant difference between two means
	1	2	3	4		
Ratio of concentrates to hay at 12 weeks ...	9:1	9:1	1:3	1:3	—	—
Diet after 14 weeks	Concentrates	Hay	Concentrates	Hay	—	—
No. of calves	6	6	6	6	—	—
Cross-section of rumen wall:						
Thickness of muscle (mm)	2.6	2.6	2.6	1.8	±0.21	0.6
Length of papillas (mm)	9.1	5.9	6.9	4.9	±0.33	1.0
Total thickness of muscle and papillas (mm)	11.6	8.5	9.5	6.7	±0.31	0.9
Weight of 6 × 6 cm section of rumen wall (g)	43.6	29.6	32.7	24.3	±1.7	5.2

Table 11. *Comparison of the length of rumen papillas in calves at 17 weeks, after changes in the diet at 14 weeks, with values obtained by Stobo *et al.* (1966) in calves given corresponding high-concentrate or high-roughage rearing diets to 12 weeks of age*

	Treatment no.			
	1	2	3	4
Length of papillas (mm)				
At 12 weeks (Stobo <i>et al.</i> 1966)	7.4	7.4	4.2	4.2
At 17 weeks (this experiment)	9.1	5.9	6.9	4.9
Difference	+1.7	-1.5	+2.7	+0.7

These findings, supported by the observations on surface appearance, indicate that the rumen mucosa changed rapidly during the period 14-17 weeks in response to different diets.

## DISCUSSION

The results of this experiment show clearly that high-concentrate diets given to calves weaned at 5 weeks of age promoted much more rapid growth than high-roughage diets, both in the rearing period to 14 weeks of age, and also in the succeeding period from 14 to 17 weeks, irrespective of previous diet. Measurements at 17 weeks of age suggest that there was a rapid increase in the weight of contents of the alimentary tract after the change of diet at 14 weeks from high-concentrate to all-hay, and a corresponding decrease in contents when the diet was changed from one high in roughage to one of all-concentrates. However, the salient features of the experiment were the complete absence of the effect of previous diet on the ability of the calf to digest either concentrates or hay, and the rapidity with which it was possible to bring about extensive changes in papillary development, by an almost complete change of diet.

The performance of the calves from 3 to 12 weeks of age was almost the same as the results obtained previously (Stobo *et al.* 1966) with calves given the same levels of concentrate intake. Despite slight differences between the two experiments in the amounts of hay consumed, the assumption was made that factors, such as weight of contents of the different organs of the alimentary tract, volume displacement of the intact organs, weight of tissue forming the organs, and the extent of rumen development, were identical in calves at 12 weeks of age in the experiment now described to values obtained by Stobo *et al.* (1966) for calves given the same levels of concentrates. Thus, the mean values obtained in treatment 5 of the experiment of Stobo *et al.* (1966) were used in treatments 1 and 2 of this experiment and those obtained in treatment 1 of the previous experiment were used in treatments 3 and 4 of this experiment, to allow an estimate to be made of the effect of changing the diet of the calf at 14 weeks of age to one consisting solely of concentrates or hay.

From the values obtained at post-mortem, it is clear that considerable changes occurred in the weight of contents of the reticulo-rumen and omasum during the 3-week period following the change in diet. Table 12 gives an estimate of the changes in weight of contents of the alimentary tract by comparing the weight of contents at slaughter with values calculated from measurements of live weight at 14 weeks and daily concentrate consumption in the 14th week using the partial regression coefficients determined previously (Stobo *et al.* 1966). The weight of contents of the reticulo-rumen increased by 62% when hay was given in place of the high-concentrate diet (treatment 2) and fell by 43% when concentrates replaced the high-roughage diet (treatment 3). These compare with a 31% increase when hay followed a high-roughage diet (treatment 4) and a 21% reduction when concentrates followed a high-concentrate diet (treatment 1).

The finding that the weight of contents of the reticulo-rumen was approximately twice as great with calves given hay as with calves given concentrates is in excellent agreement with the observations of Freer & Campling (1963), who obtained a similar ratio with adult cows given diets consisting solely of hay or concentrates. This ratio between the two diets was almost the same at 6 h after feeding and at 24 h after the last meal. These workers found that concentrates were retained for a shorter period

in the reticulo-rumen than hay, as shown previously by Paloheimo & Mäkelä (1959), and no doubt this factor contributed greatly to the low weight of contents of the reticulo-rumen obtained with concentrate diets in our experiment.

