J. Physiol. (1961), **155**, *pp.* 134–147
With 9 text-figures
Printed in Great Britain

THE ELECTROMAGNETIC MEASUREMENT OF THE FLOW OF DIGESTA THROUGH THE DUODENUM OF THE GOAT AND THE SHEEP

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(*Received* 17 *August* 1960)

The quantitative aspects of digestion are of particular importance in ruminants, in which food is subjected to microbial fermentation in the reticulo-rumenal sac before being exposed to gastric and intestinal digestion lower down the alimentary tract. An assessment of the nutritional importance of microbial activity, which includes both break-down and synthesis of food material, requires as a basic measurement the quantity of material leaving the stomach over a suitable period of time.

Phillipson (1952) measured directly the volume of digesta leaving a duodenal cannula. In some of his experiments the duodenum was blocked by an inflated balloon, which reduced the amount of flow; in others, the material flowing out was not returned to the duodenum, and this increased the amount of flow. He suggested that the values obtained by these two methods represented the lower and upper limits, respectively, of the range of true values, which would probably be between 350 and 800 ml./hr.

More recently Hogan & Phillipson (1960) have published the results of experiments performed on sheep with re-entrant duodenal fistulae. Flow through the duodenum was measured by collecting material from the cannula nearest to the stomach and then returning it to the duodenum at short intervals. By this method a mean flow rate of 360 ml./hr was obtained.

In the experiments to be described the flow of digesta through the duodenum has been recorded and measured by a method which avoids the removal of material from the duodenum, or the application of any stimulus known to affect the rate of emptying of the stomach. It is based on the method of recording blood flow in unopened vessels described by Wetterer (1938) and Katz & Kolin (1938) and more recently by Richards & Williams (1953), which uses the principle of electromagnetic induction.

METHODS

Animals. Seven cross-bred goats and four Clun Forest cross-bred sheep were used. They were brought from pasture to the animal house and accustomed to indoor feeding for 2–3 weeks before operation. They were fed twice daily, at 9.0 a.m. and 4.30 p.m., the goats receiving good quality hay and concentrates. The sheep received hay only, because concentrates tended to produce blockage of the cannulae. The animals were kept in stands which were designed both to limit movement and thereby prevent damage to the cannulae and to make possible the measurement of food intake and faeces output.

Operative procedure. Anaesthesia was induced by pentobaribitone sodium I.V. and was then maintained by cyclopropane and oxygen in closed circuit after tracheal intubation. The duodenum was exposed and, after ligation of the mesenteric vessels, transected about 2 in. (5 cm) beyond the pylorus. A Perspex cannula of $\frac{3}{4}$ in. (9 mm) internal diameter and about 2 in. in length was fixed in each open end. The cannulae were brought out through stab wounds in the abdominal wall, and joined by polythene tubing and Perspex right-angle bends. It was found that by inserting the cannulae in the open ends of the duodenum larger cannulae could be employed than if the ends of the duodenum were closed and the anti-mesenteric border cannulated. A successful preparation remains useful for 3–6 months, occasionally longer. After recovery from the operation, food intake and faeces output return to the pre-operative levels, and the animal maintains or gains body weight.

Apparatus. The principle of the recording method is stated by Richards & Williams (1953) as follows: 'When a conductor of length l cm moves with a velocity of v cm/sec through a magnetic field of H gauss, an e.m.f. is induced such that $e = Hvl\ 10^{-8}$'. In this application, duodenal contents are the moving conductor, and if they flow through a rigid tube of uniform cross-sectional area the diameter of that tube is equivalent to the length of the conductor. The velocity will be directly proportional to the volume flow in unit time. If the voltage change is recorded on moving paper and if the over-all calibration curve is linear, then the areas between the voltage curve and base line will be proportional to the volume of duodenal contents flowing through the tube in unit time.

The electro-magnetic flowmeter consists of the electrode-holding block, non-polarizable electrodes, a large permanent magnet and electrical recording equipment. The electrode holder is formed from a block of Perspex, shaped so that it can be fitted between the pole-pieces of the magnet and locked in position by a Perspex nut on a brass screw. It includes a central tube through which the duodenal contents pass, and smaller holes which are a close fit for the electrodes and which communicate with the central tube in the correct plane by narrow drilled channels which are filled with agar-saline jelly. It is important that no movement of the electrodes relative to the magnet should be allowed (Fig. 1). The electrodes are miniature calomel half-cells similar to those described by Richards & Williams (1953).

