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# The effect of diet composition and level of feeding on digestion in the stomach and intestines of sheep

By J. W. G. NICHOLSON* and J. D. SUTTON
*National Institute for Research in Dairying, Shinfield, Reading*

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1. Four wether sheep, each fitted with re-entrant duodenal cannulas and a rumen cannula, were used to determine the relative quantitative importance of digestion in the stomach compared with that in the intestines when diets of low (HM1) and high starch (CM1) content were fed at 0·9 times maintenance and when the high-starch diet was fed at 1·7 (CM2) and 2·3 (CM3) times maintenance. Paper, impregnated with chromic oxide, and polyethylene glycol (PEG) were administered.

2. An apparatus is described which allowed one operator to collect, record, sample and return the duodenal digesta from two sheep simultaneously.

3. Total digestion was determined by faeces collections over 7–10 day periods, and digestion in the stomach by measuring the total flow of digesta from the abomasum to the duodenum over two 24 h periods with two or three sheep on each ration. Flow values were adjusted to give 100% recovery of chromic oxide.

4. The recoveries of chromic oxide and PEG were similar and it was concluded that either marker was satisfactory for adjusting 24 h flow values. Disadvantages of using PEG are discussed.

5. There was relatively little difference between rations HM1 and CM1 in the proportion of digestible organic matter and energy digested in the stomach. Only 57·1% of the total dry-matter digestion occurred in the stomach for ration HM1 compared with 65·0% for ration CM1 reflecting a smaller net gain in ash for ration CM1. Doubling the level of intake (ration CM2) resulted in a decrease in the proportion of digestible dry matter, organic matter and energy digested in the stomach. When the level was increased still further with ration CM3, the proportion continued to decrease with one sheep but increased with the other.

6. All but 5–11% of the digestible starch (measured as $\alpha$-linked glucose polymer) was fermented in the stomach, the lowest proportion being with ration HM1.

7. The amount of nitrogen reaching the duodenum was approximately equal to the amount ingested with rations HM1 and CM1 but considerably greater with the other two rations. All rations contained approximately 2% nitrogen.

8. Calculation of the estimated loss of energy as methane and heat of fermentation suggested that 50–54% of the digestible energy was absorbed as volatile fatty acids.

Ruminant animals utilize digestible energy provided in excess of maintenance requirements more efficiently when the rations contain a high proportion of concentrates than when they consist mainly of roughages. Experiments conducted with respiration chambers showed differences in the efficiency of utilization for fattening of energy from the volatile fatty acids (VFA) infused into the rumen of sheep, acetic being less efficiently utilized than the others (Armstrong & Blaxter, 1957). Because high-roughage rations produce a higher proportion of acetic acid in the total VFA than do high-concentrate rations (Bath & Rook, 1963), this is one possible explanation for the differences observed between the two types of ration. However, feeding the VFA in various forms has failed to confirm this (Ørskov & Allen, 1966; Bull, Johnson & Reid, 1967).

Fermentation in the rumen of energy-yielding nutrients that are capable of being

* Present address: Research Station, Canada Department of Agriculture, Fredericton, NB, Canada.

digested by the animal's enzymes is wasteful of energy (Blaxter, 1967). If an increase in the proportion of concentrates in a ration led to an increase in the amounts of digestible carbohydrates escaping rumen fermentation, as was found by Karr, Little & Mitchell (1966) and Tucker, Mitchell & Little (1968), the overall efficiency of energy utilization would be improved.

The quantitative aspects of rumen fermentation are still poorly defined in spite of recent interest in this subject (Hogan & Phillipson, 1960; Harris & Phillipson, 1962; MacRae & Armstrong, 1966; Sineshchekov, 1965; Ridges & Singleton, 1962; Hogan & Weston, 1967) and there is wide disagreement in estimates of the amounts of fermentation products absorbed from the rumen (see Warner, 1964).

Sheep were used to determine the relative quantitative importance of digestion in the stomach compared with that in the intestines when diets of low and high starch content were fed at 0·9 times maintenance and when the high-starch diet was fed at 1·7 and 2·3 times maintenance. The results showed relatively small differences between the high-roughage and high-concentrate rations fed at maintenance in the proportion of digestible energy digested in the stomach but a marked decrease at the higher levels of intake.

## EXPERIMENTAL

*Animals.* Four cross-bred wether sheep, about 1 year of age, were used in various phases of this work. They were held in digestion crates throughout the experiment. Each sheep was fitted with a rumen cannula and re-entrant duodenal cannulas. The duodenal cannulas in sheep 13 and 48 were of flexible plastic (Ash, 1962) and those in sheep 33 and 83 of rigid perspex. In sheep 48, 22 and 83 both cannulas were inserted immediately after the pylorus but in sheep 13 the distal cannula was inserted a few centimetres caudal to the point of entry of the common bile duct, leaving about 10 cm of intestine as a blind sac. No differences in digestion were detected between this sheep and the other three. Observations on each of the dietary treatments were obtained with two of the sheep (13 and 33). Sheep 48 was removed after the first treatment period when excessive leakage developed around the duodenal cannulas, and was replaced with 83. Sheep 83 also developed serious leakage around one duodenal cannula before completion of the fourth treatment period. Results with this sheep are available for the second and third treatments.

*Dietary treatments.* The following four rations were given in successive periods (amounts in g air dry feed/day): 450 chopped hay, 150 dairy cubes (HM 1); 90 hay, 150 dairy cubes, 200 flaked maize (CM 1); 160 hay, 150 dairy cubes, 500 flaked maize (CM 2); and 230 hay, 150 dairy cubes, 850 flaked maize (CM 3). The first two rations were expected to supply the maintenance energy requirements (Agricultural Research Council, 1965) of the sheep while CM 2 and CM 3 were to provide two and three times the requirements respectively. The ratio of hay to concentrates was 75:25 for ration HM 1 and 20:80 for the three rations CM 1, CM 2 and CM 3. The feed was given in two equal portions at 06.00 h and 17.00 h. Feed refusals and water consumption were recorded once per day at 16.30 h. Each sheep was given 7 g/day of a cattle mineral mix (Churn Cattle Mineral Mix; British Glues and Chemicals Ltd, London, WC1); salt blocks providing a wide range of minerals (Mineral Salt Lick; Bell and Son Ltd, Liverpool) were available at all times.

*Collections.* Each ration was given for at least 3 weeks before any collections were made. Overall digestibility was determined by total collection of faeces using a harness and canvas bag arrangement. Faeces were collected for a total of 7–10 days from each sheep on each ration; most collections consisted of two periods of 3–5 days separated by a duodenal collection. Digestibility in the stomach was determined by means of two 24 h total collections of the duodenal contents from each sheep on each ration, by a technique similar to that of Harris & Phillipson (1962). Samples of rumen fluid were obtained via the rumen cannula 3, 6, 9 and 11 h after the morning feeding on 1 day following each faecal collection period.

