SOME EFFECTS OF VARYING THE QUANTITY OF POORLY DIGESTED MATERIALS PASSING THROUGH THE FORE-STOMACH AND INTESTINAL TRACT OF SHEEP

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ABSTRACT

Two experiments were conducted in order to investigate the effects of independently varying the quantity of non-digested dry matter passing through the fore-stomach and intestinal tract of sheep upon frequency of reticular contractions, intestinal rate of passage and the fecal excretion of some organic and inorganic nutrients.

In experiment I, two sheep were fed ad libitum on alfalfa-brome hay pellets and received the following duodenal infusion treatments during two periods: no infusion, water, 0.86 per cent glucose solution and a 6.0 per cent alpha-cellulose suspension. The infusion treatments did not appear to have any significant effect upon intestinal passage time, which ranged from 7.5 to 10.5 hours, or upon apparent nitrogen digestibility. Variations in ad libitum hay intake could not be attributed to any treatment effect. Fecal dry matter output had a tendency to remain relatively constant on all treatments. When 6 litres per day of fluid were infused into the duodenum, the sheep reduced their voluntary water intake by an amount approximately equal to that infused.

In experiment II, four sheep were fed either on all-hay or a high-grain ration and received duodenal infusions of either water or an alpha-cellulose suspension. Rations and infusion treatments were applied in a 2x2 factorial arrangement.

The hay ration with cellulose infusion (HC) resulted in the largest fecal dry matter output and the shortest intestinal retention time. The grain ration with water infusion (GW) resulted in the smallest fecal dry matter output and the longest intestinal retention time. The hay with water infusion (HW) and grain with cellulose infusion (GC) resulted in approximately equal fecal dry matter outputs which were intermediate between those of HC and GW. Variations among treatments in intestinal passage time could largely be accounted for by variations in fecal dry matter output. This negative relationship appeared to be curvilinear. Taking the reciprocal of intestinal retention time (rate of passage) transformed the relationship with fecal dry matter output to a positive linear form.

The activity of the reticulum was affected by the quantity of feed residues in the intestinal tract as well as the quantity in the fore-stomachs. The infusion of cellulose into the duodenum was accompanied by a significant increase in frequency of reticular contractions when grain was fed. The frequency was higher for the hay ration than the grain ration and cellulose infusion with the former appeared to have little or no effect upon the reticulum. A well defined diurnal rhythm was noted in the activity of the reticulum. Peak activity of the reticulum coincided with the two daily feeding times.

Dietary cellulose digestibility was equal for both the hay and grain rations. Estimates of intestinal digestion of infused cellulose, based upon the difference in fecal excretion of cellulose between the two infusion treatments, indicated that slightly more was digested when cellulose was infused with the hay ration (32%) than with the grain ration (23%).

Fecal nitrogen excretion was positively related to fecal dry matter output and this relationship appeared to be independent of the dietary source of the nitrogen. Nitrogen retention was significantly greater on the grain ration than on the hay ration but was not significantly affected by cellulose infusion.

Fecal losses of sodium and potassium calculated as a per cent of intake were significantly increased by cellulose infusion. It was noted that the concentration of these electrolytes in the fecal water was not affected by treatment, indicating that fecal excretion of water and electrolytes are probably interdependent. In addition, fecal dry matter concentration was not significantly different among treatments.

Apparent digestibility of ash was significantly greater for GW than for HC, however, other treatment comparisons revealed no other significant differences in ash digestibility.

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INTRODUCTION

The extent to which a ration becomes digested by a ruminant animal depends upon fermentation activity within the rumen, hydrolytic activity in the tract posterior to the rumen and the capacity of the mucosal surfaces of the alimentary tract to absorb the products of fermentation and hydrolysis. The rate of each of these processes will bring about a given quantitative change depending on the length of time that the ingesta spends under its influence.

Evidence is available which indicates that variations in intestinal retention time of digesta are related to variations in dry matter intake, ration digestibility and fecal dry matter output. Short intestinal retention times have been associated with increased fecal losses of water and magnesium and other observations have indicated that greater fecal losses of phosphorus and nitrogen may occur when the daily fecal dry matter output is increased.

The present study was designed to obtain further information concerning the relationship between non-digested dry matter output and intestinal retention time in sheep and to determine whether a shortened intestinal retention time is associated with an increased fecal excretion of various nutrients. The quantity of digesta passing through the alimentary tract was varied independently for the forestomachs and intestine by feeding a high grain or a high roughage ration and by the infusion of either alpha-cellulose suspension or water into the duodenum. The effects of these treatments on reticular movements, intestinal retention time and the fecal excretion of some organic and inorganic nutrients were studied.

LITERATURE REVIEW

Retention Time of Feed Residues in the Digestive Tract.

The time spent by feed in the digestive tract of ruminants is directly related to the mean dry matter digestibility, according to Blaxter, Graham and Wainman (1956). The authors studied the effect of level of feed intake and physical form of the ration on digestibility and retention times in sheep. The animals were fed three differently prepared rations at each of three levels of intake. Dried grass was fed in the long form, medium ground as cubes and finely ground as cubes. The higher the feed intake the shorter was the retention time and the lower was the digestibility. The more finely ground ration was found to have a shorter retention time than the coarser rations and also a lower digestibility. There appeared to be an upper limit of about 81 per cent to the potential digestibility. This limit was approached when feed was retained in the tract for 55 - 60 hours. Determination of the retention time of feed was based on the method of Balch (1950) and involved counting the number of previously stained feed particles appearing in the feces in successive intervals of time.

In order to obtain estimates of the relative times spent by feed in various part of the digestive tract, Blaxter _et al._

(1956) undertook a mathematical analysis of the fecal excretion data based upon a concept that regarded the digestive system as a kinetic process. Two rate constants K_1 and K_2 described the passage of food from the rumen and abomasum respectively. A delay factor τ represented the time taken for digesta to pass from the duodenum to the feces. The calculated rate constant K_2 for abomasal emptying was relatively uniform for all treatments. The rate constant K_1 for rumen emptying and the intestinal delay factor τ both were affected by treatments. K_1 was larger at the higher levels of feed intake and when the feed was ground to a finer state. Larger values of K_1 were associated with small values of τ. The authors were unable to conclude whether one factor is a determinant of the other but they suggested that either τ, as well as K_1, is an event occurring in the rumen or that a rapid flow from the rumen (a large K_1 value) causes a decreased intestinal retention time.

The quantity of indigestible dry matter or "ballast" present in the digestive tract was calculated. The amount of "ballast" was greatest immediately following ingestion of a meal and declined to a minimum immediately prior to the next meal. Thus, feeds that are highly digestible and which have a rapid rate of passage will give rise to smaller quantities of "ballast". The authors discussed the importance of this concept as it relates to distention of the digestive tract which possibly imposes a limit to voluntary intake of roughage.

Blaxter, Wainman and Wilson (1961) compared the voluntary intake by sheep of low, medium, and high quality roughages. The voluntary intake of the high quality roughage was 186 per cent of that of the low quality roughage and the high quality roughage had a rate of passage through the alimentary tract which was about 200 per cent as rapid as the low quality roughage. The "fill" of the digestive tract, however, was approximately the same for all qualities of forage.

Campling and Balch (1961) studied the effect of altering the quantity of digesta in the reticulo-rumen upon the voluntary intake of roughages by cows. When the swallowed boluses of hay were collected and removed via a rumen fistula during a three hour period while the cows were eating, it was noted that the cows increased the time spent eating and consumed about 177 per cent of their normal voluntary intake. A change of 1 pound of dry matter with its associated water in the rumen contents resulted in an inverse change of 0.6 pounds in the voluntary intake of hay. It was concluded by Campling, Freer and Balch (1961), (1962) that the time taken for particles of roughage to be reduced to a size that could pass from the reticulo-rumen to the omasum may be the major factor determining the retention time of feed residues in the rumen and thereby may partly regulate the voluntary intake of roughage by the cow. Straw was found to disappear from the reticulo-rumen more slowly than hay. When 75 grams or 150 grams per day of urea was infused into the rumen of cows receiving straw there was an increase of 40 per cent in voluntary intake. This large increase in voluntary intake was explained on the basis of a higher fermentation rate occurring in the rumen when urea was infused. Fermentation rate was estimated by recording the time required for a given loss of weight from cotton threads suspended in the rumen. This gives an index of cellulose digestion. The higher fermentation rate led to a more rapid breakdown of straw particles and was accompanied by a decrease in retention time of straw residues in the rumen. The digestibility of the organic matter of straw was increased from 41 per cent to 50 per cent by the infusion of 150 grams per day of urea. This was due mainly to an increase in crude fiber digestibility. At ad libitum intakes of roughage offered once daily to cows, the various factors of digestion in the rumen and rate of passage through the tract appear to operate in such a way as to result in a constant weight of dry matter in the rumen immediately prior to feeding.

Campling, Freer, and Balch (1963) compared the voluntary feed intake of cows receiving hay in the long form and in the ground, pelleted form. It was rationalized that grinding would reduce the particle size of the roughage and lead to a faster passage out of the reticulo-rumen. At submaximum levels of intake this was found to be true, but at ad libitum intakes the mean retention time of both long and ground hay in the alimentary tract of the cows was the same. There was no difference in voluntary intake of the two rations although the digestibility of the ground hay was much lower than that of the long hay. Examination of the excretion patterns of stained long hay and stained ground hay revealed that the latter had a faster initial excretion but a slower later excretion. Since digestibility, on the average, was lower for the ground hay and there was no change in retention time for the whole gut associated with physical form of the diet, the amount of dry matter in the alimentary tract must have been greater with ground hay. However, the quantity of digesta in the reticulo-rumen was slightly less when ground hay was fed. The authors, therefore, suggest that the hind gut must have contained more dry matter when this ration was fed.

Examples may be cited in which other researchers have found grinding of roughages to result in greater feed consumption. For sheep, Meyer et al. (1959); Lloyd, Crampton, Donifer and Beacom (1960); and Van der Merwe, Ferreira, Vosloo and Labuschagne (1960) report that grinding increased roughage intake. Wallace and Hubbert (1959) found an increase of 31 per cent in the intake of ground feed by small steers but observed no difference in dry matter digestibility between the long and ground hay. The opinion is expressed that the influence of grinding on voluntary intake of a diet is determined by the extent to which both the retention time and digestibility are altered by grinding (Campling et al. (1963). These authors concluded that voluntary intake is regulated in relation to the amount of digesta in the reticulo-rumen and that for long hay the rate of breakdown of feed particles probably limited the rate of disappearance from the rumen. With the diet of ground hay, the implication is made that the rate of elimination of digesta from the hind gut imposes a limit on emptying of the reticulo-rumen and thus grinding was not effective in enhancing voluntary intake. One other factor that may be of considerable importance as an alternate explanation is that the high dry matter concentration of the digesta in the immediate area of the reticulo-omasal orifice might in itself impose an upper limit to rate of rumen emptying. Although the total digesta in the reticulo-rumen of cows fed ground hay had the same over-all dry matter concentration as when long hay was fed, it was noted that the digesta at the reticulo-omasal orifice contained 11.8 per cent dry matter and 4.1 per cent dry matter for the respective rations of ground and long hay.

Freer and Campling (1965) made recordings of the frequency of reticular contractions of cows by means of air-filled balloons placed inside the reticulum. The frequency of contraction was greatest when the cows were eating and lowest when they were resting. The frequency during periods of rumination was intermediate in magnitude. There was a direct relationship between the mean daily number of reticular contractions and the level of feed intake. With diets of concentrates and ground hay the frequency of contraction was lower than with a similar intake of long roughage. Although most of the change in total daily number of contractions associated with a particular dietary change could be explained by increases or decreases in times spent eating and ruminating, there were also apparent differences in the frequency of contractions during resting that could be associated with ration differences. The total daily number of reticular contractions with ground hay was 1414 compared with 1755 for long hay. It is pointed out that residues of long hay may have provided greater mechanical stimulation to the alimentary tract than ground hay. Another possibility is that the greater quantity of dry matter in the hind gut when ground hay was fed caused an inhibition of reticular activity. There is some evidence that distention of the duodenum and abomasum can inhibit reticular frequency and amplitude of contraction. Phillipson (1939), Ash (1965) and Stevens, Sellers and Spurrell (1960) have indicated that controlling effects of the abomasum upon omasal activity might have important effects upon ingesta transfer. Titchen (1958) in a study of decerebrate sheep found that distention of the abomasum and manipulation of the pylorus caused a reflex inhibition of the frequency and/or amplitude of reticular contractions. While there is little doubt that such control mechanisms operate on a short-term basis and are effective in regulating diurnal patterns of digesta flow, the prediction of long term controlling effects based upon short term observations should probably be made with some reservation.

Freer, Campling and Balch (1962) concluded that a change in the quantity of digesta transferred to the omasum per contraction of the reticulum was more important than a change in the mean frequency of contraction in effecting a change in the mean daily passage of organic matter out of the rumen. It was found that the daily _ad libitum_ intake of organic matter was directly related to the weight of organic matter transferred to the omasum during each reticular contraction. In the second experiment of Freer and Campling (1965) the quantity of organic matter transferred to the omasum per contraction of the reticulum was 2.5 grams when long hay was fed and 4.8 grams when ground hay was fed. With the latter feed the frequency of reticular contractions was much lower, although there was a greater total daily transfer of organic matter than when long hay was fed. As mentioned earlier there was no change in voluntary intake. The authors suggest that with the diet of ground hay, the amount of organic matter transferred per reticular contraction was limited to 4.8 grams either by the high dry matter concentration of the transferred digesta (11.8 per cent) or by the large amount of digesta in the hind gut. If the latter alternative was the operative factor, then, it must necessarily follow that a lower limit to intestinal retention time had been reached. Campling, et al. (1962) observed no significant change in retention time of digesta in the hind gut of cows when the digestibility and daily intake of straw was increased by infusion of urea into the rumen.

The retention time of feed residues in the alimentary tract posterior to the reticulo-rumen has not received as much study as over-all retention time in ruminant animals. Ewing and Wright (1917), as cited by Castle (1956c), fed a given meal to cattle and slaughtered the animals at time intervals thereafter. After measuring the quantities of digesta in various compartments of the tract, they arrived at an estimate of 14.5 hours for the retention time in the small and large intestines. Since some of the feed consumed at a meal passes out of the rumen almost immediately, it has been common practice to regard the time required for excretion of 5 per cent of a stained meal as an index of retention time in the post-rumenal portion of the digestive tract. Experiments of Balch (1950) and Castle (1956c) showed that the 5 per cent excretion time of a stained meal was 3 - 6 hours longer than the retention time of stained particles introduced per fistulum into the abomasum of cows or the duodenum of goats, although there was a significant positive correlation between the values obtained by the two methods. Castle (1956c) reports intestinal retention times which ranged from 11.0 to 14.4 hours for goats.

Coombe and Kay (1965) published values for retention time of digesta in the small and large intestines of sheep fitted with duodenal and ileal re-entrant cannulae. Three different markers were used; small polyvinyl chloride discs, stained particles of finely milled straw and polyethylene glycol. The daily dry matter intake of the sheep ranged from 333 grams to 1008 grams. Hay and dried grass which differed in digestibility were fed.

