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THE PASSAGE OF DIGESTA FROM THE ABOMASUM OF SHEEP

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It is frequently stated that the passage of food through the stomach of the ruminant is a continuous process and this conception is based on the fact that normally food is always found in all parts of the stomach after slaughter, even after a 24 hr. fast. Studies on the rate of disappearance of stained particles from the rumen and their appearance in the faeces can be explained on this assumption while the well-known continuous cycle of contraction of the stomach pouches suggests continual mixing and propulsion of food. There is no information, however, on the quantities of food passing from the stomach—whether it stops completely at intervals through the day and night—or on the manner in which the rate of passage is influenced by feeding or rumination. The experiments to be described were undertaken in an attempt to assess the quantity of food leaving the stomach of sheep maintained on constant rations and to study the flow of food residues to the intestines.

METHOD

The flow of food from the abomasum was measured directly by diverting the flow outside the body through a cannula.

Permanent exteriorization of the flow was achieved in one sheep. This method was based on a technique described by Markowitz (1949) for the exteriorization of the flow of digesta along the small intestine of the dog. The duodenum was sectioned approximately 1½ in. below the pylorus and the two cut ends were closed by continuous sutures involving the mucosa and submucosal tissues. The closed ends were then inverted and buried by a further continuous suture. An ebonite cannula was inserted into the pyloric part of the abomasum and another into the duodenum. These were exteriorized through stab wounds in the abdominal wall, on either side of the operation wound, so that each cannula was an equal distance from the vertebral column of the sheep. The operation wound was then closed and the two cannulae joined by a glass tube bent at each end to fit the shafts of the two cannulae to which it was joined by rubber tubing.

One sheep in which the flow of food from the abomasum to the duodenum was permanently exteriorized was maintained in good condition for 3 weeks after the operation. After this time its

* This research was started in the Agricultural Research Council's Unit of Animal Physiology, Cambridge.

appetite deteriorated and the experiment was terminated. Subsequent attempts to exteriorize the flow in this way failed and other means of achieving this end were sought.

The first modification was to insert the cannulae into the pyloric part of the abomasum and into the duodenum without dividing the duodenum. No difficulty was encountered in collecting food from the abomasal cannula but the pylorus proved to be an ineffective barrier in preventing back-flow of food from the duodenum to the abomasum, so that food once collected could not be reintroduced into the duodenum without some reappearing from the abomasal cannula.