An apparatus (Pl. 1 and 2) was developed which allowed one operator to collect, record, sample and return the duodenal digesta from two sheep simultaneously while also collecting contents from a donor sheep. The digesta from the proximal cannula were collected in 100 ml graduated cylinders and weighed when the cylinders were full or at 15 min intervals. Before being sampled, the digesta were mixed by inverting the cylinder rapidly several times. A glass tube, 7 mm internal diameter, was dipped to the bottom of the cylinder and a finger placed over the end of the tube which was then withdrawn; this procedure was repeated about five times until a known proportion, 20–30%, of the contents was removed. The sample was saved for analysis and was replaced with a similar amount of digesta from a donor sheep given the same ration, including the indigestible markers.

The rate at which the digesta were returned by the automatic device was varied by remote control enabling the operator to adjust the rate of return of contents to the distal cannula to the rate of flow from the proximal cannula without approaching or in any way disturbing the animal. The sheep were accustomed to the collection procedures by several short collection periods before the beginning of the experiment and were kept under 24 h illumination for the 10- to 14-day period over which collections were made on each ration. Paper impregnated with chromic oxide, 2·5 g containing about 0·88 g of chromic oxide, was administered twice daily via the rumen cannula to each sheep, commencing at least 6 days before any collection. Flow from the duodenum was corrected when recovery of the chromic oxide at this point differed from the daily dose administered (Bruce, Goodall, Kay, Phillipson & Vowles, 1966). A solution of polyethylene glycol (PEG, average molecular weight 4000), 25 mg/ml, was infused into the rumen of sheep 13 and 33 over the same period at 30 ml/h to provide a comparison of a water-soluble marker with the insoluble chromic oxide; the PEG was not infused during the faecal collections on ration CM3.

Duodenal and faecal collections were interspersed according to the following restrictions: (1) three sheep receiving the same ration were required, (2) faecal collections were begun not less than 24 h after the end of a duodenal collection, (3) at least 1 week elapsed between duodenal collections from any one sheep, (4) when a sheep acted as a donor animal the contents removed were replaced with an equal volume of physiological saline and no collections were taken from this animal for at least 1 week.

*Digesta return apparatus* (*Pl.* 1 *and* 2). The digesta return apparatus consisted of a reservoir in which the duodenal contents were stirred continuously by a laboratory stirrer with a multi-blade rotor to prevent settling of solid particles. The reservoir was primed with about 300 ml donor contents before the start of each collection. The digesta flowed by gravity through rubber tubing which was closed off by a solenoid-operated pinch clamp. The pinch clamp was controlled by a remotely operated simmerstat which varied both the frequency and duration of the return surges to simulate the rate of outflow of the contents from the duodenum. The ratio of open time to closed time of the pinch clamp was varied from 2 sec every 4 min to being open

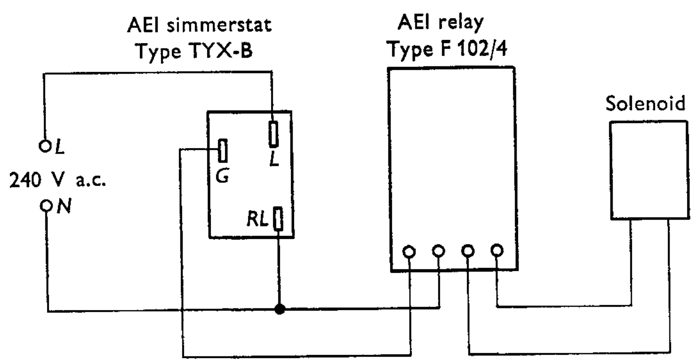


Fig. 1. Wiring diagram of the system for controlling the rate of return of duodenal contents from the reservoir to the distal cannula of the sheep. Live (*L*) and neutral (*N*) terminals from the mains power supply are indicated; the labelling of the simmerstat terminals (*L*, *G* and *RL*) is also shown. Further details are given on p. 588.

continuously by a combination of simmerstat regulator (Type TYX-B; Associated Electrical Industries Ltd, Harlow, Essex) and hot-wire relay (Type F 102/4; AEI Ltd) as shown in Fig. 1. Insulating tape was wrapped around the heater coil and bimetal strip of the simmerstat to decrease the on-time:off-time ratio at the lower end of its scale. The inherent time delay in the action of the hot-wire relay was used to reduce even further the on-time:off-time ratio at the lower end of the simmerstat scale.

The digesta were warmed nearly to body temperature, before entering the distal cannula, by passing through an aluminium tube in a warm-water jacket.

*Chemical analyses*. The samples of duodenal digesta collected over each 6 h period for each sheep were bulked and one portion was freeze-dried to provide dry-matter values. This dried material was used for the determination of gross energy by bomb calorimetry, ash by heating for 16 h at 600° and chromic oxide by a modification (J. F. D. Greenhalgh, personal communication) of the method of Stevenson & de Langen (1960). The remaining portion of the digesta was stored at −17° and later analysed for total nitrogen by the Kjeldahl method, PEG by the method of Smith (1958) and starch by the enzymic procedure of MacRae & Armstrong (1968) which measures α-linked glucose polymers.

The faecal samples were analysed similarly. The rumen fluid samples were analysed for VFA by gas chromatography (Sutton & Johnson, 1969).

## RESULTS

The average compositions of the feeds and of the four rations are shown in Tables 1 and 2 respectively. The hay was fed chopped into 5–10 cm lengths. Although it appeared to be of good quality from visual assessment and chemical analyses, small refusals occurred with ration HM 1. The average daily energy intakes of the four rations HM 1, CM 1, CM 2 and CM 3 provided 84, 91, 167 and 234% of maintenance requirements (Agricultural Research Council, 1965) based on the average weight of the sheep at the start of the experiment. There was little weight change in the sheep during the periods in which they were given rations HM 1 and CM 1, but gains in weight were appreciable when the other two rations were given.

