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## DIGESTION IN THE ABOMASUM AND INTESTINE OF THE RUMINANT

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### Flow of digesta in the intestine of the ruminant

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#### *The hind-gut*

There appear to be two distinct definitions of the hind-gut; one is based on phylogeny and the other on embryology. In most vertebrates a pylorus separates the stomach from the intestine and primitively, it would seem, the two regions served different purposes. The region anterior to the pylorus, termed the fore-gut, was merely a connecting link with the pharynx or a storage chamber; the intestine, termed the hind-gut, was responsible for digestion and absorption. However, in most vertebrates there is some overlapping of function between the two regions (Romer, 1962).

The embryonic alimentary tract consists of two simple tubes, the fore-gut and hind-gut, connected to the yolk sac. The fore-gut transforms into the mouth, pharynx and digestive canal to a point far along the small intestine. The hind-gut develops into the rest of the small intestine and the whole of the large intestine (Arey, 1944). For the purposes of this short review the hind-gut will be considered to consist of the ileum and large intestine, the form of which in the ox, sheep and goat is similar.

The terminal part of the ileum is straight and runs cranially between the caecum and colon and is attached to the former by the ileocaecal fold. The caecum is a simple tubular structure with a blind end which points in the general direction of the pelvis. Ruminants in general have relatively small caeca in comparison with those herbivores with simpler stomachs (Flower, 1872). There is no clear demarcation between caecum and colon but the site of the ileo-caecal valve is the acknowledged junction. The proximal colon is a comparatively wide tube which is looped on itself before it narrows to form the spiral colon. This part of the large intestine consists of tightly and regularly arranged centripetal and centrifugal coils. The number of centripetal coils in the three species are ox 1-2.5, sheep 2-4, and goat 2.5-3.5. The incidence of aberrant coiling is about 20% in the sheep and 3% in the ox (Smith, 1956). The spiral colon is considered to end near the dorsal level of the colon and is continued thereafter by the distal colon which leads into the rectum.

The caecum and colon of sheep contain approximately 11% of the total digesta of the alimentary tract and 13–16% of the total dry matter (Boyne, Campbell, Davidson & Cuthbertson, 1956; Rogerson, 1958).

The consistency of the digesta flowing through the ileum and into the caecum is relatively fluid; in sheep fed on hay or dried grass the concentration of dry matter is 5–9% (Hogan, 1957; Goodall & Kay, 1965). The concentration of dry matter in the caecum is about 14% and progressive dehydration occurs as material flows through the spiral colon. At the beginning of the centrifugal coils in sheep and goats the digesta are semi-solid and pellet formation takes place. These changes appear to be less intense in the colon of the ox. Estimates of the net quantity of water absorbed by the large intestine of sheep vary from 1 to 4 l./day (Hogan & Phillipson, 1960; Goodall & Kay, 1965) but these values are likely to be minimal ones, since account is not taken of the water secreted by the caecum and colon, some of which may be re-absorbed. Appreciable volumes of fluid are necessary for the transport of the solid fraction of digesta through the stomach and small intestine and most of this is provided by the gastro-intestinal secretions. It is not known how much fluid is normally secreted by the large intestine but under experimental conditions caecal pouches secreted 20 ml/h and an isolated loop of the whole spiral colon 50 ml/h (Kay, 1963). A characteristic of large intestinal secretions is that they are very mucous and this presumably provides the lubrication for the transport of solid material and partly compensates for the loss of water. Measurements of flow of digesta either from the caecum to the colon or through the different segments of the spiral colon do not appear to have been made. One reason for this omission is the lack of suitable methods for measuring the flow of semi-solid material.