The permament magnet is made of Alcomax III (Messrs Jessop Sheffield) and has mild-steel pole pieces separated by a $\frac{1}{2}$ in. (12 mm) gap, the field strength across which is 10,000 gauss. It rests on a wooden platform suspended from a stand by ropes passing over pulleys and is counter-balanced by lead weights so as to allow adjustment in height for different sizes of animal.

The recording apparatus consists of a push-pull DC pre-amplifier and oscilloscope with moving film camera.

Experimental. Recordings are made with the animal standing, lightly restrained between two Pavlov stands which prevent lateral movements. The duodenal cannulae are connected to each end of the central tube of the electrode holder by an 8 in. (20 cm) length of polythene tubing, the flexibility of which allows some movement of the animal without movement of the magnet (Fig. 2). The animals are well accustomed to handling before operation and quickly become used to the laboratory, so that continuous recordings can be made for periods of up to 3 hr.

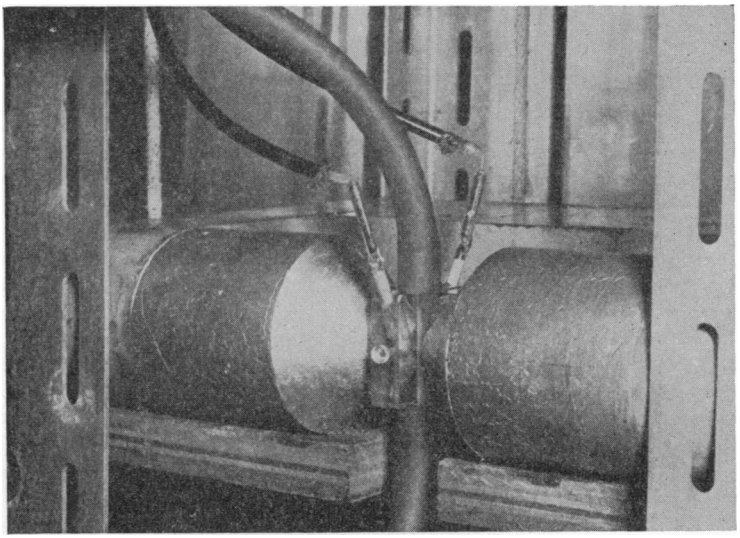

Fig. 1. The permanent magnet on its counter-balanced wooden platform. The electrodes in the Perspex block are rigidly fixed between the pole pieces, and the polythene tubing connects with the central tube of the electrode holder.

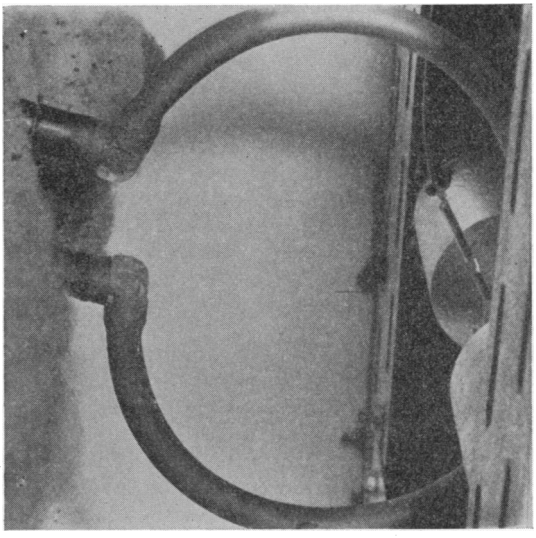

Fig. 2. The flexible connexion between the duodenal cannulae and the electrode holder, which allows some movement by the animal.

The areas between velocity tracing and base line are measured by planimeter, and the relationship between area and volume is established by direct calibration, which has been done by two methods. In the first, measured volumes of sodium chloride solution or duodenal contents are allowed to pass through the Perspex tube of the electrode holder; in the second, digesta from the lower duodenal cannula are allowed to pass through the flowmeter for short periods, but instead of returning them to the upper cannula they are collected and measured.