Table 1. *Dry-matter percentage and composition of the dry matter of feeds*

| | | per 100 g dry matter | | | | |
|---|---|---|---|---|---|---|
| | Dry matter (g/100 g feed) | Organic matter (g) | Ash (g) | Starch (g) | Protein (N × 6·25) (g) | Gross energy (kcal) |
| Hay | 90·6 | 92·3 | 7·7 | 0·9 | 12·0 | 441·6 |
| Dairy cubes | 90·1 | 92·6 | 7·4 | 29·5 | 20·3 | 428·5 |
| Flaked maize | 89·1 | 99·0 | 1·0 | 72·1 | 9·4 | 437·1 |

Table 2. *Composition of the dry matter of the rations*

| Ration | Organic matter (g/100 g) | Ash (g/100 g) | Protein (N × 6·25) (g/100 g) | Starch (g/100 g) | Gross energy (kcal/g) |
|---|---|---|---|---|---|
| HM1 | 90·7 | 9·3 | 13·4 | 8·1 | 4·314 |
| CM1 | 93·8 | 6·2 | 14·2 | 41·8 | 4·275 |
| CM2 | 95·6 | 4·4 | 11·6 | 49·5 | 4·331 |
| CM3 | 96·3 | 3·7 | 11·2 | 52·5 | 4·323 |

*Digesta flow and recovery of markers.* Flow from the abomasum into the duodenum was highly variable for the 15 min recording intervals both between sheep and for different intervals with the same sheep. No clear relationship was detected between rate of flow and eating, ruminating or resting by the sheep. Although the sheep were accustomed to the collection procedures before the experiment there were large differences in the recovery of chromic oxide in the digesta passing the duodenum in 24 h (Table 3). Recoveries of chromic oxide range from 67·8 to 106·7% with an average of 87·1%. In one collection from sheep 13, recovery was only 45·0%; the values for this collection have been omitted. The variation in recovery did not decrease as the experiment progressed nor did the mean recovery increase. The variability within the sheep and between sheep in the flow of digesta was greatly reduced by adjusting the flow of nutrients reaching the duodenum to give 100% recovery of chromic oxide.

With sheep 13 and 33 the average recovery of PEG (Table 3) was very similar to that of chromic oxide for the whole experiment although for individual collections the recovery of PEG ranged from 78 to 113% of the recovery of the chromic oxide.

Recovery of chromic oxide in faeces averaged 102% for the whole experiment but tended to be rather higher (about 104%) when faeces were collected in two 4- to 5-day periods beginning within 30h of a duodenal collection. Recovery of PEG in faeces averaged only 95%.

Table 3. *Flow of digesta to the duodenum (g/24 h) before and after adjustment for* 100% *recovery of chromic oxide* ($Cr_2O_3$), *percentage recovery of* $Cr_2O_3$ *and of polyethylene glycol (PEG) and the ratio of the recovery of PEG to that of* $Cr_2O_3$

| Sheep no. | Flow | Adjusted flow | Percentage recovery $Cr_2O_3$ | Percentage recovery PEG* | PEG recovery* / $Cr_2O_3$ recovery |
|---|---|---|---|---|---|
| | | Ration HM1 | | | |
| 13 | 5563 | 6751 | 82·4 | 78·7 | 0·96 |
| | 7613 | 10097 | 75·4 | 85·5† | 1·13† |
| 33 | 6427 | 7379 | 87·1 | 78·9 | 0·91 |
| | 6273 | 7202 | 87·1 | 78·5 | 0·90 |
| 48 | 9461 | 8867 | 106·7 | — | — |
| | 8161 | 9490 | 86·0 | — | — |
| Mean | 7250 | 8298 | 87·4 | 80·4 | 0·98 |
| | | Ration CM1 | | | |
| 13 | 4326 | 4583 | 94·4 | 75·6 | 0·80 |
| | 3939 | 5197 | 75·8 | 74·2 | 0·98 |
| 33 | 4069 | 4195 | 97·0 | 75·5 | 0·78 |
| | 4922 | 4835 | 101·8 | 96·1 | 0·94 |
| 83 | 4584 | 4626 | 99·1 | — | — |
| | 4712 | 5050 | 93·3 | — | — |
| Mean | 4425 | 4748 | 93·6 | 80·4 | 0·88 |
| | | Ration CM2 | | | |
| 13 | 5700 | 8411 | 67·8 | 72·6 | 1·07 |
| | 7863 | 9292 | 84·6 | 90·7 | 1·07 |
| 33 | 7311 | 8721 | 83·8 | 93·8 | 1·12 |
| | 7562 | 9462 | 79·9 | 85·5 | 1·07 |
| 83 | 7309 | 9766 | 74·8 | — | — |
| | 8444 | 8458 | 99·8 | — | — |
| Mean | 7365 | 9018 | 81·8 | 85·7 | 1·08 |
| | | Ration CM3 | | | |
| 13 | 12223 | 12750 | 95·9 | 88·4 | 0·92 |
| | 12385 | 13075 | 94·7 | 86·9 | 0·92 |
| 33 | 8976 | 12712 | 70·6 | 69·9 | 0·99 |
| | 9609 | 12343 | 77·8 | 75·4 | 0·97 |
| Mean | 10798 | 12720 | 84·8 | 80·2 | 0·95 |

* Calculated for sheep 13 and 33, the only sheep infused with PEG.
† Estimated from the flow for the last 18 h of the 24 h collection. Flow was too small in the first 6 h to allow analysis for PEG.

*Calculation of digestibility.* In this paper the disappearance of feed components before the duodenum will be referred to as digestion in the stomach, and the difference between the amounts of feed components ingested and the amounts excreted in the faeces will be referred to as total digestion.

Since small amounts of ration HM 1 were left uneaten, total digestion was calculated from the average daily feed intake for the period beginning 1 day before the start of the collection and ending 1 day before the end. Digestion in the stomach was calculated from the average intake of the ration on the day preceding the collection and the day during which the collection began. The other rations were completely consumed.

In calculating digestion in the stomach, the flow of nutrients was adjusted for recovery of chromic oxide. Faeces were collected for 8–10 days for each sheep on each

Table 4. *Amounts of dry matter consumed, passing to the duodenum and excreted in the faeces (g/24 h) for each sheep on each diet and the proportion digested in the stomach and throughout the tract*

(Flow rates of duodenal contents were adjusted to give 100% recovery of chromic oxide)