#### *Re-entrant cannulas*

Re-entrant cannulas are widely used to study flow through the duodenum and jejunum, the contents of which are usually quite fluid, and the method is also applicable to the ileum. The technique was originally described by Crocker & Markowitz (1936) and used by Wasteneys, Crocker & Hamilton (1941–2) to estimate the extent of digestion in the small intestine of dogs. Briefly, the intestine is transected at a predetermined point and the cut ends are inverted and closed by over-sewing a clamp. The continuity of the lumen of the intestine is restored by suturing a suitably designed cannula into the closed intestinal stumps. The barrels of the cannulas are exteriorized through the abdominal wall and joined by a tube.

The basic design of the cannulas is either a straight or curved barrel, joined to a gutter-shaped internal flange which is sewn into the lumen of the intestine through an incision on the anti-mesenteric border (Phillipson, 1952). An alternative type of cannula used by Singleton (1961) was sewn into the open ends (see Vaughan-Williams, 1954) of the transected intestine of sheep and goats. Cannulas are usually machined from Perspex (Hogan & Phillipson, 1960; Harrison & Hill, 1962) or moulded from a suitable plastic (Ash, 1962; Brown, Armstrong & MacRae, 1968). Titanium, a strong but light metal, has also been used for the manufacture of cannulas (F. A. Harrison, personal communication). It is possible to insert two or

three pairs of re-entrant cannulas at different sites in the small intestine of an individual sheep at one operation (Hogan, 1957; Scott, 1965; Brown *et al.* 1968).

Although the method involves considerable surgical interference, young animals usually make a rapid recovery from the operation. The weight changes of sheep fitted with duodenal or ileal re-entrant cannulas were recorded by Harris & Phillipson (1962) and Bruce, Goodall, Kay, Phillipson & Vowles (1966). Both groups reported that their sheep lost about 5 kg body-weight in the first 2-3 months after operation although the amounts of food consumed by the operated sheep were not markedly different from those of the unoperated 'control' animals.

The intestine is capable of propelling and accommodating large volumes of digesta and it is important that the insertion of a rigid tube into the lumen should not impede flow. The overt effect of a complete blockage of re-entrant cannulas is a complete loss of appetite. An insidious effect of partial impedance is hypertrophy of the musculature of the intestinal wall oral to the cannulas. This tends to occur in the ileum and is presumably a result of the additional force required to propel the viscous digesta of the lower ileum through the re-entrant cannulas (Bruce *et al.* 1966). In general, compensation appears to be adequate since the digestive performance of sheep with re-entrant cannulas does not differ markedly from that of normal animals. The useful experimental life of many cannulated sheep may be as long as 18 months.

In order to measure flow through re-entrant cannulas, it is usual to collect the digesta from the proximal cannula in 50-100 ml fractions, measure the volume or weigh the contents exactly, and then introduce the material slowly into the distal cannula. Precautions are taken to maintain the temperature of the digesta outside the body. Samples removed for analysis are replaced by the addition of similar material collected previously, either from the same animal or a donor on the same diet. Thus, a direct measurement of flow and representative samples of digesta are obtained simultaneously.

The procedure deviates from the normal sequence of events in the duodenum and jejunum. Flow through closed Perspex loops takes the form of gushes which occur in groups of about four and they are separated by a varying but usually short period of quiescence. Further the aboral gushes may be followed by retrograde flows and with the manual method of measurement this will be prevented. A quantitative estimate of the peristaltic-antiperistaltic flows through closed re-entrant cannulas in the duodenum was made by Singleton (1961) using an electromagnetic flowmeter. Expressing retrograde flow as a percentage of total aboral flow, a mean value of 40% (range 2-56%) was obtained for retrograde flow in goats, while in sheep the mean was 5% (range 0-17%). As a basis for judging the accuracy of the manual method of collection, chromium sesquioxide incorporated into a paper was used as a marker (Harris & Phillipson, 1962; Bruce *et al.* 1966). The mean recovery of chromium sesquioxide from duodenal digesta was about 84-90% of the dose administered. In contrast, the mean recovery of the compound from ileal contents exceeded the amount given by 2%; in sixteen experiments the amount recovered exceeded the theoretical on nine occasions and was less on