By the first method calibration is precise. The curves obtained are regular, and the areas easy to measure by planimeter. The second method produces a tracing similar to those obtained during actual experiments, except that antiperistaltic flow is prevented. The areas to be measured are smaller and less regular and include some caused by oscillation of the column of fluid due to movements of the animal, so that the error involved in planimeter measurement is greater.

RESULTS

Calibration

The passage through the flowmeter of measured quantities of sodium chloride solutions or abomasal contents produces results similar to those described by Richards & Williams (1953) in that, when area is plotted against volume, there is a straight-line relationship, the line passing through the origin. The results of calibration with NaCl solution 0·9 g/100 ml. and duodenal contents are shown in Fig. 3, the line being a regression of area on volume. A comparison of means of the areas obtained with saline and duodenal contents shows no significant difference between the two ($P > 0{\cdot}4$). The results of calibration on the animal are shown in Table 1. By this method all experimental error of measurement is included.

Pattern of flow through the duodenum

The tracings (Figs. 4 and 5) confirm Phillipson's observation (1952) that flow occurs mainly in gushes, separated by intervals of different lengths, but also show that flow occurs in both directions, a flow of material from the stomach being usually, but not invariably, followed by a smaller return flow, represented by the area below the base line. Small spurts of retrograde flow also occur independently of the main aboral gushes (Fig. 5).

The tracings are primarily a record of velocity change. In any one animal differences occur in the form of individual flows, the rates of acceleration and deceleration and the peak velocity and duration, producing a considerable range of variation in the volume ejected at each gush. The highest peak velocities observed in goats have been of the order of 18 cm/sec but more usually lie within the range 7–11 cm/sec. In sheep the velocities tend to be lower, within the range 4–9 cm/sec, but occasionally as high at 12 cm/sec.

As well as this variation in the volume of individual flows, there is also variation in frequency, and in the size and incidence of the return flows.

The amount of to-and-fro movement is much greater in goats than in sheep, as can be seen from the tracings in Figs. 4 and 5, and from the histograms (Figs. 7 and 8). Feeding has no regular effect on the pattern of flow in animals fed by the normal routine. If an animal is deprived of food for 24 hr the flow is very much reduced and a subsequent feed is immediately followed by an increased rate of flow. Although rumination can occur without any obvious regularity of the duodenal flow it is often accompanied by a flow pattern in which the gushes occur in groups of two to six, separated by short intervals (Fig. 6).

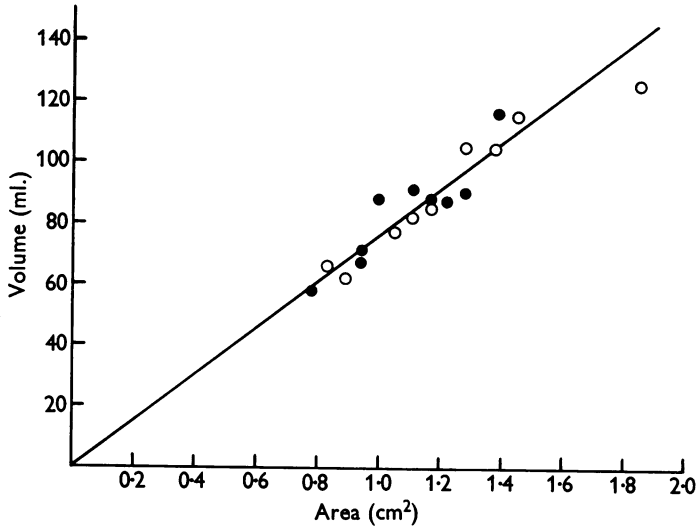

Fig. 3. Calibration of the flowmeter by passing measured quantities of saline (○) and duodenal contents (●) through it. The line is a regression of volume on area.

TABLE 1. Calibration on the animal

Animal no.	Duration of expt. (min)	Volume collected (ml.)	Area measured (cm^2)	Vol./cm^2
31	10	130	1·183	110
31	14	100	0·833	120
31	10	245	2·150	114
31	9	270	2·266	119
31	12	325	2·75	118
61	7	100	0·866	115
52	10	425	3·600	118

Mean vol./cm^2 = 116·3 ± S.E. 1·32.