The retention times of digesta in the small intestine ranged from 2.25 to 4.50 hours and in the large intestine from 10.2 to 26.5 hours. The soluble marker, polyethylene glycol, was found to be retained significantly longer in the small intestine than the solid markers. This would indicate the possibility of there being a preferential retention of fluid in the small intestine. There was, however, no significant difference in rate of passage of the soluble and solid markers through the small plus large intestine or through the large intestine alone. The retention times reported here for the small plus large intestines of sheep are greater than those reported by Castle (1956c) for goats. The latter author, however, fed the goats at *ad libitum* levels whereas the feed intake of the sheep was limited. Coombe and Kay (1965) noted that intestinal retention time was related to the level of feed intake, a concept previously predicted by Blaxter *et al.* (1956). It is pointed out that when feed consumption is increased the intestines must either dilate to accept a larger volume, or increase the concentration of dry matter in the digesta or propel a larger volume more rapidly. The work of Goodall and Kay (1965) indicates that the dry matter concentration of ileal digesta remains constant but the volume of digesta varies with level of feed intake. This means that either distention of the intestines or faster propulsion of digesta occurs when feed intake is increased. The constant dry matter concentration of ileal digesta found by the latter authors differs from the concept of Purser and Moir (1966) as it applies to rumen dry matter concentration. Coombe and Kay (1965) regard faster propulsion as the most important response of the intestines to larger quantities of digesta, but they also propose that a certain degree of intestinal distention occurs which acts as a stimulus to increased propulsive motility of the intestines.

Increased digestibility has been associated with decreased retention time in the rumen (Campling et al.; 1961, 1962) but is apparently associated with increased intestinal retention time. Coombe and Kay (1965) found that increased digestibility and decreased feed intake both resulted in a slower rate of passage of digesta through the intestines. Rationalizing that intestinal retention time may be more dependent upon the quantity of non-digestible residues passing through the tract than on dry matter intake, the authors calculated correlation coefficients pertinent to this question. There were significant negative correlations between intestinal retention time and the following parameters: dry matter intake, total fecal output, fecal water output and fecal dry matter output. The correlation with fecal dry matter output was not as good as expected and had a value of -0.87 whereas the correlation with dry matter intake was -0.98. It was found that the percentage of dry matter in the feces had a moderate positive correlation with intestinal retention time but it was not statistically significant.

Volume Relationships of the Ruminant Digestive Tract.

Due to anatomical reasons it has not yet been possible to quantitively collect the fluid which flows into the omasum through the reticulo-omasal orifice. Thus, estimates of the outflow from the reticulo-rumen are limited to those obtained by dilution techniques as described by Hyden (1961), Murray, Reid and Sutherland (1962) and Purser and Moir (1966). Thus, estimates of rumen volumes of sheep have ranged from 2.5 litres to 7.6 litres and outflow rates of the order of 300 millilitres per hour are not uncommon. Direct measurements have been made, however, of fluid volumes passing from the omasum into the abomasum. Oyaert and Bouchaert (1961) used a funnel in the proximal abomasum fitted with a side arm for diverting the omasal outflow. By following the concentrations of polyethylene glycol in the digesta they found average hourly flows of 442 - 810 millilitres in sheep. Keeping in mind that the omasum is considered to be an organ involved in the absorption of large quantities of water these values would appear to be too large when compared to rumen outflow data. Boyne et al.(1956) and Gray et al.(1954) estimated that approximately 43 per cent of the water of the digesta entering the omasum is absorbed before reaching the abomasum. Therefore, one would expect the volumes passing from the omasum to the abomasum to be much lower than rumen outflow estimates. In the experiments of Oyaert and Bouchaert (1961) the collected digesta was not returned to the abomasum and the authors noted that the animals drank more water than normally. This would tend to dilute the rumen contents. Ash (1965) measured flow through an abomasal re-entrant cannula placed beneath the omaso-abomasal orifice. It was observed that the flow from the omasum was doubled by failure to return the collected digesta through the distal cannula and was associated with increased frequency of reticular contractions. Conversely, if excess rumen fluid was placed in the abomasum then the outflow from the omasum was depressed. This depression was accompanied by a decrease in the frequency and amplitude of contractions of the reticulum. The addition of various quantities of rumen fluid into the rumen resulted in an increased outflow from the omasum in proportion to the amount introduced. From these results it is indicated that controlling effects are imposed upon flow through the omasum by the quantities of digesta in the rumen and in the abomasum.

Phillipson and Ash (1965) reported that omasal outflow volumes are dependent upon dietary characteristics and the degree to which feed is fermented in the rumen. Increasing the feed intake of sheep from 400 to 1100 grams per day of long dried grass resulted in an increase in volume of omasal outflow from 130-150 millilitres to 250 - 346 millilitres per hour. Grinding and pelleting of the grass reduced the rate of flow. An all concentrate ration resulted in lower volumes than those recorded when long roughages were fed. When 400 - 800 grams per day of ground, pelleted barley was fed the omasal outflow was 77 - 157 millilitres per hour. It was rationalized that omasal flow volume is related to the quantity of dry matter that escapes fermentative digestion in the rumen; the higher flow volumes when roughages were fed being associated with a greater amount of dry matter leaving the rumen than when barley was fed. These rates of omasal outflow are lower than most estimates of rumen outflow and appear realistic in view of the water absorbing capacity of the omasum. Oyaert and Bouchaert (1961), however, obtained evidence that a portion of the rumen fluid that enters the omasum is retained for some time and a portion passes directly through to the abomasum. The direct passage of rumen fluid to the abomasum was observed radiologically by Benzie and Phillipson (1957).

Estimates of the volume of digesta flowing from the abomasum to the duodenum have been made using sheep fitted with duodenal re-entrant cannulae. With this type of surgical preparation, Hogan and Phillipson (1960) and Harris and Phillipson (1962) collected all the digesta flowing from the proximal cannula and at intervals measured the amounts collected and then returned the digesta through the distal cannula. Hogan and Phillipson (1960) obtained a mean flow value of 360 millilitres per hour for sheep eating 1000 grams of feed provided in two equal meals daily. No diurnal trends in abomasal flow were observed. Harris and Phillipson (1962) corrected the flow volumes recorded for 100 per cent recovery of chromium sesquioxide and reported an average flow of 416 millilitres per hour when sheep were receiving 750 grams of hay in two equal meals daily. A diphasic, diurnal flow pattern occurred with maximum rates coinciding with feeding times. Phillipson (1952) made the observation that failure to return collected digesta into the duodenum caused an abnormally high flow from the abomasum and that inflation of a balloon in the duodenum depressed flow. It has therefore been suggested that abomasal outflow is controlled by the quantity of digesta in the duodenum in a similar manner in which digesta in the abomasum controls omasal outflow. Singleton (1961), using an electromagnetic flowmeter to measure the volume of digesta passing through a closed loop of a duodenal re-entrant cannula, estimated flow rates of 464 to 493 millilitres per hour in sheep fed 700 grams of hay per day. The measurements were made without disconnecting the cannulae and thus should not have interfered with the flow of digesta. The recording periods, however, were limited to only 1 to 3 hours duration. Anti-peristalsis occurred at frequent intervals and a considerable amount of back-flow was evident. The back-flow was more pronounced in goats than in sheep, however, the author was unable to conclude that this represented a species difference as the goats received rations different from those fed to the sheep. Phillips and Dyck (1964) studied abomasal outflow in sheep by means of a marker-dilution technique employing polyethylene glycol. For high straw rations and high starch rations the volumes of flow were 484 and 295 millilitres per hour respectively. For the high straw ration a greater quantity of dry matter escaped digestion in the reticulo-rumen. A monophasic, diurnal flow pattern was evident with the once a day feeding regime, the peak flow rates occurring just prior to and during feeding.

The various abomasal flow rates that have been determined are similar in magnitude to rumen outflow rates. Hogan (1964) pointed out that estimated abomasal secretory volumes are approximately equal to the volume of water absorbed in the omasum. However, on ad libitum feeding of sheep, that author found that the volume entering the duodenum was always greater than that leaving the reticulorumen. It was concluded that on ad libitum intakes the volume of abomasal secretion exceeds omasal water absorption. Masson and Phillipson (1952) in experiments with sheep calculated daily abomasal secretory volumes of 5 - 6 litres. Based on the chloride concentrations of omasal and abomasal digesta, these authors considered that the ratio of gastric juice to omasal contents was approximately 2.1 or greater.

The volume of digesta passing from the terminal ileum of sheep has been measured by Hogan and Phillipson (1960). Re-entrant cannulae were established at the terminal ileum and digesta was collected from the proximal cannula, measured, and returned through the distal cannula. Flow from the ileal cannula was intermittent and the volumes collected, when averaged over 12 hours, ranged from 160 to 240 millilitres per hour. These are similar to the mean flow rates of 140 and 150 millilitres per hour recorded by Bullen, Scarisbrick and Maddock (1953) as cited by Hogan and Phillipson (1960). Observations of Goodall and Kay (1965) confirm the intermittent nature of the flow of digesta from the ileum of sheep. They reported that a series of flows would occur during a period of 30 minutes alternating with a period of inactivity. Hogan and Phillipson (1960) indicated that a net absorption of about 4 litres of water per day occurred during passage of digesta through the small intestine and a similar quantity disappeared during passage through the large intestine. It is apparent that, of the large volume of water that enters the duodenum from the abomasum, only a small percentage is excreted in the feces. Considering that various secretions such as bile, pancreatic juice and those from intestinal mucosal glands are poured into the lumen of the gut, to become reabsorbed in part or in total, the small and large intestines together must have a tremendous water-absorbing capacity.

Movements of the Digestive Tract.

With respect to both ruminants and non-ruminants, the passage of digesta along the alimentary tract has been attributed largely to the co-ordinated movements of various segments of the tract. The qualitative observations of Stevens, Sellers and Spurrell (1960) demonstrate the inter-relationships between the movements of the structures of the forestomachs of dairy cattle. The experiments conducted were short-term in nature with durations of only 1 or 2 hours. Recordings were made of pressure changes in the rumen, reticulum, omasal canal, omasal body and the abomasum. Flow of digesta was estimated by fluoroscopic examination, palpation, a funnel reservoir system and by the use of the Pitot tube principle. Integration of the motility of the various segments of the fore-stomachs was apparent and is described as follows: The rumen undergoes two cycles of contraction, the primary cycle always being preceded by contraction of the reticulum while the secondary cycle can occur without a prior reticular contraction. The omasal canal exhibits pressure changes which are integrated with the primary and secondary cycles of the rumen. It was observed that flow of fluid from the reticulum to the omasal canal could occur on two distinct occasions during a reticulo-omasal cycle. Flow could occur during the second reticular contraction and also during relaxation of the omasal canal following its contraction. The relaxation of the omasal canal was deemed to be the more important event of the two in transferring material from the reticulum to the omasum as it had a longer duration. Based on palpation, reticulo-omasal flow accompanying the second reticular contraction was noticed only at the peak of the contraction. Measurements made in the omasal canal indicated that flow velocity was the greatest and of longest duration during relaxation of the omasal canal. Contraction of the omasal body did not occur regularly in every reticulo-omasal cycle. When it did occur, it began its wave of contraction after the primary contraction of the omasal canal. The greatest volume of omaso-abomasal flow was noted to accompany contractions of the omasal body, however, at rare intervals the omaso-abomasal orifice was closed during omasal body contractions. At these times, a backflow of digesta into the reticulum was palpated.

The authors have described the function of the omasum as a two-stage pump. The first stage of action is the aspiration of fluid into the canal when the pressure differential between the reticulum and omasal canal is favourable, followed by the expression of fluid between the leaves of the omasum into the omasal body by contraction of the canal. The second stage is the expulsion of digesta into the abomasum when the omasal body undergoes contraction.

The reticulo-rumen was distended by insufflation of N_2 and observations were made simultaneously on the omasal activity. Distention of the reticulo-rumen within expected physiological ranges did not affect the amplitude of omasal contraction. Also, emptying of the rumen had no effect upon the activity of the omasum. It did appear, however, that the abomasum exerted a controlling effect upon the omasum. Distention of the abomasum by injecting 1500 millilitres of water into a balloon contained in the lumen decreased the amplitude of both the omasal canal and omasal body contractions. No effect upon rumen or reticular motility was noted during the resulting omasal inhibition. Rapidly emptying the abomasum enhanced the amplitude of omasal canal contractions.

Because of the intermittent occurrence of the omasal body contractions, the authors suggest that this event is partly dependent upon omasal distention. To support this idea, they explained that rapid filling of the omasum with water from the funnel reservoir system was followed by omasal body contraction.

According to Dukes (1955) the most important propulsive activity of any portion of the digestive tract is the rhythmic, peristaltic rushes are usually initiated in the small intestine by distention of the gut caused by the presence of ingesta, although waves of contraction may occur in the absence of digesta and sometimes are initiated by a gastric wave reaching the pylorus. Early studies with sheep (Dukes and Sampson; 1937) revealed the occurrence in the small intestine of rhythmic segmentations, pendular movements and peristaltic rushes. Considerable periods of relative inactivity of the small intestine were also observed. This may be related to the observation that the flow of digesta from the terminal ileum is intermittent (Hogan and Phillipson; 1960), and Goodall and Kay; 1965). The caecum and colon both showed powerful propulsive movements and often displayed rhythmic back and forth movements of digesta. There was no influence of rumen motility on cecal motility as judged by recording the frequency of contractions of these two organs during the time that the animal was being fed hay. This does not necessarily exclude the possibility of a correlation between rumen motility and cecal motility on a long term basis. For example, increasing the daily intake of a ration has been shown to result in an increase in the mean number of reticular contractions daily (Freer et al; 1962). At the same time there would be a larger quantity of fecal residues excreted daily. This would be expected to stimulate increased caecal motility. As I have already mentioned, Coombe and Kay (1965) suggested that intestinal distention may be the necessary stimulus to increased propulsive motility of the intestinal tract.

Qualitative and Quantitative Aspects of Intestinal Digestion.

Estimates have been made of the concentrations of nutrients in the various sections of the intestinal tract. Boyne et al. (1956) in a slaughter experiment with sheep analysed the digesta removed from each segment of the gut. The concentration of nitrogen was found to increase markedly in the proximal small intestine from the concentration found in the abomasum. Progressing distally from the proximal small intestine there was a gradual reduction in nitrogen concentration.

The high concentration in the first segment of the small intestine was attributed to additions of nitrogenous substances rather than a more rapid rate of absorption of products of carbohydrate digestion. It was noted that the ratio of energy to insoluble ash was highest in the proximal small intestine and decreased distally from this rate. The concentration of volatile fatty acids was greatest in the caecum, colon and distal small intestine and lowest in the abomasum. The presence of significant concentrations in the lower part of the small intestine suggested the possibility that some microbial fermentation was occurring in this region. The significance of intestinal fermentation would lie partly in the postulated synthesis of certain vitamins valuable to the animal but also partly in the possible cellulolytic activity of micro-organisms. Gray (1947) estimated that 30 per cent of the digested cellulose was broken down in the large intestine. Goodall and Kay (1965), however, cite unpublished results which indicated that approximately 12 per cent of the dietary cellulose that becomes digested is degraded in the large intestine of sheep.

Hogan and Phillipson (1960) reported that of 275 grams of dry matter digested by sheep during a 12 hour period, 11 per cent was digested in the small intestine and 19 per cent in the large intestine. The ration consisted of 300 grams of hay plus 200 grams of concentrate. Harris and Phillipson (1962) in a study of sheep consuming 750 grams of hay daily, found intestinal losses of organic matter, nitrogen and ash to be approximately 82 grams, 7 grams and 48 grams respectively. Phillips and Dyck (1964) estimated the extent of digestion of organic matter in the intestines of sheep fed high straw and high starch rations. In the intestines the residues of gastric digestion of the high starch rations were apparently digested to a significantly greater extent than were the residues of the high straw rations.

Horrocks and Phillips (1964) conducting a slaughter experiment analysed the gut contents of European and Zebu steers. Sodium and potassium concentrations both declined in each successively distal segment of the intestinal tract which indicated a marked absorption of these elements prior to the excretion of the residues. Absorption of phosphorus was found to occur from the distal small intestine. The results for calcium and magnesium suggested possible secretions of these elements into the small intestine, however the authors state that particular sites for their absorption could not be determined as the concentration changes were small and variable.