Table 12. *Mean weight of contents of various parts of the alimentary tract of calves given diets containing concentrates and hay in the ratio of either 9:1 or 1:3 from 12 to 14 weeks, calculated from regression equations obtained by Stobo et al. (1966), together with the weight of contents recorded when the calves, which were slaughtered at 17 weeks of age, had received either concentrates or hay during the preceding 3-week period*

Ratio of concentrates to hay 12-14 weeks	Treatment no.				Regression equation used in the calculations (from Stobo <i>et al.</i> 1966)
	1	2	3	4	
Diet after 14 weeks	Concentrates	Hay	Concentrates	Hay	
Rumen contents (kg):					
At 14 weeks (calculated)	9.11	8.80	10.66	11.11	$y = 9.20 + 0.194(x_1 - 69.0)$
At 17 weeks	7.23	14.29	6.06	14.50	$-3.89(x_2 - 1.35)$
Change from 14 to 17 weeks	-1.88	+5.49	-4.60	+3.39	
Omasum contents (g):					
At 14 weeks (calculated)	251	234	166	198	$y = 242 + 10.5(x_1 - 69.0)$
At 17 weeks	119	759	95	647	$+327(x_2 - 1.35)$
Change from 14 to 17 weeks	-132	+525	-71	+449	$-168(x_2^2 - 2.20)$
Abomasum contents (g):					
At 14 weeks (calculated)	752	748	671	679	$y = 704 + 2.70(x_1 - 69.0)$
At 17 weeks	711	752	774	734	$+3.61(x_2 - 1.35)$
Change from 14 to 17 weeks	-41	+4	+103	+55	
Intestine contents (kg):					
At 14 weeks (calculated)	2.66	2.65	2.04	2.06	$y = 2.35 + 0.0039(x_1 - 69.0)$
At 17 weeks	3.40	2.87	2.37	2.68	$+0.288(x_2 - 1.35)$
Change from 14 to 17 weeks	+0.74	+0.22	+0.33	+0.62	
Total contents of alimentary tract (kg):					
At 14 weeks (calculated)	12.85	12.51	13.60	14.10	$y = 12.49 + 0.212(x_1 - 69.0)$
At 17 weeks	11.46	18.67	9.30	18.56	$-3.72(x_2 - 1.35)$
Change from 14 to 17 weeks	-1.39	+6.16	-4.30	+4.46	
Live-weight increase 14-17 weeks (kg)	+20.2	+5.8	+9.8	+8.2	
Live-weight increase 14-17 weeks after allowing for changes in weight of contents of alimentary tract (kg)	+21.6	-0.4	+14.1	+3.7	

$y$  = weight of contents;  $x_1$  = live weight at 14 weeks (kg);  $x_2$  = daily consumption of concentrates in 14th week (kg).

Trends in the weight of contents of the omasum were similar to those occurring in the reticulo-rumen, except that the increase in contents when calves were changed to an all-hay diet was greater than the decrease when concentrates were given as the sole diet. It would seem reasonable to argue that the retention time in the omasum was greater for hay than for concentrates, although there was no experimental evidence to support this.

The volume displacement of each intact stomach compartment (l.) was found to be closely related to the weight of its contents. The regression coefficients were:

Reticulo-rumen (kg)	$b = 1.35 \pm 0.21^{***}$
Omasum (g)	$b = 0.0017 \pm 0.00011^{***}$
Abomasum (g)	$b = 0.0017 \pm 0.0008^*$

\* Significant at  $P < 0.05$ . \*\*\* Significant at  $P < 0.001$ .

It is clear, therefore, that there is considerable elasticity in the walls of the reticulo-rumen and omasum, which are capable of stretching to accommodate the increase in bulk of contents when only hay is given, and of contracting to a much more compact size when only concentrates are given.

The finding that the weight of tissue forming the reticulo-rumen was related to empty body weight indicates that growth of rumen tissue occurs rapidly in the fast-growing calf. However, the results for volume displacement and thickness of the rumen wall show that much of this increase in weight of tissue has come about as the result of papillary development rather than as growth of the muscular wall. This supports the observations in the lamb by Sinclair & Kunkel (1959) and confirms the conclusions of Stobo *et al.* (1966) that a well-developed rumen mucosa is associated with high rates of live-weight gain in the ruminant calf.

Harrison, Warner, Sander & Loosli (1960) found that the rumen papillas had almost disappeared in calves changed from a diet of concentrates or of hay, at 16 weeks of age, to one of milk for a further 18 weeks, whereas retrogression of muscular tissue was much less noticeable. A remarkable retrogression of papillas was obvious in our experiment in treatment 2, in which calves were changed from a high-concentrate to an all-hay diet, which they received for only 3 weeks. Even more marked was the rapid development of rumen papillas that took place in treatment 3, after the change from a high-hay to an all-concentrate diet.