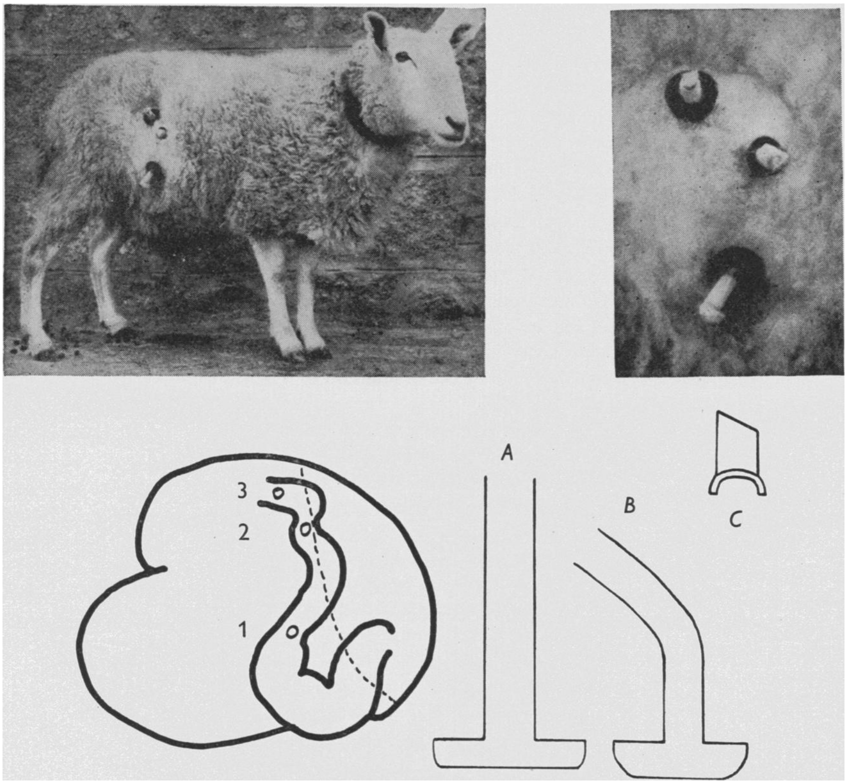

Fig. 1. A sheep fitted with three cannulae into the duodenum is shown above. An enlargement of the cannulae *in situ* is also shown. This animal, sheep no. 2, has lived normally for 2 years after the operations. A diagram of the stomach and duodenum is shown and the sites of cannulae *1*, *2*, and *3* are marked. The dotted line represents the line of the last rib and the costo-chondral arch. The drawings of the cannulae are one-half the size of those used. Straight cannulae (*A*) are inserted in positions *2* and *3*; the curved cannula (*B*) is inserted in position *1*. Diagram *C* shows the curvatures of the inner collar of each cannula.

The final method (Phillipson, 1948) is illustrated in Fig. 1. A curved cannula was inserted into the duodenum immediately caudal to the pylorus (*1*). Two more cannulae (*2* and *3*) were inserted into the lower part of the duodenum beyond the common opening of the bile and pancreatic ducts 7–10 days later. These operations did not affect the well-being of the sheep, which, with one exception, maintained their usual appetite and lived a normal life. A pyogenic infection was the cause of the one sheep's failure to make a satisfactory recovery.

Three factors had an important influence on the results of these operations. The first was the design of the cannulae. In the early operations ebonite cannulae were used in which a threaded joint united the shaft with the internal collar; this joint did not prove strong enough to prevent breakages. Subsequently Perspex cannulae were used with welded joints and these were satisfactory. The second was that the abdominal wall of the sheep is thin in the lower parts of the abdomen and in some animals a hernia-like swelling appeared at the site of the lower incision. This was not due to rupture of the abdominal muscles but rather to loss of tone of the muscle layers where they had united. The third was that after a cannula had been present in the duodenum for some months the internal collar sometimes formed a diverticulum in the wall of the duodenum, and the mucosa gradually grew over it so that free access to the lumen of the gut was hindered and ultimately lost. This occurred only when the cannula was inserted into the first part of the duodenum. Occasionally the cannulae became blocked by solid food which had dried up, or by hard mineral deposits. These could be removed mechanically.

Some of the animals used in these experiments were fitted with a cannula in the rumen. Sheep prepared in this way have been used for measurements of flow over short periods of 1½ hr. and also for long experiments lasting 10–12 hr. All three cannulae were opened during short-term collections and any material that flowed from them was collected, measured and sampled. In the large majority of instances all food flowed from cannula *1*, shown in Fig. 1. Small quantities of bile, pancreatic and duodenal juices flowed from cannula *2* and nothing from cannula *3*. If any food passed cannula *1* it appeared from cannula *2* and indicated obstruction in cannula *1*. This could be rectified by clearing cannula *1* but in one sheep food always appeared at cannulae *1* and *2*. The procedure during long-term collections consisted of inserting a small balloon into cannula *2* and inflating it sufficiently to close the lumen of the duodenum in a similar manner to that described by MacDonald (1948). Food was collected from cannula *1*, and after measuring and removing a sample it was reheated to body temperature and reinserted slowly into the duodenum through cannula *3* after it had been stained by adding small quantities of Evans Blue. This was done so that if any succeeded in passing the balloon in an oral direction it would be noticed and avoided if it reappeared at cannula *1*. This was an important precaution, for the balloon was not easily adjusted so that it closed the lumen of the intestine.

Movements of the rumen and reticulum were recorded by balloons attached to rubber tubing which were passed into these organs through a rumen cannula. The balloon was lightly inflated and the tubing attached to water manometers as previously described (Phillipson, 1939). Records of the volume of food passed from the abomasum to the duodenum were recorded by means of a large float volume recorder.

RESULTS

Permanent exteriorization of the duodenal flow

These measurements were made on the 14th, 15th and 22nd days after the operation. The experimental sheep consumed its food satisfactorily until 3 weeks had elapsed, but after this time the amount of food eaten decreased and this is shown in the measurements recorded. The tube connecting the two cannulae was kept under close observation between the dates of the operation and the measurements and when necessary it was removed and cleaned. Blockage occurred when the food contained cereal offals and for this reason hay alone was fed.

The animal, which was accustomed to being handled, was placed in a cage; the connecting tube was removed and the tubing was fixed to each cannula. The tubing from the abomasal cannula led to a measuring cylinder while a funnel was attached to the tube leading to the duodenum so that material collected from the abomasum could be reintroduced gently into the duodenum.

