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Rate of passage of digesta in sheep

1. The effect of level of food intake on marker retention times along the small intestine and on apparent water absorption in the small and large intestines

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1. Sheep given 400 and 1200 g lucerne chaff/d in equal hourly meals were infused continuously with the complex ^{51}Cr EDTA into the rumen for 5 d and then slaughtered. The retention times of ^{51}Cr EDTA along the small intestine and the apparent quantities of water absorbed in the small and large intestines were calculated.

2. The apparent quantities of water absorbed for the 400 and 1200 g food intakes were 5844 and 13110 ml/d in the small intestine and 2101 and 8520 ml/d in the large intestine respectively.

3. The mean total retention times of ^{51}Cr EDTA in the small intestine were 136 and 91 min for the sheep given 400 and 1200 g/d respectively. The marker was retained up to seventeen times longer in the ileal than in the duodenal or proximal jejunal segments.

The relative importance of different parts of the small intestine for nutrient absorption should be related, theoretically, to the quantity of nutrient presented to the mucosa and the potential of the mucosa to absorb (White, Williams & Morris, 1971; Tilson, 1972) and the time available for the process to occur.

The purpose of the experiment now presented was to determine the effect of level of food intake on the times available for digestion and absorption of nutrients in different parts of the small intestine of sheep. An aspect of water absorption from the small and large intestines was also studied.

EXPERIMENTAL

Sheep and rations

Thirteen mature Merino sheep were used. Sheep 4, 25, 26, 27, 28, 29 and 30 were given 400 g air-dried lucerne chaff/d, and their body-weights before slaughter were 34, 28, 29, 37, 37, 52 and 48 kg respectively. Sheep 1, 2, 3, 24, 31 and 32 were given 1200 g lucerne chaff/d, and their body-weights were 37, 48, 45, 46, 44 and 38 kg respectively. All sheep except 29 and 30 had permanent rumen fistulas (Hecker, 1969). Sheep 1, 2, 3 and 4 also had permanent abomasal fistulas (Jarrett, 1948). Sheep 4, 25, 26, 27 and 32 were ewes; the rest were wethers (castrated males).

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Housing and feeding

The sheep were kept in single pens in an animal house and were given their experimental rations once a day for at least 3 weeks. During the following 10 d experimental period the sheep were kept in metabolism cages and given about 1/24 of their daily intake per hour from an automatic feeding device (Minson & Cowper, 1966). Water was available *ad lib.* The experimental room was illuminated continuously.

Experimental procedure

The complex of chromium-51 with EDTA (^{51}Cr EDTA) (supplied by the Australian Atomic Energy Commission, Lucas Heights, NSW) was used as a water-soluble marker (Downes & McDonald, 1964).

After 5 d of hourly feeding, all sheep, except 3, 29 and 30, were given a single injection of ^{51}Cr EDTA in 100 ml distilled water (approximately 46 000 counts/ml per min) into the rumen. The marker solution was then infused continuously into the rumen at the rate of 0·16 ml/min for the next 5 d. The recoveries of ^{51}Cr in faeces were not determined. Total faecal outputs and their water contents were measured daily during this infusion period.

A catheter was inserted into a jugular vein of each sheep 12–48 h before slaughter on day 10. At slaughter the animals were anaesthetized with sodium pentobarbitone, weighed and killed by exsanguination. The digestive tract was then removed from each sheep, care being taken to minimize the oral and aboral flow of gut contents. Samples of digesta were taken from the rectum and were dried to constant weight at 100°. The small intestine was stripped from its mesentery and divided into five segments, each of which was about 20% of the total length. These were numbered consecutively from 1 to 5 starting at the most proximal segment. The quantities of water and dry matter present in each of the five segments of the small intestine were determined in sheep 3, 29 and 30 by draining the digesta into tared tins and drying them at 100° for 6 d. The prolonged drying time was necessary because the oven was poorly ventilated and crusts that formed on the tops of the samples slowed the release of water from the digesta.

For sheep receiving ^{51}Cr EDTA a similar procedure was followed except that single digesta samples of known wet weight were obtained from the contents of the reticulo-rumen, abomasum and each of the five segments of the small intestine, and one additional sample of digesta was taken from the small-intestinal contents closest to the ileo-caecal junction. The digesta recovered from the intestines were always dark-green in colour, except for that obtained from the first segment in one sheep, which had a creamy colour. This latter material contained no ^{51}Cr EDTA and was not included as a part of the digesta in the small intestine. The extent to which material of this nature contaminated the digesta from the other sheep is not known.