It has already been established that butyrate and, to a lesser extent, propionate stimulate papillary development (Sander, Warner, Harrison & Loosli, 1959; Tamate, McGilliard, Jacobson & Getty, 1962). In treatment 2 there was a decrease in the mean concentration of total VFA, a reduction in the proportion of propionic, butyric and higher acids and a rise in pH of the rumen liquor, whereas in treatment 3 the opposite occurred, after the change in diet.

Interpretation of the observations on papillary development is difficult in the absence of information on the daily amount of VFA produced in the rumen. No attempt was made to estimate the daily production of VFA in this experiment, since the rate of their absorption from the rumen was not known. However, from the values given in Table 6, it seems probable that the production of propionic, butyric and higher acids was greater in calves given all-concentrate diets than in those given all-hay.

The possibility that the pH of the rumen liquor also played an important part in promoting papillary development must not be discounted. Danielli, Hitchcock, Marshall & Phillipson (1945) found that absorption of VFA occurred at a faster rate when the rumen contents were acid, the higher homologues being absorbed faster at pH 5.8 than at pH 7.5. Thus, in treatment 3 it would seem that conditions were ideal for the

rapid development of rumen papillas. On the other hand, the marked retrogression of papillas in treatment 2 may have been associated with a reduction in the rate of absorption, particularly of butyrate and propionate, due to the lower concentration of these acids and to the higher pH in the rumen. The stretching of the walls of the rumen, that occurred when hay was given as the sole diet, would reduce the height and density of the papillas and, since comparison with the results obtained in a previous experiment (Stobo *et al.* 1966) suggested that the total weight of rumen tissue continued to increase at a slow rate, there would appear to have been little or no reduction in the total amount of rumen mucosa.

Most of the digestibility coefficients obtained at 13 weeks of age were very similar to values obtained when diets of hay and concentrates in different proportions were given to mature cows (Balch, 1957), 2-year-old heifers (Balch *et al.* 1960), and 12-week-old calves (Conrad & Hibbs, 1953), but the digestibility of crude fibre was considerably below the values obtained by these workers, especially when diets containing large amounts of concentrates were given, being 57% when the proportion of hay to concentrates was 3:1 and only 18% when it was 1:9. This suggests that there was a shortage of cellulose-splitting organisms in the rumen, or that the more readily available carbohydrates present, particularly in the high-concentrate diet, were attacked in preference to the fibrous fraction, as observed by Arias, Burroughs, Gerlaugh & Bethke (1951). The development of large numbers of cellulose-splitting organisms was found by Lengemann & Allen (1959) to reach adult levels at 9 weeks of age in calves given a maximum of 1.4 kg of concentrates/day. However, Bryant, Small, Bouma & Robinson (1958) and Conrad, Hibbs & Frank (1958) found that very few protozoa were present at 4 months of age in calves given high-concentrate diets if they were not given rumen inoculations from older animals. Conrad, Hibbs, Pouden & Sutton (1950) had previously shown that protozoa and some cellulose-splitting bacteria disappeared from the rumen when the proportion of concentrates in the diet was increased. These authors found that, when hay was given later, the digestibility of dry matter was reduced from the previous level of 67% to 58% and of cellulose from 65% to 54% if these organisms did not reappear in the rumen.

Except for the crude fibre fraction, the apparent digestibility coefficients of mixed diets given in period 1 did not differ from the weighted mean of the digestibility coefficients of concentrates and hay, when given separately in period 2. That the digestibility of crude fibre in period 1 was greater than in period 2 by 14% on the high-hay diet and by 4% on the high-concentrate diet suggests that there may be an optimum ratio of concentrates to hay for the development of cellulose-splitting organisms, possibly in combination with an optimum rate of passage of digesta through the alimentary tract.

In view of the difficulty of obtaining representative samples by stomach tube from non-fistulated animals, and because of the possibility that such samples might be contaminated by saliva, with a resultant increase in rumen pH and reduction in the concentration of VFA, the observations on rumen VFA concentration must be treated with caution. However, the observed rise in concentration of total VFA, reaching a peak at approximately 3–4 h after feeding, is in accordance with the findings of Balch

& Rowland (1957) and Stewart, Stewart & Schultz (1958) in adult cattle and of Gray, Jones & Pilgrim (1960) in sheep.

