

The rumen in relation to the animal

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There are three principal reasons for studying the digestive system of ruminants. The first is biological, for the ruminant represents the most developed form of herbivore in that it manages to extract more nourishment from coarse fibrous food-stuffs than any other kind; the second is agricultural, for by studying the process of digestion we may hope to find ways of feeding domestic ruminants in a more economical manner for a given purpose; the third is veterinary, for by understanding more of the normal events in the alimentary canal we may hope to obtain a better understanding of the disturbances that may occur within the alimentary tract or that are associated with it.

The papers in this Symposium summarize the main features of digestion in the reticulum and rumen, and it is necessary to relate these organs to the remainder of the alimentary tract and to see what implications it has for the whole animal. I propose in this paper to consider briefly these matters.

Extent of digestion in the reticulum and rumen

Several estimates have been made of the extent of digestion in the reticulum and rumen based on the lignin ratio which suggest that the quantity of food constituents disappearing during their sojourn there is extensive. The most recent is that of Balch (1957) in cattle. Small samples of the digesta lying in the region of the reticulo-omasal orifice were taken at 3-hourly intervals over several days and combined to form a sample thought to be representative of the material passing to the omasum. The lignin-ratio technique was applied to values for the constituents of this sample in combination with values for the weight of the proximate constituents in the food and of lignin in the faeces. This variation of the usual procedure was necessary because losses of lignin occur in the alimentary tract; it assumes that the losses occur in the rumen. The calculation shows that of the total dry matter disappearing from the alimentary tract from 43 to 83% disappeared in the reticulum and rumen. The cows were fed on a variety of rations and the mean value for disappearance of dry matter was 64%. The values for animals receiving a high proportion of concentrates in the ration are at the upper end of the range. About 80% of this loss is represented by carbohydrate. Balch points out that confirmation of these results by another method is desirable.

Another method has been used by Hogan (1957) with sheep. He adopted the method of exteriorizing the flow of food in the duodenum. This method appears to cause surprisingly little lasting disturbance to the sheep and it is possible to measure directly the total food flowing from the stomach, and return it to the duodenum. Provided this return is made frequently and rapidly the flow does not appear to be unduly disturbed. Failure to return food to the duodenum causes an increased out-flow from the stomach. The procedure has the advantage that there is no ambiguity

in the volumes measured as all the material passes to the exterior. Using this technique with sheep fed every 12 h on 300 g hay and 200 g concentrates, consisting of 2 parts linseed meal and 1 part oats, Hogan found that on an average 70% of the digested dry matter disappeared in the stomach, a value that agrees well with those found by Balch (1957) for cows fed on hay and concentrates. It should not be overlooked that Hogan's results apply to the whole stomach whereas those for the cows apply only to the first two parts of the stomach. There is no information on the extent of digestion in the omasum beyond the fact that volatile acids and chloride are absorbed, and their place is taken largely by bicarbonate. If the abomasum behaves as a simple stomach then absorption from it will be small. At any rate these results suggest that losses from these two organs are not very important.

As regards carbohydrates, therefore, digestion in the rumen is very important. It is more difficult to assess the extent of disappearance of nitrogen-containing materials as the secretions augment the nitrogen of the food, but it appears in both cows and sheep that considerable losses from the rumen occur and presumably represent the absorption of ammonia. However, losses in the intestine are more extensive when compared to the apparent digestibility of nitrogen for the whole alimentary tract. The losses of carbohydrate from the rumen and also the dissolution of protein are accompanied by the evolution of the gases, methane and carbon dioxide, the production of heat, and the production of ammonia and short-chain fatty acids. Of these the fatty acids represent the end-products of nutritional value.

Estimates of the fatty acids produced in the rumen have been made *in vitro* by incubating food with a large quantity of rumen liquor from the cow and a suitable buffered saline solution for 12 h in an atmosphere of carbon dioxide. With this method Carroll & Hungate (1954) estimated that the short-chain fatty acids supplied 10 100, 16 350 and 6870 kcal daily to cattle fed on hay, hay and grain, and pasture grass. Balch (1958), with cows fed on hay and concentrates or ground hay and concentrates, estimated that they supplied from 8400 to 18 000 kcal daily. As the daily heat production of a 1000 lb cow at maintenance is about 8000 kcal, these quantities are more than sufficient to account for the turnover of energy.

Using the method of assessing the quantity of short-chain acids passing to the liver in the portal blood stream of sheep, Schambye (1955) came to the conclusion that enough was present to account for from 300 to 600 kcal/12 h, or twice that amount daily. As the heat output of a fasting adult sheep is about 1200 kcal, these acids probably satisfy most of the maintenance demands for energy. As Fegler (1957) has recently found higher blood flows in the portal vein of sheep than Schambye did and points out the depression that occurs on anaesthetization, it seems that Schambye's estimate could be increased by about 18%.