| | | | | Proportion digested (%) | |
|---|---|---|---|---|---|
| Sheep | Food | Duodenum | Faeces | Stomach | Total |
| | | Ration HM 1 | | | |
| 13 | 552 | — | 194 | — | 64·9 |
| | 438 | 287 | — | 34·5 | — |
| | 548 | 369 | — | 32·7 | — |
| 33 | 526 | — | 185 | — | 64·8 |
| | 503 | 296 | — | 41·2 | — |
| | 540 | 318 | — | 41·1 | — |
| 48 | 555 | — | 193 | — | 65·2 |
| | 562 | 352 | — | 37·4 | — |
| | 562 | 363 | — | 35·4 | — |
| Mean | 544 | — | 191 | — | 65·0 |
| | 526 | 331 | — | 37·1 | — |
| | | Ration CM 1 | | | |
| 13 | 408 | 189 | 78 | 53·7 | 80·9 |
| | | 205 | — | 49·8 | — |
| 33 | 408 | 182 | 64 | 55·4 | 84·3 |
| | | 188 | — | 53·9 | — |
| 83 | 408 | 167 | 80 | 59·1 | 80·4 |
| | | 215 | — | 47·3 | — |
| Mean | 408 | 191 | 74 | 53·2 | 81·9 |
| | | Ration CM 2 | | | |
| 13 | 737 | 361 | 121 | 51·0 | 83·6 |
| | | 397 | — | 46·1 | — |
| 33 | 737 | 342 | 117 | 53·6 | 84·1 |
| | | 377 | — | 48·8 | — |
| 83 | 737 | 341 | 107 | 53·7 | 85·4 |
| | | 378 | — | 48·7 | — |
| Mean | 737 | 366 | 115 | 50·3 | 84·4 |
| | | Ration CM 3 | | | |
| 13 | 1108 | 507 | 209 | 54·2 | 81·2 |
| | | 567 | — | 48·8 | — |
| 33 | 1108 | 622 | 230 | 43·9 | 79·2 |
| | | 585 | — | 47·2 | — |
| Mean | 1108 | 570 | 220 | 48·5 | 80·2 |

diet except for sheep 48 on ration HM 1 when the collection lasted only 7 days; this period was considered adequate to give a reliable estimate of the total digestion and faeces were not corrected for recovery of chromic oxide. In a brief report published earlier (Sutton & Nicholson, 1968) faeces collections were corrected for chromic oxide recovery. Comparison of results calculated by the two methods showed that only small differences occurred.

The weight of PEG and chromic oxide was deducted from the dry matter, organic

Table 5. *Amounts of organic matter consumed, passing to the duodenum, and excreted in the faeces (g/24 h) for each sheep on each diet and the proportion digested in the stomach and throughout the tract*

(Flow rates of duodenal contents were adjusted to give 100 % recovery of chromic oxide)

| | | | | Proportion digested (%) | |
|---|---|---|---|---|---|
| Sheep | Food | Duodenum | Faeces | Stomach | Total |
| | | Ration HM1 | | | |
| 13 | 500 | — | 165 | — | 67·1 |
| | 406 | 223 | — | 45·1 | — |
| | 499 | 285 | — | 42·9 | — |
| 33 | 479 | — | 157 | — | 67·2 |
| | 456 | 230 | — | 49·6 | — |
| | 493 | 248 | — | 49·7 | — |
| 48 | 503 | — | 163 | — | 67·6 |
| | 508 | 276 | — | 45·7 | — |
| | 508 | 283 | — | 44·3 | — |
| Mean | 494 | — | 162 | — | 67·3 |
| | 480 | 258 | — | 46·4 | — |
| | | Ration CM1 | | | |
| 13 | 381 | 146 | 61 | 61·7 | 84·0 |
| | | 160 | — | 58·0 | — |
| 33 | 381 | 144 | 50 | 62·2 | 86·9 |
| | | 145 | — | 61·9 | — |
| 83 | 381 | 126 | 63 | 66·9 | 83·5 |
| | | 170 | — | 55·4 | — |
| Mean | 381 | 148 | 58 | 61·0 | 84·8 |
| | | Ration CM2 | | | |
| 13 | 703 | 294 | 103 | 58·2 | 85·4 |
| | | 327 | — | 53·5 | — |
| 33 | 703 | 272 | 100 | 61·3 | 85·7 |
| | | 304 | — | 56·8 | — |
| 83 | 703 | 261 | 94 | 62·9 | 86·7 |
| | | 309 | — | 56·0 | — |
| Mean | 703 | 294 | 99 | 58·1 | 85·9 |
| | | Ration CM3 | | | |
| 13 | 1065 | 408 | 187 | 61·7 | 82·4 |
| | | 471 | — | 55·8 | — |
| 33 | 1065 | 518 | 210 | 51·4 | 80·3 |
| | | 490 | — | 54·0 | — |
| Mean | 1065 | 472 | 199 | 55·7 | 81·4 |

matter and ash in the digesta and faeces; the gross energy of PEG (6306 cal/g) was similarly deducted.

*Digestibility of the rations.* The high-roughage ration was less completely digested than the high-concentrate ration in the entire digestive tract. Apparent digestibility of dry matter, organic matter and energy of the high-concentrate ration showed a curvilinear response (Tables 4–6), being slightly higher at the second level and lower at the third level than with the maintenance level of feeding. Digestibility in the

Table 6. *Amounts of gross energy consumed, passing to the duodenum, and excreted in the faeces (kcal/24 h) for each sheep on each diet and the proportion digested in the stomach and throughout the tract*

(Flow rates of duodenal contents were adjusted to give 100 % recovery of chromic oxide)

| | | | | Proportion digested (%) | |
|---|---|---|---|---|---|
| Sheep | Food | Duodenum | Faeces | Stomach | Total |
| | | Ration HM1 | | | |
| 13 | 2379 | — | 861 | — | 63·8 |
| | 1917 | 1081 | — | 43·6 | — |
| | 2373 | 1398 | — | 41·1 | — |
| 33 | 2288 | — | 810 | — | 64·6 |
| | 2191 | 1116 | — | 49·1 | — |
| | 2347 | 1209 | — | 48·5 | — |
| 48 | 2393 | — | 823 | — | 65·6 |
| | 2416 | 1316 | — | 45·5 | — |
| | 2416 | 1354 | — | 44·0 | — |
| Mean | 2353 | — | 831 | — | 64·7 |
| | 2277 | 1246 | — | 45·3 | — |
| | | Ration CM1 | | | |
| 13 | 1736 | 770 | 326 | 55·6 | 81·2 |
| | | 815 | — | 53·1 | — |
| 33 | 1736 | 765 | 264 | 55·9 | 84·8 |
| | | 715 | — | 58·8 | — |
| 83 | 1736 | 632 | 336 | 63·6 | 80·6 |
| | | 874 | — | 49·7 | — |
| Mean | 1736 | 762 | 309 | 56·1 | 82·2 |
| | | Ration CM2 | | | |
| 13 | 3186 | 1528 | 568 | 52·0 | 82·2 |
| | | 1683 | — | 47·2 | — |
| 33 | 3186 | 1401 | 548 | 56·0 | 82·8 |
| | | 1622 | — | 49·1 | — |
| 83 | 3186 | 1379 | 498 | 56·7 | 84·4 |
| | | 1542 | — | 51·6 | — |
| Mean | 3186 | 1526 | 538 | 52·1 | 83·1 |
| | | Ration CM3 | | | |
| 13 | 4777 | 2168 | 986 | 54·6 | 79·4 |
| | | 2449 | — | 48·7 | — |
| 33 | 4777 | 2678 | 1091 | 43·9 | 77·2 |
| | | 2490 | — | 47·9 | — |
| Mean | 4777 | 2446 | 1039 | 48·8 | 78·3 |

stomach showed a similar pattern except that digestibility coefficients declined for each increase in the level of feeding the high-concentrate ration.