TABLE 1. Volume of food passed from the abomasum

Experiment	Duration of experiment (hr.)	Total quantity collected (ml.)	Average volume passed per hr. (ml.)
1	7	2720	389
2	8	3525	441
3	5	1075	215

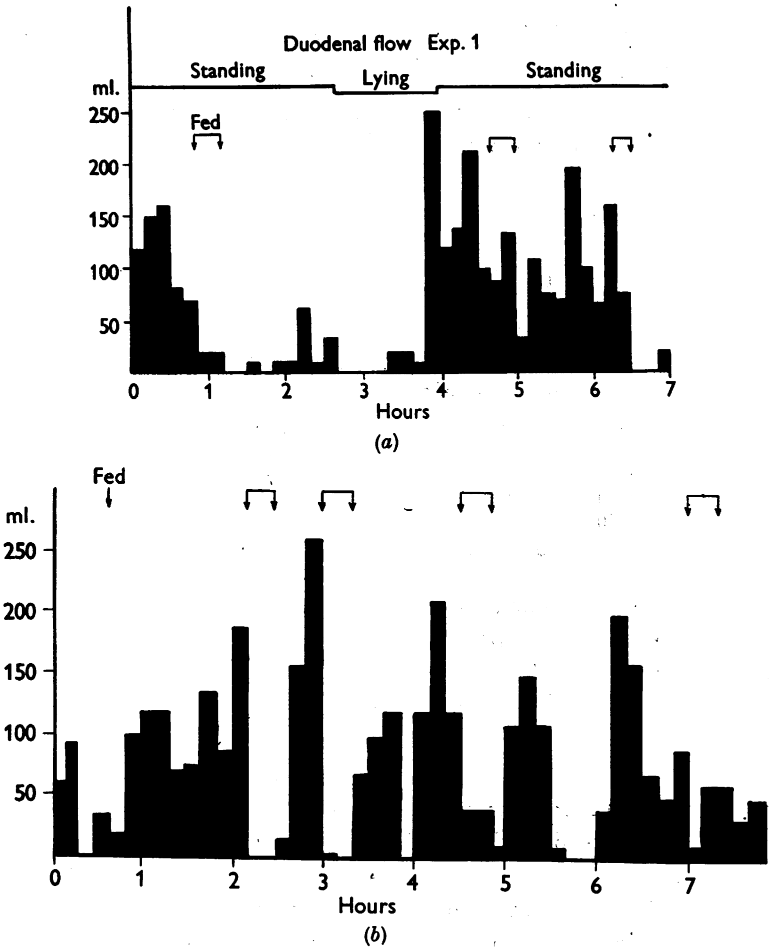

Fig. 2. The quantities collected in 15 min. intervals from the abomasum of a sheep in which the flow to the duodenum was permanently exteriorized. The arrows joined by a horizontal line indicate the period during which abomasal contents were introduced into the duodenum.

When the abomasal cannula was first opened a quick gush of food flowed through it. This was reintroduced into the duodenum and its volume was not included in the volumes subsequently passed per unit of time. Three collections were made and the quantities collected are given in Table 1.

Food passed from the abomasum at frequent intervals throughout the periods of collection except for a period during the first experiment when very little was collected for a considerable period. Each time food was reintroduced into the duodenum the volume collected during the subsequent period was reduced or ceased completely for 15 min. or more. The actual course of the first two experiments is shown in Fig. 2*a* and *b*.

Temporary exteriorization of the duodenal flow over long periods

This method has the serious disadvantage that the inflation of a small balloon in the duodenum reduces the output from the abomasum. There is no evidence to show whether the inhibiting effect of reintroducing food into the duodenum is due to the volume of the material in the duodenum, to the pressure it exerts, or to its chemical properties, such as the acidity of the material. Inflation of a small balloon, however, increased intra-lumenal pressure in only a small area, and still reduced the flow from the abomasum. This is shown by the data given in Table 2.

TABLE 2. Quantities collected from the first duodenal cannula in 30 min. intervals with and without the presence of a balloon in the lower duodenum

30 min. intervals	Series 1 (ml.)	Series 2 (ml.)	Series 3 (ml.)	Series 4 (ml.)
0–30	645	435*	765	690
30–60	305*	415	270*	235*
60–90	370	360*	305	305

* Indicates presence of a balloon.