seven. Thus, manual collection in the duodenum seems to depress flow rather than give greater flows than expected, but the almost equal distribution of recoveries in the ileum suggests that it is unlikely that a single factor, such as the method of collection, was influencing flow. While it is possible that movement of the cannulas and general activity associated with the collection procedure slightly depress gastro-intestinal motility, the manual collection and return of digesta more closely resembles normal flow through the ileum than it does through the duodenum. Digesta in the ileum flow in a steady stream towards the caecum; retrograde flow rarely occurs and sometimes the contents remain stationary (Hogan, 1957). Clearly, methods used to measure flow through re-entrant cannulas must avoid not only excessive rates of flow through failure to return digesta (Phillipson, 1952) but also reduced flow caused by the return of large volumes of digesta at one time. Although chromium sesquioxide appears to be a useful marker for checking the measurement of flow through re-entrant cannulas, it has also indicated that day-to-day variations in the retention and excretion of digesta of unoperated sheep are quite normal. Assuming that a method of measuring flow does not interfere with the transport of food material a range of values for flow through the gut may be expected.

#### *Flow of digesta through the hind-gut*

The flow of digesta through the ileum is characterized by its irregularity, whereas flow through the duodenum is virtually continuous. Goodall & Kay (1965) described ileal flow as occurring in a series of propulsions, about 20–30 ml at a time, and following each other over a period of 10–30 min; digesta were returned to the distal cannula in 100 ml fractions. These periods of activity were followed by intervals of 1–2 h, or even 5 h in some experiments, in which there was little or no flow (see also Hogan & Phillipson, 1960; Bruce *et al.* 1966). Coombe (1966) recorded two types of pressure change in the ileum, one progressive and associated with the flow of digesta and the other localized and non-propulsive. Frequently, peristalsis was followed by non-propulsive activity and there were periods of quiescence lasting 1.5 h. A similar pattern of electrical activity in the ileum was recorded by Laplace (1968); isolated bursts of potentials associated with rhythmic segmentation, and less frequently long discharges characteristic of propulsive activity, alternated with prolonged silent periods. During the periods of ileal quiescence, intense electrical discharges were recorded from the caecum and Laplace associated these with caecal emptying; this occurred less frequently on grain diets than when the sheep were fed hay. Berehoiu (1966) described a total contraction of the caecum which forces caecal contents into the sigmoid colon. Successive contractions at 12–20 min intervals occurred until the caecum was almost empty. This form of activity was considered to be related to the quantity and nature of the caecal contents.

Potential discharges associated with anti-peristalsis were rarely observed in the ileum and their intensity was much less than those accompanying peristaltic activity (Laplace, 1968). Similarly, Besselaar & Quin (1935) concluded from their studies on bowel anastomosis that retrograde flow in the upper third of the large intestine of sheep was extremely feeble or perhaps completely absent. In addition, by-passing

the ileo-caecal valve by anastomosing the ileum to the tip of the caecum caused no apparent change in the excretion of digesta.

The quantities of digesta flowing through the terminal ileum of sheep fed 600–1000 g of fodder per day varies from 1.5 to 5 kg/day (Hogan & Phillipson, 1960; Goodall & Kay, 1965; Bruce *et al.* 1966). The total amount appears to be influenced by dietary factors; dried grass gave lower values than less digestible hay. The concentration of dry matter in ileal contents shows little change and it seems that total ileal flow will be determined largely by the extent of digestion and absorption in the stomach and small intestine (Hogan, 1957). Flow rates tended to be depressed when the consumption of hay was low (Bruce *et al.* 1966). As judged by the available information, ileal flow is approximately a half to one-third of the duodenal flow.

Although Coombe (1966) found that eating decreased peristaltic and non-propulsive activity in the ileum, fluctuations in ileal flow throughout the day do not appear to be associated with either feeding or rumination. Any pattern of flow observed in the anterior sections of the gastro-intestinal tract may well be lost by delays and changes in the volume of digesta before it reaches the ileum (Goodall & Kay, 1965).

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