The samples were centrifuged at 2500 *g* for 30 min, and 3 ml portions of the supernatant fraction and ^{51}Cr EDTA infusion stock were counted with a Packard model 3002 Tricarb Scintillation Spectrometer (Packard Instrument Company Inc., Illinois, 60515, USA).

The flow-rates of water through the reticulo-rumen, abomasum and different segments of the small intestine were calculated from equation 1 (Hydén, 1961):

$$\text{Flow-rate (ml/min)} = \frac{\text{counts infused/min}}{\text{sample counts/ml}}. \tag{1}$$

The retention time of marker in each fifth of the small intestine was calculated from equation 2 (Hydén, 1961):

$$\text{Retention time (min)} = \frac{\text{digesta water (ml)}}{\text{flow-rate of water (ml/min)}}. \tag{2}$$

The apparent quantity of water absorbed from the small intestine per min was calculated by subtracting the lower of the two flow-rates of water in the distal 20% of the small intestine from the flow-rate in the abomasum. This difference was multiplied by 1440 to calculate the quantity of water absorbed/d.

The apparent quantity of water absorbed from the large intestine was calculated by two methods.

(A) The mean daily faecal water output (ml) was subtracted from the lower of the two estimated daily flow-rates of water in the distal 20% of the small intestine.

(B) The weight (g) of water per g dry matter in the rectum was subtracted from the same measurement for digesta in the terminal ileum, and the difference was multiplied by the mean daily quantity of faecal dry matter excreted and by a correction factor (1·25) to allow for an estimated 20% digestion and absorption of dry matter in the large intestine (Hogan & Phillipson, 1960; Goodall & Kay, 1965; Bruce, Goodall, Kay, Phillipson & Vowles, 1966).

Student's t test was used to determine the significance of differences between means.

RESULTS

The percentage dry-matter of abomasal contents (mean ± SE) were 8·1 ± 0·6 and 9·0 ± 0·6 for the sheep given 400 and 1200 g lucerne chaff/d respectively. The increase in the mean percentage dry-matter content of digesta between the first and the last segment of the small intestine (Fig. 1) was significant ($P < 0·001$) in sheep given 1200 g food/d but not in those given 400 g. The difference between the means for the two intake groups was significant in the first segment ($P < 0·01$) but not in the fourth segment (60–80%). The dry-matter content of digesta in the terminal ileum was not influenced by the level of food intake.

The amount of digesta was greater in the distal small intestine than in the proximal segments for each sheep studied (Fig. 2). The mean quantities of digesta in the total small intestines of the sheep given 400 and 1200 g lucerne chaff/d were 388 ± 39 and 645 ± 47 g respectively. The difference was significant ($P < 0·005$).

The mean flow-rates of water through the reticulo-rumen, abomasum, and each segment of the small intestine (Table 1) were all greater ($P < 0·05$) for sheep given 1200 g/d than for those given 400 g/d. The difference in flow-rates of water between the reticulo-rumen and the abomasum, and between the abomasum and the third

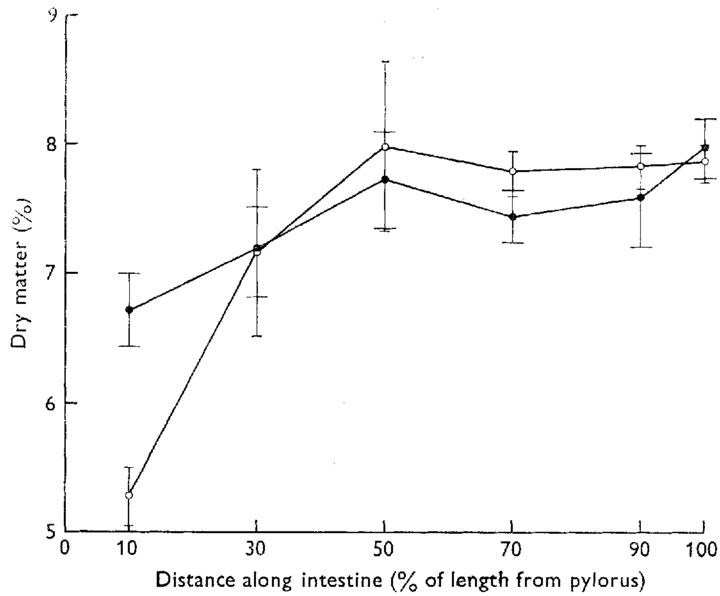

Fig. 1. Dry-matter contents of digesta along the small intestine of sheep: the vertical bars represent the standard errors of the mean. (●), seven sheep given 400 g lucerne chaff/d; (○), six sheep given 1200 g/d.

