The flow of digesta, dry matter and starch to the duodenum in sheep given rations containing straw of varying particle size

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1. Using sheep fitted with re-entrant cannulas in the proximal duodenum, and which were given a ration containing long straw, a series of three experiments was conducted in which the flow of digesta to the duodenum was measured and sampled continuously for 3 d. There appeared to be no consistent effect of this procedure on total flow of digesta to the duodenum from day to day, indicating that under our conditions a 24 h pattern of flow can be taken as representative of digesta entering the duodenum.

2. In a further series of four experiments, each lasting 3 d, rations identical in composition to that given in the first series of experiments, but differing in the physical form of the roughage component (chopped or ground), were given to the sheep. There was no consistent effect of altering the particle size of the roughage component of the diet on total daily flow of digesta, or in the dry-matter content of the digesta entering the duodenum.

3. Significantly ($P < 0.01$) more starch entered the duodenum per day when the ration included long or chopped straw than when it contained ground straw; all rations contained ground maize.

4. A peak in the flow of digesta, dry matter and starch to the duodenum occurred between 4 and 12 h after feeding the sheep.

The usual procedure adopted for obtaining information on flow-rate and representative samples of digesta has involved the use of animals prepared with re-entrant cannulas in the digestive tract and the total collection and return of all digesta flowing from the exit cannula. Goodall & Kay (1965) and Klooster, Rogers & Sharma (1969) measured the flow of digesta at the terminal ileum and distal duodenum of sheep respectively for periods of 72 and 120 h and found an increase in flow-rate from day to day. MacRae & Armstrong (1969) reported that continuous collection of digesta from sheep for periods of 24 h tended to suppress flow-rates possibly owing to disturbance of the animal. Attempts to assess any deviation from the average daily flow using indigestible markers have been made but criticism has arisen because of large variations in the concentration of the marker in the digesta and inconsistent marker recoveries.

Since confidence in the accuracy of flow-rate measurements is necessary for any meaningful conclusions to be drawn from this type of experiment, it was decided to conduct on two sheep a series of three experiments, each lasting 3 d, to measure continuously the flow of digesta at the proximal duodenum of the sheep, in order to determine whether there was any effect of experimental method on the rate of flow. The results indicate that under our conditions the experimental procedure adopted had no effect on the rates of flow of digesta to the duodenum on different days of the experiment. A further series of four experiments, each lasting 3 d, designed

Table 1. *Percentage composition of the diet**

Ration	Barley straw: Long	Barley straw: Chopped	Barley straw: Ground	Ground maize	Soya-bean meal	Mineral + vitamin supplement
A	30	—	—	54·7	12·3	3·0
B	—	30	—	54·7	12·3	3·0
C	—	—	30	54·7	12·3	3·0

* All the diets contained 88·8% dry matter, comprising: organic matter 94·2, crude protein 12·7 and crude fibre 13·1 (expressed as % of the dry matter).

to investigate, by continuous sampling, the effect of varying the particle size of the roughage component of the diet on the composition and rate of flow of digesta to the duodenum was also conducted. There was no effect on the total daily flow of digesta but amounts of starch entering the duodenum were significantly different on different rations.

EXPERIMENTAL

Sheep and housing

Two 3-year-old cross-bred castrated male sheep (nos. 1 and 2), weighing approximately 65 kg at the start of the experiments and fitted with re-entrant cannulas in the proximal duodenum when about 1 year of age, were used. They were penned individually in the metabolism laboratory under conditions of even temperature (15°) and continuous lighting. A third sheep was used as a donor (see 'Sampling of digesta').

Surgery. The cannulas were fitted using the technique described by Wasteneys, Crocker & Hamilton (1941) and were sited in the proximal part of the duodenum immediately after the pyloric sphincter. The whole operative procedure was carried out as described by Pickard (1971).

Feeds and feeding

Details of the composition of the diets are given in Table 1.

