REFLEX CLOSURE OF THE OESOPHAGEAL GROOVE AND ITS POTENTIAL APPLICATION IN RUMINANT NUTRITION

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The oesophageal groove reflex and indeed the very function of the oesophageal groove has intrigued physiologists for some considerable period and very rightly so. It has been generally agreed that the anatomical nature of the oesophageal groove enabled it to function as a continuation of the oesophagus leading from the cardia to the reticular-omasal orifice, thus prevening swallowed fluids entering the reticulum and the rume. Tiedeman & Gmelin (1826) quoted by Mangold (1929) were apparently the first workers to report that milk passed directly to the abomasum in young lambs and calves; this has been confirmed by numerous workers since.

As to its role in the functioning ruminant animal, there have been several divergent opinions. Up to about 1930, the textbooks of ruminant physiology were dominated by the view of Colin (1886) who contented that the oesophageal groove closed when boli were swallowed during rumination and that this was the main route for passage of solid matter from the rumen to the omasum and abomasum. In 1928, however, Schalk & Amadon, after studying the passage of materials from the rumen in animals with large rumen fistulae, concluded: "We can state without fear of error that the oesophageal groove functions only upon rare occasions in the mature subject as a direct route for liquids and solids from the cardia to omasum and abomasum" Wester (1926) contended that in the mature animal the oesophageal groove had the function of leading mixed food particles and liquids across from the reticulum to the omasum and abomasum.

The factors which have been reported to affect efficient closure of the oesophageal groove in the young suckling ruminant are almost too many to enumerate, but some will be referred to.

1. The age of the animal. Several workers, including Schalk & Amadon (1928) and Trautman & Schmitt (1933), held the view that irrespective of how the liquid was consumed, it normally passed to the abomasum in the young animal and as the animal grew older, some liquid would pass to the rumen and finally all liquid consumed would pass to the rumen. Trautman & Schmitt (1933) attributed this change to a regression of the development of the lips of the oesophageal groove and deterioration of the nervous mechanisms controlling it.

2. The method of drinking. Schalk & Amadon (1928) and Wise (1939) reported that if calves sucked milk from a rubber nipple, it usually passed to the abomasum, while it often passed to the rumen if it was drunk from a bucket. Schalk & Amadon (1928) also observed that when the size of the swallows was too large, the lips of the groove were pressed open and part of the liquid passed into the rumen.

3. The composition of the liquid consumed. It was quite natural that the composition of the liquid consumed was thought to play a dominant role in the

reflex closure of the oesophageal groove. Wester (1926) attempted to separate the various fractions of the milk and made some interesting observations, namely that milk sugar, butterfat and casein did not cause closure of the groove; he also ascertained that boiled milk had the same effect as unboiled milk and thereby proved that milk enzymes had no effect. He did, however, conclude that milk salts had an effect and found that this was particularly associated with the sodium ions in the milk. He also maintained a firm belief that sweet, sour or bitter substances had little effect on the groove. Interest in finding a substance causing closure was particularly important from a pharmacological point of view and Clunies Ross (1934) reported that solutions of copper sulphate stimulated closure of the groove more often than water, an observation which was confirmed by Watson & Jarrett (1944).

4. The site of delivery into the oesophagus. It is of interest here to note that Wester (1930) tested the effect on closure of swallowing and states: "I gave milk via the mouth and the groove closed but when I poured milk into the distal end of the oesophagus, the groove did not function." Other factors, such as the temperature of the liquid (Trautman & Schmitt, 1933), and the posture of the animal while drinking (Wise, Anderson & Miller, 1942), have been claimed to influence closure of the groove.