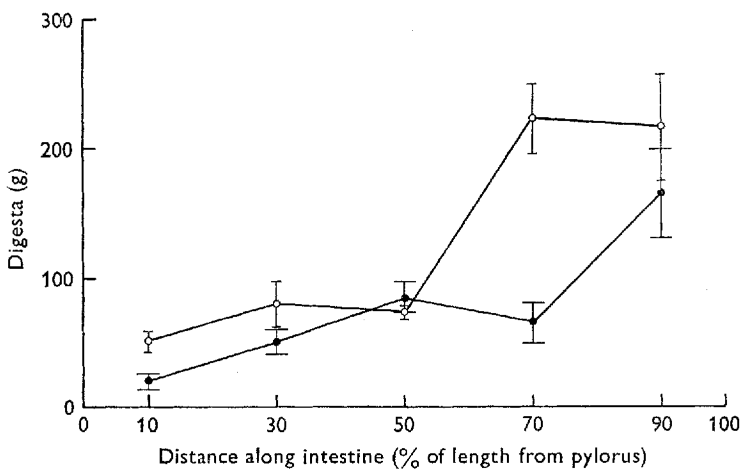

Fig. 2. Weight of digesta in successive 20% segments of the small intestine of sheep: the vertical bars represent the standard errors of the mean. (●), seven sheep given 400 g lucerne chaff/d; (○), six sheep given 1200 g/d.

segment of the small intestine (40–60%), were also larger in the sheep with the higher intake of lucerne chaff. The mean flow-rate of water along the small intestine of sheep given 400 g/d decreased progressively from the duodenum to the terminal ileum. For the 1200 g food intake the flow-rate decreased mainly along the first half of the small intestine. The increased flow-rate of water in the terminal ileum of these sheep was questioned (see p. 19) and not used in any of the calculations in this paper.

Table 1. *Flow-rates of water along the alimentary tract of sheep and the apparent quantities of water absorbed in the small intestine*

(Mean values for five animals in each food intake group)

Measurement	Flow-rate of water								Water absorbed in small intestine (ml/d)
			Intestinal segment (% of small-intestinal length)						
	Rumen	Abomasum	0–20	20–40	40–60	60–80	80–100	100*	
Sheep given 400 g lucerne chaff/d									
ml/min ± SE	4·7 ± 0·2	5·7 ± 0·5	6·0 ± 0·9	4·6 ± 0·6	3·1 ± 0·4	2·6 ± 0·3	2·1 ± 0·3	1·6 ± 0·1	5844 ± 745
ml/d	6725	8165	8640	6538	4421	3816	3038	2336	
Sheep given 1200 g lucerne chaff/d									
ml/min ± SE	8·6 ± 1·5	15·1 ± 1·6	13·6 ± 1·5	9·7 ± 1·8	5·9 ± 0·4	5·7 ± 0·5	6·0 ± 0·8	8·7 ± 1·6	13 110 ± 2194
ml/d	12 341	21 700	19 627	14 011	8568	8150	8594	12 600	

* Samples from the terminal ileum; but for sheep given 400 g/d, $n = 3$.

Table 2. *Apparent water absorption in the large intestine of sheep, calculated by two methods (A and B, see p. 15 for details)*

(Mean values with their standard errors: no. of animals in parentheses)

Method A			Method B*				
			g water/g dry-matter				
Ileal water output (ml/d) (*a*)	Faecal water output (ml/d) (*b*)	Water absorption (ml/d) ($a-b$)	Ileum† (*c*)	Rectum (*d*)	Difference ($c-d$)	Faecal dry-matter output (g/d) (*e*)	Daily water absorption (g/d) $(c-d) \times e \times 1{\cdot}25$‡
Sheep given 400 g lucerne chaff/d							
2336 ± 127 (5)	235 ± 26 (5)	2101 ± 145 (5)	11·8 ± 0·5 (5)	1·8 ± 0·2 (5)	10·1 ± 0·5 (5)	122 ± 4 (5)	1536 ± 99 (5)
Sheep given 1200 g lucerne chaff/d							
8594 ± 1090 (5)	782 ± 47 (4)	8520 ± 1050 (4)	12·2 ± 0·3 (4)	1·8 ± 0·1 (5)	10·6 ± 0·3 (4)	437 ± 2 (4)	5769 ± 143 (4)

* Values obtained by Grovum and Hecker (unpublished).
† Last segment of the small intestine.
‡ 1·25 is a correction factor to allow for an estimated 20 % digestion of dry matter in the large intestine.

