

## Digestion of concentrate and of hay diets in the stomach and intestines of ruminants

### 1. Sheep

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1. The flow of digesta to the abomasum and through the duodenum and terminal ileum was measured over 24 h periods in sheep. Pelleted diets of concentrates, principally composed of barley, and of poor-quality hay were given. The seven Scottish Blackface ewes studied were all fitted with rumen cannulas, and in addition two had simple abomasal cannulas, one a re-entrant abomasal cannula, two re-entrant duodenal cannulas, and two re-entrant ileal cannulas.

2. Paper impregnated with chromium sesquioxide was given twice daily by rumen fistula. The amounts of dry matter, starch, cellulose, total nitrogen and energy passing through the abomasum, duodenum and ileum and the amounts excreted in the faeces were measured. The flows of digesta were adjusted to give 100% recovery of chromium sesquioxide and the extent of digestion in various parts of the alimentary tract was calculated using these adjusted values. Concentrations of glucose in the blood and of volatile fatty acids (VFA) in the rumen were also measured.

3. For the concentrate diet, 69% of the digestible dry matter disappeared in the stomach (reticulo-rumen, omasum and abomasum), 17% in the small intestine and 14% in the large intestine. Values for disappearance of digestible energy were 72% in the stomach, 23% in the small intestine and 5% in the large intestine. Of the 298 g starch fed daily only 6–35 g passed through the abomasum or duodenum and only 1–4 g reached the terminal ileum. The cellulose in the diet was poorly digested.

4. For the hay diet, 67% of the digestible dry matter disappeared in the stomach, 22% in the small intestine and 11% in the large intestine. Values for disappearance of digestible energy were 81% in the stomach, 7% in the small intestine and 12% in the large intestine. Of the 33 g of starch consumed daily, from 5 to 13 g passed through the abomasum or duodenum. The cellulose in the hay was 59% digestible and virtually all this digestion took place in the stomach.

5. The concentration of VFA and the proportion of propionate in the rumen fluid, 2.5 h after feeding, were considerably greater on the concentrate diet than on the hay diet, but diet had little influence on the concentration of blood glucose.

6. The importance of the small amount of starch passing to the sheep's small intestine is discussed.

The volume and composition of the digesta passing through various sections of the digestive tract of sheep can be measured directly by causing the digesta to flow through re-entrant cannulas inserted into either the duodenum or terminal ileum (Phillipson, 1952; Sineshchekov, 1953; Hogan & Phillipson, 1960; Harris & Phillipson, 1962; Phillips & Dyck, 1964; Goodall & Kay, 1965; Bruce, Goodall, Kay, Phillipson & Vowles, 1966; Clarke, Ellinger & Phillipson, 1966). The technique has been used to determine the relative amount of digestion which occurs in the sheep's stomach, as a result of fermentative processes, compared with that taking place in the small or large intestine. Most attention has been given to the disappearance of dry matter, organic matter, nitrogen and some minerals.

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Ridges & Singleton (1962) carried out similar studies with goats, and recently Porter & Singleton (1965) have used the technique to examine the passage of carbohydrate from the stomach of a hay-fed goat. They found a complex mixture of polysaccharides in the duodenal digesta but this included very little  $\alpha$ -linked glucose, equivalent to a flow of only 3 g daily. This result supported the earlier observations of Heald (1951) and of Weller & Gray (1954), who found from rumen studies in sheep receiving roughage diets that only 1–8 g of starch flowed onwards from the rumen each day. Evidently very little  $\alpha$ -linked glucose is available for hydrolysis in the small intestine of ruminants fed on roughage diets. In cellulose and hemicellulose the glucose units are joined by a  $\beta$ -linkage and are not degraded by mammalian enzymes.

In recent years the feeding of cattle, and to a lesser extent of sheep, on all-concentrate diets, rich in starch, has become an established farming practice. On such diets, it is possible that relatively large amounts of starch may escape rumen fermentation. If so, or if substantial amounts of new starch were synthesized and stored in micro-organisms to be passed on to lower sections of the alimentary tract for digestion, this would provide the ruminant with a useful source of glucose. Blaxter (1962) has shown that absorbed glucose is used with a high efficiency for both maintenance and lipogenesis by the ruminant.

The study now described was designed to examine quantitatively the digestion of diets of concentrates, principally barley, and of hay in various sections of the gut of sheep. The animals were fitted with simple or re-entrant cannulas in the abomasum, duodenum or terminal ileum. A subsequent paper (Topps, Kay, Goodall, Whitelaw & Reid, 1968) describes similar work with young steers. These experiments show that very little starch passes to the abomasum and intestines under our conditions. The results agree with the recent findings of MacRae & Armstrong (1966) but conflict with those of Tucker, Little, Mitchell, Hayes & Karr (1966) and with those of Porter & Singleton (1966).

#### EXPERIMENTAL

*Animals.* Seven Scottish Blackface ewes were used. All except one (Annie) were about 3 years old and their weights ranged from 30 to 46 kg. Annie was 8 years old. Each sheep was fitted with an ebonite rumen cannula and all had previously been used for experimental work. Two of the ewes (Maud and Annie) had re-entrant cannulas fitted into the first part of the duodenum (Hogan & Phillipson, 1960) and two others (Ingrid and Joanna) had them fitted into the terminal part of the ileum (Bruce *et al.* 1966); the design of the cannulas is described by Ash (1962*a*). Two other sheep (Bunty and Ester) had an ebonite cannula of 12 mm internal diameter fitted into the fundus of the abomasum. These cannulas were closed by a combined cap and core which prevented solid material settling in the barrel between sampling periods. The seventh animal (Fiona) was fitted with re-entrant cannulas in the anterior part of the abomasum (Ash, 1962*b*). All surgery was performed under general anaesthesia and was completed at least 2 months before the first experiment began.