The next major contribution to the understanding of the function of the oesophageal groove was undoubtedly that of Watson (1944). Perhaps because this work was published during the war or because the major description was in a Bulletin, the work of Watson has not received the attention it rightly deserves, and many modern texibooks are still influenced by the somewhat erroneous conclusions of Wester (1926). It is appropriate here to quote in full, one of Watson's main conclusions: "The passage to the abomasum of liquids sucked by the lamb is not determined by the temperature or the composition of the liquid, by the posture assumed by the animals while sucking, nor by the act of sucking itself. It is the result of the actuation of the pattern of behaviour which surrounds the act of suckling". He was, however, also led to conclude: "The passage to the abomasum of suspensions given into the mouth is shown to have been due to mechanical stimulation of regions of the mouth and pharynx arising from the presence in the mouth of the mouthpiece of the delivery tube and the wire bit used to guide it and the passage through the mouth of the liquid given". In reaching the latter conclusion, he was undoubtedly influenced by Trautmann & Schmitt (1933) who concluded that the function of the oesophageal groove was controlled by a reflex activated from the mouth and pharynx. Comline&Titchen (1951) later demonstrated that in decerebrate calves, stimulation of the pharyngeal receptors by the swallowing of fluids or stimulation of the laryngeal nerve reflexly caused contraction of the muscle of the groove.

When the later Mr. D. Benzie and I. (\emptyset rskov & Benzie, 1969) became interested in exploring the oesophageal groove as a route by which protein and other nutrients could be made to by-pass the rumen, we were not aware of the work of Watson (1944) and made further trials on the use of salt solutions; however, we were unable to demonstrate by radiography any effect of the salt on the course taken by swallowed liquid. We did not pursue the study of copper sulphate since the sheep would soon have been overcome by copper poisoning, as protein suspensions, would have to be fed at least once daily while pharmaceutical compounds generally are administered once or twice yearly.

The nature of the reflex

Drawn by a rather stray and very inconclusive observation that the youngest animals used in the study of salt solutions had barium marker in the abomasum more often than the other sheep, we were led to believe that the time that had advanced since the sheep was reared was important i.e. the time interval in which the oesophageal groove had not functioned. We weaned lambs at two weeks of age and taught them to drink milk from a bottle fitted with a teat. At 4-5 weeks of age, milk was replaced by a suspension of soyabean meal and vegetable oil. When the same feeding regime was maintained, the suspension always passed directly to the abomasum even if it was replaced by water alone or by other types of suspension. These results are summarized in Table 1.

To ascertain if it was the voluntary act of drinking which was responsible for closure, the same suspensions were given as the only source of liquid in a trough so that the animals were forced to drink these suspensions for quenching their thirst. When this was done, the suspensions passed invariably to the reticulum and rumen.

At this stage, we became aware of the work of Watson (1944) and it can be seen that our observations confirmed the earlier observation, since Watson also observed that when animals drank to quench their thirst, the liquid would pass to the forestomachs.

In a further series of trials (\emptyset rskov, Benzie & Kay, 1970) we tested whether the act of sucking from a nipple was a necessary stimulus for closure of the groove, or whether the different responses of the groove to sucking and drinking were parts of the total complex behaviour

Site of herium

Table 1

Expt 3: effect of method of administration and type of liquid suspension on the site at which $BaSO_4$ could be found in the stomach of the sheep

	Method of administration	No. of observations	Site of Dalium		
Type of suspension			Mean of scores	Range of Scores	
Water	Drench	6	2,5	1-5	
	Involuntary from teat of bottle	4	2,2	1-3	
	Voluntary from teat of bottle	3	5,0	5	
Milk	Drench	3	3,6	2-5	
	Involuntary from teat of bottle	2	1,5	1-2	
	Voluntary from teat of bottle	2	5,0	5	
10% liquid suspension protein concentrate	Drench	3	2,0	1-4	
	Involuntary from teat of bottle	2	1,0	1-3	
	Voluntary from teat of bottle	2	5,0	5	

Score: 1 = all the reticulo-rumen; 2 = most in the reticulo-rumen and a trace in the abomasum; 3 = equally in the reticulo-rumen and abomasum; 4 = a trace in the reticulo-rumen but most in the abomasum and intestine; 5 = all the marker in the abomasum and intenstine.