According to Coombe and Kay (1965), a time limit may be set to digestion and absorption of digestion products by a rapid rate of passage through the intestines. There is some evidence that water absorption may be reduced by a rapid rate of passage and these authors mentioned that large amounts of water and salts have appeared in the feces about an hour following the release of accidental blockage of ileal re-entrant cannulae.

Castle (1956a,b) and Blaxter et al. (1956) in studies with goats and sheep, respectively observed positive correlations between intestinal retention time and fecal dry matter concentration. Hintz and Loy (1966) found a similar relationship in horses. This suggests an effect of passage time on water absorption. Castle (1956c), however, found no such relationship during another experiment with goats.

The literature contains few reports describing the relationship between intestinal passage time and fecal losses of specific nutrients other than water. Smith (1963) obtained data which indicated that magnesium absorption in milk fed calves is higher when the passage time of digesta through the small intestine is longer. However, in a study with adult rats Smith (1966) found no difference in endogenous magnesium excretion when either 5 per cent or 10 per cent cellulose was added to the basal ration even though fecal dry matter output was greatly increased by these treatments. Kleiber, Smith, Ralston and Black (1951) reported that fecal excretion of phosphorus was positively correlated with total fecal output in the cow.

Yang and Thomas (1965) used a lignin ratio technique to study the absorption and secretion of various nutrients along the alimentary tract of young calves. There was net absorption of calcium from the rumen and the lower gastrointestinal tract but in the upper small intestine there was a definite secretion of this element. In one trial reported by these authors, total per cent calcium absorption was significantly greater on the low fiber ration than on the high fiber ration but in a second trial there was no significant effect of dietary fiber level upon total per cent calcium absorption.

Nitrogen excretion in rats has been positively correlated with fecal output by Mitchell (1924). That a similar relationship occurs in pigs, has been demonstrated by Cunningham, Friend and Nicholson (1962). These authors fed a basal ration with various levels of wood cellulose added. There was a significant increase in fecal dry matter excretion as the level of cellulose was increased. This was accompanied by a marked increase in fecal nitrogen excretion although the protein intake was the same for all treatments. The extra fecal protein excreted was approximately equal to the weight of 14 per cent of the extra fecal crude fiber excreted. While the passage time through the digestive tract of the pigs was not determined, one might expect that the increased fecal output would be accompanied by a shorter passage time. Whiting and Bezeau (1957) also report that increasing the cellulose content of the ration for pigs significantly reduced the true and apparent digestibility of the protein and increased metabolic fecal nitrogen excretion.

Considering the examples cited above, it is obvious that the dietary intake of certain nutrients necessary to meet an animal's basic requirement may be significantly influenced by variations in the physical form and digestibility of the ration.

EXPERIMENTAL METHODS

Experiment I (Preliminary)

This experiment was conducted in order to study the effects of infusing large volumes of fluid into the duodenum of sheep upon *ad libitum* feed intake, water consumption, intestinal retention time, and dry matter and nitrogen digestibility.

Animals and Diets

Two Suffold wethers, which had been surgically fitted with duodenal re-entrant cannulae 6 months previously, were used. The observations were made during two experimental periods. Ground, pelleted, alfalfa-bromegrass hay was fed *ad libitum* throughout the experiment, however, the hay fed during period I was from an earlier cutting than that fed during period II. The dry matter and nitrogen contents of the respective hays are listed in Table I. A mineral supplement consisting of 1 part bonemeal, 1 part calcium phosphate and 1 part sodium chloride was fed *ad libitum* throughout the experiment.

Table I: Composition of the hays fed during experiment I

Period	Dry matter (%)	Nitrogen (%)
I	91.91	3.49
II	88.79	2.71

Treatments

Period I consisted of a 14-day pre-infusion subperiod followed immediately by a 14-day subperiod during which sheep 4154 received a duodenal infusion of 6 litres/day of tap water and sheep 4135 received an infusion of 6 litres/day of a 0.83 per cent glucose solution. The glucose treatment was expected to provide an amount of digestible energy approximating that derived from intestinal digestion of alpha-cellulose and therefore to serve as a control for infused digestible energy.

Period II consisted of 35 days during which the duodenal infusion of 6 litres/day of tap water was compared with the duodenal infusion of 6 litres/day of a 6 per cent suspension of alpha-cellulose powder*. A simple changeover regime was applied (Table II).

In both periods I and II, during the last eight days of each subperiod, the daily intakes of feed and water were recorded and total feces and urine excretions were collected and recorded. Intestinal passage times were estimated on the second and seventh day of each eight-day collection period. During each period the animals were kept in metabolism crates.

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* Alphacel. Nutritional and Biochemical Corporation, Cleveland, Ohio.

Table II: Treatment Schedule of Experiment I.

Sheep			Length of Period (Days)
Period	4154	4135	
I	No infusion	No infusion	14
	water	glucose soln.	14
II	alpha-cellulose	water	18
	water	alpha-cellulose	17

Infusion Technique

Fluids (see Treatments) were administered to the duodenum via 1/8 inch I.D. "Jayon" P.V.C. tubing assembled to a peristaltic pump which was adjusted to deliver a volume of approximately 250 millilitres per hour. Infusion was continuous throughout each 24 hour period except for one-half hour each morning when the pump was stopped to allow measurement of the fluid remaining in the reservoirs and to refill the latter with fresh fluid. The infused fluids were warmed to about 38 degrees centigrade before entering the duodenum by suspending a coil of the infusion delivery tube in a warm water bath.

Cellulose powder rapidly settles out of suspension in water, but preliminary studies indicated that a 0.2 per cent agar solution greatly retarded the settling out of the alpha-cellulose. In order to maintain a uniform distribution of the alpha-cellulose in the reservoirs over long periods, continuous agitation was necessary and was accomplished by bubbling air slowly through the fluid.

Estimation of Intestinal Retention Time (R_i)

At 9:30 A.M. on day two and day seven of each collection period, one gram of sieved fecal particles, stained red with Basic Fuchsin, was introduced into the distal duodenal cannula. Forty millilitres of warm water were used to flush all the stained particles into the lumen of the duodenum. This procedure was completed within five minutes for each sheep.

Feces samples were collected at intervals for thirty-six hours following the introduction of the stained particles into the duodenum. In order to estimate the number of stained particles excreted during each time interval, ten grams of moist feces from a given sample were macerated by mortar and pestle with fifty millilitres of water and the number of stained particles in four millilitres of this suspension were counted using a X5 magnification lens. The concentration of stained particles in a given feces sample was calculated by multiplying the mean of duplicate counts by the dilution factor. Mean particle-hours was calculated by multiplying the number of stained particles excreted in a given time interval by the mean time taken for those particles to appear in the feces. The sum of these values for all collections divided by the total number of stained particles excreted gave intestinal retention time in hours. A mean intestinal retention time was calculated for each period from the values obtained on day two and day seven.

Feces Collection

The total feces production was collected in canvas bags and weighed daily and 10 per cent aliquots were frozen and stored in polyethylene bags for future analysis. Eight-day composite feces samples were prepared by mixing the daily aliquots in a "Hobart" mixer for 10 minutes.

Analysis of Feed and Feces

Dry matter was determined on feed, feces and alpha-cellulose by drying to constant weight in a forced-air drying cabinet at 80 degrees centigrade. The samples of dried feed and feces were ground in a Wylie mill and subsequently analysed for total nitrogen according to the Kjeldahl procedure (A.O.A.C.; 1960).

Experiment II

In experiment II treatments were used which would give rise to a fairly wide range of predictable fecal dry matter outputs and at the same time allow for a constant oral intake of dry matter and other nutrients. Feeding either a high grain or a high roughage ration and infusing into the duodenum either water or an alpha-cellulose suspension were used to independently vary the quantities of non-digested residues passing through the forestomach and the lower intestinal tract respectively.

Animals

Four Western Range Wethers weighing between 45 and 50 kilograms were surgically fitted with rumen and duodenal cannulae (machined from "Delrin") at least two months prior to the start of the experiment. The animals were kept in individual stalls prior to and between experimental periods. For the experimental periods the animals were moved into metabolism crates. The sheep were trained by exposing them to the experimental routine several times before starting the experiment.

Treatment

Two rations (all hay or 75 per cent grain, 25 per cent hay) were fed along with two infusion treatments (water or alpha-cellulose) in a 4x4 Latin Square. The four treatments were as follows:

1. Hay ration with water infused into the duodenum.
2. Hay ration with alpha-cellulose infused into the duodenum.
3. High grain ration with alpha-cellulose infused into the duodenum.
4. High grain ration with water infused into the duodenum.

It was calculated that treatments 1 and 3 would result in approximately equal daily fecal dry matter outputs.

During the remainder of this paper these treatments will be designated HW, HC, GC and GW respectively.

Each sheep received each treatment in a randomized sequence based on a 4x4 Latin square. The animals were allowed 14 days to become adjusted to each ration prior to each 10 day collection period. Four days prior to each collection period the animals were moved into the metabolism crates and the infusion treatments were begun.

Rations

The rations (Table III) were fed at the level of 1200 grams per day, divided into two equal portions offered at 8:30 AM and 4:30 PM. There were no refusals and the feed was generally consumed within 30 - 45 minutes. The hay consisted of a second cutting alfalfa-bromegrass mixture and was fed in a ground, pelleted form. Coarsely ground barley formed the basis of the grain ration. An attempt was made to approximately equalize daily intake of nitrogen and the major mineral elements for both rations. This was done by the addition of various mineral and nitrogen supplements to the 1200 grams of hay or grain ration (table III).

Table III Ration Composition (grams/day)

Ingredient	Hay Ration	Grain Ration
Alfalfa-Brome Hay Pellets	1200.0	300.0
Barley	-	870.0
Soybean meal	-	30.0
NaCl	6.0	6.2
Calcium Phosphate	11.7	-
Potassium Acetate	-	16.5
Potassium Bicarbonate	-	16.5
Bone meal	-	7.1
Calcium Carbonate	-	14.0
Magnesium Chloride	-	7.6
Total	1217.7	1267.9

Enough daily allotments of each ration for the whole experiment were weighed and dispensed into polyethylene bags before the start of the experiment.

Infusion of Fluids into the Duodenum

Four litres per day of either tap water or a 6 per cent suspension of alpha-cellulose powder were infused. The latter resulted in the addition of approximately 200 grams per day of alpha-cellulose to the duodenal contents.

Preparation of the cellulose suspension and the infusion technique was the same as that described for experiment I.

Estimation of Intestinal Passage Time

The technique used for estimating intestinal passage time was basically the same as that described for the preliminary experiment, however, the feces were examined for the presence of stained particles during intervals up to 56 hours following the introduction of particles into the duodenum.

In this experiment the excretion pattern of stained particles administered on the second day of the collection period was determined.

Recording of Reticulum Movements

Pressure changes occurring in the reticulum of each sheep were recorded on a kymograph. A small balloon inflated with air and connected by "Jayon" tubing to a tambour-ink recorder was placed into the reticulum via the rumen cannula. This system proved satisfactory for determining the frequency of reticular movements.

Reticular movements were recorded during eight half-hour periods for each of the first six days of each collection period. On each of these days eight different half-hour periods were sampled so that, at the end of six days, reticulum motility for each of the forty-eight half-hour periods of the day had been sampled once. An automatic timer capable of switching on the kymograph for any half-hour period during the day or night was used. It was re-set daily to record at the appropriate times. The forty-eight half-hour intervals were assigned numbers drawn from a random number table and when these numbers were ranked they formed the basis of the sampling schedule.

The daily frequency of reticulum contractions was calculated by summation of the numbers recorded during the forty-eight half-hour periods.

Collection of Feces and Urine

Feces were collected and sampled in the same manner as described for the preliminary experiment.

Urine was collected in large bottles, under a layer of Toluene, from a polyethylene covered tray situated beneath the floor of the metabolism crate. The daily urine volume for each sheep was recorded and a 5 per cent aliquot was frozen and stored in a polyethylene bottle. At the end of each collection period a composite urine sample for each sheep was prepared by combining the daily aliquots.

Chemical Analysis

Dry matter and nitrogen content of feed and feces samples were determined by the methods outlined for experiment I.

Cellulose content was determined on feed, alpha-cellulose and feces according to the method of Crampton and Maynard (1938).

Sodium and potassium were determined by flame photometry. Feed and feces samples were first subjected to wet ashing with concentrated nitric acid and concentrated perchloric acid (2.5 to 1 mixture). The ash was dissolved and diluted with deionized water and the resulting solution analysed in the flame photometer. Urine samples were diluted with deionized water and the readings were taken directly in the flame photometer without prior ashing.

Calcium and magnesium determinations were made by atomic absorption spectrophotometry. The feed and composite feces samples were first ashed in a muffle furnace at 600 degrees centigrade for 2 hours and the ash subsequently dissolved in concentrated HCl. The acid solution was diluted with a lanthanum solution and deionized water to give the appropriate concentration of either calcium or magnesium as well as a final concentration of 1 per cent lanthanum.

Statistical Analysis

The data from experiment II were examined by analysis of variance for a 4x4 Latin Square. The differences between treatments were tested for significance using Duncan's New Multiple Range test (Steel and Torrie (1960)).

RESULTS

Experiment I

Feed Intake

Although there was a gradual decline in the *ad libitum* feed intake of each sheep from the beginning to the end of the experiment this parameter did not appear to be markedly affected by the infusion treatments. (see figure 1 and Table IV).

The *ad libitum* intake of sheep 4154 was approximately the same on both the water and cellulose treatments during period II. For sheep 4135 the feed intake on the cellulose treatment was lower than on the water treatment.

Daily water intake and excretion

During period I (no infusion) the daily voluntary consumption of water was 7.4 litres and 10.0 litres for sheep numbers 4154 and 4135 respectively. The infusion of fluid into the duodenum reduced the daily voluntary consumption of water by a volume approximately equal to that infused (Table V). Thus the total daily water intake was not changed by the infusion treatments. For both sheep fecal water output was highest for "no infusion" and lowest for "cellulose infusion".

Intestinal Retention Time (R_i)

The time taken for digesta to pass through the intestinal tract was estimated to range from 7.67 to 10.52 hours.

TABLE IV

Sheep	Period	Infusion Treatment	Feed Intake (gm/day)	Fecal Dry Matter Concentration (%)	Fecal Dry Matter Output (gm/day)	Dry Matter Digestibility (%)	R_i* (hrs.)	Dry Matter Infused (gm/day)	Indigestible DM in Intestinal Tract ** (gm)
4154	I	None	3014	29.55	1141	58.83	8.64	-	411
		Water	2820	30.60	1108	57.26	10.52	-	486
	II	Water	2337	37.35	968	53.51	9.99	-	403
		Cellulose	2338	33.73	1208	49.81	10.06	329	506
4135	I	None	3390	24.70	1251	59.85	7.67	-	400
		Glucose	3018	28.81	1227	56.52	8.14	48	416
	II	Water	2792	27.82	1167	53.17	8.43	-	410
		Cellulose	2061	33.52	1154	46.79	10.39	324	500

* See Experimental Methods.