*Diets.* Two diets were used: milled and pelleted grass hay, and pelleted concentrates. The concentrates consisted of (g/kg): barley (grain with husk), 850; soya-bean meal,

75; white fish meal, 36; molasses, 11; limestone, 13; dicalcium phosphate, 9; sodium chloride, 6; ferrous sulphate, 0.3; copper sulphate, 0.02; cobalt sulphate, 0.002; vitamin A, 6300 i.u./kg; vitamin D, 1500 i.u./kg. The composition and apparent digestibility of the diets are shown in Table 1.

Table 1. *Composition of the diets (g/100 g food) and their digestibility*

	Water	Cellulose	Total nitrogen	Starch A*	Starch E†	Digestibility of dry matter (%)
Period 1:						
Concentrate	14.2	5.5	2.6	45.9	46.1	79.9
Hay	13.0	36.1	1.2	6.6	4.2	46.6
Period 2:						
Concentrate	15.3	4.7	2.4	45.5	49.0	81.7
Hay	14.5	35.8	1.1	7.2	3.9	49.9
Period 3:						
Concentrate	14.4	5.5	2.7	45.1	46.7	83.6
Period 4:						
Hay	9.2	31.0	1.6	6.5	4.1	61.8

The concentrate and hay diets had a mean sugar content of 4.1 and 3.1% respectively.

\* Determined by the anthrone method (Clegg, 1956).

† Determined by an enzymic method (MacRae & Armstrong, 1966).

Table 2. *Plan of the experiment, with the sequence and duration of giving the diets to the sheep and the times of collection of samples*

Period and starting date	Days	
1 (7 Oct. 1965)	1-19	Ester, Maud and Ingrid changed gradually from dried grass to concentrate diet
	12	Bunty, Annie and Joanna changed from dried grass to hay diet
	24-37	Faeces and urine collected
	25 and 31	Blood and rumen contents sampled
	27 and 33	Flow of digesta measured over 24 h
2 (20 Dec. 1965)	1-21	Bunty, Annie and Joanna changed gradually from dried grass to concentrate diet
	14	Ester, Maud and Ingrid changed from dried grass to hay diet
	25-41	Faeces and urine collected
	27 and 39	Blood and rumen contents sampled
	30 and 36	Flow of digesta measured over 24 h
3 (7 Feb. 1966)	1-21	Fiona changed gradually from dried grass to concentrate diet
	26-43	Faeces and urine collected
	42	Blood and rumen contents sampled
	29 and 38	Flow of digesta measured over 24 h
	4 (15 Apr. 1966)	1
16-30		Faeces and urine collected
24		Blood and rumen contents sampled
20 and 26		Flow of digesta measured over 24 h

*Feeding and sampling.* The main part of the work was undertaken with six sheep and was followed by experiments with a seventh sheep, Fiona, to obtain corroborative results. The six sheep were paired according to type of cannulation and one of each pair was allocated to two groups of three animals. For the first half of the main experi-

ment one group was given the concentrate diet and the other the hay diet; the dietary treatments were then interchanged. A plan of the whole experiment is shown in Table 2.

During experimental periods the sheep were housed in metal metabolism cages (Duthie, 1959) which allowed faeces and urine to be collected separately. Water was freely available and the mean voluntary intake was measured over 14- or 15-day periods. The daily ration was either 850 g hay cubes or 650 g concentrate cubes, and these amounts supplied about 1700 and about 1900 kcal of digestible energy respectively. Usually the full ration was consumed but any uneaten food was collected and weighed daily. The food was divided equally into two meals given at 09.00 and 16.00 h. At these times 3 g of paper impregnated with chromium sesquioxide were inserted via the cannula into the rumen of each sheep to serve as an indigestible reference substance. This supplied 1.85 g of chromium sesquioxide ( $\text{Cr}_2\text{O}_3$ ) daily.

The flow of digesta through the duodenum or ileum of the sheep fitted with re-entrant cannulas was recorded and a representative sample was taken by the technique described by Bruce *et al.* (1966). Two 24 h collections, separated by an interval of 6 days, were made on each diet. At the same time 30 ml samples of digesta were withdrawn at hourly intervals from the abomasal cannulas of Ester and Bunty and were pooled to make a sample representative of the 24 h. Digesta collected on an earlier occasion was used to restore the volume of digesta being returned to the animals with re-entrant cannulas, but this proved impracticable with Ester and Bunty. The samples were frozen by solid carbon dioxide during collection and subsequently stored at  $-20^\circ$  until analysed. The pH of samples of digesta was measured with a Cambridge pH meter at 2 h intervals. The behaviour of each sheep was recorded during the collection periods by noting at 15 min intervals whether or not she was ruminating.

Food intake and faecal output were recorded for a 12-day period, which included the two digesta collection days, and a representative sample of faeces was taken for analysis. One or two days before each 24 h collection blood and rumen samples were withdrawn from the sheep immediately before the morning feed and 2.5 h later. Previous measurements had shown that, with both diets, the pH of the rumen contents reached a minimum about 2.5 h after feeding and this was assumed to correspond to maximal concentration of volatile fatty acids (VFA). About 5 ml of blood were withdrawn from the jugular vein into heparinized tubes and immediately analysed for blood glucose. Approximately 100 ml of rumen contents were obtained by suction from varying depths of the rumen and strained through gauze into a centrifuge tube kept in iced water. The solid material obtained by straining and any excess sample were returned to the rumen with the aid of a little water. The strained rumen liquor was centrifuged at 1800g for 10 min and 20 ml of the supernatant liquid were acidified with 1 ml of 10 N- $\text{H}_2\text{SO}_4$  and stored at  $0^\circ$  for determination of VFA.

*Chemical analysis.* Food, digesta and faeces were dried at  $105^\circ$  for 48 h; they were then ashed at  $570^\circ$  and the weights of dry matter and organic matter calculated. Chromium sesquioxide was determined in weighed samples of ash of the faeces and digesta by the procedure of Christian & Coup (1954). Nitrogen in the fresh samples was determined by the macro-Kjeldahl method.