From:

ØRSKOV, E.R. & BENZIE, D., 1970. Br. J. Nutr. 23, 415.

patterns associated with the two quite different acts. We therefore associated the act of sucking with rather different stimuli by training bottle-fed lambs to suck milk from a trough identical with their water trough. This was soon accomplished, the lambs sucking the milk up with enthusiastic tail-wagging and head-butting movements. At 4-5 weeks of age we replaced milk by other protein suspensions or by water alone. When we maintained the same feeding regime as that used with bottle feeding, it was clear that method of drinking was unimportant because efficient closure of the groove was also achieved with trough feeding. It was also clear that one of the conclusions of Watson (1944), that closure was due to mechanical stimulation in the mouth and pharynx arising from the mouthpiece of the delivery tube, was untenable.

We were therefore confronted with rather a paradox: If fluids were given via the mouth, either as a drench or to quench the thirst, the oesophageal groove did not function, yet if they were given from a bottle or a trough as an extension of the regime used during the rearing period, then the oesophageal groove closed. If the closure was dependent upon the liquid stimulating nervereceptors in the mouth, then we should expect closure in both circumstances. The paradox could, however, be resolved if we were dealing with a conditioned reflex. To test this we inserted into the upper oesophagus a smaller catheter which was long enough to enable a person to stand behind the animal and, without disturbing, it, inject a suspension of barium sulphate into the oesophagus. The result of this study was that if the lambs were resting quietly, the barium would pass to the reticulum and the rumen; however, if the usual stockman was in sight with the liquid feed receptacle (trough or bottle, depending on regime used) beyond its reach, then the groove closed and barium passed to the abomasum although no liquid had entered the mouth. In further studies it also became apparent that the time of groove closure was dependent upon whether the lambs were able to distinguish between the routine feeding procedure, which unequivocally signalled feeding time, and the teasing procedure used in the experimental situation. It was therefore apparent that visual and other stimuli signalling feeding time became responsible for groove closure so that it no longer depended upon receptors in the mouth and pharynx but it functioned as a conditioned reflex. This is perhaps best defined by the scientist who defined the concept, Pavlov (1927).

"Conditioned reflexes are phenomena of common and widespread occurrence: Their establishment is an integral function in everyday life. We recognize them in ourselves and in other people or animals under such names as 'habits' and 'training' and all of these are really nothing more than the results of an establishment of new nervous connections during the post-natal existence of the organism. They are, in actual fact, links connecting definite extraneous stimuli with their definite response reactions."The oesophageal groove reflex is probably only one of many reflexes affecting digestion, secretion and motility of the stomach which may be conditioned to respond to new and external stimuli. It is also of interest that Kay & Ruckebusch (1971) showed that sucking of milk influenced the movements of the rumen and reticulum as well as the oesophageal groove. Being a conditioned reflex, it can be extinguished, for instance by feeding ad libitum of the liquid destined to by-pass the rumen.

Establishment of this reflex in mature animals, which had not previously been trained, has so far only been successful with a proportion of animals.

Motive for studying the mechanism of the oesophageal groove

It is interesting to look at the motives of the scientists who, during the last century, have contributed towards an understanding of this intriguing function. Apart from the driving curiosity which underlies most research, some scientists were interested in the mechanism of groove closure strictly from the point of view of understanding the function and physiology of the ruminant stomach. Such an academic approach was adopted, for instance, by Colin (1886),, Trautman & Schmitt (1933), Wester (1926) and Comline & Titchen (1952). However, Wester (1930), in a more practical mood article (Wester, 1930), asks rhetorically: "To what use can the vet put these findings? " (referring to the apparent effects of salt solutions) and continues: "It will be of great value when one can with certain medicines be able to get them with precision into the abomasum instead of the reticulum as in the reticulum and rumen it first becomes diluted and then after a very long time is conveyed to the abomasum." This pharmacological application was undoubtedly also the motive which Clunies Ross (1934) and Watson & Jarrett (1944) had in mind when they examined the use of copper sulphate to increase predictability of directing medicaments, such as anthelmintics directly to the abomasum without groove closure. If the medicament entered the rumen not only would the particular compound be diluted but it might be wholly or partly destroyed through the action of microorganisms. Our reason for wishing to gain an understanding of the function of the groove was strictly nutritional, namely a desire to be able to by-pass the rumen with high quality protein and other nutrients which might suffer as a result of rumen fermentation, and some results of using the groove for this purpose will be referred to later.