In many of the experiments the quantity collected during the first period exceeded those of subsequent periods; this was more marked in some sheep than others. The four periods of collection given in Table 2 were made on the same sheep (no. 478), and it is clear that the presence of the balloon reduced the flow.

Owing to the inhibitory influence of the balloon the results of long collections extending over 10–12 hr. represent a flow that is less than normal. Even so the information obtained is of value for it is better to know a lower limit than no limit at all.

The course of events during four collections are illustrated in Fig. 3. The quantity passed from the stomach per hour tended to diminish with time, although in each experiment there was a marked response to a feed of meals but little response to a feed of hay.

The inhibitory effect of reintroducing food into the lower part of the duodenum was the same in these experiments as in those found on the first sheep.

The total quantities collected are shown in Table 3 and the average amount of food passed per hour from the duodenum under these conditions varied from 309 to 413 ml. In Exp. 5 the rate of flow was poor and after 6½ hr. the balloon was removed; the immediate response to this was that the flow recommenced and was maintained at a higher rate than in any of the previous experiments. This provides a striking confirmation of the inhibitory effect of local pressure in the lower part of the duodenum upon the rate of passage of food into the upper part.

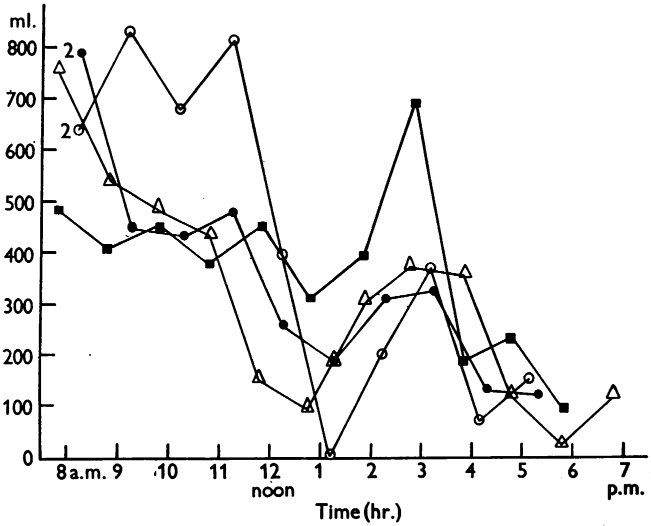

Fig. 3. The quantities collected per hour from the duodenum through cannula *1*. The sheep were fed at 7 a.m., 11 a.m., and 4 p.m. The first and last feeds consisted of hay; the main feed consisted of a mixture of meal given in Table 4. Collections from sheep 2 are marked by △, ○ or ■. Collections from sheep 494 are marked by ●.

TABLE 3. The quantities of food collected from the duodenum over periods of 6–12 hr.

Experiment	Duration of collection (hr.)	Total quantity collected (ml.)	Average quantity passed/hr. (ml.)
1	11	4086	371
2	12	3751	313
3	$10\frac{1}{2}$	3485	329
4	10	4126	413
5	$6\frac{1}{2}$	2010	309
	$1\frac{3}{4}$	988*	565*

* Indicates period during which balloon was removed from duodenum.

Temporary exteriorization of the flow for short periods

A large number of collections lasting $1\frac{1}{2}$ hr. was made in which no balloon was present and during which no food was returned to the duodenum. The quantities passed during these collections were much larger and the rate of flow was steady in most instances throughout the whole period. In one sheep, no. 478, the flow always diminished with time; this was not a constant finding with the other sheep, indeed the flow during the second half of the experimental period often exceeded that of the first. The results are shown in Table 4.

TABLE 4. Volume of food passed from the duodenal cannula during measurements lasting 1½ hr.

Sheep	No. of measurements	Quantities collected/hr. Variation (ml.)	Quantities collected/hr. Average (ml.)	Food Hay (g.)	Food Meals (g.)
1	9	1504–1864	1608	1800	225 *A*
1	5	797–1157	1038	2025	—
1	4	643–889	798	1012	—
2	12	657–1277	988	600	600 *A*
2	15	667–1130	818	600	600 *B*
2	8	470–1017	783	1200	—
4	10	583–1030	877	900	225 *A*
4	11	483–672	589	900	225 *B*
12	4	467–800	626	600	600 *B*
478	17	657–1025	823	900	225 *A*
478	7	650–950	735	780–880	—
494	10	623–940	796	900	225 *A*
495	10	643–930	794	900	225 *A*