The starch was almost completely digested with all the rations (Table 7). Most of the digestion occurred before the duodenum. The starch was least well digested in the stomach and in the entire tract with ration HM 1; with the other rations the coefficients of digestion in the stomach fell slightly as the level of starch intake increased but there was no such tendency with total digestion.

Table 7. *Amounts of starch consumed, passing to the duodenum, and excreted in the faeces (g/24 h) for each sheep on each diet and the proportion digested in the stomach and throughout the tract*

(Flow rates of duodenal contents were adjusted to give 100 % recovery of chromic oxide)

| | | | | Proportion digested (%) | |
|---|---|---|---|---|---|
| Sheep | Food | Duodenum | Faeces | Stomach | Total |
| | | Ration HM 1 | | | |
| 13 | 44·9 | — | 1·1 | — | 97·6 |
| | 43·8 | 5·6 | — | 87·3 | — |
| | 45·0 | 5·4 | — | 88·0 | — |
| 33 | 44·7 | — | 1·3 | — | 97·1 |
| | 44·5 | 6·0 | — | 86·4 | — |
| | 44·9 | 6·1 | — | 86·3 | — |
| 48 | 45·0 | — | 0·9 | — | 97·9 |
| | 45·2 | 5·8 | — | 87·3 | — |
| | 45·2 | 6·0 | — | 86·8 | — |
| Mean | 44·9 | — | 1·1 | — | 97·5 |
| | 44·8 | 5·8 | — | 87·0 | — |
| | | Ration CM 1 | | | |
| 13 | 168·4 | 6·9 | 0·5 | 95·9 | 99·7 |
| | | 8·8 | — | 94·8 | — |
| 33 | 168·4 | 6·3 | 0·5 | 96·3 | 99·7 |
| | | 7·5 | — | 95·6 | — |
| 83 | 168·4 | 2·8 | 0·4 | 98·3 | 99·8 |
| | | 8·6 | — | 94·9 | — |
| Mean | 168·4 | 6·4 | 0·5 | 96·0 | 99·7 |
| | | Ration CM2 | | | |
| 13 | 362·6 | 10·8 | 0·6 | 97·0 | 99·8 |
| | | 21·9 | — | 94·0 | — |
| 33 | 362·6 | 15·3 | 0·6 | 95·8 | 99·8 |
| | | 29·7 | — | 91·8 | — |
| 83 | 362·6 | 15·4 | 0·7 | 95·8 | 99·8 |
| | | 25·1 | — | 93·1 | — |
| Mean | 362·6 | 19·7 | 0·6 | 94·6 | 99·8 |
| | | Ration CM3 | | | |
| 13 | 578·6 | 28·4 | 1·7 | 95·1 | 99·7 |
| | | 37·9 | — | 93·5 | — |
| 33 | 578·6 | 39·4 | 3·2 | 93·2 | 99·4 |
| | | 32·1 | — | 94·5 | — |
| Mean | 578·6 | 34·4 | 2·5 | 94·1 | 99·6 |

The apparent digestibility of nitrogen was lowest for ration HM1 (Table 8); with the high-concentrate rations the mean digestibility declined with each increase in level of intake, the decline being especially large between rations CM2 and CM3.

The amount of nitrogen reaching the duodenum was approximately equal to that consumed with rations HM1 and CM1. With ration CM2 and CM3 the mean nitrogen flows were 17·7 and 30·1 g/24 h, greatly exceeding the daily consumption of 13·7 and 19·7 g/24 h respectively. The nitrogen content of the four rations did not

Table 8. *Amounts of nitrogen consumed, passing to the duodenum, and excreted in the faeces (g/24 h) for each sheep on each diet and the proportion digested in the stomach and throughout the tract*

(Flow rates of duodenal contents were adjusted to give 100% recovery of chromic oxide)

| | | | | Proportion digested (%) | |
|---|---|---|---|---|---|
| Sheep | Food | Duodenum | Faeces | Stomach | Total |
| | | Ration HM1 | | | |
| 13 | 11·8 | — | 4·4 | — | 63·0 |
| | 9·9 | 9·6 | — | 2·3 | — |
| | 11·7 | 14·6 | — | −24·2 | — |
| 33 | 11·4 | — | 4·3 | — | 62·1 |
| | 11·0 | 10·3 | — | 6·1 | — |
| | 11·6 | 11·1 | — | 4·2 | — |
| 48 | 11·8 | — | 4·5 | — | 61·6 |
| | 11·9 | 12·4 | — | −3·6 | — |
| | 11·9 | 13·7 | — | −14·8 | — |
| Mean | 11·7 | — | 4·4 | — | 62·2 |
| | 11·3 | 12·0 | — | −5·4 | — |
| | | Ration CM1 | | | |
| 13 | 9·2 | 9·5 | 2·5 | −3·4 | 72·3 |
| | | 10·1 | — | −10·6 | — |
| 33 | 9·2 | 8·4 | 2·2 | 8·1 | 76·0 |
| | | 9·0 | — | 1·9 | — |
| 83 | 9·2 | 6·7 | 2·7 | 26·6 | 70·6 |
| | | 9·8 | — | −7·5 | — |
| Mean | 9·2 | 8·9 | 2·5 | 2·6 | 73·0 |
| | | Ration CM2 | | | |
| 13 | 13·7 | 18·1 | 4·0 | −32·9 | 70·5 |
| | | 19·6 | — | −43·6 | — |
| 33 | 13·7 | 17·2 | 4·1 | −26·2 | 70·1 |
| | | 18·0 | — | −32·2 | — |
| 83 | 13·7 | 15·2 | 3·6 | −11·2 | 73·7 |
| | | 18·1 | — | −32·4 | — |
| Mean | 13·7 | 17·7 | 3·9 | −29·8 | 71·4 |
| | | Ration CM3 | | | |
| 13 | 19·7 | 25·5 | 7·3 | −29·5 | 62·8 |
| | | 28·8 | — | −46·1 | — |
| 33 | 19·7 | 33·7 | 6·9 | −71·1 | 64·9 |
| | | 32·4 | — | −64·6 | — |
| Mean | 19·7 | 30·1 | 7·1 | −52·8 | 63·8 |

vary widely, being 2·1, 2·2, 1·9 and 1·8% for the rations HM 1, CM 1, CM 2 and CM 3 respectively.