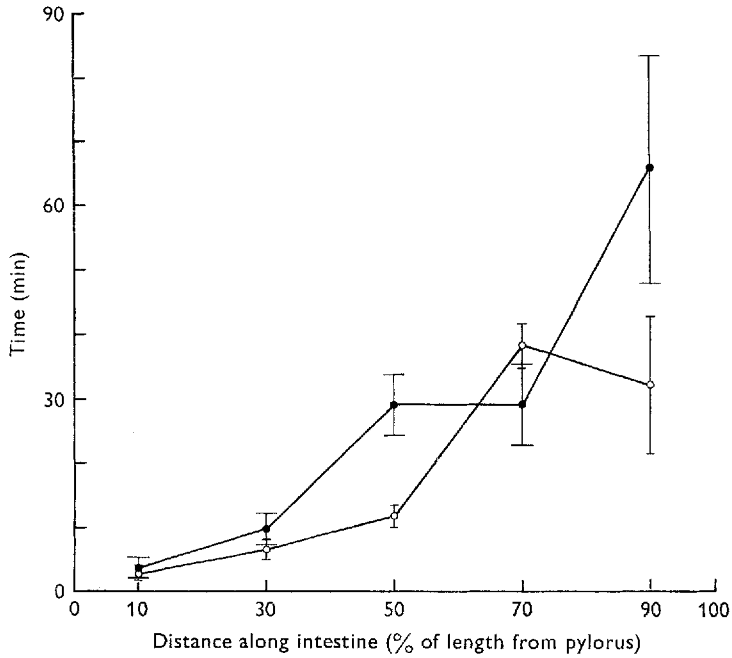

Fig. 3. Retention times of ^{51}Cr EDTA in successive 20 % segments of the small intestine of sheep: the vertical bars represent the standard errors of the mean. (●), five sheep given 400 g lucerne chaff/d; (○), five sheep given 1200 g/d.

The apparent quantities of water absorbed daily from the small intestine (Table 1) were 5844 ± 745 and $13\,110 \pm 2194$ ml for lucerne chaff intakes of 400 and 1200 g/d respectively. The difference between the means was significant ($P < 0.025$).

The apparent quantities of water absorbed from the large intestine (Table 2) were significantly greater ($P < 0.01$) for sheep given 1200 g than those given 400 g. The means for method B were about 70% of those for method A. The level of food intake did not influence the water content of digesta in the rectum.

Marker was retained in the distal small intestine longer than in the proximal small intestine of each sheep. The mean retention times (Fig. 3) with daily intakes of 400 and 1200 g lucerne chaff were about seventeen and ten times larger respectively, in the last 20% of the small intestine than in the first 20% of the length of this organ. The mean total retention times of 136 ± 22 and 91 ± 9 min for daily food intakes of 400 and 1200 g respectively were significantly different using a one-tailed test ($P < 0.05$).

DISCUSSION

In this study it was assumed that the slaughtering procedure did not alter the dry-matter content of the digesta along the gut. However, some epithelium from the small intestine may have been shed into the lumen causing some dilution of the water in the digesta (Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958). The extent of shedding was not measured.

The sheep used in this experiment were allocated to the treatments without regard to sex. Ewes constituted four out of the seven sheep given 400 g lucerne chaff/d and one out of six sheep given 1200 g. We have interpreted the differences in results between treatments as effects of level of food intake rather than of sex.

Warner (1969) found that ^{51}Cr EDTA was occasionally bound to particulate digesta in the reticulo-rumen of some sheep. The calculated increase in the flow-rate of water in the terminal ileum of sheep eating 1200 g lucerne chaff/d was unreasonable because the dry-matter percentage of the digesta did not change (Fig. 1). Binding of ^{51}Cr EDTA to particulate matter in the terminal ileum would create this effect, but no substantiating evidence was obtained in this experiment. Overestimation of the ileal flow-rates of water would decrease rather than increase the gradient of retention times along the small intestine and would account for the discrepancy between the two methods of estimating water absorption from the large intestine (Table 2).

In this study, digesta in the duodenum contained about 6% dry matter and that in the terminal ileum about 8% dry matter, which are within the ranges of 5·2 and 8·1, 4·3 and 6·3, 4·1 and 7·3, and 5·3 and 9·3 reported by Hogan & Phillipson (1960), Badawy & Mackie (1964), Bruce *et al.* (1966) and Cloete (1966) respectively.

The ileal region of the small intestine contained more digesta than the duodenal and jejunal segments; this was also found in sheep by Elsden, Hitchcock, Marshall & Phillipson (1945–6) and Badawy *et al.* (1958). The quantity of digesta in the small intestine was positively related to the level of food intake. No similar observation for ruminants has been found in the literature.