For rations A and B the straw was given separately from the remainder of the ration which was mixed and pelleted. For ration B the straw was chopped to a maximum length of 2·5 cm, and for ration C it was ground sufficiently to pass through an 8 mm screen before being mixed and pelleted with the remainder of the ration. Details of the sieve analysis of the ground straw and also of the complete diet containing 30% ground straw (ration C) are given in Table 2. The sheep were given 900 g of ration A, B or C once per day at 09.00 hours for 3 d and when the ration was changed at least 3 weeks were allowed for the sheep to adapt to the new ration. Water was available to the sheep at all times.

Sampling of digesta

On the days of sampling the sheep were placed in metabolism crates, to which during their 2 years of experimental life they had become thoroughly accustomed, to restrict movement and to facilitate access to the cannulas. The piece of tubing

Table 2. *Sieve analysis of the ground barley straw and of the complete diet containing 30% of ground barley straw (ration C)**

Sieve mesh	Percentage particle size distribution	
	Ground barley straw	Ration C
3 mm	7·43	0·86
1204 μm	13·51	19·38
853 μm	21·80	18·92
699 μm	9·79	8·68
599 μm	9·38	8·87
500 μm	7·38	7·52
422 μm	5·60	4·60
295 μm	8·73	9·99
178 μm	8·23	9·42
124 μm	3·41	4·54
Base	4·73	7·24

* See Table 1 for detailed composition.

joining the two cannulas was removed and separate lengths of dialysis tubing (Visking tubing 24/32) were attached to each cannula. The tubing attached to the exit cannula was arranged so that digesta were delivered into a plastic measuring cylinder placed in a water-bath at body temperature. The open end of the tubing attached to the return cannula was fastened to a plastic funnel clamped to the crate some 40–50 cm above the cannula so allowing the return of digesta to the duodenum. This arrangement did not prevent the sheep from lying or standing. The sheep remained in the crates throughout the 3 d during which samples were taken. The measuring cylinders were replaced whenever they contained approximately 50 ml digesta and the exact volume was measured. The pH of the sample was then determined using a glass-calomel-electrode system with automatic temperature adjustment, and a Pye reading meter. A 10% sample of the digesta was then taken, the remainder being returned to the duodenum through the funnel.

The samples taken within 1 h were pooled, weighed and frozen at $-15°$ for storage. At the end of each hour, a volume of digesta, equal to that removed for analysis during that period, taken immediately before use from a third sheep (donor) on the same feeding regimen, was returned to the duodenum.

Samples of the food were taken just before, during and at the end of an experiment. Subsamples were then taken for analysis.

A sample of the faeces voided during an experiment was taken at the end of the 3 d period. This was dried at 40° and finely ground before analysis.

Analysis

The pooled hourly samples of digesta were freeze-dried and reweighed to obtain dry-matter values. They were bulked into 4-hourly samples and these were then analysed for starch by the enzymic method of MacRae & Armstrong (1968), except that the final glucose concentration was measured by an alternative glucose oxidase method (God-Perid-Method; Boehringer Mannheim GMBH, Mannheim, Germany). Samples of food and faeces were also analysed for starch.

Table 3. *Flow of digesta (ml/d) to the duodenum of sheep given 900 g/d for 3 d of a long-straw ration (A)**

	Expt 1	Expt 2	Expt 3	Mean	SE
		Sheep no. 1			
Day 1	5527	5762	6970	6086	455·4
Day 2	5875	6502	6459	6269	206·0
Day 3	6122	6122	6233	6159	37·6
General mean	5841	6129	6554	—	—
		Sheep no. 2			
Day 1	5923	6259	7698	6627	554·5
Day 2	6978	6217	6539	6578	224·6
Day 3	7158	6804	6676	6879	146·8
General mean	6686	6427	6904	—	—

* See Table 1 for detailed composition.

Experimental design

Expts 1–3. To measure flow of digesta and dry matter to the duodenum; sheep given straw in the long form (ration A).

Expts 4–7. To measure the effect of particle size of the roughage component of the diet on the flow of digesta and dry matter to the duodenum:

Expts 4 and 5; sheep given chopped straw (ration B).

Expts 6 and 7; sheep given ground straw (ration C).