Freeze-dried samples of digesta and oven-dried samples of food and faeces were used in the following analyses. Cellulose was measured by the method of Crampton & Maynard (1938). Calorific values were measured in an adiabatic bomb calorimeter (A. Gallenkamp and Co. Ltd, London). The 'starch' content of the samples was measured both by the 'anthrone' method (Clegg, 1956) and by the enzymic method of MacRae & Armstrong (1966). The latter determination measures  $\alpha$ -linked glucose polymers. The material was hydrolysed enzymically with a preparation with mixed amylase activity obtained from *Aspergillus niger* fermentation broths (Agidex; Glaxo Research Ltd) and the glucose formed was determined by the glucose oxidase method of Huggett & Nixon (1957), using *o*-dianisidine as an oxygen acceptor.

Blood glucose levels were determined by the same glucose oxidase method. The VFA were steam-distilled from the acidified rumen liquor and the distillate was titrated against standard NaOH, under CO<sub>2</sub>-free conditions, to give the total concentration of VFA. The proportions of acetic, propionic and butyric acids were determined by the gas chromatographic technique of James & Martin (1952).

#### RESULTS

*Appetite.* On two occasions whilst receiving the hay diet Ingrid's ileal cannula became blocked overnight with food particles. When this happened she refused her morning feed but after removal of the blockage she began to eat again within a few hours. Throughout this period, however, Ingrid failed to eat her full rations. Joanna and occasionally Annie refused part of the concentrate ration, though for no evident reason. With these exceptions, the animals ate their full rations promptly, generally taking about 20 min to consume a meal of hay cubes, and 5 min for a meal of concentrates.

*Water intake.* With the exception of Ester, the sheep drank about as much water on the concentrate diet, 1620 ml/24 h  $\pm$  620 SD, as on the hay diet, 1430 ml/24 h  $\pm$  370 SD. Ester drank much more, 5780 ml/24 h on the concentrate ration and 2670 ml/24 h on the hay ration, but the reason for this was not apparent.

*Body-weight.* The weights of the sheep remained fairly constant except that Ester and Annie lost from 3 to 6 kg when given the concentrate diet, and Ingrid lost a similar amount on the hay. All seven sheep remained in approximate nitrogen balance on each diet.

*Rumination.* The time devoted to rumination, averaged for seven sheep over 2 h periods during the 24 h collections, and the average hourly flow of duodenal and ileal contents are shown in Fig. 1. As noted previously (Harris & Phillipson, 1962), the flow of duodenal digesta tended to be highest during the period between midnight and midday when most rumination occurred. There was no consistent diurnal pattern of ileal flow. The sheep spent an average of 4.8 h ruminating daily when given the hay but only 2.0 h when given the concentrates. On the concentrate diet, rumination tended to occur for only a few minutes at a time and boluses were chewed in a more brief and desultory manner than when hay was given.

*Flow of digesta.* The flow of digesta recorded over the 24 h periods for five sheep, the

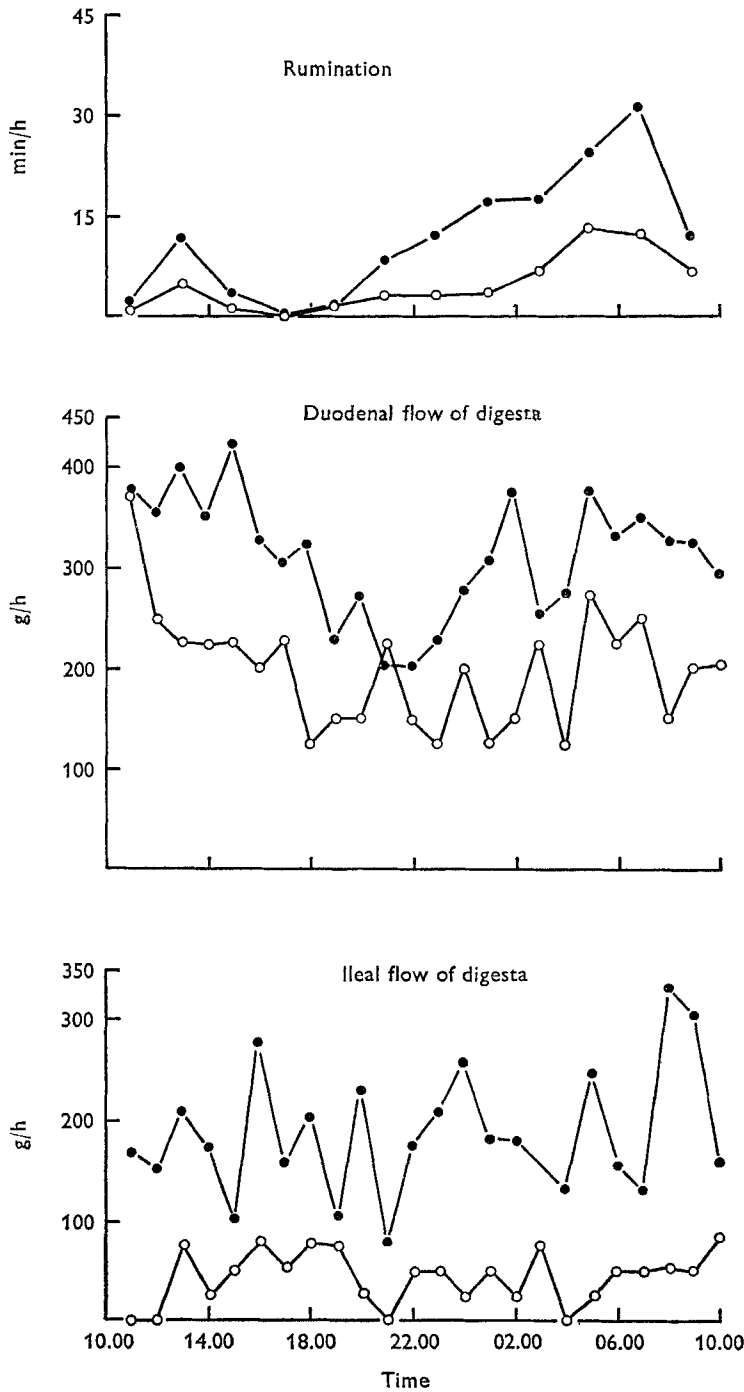


Fig. 1. Diurnal patterns of rumination and of digesta flow. The rations were given as two equal meals at 09.00 and 16.00 h. Each point is the mean value for either seven sheep (rumination) or two (digesta flow). O, sheep given concentrate ration; ●, sheep given hay ration.