The concentration of total VFA in the rumen has been found to reach adult levels at about 6 weeks of age in calves given a high-roughage diet (Conrad *et al.* 1958) and at 7–8 weeks of age in calves given a high-concentrate diet (Lengemann & Allen, 1955; McCarthy & Kesler, 1956). In our experiment when the calves were 8 weeks of age the mean concentrations of VFA in rumen samples, taken 2½ h after food was given, were 8.9 and 7.9 m-equiv./100 ml for high-hay and high-concentrate diets respectively and were in close agreement with values obtained 3 h after feeding by these other workers. Although the concentration of VFA did not alter markedly between 8 and 14 weeks of age, the increase in volume of rumen contents, which is almost certain to have occurred, must indicate an increase in total production of VFA between these ages.

At about 14 weeks of age, the proportion of individual VFA in the rumen of calves given high-roughage diets was shown by Conrad *et al.* (1958) to be acetic 72%, propionic 19% and butyric 9%; whereas with calves given high-concentrate diets Lengemann & Allen (1955) found values of acetic 59%, propionic 21%, butyric 14% and others 6%. Despite fairly close agreement between these results and those of our experiment, the values give no indication of the amounts of each individual acid produced, because the rate at which the acids disappear from the rumen are probably different for each acid. Moreover, changes in volume of rumen contents are likely to occur with time after feeding, particularly on high-roughage diets, and probably confound the results. However, by calculating the concentration of each acid present at different times, it was found that in calves on all-concentrate diets propionic acid accounted for up to 40% and butyric acid up to 30% of the increase in VFA that occurred between feeding and 3 h after feeding, whereas on all-hay diets acetic acid accounted for 100% of the increase in VFA during the first hour after feeding, followed by an increase in propionic acid to 30% and of butyric acid to 15% of the total increase in VFA at 3 h after feeding.

It is well established that VFA are absorbed from the rumen, but not all the VFA appears in peripheral blood. Kiddle, Marshall & Phillipson (1951) first showed that the concentration of butyrate in portal blood was less than that expected in relation to its absorption from the rumen. Later work by Pennington (1952) established that rumen epithelial cells metabolized butyrate and produced an increase in the concentration of ketone bodies in the portal blood, as shown by Annison, Hill & Lewis (1957). Reid (1950) had previously shown that propionate was removed by the liver with the production of glucose.

It thus becomes apparent that, whereas the calf given a diet consisting mainly of roughage utilizes considerable amounts of acetate as a source of energy to the tissues, the calf given a high-concentrate diet relies more on glucose as its energy source. This is in agreement with the findings of this experiment, that the VFA concentration in peripheral blood was higher, and blood sugar concentration was lower, in hay-fed than in concentrate-fed calves.

The concentrations of plasma reducing sugars in calves given the high-hay diet are in agreement with values reported in 3-month-old calves reared on the high-roughage

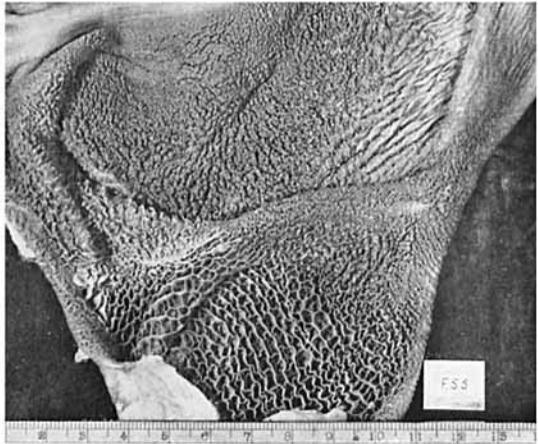
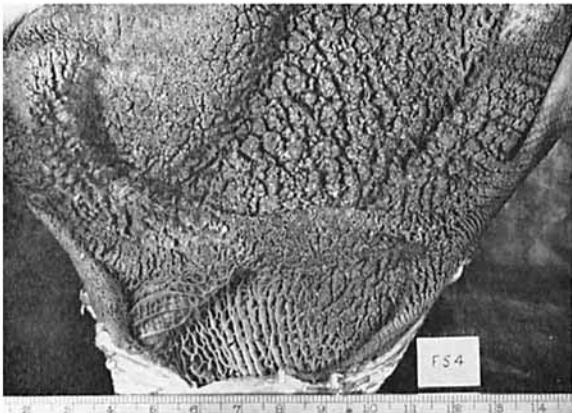
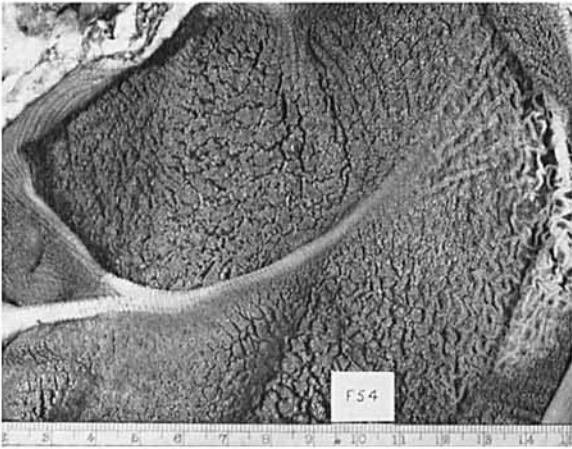
system (Hibbs, Conrad & Pounden, 1952; Hibbs, Conrad, Pounden & Frank, 1956). The concentrations found in calves given high-concentrate diets were up to 20 mg/100 ml higher than values reported by Preston & Ndumbe (1961) in calves between 10 and 16 weeks of age, given all-concentrate diets at a daily rate of 8% of the metabolic body size ( $\text{kg}^{0.74}$ ). In period 2 of our experiment, concentrates were given at 10% (treatment 1) and 9.5% (treatment 3) of metabolic body size ( $\text{kg}^{0.73}$ ).