** Indigestible DM in intestinal tract = $\frac{\text{fecal DM}}{24} \times R_i$

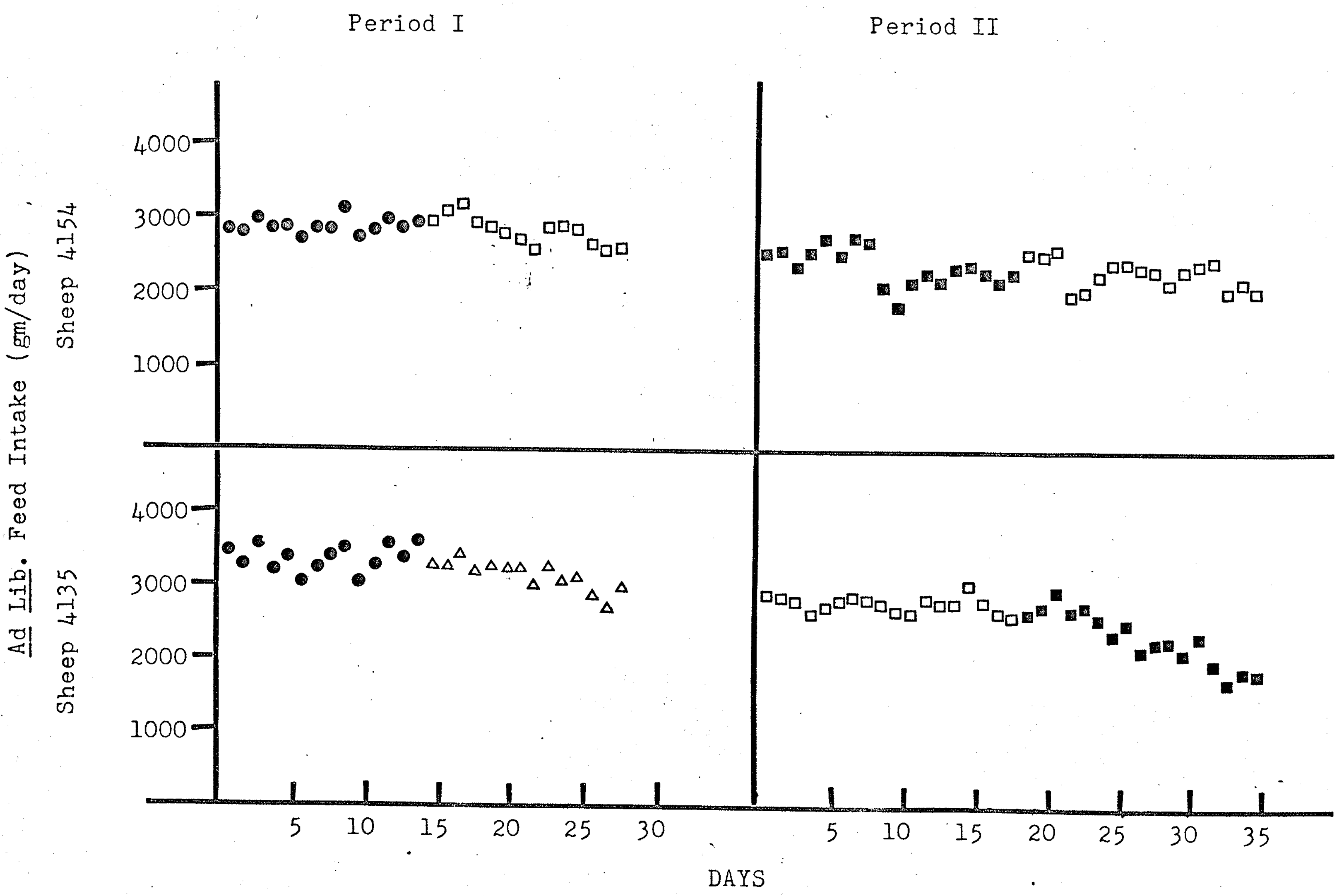


Figure 1: Feed Intake of Sheep during Experiment I.

● - No Infusion

□ - Water Infusion

△ - Glucose Infusion

■ - Cellulose Infusion

TABLE V

Daily Water Intake and Excretion (litres per day)

Sheep	Period	Infusion Treatment	Water Consumed	Water Infused	Total Water Intake	Fecal Water	Urine Volume
4154	I	None	7.41	nil	7.41	2.71	2.85
	II	Water	2.28	6.24	8.52	2.51	2.97
		Water	0.95	5.91	6.86	2.37	2.28
		Cellulose	1.03	5.86	6.89	1.63	2.80
4135	I	None	10.00	nil	10.00	3.81	3.60
	II	Glucose	4.79	5.80	10.59	3.03	3.98
		Water	2.53	6.34	8.87	3.03	2.98
		Cellulose	1.39	5.82	7.21	2.29	2.43

The shortest retention times recorded for both sheep occurred when no infusions were being made and the longest retention times occurred when cellulose or water was infused (Table IV).

Dry Matter Digestibility

The infusion of either water or 0.86 per cent glucose solution during period I did not have marked effects upon dry matter digestibility (Table IV). The hay fed during period II had an apparent dry matter digestibility slightly lower than for the hay fed during period I. The infusion of cellulose during period II caused a reduction in apparent digestibility. In the latter case digestibility was calculated on the basis of total dry matter intake (dry matter consumed plus dry matter infused via the duodenum).

Apparent Nitrogen Digestibility

The hay fed during period II had a lower apparent nitrogen digestibility than that fed during period I. For neither of the two hays fed did there appear to be any marked effect of the duodenal infusion treatments upon nitrogen digestibility (Table VI). For sheep 4154 during period II the nitrogen intake on both the water treatment and cellulose treatment was the same. The fecal excretion of nitrogen was also equal on both treatments although the daily fecal dry matter output was much higher for the cellulose treatment.

TABLE VI

Sheep	Period	Infusion Treatment	Nitrogen Intake (gm/day)	Fecal Nitrogen Excretion (gm/day)	Nitrogen Digestibility %
4154	I	No infusion	100.34	25.74	74.35
		Water	93.88	22.83	75.69
	II	Water	58.24	19.50	66.51
		Cellulose	58.37	19.04	67.39
4135	I	No infusion	112.87	30.66	72.84
		Glucose	100.48	25.97	74.15
	II	Water	69.72	21.68	68.91
		Cellulose	51.33	17.09	66.70

Experiment II

Intestinal Retention Time

The intestinal retention time (R_i) for the GW treatment was significantly ($P<0.05$) longer than those for the GC, HW, and HC treatments (Table VII). There were no significant differences among the latter three treatments. It may be noted, however, that consistently shorter retention times were found for HC compared with HW treatments.

There appeared to be a curvilinear relationship between R_i and daily fecal dry matter output (Figure 2). For comparative purposes the data from experiment I have also been included on this graph. This relationship is examined in detail in the discussion.

Frequency of Reticular Contractions

There was a marked tendency for the number of reticular contractions to be greater for the hay than for the grain ration (Table VII). Cellulose infused into the duodenum resulted in a consistent increase in reticular motility over the level observed in the corresponding water infusion treatment, but this effect of cellulose infusion was greater when grain was being fed. The mean reticular frequency of contraction for the GW treatment was significantly ($P<0.05$) lower than for GC, HW, and HC treatments, but there were no significant differences amont the latter three. There were highly significant ($P<0.01$) differences among sheep in number

TABLE VII

Fecal excretion and digestibility of dry matter, Intestinal Retention Time and number of Reticular Contractions daily. (Experiment II)

Sheep	Treat.	D.M. Infused (gm/day)	Fecal D.M. Output (gm/day)	D.M. Digestibility (%)	Ri (hours)	No. of Retic. Contractions Daily
130	HC	235	738	45.75	13.18	1705
	HW		518	53.95	15.60	1608
	GC	205	468	65.72	13.70	1632
	GW		290	74.99	18.52	1511
54	HC	242	684	49.97	13.13	1601
	HW		533	52.67	15.03	1551
	GC	203	525	61.51	14.21	1619
	GW		249	78.56	27.07	1499
43	HC	228	693	48.84	11.21	1533
	HW		513	54.38	12.36	1501
	GC	224	461	66.69	15.66	1555
	GW		321	72.34	20.24	1416
49	HC	209	717	46.31	10.19	1825
	HW		559	50.34	10.96	1822
	GC	216	467	66.13	13.54	1640
	GW		263	77.35	16.55	1597
Mean	HC	229	708^{a}	47.72	11.93^{a}	1666^{a}
	HW		531^{b}	52.84	13.49^{a}	1621^{a}
	GC	212	480^{c}	65.01	14.28^{a}	1612^{a}
	GW		281^{d}	75.81	20.60^{b}	1506^{b}
			($p<0.01$)		($p<0.05$)	($p<0.05$)

Means with different superscript letters are significantly different.

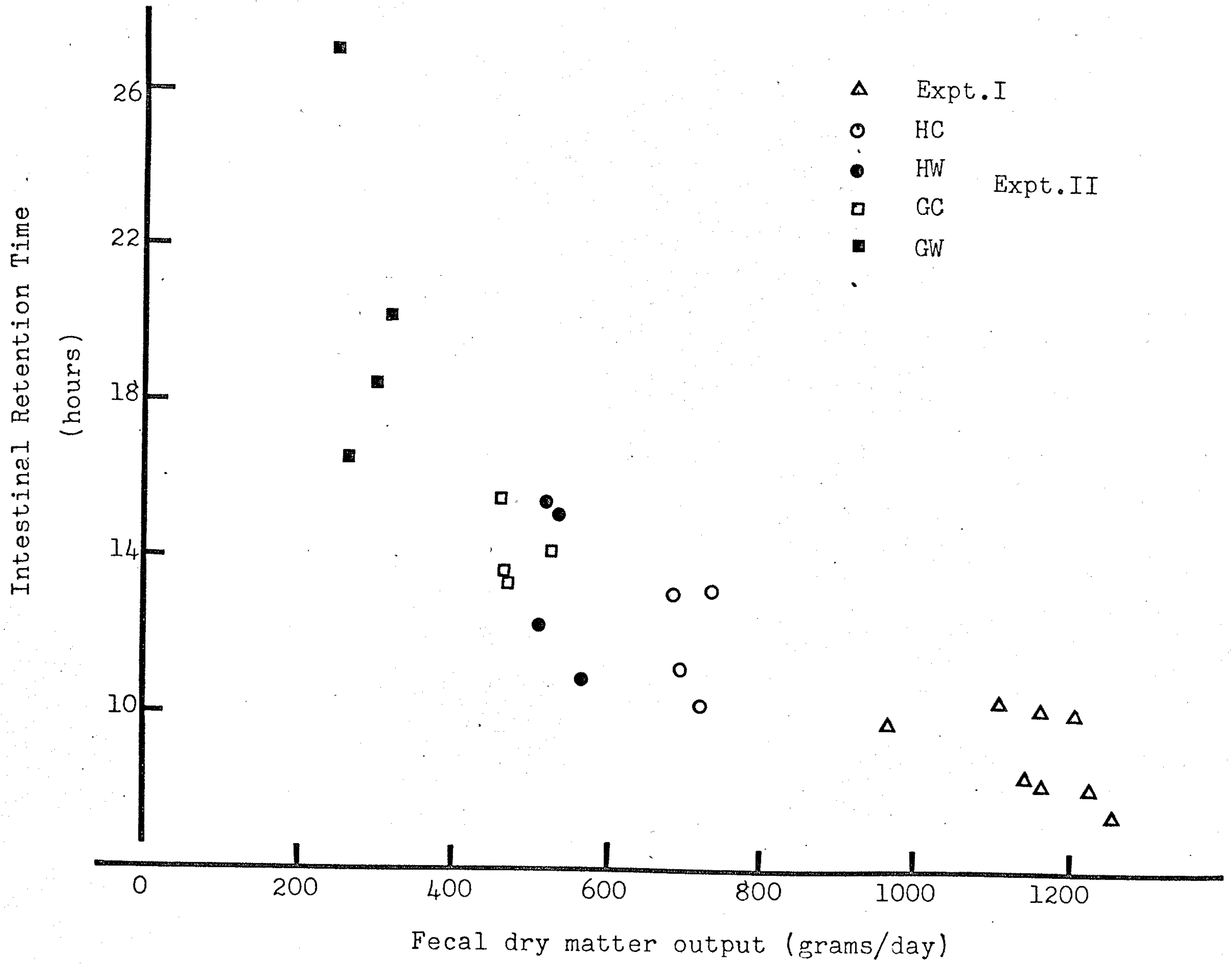


Figure 2: Relationship between intestinal retention time and fecal dry matter output.

Table III (a)

Daily dietary intake of various ration components. (Experiment II)

	Hay	Grain
Dry Matter (gm.)	1126.0	1161.0
Cellulose (gm.)	401.0	161.0
Nitrogen (gm.)	22.13	22.46
Ash (gm.)	121.27	81.87
Sodium (mEq)	187.8	129.8
Potassium (mEq)	546.6	531.7
Calcium (gm.)	10.15	8.57
Magnesium (gm.)	3.34	2.81

of reticular contractions per day.

A diurnal variation in frequency of reticular contractions was indicated (Figure 3a and 3b). A definite pattern of activity of the reticulum was apparent regardless of treatment, with frequencies rising during the hour prior to each feeding and reaching a peak at the feeding times 8:30 A.M. and 4:30 P.M. The frequency mid-way between feedings and at night between 6:00 P.M. and 2:00 A.M. was lower for the GW treatment than for all other treatments.

Fecal Dry Matter Output and Apparent Dry Matter Digestibility

There was a significant (Table VII) treatment effect upon daily fecal dry matter output and on dry matter digestibility ($P<0.01$). The infusion of cellulose into the duodenum increased fecal dry matter output by approximately 200 grams daily when grain was being fed and by approximately 180 grams daily when hay was being fed. In one case (sheep 54 receiving the grain ration) cellulose infusion caused an increase in daily fecal dry matter excretion by an amount greater than the quantity of cellulose dry matter infused. The mean dry matter digestibilities of the grain and hay rations with water infusion were 75.81 and 52.84 per cent respectively.

Intake, Excretion, and Digestibility of Cellulose

The four treatments used in this experiment resulted in wide variations in total daily cellulose intake by the

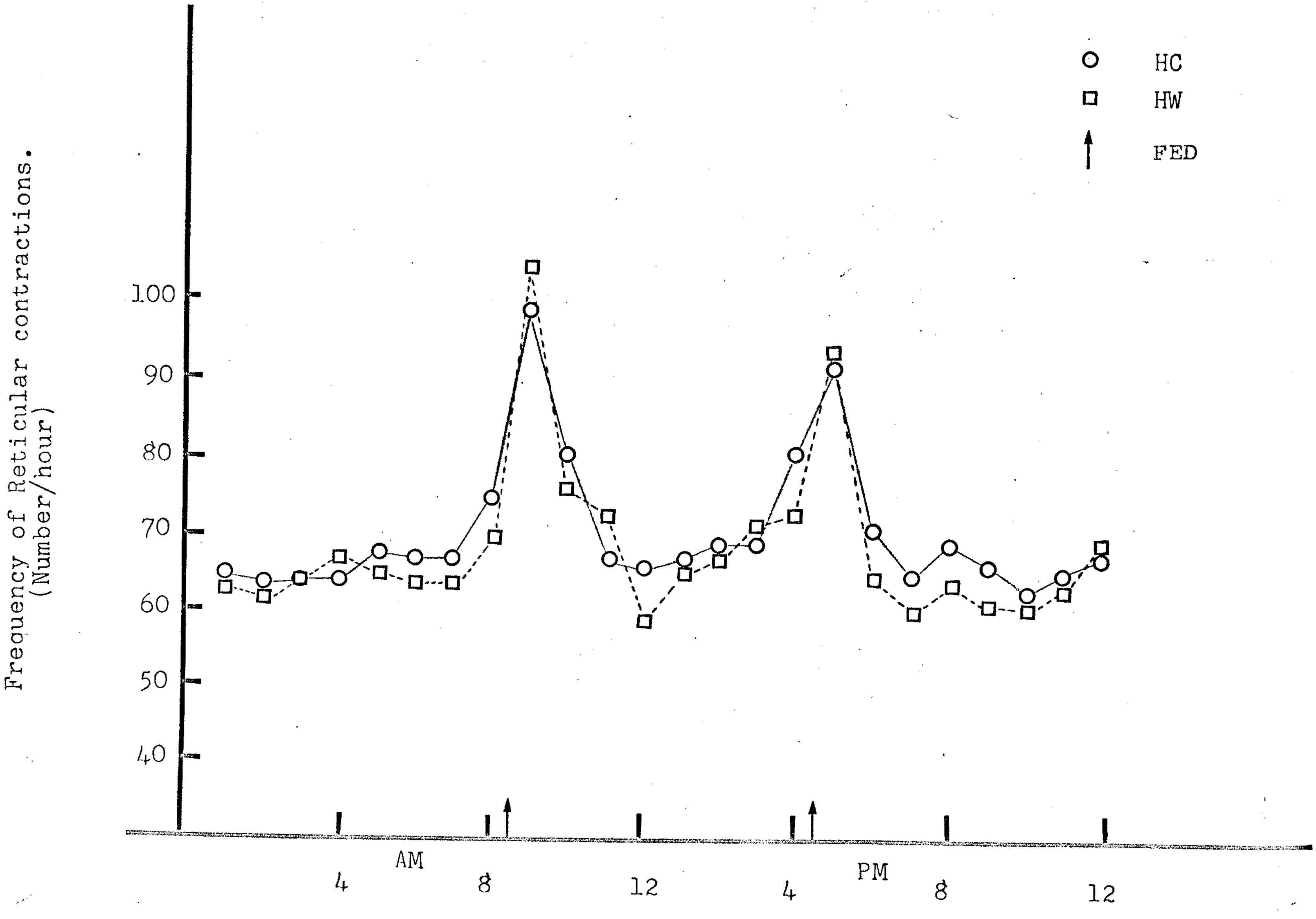


Figure 3(a): Diurnal variation in hourly frequency of Reticular Contractions. (Experiment II).