*Proportion of digestion occurring in the stomach.* The proportion of total digestion that occurred in the stomach is given in Table 9. There was relatively little difference between rations HM 1 and CM 1 in the proportion of digestible organic matter and energy digested in the stomach. However, only 57·1% of the total dry-matter digestion occurred in the stomach for the ration HM 1 compared with 65·0% for ration CM 1. This was due to the smaller net gain in ash content during passage of digesta through the stomach on ration CM 1 than on ration HM 1.

Table 9. *Percentage of total digestion occurring in the stomach of each sheep on each diet*

| Sheep no. | Dry matter | Organic matter | Gross energy | Starch |
|---|---|---|---|---|
| | | Ration HM 1 | | |
| 13 | 51·8 | 65·6 | 66·4 | 89·8 |
| 33 | 63·5 | 73·8 | 75·5 | 88·9 |
| 48 | 55·8 | 66·6 | 68·2 | 88·9 |
| Mean | 57·1 | 68·7 | 70·0 | 89·2 |
| | | Ration CM 1 | | |
| 13 | 64·0 | 71·2 | 66·9 | 95·6 |
| 33 | 64·8 | 71·4 | 67·6 | 96·2 |
| 83 | 66·2 | 73·2 | 70·3 | 96·8 |
| Mean | 65·0 | 71·9 | 68·3 | 96·2 |
| | | Ration CM 2 | | |
| 13 | 58·1 | 65·3 | 60·3 | 95·7 |
| 33 | 60·9 | 68·9 | 63·5 | 94·0 |
| 83 | 60·0 | 68·6 | 64·2 | 94·5 |
| Mean | 59·7 | 67·6 | 62·7 | 94·7 |
| | | Ration CM 3 | | |
| 13 | 63·4 | 71·3 | 65·1 | 94·6 |
| 33 | 57·6 | 65·6 | 59·5 | 94·4 |
| Mean | 60·5 | 68·5 | 62·3 | 94·5 |

An approximate doubling of the level of intake of the high-concentrate ration resulted in a decrease in the proportion of digestible dry matter, organic matter and energy that was digested in the stomach. When the level of intake was increased still further with ration CM 3, the proportion continued to decrease with sheep 33 but increased with sheep 13.

Almost all the digestible starch was digested before the duodenum, the lowest proportion being with ration HM 1 when the level of intake was lowest.

*Rumen VFA.* The molar proportions of VFA in the rumen fluid (Table 10) were typical for the rations being fed though there were considerable differences among sheep. The low level of the high-concentrate ration resulted in a lower proportion of propionic acid and a higher proportion of butyric acid than did the high-roughage ration. As the level of feeding the high-concentrate ration increased, the proportions of acetic and butyric acids tended to decrease and that of propionic acid to increase.

Table 10. *Concentrations and molar proportions of volatile fatty acids (VFA) in the rumen contents of each sheep on each diet*

| Sheep | Total VFA (m-moles/l.) | Molar % | | | | | |
|---|---|---|---|---|---|---|---|
| | | Acetic | Propi-onic | Iso-butyric | n-Butyric | Iso-valeric | n-Valeric |
| | | | Ration HM1 | | | | |
| 13 | 52·7 | 69·6 | 19·8 | 1·4 | 7·6 | 1·0 | 0·6 |
| 33 | 47·1 | 69·5 | 19·3 | 1·5 | 7·7 | 1·3 | 0·7 |
| 48 | 53·8 | 69·7 | 19·6 | 1·2 | 8·2 | 0·8 | 0·5 |
| Mean | 51·3 | 69·6 | 19·6 | 1·4 | 7·8 | 1·0 | 0·6 |
| | | | Ration CM1 | | | | |
| 13 | 69·5 | 67·8 | 18·1 | 1·1 | 11·6 | 1·6 | 0·4 |
| 33 | 53·2 | 70·4 | 15·0 | 1·0 | 11·7 | 1·6 | 0·3 |
| 83 | 62·6 | 61·8 | 18·5 | 0·7 | 16·1 | 1·8 | 1·1 |
| Mean | 61·8 | 66·7 | 17·0 | 0·9 | 13·1 | 1·7 | 0·6 |
| | | | Ration CM2 | | | | |
| 13 | 98·4 | 60·5 | 28·6 | 0·8 | 7·3 | 1·4 | 1·4 |
| 33 | 75·7 | 63·1 | 20·8 | 1·1 | 12·2 | 1·5 | 1·3 |
| 83 | 72·3 | 63·2 | 22·4 | 1·3 | 9·4 | 2·6 | 1·1 |
| Mean | 82·1 | 62·3 | 23·9 | 1·1 | 9·6 | 1·8 | 1·3 |
| | | | Ration CM3 | | | | |
| 13 | 109·2 | 61·3 | 24·6 | 1·3 | 10·0 | 1·6 | 1·2 |
| 33 | 84·7 | 53·3 | 34·5 | 0·8 | 7·9 | 0·7 | 2·8 |
| Mean | 97·0 | 57·3 | 29·6 | 1·0 | 9·0 | 1·1 | 2·0 |

## DISCUSSION

### *Duodenal flow and recovery of markers*

Hogan & Phillipson (1960) noted that failure to return contents to the duodenum during collections increased the flow rate from the duodenum from 514 to 848 ml/h and that flow ceased for a period when digesta were returned to the duodenum. Ash (1961) found that flow from the pylorus was inhibited when a balloon was inflated in the duodenum. Harris & Phillipson (1962) obtained low flow rates with two sheep not previously accustomed to the collection procedures, indicating the importance of training. Our apparatus for the collection and return of digesta was designed to reduce apparent psychological and physical disturbance of the animal to a minimum. Casual observation of the animals did not disclose any obvious changes in their diurnal pattern of eating, resting and ruminating on collection days compared with other days. The apparatus functioned well from this point of view as well as eliminating much of the work necessary in the slow return of digesta by manual means.

Although the animals did not appear to be upset by the collection procedures, the average recovery of chromic oxide in the 24 h collections of duodenal contents was only about 87% of the amount administered daily. Similar results were obtained by Harris & Phillipson (1962), Bruce *et al.* (1966) and Topps, Kay & Goodall (1968). There is, no doubt, considerable day-to-day variation in flow which is reflected in the range of percentage recoveries of chromic oxide in our results. However, the fact that the recoveries averaged less than 100% indicates that the procedures employed did depress flow rates despite the attempts to match the return of contents closely to the way in which they flowed from the abomasum. The low recovery of chromic oxide did not appear to be due to the lack of training of the animals as recovery did not increase during the 6 months of the experiment.

The broad similarity of recovery of PEG and of chromic oxide in the 24 h duodenal collections showed that flow of the liquid phase of the digesta was reduced as much as that of the solid material. Further work would be necessary to examine the apparent differences among rations in the ratio of recovery of the two markers. Our results suggest that, at least where all digesta reaching the duodenum are collected for 24 h, either soluble or insoluble markers can be used.