Additionally, Expts 1 and 2, and 4–7, were to measure the flow of starch to the duodenum (all rations contained ground maize) and the pH of the duodenal digesta.

RESULTS

Effect on total daily flow of digesta and dry matter. Expts 1–3

The total daily amounts of digesta flowing to the duodenum of each of two sheep when given ration A are given in Table 3.

There appeared to be no definite pattern of flow from day to day but, as indicated by the standard errors of the means of the daily totals, there appeared to be a greater variation with both sheep in total flow on day 1 than on days 2 and 3 but none of these differences was significant.

The average daily dry-matter content of the digesta flowing to the duodenum of the sheep is given in Table 4. The dry-matter percentage of the digesta was fairly constant from day to day and between sheep.

Effect of the particle size of the roughage component of the diet

Total daily flow of digesta and dry matter. Expts 4–7. The daily flow of digesta to the duodenum of the two sheep given either the chopped-straw diet (ration B) or the ground-straw diet (ration C) is given in Table 5. As in Expts 1–3 (Table 3), there was no definite pattern of flow from day to day but generally the total flow tended to decrease from day 1 to day 3.

There appeared to be no consistent effect of particle size of the roughage component

Table 4. *Average daily dry-matter percentage of digesta entering the duodenum of sheep given* 900 *g/d for* 3 *d of a long-straw ration* (*A*)*

	Expt 1	Expt 2	Expt 3	Mean
		Sheep no. 1		
Day 1	6·54	6·70	6·63	6·6
Day 2	6·47	6·61	6·38	
Day 3	6·58	6·79	6·90	
		Sheep no. 2		
Day 1	6·14	6·56	6·35	6·4
Day 2	5·88	6·39	6·36	
Day 3	6·12	6·47	6·87	

* See Table 1 for detailed composition.

Table 5. *Flow of digesta* (*ml/d*) *to the duodenum of sheep given* 900 *g/d for* 3 *d, of a chopped-straw ration* (*B*)* *or ground-straw ration* (*C*)*

	Ration B			Ration C		
	Expt 4	Expt 5	Mean	Expt 6	Expt 7	Mean
			Sheep no. 1			
Day 1	6913	6899	6906	6406	6658	6532
Day 2	6772	6380	6576	6394	6471	6433
Day 3	6357	6390	6374	6283	5900	6092
General mean	6680	6823	—	6361	6309	—
			Sheep no. 2			
Day 1	8284	7794	8039	7432	8113	7773
Day 2	7362	7680	7521	6388	8866	7627
Day 3	7041	7507	7274	6661	8266	7447
General mean	7592	7690	—	6827	8404	—

* See Table 1 for detailed composition.

on total daily flow of digesta to the duodenum, since with sheep no. 1 there was little difference between the mean daily flow of digesta entering the duodenum with ration A, B or C, but with sheep no. 2 there was an increase in the mean daily total amount of digesta entering the duodenum when the straw component of the diet was chopped or ground. However, there was no significant difference between the mean daily flow of digesta on any of the rations, although the general mean daily flow of digesta from sheep no. 2 was significantly higher ($P < 0{\cdot}05$) than the flow from sheep no. 1.

The daily average dry-matter percentages of the digesta entering the duodenum of the two sheep when given ration B or C are presented in Table 6. As in Expts 1–3, when ration A was given, the amounts of dry matter entering the duodenum followed closely the total daily flow of digesta to the duodenum, since the percentage of dry matter in the digesta was again reasonably constant.

Table 6. *Average daily dry-matter percentage of digesta entering the duodenum of sheep given 900 g/d for 3 d of a chopped-straw ration (B)* or a ground-straw ration (C)**

	Ration B		Ration C	
	Expt 4	Expt 5	Expt 6	Expt 7
		Sheep no. 1		
Day 1	6·64	6·26	6·27	6·91
Day 2	6·18	6·03	5·85	6·36
Day 3	6·45	5·60	6·06	6·57
		Sheep no. 2		
Day 1	6·21	5·62	6·09	6·09
Day 2	6·04	5·60	5·88	5·78
Day 3	6·54	5·47	5·99	5·77

* See Table 1 for detailed composition.