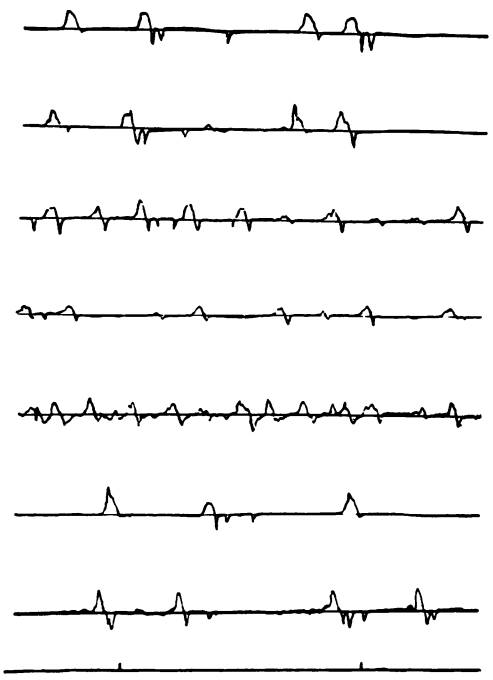

Fig. 4. Examples of flow records from goats, illustrating the variation which occurs. The areas above the base line represent aboral flow, those below retrograde flow. Time marker, minutes.

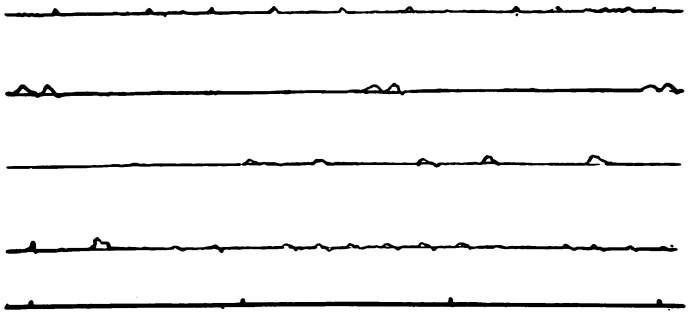

Fig. 5. Representative tracings from sheep. The aboral flows tend to be smaller than in goats, and the quantity of retrograde flow much less. Time marker, minutes.

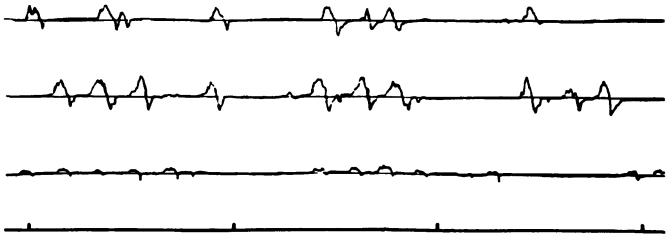

Fig. 6. Examples of a flow pattern often seen during rumination, in which gushes occur in groups separated by intervals. Time marker, minutes.

The quantity of material leaving the stomach

The first experiments, performed on five goats, consisted of relatively short periods of recording, lasting up to 80 min and all between the hours of 9.0 a.m. and 10.0 p.m. The results are summarized in Table 2 and show the extent of variation in rates of flow. The histograms in Fig. 7 show the short-term variation which occurs between successive 5-min periods. It is apparent from these results that the volumes of aboral and retrograde flow can vary independently, and that the volume of retrograde flow has a considerable influence on the net volume of material leaving the stomach. Over such short periods there is occasionally more retrograde than aboral flow, as shown by the white areas below the base line. Intervals of up to 15 min during which there is no flow in either direction occur quite commonly.

TABLE 2. Results of short experiments on five goats expressed as flow

No. of expts.	Goat no.	Wt. (kg)	Mean aboral flow (ml./hr)	Mean retrograde flow (ml./hr)	Mean net aboral flow (ml./hr)	Range	S.D.	Coef. of variation
6	13	35	868	475	392	117–684	116	42
23	31	41	2037	1143	893	174–1925	511	57
8	21	33	863	279	584	191–858	255	44
22	41	34	2839	1520	1319	282–2025	483	37
7	23	25	1251	419	803	307–1180	343	43

Similar periods from short-term experiments on a sheep are shown in Fig. 8. The same kind of variation occurs, but the proportion of retrograde to aboral flow is always smaller and the net rate of flow through the duodenum is always less than in goats. This can be explained in part by the higher dry-matter content of the duodenal contents in sheep (5–6 %) compared with goats (3–4 %). Furthermore, as the sheep were receiving no concentrates this might well have reduced the volumes of saliva and gastric secretion.