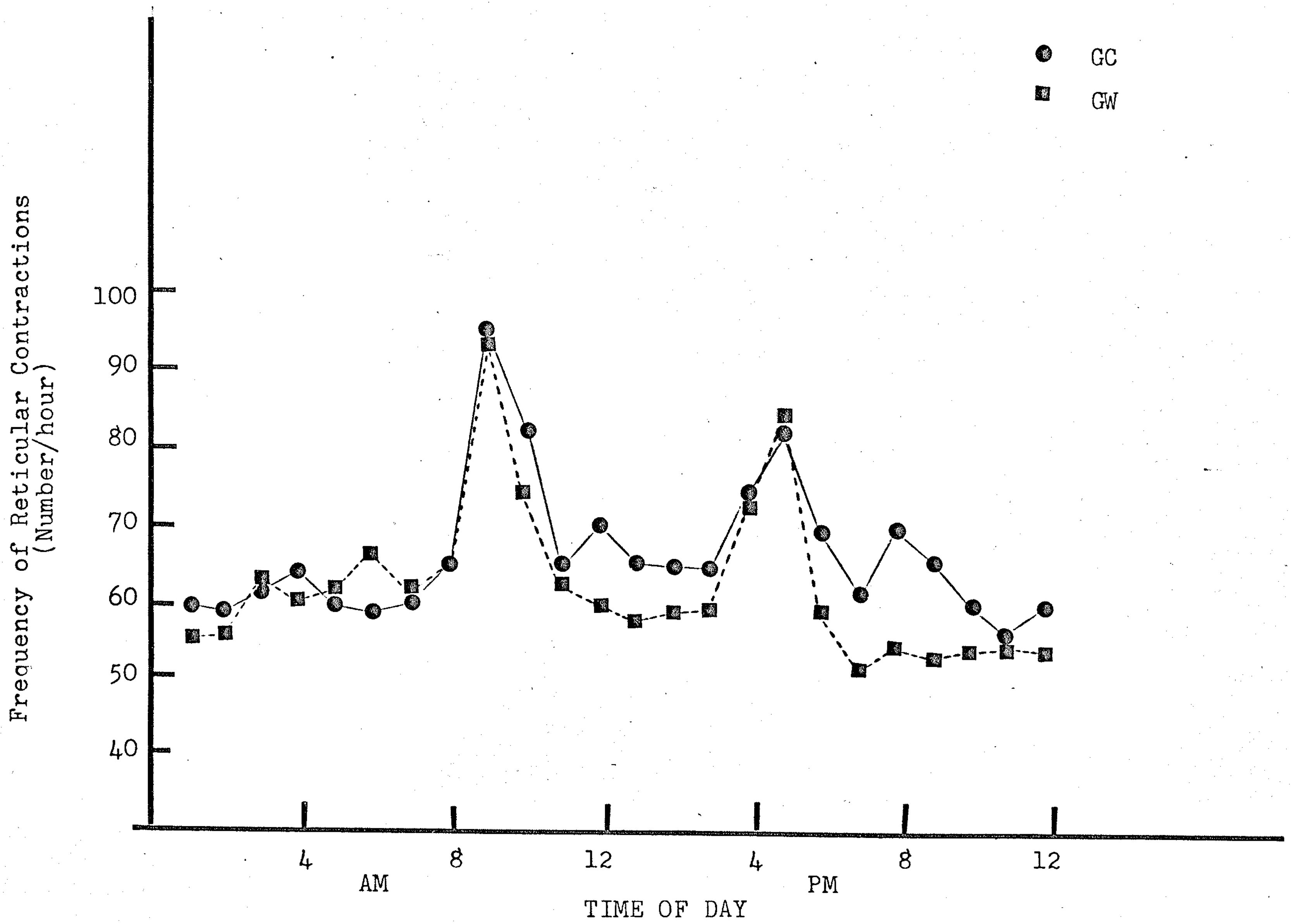


Figure 3(b): Diurnal variation in Hourly Frequency of Reticular Contractions. (Experiment II) sheep (Tables IIIa and VIII). Dietary intake of cellulose was 401 grams per day on the hay ration and 161 grams per day on the grain ration. The daily amount of cellulose infused was approximately 200 grams.

The digestibility of cellulose of both rations was the same during water infusion and had an average value of 50 per cent. The infusion of cellulose into the duodenum caused a significant decrease ($P<0.05$) in apparent cellulose digestibility on the hay rations and a highly significant decrease ($P<0.01$) on the grain ration (Table VIII).

The extra fecal cellulose excretion on the cellulose treatments was calculated by difference from the appropriate water control. Based upon the difference method, an estimate was made of the intestinal digestion of infused cellulose. The values thus calculated for intestinal cellulose digestibility ranged from 11 per cent to 36 per cent of the infused cellulose. The mean digestibility values were 32 and 23 per cent for the hay and grain rations respectively.

Water Intake, Excretion, and Apparent Balance

Approximately 4 litres per day of water were infused into the duodenum and the sheep voluntarily consumed amounts which ranged from about 0.5 to 5.4 litres per day, including water in the feed (Table IX). Slightly higher total water intakes occurred when grain was being fed than when hay was fed, how-

TABLE VIII

Experiment II: Daily intake, fecal excretion and digestibility of cellulose. (Values for individual sheep and treatment means.)

Sheep	Treat.	(A) Cellulose Infused into the duodenum (gm/day)	Fecal Cellulose (gm/day)	Cellulose Digestibility (%)	(B) Extra Fecal Cellulose (gm/day)	Intestinal digestion of infused Cellulose $\frac{(A-B)}{A}$ (%)	(SE)
130	HC	213	358	41.72	154	27.65	
	HW		204	49.21			
	GC	186	208	39.92	121	34.85	
	GW		87	45.75			
54	HC	220	320	48.37	138	36.69	
	HW		182	54.50			
	GC	184	233	32.40	163	11.68	
	GW		71	56.13			
43	HC	207	327	46.28	145	30.08	
	HW		182	54.65			
	GC	203	223	38.81	133	34.50	
	GW		90	44.25			
49	HC	190	333	43.58	126	33.84	
	HW		208	48.19			
	GC	174	228	32.02	154	11.44	
	GW		74	54.31			
MEAN	HC	208	335	44.99^{ad}	141	32.06	(1.99)
	HW		194	51.64^{ac}			
	GC	187	223	35.79^{bd}	143	23.12	(6.67)
	GW		81	50.11^{ac}			

Means with different superscript letters are significantly different.

ab ($p<0.01$) cd ($p<0.05$)

TABLE IX

Experiment II: Water intake, excretion and apparent balance and fecal dry matter concentration. (Values for individual sheep and treatment means)

Sheep	Treatment	Total Water Intake litres/day	Fecal Water output litres/day	Urine volume litres/day	Apparent Balance litres/day	Fecal Dry Matter Concentration %
130	HC	6.54	1.16	4.45	0.93	38.89
	HW	7.92	0.82	5.88	1.22	38.71
	GC	8.98	1.03	5.75	2.20	31.21
	GW	7.52	0.38	5.70	1.44	43.66
54	HC	5.23	1.10	3.25	0.88	38.27
	HW	5.28	0.76	3.54	0.98	41.33
	GC	4.51	0.97	2.46	1.08	35.24
	GW	4.94	0.31	3.00	1.62	44.30
43	HC	5.33	0.96	3.62	0.76	42.03
	HW	5.80	0.81	3.55	1.44	38.75
	GC	5.37	0.93	3.16	1.28	33.21
	GW	6.32	0.63	4.49	1.20	33.88
	HC	4.67	1.45	2.18	1.05	33.12
	HW	4.68	1.01	2.83	0.85	35.74
	GC	5.45	0.91	3.30	1.24	33.88
	GW	6.76	0.52	3.66	2.57	33.41
Mean	HC	5.44	1.17^{a}	3.38	0.91	38.08
	HW	5.92	0.85^{b}	3.95	1.12	38.63
	GC	6.08	0.96^{ab}	3.67	1.45	33.38
	GW	6.38	0.46^{c}	4.21	1.71	38.81
		N.S.	$(p<.01)$	N.S.	N.S.	N.S.

Means with different superscript letters are significantly different.

ever, there were no significant treatment effects upon total daily water intake.

Daily fecal water excretion on the GW treatment was significantly lower ($P<0.01$) than for all other treatments. There was also a significant ($P<0.01$) difference between HC and HW treatments. Thus, when either hay or grain was fed the infusion of cellulose resulted in a significant increase in fecal water excretion.

Nitrogen Intake, Excretion, and Balance

Daily nitrogen intake was similar on all treatments (Table IIIa).

There was a significant ($P<0.01$) treatment effect upon fecal nitrogen excretion with HC>HW and GC>GW but the difference between GC and HW was not statistically significant (Table X). Thus cellulose infusion greatly increased fecal losses of nitrogen when either ration was fed.

There were no significant effects due to treatment on urinary nitrogen excretion although the difference between GC and HW approached significance.

Nitrogen balance was significantly ($P<0.05$) greater when grain was fed than when hay was fed. Within each ration, cellulose infusion had no significant effect upon nitrogen balance (Table X). The various parameters of nitrogen balance are illustrated in figure 4.

Fecal nitrogen concentration was consistently the lowest for HC treatment in which there was the greatest quantity of fecal dry matter. Fecal nitrogen concentration progressively increased from treatment to treatment in the following order: HC < HW < GC < GW. In spite of the decreased fecal nitrogen concentration associated with an increased fecal dry matter output, there was a marked positive relationship between fecal dry matter output and total daily fecal nitrogen excretion (Figure 5).

Intake and Excretion of Inorganic Elements

The mean daily intakes of sodium, potassium, calcium, and magnesium, for each treatment are listed in Table IIIa. Fecal and urinary excretions and daily balance of sodium and potassium and fecal excretion of calcium and magnesium were calculated as a percentage of daily intake for comparative purposes and the mean values are presented in Table XI.

Sodium. Fecal excretion of sodium appeared to be related to daily fecal dry matter excretion. There was a significantly ($P<0.05$) lower fecal sodium excretion for treatment GW than the other treatments. The differences among HC, HW, and GC were not significant. The urinary sodium excretion for the GW treatment was significantly higher ($P<0.05$) than for HC and HW treatments, but did not differ significantly from GC. Treatment differences in sodium balance were subject to large variations and were not significant. Actual amounts of sodium excreted in the feces and urine are shown in Appendix Table III.

Potassium. There were no significant differences between HC and GC or HW and GW with respect to fecal potassium excretion. The infusion of cellulose into sheep on the grain ration was accompanied by a significant increase in fecal potassium excretion ($P<0.05$) over and above that observed during water infusion. Cellulose infusion into sheep on the hay ration did not result in a significant increase in fecal potassium excretion.

A comparison of treatment effects indicates that the HW treatment was accompanied by a urinary potassium excretion which was significantly greater ($P<0.05$) than both GC and GW. The urinary excretion of potassium on HW did not, however, differ from the HC treatment.

The potassium balance on the GW treatment was larger ($P<0.01$) than for the other three treatments.

Actual amounts of potassium excreted in the feces and urine are shown in Appendix Table IV.

Calcium. Fecal excretion of calcium was significantly ($P<0.05$) lower for treatment GW than for all other treatments. For treatments HC, HW and GC, approximately 100 per cent of the calcium intake was excreted in the feces.

Magnesium. Fecal excretion of magnesium was significantly ($P<0.05$) lower for treatment GW than for treatments HW and HC. No other treatment comparisons revealed significant differences in fecal magnesium excretion.

Ash. Fecal excretion of ash was significantly ($P<0.05$) lower for treatment GW than for treatment HC. No other treatment comparisons revealed significant differences in fecal ash excretion.

Actual amounts of calcium, magnesium, and ash excreted in the feces of individual sheep are shown in Appendix Table V.