Table 7. *Mean values with their standard errors for daily totals of digesta (ml) flowing to the duodenum during seven experiments, each of 3 d duration, on each of two sheep*

		Mean daily flow	SE
Sheep 1	Day 1	6448	222
	Day 2	6408	102
	Day 3	6201	64
Sheep 2	Day 1	7357	346
	Day 2	7147	350
	Day 3	7154	213

Flow of digesta. Expts 1–7

The daily totals of digesta entering the duodenum during all seven experiments conducted with sheep nos. 1 and 2 are presented in Table 7. The standard errors of the means were much lower for sheep no. 1 and decreased each day from day 1 to day 3. The mean total daily flow of digesta to the duodenum also decreased with the duration of the experiments for sheep no. 1, but for sheep no. 2 the value was slightly higher on day 3 than on day 2. There was no significant difference between the means of the total flow (Table 7) on any 2 d with either sheep.

Flow of starch. Expts 1–2 and 4–7

The average total daily amounts of starch entering the duodenum of the two sheep during two experiments with each of the three rations are given in Table 8. The results showed that considerable amounts of starch, up to 20% of the daily intake, flowed to the duodenum each day when the sheep were given a ration containing approximately 50% ground maize and 30% long (ration A) or chopped (ration B) barley straw. When, however, the 30% barley straw was given milled and pelleted with the rest of the ration (C), only about 8% of the daily intake of starch flowed to the proximal duodenum. The difference between the amounts of starch reaching the duodenum with ration C and the other two rations (A and B) was significant ($P < 0{\cdot}01$); there were no significant differences between sheep and days of experiment. On average, 3·7 g starch/d were measured in the faeces of the sheep

Table 8. *Amounts of starch flowing to the duodenum of two sheep given* 900 *g/d for* 3 *d of a long-straw* (*A*)*, *chopped-straw* (*B*)* *or ground-straw* (*C*)* *ration*

Ration	Sheep no.	Expt no.	Amount of starch at duodenum (g/d) Mean	SE	Amount of starch as % of daily intake
A	1	1	57·8	6·2	17·0
	—	2	75·9	3·7	22·3
	2	1	53·4	3·9	15·7
	—	2	54·4	1·9	16·0
B	1	4	76·9	7·6	22·6
	—	5	55·7	3·8	16·4
	2	4	78·2	4·9	23·0
	—	5	52·2	2·9	15·4
C	1	6	29·9	1·1	8·4
	—	7	26·6	1·4	7·5
	2	6	26·2	2·8	7·4
	—	7	30·2	2·8	8·5

* See Table 1 for detailed composition.

Table 9. *Average daily pH of duodenal digesta in two sheep given* 900 *g/d for* 3 *d of a long-straw* (*A*)*, *chopped-straw* (*B*)* *or ground-straw ration* (*C*)*

	Ration A		Ration B		Ration C	
	Expt 1	Expt 2	Expt 4	Expt 5	Expt 6	Expt 7
			Sheep no. 1			
Day 1	2·59	2·62	2·67	2·70	2·63	2·68
Day 2	2·55	2·60	2·72	2·68	2·63	2·67
Day 3	2·62	2·60	2·73	2·70	2·65	2·70
			Sheep no. 2			
Day 1	2·85	2·82	2·86	2·92	2·82	2·93
Day 2	2·85	2·79	2·94	3·00	2·76	2·92
Day 3	2·94	2·05	3·00	2·95	2·82	2·89

* See Table 1 for detailed composition.

when they were fed on the long- or chopped-straw diets. This was slightly more than the 3·3 g starch/d which was present in the faeces when the sheep were receiving the ground-straw diet.

pH of duodenal digesta

The average pH of duodenal digesta on each day of six of the experiments is given in Table 9. There was no significant difference between the mean pH on any ration but sheep no. 2 had a significantly ($P < 0{\cdot}05$) higher mean duodenal pH than sheep no. 1.