Although both PEG and chromic oxide gave similar estimates of variations in duodenal flow, disadvantages were found with PEG. Firstly, its recovery in faeces was not complete. Average recovery of PEG in faeces was only 94·8% for sheep 13 and 33 on rations HM 1, CM 1 and CM 2 compared with the recovery of 103·5% of the chromic oxide administered. Hydén (1955) was also unable to recover PEG in faeces quantitatively. A second disadvantage was that the PEG formed an appreciable fraction of the dry matter, organic matter and gross energy of the digesta and faeces. The percentage of the gross energy of faeces that came from PEG reached about 27% when ration CM 1 was given. A radioactive form of PEG that could be administered in much lower concentrations would be an advantage.

### *Digestion of dry matter, organic matter and energy*

The apparent digestion coefficients for dry matter, organic matter and energy were higher for the high-concentrate rations than for the high-roughage ration both in the stomach and in the entire digestive tract. The percentages of total dry matter and organic matter digestion that occurred in the stomach were highest for the high-concentrate ration given at maintenance level. Differences among the other rations were small and varied among the sheep.

The proportion of digestible energy that was digested in the stomach was consistently smaller than the proportion of organic matter that was so digested when the high-concentrate rations were given, but not when the high-roughage ration was given. This reflected the considerable increase in energy concentration of the organic matter from the high-concentrate rations during its passage through the digestive tract. The average concentrations of gross energy in the organic matter (kcal/g) of the feed, duodenal contents and faeces respectively were 4·76, 4·83 and 5·13 for ration HM 1, 4·56, 5·15 and 5·33 for ration CM 1, 4·53, 5·19 and 5·43 for ration CM 2 and 4·49, 5·18 and 5·22 for ration CM 3. These differences may have been due simply to the higher digestibility of the non-lipid materials from high-concentrate rations than from the high-roughage rations resulting in a concentration of the lipid fraction.

### *Digestion of starch*

With all the rations almost all the starch was digested. Even at the highest level of starch intake, only 2–3 g of starch reached the faeces daily. Most of the starch was fermented in the rumen; only 5–11% of the amount ingested reached the duodenum. The contribution of microbial starch to the starch found in the duodenum is not known so the true digestibility of starch cannot be calculated. The proportion of ingested starch reaching the duodenum was greatest on ration HM1 in which most of the starch came from the dairy concentrate which included 20% barley and 20% ground maize. With the high-concentrate rations, a fourfold increase in the amount of flaked maize fed caused only a very slight increase in the proportion of starch that escaped fermentation.

These results are in general agreement with those obtained in similar experiments by MacRae & Armstrong (1966), Topps, Kay & Goodall (1968) and Ørskov & Fraser (1968) with sheep fed rations containing rolled barley and by Topps, Kay, Goodall, Whitelaw & Reid (1968) with steers fed similar rations. However, Karr *et al.* (1966) and Tucker *et al.* (1968) reported that over 30% of ingested starch reached the duodenum of sheep and of steers when they were fed various amounts of cracked maize. Wright, Grainger & Marco (1966) also found considerable amounts of starch in the abomasum of sheep fed ground maize.

The reason for the difference in results from various experiments is not clear. Part of the explanation may lie in the different analytical procedures used for determining starch (Topps & Kay, 1969). The physical form in which the grain is given may also be important (E. R. Ørskov, personal communication). The reported effects of the amount of starch ingested vary. In general, as in our experiments, the proportion of ingested starch reaching the duodenum has not varied greatly with level of starch intake (Topps, Kay, Goodall *et al.* 1968; Tucker *et al.* 1968) but small increases have been reported in some other experiments (Karr *et al.* 1966; Ørskov & Fraser, 1968).

### *Digestion of nitrogen*

The amount of nitrogen reaching the duodenum was approximately equal to the amount ingested with the two rations fed at maintenance but considerably greater with the other two rations. Increases in the nitrogen content of digesta during their passage through the stomach have been reported previously when rations low in digestible crude protein were fed to sheep (Harris & Phillipson, 1962; Clarke, Ellinger & Phillipson, 1966; Hogan & Weston, 1967; Topps, Kay & Goodall, 1968). The daily increase of over 10 g nitrogen in our experiments when ration CM3 was fed was considerably greater than the increases reported elsewhere yet the crude protein content of the ration was not low.

The passage of nitrogen along the digestive tract when low-roughage rations are fed at high levels does not appear to have been examined previously. The results of the present experiments suggest that it is worthy of further study. In particular it would be important to know how much of the increase in nitrogen at the duodenum was due to synthesis of microbial protein. Hogan & Weston (1967) calculated that, in sheep, about 15 g microbial protein were synthesized per 100 g organic matter digested in the rumen.

*Partition of apparently digested energy*

In Table 11 an attempt has been made to partition the apparently digested energy of the four rations. The proportion of digestible energy that was digested in the stomach ranged from 62 to 70%. Of the energy digested in the stomach a considerable proportion is lost. The amounts of energy lost as methane in our experiments were estimated from an equation published by Blaxter & Clapperton (1965) relating methane losses (cal/100 cal gross energy ingested) to the digestibility and level of intake of the ration:

$$CH_4 = 1.30 + 0.112D + L(2.37 - 0.050D),$$

where $D$ is the digestibility at the maintenance level of feeding and $L$ is the level of feeding as a multiple of maintenance.

Table 11. *Partition of apparently digested energy (% of total digested energy)*

(See this page for the assumptions made in deriving these estimations)

| | Stomach | | | | |
|---|---|---|---|---|---|
| Ration | Heat | Methane | VFA | Total | Intestine |
| HM1 | 4.2 | 12.1 | 53.7 | 70.0 | 30.0 |
| CM1 | 4.1 | 10.8 | 53.4 | 68.3 | 31.7 |
| CM2 | 3.7 | 9.3 | 49.7 | 62.7 | 37.3 |
| CM3 | 3.7 | 8.2 | 50.4 | 62.3 | 37.7 |

Losses of energy as heat of fermentation also occur and were estimated to be about 6% of the fermented energy (Marston, 1948; Houpt, 1968). It was assumed that the only other major component of the net energy exchange out of the stomach was the absorption of VFA. The results suggest that VFA absorbed from the stomach formed about 50–54% of the digestible energy of these rations. The proportion was similar for the high-roughage and high-concentrate rations fed at maintenance but was smaller at the two higher levels of intake.