TABLE X

Nitrogen Excretion and Balance
as a percent of intake. (Experiment II)

Sheep	Treat.	Fecal-N	Urine-N	N-Balance
		(as % of daily N-Intake)		
130	HC	48.44	38.45	13.10
	HW	39.77	47.72	12.52
	GC	38.69	34.33	26.98
	GW	27.60	26.49	45.90
54	HC	44.65	36.42	18.93
	HW	34.70	42.11	23.18
	GC	36.33	38.69	24.98
	GW	23.20	49.51	27.29
43	HC	41.98	40.67	17.35
	HW	35.16	45.32	19.07
	GC	34.73	41.59	23.69
	GW	30.23	39.54	30.23
49	HC	41.57	44.60	13.83
	HW	38.18	53.19	8.63
	GC	32.72	35.75	31.52
	GW	25.96	45.28	28.76
Mean	HC	44.16^{a}	40.04	15.80^{a}
	HW	36.95^{b}	47.09	15.85^{a}
	GC	35.61^{b}	37.59	26.79^{b}
	GW	26.75^{c}	40.21	33.05^{b}
		($p<0.01$)	N.S.	($p<0.05$)

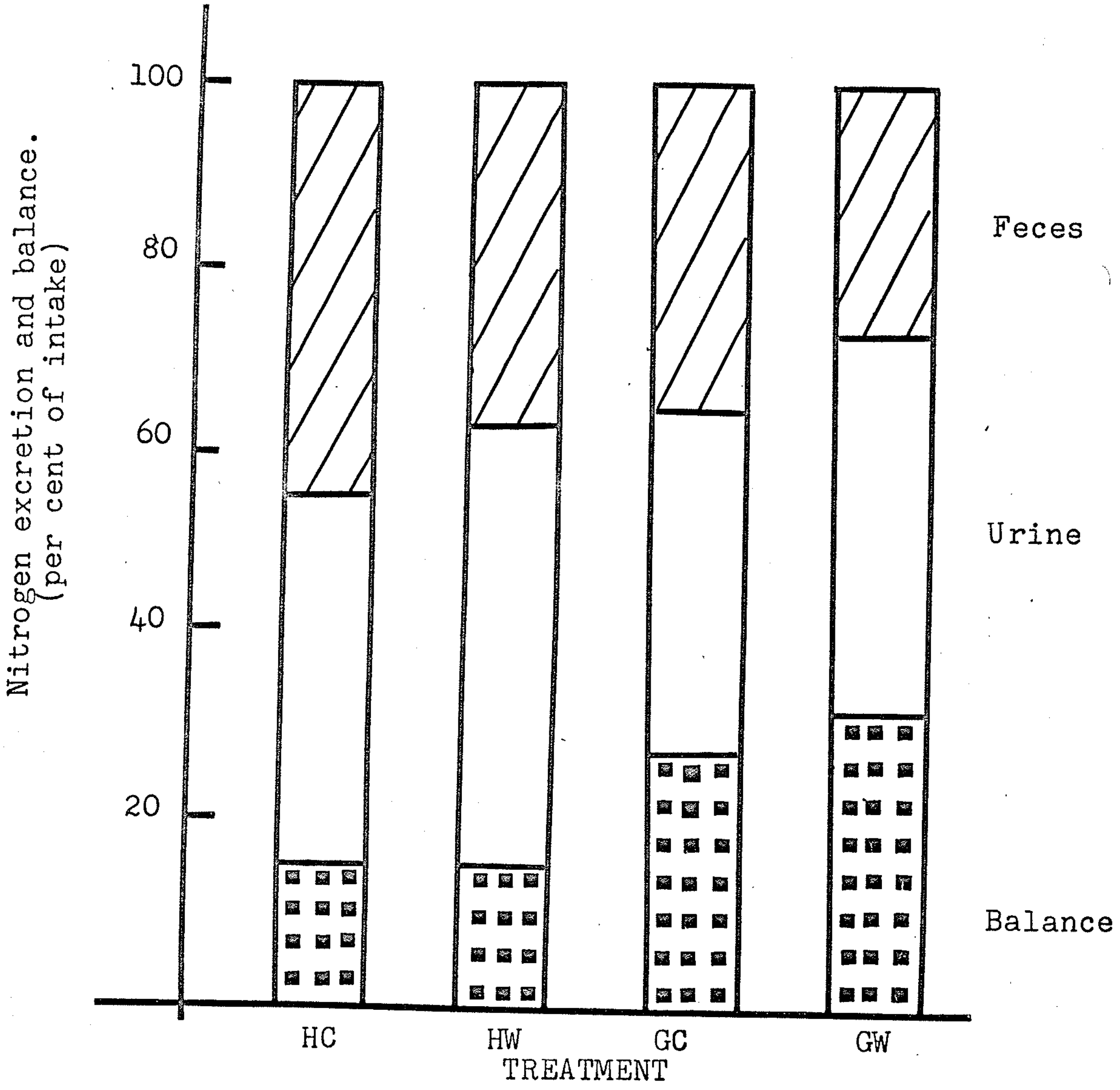


Figure 4: Treatment effects upon Nitrogen excretion and balance. (Experiment II).

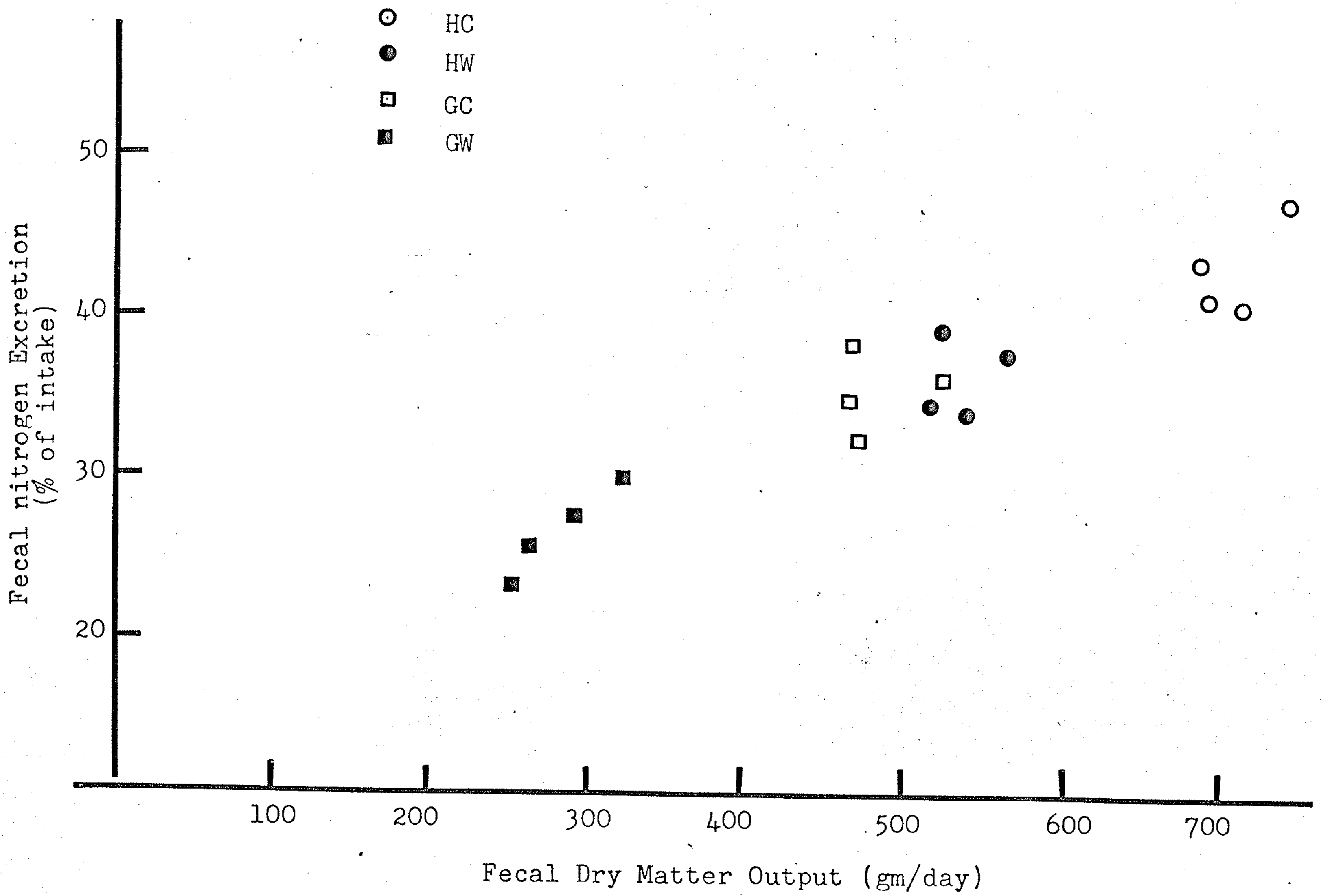


Figure 5: The relationship between daily fecal dry matter output and fecal nitrogen excretion. (Experiment II)

Table XI

Mean daily excretion of inorganic elements and ash (Experiment II). (as a percentage of daily intake).

Inorganic Constituent	Treatment	Feces	Urine	Balance
Sodium	HC	34.86^{a}	57.59^{a}	7.55
	HW	25.29^{a}	52.92^{a}	21.79
	GC	29.34^{a}	70.35^{ab}	0.31
	GW	12.26	78.82^{b}	8.92
Potassium	HC	8.16^{ab}	85.31^{ab}	6.53^{A}
	HW	6.61^{ac}	88.91^{b}	4.48^{A}
	GC	9.61^{b}	82.22^{a}	8.17^{A}
	GW	4.20^{c}	80.29^{a}	15.51
Calcium	HC	100.02^{a}		
	HW	102.04^{a}		
	GC	98.30^{a}		
	GW	85.54		
Magnesium	HC	77.93^{a}		
	HW	73.38^{a}		
	GC	65.99^{ab}		
	GW	57.23^{b}		
Ash	HC	56.44^{a}		
	HW	54.98^{ab}		
	GC	54.06^{ab}		
	GW	50.75^{b}		

Means with different superscript letters are significantly different.

a, b ($P<0.05$).

A ($P<0.01$).

DISCUSSION

The results of experiment II demonstrate an inverse relationship between intestinal retention time and the quantity of dry matter being transferred through the intestinal tract of mature sheep. This relationship was not, however, readily apparent in experiment I during which the animals were consuming hay ad libitum. It is possible that in the latter case the variations in quantity of dry matter passing through the intestinal tract were not large enough to be reflected by marked variations in rate of passage. Since the ad libitum intakes of hay were large the fecal dry matter outputs were also correspondingly high (Table IV). Stained particles introduced into the duodenum were excreted rapidly in all cases during experiment I and the calculated retention times ranged from approximately 7.5 to 10.5 hours. These estimates are lower than those found in experiment II or those reported by Coombe and Kay (1965). The latter authors, however,obtained estimates from sheep producing very low fecal dry matter outputs. For sheep 4154 during period II of experiment I the duodenal infusion of cellulose increased the daily fecal dry matter output by approximately 240 grams (25 per cent) but the intestinal retention time was not changed. In addition, the ad libitum feed intake was not altered during cellulose infusion with this particular sheep. In general, it is difficult to draw any major conclusions from experiment I with respect to the relationship between fecal dry matter output and intestinal retention time. The number of observations are too few and the results were complicated by the variations observed in voluntary feed intake. An observation that may be significant, however, was that with the exception of sheep 4154 during period II, the fecal dry matter output from a given ration remained fairly constant in spite of variations in feed intake.

Castle (1956b) reports a mean intestinal retention time of 13 hours for goats fed hay ad libitum and calf nuts in comparison to values of 18 - 25 hours obtained from sheep on restricted feed intakes by Coombe and Kay (1965) who found that intestinal retention time is negatively correlated to both dry matter intake and fecal dry matter excretion. This finding supports the results of earlier work carried out by Blaxter _et_ _al_. (1956). In view of the above reports the very low estimates of intestinal retention time recorded in experiment I of the present study would not appear to be unrealistic since the fecal dry matter excretions by these sheep were extremely large.

The inverse association noted between intestinal retention time and fecal dry matter output in experiment II confirms the findings of Coombe and Kay (1965). The treatments in experiment II gave rise to wide variations in fecal dry matter output within a range that falls between the values reported by Coombe and Kay (1965) and those for experiment I. The estimates of intestinal retention time similarly fall into the range between those of the above authors and experiment I of the present study.

When the hay ration was being fed, the duodenal infusion of over 200 grams of cellulose dry matter per day did not result in as large a decrease in intestinal retention time as a similar infusion when the sheep were consuming the grain ration (Table VII). Moreover, when intestinal retention time was plotted graphically against fecal dry matter output (Figure 2) the negative relationship did not appear linear over the entire range of fecal dry matter outputs studied. Rather, there appeared to be an inflection of the curve in the lower portion of the fecal dry matter output range. Although the number of observations which fell in this region of the range were few, their distribution on the graph suggested that when the fecal dry matter output was small either the random variation associated with estimating retention time was larger or that a small unit change in fecal dry matter output was accompanied by a large change in retention time of digesta.

The relationship between intestinal retention time and fecal dry matter output found in the present study and that found by Coombe and Kay (1965) appeared to be described by differently sloped curves (Figure 6). The possibility was considered that the relationship between intestinal retention time and fecal dry matter output is curvilinear over a wide range. Since the same method was used to estimate intestinal passage time it was decided to incorporate the data of Coombe and Kay (1965) with those from the two experiments in the present study. The reciprocal of each retention time was calculated and subsequently corrected for metabolic body weight of the sheep. The reciprocal of retention time represents rate of passage through the intestine. When these corrected rates of passage from all three experiments were plotted against fecal dry matter outputs a positive linear relationship was apparent. A positive correlation of 0.972 (S.E. ± 0.041) was calculated between $\frac{W^{.75}}{R_i}$ $\left(\frac{\text{metabolic body weight}}{\text{intestinal retention time}}\right)$ and daily fecal dry matter output using the data from all three experiments. Calculations based upon the data from experiment II alone indicated a positive correlation of 0.860 (S.E.± 0.135) between $\frac{W^{.75}}{R_i}$ and daily fecal dry matter output. Taking the reciprocal of intestinal retention time thus appeared to transform the relationship with fecal dry matter to a linear form (Figure 7).

The two regression equations which describe this bivariate relationship for the data from all three experiments as well as the equations for the data from experiment II alone are presented below:

Regression equations for data from all three experiments:

(a) $\frac{W^{0.75}}{R_i} = 0.295 + 0.0022\ DM$

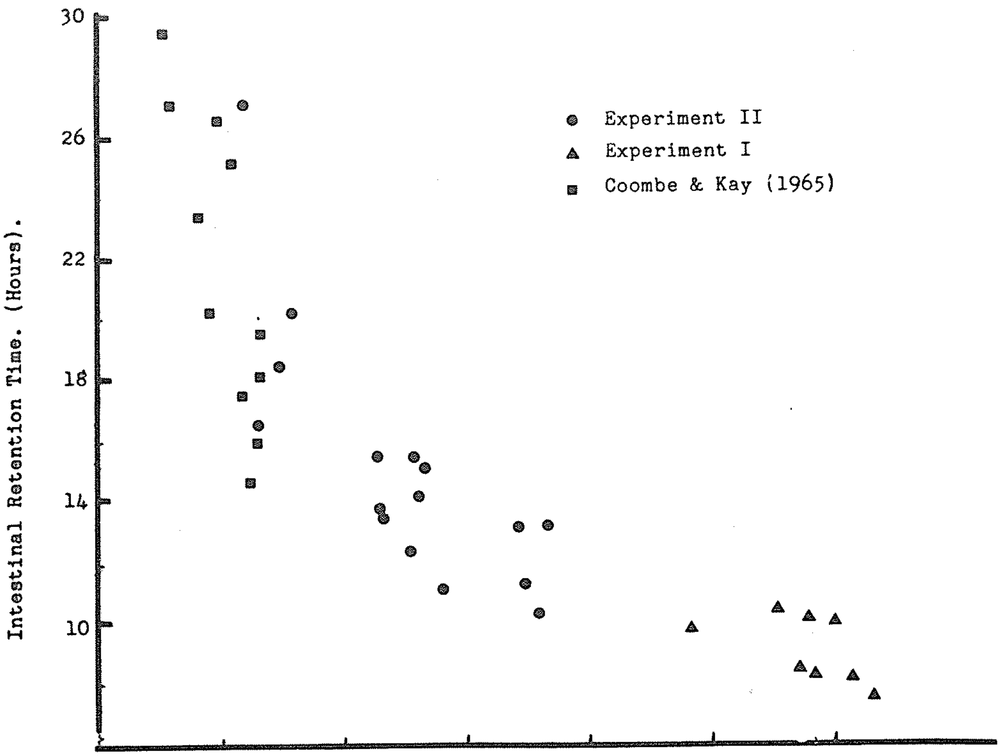
(b) $DM = 429.57\ \frac{W^{0.75}}{R_i} - 95.98$

Regression equations for data from experiment II only:

(a) $\frac{W^{0.75}}{R_i} = 0.556 + 0.0016\ DM$

(b) $DM = 465.95\ \frac{W^{0.75}}{R_i} - 131.88$

It should be pointed out that to regard changes in fecal dry matter output as the cause of changes in intestinal rate of passage is an oversimplification. Variations in intestinal passage time likely contribute to variations in fecal dry matter output because according to Blaxter et al. (1956) the longer the retention time the more complete will be the digestion of feed residues. Bearing this reservation in mind, however, one can usefully consider fecal dry matter output as an index of non-digestible dry matter intake of an animal. To consider variations in the latter as a causative factor contributing to variations in intestinal propulsion would not seem objectionable. Thus, comparing the regressions of fecal output on rate of passage obtained using data from all three



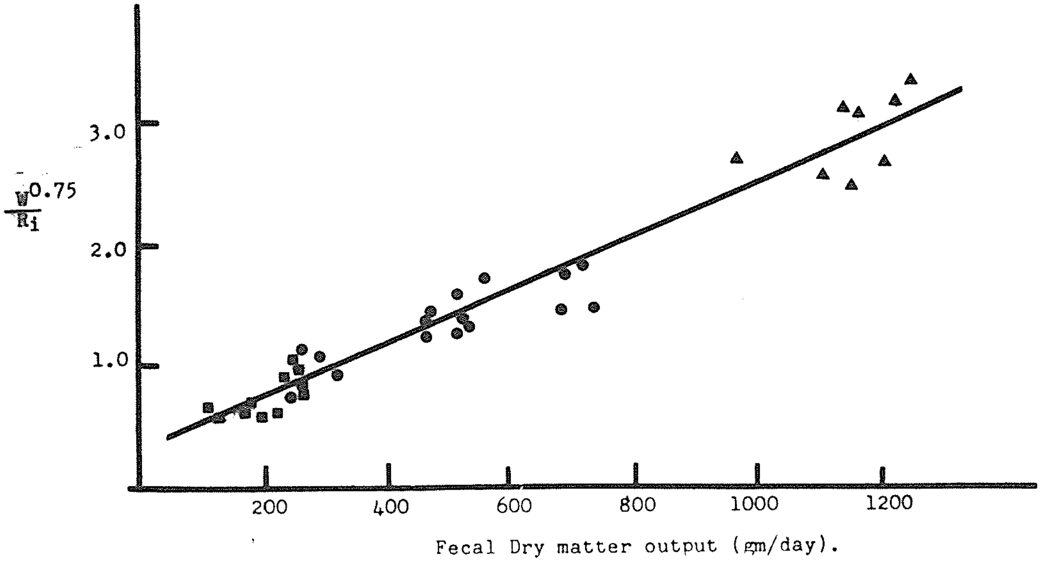


Figure 6: (Above) Intestinal Retention Time v.s. Fecal Dry Matter Output.