Patterns of flow of digesta, dry matter and starch to the duodenum

The patterns of flow of digesta, dry matter and starch, compiled from the 4-hourly values throughout the 3 d, when the sheep were given a ration containing long (A), chopped (B) or ground (C) barley straw are shown in Figs 1 (Expts 1–3: flow of

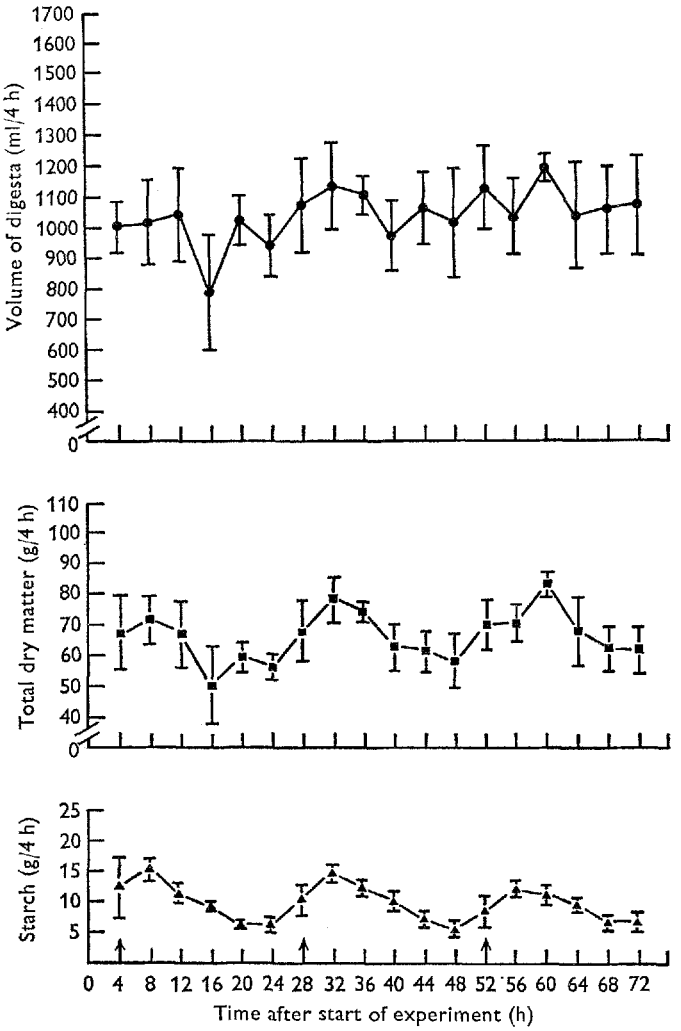

Fig. 1. Expts 1–3. Patterns of flow of digesta (●—●), dry matter (■—■) and starch (▲—▲) (starch was estimated only in Expts 1 and 2) to the duodenum of the sheep over a period of 3 d, when given a long-barley straw and pelleted ground cereal ration (A) (see Table 1 for detailed composition). The vertical bars represent the standard errors of the mean for three experiments on each of two sheep. The sheep were fed at the beginning of the 4-hourly periods indicated by the arrows.

starch was estimated only for Expts 1 and 2), 2 (Expts 4 and 5) and 3 (Expts 6 and 7) respectively. Of the three rations, A appeared to give the least variable pattern of flow of digesta over the 3 d of the experiment; rations B and C gave rise to an increase in the flow of digesta in the 12 h after each feed. This is reflected in the patterns of flow of dry matter and starch to the duodenum, but when ration C was given the amounts of starch flowing to the duodenum were very much reduced.

There was no definite pattern of flow from day to day over the 3 d periods except that when the sheep were given ration A, the flow of digesta appeared to rise steadily throughout the experiment. This did not occur with the other rations.