Management of feeding system using the oesophageal groove to by-pass the rumen

When devising a management system for by-passing the rumen with part of the food one must distinguish clearly between the two different motives for drinking, namely drinking to quench thirst and drinking as a state of juvenile excitement. This distinctive behaviour can only be achieved when water is freely available so that animals can quench their thirst whenever they desire. The liquid suspensions designated to by-pass the rumen should always be given in restricted quantities as an extension of the milk feeding period and the feeding method and regime used for rearing should be followed. Dry food which will ferment in the rumen can be given ad libitum or in restricted quantities, depending on circumstances. It is extremely important that these rules are adhered to. Periods of feeding ad libitum with the liquid supplement

Table 2

Treatment	Dry-matter intake (g/day)	Nitrogen intake (g/day)	Urinary nitrogen (g/day)	Faecal nitrogen (g/day)	Retained nitrogen (g/day)
Barley + liquid protein supplement	883	22,91	6,50	6,63	9,78
Barley + dry protein supplement	931	22,77	8,68	6,18	7,90
S.E. of treatment differences	+ 21	± 0,68	±0,59	±0,57	±0,91

Comparison of nitrogen balance of 11 lambs when they received protein supplements in liquid or in dry form as additives to a basal ration of barley

From: ØRSKOV, E.R. & FRASER, C., 1969. J. agric. Sci. Camb. 73, 469.

Table 3

Influence of amino-acid supplementation via oesophageal groove of nitroten balance in lambs receiving a purified diet where urea provided $95 \frac{\pi}{6}$ of the nitrogen

Treatment	Dry-matter intake (g/day)	Nitrogen intake (g/day)	Urinary nitrogen (g/day)	.Faecal nitrogen (g/day)	Retained nitrogen (g/day)
Control	774	21.1	119	4 5	4.7
Control + methionine	788	21,4	10.9	4,6	5,8
Control + methionine + lysine	780	21,2	11,4	4,4	5,5
Control + lysine	786	21,3	12,9	4,3	4,1
S.E. of treatment differences		±0,11	± 0,26	± 0,30	±0,24

will extinguish the reflex in some animals presumably because the liquid is no longer presented to an animal displaying eager anticipation, (see Lawlor, Hopkins & Kealy, 1971).

Concentration of liquid suspensions

It may legimately be asked whether the feed has to be a liquid suspension or whether it is possible to maintain the function of the oesophageal groove with dry feeding. We (E.R. Ørskov & G. Wenham, unpublished) have recently carried out an experiment in which milk diets given to lambs trained to drink from a trough were prepared with less water and less so that in the end dried milk substitute was given. As long as it was possible for the lambs to sip the suspensions, i.e. up to about 50% of water, radiography demonstrated that the groove functioned normally. When, with dry or nearly dry feeding, it was necessary for the lambs to chew and salivate before swallowing, an interesting situation arose. At first the lambs showed all the normal excitement of a sucking juveniles at feeding times but at the same time, there was evidence of intense frustration. The oesophageal groove was seen to close on the first few occasions. However, after 2-3 days, the reflex apparently became extinguished and the material entered the rumen. By re-introducing liquid after a few days, it was possible to restore the normal closure.

Using the oesophageal groove to by-pass the rumen as a means of improving protein utilization

It has already been mentioned that our initial motive for exploring the oesophageal groove was to prevent the fermentation of protein in the rumen. This was stimulated by the work of McDonald (1948) and Chalmers & Synge (1954) and by that of Ferguson, Hemsley & Reis (1967).