Cr<sub>2</sub>O<sub>3</sub> content of these digesta, and the calculated flow of digesta required to give 100% recovery of the Cr<sub>2</sub>O<sub>3</sub> given daily, are shown in Table 3. Mean daily faecal output and calculated daily flows of digesta through the abomasum of Bunty and of Ester are also given. The weight of Cr<sub>2</sub>O<sub>3</sub> passing through the re-entrant cannulas

Table 3. *Digesta flow (values for two 24 h collections) and faecal output, before and after adjustment for 100% recovery of chromium sesquioxide, and the amount of chromium sesquioxide recovered (g/24 h) in seven sheep receiving two diets*

Sheep	Cannula	Digesta			Faeces		
		Measured flow	Cr <sub>2</sub> O <sub>3</sub> recovered	Adjusted flow	Measured output	Cr <sub>2</sub> O <sub>3</sub> recovered	Adjusted output
Concentrate diet							
Fiona	Abomasal	5195	1.45	6650	194	1.59	225
		5281	1.89	5170			
Bunty		—	—	5200	142	1.74	151
		—	—	6430			
Ester		—	—	5570	215	1.77	226
		—	—	5160			
Annie	Duodenal	5379	1.71	5820	143	1.52	174
		3657	1.15	5880			
Maud		5684	1.62	6500	208	1.77	218
		4519	1.37	6100			
Joanna	Ileal	964	0.94	1900	164	1.76	172
		1032	1.96	975			
Ingrid		1413	*	—	234	1.60	271
		914	1.30	1300			
Hay diet							
Fiona	Abomasal	9069	1.60	10520	764	1.82	779
		10455	1.74	11082			
Bunty		—	—	9180	725	1.76	761
		—	—	8770			
Ester		—	—	7240	791	1.81	807
		—	—	7810			
Annie	Duodenal	6989	1.60	8090	700	1.80	721
		8352	1.58	9779			
Maud		7207	1.48	9009	775	1.83	783
		7533	1.83	7616			
Joanna	Ileal	4813	1.71	5207	776	1.80	799
		4037	1.29	5780			
Ingrid		4588	2.36	3596	663	1.52	809
		4810	1.56	5600			

\* Cr<sub>2</sub>O<sub>3</sub> not determined.

Table 4. *Mean values and standard deviations for pH of digesta collected over four 24 h periods from three pairs of sheep receiving two diets*

Diet	Abomasal digesta	Duodenal digesta	Ileal digesta
Concentrate	2.35 ± 0.33	2.80 ± 0.43	7.73 ± 0.23
Hay	2.69 ± 0.45	2.46 ± 0.39	7.93 ± 0.18

Table 5. Amounts of dry matter consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments) and excreted in the faeces (g/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet						Hay diet					
	Food	Abomasum	Duodenum	Ileum	Faeces		Food	Abomasum	Duodenum	Ileum	Faeces	
Bunty	551	212	—	—	89		740	491	—	—	350	
Ester	558	235	—	—	112		727	448	—	—	353	
Annie	529	237	—	—	100		740	473	—	—	325	
Maud	558	239	—	—	114		727	475	—	—	360	
Joanna	516	—	256	—	86		740	—	400	—	380	
Ingrid	558	—	195	—	134		543	—	491	—	355	
		—	305	—	114			—	488	—		
		—	254	—	86			—	490	—		
		—	—	173	86			—	—	418		
		—	—	113	134			—	—	424		
		—	—	139*	134			—	—	266		
		—	—	124	124			—	—	478		

\* Based on measured flow rate.



during the 24 h collection periods was usually less than the amount introduced into the rumen, 1.85 g daily. As a result, the recorded duodenal flow averaged only 83 % of the calculated 24 h flow, the ileal flow 86 % and the faecal output 93 %.

Abomasal and duodenal flows were about 1.5 times greater and ileal flow was nearly 4 times greater on the hay diet than on the concentrate diet.