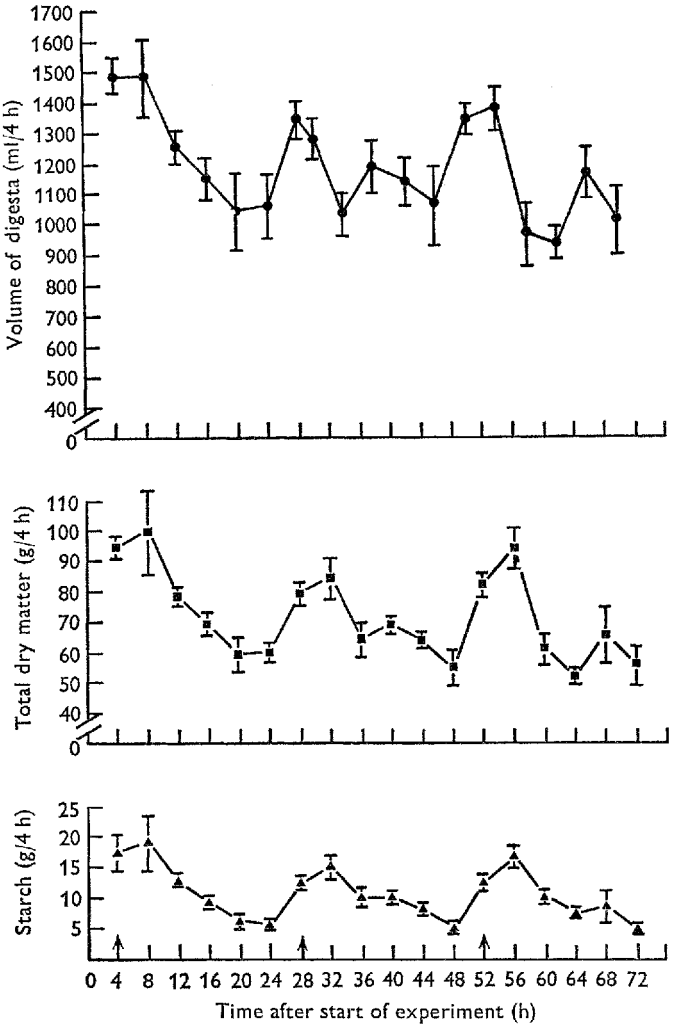

Fig. 2. Expts 4 and 5. Patterns of flow of digesta (●—●), dry matter (■—■) and starch (▲—▲) to the duodenum of the sheep over a period of 3 d, when given a chopped-barley straw and pelleted ground cereal ration (B) (see Table 1 for detailed composition). The vertical bars represent the standard errors of the mean for two experiments on each of two sheep. The sheep were fed at the beginning of the 4-hourly periods indicated by the arrows.

DISCUSSION

Effect on total flow of digesta and dry matter

The results of this investigation appear to be contrary to the finding of Klooster *et al.* (1969), who reported that the flow-rate of digesta through the distal duodenum tended to increase with time. Goodall & Kay (1965) also observed a similar pattern of flow of digesta at the terminal ileum of sheep over 72 h periods. There was no indication from our study that flow was suppressed over the first 24 h, as might have been expected from the findings of MacRae & Armstrong (1969), and