The volume flowing in 24 hr

The practical limit for a period of continuous recording is about 3 hr. After this length of time some animals became restless and, as they must remain standing during the whole recording period, it was considered that longer periods would interfere unduly with their normal habits. The amount of variation in the volumes flowing over short periods (about 1 hr) is too great for a mean value to be representative of all hours of the day, and an estimate of the total flow in 24 hr obtained from it would not take into account any longer-term variations or diurnal rhythms which might occur. If the volume of flow over any particular period of the day is similar from day to day, a better estimate might be obtained by recording each

3-hr period of the day on a different day and covering each of the 24 hr in as short a period as practicable. An examination of the results of the short experiments on goats indicated that the hourly flow rates for the morning were of the same order, and different from those in the afternoon (Table 3). These experiments were not planned to show this point, and begin and end at different times of day, but they do suggest a certain degree of consistency at about the same time of each day. It might be expected that longer recording periods such as 3 hr beginning and ending at the same time each

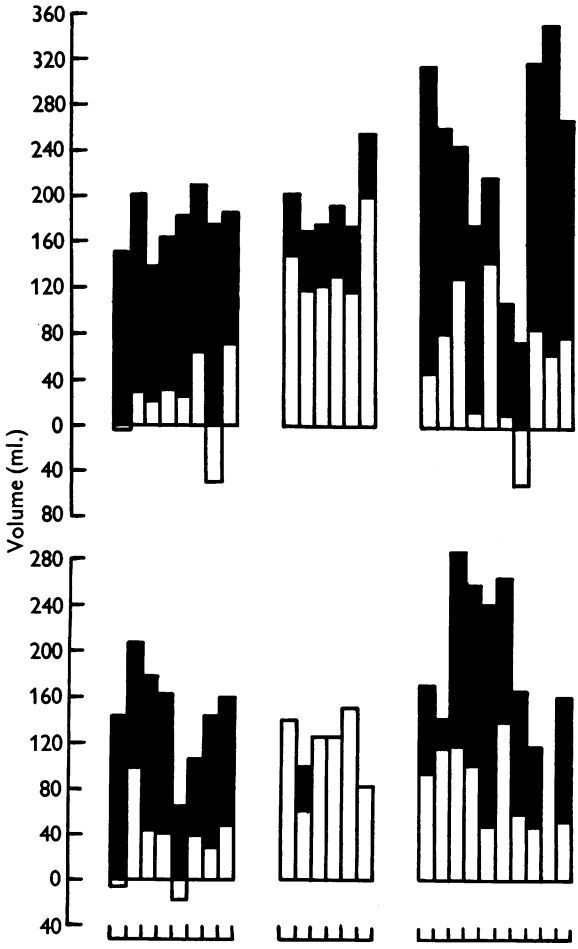

Fig. 7. Quantities of duodenal contents flowing backwards and forwards in successive 5-min periods in six experiments on the same goat. The total height of each block represents the quantity leaving the stomach and the black area denotes the proportion returned as retrograde flow. The white areas thus represent net aboral flow: occasionally, over these short periods, this quantity is negative.

day would show less variation, and this is confirmed by the experiments on sheep 929 (Table 5).

Six 24-hr estimates were made on this basis, two on one goat, and one each on another goat and on three sheep. The results are summarized in the histograms (Fig. 9) and in Table 4. From the histograms it can be seen that the goats show a regular tendency to a period of reduced flow in the