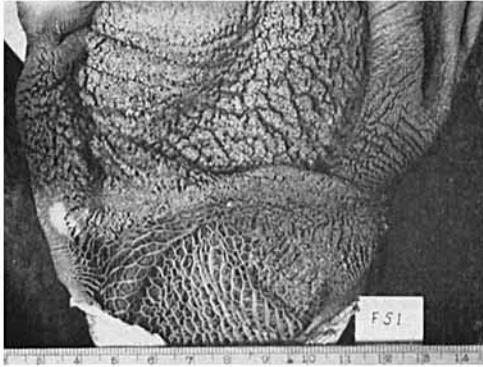
The extent to which the higher plasma glucose concentrations, obtained on concentrate diets as opposed to hay, may be attributed to the glucogenic effect of propionate, or to glucose formed by hydrolysis of starch in the intestine, is uncertain, since little is known of the extent to which starch can bypass the rumen. Preston & Ndumbe (1961) also observed a temporary depression in blood glucose of concentrate-fed calves 3 h after feeding, but to a minimum level of about 60 mg/100 ml. These workers postulated that the decline in blood glucose after feeding was the result of additional requirements for glucose in metabolizing VFA mixtures low in propionic acid, a condition they assumed to exist. The results of our experiment have shown that, in fact, the molar percentage of propionic acid in the rumen contents of concentrate-fed calves is very high (mean value 28.4% of total VFA). Moreover, the proportion of propionic acid actually increased at the time when plasma glucose levels were at their minimum. However, it may be that the increase in concentration of butyrate, which occurred 3 h after feeding, and which would be expected to have a higher specific absorption rate than propionate at a pH 5.8–6.2 had a depressing effect on plasma glucose, since the available evidence suggests that butyrate, as well as acetate, is not glucogenic and may even depress blood glucose levels (Storry & Rook, 1961; Blaxter, 1962).

The rise in plasma glucose concentration that occurred 3 h after feeding was accompanied, in most instances, by a decrease in the concentration of butyrate. However, it may be that the hydrolysis of dietary starch to glucose in the intestine had an effect on blood glucose levels, which were shown by Preston & Ndumbe (1961) to rise gradually to maximum levels 8–12 h after food was eaten.

In conclusion, the findings of this experiment have demonstrated the marked ability of the ruminant calf to adapt itself rapidly to severe changes in its diet, enabling it to digest a virtually new diet as efficiently as can a similar animal given the diet for a considerable period of time. It was apparent that the metabolic processes that occurred within the growing calf differed between high-concentrate and high-roughage diets, and that changes in the diet resulted not only in a transition in the metabolic processes, but also in a rapid transformation in the anatomical development of the reticulo-rumen and omasum.

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## EXPLANATION OF PLATES

Rumen development in the ventral sac (top) and the anterior dorsal sac in the region of the rumino-reticular fold (middle) in 17-week-old calves given a diet consisting solely of concentrates or hay after a rearing diet high in concentrates or in roughage (scale graduated to 0.1 in). The cross-section photograph (bottom) shows muscle thickness and papilla length in the anterior dorsal sac just caudal to the rumino-reticular fold (scale graduated to 0.5 mm).

## PLATE 1

F 54. Rumen development in a calf given concentrates as the sole diet after a rearing diet high in concentrates (treatment 1).

F 55. Rumen development in a calf given hay as the sole diet after a rearing diet high in concentrates (treatment 2).

## PLATE 2

F 51. Rumen development in a calf given concentrates as the sole diet after a rearing diet high in roughage (treatment 3).

F 94. Rumen development in a calf given hay as the sole diet after a rearing diet high in roughage (treatment 4).

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