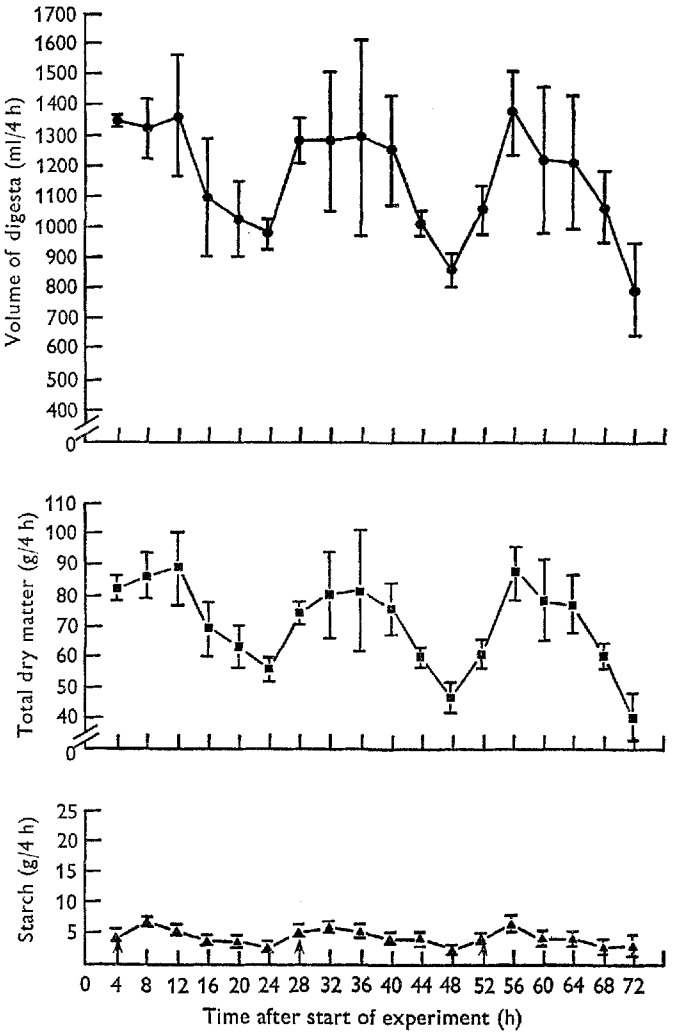

Fig. 3. Expts 6 and 7. Patterns of flow of digesta (●—●), dry matter (■—■) and starch (▲—▲) to the duodenum of the sheep over a period of 3 d, when given a pelleted ground barley straw and ground cereal ration (C) (see Table 1 for detailed composition). The vertical bars represent the standard errors of the mean for two experiments on each of two sheep. The sheep were fed at the beginning of the 4-hourly periods indicated by the arrows.

in fact the mean daily flow of digesta to the duodenum when the sheep were given rations B and C (chopped and ground straw respectively) decreased slightly from day 1 to day 3.

The fact that there were no statistically significant differences between the mean daily total flow on any 2 d and the absence of any definite pattern of flow from day to day over the experimental period, suggest that under our conditions a 24 h collection of digesta can be taken as representative of flow-rate and composition of digesta entering the duodenum.

Effect of particle size of the roughage component of the diet

Total daily flow of digesta and dry matter. There are many reports of the effects, upon ruminant digestion, of grinding and pelleting of all-roughage diets, but there is little information on the effects of grinding and pelleting mixtures of roughage and cereals. A decline in the digestibility of ground material has been associated with a faster rate of passage (Blaxter, Graham & Wainman 1956; Rodrigue & Allen, 1960; Campling & Freer, 1966) and a restricted feeding regimen, since Campling & Freer (1966) found no difference in the retention time of stained ground and long roughages when offered *ad lib.* to cattle. Unfortunately it is not possible from results of the present study to speculate on the effect of particle size of the roughage component of a mixed roughage and cereal diet on the rate of passage of digesta along the alimentary tract, but there appears to be no consistent effect on the total daily flow of digesta from the abomasum. Weston & Hogan (1967) reported a higher rate of flow of digesta (l/100 g organic-matter intake) from the abomasum when chopped lucerne hay was given than when ground lucerne hay was offered to sheep but this was not so with wheaten hay. Although one of our sheep (no. 2) showed an increased flow of digesta to the duodenum when the straw was offered in the chopped or ground form, the other sheep (no. 1) exhibited very little difference in total daily flow of digesta to the duodenum with any of the rations.

Phillips & Dyck (1964) and Topps, Kay & Goodall (1968) have reported increases in the flow of digesta to the duodenum associated with changing from ground to long roughages, but their results are not comparable with those of our study since the total dry-matter intake or the proportion of long roughage in the diet, or both, were changed. There was no significant effect of the particle size of the roughage component of the diet on duodenal pH.