A = Maize meal 2 parts
Crushed oats 1 part

B = Ground maize 4 parts
Crushed oats 1 part
Wheat bran 1 „
Linseed meal ½ „
Fish meal ½ „

These values given for the quantity of food passed to the duodenum per hour are undoubtedly greater than the physiological rate of passage, for no food entered the lower part of the duodenum or the small intestines. They serve two purposes; they set a maximum limit to the quantity of food passed from the stomach and they indicate that there is variation in the quantities passed by the same sheep when equal quantities of different feeds are given. Sheep 1 was examined first at Cambridge where it passed approximately 800 ml./hr. when maintained on a hay ration. After its arrival in Aberdeenshire its appetite increased until it ate far more food daily than local sheep. The increase in appetite was reflected in the amount of material collected from the duodenum.

Comparison of the values found for sheep 1, 2, and 4 shows clearly that when the ration consists of hay and meals greater volumes of material pass to the duodenum than when the ration consists of hay alone. In addition a comparison of the values found for sheep 2 and 4 suggests that different mixtures of meals are also associated with different volumes passed to the duodenum, for mixture *A* produced larger volumes than mixture *B* (see Table 4).

The continuity of the flow

The contents of the abomasum of sheep after slaughter rarely exceed 800 ml. and for this reason it is impossible to account for the quantities collected during 1½ hr. or for longer periods as representing only the material already present in the abomasum. Passage of food from the anterior parts of the stomach must have continued during these experiments. Tracings of the pressure changes occurring in the reticulum and rumen during collections from the abomasum, an example of which is given in Fig. 4, show that the normal cycle of movement continued unimpeded.

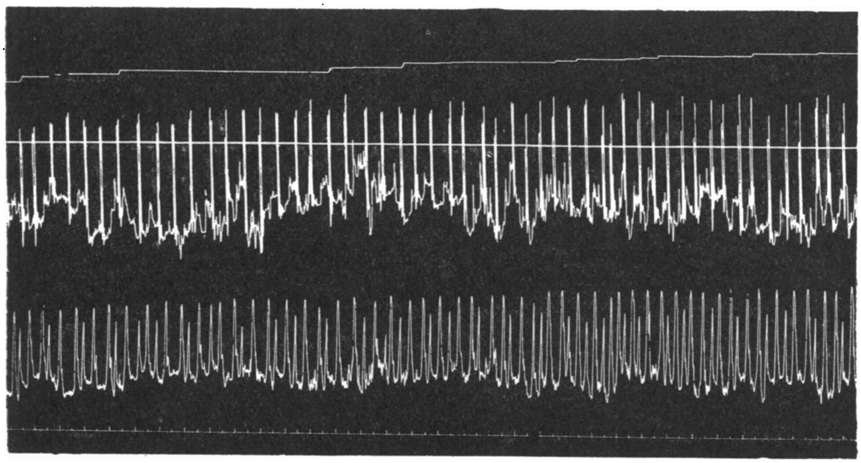

Fig. 4. The lower tracing shows the pressure changes occurring within the rumen; the middle tracing shows the pressure changes occurring in the reticulum, while the upper tracing shows the volume of material passed from the duodenal cannula *1*. The white line traversing the pressure tracings from the reticulum is the base line of the volume recorder. Time in 30 sec intervals; the larger excursion representing 60 sec. intervals.

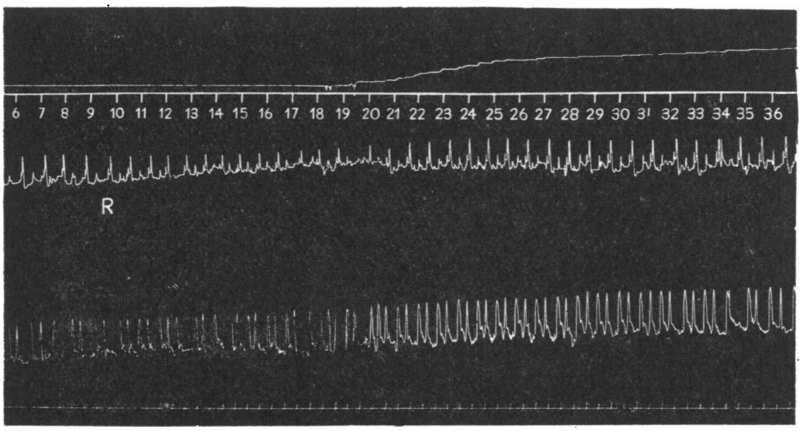

Fig. 5. Lower tracing is taken from the rumen, the middle from the reticulum and the upper from the volume recorder. *R* represents the start of rumination. Time in 30 sec. intervals.