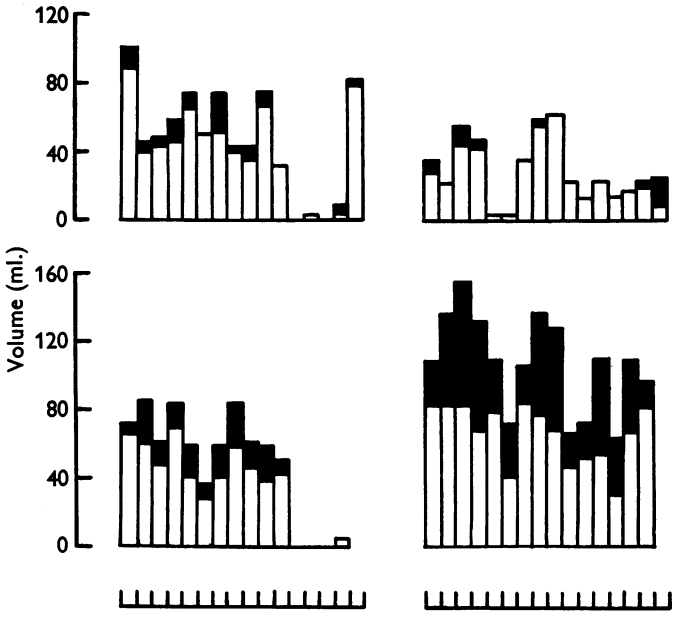

Fig. 8. Quantities of duodenal contents flowing in successive 5-min periods in four experiments on one sheep. The black areas show retrograde flow, the white areas the net amounts leaving the stomach.

TABLE 3. Comparison of flow rates between morning and afternoon experiments on goat 31

Experiments between 9.0 a.m. and 2.0 p.m.		Experiments between 2.0 and 5.0 p.m.	
Time of commencement	Net aboral flow (ml./hr)	Time of commencement	Net aboral flow (ml./hr)
9.35	208	2.20	988
11.30	348	2.25	720
11.40	780	2.25	950
11.50	568	2.25	914
11.50	711	2.25	1100
1.0	270	2.45	1209
1.0	174	2.50	804
1·0	499	2.55	1146
Mean	444	Mean	879
S.D.	230	S.D.	215

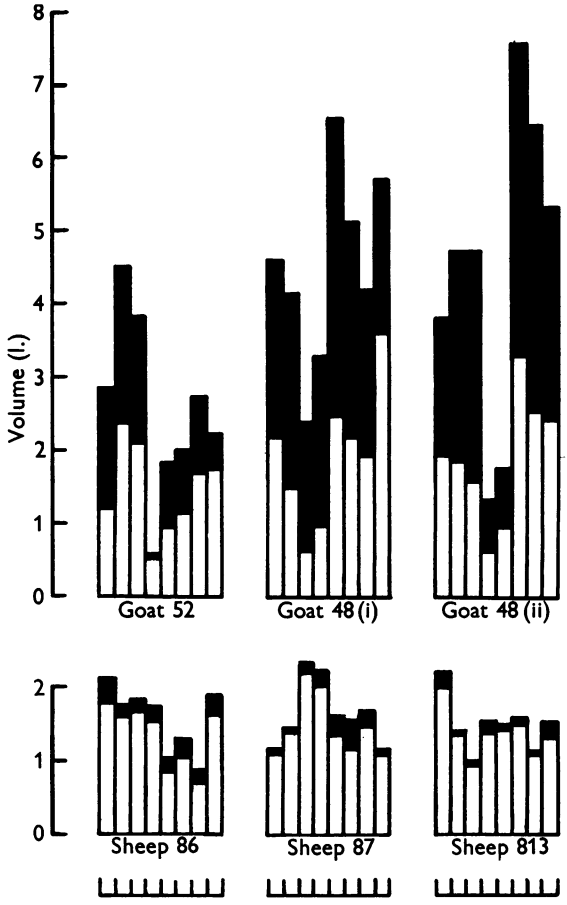

Fig. 9. Histograms showing the pattern of flow over a composite 24 hr, in eight 3-hr periods, beginning with 10.30 p.m.–1.30 a.m. recorded on different days. Above are three results from two goats all showing a period of reduced flow in the early morning. Below are the results from three sheep which show no consistent pattern. Retrograde flow is black, net aboral flow white.

TABLE 4. The volume of duodenal flow in 24 hr obtained by adding eight 3-hr periods covering every hour of the day

Animal	Body wt. (kg)	Food intake: Hay (g)	Food intake: Concentrates (g)	Aboral flow (ml./24 hr)	Retrograde flow (ml./24 hr)	Net aboral flow (ml./24 hr)	Mean hourly flow (ml.)
Goat 52	33	581	267	21,024	8,661	12,363	515
Goat 48 (i)	33	900	400	37,506	21,439	16,067	669
Goat 48 (ii)	34	780	400	36,314	20,878	15,436	643
Sheep 86	60	596	—	12,644	1,505	11,139	464
Sheep 87	68	781	—	13,140	1,304	11,836	493
Sheep 813	62	627	—	11,991	755	11,236	468

early morning which might be related to the unequal interval between feeds, although the sheep on a similar feeding routine show no regular pattern.