The flow-rates of water through the fore-stomachs and along the small intestine were positively related to the level of food intake. Such increases in the flow-rates of digesta through the duodenum and ileum of sheep have been associated with increases in peristaltic activity (Coombe, 1966). The mean flow-rates of water through the abomasum in sheep eating 400 and 1200 g lucerne chaff/d were 8165 and 21 700 ml/d respectively. These means are high for the food intake. Hogan (1964) obtained digesta flow-rates at the duodenum of 7300 g/d for a sheep eating 800 g of lucerne chaff and 13 300–29 100 g/d for sheep eating 1700 g/d. Hogan & Phillipson (1960) measured duodenal flow-rates of digesta of 8640 g/d with sheep given 300 g meadow hay and 200 g concentrate/d. Phillips & Dyck (1964) obtained an average duodenal flow-rate of water of 11 616 ml/d for sheep eating a ground and pelleted roughage ration that supplied 542 g of organic matter daily. Cloete (1966) found that 6380 g digesta passed the pylorus daily in sheep given 550 g grass cubes. The hourly feeding technique used in this experiment may have been responsible for the high values, since Harrison & Hill (1962) showed that the flow-rate of water past the pylorus was about doubled when sheep were fed three times daily instead of once.

The mean flow-rates of water in the terminal ileum of sheep given 400 and 1200 g lucerne chaff/d were 2336 and 8594 ml/d respectively. These values are larger, relative to the food consumed than flow-rates reported previously, which range from 1490 to 4870 g/d for daily food intakes of 500–900 g (Hogan & Phillipson, 1960; Badawy & Mackie, 1964; Goodall & Kay, 1965; Bruce *et al.* 1966; Cloete, 1966).

The apparent quantities of water absorbed/d from the small and large intestines

(Tables 1 and 2) do not account for the volumes of secretions subsequently absorbed. The volumes secreted would have been substantial for the former, but probably negligible for the latter. Also, the small intestinal secretions would have been greater in the sheep given the high intake than in those given the low intake.

The apparent volumes of water absorbed from the small intestine were larger than the range of 3300 to 5700 ml for sheep calculated from the experiments of Hogan & Phillipson (1960), Badawy & Mackie (1964), Bruce *et al.* (1966) and Cloete (1966). The significant increase in water absorption in the small intestine with increased intake was accompanied by a significant decrease in the retention time of ^{51}Cr EDTA, therefore the absorption process must have been more rapid. Water absorption must also have been more rapid in the proximal half of the small intestine than in the distal half because more water was absorbed in the proximal part even though the retention time of ^{51}Cr EDTA was relatively small. The results of Hydén (1961) also showed that the proximal small intestine of sheep absorbed more water than the distal parts.

The relatively large retention time of marker in the ileum compared with that in the duodenum and jejunum (Fig. 3) must be considered in assessing potentials for digestion and absorption in different parts of the small intestine of the sheep. Reynell & Spray (1956), Cramer & Copp (1959), Marcus & Lengemann (1962) and Sikov, Thomas & Mahlum (1969) have shown that markers move faster through the proximal small intestine than through the distal small intestine in the rat. The results of Cramer (1959) for fed rats also support this conclusion. However, Dillard, Eastman & Fordtran (1965), working with humans, reported that fluid pumped at a constant rate moved more slowly through the jejunum than through the ileum. This indicates that the gradient of marker retention times along the human small intestine may be different from those in sheep and rats.

The mean small-intestinal retention times of 136 and 91 min are within the range of 1–2 h, and 3 h obtained for sheep by Hydén (1961) and Coombe & Kay (1965) respectively. These retention times were smaller for larger food intakes in the work of Coombe & Kay (1965) but, unlike our findings, the effects were not significant. Information on the rate of passage of digesta is useful in nutritional studies because the net quantities of magnesium absorbed from the small intestine of the calf were positively related to corresponding transit times of marker (Smith, 1963). Also, Barreiro, McKenna & Beck (1968) have reported a significant positive correlation between the extent of xylose absorption and the transit time of marker in the human jejunum.

Dillard *et al.* (1965) showed that flow-rates of fluid up to 7 ml/min in the human jejunum and ileum were accommodated by increased lumen diameter, but that flow-rates faster than 7 ml/min caused the transit time of marker to decrease. In our study the faster flow-rates of fluid were apparently accommodated more by an increase in the mean diameter of the small intestine than by a decrease in retention time. The effect of still higher flow-rates on the volumes of digesta and its retention time in sheep is unknown.

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