Records of the volume of material collected were also made. Food flowed from the duodenal cannula at regular intervals except for periods of 15 or even 30 min. which occurred at unpredictable intervals and in which no material was collected (Fig. 5). Cessation of flow bore no close relation to the movements of the reticulum and rumen. This cycle of movement never stops although its frequency alters particularly with feeding (Fig. 6); and although in some instances a low frequency was associated with a low flow from the duodenum or with cessation of flow a close examination of all the records shows that the relationship, if it exists, is of minor importance compared with other factors affecting the flow.

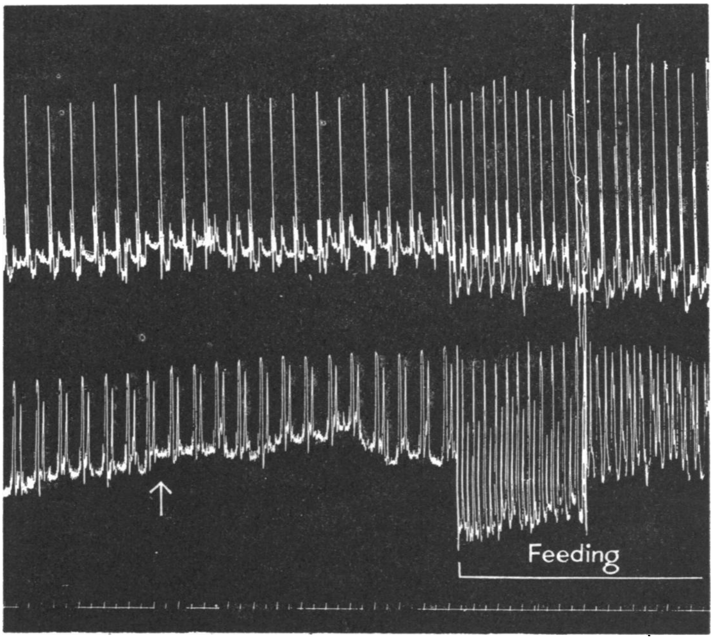

Fig. 6. The upper tracing is taken from the reticulum and the lower from the rumen. The arrow indicates the reintroduction of food into the duodenum. Time in 30 sec. intervals.

Short-term collections of $1\frac{1}{2}$–2 hr. have been made from 8 a.m. to 1 a.m. at different times and quantities comparable to those given in Table 4 were collected so that there is reason to believe that the passage of food from the stomach to the duodenum continues, with only short periods of rest, for at least 17 out of the 24 hr.

The effect of feeding and of rumination

The influence of feeding was not constant. A feed of hay often decreased the volume collected during the succeeding period. The length of the depression was variable but it seldom exceeded 15 min. and was usually less; after this period the flow returned to its previous level and often exceeded it. Similar immediate responses were noted after feeding meals but the subsequent effect was to increase the quantity collected. This is clearly illustrated in Fig. 3.

Rumination was associated with a steady flow of material from the duodenum which started soon after rumination commenced. The quantities passed were not in excess of those previously collected, but their appearance was more rhythmical for some passed from the cannula (on occasions only a few drops, but at fairly regular intervals after regurgitation) before the bolus was swallowed. The time relation and continuity of these observations are given in Table 5.

TABLE 5. The relation between the appearance of food from the duodenal cannula and the stages of rumination

a = interval between regurgitations and the appearance of food. b = interval between appearance of food and swallowing. c = interval between swallowing and regurgitation. Time in sec.

Example 1			Example 2			Example 3		
a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
17	24	5	39	11	5	32	29	6
20	21	6	22	29	3	31	26	8
24	30	7	21	33	4	21	33	7
20	31	7	—	53	5	30	32	16
23	31	6	31	24	5	—	57	4
22	32	6	22	35	5	29	33	6
22	21	4	—	52	3	—	53	4
25	29	7	27	28	5	—	66	15
16	38	12	32	25	5	—	54	—

The sequence of events was occasionally broken by the failure of food to pass to the duodenum and sometimes this was observed several times in succession.