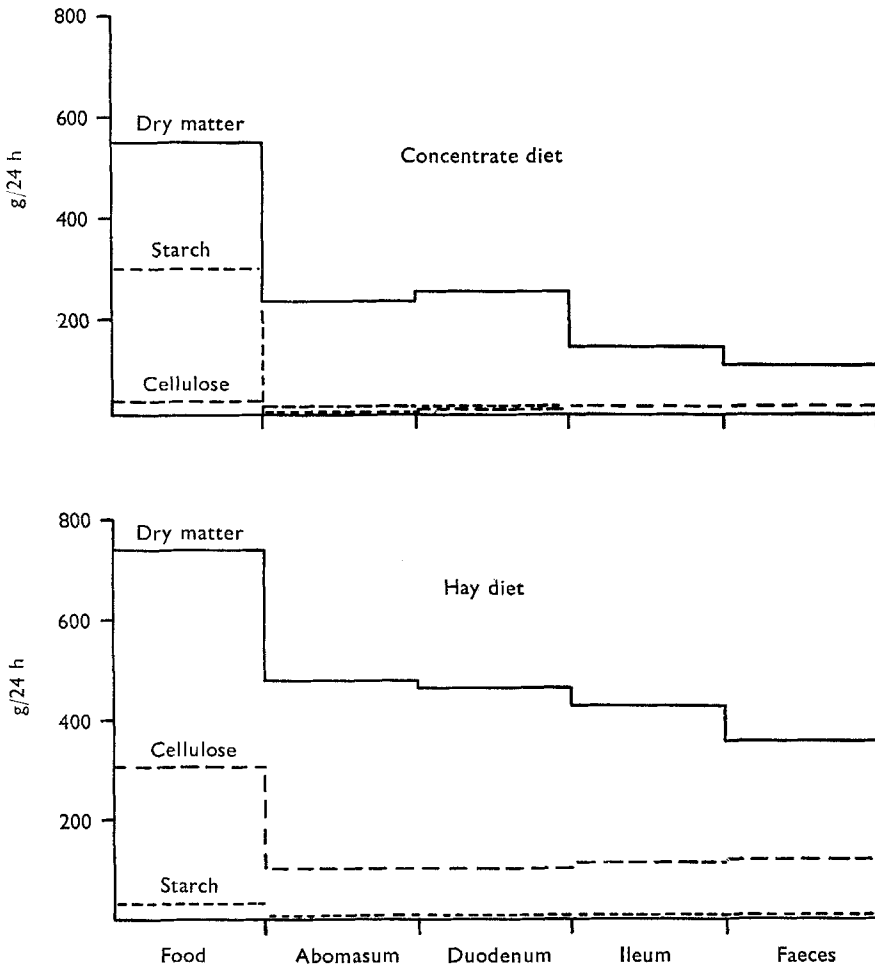


Fig. 2. Mean amounts of dry matter, starch and cellulose in the food (six sheep), in the abomasal, duodenal and ileal digesta (two sheep each) and in the faeces (six sheep).

*pH of digesta.* The mean pH values of the digesta are given in Table 4. The pH of the abomasal digesta, and also of the ileal digesta, tended to be higher with the hay diet than with the concentrates, whilst a converse trend was found with material flowing through the duodenum, but none of these differences achieved statistical significance.

*Amounts of various constituents passing through the digestive tract.* Tables 5–10 give the quantities of dry matter, starch (two tables), cellulose, nitrogen and energy found

in the food, digesta and faeces of the six sheep given each diet. The corresponding results for Fiona are shown in Table 11. The mean values for dry matter, starch and cellulose are shown diagrammatically in Fig. 2.

The results of the main experiment showed that, of the apparently digestible dry matter of the hay diet, some 67% (range 65–72%) disappeared from the stomach (throughout this paper the term 'stomach' refers to reticulo-rumen, omasum and abomasum, and the term 'forestomach' refers to reticulo-rumen and omasum), about 22% from the small intestine (by difference between the sheep with duodenal or abomasal cannulas and Joanna with ileal cannulas), and about 11% from the large intestine. Values for the second sheep with ileal cannulas, Ingrid, unfortunately had to be disregarded since her variable food intake and faecal output did not permit comparisons of digesta flows measured over 24 h with mean food and faeces values. Fiona received a much more digestible hay ration and in her case 46% of the digestible dry matter disappeared from her forestomach.

When the concentrate diet was given, 69% (range 63–71%) of the digestible dry matter disappeared from the stomach, 17% from the small intestine and 14% in the large intestine. The latter value is again based only on Joanna; the apparent changes in dry matter in digesta passing through Ingrid's large intestine suggest that ileal flow had been underestimated. Values for Fiona indicated the loss of 64% of digestible dry matter from the forestomach.

The corresponding values for organic matter (dry matter minus ash) indicated that on the concentrate and hay diets, respectively, 76 and 83% of the apparently digestible organic matter disappeared from the stomach, 19 and 7% from the small intestine and 5 and 10% from the large intestine.

The results shown in Tables 6 and 7 for starch show that of the 298 g starch supplied daily in the concentrate diet only 6–35 g reached the abomasum or duodenum. The amounts passing from the stomach on the hay diet were smaller still. With both diets, most, if not all, of this starch seemed to be hydrolysed in the small intestine, although somewhat contrary and inexplicable results were obtained with Joanna when her ileal digesta were analysed for starch by the enzymic method. In general, however, reasonably close agreement was obtained between the values for starch content obtained by the two analytical methods. The anthrone method usually gave slightly higher results than the enzymic method. No free glucose was present in the digesta or faeces.

Table 8 shows that some 28% of the small amount of cellulose contained in the concentrate ration, and 59% of the large amount in the hay ration, were digested. With both diets cellulose digestion seemed confined to the stomach.

On a net basis there was a considerable addition of total nitrogen to the stomach contents of the sheep when they were given hay cubes (Table 9). Although the dietary N content of the concentrate ration was approximately 50% greater than that of the hay cubes, the amounts of nitrogen passing to the small intestine were similar for the two diets. Some 8 g of this nitrogen disappeared from the small intestine, and a further 1–2 g from the large intestine.

The pattern of energy disappearance along the digestive tract paralleled that of the dry-matter losses (Table 10). When the concentrate ration was given, about 72% of

Table 6. Amounts of starch, determined by the anthrone method (Clegg, 1956), consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments), and excreted in the faeces (g/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet						Hay diet					
	Food	Abomasum	Duodenum	Ileum	Faeces		Food	Abomasum	Duodenum	Ileum	Faeces	
Bunty	288	8.0	—	—	1.7		55.4	6.6	—	—	3.7	
Ester	296	9.8	—	—	1.5		55.8	9.4	—	—	4.8	
Annie	276	15.1	—	—	1.8		55.4	9.6	—	—	3.2	
		25.7	—	—	—			9.7	—	—	—	
		—	31.3	—	1.8			—	4.8	—	—	
		—	7.1	—	—			—	7.8	—	—	
Maud	296	—	31.9	—	1.8		55.8	—	8.9	—	4.8	
		—	21.6	—	—			—	9.1	—	—	
Joanna	269	—	—	5.3	1.8		55.4	—	—	3.2	3.8	
		—	—	6.4	—			—	—	5.9	—	
Ingrid	296	—	—	3.5*	1.8		41.7	—	—	3.0	4.3	
		—	—	3.9	—			—	—	6.7	—	

\* Based on measured flow rate.