Figure 7: (Below) Intestinal Rate of Passage v.s. " " " " .

experiments and from experiment II alone, the two were not found to be significantly different. Therefore the transformed data from each of the three experiments considered here appears to describe a common relationship between intestinal rate of passage and fecal dry matter output.

Since rates of passage were corrected for body weight of the sheep, the main objections to making inferences based on the combined data are that the rations used by Coombe and Kay (1965) were chemically different from those used in the two experiments of the present study, and that duodenal infusions carried out in the present study might have caused abnormal responses. However, variations due to chemical differences between rations did not seem to be very marked in experiment II since most of the variation in rate of passage could be related to fecal dry matter output. In addition the results of experiment I suggest that infusing a large volume of water into the intestine does not have any marked effect upon intestinal rate of passage. Also, in regard to this point, there was the observation that voluntary water consumption during infusion was reduced by an amount equal to the quantity of fluid infused. Benzie and Phillipson (1957) obtained evidence from radiographic studies that large proportions of the water consumed by a sheep passes directly from the oesophagus to the abomasum without being held for any significant length of time in the forestomach. Therefore, infusion of water into the duodenum may not greatly change the situation from that which occurs when water is consumed orally.

From the foregoing consideration of the combined data of Coombe and Kay (1965) and of the present study the following general conclusion was made with respect to the relationship between fecal dry matter output and rate of passage: The intestinal rate of passage $\left(\frac{1}{R_i}\right)$ is directly proportional to daily fecal dry matter output of the sheep and inversely proportional to the size of the animal. That is:

$$\frac{1}{R_i} \propto \frac{DM}{W}$$

or $R \propto \frac{W}{DM}$

where R_i represents intestinal retention time.

W represents body weight.

DM represents daily fecal dry matter output.

When fecal dry matter output approaches zero, the time spent by digesta in the intestinal tract will approach infinity. The relationship between retention time and fecal dry matter will be described by a hyperbolic curve. Plotting the reciprocal of retention time against fecal dry matter results in a linear relationship which the data appears to fit. The choice of $W^{0.75}$ as a correction factor for body size of the animals was based upon the rationale that a factor affecting nutrient availability such as rate of passage through the digestive tract, may be adjusted to metabolic size of the animal. If accurate estimates of gut length were available this perhaps would be the ideal parameter to use for adjusting rate of passage, however, Dukes (1955) outlines some of the difficulties in obtaining such estimates. Brody (1945) reports that intestinal weight in cattle is related to the 0.45 power of body weight however, no value is reported for the relationship in sheep.

Although the use of $W^{0.75}$ in the present study is rather arbitrary, this aspect could be tested experimentally by using animals which vary markedly in body size and by feeding the animals so that a constant fecal dry matter output would be obtained. It should thus be possible to establish the true relationship between intestinal rate of passage and body size. In addition to the question of body size of the animal, further experimentation would clearly be desirable concerning the effect of non-digested dry matter upon rate of passage since the hypothesis presented above is based upon data from three separate experiments.

It is apparent from the present study that events occurring in the reticulo-rumen of the sheep are subject to a certain degree of modification brought about by changes occurring in the lower intestinal tract. Duodenal infusion of cellulose resulted in a significant increase in the daily frequency of reticular contractions when the grain ration was being fed. There was also a tendency for the frequency to be higher on the hay ration when cellulose was infused than when water was infused although the difference did not reach significance. The hay-water treatment resulted in a higher reticular frequency than the grain-water treatment and this might be associated with greater mechanical stimulation to the reticulo-rumen and also the greater quantity of digesta leaving the rumen when hay was fed. This observation is in agreement with that reported by Freer and Campling (1965) in a study with cows.

The observed increase in reticular frequency accompanying cellulose infusion was not anticipated since previous reports of feed-back control of digesta flow volumes (Harris and Phillipson; 1962, Oyaert and Bouchaert; 1961) indicated that distention of a portion of the alimentary tract reduces outflow from the preceding portion. There is also previous evidence that distention of the duodenum and abomasum can reduce the frequency of reticular contraction (Titchen; 1958 and Ash; 1965). The latter author has shown that distention of the duodenum with an inflated condom reduces the frequency and force of the contractions of the reticulum, although running abomasal contents through an isolated loop of duodenum had very little effect upon the reticulum. Based upon these observations Ash (1965) concluded that the volume of the contents of the duodenum rather than any chemical effect was the operative factor in controlling the motility of the reticulum. In the present study it appeared that a positive rather than a negative feed-back control operated as a result of increasing the volume of flow through the duodenum by cellulose infusion.

If the frequency of reticular contractions is an important variable determining the rate of rumen emptying, then in experiment II the infusion of cellulose should not have had any significant retarding effect upon the rate of stomach emptying and there is a possibility that in the case of sheep consuming the grain ration, the rate of stomach emptying may even have been accelerated. On the other hand, Freer, _et al_. (1962) concluded that a change in quantity of digesta transferred from the rumen of cows per contraction of the reticulum was more important than a change in the mean frequency of contraction in determining the rate of rumen emptying. These same authors in a subsequent publication (Campling, _et al_.; 1963) suggested that feeding of ground hay to cows might lead to distention of the hind gut and consequently impose a limit to stomach emptying and to voluntary feed intake. While it is reasonable to suppose that the intestinal tract of an animal does have a definite limit to its capacity the important question is whether this limiting capacity is ever reached before other factors assume a dominant role in controlling ingesta transfer. In experiment II it appears that a limiting intestinal distention was not reached. In experiment I the intestinal rate of passage was not markedly changed by cellulose infusion and it might be concluded that rate of passage was at or very near to its upper limit. Although variations did occur in *ad libitum* feed intake by sheep in this experiment there was no conclusive evidence that duodenal cellulose infusion or intestinal dry matter *per se* reduced the *ad libitum* feed intake. Further experimentation is clearly needed to obtain more information on this point.

There are two possible explanations for the effect of cellulose infusion upon the motility of the reticulum as noted in experiment II. Either the cellulose caused a reflex stimulation of the reticulum due to its mechanical effect upon the duodenum, or the cellulose, by causing an increase in digesta volume within the duodenum, resulted in a dilution of chemical metabolites that normally exert inhibitory effects upon the activity of the reticulum. The first alternative seems unlikely since there is much evidence which supports an inhibitory role for mechanical distention. Also, it is not certain that the slow, continuous infusion of cellulose in the present experiment would lead to a significant distention of the duodenum. In all probability, the volume of intestinal contents would be increased by cellulose infusion, but this volume increase may not have been great enough or may not have occurred rapidly enough to cause an inhibition of the reticulum. The quantity of non-digestible dry matter in the intestinal tract (Appendix Table VII) was increased by cellulose infusion and, in general, was closely related to fecal dry matter output. The increase in intestinal rate of passage accompanying an increase in fecal dry matter output was not large enough to result in a constant quantity of non-digested dry matter in the intestine. The observed increase in the intestinal content of non-digested dry matter supports the contention that the digesta volume was indeed greater when cellulose was infused.

Information is lacking concerning the effect upon reticular motility of concentrations of chemical metabolites in the duodenal digesta. In most mammals, fat is known to have a negative feedback effect upon stomach emptying mediated via the humoral agent enterogastrone (Dukes; 1955). Possibly other metabolites such as volatile fatty acids, proteins, sugars and inorganic electrolytes in high concentration may exert a similar negative feed-back effect upon reticular motility. In humans, gastric emptying has been shown to be retarded by ingestion of hyperosmotic sucrose solutions (Hunt, MacDonald and Spurrell; 1951). These authors considered that the entrance of hyperosmotic fluid into the duodenum caused an inhibition of stomach emptying by some feedback mechanism.

The difference in response to cellulose infusion between the hay and grain rations lends support to the postulation of a chemical feedback inhibition of the reticulum. With the hay ration, the concentration of metabolites entering the duodenum may already have been diluted to such a low concentration that there was little or no chemical inhibition operating. Phillips and Dyck (1964) reported that greater volumes of fluid enter the duodenum when a high roughage ration is fed than when a high starch ration is fed. Further dilution of digesta derived from a hay ration would be expected to result in little or no increased motility of the reticulum under such circumstances. On the other hand, duodenal digesta derived from the grain ration could have conceivably contained a concentration of chemical metabolites high enough to result in a feedback inhibition of reticular motility. Under such conditions the duodenal infusion of cellulose, which itself is quite chemically inert, may have been able to overcome the chemical inhibition by diluting the duodenal contents below a certain critical concentration. While the evidence for chemical inhibition of the reticulum in the present study is only indirect, the data obtained can logically be explained by postulating such a mechanism.

The diurnal variation in frequency of reticular contractions (Figure 3) that was noted in experiment II closely resembles the diurnal pattern of abomasal outflow volumes reported by Harris and Phillipson (1962) for sheep fed twice daily. This provides further evidence that events occurring in various portions of the ruminant digestive tract are well integrated. The reticulum had periods of peak activity corresponding in time with the two daily feedings. During the hour prior to each feeding the reticular frequency had already begun to increase and following feeding the frequency remained higher than the average of the non-feeding periods for about two hours. The rise prior to feeding might have occurred as the result of conditioning the animals to a uniform feeding schedule and the activities in the barn may have signalled the approach of feeding time. The higher frequency noted during the hour following feeding was more pronounced at the morning than at the afternoon feeding. The hourly frequencies were generally lowest during the evening and at night. Had records been kept of the times that the animals spent ruminating these might have greatly assisted the interpretation of the results.

The only treatment effect noted in the reticular frequency pattern was that the grain-water treatment resulted in a lower frequency, during the middle of the day and during the evening and night, than the other treatments. If there was a chemical inhibition operating to control the reticulum its greatest effect was exerted at the times just mentioned. These times would correspond approximately with the times of depressed flow from the abomasum to the duodenum as noted by Harris and Phillipson (1962). The relative importance of the various proposed control mechanisms of the alimentary tract are difficult to appraise, however, in the present study intestinal rate of passage and the frequency of reticular movements were positively associated. That the intestines and the reticulum are very well integrated in their activities is, therefore, apparent.

The mean dry matter digestibilities of the hay and grain rations observed during duodenal water infusion in experiment II were within the ranges commonly reported in the literature (Kromann and Meyer; 1956, Egan; 1965 and Forsyth; 1964). The infusion of cellulose decreased the apparent dry matter digestibilities considerably, however, it must be borne in mind that digestibility was calculated as a percentage of total dry matter intake (i.e. dry matter consumed + dry matter infused.) It was expected that only a small amount of the infused cellulose would be digested in the intestinal tract. According to Goodall and Kay (1965) only about 12 per cent of the dietary cellulose which becomes digested is degraded in the large intestine of the sheep. Gray (1947), on the other hand, estimated that 30 per cent of the cellulose digestion occurred in the large intestine. As suggested by Coombe and Kay (1965), the extent of intestinal fermentation may be modified by variations in the intestinal retention time of digesta.

The estimates of intestinal cellulose digestion made in the present study appear to be in agreement with the value reported by Gray (1947). However, since the present estimates were calculated on the basis of a difference in fecal cellulose excretion between the cellulose and water treatments they may not be too reliable. Such a calculation necessitates the assumption that the duodenal cellulose infusion had no effect upon the digestion of the diet in the upper alimentary tract. This assumption does not appear to be valid in view of the significant effect that duodenal cellulose infusion had upon the activity of the reticulum while sheep were consuming the grain ration. For the hay ration the mean intestinal cellulose digestibility had a much smaller standard error than for the mean calculated for the grain ration (Table VIII). Perhaps this is related to the small effect that cellulose infusion had upon the reticulum when hay was being consumed. Since cellulose infusion resulted in a greater depression of overall cellulose digestibility on the grain ration than on the hay ration one might be tempted to suggest that rumen emptying was accelerated along with the frequency of reticular contractions.

One must not neglect the enhanced intestinal rate of passage that occurred to such a marked extent when cellulose was infused during consumption of the grain ration. This may also have contributed to the lower cellulose digestibility. Considering that almost all the intestinal passage times recorded during experiment II were less than 20 hours, however, it is questionable whether intestinal cellulose digestibilities as high as 30 per cent could possibly occur. Balch and Johnson (1950) reported that the percentage reduction in weight of cotton thread placed in the rumen was not very pronounced within a period of 24 hours. However, cotton thread has cellulose of a larger molecular size (3000 - 5000 glucose units) than alpha-cellulose (200 - 500 glucose units) and therefore the former is probably a more severe test of cellulose digestion. The powdered alpha-cellulose may be more readily attacked by micro-organisms than the native cellulose of most feedstuffs and this could explain the high apparent intestinal digestibilities calculated for infused cellulose in the present study.

A reliable estimate of the intestinal digestion of some component such as cellulose probably cannot be obtained by the difference method based on an infusion technique as used in experiment II. The associative effects of intestinal infusions upon rumen function must always be considered and it is suggested that for a given infusion treatment the associative effect upon the rumen may be different when different rations are fed.

Although an increase in fecal dry matter output in experiment II was associated with a greater total daily fecal water excretion there was no significant treatment effect upon fecal dry matter concentration (Table IX). The fecal dry matter concentration has sometimes been used as an index of the efficiency of water absorption and several authors (Castle; 1956, Blaxter _et_ _al_.; 1956 and Hintz and Loy; 1966) have reported a positive correlation between intestinal retention time and fecal dry matter concentration in experiments with goats, sheep and horses respectively. This relationship was not apparent in the present study. It is conceivable, however, that variations in the fecal concentration of electrolytes may alter fecal water excretion and thus modify the effect upon the latter of variations in intestinal passage time. Some limited evidence for this may be found in experiment II. There were no significant differences among treatments in the concentration of sodium plus potassium in fecal water (Appendix Table II). The fecal excretion of water and electrolytes appeared to be interdependent since there were no significant treatment effects upon fecal dry matter concentration.