An estimate of the quantity of food passing to the duodenum under normal conditions

The direct measurements made of the quantities of food passing to the duodenum can only be accepted as setting a lower and an upper limit to the probable quantities passed in the normal sheep. The inclusion of a marker in the food appears to be the most suitable method of obtaining a measure of the true flow but the problem of finding a suitable marker has yet to be solved. Materials such as barium sulphate and iron oxide tend to settle out of the food especially in the rumen. Theoretically an inert part of the food would be the most suitable marker and for this purpose lignin has been used, but as its chemical constitution is not fully understood its estimation is empirical and the results controversial.

When hay is fed estimates of food residues are a possible way of obtaining a value for the material flowing along the duodenum, for most of the digestion of hay occurs in the rumen. Food residues were separated from samples of 500 ml. of duodenal contents by allowing them to settle through a column of water. A glass tube 4 ft. long with a diameter of 2 in. was used. The lower end was fitted by a ground-glass joint to a glass jar with the capacity of a litre. A stopcock was fitted to the glass tube immediately above the glass joint. The ground-glass joint was sealed with a thick layer of heavy tap grease and the whole apparatus was filled with water except for a space at the top of the tubing which was sufficient to contain 500 ml. A 500 ml. sample of duodenal contents was poured into this space and the food residues were allowed to settle for 18 hr. The supernatant fluid was removed through the stopcock and the remainder was removed by suction. The residue was resuspended in 500 ml. of water and allowed to settle again through the 4 ft. column of water. This process was repeated three times and the residue was finally dried and weighed. A sample of the supernatant fluid was collected after each 18 hr. period and the fine particles in it were allowed to settle for a further 24 hr. The fine sediment thus obtained was dried, weighed and the total calculated.

This method removed soluble material and microscopic examination of the coarse sediment showed that relatively few bacteria remained attached to the large plant particles. An appreciable amount of bacterial debris was present in the fine sediment which developed on allowing the suspension to settle for 24 hr.

The faeces of the sheep were collected every 24 hr. and a 100 g. sample was mashed into an even pulp with water, the final volume being adjusted to 500 ml. The same procedure was then followed as that used for duodenal contents.

The quantities of dried residues obtained from sheep maintained on a diet of hay alone are given in Table 6. It can be seen that the coarse residues are 4–5 times greater than the fine residues of the duodenal contents but they are approximately 10 times greater with the faeces.

TABLE 6. The quantities of coarse and fine food residues in duodenal contents and faeces

Duodenal contents			Faeces		
Coarse food residues (g./100 ml.)	Fine food residues (g./100 ml.)	Total (g./100 ml.)	Coarse food residues (g./100 g.)	Fine food residues (g./100 g.)	Total (g./100 g.)
2·84	0·59	3·43	28·84 *	2·80	31·64
2·56	0·52	3·08	27·20	3·66	30·86
2·77	0·56	3·33	30·04	4·06	34·10
2·16	0·50	2·66	30·79	2·67	33·46
2·54	0·45	2·99	28·68	2·55	31·22
2·70	0·50	3·20	27·18	3·18	30·36
2·62	0·56	3·18	—	—	—
2·22	0·48	2·70	—	—	—

* Duplicate samples.

The quantity of moist faeces passed by this sheep over a period of a month varied from 955 to 1105 g. daily, the average figure being 1043 g. The average quantity of food residues passed in the faeces was 31·8 g./100 g. faeces which gives a total of 332 g./24 hr.

The average quantity of food residues in duodenal contents was 3·1 g. and this, when divided into the daily quantity passed in the faeces, suggests that not less than 10·7 l. of food passed through the duodenum of this sheep when it was eating 1200 g. of hay daily. This estimate does not allow for further digestion that occurs in the intestine, but of the two principal constituents fed, namely cellulose and the pentosans, the quantities disappearing in the intestine are small compared to the quantities disappearing in the rumen.

DISCUSSION

It has been known for a long time that if the digesta leaving the stomach of the dog are allowed to flow from the duodenum through a cannula the stomach empties more rapidly than normally. The reintroduction of the digesta so obtained into the intestine beyond the duodenal cannula produces a normal emptying time of the stomach (Alvarez, 1928). The experiments recorded here show that the same principle is true for the sheep, for the reintroduction of the material collected from the abomasum or first part of the duodenum into the lower part of the duodenum reduced the rate of flow from the abomasum. For this reason it is obvious that the quantities of digesta flowing from the upper part of the duodenum during short collections were greater than normal as none of the material was reintroduced into the intestine again. Distension of the duodenum or small intestine of the dog inhibits the movements of other parts of the alimentary tract (Pearcy & van Liere, 1926; Youmans, Meek & Herrin, 1938) while distension of the abomasum of sheep inhibits the movements of the reticulum (Phillipson, 1939). The use of a small balloon to prevent back-flow of the reintroduced food also reduced the rate of passage of digesta from the abomasum to the duodenum as could be expected from previous work on dogs and for this reason the rate of flow during long collections when this device was employed was less than normal.