The recent work of Armstrong & Blaxter (1957*a,b*) indicates that at levels of feeding up to the maintenance level the value of the mixture of short-chain fatty acids to the animal as a source of energy is fairly constant irrespective of the quantities of each individual acid absorbed. The addition of individual acids to the rumen contents of a sheep fed on a plane of nutrition higher than maintenance, however, shows first that the value of each acid is less at the higher level than at maintenance

level and second that acetic acid causes a greater heat increment than propionic or butyric acid. In other words, for production purposes rations that favour the formation of propionic and butyric acids should be more valuable than those that favour the production of acetic acid.

In this connexion it is interesting to compare the fatty-acid mixture in cows fed on a variety of rations, and it can be seen from the data of Balch & Rowland (1957) that the proportions of propionic and butyric acids increase as the concentrate part of the ration increases. In particular, foods rich in starch increase the proportion of propionic acid.

From the point of view of the energy metabolism of the cow, then, the quantity of acids produced appears to be large enough to satisfy a substantial part of their demands and the mixture of acids produced is not without significance for productive purposes. As yet very little is known of the abomasal and intestinal phases of digestion and a great deal more attention will have to be paid in the future to the materials passing to the intestine and to their mode of assimilation.

Absorptive capacity of the intestinal tract

One of the conditions of terrestrial life is the necessity of conserving water and sodium. It seems that the ruminant is unusually good at carrying out these two tasks because (1) the quantity of water secreted in its alimentary tract is very large and is necessary in order to maintain adequate conditions in the rumen and to transport food through the stomach and gut, and (2) the quantity of sodium in most of the foodstuffs eaten is small compared to the quantity of potassium, since plants concentrate potassium from the soil.

In sheep, Kay (1959) estimates that the total daily salivary output is between the limits of 6 and 16 l., which is greater than the total plasma volume. As the parotid secretions and the secretions of the miscellaneous cheek and buccal glands form the bulk of the saliva secreted and contain a somewhat greater concentration of sodium than the plasma (158–185 m-equiv./l. for saliva as opposed to 140–145 for plasma), the quantity of sodium passing to the rumen represents a slightly greater drain on the animal than the water involved. Abomasal juice represents a drain of about another 5 l. daily but little is yet known of the volume of the intestinal, pancreatic and biliary juices secreted into the gut. It is probable that the sodium content of the watery secretions into the gut is close to that of plasma with which such secretions are usually close to isotonicity and under normal circumstances it is improbable that sodium is substituted to any great extent by potassium. The exception to this generalization is the abomasal juice, in which the sodium ion is substituted to a large extent by the hydrogen ion. Only in secretions rich in mucus, or in other large molecules, is the sodium concentration likely to be considerably less than that of plasma. The quantity excreted daily in the faeces is only about 400–500 ml a day of water and 50–60 m-equiv. of sodium. Both sodium and water are known to be absorbed from the rumen and omasum and there is no doubt that absorption also occurs along the remainder of the tract, particularly in the large intestine. It is of interest that in conditions of sodium depletion the sodium content of the saliva is

lowered and its place is taken by potassium; there is also a diminution of the volume secreted. How far this finding applies to other secretions is not known but economy in sodium is certainly made as regards its supply to the rumen.

The principal point I wish to emphasize is that the digestive system of cattle demands a considerable turnover of the animal's resources owing to its capacity and the nature of the events inside it. A study of the rates of turnover of body constituents such as water, sodium, other mineral elements and nitrogen under various circumstances may help in the end to understand why occasionally things go wrong.

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The application of recent scientific information through the feeding-stuffs industry

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In the early days of scientific feeding the daily diet of ruminants was thought of as a whole, much as rations for monogastric animals are regarded today. Kühn (1892-3) popularized the view already held in Germany by other workers that for convenience of practical rationing the daily diet might be considered as consisting of a portion for the maintenance of an animal in normal health, made up mainly of roughages, and a portion for the production of milk, made up of more concentrated feeds. This concept proved so convenient that it has become the standard basis of theoretical rationing. The need for maximum use of home-grown feeds, which developed in 1940, and the subsequent economic controversy about the best use of roughages and concentrates for the most economic milk yields, has tended to give the impression that two schools of dairy nutritional thought have developed: one which advocates maximum use of home-grown feeds, and the other which supports highest yields by the optimum use of concentrates. It is perhaps remarkable that the protagonists of both views advance them in the cause of maximum profitability for the farmer.

The truth is that the feeding-stuffs industry in recent years has increasingly held the view that dairy concentrates, whether purchased or home-grown, are