In the first experiments on feeding protein in this manner (Ørskov & Fraser, 1969), we showed that protein utilization was substantially improved when it by-passed the rumen instead of being partly destroyed in the rumen.

This is illustrated in Table 2 showing that urinary nitrogen was reduced (P < 0,01) and nitrogen retention increased (P < 0,05). We later showed (\emptyset rskov, Fraser & Corse, 1970) that the improvement in the supplementary protein utilization that was achieved was in the region of 30% with soy protein, casein and white fish meal. Further we showed that methionine was apparently the limiting amino acid in microbial protein for growth. This was demonstrated both by comparing solutions of methionine with solutions of lysine (\emptyset rskov & Fraser, 1970) (Table 3) and by the fact that protein supplements high in sulphur containing amino acids apparently provided the best combinations with microbial protein (\emptyset rskov, Fraser & Corse, 1970).

is important for if it is adequate and the food contains less than that required for microbes, then non-protein nitrogen can be used and no protein supplementation is required. During early growth of ruminants and most of the lactation period for high yielding cows, microbial protein is inadequate to meet the protein requirement. During this time protein in excess of that synthesized in the rumen must be made available to the animal and if rumen fermentation of the supplement is prevented a higher efficiency of utilization can be achieved.

Protein supplementation combined with use of non-protein nitrogen

When the protein supplement is given so that it is sub-

Table 4

Crude protein intake and disappearance in various segments of the digestive tract in sheep receiving rolled barley diets supplemented with either fish meal or combinations of fish meal and urea

(Each value is the mean of five observations adjusted to equal dry-matter intake at 1025 g/day)

Treatment	Intake	Disappearance in rumen	Passing abomasum	Disappearance in small	Disappearance in large	Excreted in faeces
	(g/day)	(g/day)	(g/day)	intestine (g/day)	intestine (g/day)	(g/day) (g/day)
Unsupple-						
mented	97	-33	131	80	10	
Fish meal level 1	124	-20	144	07	10	44
Fish meal level 2 Fish meal level 1	160	6	154	104	15	42 39
+ urea level 1 Fish meal level 2	163	21	142	96	12	37
+ urea level 2	213	73	140	90	14	40
S.E. of treatment						
means	_	8,2	7,4	6,8	2,8	2,4

From: ØRSKOV, E.R. & FRASER, C., 1972. Proc. Nutr. Soc. 31, 25A

In assessing whether protein utilization is improved . by preventing the rumen fermentation of dietary protein through the use of the oesophageal groove, experiments must be adequately designed and it must be remembered that it is not possible to increase protein deposition simply by making more available. Comparisons must be made at intakes of protein below those requirements which have been estimated with dry feeding, since the losses incurred during fermentation of the protein have been taken into account in this assessment. In this respect it must be emphasized that most proteins are only partly destroyed in the rumen. From our work with fish meal (\emptyset rskov, McDonald & Fraser, 1971b) it seems that the destruction amounts to about 60%.

As in any consideration of protein requirements of ruminants, the important question is whether the microbial protein formed during fermentation of the carbohydrates is adequate to meet the requirements of the animal. This

jected to fermentation in the rumen, it is wholly or partly converted to ammonia and volatile fatty acids. The ammonia formed could be incorporated into microbial protein if nitrogen was limiting in the same manner as ammonia formed from the hydrolysis of urea. The extent of deamination of the protein does not appear to be related to the ammonia requirement by the bacteria, in fact in one experiment with soya bean meal we observed that the destruction of protein in the rumen increased progressively as its concentration in the diet was increased (Ørskov, Fraser & McDonald, 1971a). We have further shown (Ørskov & Fraser, 1972) that urea does not appear to reduce the degradation of dietary protein. This is illustrated in Table 4 showing that the amount of protein entering the abomasum was not influenced by urea supplementation with the fish meal. It is important to keep this concept in mind when making recommendations on the use of non-protein nitrogen in diets for ruminants. The position



Fig. 1. – The effect of acetic acid (---) or glucose (---•--) on yield of milk fat in comparison with a control diet (-----).

may be clarified if one considers two different nutritional situations.