Although several assumptions have been necessary in making these estimates of the contribution of ruminal VFA to the energy requirements of sheep, these values agree closely with recent more direct determinations of VFA production in the rumen by the use of isotope dilution techniques in sheep fed rations largely consisting of roughages (Gray, Weller, Pilgrim & Jones, 1967; Leng, Corbett & Brett, 1968; Weston & Hogan, 1968). The degree of agreement between such widely different techniques is encouraging.

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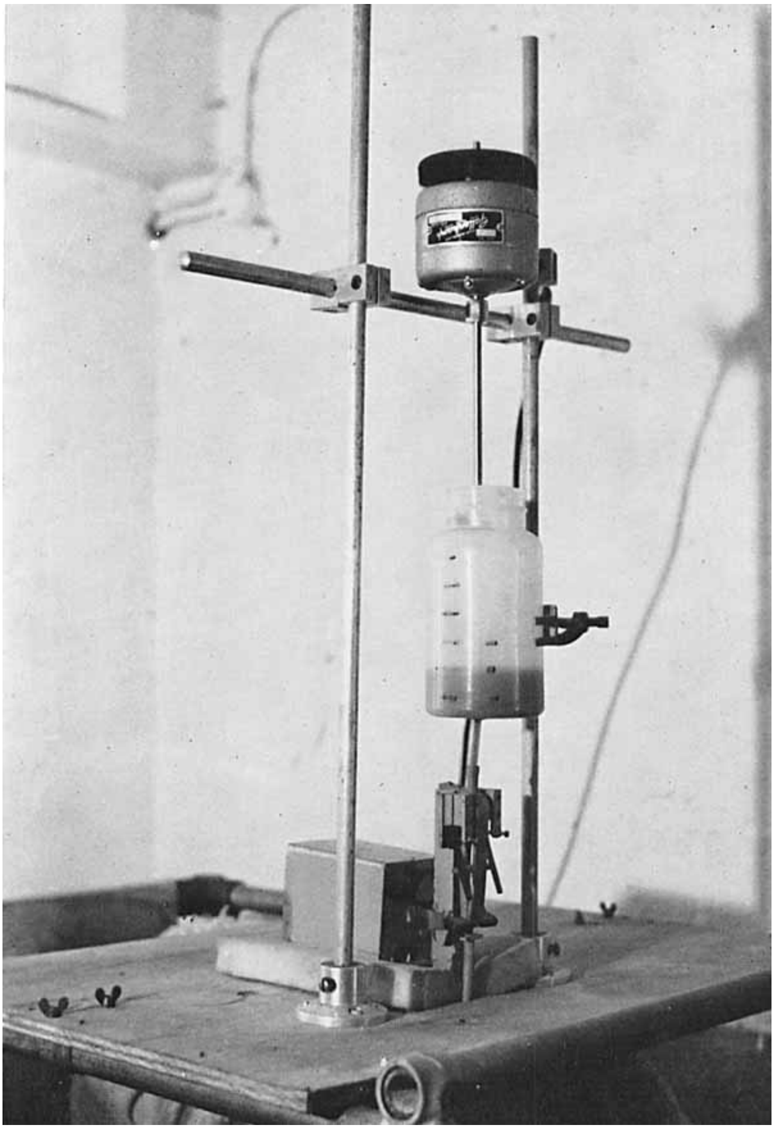

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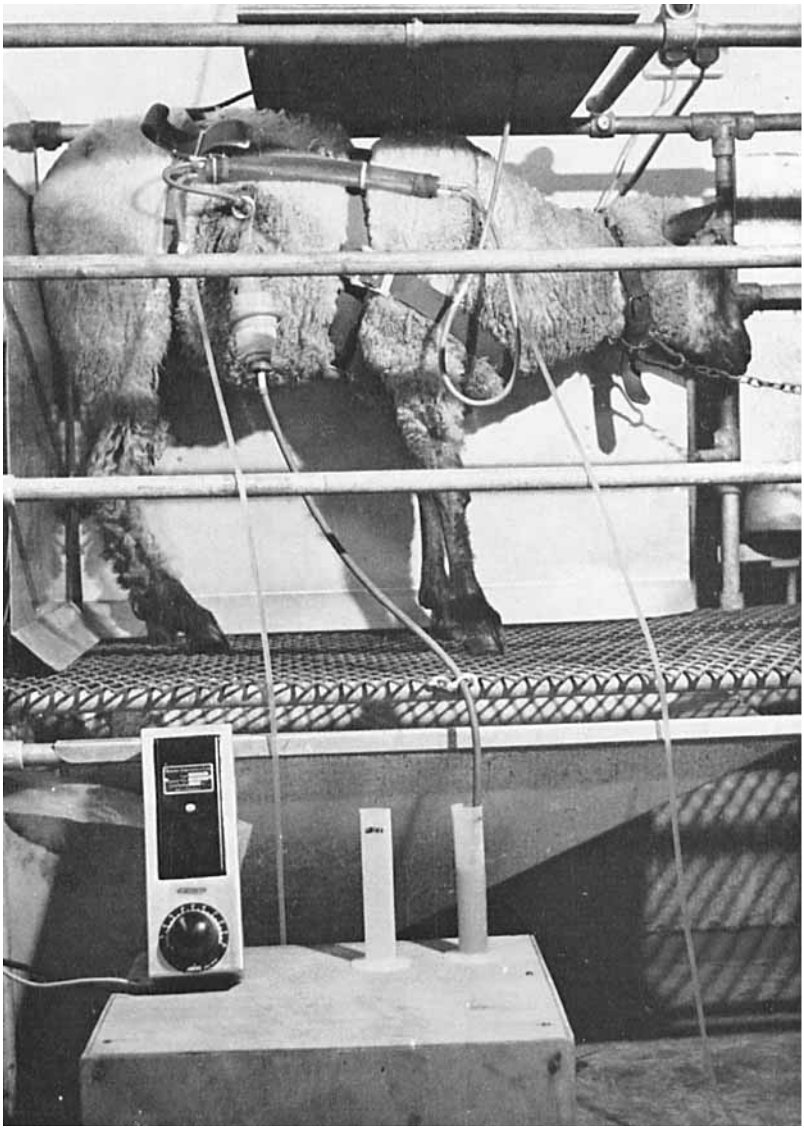

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## EXPLANATION OF PLATES

### Plate 1

Apparatus for returning the duodenal contents to the sheep. Stirrer, reservoir of duodenal contents and the solenoid-operated pinch clamp mounted on top of the digestion crate are shown.

### Plate 2

Sheep in digestion crate during the collection of duodenal contents. Contents leaving the proximal (lower) cannula are collected in the 100 ml cylinders. Contents being returned after sampling pass through the warm-water jacket on the side of the sheep before entering the distal (upper) cannula. The modified simmerstat for controlling remotely the rate of opening of the solenoid valve (Pl. 1) is also shown.

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