Table 7. Amounts of starch, determined by an enzymic method (MacRae & Armstrong, 1966), consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments) and excreted in the faeces (g/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet						Hay diet					
	Food	Abomasum	Duodenum	Ileum	Faeces		Food	Abomasum	Duodenum	Ileum	Faeces	
Bunty	310	6.6	—	—	1.2		35.2	13.2	—	—	3.6	
Ester	297	13.2	—	—	1.0		32.9	5.3	—	—	5.0	
Annie	298	21.7	—	—	1.4		35.2	6.7	—	—	—	
Maud	297	—	34.7	—	—		—	—	10.0	—	3.2	
Joanna	290	—	5.7	—	—		—	—	11.2	—	—	
Ingrid	297	—	30.4	—	1.1		32.9	—	6.1	—	5.1	
		—	21.7	—	—		35.2	—	7.3	—	3.7	
		—	—	1.7	1.2		—	—	—	9.9	—	
		—	—	1.4	—		—	—	—	9.8	—	
		—	—	3.8*	1.3		24.6	—	—	2.2	5.0	
		—	—	3.6	—		—	—	—	5.5	—	

\* Based on measured flow rate.

Table 8. Amounts of cellulose consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments), and excreted in the faeces (g/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet					Hay diet				
	Food	Abomasum	Duodenum	Ileum	Faeces	Food	Abomasum	Duodenum	Ileum	Faeces
Bunty	30	18	—	—	21	307	105	—	—	127
Ester	36	21	—	—	23	304	97	—	—	111
Annie	29	19	—	—	28	307	100	—	—	86
Maud	36	12	20	—	24	304	112	79	—	128
Joanna	28	—	16	—	17	307	—	98	—	138
Ingrid	36	—	23	29	24	227	—	110	120	127
		—	14	19	24		—	128	99	
		—	—	20*	18		—	—	62	
		—	—	18			—	—	152	

\* Based on measured flow rate.

Table 9. Amounts of total nitrogen consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments), and excreted in the faeces (g/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet						Hay diet					
	Food	Abomasum	Duodenum	Ileum	Faeces		Food	Abomasum	Duodenum	Ileum	Faeces	
Bunty	15.5	12.2	—	—	2.8		9.9	13.9	—	—	5.5	
Ester	16.8	11.6	—	—	4.2		9.6	12.5	—	—	5.9	
Annie	14.8	14.1	—	—	2.7		9.9	13.5	—	—	6.1	
Maud	16.8	—	14.0	—	—		—	—	13.1	—	—	
			10.0	—	—		—	—	15.5	—	—	
			16.8	—	3.3		9.6	—	14.4	—	5.5	
			15.6	—	—		—	—	13.5	—	—	
Joanna	14.5	—	—	5.0	2.7		9.9	—	—	5.8	6.3	
			—	3.5	—		—	—	—	9.1	—	
Ingrid	16.8	—	—	5.7*	5.5		7.2	—	—	5.0	5.5	
			—	4.6	—		—	—	—	7.1	—	

\* Based on measured flow rate.

Table 10. Amounts of energy consumed, passing to the abomasum, duodenum or terminal ileum (values for two experiments), and excreted in the faeces (kcal/24 h) of six sheep receiving two diets

(Values are based on flow rates and on faecal outputs adjusted to give 100% recovery of chromium sesquioxide)

Sheep	Concentrate diet					Hay diet				
	Food	Abomasum	Duodenum	Ileum	Faeces	Food	Abomasum	Duodenum	Ileum	Faeces
Bunty	2383	817	—	—	340	3329	2047	—	—	1591
		932	—	—	—		1839	—	—	
Ester	2393	987	—	—	439	3218	1889	—	—	1579
		972	—	—	—		1875	—	—	
Annie	2287	—	995	—	374	3329	—	1636	—	1442
		—	684	—	—		—	2025	—	
Maud	2393	—	1224	—	439	3218	—	2031	—	1603
		—	1005	—	—		—	1961	—	
Joanna	2231	—	—	613	330	3329	—	—	1741	1687
		—	—	397	—		—	—	1837	
Ingrid	2393	—	—	524*	547	2404	—	—	1047	1596
		—	—	463	—		—	—	1855	

\* Based on measured flow rate.

the digestible energy was accounted for by breakdown processes in the stomach (the corresponding value for Fiona was 67%). Of the remainder 23% was digested in the small intestine and 5% in the large intestine. When hay cubes were given the

Table 11. *Amounts of dry matter, starch, cellulose and total nitrogen (g/24 h) and of energy (kcal/24 h) consumed, passing to the abomasum (values for two experiments) and excreted in the faeces of a sheep receiving two diets*

(Values are based on flow rates and on faecal outputs of sheep Fiona, adjusted to give 100% recovery of chromium sesquioxide)

Constituent	Concentrate diet			Hay diet		
	Food	Abomasum	Faeces	Food	Abomasum	Faeces
Dry matter	556	264 287	106	772	540 567	300
Starch A*	293	9.5 28.3	2.3	55.4	8.6 11.0	4.4
Starch E†	335	14.0 40.4	1.4	34.4	12.7 15.6	3.3
Cellulose	31	14 17	16	240	114 121	84
Nitrogen	17.2	15.6 17.7	8.4	13.5	18.6 20.0	6.6
Energy	2389	977 1175	425	3444	2167 2284	1347

\* Determined by the anthrone method (Clegg, 1956).

† Determined by an enzymic method (MacRae & Armstrong, 1966).

Table 12. *Mean values and standard deviations for blood glucose concentrations, and concentrations and molar proportions of volatile fatty acids (VFA) in the rumen, of seven sheep receiving two diets*

	Concentrate diet		Hay diet	
	Before feeding*	After feeding†	Before feeding*	After feeding†
Blood glucose (mg/100 ml)	40.6 ± 3.1	44.1 ± 2.9	41.0 ± 4.6	42.1 ± 3.8
Total VFA (m-equiv./l.)	54.7 ± 12.7	94.6 ± 13.0	56.0 ± 9.7	79.7 ± 8.9
Acetic acid (%)	48.6 ± 8.7	44.5 ± 4.9	65.8 ± 4.3	63.3 ± 2.8
Propionic acid (%)	24.7 ± 6.6	34.6 ± 7.8	22.3 ± 2.5	24.6 ± 2.7
Butyric and higher acids (%)	26.7 ± 4.4	20.9 ± 4.5	11.9 ± 4.7	12.1 ± 1.5

\* Given at 09.00 h.