The differences in the absolute quantities of sodium excreted in the feces arising from the hay and grain rations reflected the differences in total daily intake of sodium between these two rations. The hay ration contained a higher level of sodium than the grain ration. When fecal sodium excretion was calculated as a percentage of daily intake, the grain-water treatment differed significantly from the other three. Although, in the case of the hay ration there appeared to be an increase in fecal sodium output with cellulose infusion, this increase was not significant. The effects of cellulose infusion on fecal sodium and potassium excretion indicate that the intestinal tract is an important site for the absorption of these ions. Absorption of sodium and potassium from the intestinal tract has previously been reported in sheep by Parthasarathy (1952) as cited by Phillipson (1955) and in steers by Horrocks and Phillips (1964).

The increased fecal excretions of these ions could well be related to the increased intestinal rates of passage accompanying cellulose infusion. Another possibility is that the cellulose reduces the number of ions that are capable of achieving a close enough proximity to the mucosal surface for absorption. Since the major sources of dietary potassium in the case of the grain ration were the potassium salts of acetate and bicarbonate and in the case of the hay ration the potassium inherent in the plant material, one might expect a ration difference in the availability of this ion for absorption. This, however, does not appear to be the case. It is likely that the cellular potassium of the hay ration was readily released during the fermentation process which occurs in the rumen.

While it may be concluded from this study that the intestinal absorption of sodium and potassium can be reduced significantly by increasing the quantity of cellulose passing through the intestinal tract it must be remembered that the dietary intakes of these minerals were more than adequate to meet the requirements of the animals. As Campbell (1964) has demonstrated, by feeding potassium deficient rations to sheep, the animals can economize in this element by greatly reducing both its fecal and urinary excretion. There is always, however, some unavoidable loss of potassium in the feces.

The fecal excretion of calcium and magnesium (calculated as per cent of intake) was high for all treatments. The 100 per cent fecal excretion of calcium for treatments HC, HW and

GC may be attributed partly to the high dietary intake of this mineral. Also, since the sheep used in the present study were mature wethers, one would not expect a very appreciable net retention of calcium. Thus, excretion of calcium (which occurs mainly via the feces of ruminants, Comar and Bronner; 1964) should approximately balance calcium intake.

Fecal excretion of magnesium (calculated as per cent of intake) was lower than for calcium. Although urinary excretion of calcium and magnesium were not determined in the present study, other workers (Thorlacius, 1965 in a study with cattle and Suttle and Field, 1966 in a study with sheep) have found that only a small percentage of calcium excretion occurs via the urine while urinary magnesium output can be quite large.

While fecal calcium excretion appeared to be increased by cellulose infusion on the grain ration, there was no significant effect of cellulose infusion upon calcium excretion when hay was fed to the sheep or upon magnesium excretion for either ration. Yang and Thomas (1965), in a study with young dairy calves, found that total feed to feces digestibility of calcium was reduced during one trial when the fiber content of the ration was raised.

If, under conditions of marginal sodium, potassium and calcium intake, the effects of cellulose upon fecal excretion of these minerals are the same as observed in the present experiment, then the level of fiber in the ration could have some significance in determining the mineral economy of the animals.

Apparent sodium and potassium balances calculated from the data of experiment II are quite variable. Urinary excretions and balances of potassium were significantly affected by both sheep and period differences. The work of Campbell (1964) and Driedger (1966) indicated that the raw wool of sheep can contain significant amounts of potassium. This may indicate that the sweat glands are another avenue for excretion of this mineral. In the present study, such losses were not considered in calculating the apparent balances. The intakes of sodium were different on the two rations fed in experiment II and this factor might be expected to introduce variability into the estimates of excretion and balance.

The high apparent nitrogen digestibilities observed in experiment I and the lack of effect of change in fecal dry matter output upon fecal nitrogen excretion may have been due to the very high daily nitrogen intake by the sheep. When the nitrogen content of the ration is high, significant losses of nitrogen can occur during passage of the digesta through the stomachs. This was noted by Hogan and Phillipson (1960). On the other hand, Harris and Phillipson (1962) observed that the quantity of total nitrogen leaving the abomasum daily was greater than the daily quantity of nitrogen consumed. The latter authors suggested that this may be expected on a low nitrogen intake and that the source of the additional nitrogen leaving the abomasum may be either salivary urea, urea transported from the blood across the rumen epithelium or abomasal secretions. When the nitrogen content of the feed is high it is possible that a rapid formation of ammonia as a result of bacterial fermentation will lead to considerable amounts of nitrogen being lost from the rumen in this form.

Under the conditions of experiment I it is suggested that the proportion of the total nitrogen digestion which occurred in the intestinal tract was small and therefore any variations in intestinal absorption of nitrogen might not be expected to show up significantly in a comparison of overall digestibility coefficients.

The results of experiment II, where the daily nitrogen intake on both rations was of the order of 22 grams per day, indicate that there was a marked effect on nitrogen digestibility of changes in the quantity of poorly digested material passing through the intestinal tract. Comparisons between treatment effects upon fecal and urinary excretions and apparent daily balance of nitrogen can readily be made in figure 4. The increased fecal nitrogen excretion associated with cellulose infusion might be due to the increased intestinal rate of passage. As rate of passage and fecal dry matter output were interdependent in the present study it cannot be said which one most affected the fecal nitrogen losses. Since there was no significant difference in fecal nitrogen excretion between the hay-water and the grain-cellulose treatments, where fecal dry matter outputs were similar, it is suggested that dietary source of nitrogen has little effect on fecal nitrogen losses. Further support for this contention may be found by examination of figure 5. Forsyth (1964), who fed sheep on rations composed of hay and corn in varying proportions, described a similar trend but the results were less convincing than in the present study. That author determined the amino acid composition of duodenal digesta and found that ration differences in protein quality were largely removed by the time the digesta entered the duodenum. It was concluded, therefore, that protein of a relatively uniform amino acid composition was presented to the intestinal mucosa regardless of ration differences in protein composition. A similar observation was made by Nasset et al.

(1963) in a study with dogs.

The nitrogen balances calculated for each treatment in experiment II are similar in magnitude to those reported by Forsyth (1964). It is noted that feeding the grain ration led to a significantly greater positive nitrogen balance than the hay ration. Two possible reasons for a higher nitrogen balance on the grain ration might be put forward. Either the protein being absorbed from the intestinal tract when the grain ration was fed was of a higher quality than when the hay ration was fed or the greater digestible energy intake on the grain ration contributes to the enhanced nitrogen balance. Cellulose infusion caused a reduction in nitrogen balance when grain was being fed but not when hay was fed (Figure 4). This observation supports the idea of a ration difference in quality of intestinal protein but is not conclusive evidence since the effect of cellulose infusion on the grain ration was not significant. Such a proposal is contrary to the evidence in the literature already cited regarding the quality of intestinal protein. It seems more likely that the enhanced nitrogen balance of sheep on the grain ration was due to the probable greater digestible energy intake that occurred when grain was fed. This would be in agreement with the findings of Head (1953) who reported that higher nitrogen retentions occurred in sheep when the starch equivalent of the ration was increased.

SUMMARY

1. Two experiments were conducted in order to study the relationship between intestinal rate of passage and fecal dry matter output in mature sheep. The effect of variation in fecal dry matter output upon the digestibility of certain nutrients was also examined.

2. Experiment I involved two sheep on *ad libitum* intakes of ground pelleted hay.

3. From experiment I it was concluded that the infusion of large volumes of water into the duodenum of sheep had very little effect upon digestibility of dry matter or nitrogen. Infusion of water was accompanied by a reduced oral consumption of water. The reduction in the latter approximated the volume infused.

4. Infusion of alpha-cellulose into the duodenum had no effect upon nitrogen digestibility.

5. The infusion treatments did not appear to affect *ad libitum* hay intake. While the latter was subject to some non-specific variation, the daily fecal dry matter outputs from a particular hay remained relatively constant with one exception.

6. Intestinal retention times of sheep consuming hay pellets *ad libitum* ranged from 7.5 to 10.5 hours.

7. In experiment II, four sheep were fed each of two rations which differed widely in dry matter digestibility. The sheep also received duodenal infusions of either water or alpha-cellulose suspension. Rations and infusion treatments were applied in a 2x2 factorial arrangement. Hay with cellulose infusion (HC) had fecal dry matter outputs of 700 grams per day while grain with water infusion (GW) had fecal dry matter output of about 280 grams daily. The Hay-water (HW) and grain-cellulose (GC) treatments resulted in similar fecal dry matter outputs ranging from 461 to 560 grams per day.

8. Mean intestinal retention times were 11.93, 13.49, 14.28 and 20.60 hours for treatments HC, HW, GC, and GW respectively. The mean for treatment GW was significantly ($P<0.05$) greater than for the other three treatments.

9. A positive correlation ($P<0.01$) was found between daily fecal dry matter output and the inverse of retention time (rate of passage) when the latter was corrected for metabolic body size of the sheep ($r = 0.860 \pm 0.135$).

10. The mean daily frequency of reticular contractions was 1621 for HW and 1506 for GW. The duodenal infusion of cellulose while animals were consuming the grain ration was accompanied by an increase ($P<0.05$) in daily number

of reticular contractions. This indicates that events occurring in the intestinal tract had a controlling effect upon fore-stomach function. The significance of this observation is discussed in relation to a possible chemical feedback control mechanism.

11. The activity of the reticulum was shown to have a consistent pattern of diurnal variation with increases in frequency during the hour prior to each feeding time and peak frequencies occurring at feeding times.

12. Dietary cellulose digestibility was the same for both the hay and grain rations and had a mean value of 50 per cent.

13. The digestibility of infused alpha-cellulose was estimated by the difference in fecal cellulose excretion from the appropriate water control. For sheep on the hay ration, 32 per cent of the infused cellulose was digested and on the grain ration 23 per cent of infused cellulose was digested. The assumptions involved in obtaining this estimate have been discussed.

14. Fecal nitrogen excretion was directly related to fecal dry matter output. The infusion of cellulose increased fecal nitrogen excretion when either ration was being fed ($P<0.01$), however, cellulose infusion had no significant effect on nitrogen balance.

15. Nitrogen balance was significantly ($P<0.05$) higher when sheep were consuming the grain ration than when they were consuming the hay ration.

16. Cellulose infusion significantly ($P<0.05$) increased fecal losses of potassium for both the hay and grain rations.

17. Cellulose infusion significantly ($P<0.05$) increased fecal losses of sodium when sheep were consuming the grain ration.

18. Cellulose infusion on the grain ration significantly ($P<0.05$) increased fecal excretion of calcium.

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APPENDIX

TABLE I

Nitrogen Excretion and Balance (gm/day)

Treatment

Sheep	GW	GC	HW	HC
		(Feces)		
130	6.20	8.69	8.80	10.72
54	5.21	8.16	7.68	9.88
43	6.79	7.80	7.78	9.29
49	5.83	7.35	8.45	9.20
		(Urine)		
130	5.95	7.71	10.56	8.51
54	11.12	8.69	9.32	8.06
43	8.88	9.34	10.03	9.00
49	10.17	8.03	11.77	9.87
		(Balance)		
130	10.31	6.06	2.77	2.90
54	6.13	5.61	5.13	4.19
43	6.79	5.32	4.22	3.84
49	6.46	7.08	1.91	3.06

TABLE II

Concentrations of Sodium and Potassium
in Fecal Water.
All values in mEq/litre.

Sheep	Treat.	Na^+	K^+	$Na^+ + k^+$
130	HC	52.31	46.13	98.44
	HW	42.42	48.76	91.18
	GC	29.38	64.20	93.58
	GW	28.29	47.60	75.89
54	HC	50.54	37.49	88.03
	HW	70.95	38.57	109.52
	GC	34.18	66.38	100.56
	GW	25.59	43.83	69.42
43	HC	55.04	33.86	88.90
	HW	59.38	38.67	98.05
	GC	40.67	35.01	75.68
	GW	46.52	48.74	95.26
49	HC	64.14	35.40	99.54
	HW	53.04	43.80	96.84
	GC	56.37	45.74	102.11
	GW	42.73	51.70	94.43

TABLE III

Sodium Excretion (mEq/day)

Treatment

Sheep	GW	GC	HW	HC
		(Feces)		
130	11	30	35	61
54	8	33	54	56
43	29	38	48	53
49	22	51	53	93
		(Urine)		
130	91	103	97	122
54	120	87	110	127
43	89	97	97	107
49	110	78	94	77

TABLE IV.

Potassium Excretion (mEq/day).

Treatment

Sheep	GW	GC	HW	HC
		(Feces)		
130	18	66	40	54
54	14	64	29	41
43	31	32	31	32
49	27	42	44	51
		(Urine)		
130	285	388	448	451
54	498	507	449	498
43	481	489	510	430
49	444	365	536	487

Table V

Fecal excretion of Calcium, Magnesium, and Ash for individual sheep (Experiment II).

Sheep	Treatment	Calcium	Magnesium (gm/day)	Ash
130	HC	10.51	2.44	69.74
	HW	10.58	2.31	66.29
	GC	8.99	1.82	44.38
	GW	6.64	1.51	38.03
54	HC	9.86	2.65	68.46
	HW	10.47	2.54	68.56
	GC	8.07	2.21	46.29
	GW	8.01	1.82	40.29
43	HC	10.27	3.13	66.10
	HW	10.09	2.40	64.06
	GC	8.83	1.74	43.98
	GW	7.84	1.64	44.90
49	HC	9.97	2.18	69.49
	HW	10.23	2.54	67.81
	GC	7.80	1.64	42.40
	GW	6.83	1.47	42.99

TABLE VI
Mean Squares for various measurements made in Experiment II

Measurement	Period	Sheep	Treatment	Error
Ri	1.37	13.90	58.04	6.79
Daily number of reticular contractions	4848.57	34,188.40	18,384.07	2068.32
Daily fecal dry matter output	2418.57	38.07	123,560.23	236.73
Cellulose digestibility (percent)	39.64	14.24	204.50	9.71
Fecal dry matter concentration (percent)	16.75	23.44	26.63	8.60
Total water intake	0.47	6.00	0.62	0.62
Fecal water output	0.026	0.023	0.353	0.013
Daily urine volume	0.25	5.22	0.52	0.30
Apparent water balance	0.31	0.11	0.50	0.14
Fecal Nitrogen Excretion (percent of intake)	13.51	14.15	204.22	1.66
Urinary Nitrogen Excretion (percent of intake)	44.65	43.57	66.68	28.30
Apparent Nitrogen Balance (percent of intake)	82.34	11.28	290.86	21.63

TABLE VI cont'd

Measurement	Period	Sheep	Treatment	Error
Fecal concentration of Na^+ plus K^+ (mEq/litre of fecal water)	88.42	66.29	158.84	132.36
Fecal Na^+ excretion (percent of intake)	8.83	133.35	327.65	43.87
Urinary Na^+ excretion (percent of intake)	57.70	112.57	560.17	97.28
Apparent Na Balance (percent of intake)	29.28	38.44	323.05	77.11
Fecal K^+ excretion (percent of intake)	7.99	4.04	21.44	2.38
Urinary K^+ excretion (percent of intake)	336.97	254.21	56.78	10.15
Apparent K^+ Balance (percent of intake)	432.77	207.31	92.52	7.36
Fecal ash excretion (% of intake)	10.85	1.64	23.26	4.73

Table VII

Amount of indigestible dry matter in the intestinal tract (Experiment II).

Sheep	Treatment	$\frac{\text{Fecal DM}}{24} \times R_i$ (gm.)
130	HC	405
	HW	337
	GC	267
	GW	224
54	HC	373
	HW	334
	GC	311
	GW	281
43	HC	324
	HW	264
	GC	302
	GW	271
49	HC	304
	HW	255
	GC	263
	GW	182
Mean	HC	351
	HW	299
	GC	286
	GW	241