The large amount of retrograde flow shown by goat 48 in both experiments is in part due to an artifact caused by the use of a different preamplifier which had an unbalanced input. This produced spurious potentials due to movements of the animal but as they were randomly positive and negative they make little difference to the value for net aboral flow.

TABLE 5. Replicate recordings on sheep 929 over the period 10 a.m.–1.0 p.m.

Aboral flow (ml.)	Retrograde flow (ml.)	Net aboral flow (ml.)
1358	172	1188
1631	294	1337
1369	160	1209
1800	201	1599
2067	662	1405

Mean net aboral flow 1162 ml. ± S.D. 144, coefficient of variation 12·4 %.

TABLE 6. Total quantities of dry matter and crude fibre digested, calculated from food and faeces analysis, and proportion digested in the reticulo-rumen, calculated from duodenal flow measurement and analysis of duodenal contents

Animal	Total dry matter digested (g)	Dry matter apparently disappearing in the stomachs (g)	Total crude fibre digested (g)	Crude fibre apparently digested in the stomach (g)
Goat 52	425	239 (56 %)	100	101 (101 %)
Goat 48 (i)	702	444 (63 %)	154	146 (95 %)
Goat 48 (ii)	679	369 (54 %)	164	138 (83 %)
Sheep 86	376	−80 (−21 %)	96	48 (48 %)
Sheep 87	447	92 (21 %)	98	77 (79 %)
Sheep 813	341	140 (41 %)	155	129 (83 %)

DISCUSSION

The results of the calibration experiments indicate that the electromagnetic method of flow measurement is extremely accurate and that when the calibrations are performed on the animal, so that all possible error of measurement is included, the total error is negligible. Accepting that the measurements themselves are accurate, other objections can be raised as to the validity of the results. Transection and cannulation of the duodenum might affect the mechanisms which control the emptying of the stomach. In particular, the backward and forward movement of digesta in the duodenum might be a feature of this preparation, and may not occur in the intact animal. It is well known, however, that backward and forward movements have been observed radiologically in the duodenum of man, and there is no reason to doubt their occurrence in animals. The

return of food intake and faeces output to pre-operative levels after the animals had recovered from the surgical interference, and the maintenance of body weight, suggest either that the animals were not unduly affected or that they were rapidly adjusted to the condition. In addition, long periods occurred, particularly in the sheep, when the retrograde flow was almost negligible and the independent variation of retrograde flow might mean that it is part of the mechanism which controls the rate of stomach emptying. The to-and-fro movement may also be significant with regard to the point of entry of pancreatic secretion and bile, which is about a foot beyond the pylorus, in that these secretions would be carried forward and so would affect the pH in the first part of the duodenum. The results obtained from sheep are too few to justify the conclusion that as a species they differ from goats. The smaller amount of backward and forward movement could well be due to the difference in diet.

The methods of measurement used by Phillipson (1952) and by Hogan & Phillipson (1960) would prevent the occurrence of retrograde flow, and so might alter the values obtained. Expressing retrograde flow as a percentage of total aboral flow occurring over periods of at least an hour and ignoring the results obtained on goat 48 where artifacts occurred, a mean value of 40 % with a range of 2–56 %, is obtained for retrograde flow in goats, while for the sheep the mean is 5 %, with a range of 0–17 %.

The total quantity of material leaving the stomach in 24 hr will depend not only on the size of the animal and on its food and water intake, but also on the amount of digestion and absorption occurring in the reticulo-rumen and the volumes of salivary and gastric secretions, which in turn will be influenced by the composition of the food. An ideal method of measurement would be applicable to the animal without producing any disturbance of its normal behaviour, so that recordings could be made over several successive days without the animal being moved from its usual accommodation.