† 2½ h after feeding.

mean values for disappearance of digestible energy were 81% in the stomach, 7% in the small intestine and 12% in the large intestine. In Fiona a much lower value, of 58% for disappearance of digestible energy in the forestomach, was observed.

*Concentrations of blood glucose and of VFA in the rumen.* Table 12 shows the blood glucose concentrations and the VFA concentrations and molar proportions in the



seven sheep on each diet. Diet had little or no effect on concentrations of glucose. When,  $2\frac{1}{2}$  h after feeding, the pH of the rumen contents had been shown to reach a minimum, the concentration of total VFA and the proportion of propionate were considerably greater on the concentrate diet than on the hay cubes. At both sampling times, the proportion of acetate in the rumen of concentrate-fed sheep was considerably less and that of butyrate and higher acids was considerably more than that found in the sheep receiving hay cubes.

#### DISCUSSION

The main aim of the study was to see if large quantities of starch can escape rumen fermentation and pass to the small intestine of sheep when they are given a diet rich in starch. The results clearly show that only small amounts, ranging from 6 to 35 g daily, reached the abomasum or duodenum. At most this represents only 6% of the dietary intake of 298 g daily. This finding is consistent with the results of MacRae & Armstrong (1966), who reported finding only 17–22 g of  $\alpha$ -linked glucose polymers in the duodenal contents of sheep receiving a diet of 200 g hay and 700 g rolled barley daily. On the other hand, it is at variance with the results contained in a brief report by Tucker *et al.* (1966). These workers showed that with diets containing 40, 60 or 80% ground maize, and which supplied daily 326, 462 or 580 g starch to wether sheep, between 120 and 144 g starch passed to the abomasum. Porter & Singleton (1966) also found that about a third of the starch consumed by sheep receiving a ration of 1300 g hay and 200 g concentrate reached the intestine. The work of Wright, Grainger & Marco (1966) again indicates that under some conditions appreciable amounts of starch may escape fermentation in the rumen. These workers analysed the contents of the abomasum of sheep killed at various intervals after a meal of concentrates rich in maize. Starch, as a percentage of dry matter, was high enough 3 h after feeding to suggest that substantial amounts may pass to the intestines, though with no measure of the digestibility of dry matter in the rumen or of flow through the abomasum it is not possible to assess this amount quantitatively. It is difficult to postulate a reason for these discrepancies between results from different centres. It is conceivable that differences in the fermentation of maize starch and barley starch, or differences in levels of feeding, methods of sampling and analysis could be responsible, but none of these factors offers a very plausible explanation. Nevertheless, at present it may be concluded that only small amounts of starch are available for hydrolysis in the small intestine of sheep given restricted amounts of concentrate diet composed principally of barley.

Although small in quantity this starch may make a useful contribution to the glucose available to the animal. Armstrong (1965) summarized the evidence available on glucose metabolism in sheep. The requirement of a non-pregnant sheep is estimated to be 89 g daily. Armstrong suggested that, since little glucose is available for absorption from the intestine when roughage diets are given, most of this essential metabolite must be derived from the propionate formed in the rumen. Our results suggest that propionate must remain the principal source of glucose, even when con-

concentrate diets containing large amounts of starch are given. Our next paper (Topps *et al.* 1968) further considers this important aspect of metabolism.

The hay cubes supplied the sheep with only about 34 g of starch daily. Although very little reached the abomasum or duodenum, this amount was greater relative to intake than when concentrates were given, suggesting that much of it may have been of microbial origin. Unfortunately, the analytical methods used did not differentiate food starch from microbial starch. The amount of starch in the duodenal contents of sheep given hay cubes agreed well with the values of Heald (1951), Weller & Gray (1954) and Porter & Singleton (1965).

Although the two procedures for determining starch usually gave similar results, those obtained by the anthrone method were often a little higher than those by the enzymic method. This may be explained by the presence of certain mucopolysaccharides which gave a slight colour reaction with anthrone. Mucin bought as a chemical (Koch-Light) gave a colour reaction equivalent to 8% that of potato starch (British Drug Houses Ltd).

The extent of the disappearance of other dietary constituents in various parts of the gut is consistent with the findings of earlier workers. The fact that 90% or more of the cellulose digested disappeared in the stomach agrees with the results of Porter & Singleton (1965) and of Bruce *et al.* (1966). The low overall digestibility of the small amount of cellulose in the concentrate ration was probably due to a depression of the cellulolytic flora caused by a preponderance of starch in the diet (Belasco, 1956).

The disappearance of approximately 70% of the digestible dry matter in the sheep's stomach agrees with the findings of Hogan & Phillipson (1960). The fact that more than half of the post-ruminal digestion of the dry and organic matter of the diets occurred in the small intestine illustrates the importance of enzymic digestion in the ruminant. The substances digested included nearly all of the starch and most of the nitrogenous compounds flowing from the abomasum.

When the sheep were given the concentrate diet the amount of nitrogen passing through the abomasum was similar to the amount consumed, but when hay was given there was a substantial net addition of nitrogen to the stomach contents. Similar changes in the nitrogen content of digesta have been recorded by Harris & Phillipson (1962) and by Clarke *et al.* (1966). This effect is of great importance to the ruminant in helping it to overcome a deficiency of dietary nitrogen.

The disappearance of energy along the digestive tract parallels that of dry and organic matter. It is interesting to note that quite a large amount of energy, 209 kcal/24 h, was lost by food residues passing through the large intestine when hay was given, whereas only 88 kcal/24 h were lost when concentrates were given. It is not clear what substances were being fermented since there was little digestion of cellulose and nitrogenous compounds. Possibly, hemicelluloses of the diet and mucopolysaccharides secreted into the small intestine were yielding to bacterial attack.