Total daily flow of starch. The apparent disagreement between many workers as to the extent of the flow of starch from the abomasum of sheep and cattle can be partly explained by the type and processing of the cereal used. MacRae & Armstrong (1966) and Topps *et al.* (1968) used rations based on barley, and Sutton & Nicholson (1968) reported similar amounts of starch reaching the duodenum when flaked maize was given to sheep. However, when sheep were given cracked or ground maize, Wright, Grainger & Marco (1966) and Tucker, Mitchell & Little (1968) reported large amounts of starch escaping from rumen fermentation. More recently, Beever, Coelho da Silva & Armstrong (1970) have shown ground maize to be more resistant to rumen fermentation than flaked maize, as measured by duodenal starch levels.

The results of our investigation are in general agreement with other published results (Tucker *et al.* 1968) in terms of total daily duodenal starch levels, and they indicate that the particle size of the roughage component of the ration may also have a significant effect upon the amounts of starch that escape fermentation in the rumen and enter the duodenum and thereby become available for digestion in the small intestine.

Although many previous experiments have been conducted using long- and

ground-roughage rations, none has been reported where the aim was to examine possible effects of particle size of the ration on duodenal starch concentrations. Porter & Singleton (1966) gave a hay and concentrate ration to three sheep and observed that about one-third of the starch ingested disappeared from the intestines of the sheep eating most hay (1300 g/d) and only 10% was apparently digested beyond the rumen in the sheep eating 700 or 1000 g of hay/d.

Substituting chopped dried grass for 40% of a diet of rolled barley and protein supplement, Ørskov & Fraser (1968) found an increase from 7·5 to 13% in the percentage of starch eaten that escaped fermentation. The authors suggested that the addition of the dried grass brought about an increase in the rate of passage of the smaller particles of cereal from the rumen.

Since the particle size of the diet has been shown to affect the rate of passage of digesta from the rumen (Blaxter & Graham, 1956), the differences observed in our experiments between the long- and chopped-roughage diets on the one hand, and the ground-roughage diet on the other, may be due to the longer retention time of the longer material in the rumen, resulting in a faster rate of passage of the smaller (cereal) particles from the rumen before fermentation could be completed.

Our results support this theory since the peak starch flow tended to occur within a few hours of feeding and always in the first 12 h after feeding (see Figs 1–3), suggesting that the greater part of the starch escaping to the duodenum at this time was of immediate dietary origin.

There was little difference between rations in the amounts of starch that were present in the faeces. It would appear that with all the rations intestinal digestion of starch was sufficient to remove most of the starch entering the intestines, since the total amount of starch present in the faeces represented only about 1% of the total daily intake.

Patterns of flow of digesta, dry matter and starch to the duodenum

Phillips & Dyck (1964) measured the flow-rate of duodenal digesta in sheep given a pelleted ration and reported a diurnal rhythm in the pattern of flow of digesta through the duodenum. The sheep were allowed to eat as much as they would in 2 h. They found that the highest rates of flow occurred at the time of feeding and for 1 or 2 h before feeding. The lowest flow-rates occurred 6–12 h after feeeding. The present results do not support these findings since the flow-rate of digesta to the duodenum was generally at its lowest in the 4 h before feeding and reached a maximum from 4–12 h after feeding. This was particularly evident when the sheep were given the ground-straw ration and, to a lesser extent, the chopped-straw ration, but when the long-straw ration was given there was only a slight tendency for the pattern of flow of digesta to rise after feeding. These results indicate that when the particle size of the ration was decreased the initial rate of flow of digesta from the reticulo-rumen was increased; Pickard (1971) giving similar rations to sheep, did not, however, observe this effect.

The patterns of flow of dry matter followed very closely those of digesta on each of the three rations, indicating that there was little change in the percentage of dry matter in the digesta throughout the day. The pattern of starch flow was also similar

to that of digesta and dry matter except when the sheep were given the ground-straw ration. With the latter ration the flow of starch was very much reduced and the rate was steadier.

We suggest our results support the theory that in diets composed of long straw and milled cereals, small particles of cereals rapidly pass from the rumen to the abomasum. Replacing the long straw by milled straw increases the retention of cereal particles in the rumen, resulting in more complete fermentation and reduces the amount of starch passing to the abomasum and intestines.

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