The method described here, by which the daily output is estimated by adding together the quantities recorded in 3-hr periods, assumes that (1) flow during a given 3-hr period does not vary significantly from day to day and (2) the volume of flow measured in the laboratory is representative of what would occur if the animal had not been disturbed. The first assumption was tested by performing replicate recordings of the flow over the same 3-hr period of successive days. The results are shown in Table 5. If we assume that all periods would have a similar coefficient of variation, and that each period is independent of the others, an estimate of the error from this source can be made for each experiment thus

$$\text{S.E. (24 hr)} = C\sqrt{(\Sigma_1^8 x^2)},$$

where C = coefficient of variation, x = volume flowing in 3-hr period. Calculated in this way the S.E. of the six 24-hr experiments lie between $\pm 4{\cdot}5$ and $\pm 4{\cdot}8\,\%$ of the totals.

Alternatively, if we assume that all 3-hr periods would have a similar standard deviation rather than C, the S.E. of the total would be

$$\sqrt{n_\rho}(\text{S.D.}/\sqrt{n_r}),$$

where n_ρ = number of periods added together, n_r = number of replicates. By this method, the S.E. would be ± 211 ml., which is less than 2 % of the 24-hr flow values.

The second assumption, that flow recorded in the laboratory is not different from what would occur if the animal were undisturbed, cannot be tested directly, but an assessment of the total error can be made by comparing the quantities of dry matter and crude fibre apparently digested in the stomachs with the results of other workers obtained by different methods. The values of Table 6 have been calculated from results of chemical analyses of food, duodenal contents and faeces which are to be presented in another paper.

Hogan & Phillipson (1960), using a similar preparation, measured duodenal flow directly in sheep by collecting material from the lower cannula, measuring its volume and reintroducing it into the upper cannula at short intervals. They found a mean flow rate of 360 ml./hr through the duodenum. On the basis of this measurement they report that 70 % of the digested dry matter was digested in the stomach. The sheep were fed on a diet similar to that of the goats in the present experiments, which show an apparent disappearance of only 54–63 % of the dry matter in the stomachs. This lower value could be accounted for by the 24-hr flow estimates being too high, but the proportions of the crude fibre digested which disappear between mouth and pylorus suggest that they are, if anything, slightly low.

Gray (1947), using a lignin-ratio technique, reported that 70 % of the cellulose digested in sheep was digested in the rumen, and Hale, Duncan & Huffman (1940) by a similar method found a corresponding value of 85 % in cows. It is surprising that Hogan & Phillipson should obtain a relatively low value for duodenal flow, as their method of measurement would prevent retrograde flow and they removed 10 % of each sample before returning it to the duodenum, which would tend to increase the rate of stomach emptying.

The sheep in the present experiments were fed on hay only, so that in the absence of readily fermentable concentrate it is to be expected that less of the digestible dry matter would disappear in the reticulo-rumen. The result for sheep 86 appears to be a considerable over-estimate of duodenal flow, as more dry matter appears at the duodenum than was eaten. This in

itself is not impossible, since the dry matter of duodenal contents contains 14–25 % ash (Masson & Phillipson, 1952) compared with 5–7 % in that of hay, and other constituents of saliva and gastric juice may be present. By comparison with the rumenal digestion of crude fibre in the other two sheep it would appear to be an over-estimate of about 27 %. This sheep had a particularly nervous temperament, and it may well be that duodenal flow was greater in the laboratory than when the animal was undisturbed.

SUMMARY

1. An electromagnetic method of recording the flow of digesta through the duodenum of small ruminants is described.

2. The flow pattern shows peristaltic-antiperistaltic movement; in goats about 40 % of the material leaving the stomach is returned to it and in sheep about 5 %.

3. In periods of up to 1½ hr of recording during the day the mean net aboral duodenal flow ranged from 400 to 1300 ml./hr for different goats.

4. Estimates of the total flow through the duodenum per day were made in six separate experiments carried out on two goats and three sheep. Goats on a diet of hay and concentrates had a duodenal flow rate of 12–15 l./day, and sheep on a diet of hay 11 l./day.

5. The errors involved in these estimations are discussed.

I wish to thank Drs T. G. Richards and T. D. Williams for helpful advice on apparatus, Messrs J. McCarthy and J. Stowell for technical assistance, and Mrs A. P. Ridges who assisted with part of the 24 hr recording. Special thanks are due to Professor E. G. White for his continued interest in these experiments, and for the provision of accommodation in the Department of Veterinary Preventive Medicine. The work was supported by a grant from the Agricultural Research Council.

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