Previous measurements of the flow of digesta through the duodenum have shown it to be related to both the amount of food eaten and its roughage content. Hogan (1964) estimated the duodenal flow of sheep to be 7–11 l./24 h when 700–800 g hay were given and 13–29 l./24 h when 1700 g were given. Phillips & Dyck (1964) found the flow to be

increased by raising the straw content of the ration given. These two effects adequately explain the differences in volume of flow of duodenal digesta between the hay cubes and the concentrate diet. Flow of digesta through the ileum was still more closely related to the intake of indigestible matter, as observed previously by Goodall & Kay (1965).

The values for the flow and composition of digesta that were obtained by withdrawing frequent small samples from an abomasal cannula were very similar to those obtained by the more tedious procedure of measuring and sampling flow through re-entrant cannulas placed in the first part of the duodenum. As sheep with re-entrant cannulas are also the more difficult to prepare and manage, this suggests that in some instances abomasal sampling may provide a convenient alternative.

With both diets the concentration of glucose in jugular blood showed little change after feeding. Anison, Hill & Lewis (1957) suggested that the lack of a response of glucose concentration in portal blood to feeding indicates that very little carbohydrate is absorbed as glucose from the alimentary tract. If this suggestion is valid, the smallness of the increase in blood sugar after the concentrate ration has been given may be regarded as supporting the evidence that little starch reaches the intestine.

The patterns of ruminal VFA associated with the two diets were typical for a hay diet (Bath & Rook, 1963) and for a diet high in starchy concentrates (Balch & Rowland, 1957). Blaxter (1962) has shown that this pattern of VFA, in particular the proportion of acetate, is closely related to the net availability of the metabolizable energy of the diet for lipogenesis. Our view on the significance of this relationship for concentrate diets would need to be re-examined if appreciable amounts of starch were digested in the intestine to give glucose which is used with a high efficiency for lipogenesis. Our results indicate that any consequences of intestinal digestion of glucose are likely to be small.

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#### REFERENCES

- Anison, E. F., Hill, K. J. & Lewis, D. (1957). *Biochem. J.* **66**, 592.  
 Armstrong, D. G. (1965). In *Physiology of Digestion in the Ruminant*, p. 272. [R. W. Dougherty, editor.] London: Butterworths.  
 Ash, R. W. (1962*a*). *Anim. Prod.* **4**, 309.  
 Ash, R. W. (1962*b*). *J. Physiol., Lond.* **164**, 4*P*.  
 Balch, D. A. & Rowland, S. J. (1957). *Br. J. Nutr.* **11**, 288.  
 Bath, I. H. & Rook, J. A. F. (1963). *J. agric. Sci., Camb.* **61**, 341.  
 Belasco, I. J. (1956). *J. Anim. Sci.* **15**, 496.  
 Blaxter, K. L. (1962). *The Energy Metabolism of Ruminants*. London: Hutchinson.  
 Bruce, J., Goodall, E. D., Kay, R. N. B., Phillipson, A. T. & Vowles, L. E. (1966). *Proc. R. Soc. B* **166**, 46.  
 Christian, K. R. & Coup, M. R. (1954). *N.Z. J. Sci. Tech.* A **36**, 328.  
 Clarke, E. M. W., Ellinger, G. M. & Phillipson, A. T. (1966). *Proc. R. Soc. B* **166**, 63.  
 Clegg, K. M. (1956). *J. Sci. Fd Agric.* **7**, 40.  
 Crampton, E. W. & Maynard, L. A. (1938). *J. Nutr.* **15**, 383.  
 Duthie, I. F. (1959). *Lab. Pract.* **8**, 408.

- Goodall, E. D. & Kay, R. N. B. (1965). *J. Physiol., Lond.* **176**, 12.
- Harris, L. E. & Phillipson, A. T. (1962). *Anim. Prod.* **4**, 97.
- Heald, P. J. (1951). *Br. J. Nutr.* **5**, 84.
- Hogan, J. P. (1964). *Aust. J. agric. Res.* **15**, 384.
- Hogan, J. P. & Phillipson, A. T. (1960). *Br. J. Nutr.* **14**, 147.
- Huggett, A. St G. & Nixon, D. A. (1957). *Lancet* *ii*, 368.
- James, A. T. & Martin, A. J. P. (1952). *Biochem. J.* **50**, 679.
- MacRae, J. C. & Armstrong, D. G. (1966). *Proc. Nutr. Soc.* **25**, xxxiii.
- Phillips, G. D. & Dyck, G. W. (1964). *Can. J. Anim. Sci.* **44**, 220.
- Phillipson, A. T. (1952). *J. Physiol., Lond.* **116**, 84.
- Porter, P. & Singleton, A. G. (1965). *Biochem. J.* **96**, 59P.
- Porter, P. & Singleton, A. G. (1966). *J. Physiol., Lond.* **186**, 145P.
- Ridges, A. P. & Singleton, A. G. (1962). *J. Physiol., Lond.* **161**, 1.
- Sineshchekov, A. D. (editor) (1953). *Fiziologiya pitaniya sel'skokhozyaistvennykh zhivotnykh*. Moscow: Sel'khozgiz. (The nutritional physiology of farm animals. English translation 1964. National Lending Library for Science and Technology, Boston Spa, Yorkshire.)
- Topps, J. H., Kay, R. N. B., Goodall, E. D., Whitelaw, F. G. & Reid, R. S. (1968). *Br. J. Nutr.* **22**, 281.
- Tucker, R. E., Little, C. O., Mitchell, G. E., Hayes, B. W. & Karr, M. R. (1966). *J. Anim. Sci.* **25**, 911.
- Weller, R. A. & Gray, F. V. (1954). *J. exp. Biol.* **31**, 40.
- Wright, P. L., Grainger, R. B. & Marco, G. J. (1966). *J. Nutr.* **89**, 241.