These experiments, however, serve the purpose of setting limits to a measurement which it is important to know. The average value for long-term collections was approximately 350 ml./hr., while the average figure for short-term collections was approximately 800 ml./hr. The true range of values lies between these two extremes and the calculations based upon the food residues support this statement for they show that for the sheep concerned, which weighed approximately 60 kg., the flow was not less than 440 ml./hr. An assessment of the small quantities of cellulose and pentosans digested in the intestine indicates that the true figures for this sheep would be approximately 500 ml./hr. The most exact data were obtained from the first sheep of this series in which over two 8 hr. periods the rates of flow were 389 and 441 ml./hr. while the sheep retained its normal appetite. In this animal all the digesta collected, except for the small quantities retained as samples, was returned to the duodenum so that the emptying of the abomasum was, presumably, normal. This sheep weighed approximately 40 kg.

The mechanism governing the flow of food into the abomasum is as important as that governing the outflow from the abomasum to the duodenum. This mechanism is not yet understood and so it is impossible to find out whether it is influenced by the quantities of food in the duodenum and small intestines. In these experiments no apparent correlation was observed between the rate at which digesta flowed from a cannula in the pyloric part of the abomasum and the frequency of contractions of the reticulum and rumen. The regular cycle of movement in the reticulum and rumen suggests that the passage of food from the reticulum to the omasum occurs at a definite stage in the cycle. This is supported by the fact that, in the cow, pressure changes that have been recorded from the interior of the omasum are as regular as those in the reticulum and rumen and are related to them in time. There appear to be two possible explanations to account for the fact that flow from the abomasum may cease for as long as 15 or 30 min. after a feed of hay. The first is that passage of food into and through the omasum is independent of the movements of the reticulum; the second is that the entry of food into the omasum is governed by its consistency. A relation between consistency and the flow of food was found in long collections, for after the sheep was fed on millers' offals and other fine meals the rate of passage of digesta from the abomasum was increased while after the sheep ate hay there was no increase and often a decrease in the rate of flow. Feeding, however, invariably increases the frequency of the movements of the reticulum and rumen; while rumination, which results in the food present in the reticulum being in a fine state of division, causes a regular rhythm and a more regular passage from the abomasum than occurs at other times. The consistency of the contents of the reticulum appears to be important in determining the rate at which digesta pass into the omasum but the possibility of independent control still remains. The passage of food therefore from the large reservoir formed by the reticulum and rumen together to the duodenum is a more complicated process to study than the emptying of the stomach of a dog, and although the statement that it is a continuous process appears to be substantially correct the rate of flow may vary considerably or flow may cease completely at different times throughout the day.

SUMMARY

1. The quantity of digesta passed from the stomach of one sheep in which flow to the duodenum was permanently exteriorized was found to be 389 and 441 ml./hr. on two separate occasions.

2. The quantity of digesta passed in two sheep in which the flow along the duodenum was temporarily exteriorized by the inflation of a balloon in the duodenum varied from 309 to 413 ml./hr.

3. The inflation of a balloon in the duodenum reduced the outflow of digesta from the abomasum to the duodenum.

4. The reintroduction of digesta into the duodenum temporarily stopped or reduced the passage of digesta from the abomasum.

5. The quantities of digesta passing from a duodenal cannula placed immediately caudal to the pylorus varied from 467 to 1277 ml./hr. with sheep consuming 1125 or 1200 g. of dry food daily when the material collected was not reintroduced into the intestine.

6. The quantities passed from the duodenum during collections lasting 1½ hr. was influenced by the quality of the food eaten.

7. An increase in the flow of digesta from the abomasum was found after a feed of cereal offals and meals but not after a feed of hay.

8. The flow of digesta from the duodenum was more regular when the sheep was ruminating than when it was otherwise occupied.

9. No relationship was found between the frequency of the movements of the reticulum and the quantities of food passing to the duodenum.

10. Digesta passes to the duodenum of sheep in gushes at irregular intervals for 17 out of 24 hr. Periods of 15–30 min. between gushes may occur particularly if the sheep has recently consumed hay.

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