1. The requirement of the animal can be met by microbial protein produced as a result of rumen fermentation.

This situation occurs in the later stage of growth of young animals, during most of the gestation period and in late lactation. It also occurs when a low level of nutriton is imposed at any stage, except perhaps for wool growth. If the basal feed contains less protein than that required by the rumen micro-organisms, then non-protein nitrogen such as urea can be added to meet the additional requirement and no supplementation with pre-formed protein is required.

2. The protein needs of the animal are not met by microbial protein. This occurs in the young fast-growing animals, and in part of the lactation period of high-yielding cows; also, in sheep with a high potential for wool growth. To realize the animal's potential for growth, protein supplements must be given.

a. Protein supplements can be given so that they are protected from microbial fermentation either chemically or given so that the rumen is by-passed.

In this case, non-protein nitrogen can be used if necessary to bring the nitrogen concentration in the basal feed up to that which together with recycled nitrogen is adequate for the rumen microbes, and the required supplements can be given in addition.

b. Protein supplements are not protected.

In this case a response to non-protein nitrogen such as urea can seldom be expected. This is because the nitrogen content of most basal feeds is so close to the needs of microbes so that the inevitable degradation of some of the protein supplement usually provides ammonia in excess. In spite of this it is not an uncommon practice to include urea as part of unprotected protein supplements given so that they are subjected to rumen degradation.

Postruminal digestion of carbohydrates

The use of the oesophageal groove to by-pass the rumen, is, of course not limited to protein. When carbohydrates are fermented in the rumen, energy losses in heat and methane occur which amount to 15 to 20% of the energy. In the case of carbohydrates of g-linked configuration, this is inevitable since mammals do not possess enzymes capable of hydrolysing these linkages. In the case of carbohydrates of a-linked configuration, which are fed to ruminants in large quantities in some areas of the world, potential increases in the efficiency of energy utilization is possible. Comparisons of the enzyme concentrations in the small intestine between pigs and sheep (Walker, 1959), however, indicated that sheep had a lesser capacity to digest carbohydrates. On the other hand, Clary, Mitchell, Little & Bradley (1969) showed that enzyme secretions were related to the substrate digested and the question of whether the ruminant had sufficient ability to adapt to its enzymes in this way became of interest. During the past few years we have sudied the effect on the capacity to digest α -linked glucose polymers when they were given for long periods. While a detailed description of this work is not possible here, a brief summary of the work so far on digestion of the most relevant carbohydrates seems appropriate.

Starch

Ørskov, Fraser & Kay (1969) noticed that when substantial amounts of starch escaped rumen fermentation, a rise occurred in the total α -linked glucose polymers which passed the terminal ileum indicating an inefficient digestion in the small intestine. In more recent work (Mayes & Ørskov, 1972), we have studied the capacity for digestion in the small intestine of sheep of pregelled starch given by infusion via the abomasum for periods of up to four weeks. The results of this work again confirmed the limited capacity. for starch digestion of the small intestine and no change with time was apparent. However, by separating the carbohydrate fractions in the terminal ileum into starch (precipitable in hot ethanol), oligosaccharides and glucose, it was shown that starch was almost completely removed and by far the greatest fraction consisted of oligosaccharides. This indicated that the limiting factors may not be amylase activity but intestinal maltase activity. Further work involving determination of the total maltase activity of the gut indicated that at the pH optimal for enzyme activity the sheep would be able to digest no more than about 250 g starch/24 h. No detectable change in the maltase activity occurred with time (Mayes, 1971).

Sucrose

Long periods of feeding sucrose via the oesophageal groove, showed that the sheep had virtually no capacity to digest it and no increase in digestion occurred with time (Ørskov, Mayes & Mann, 1972). The disappearance of small amounts of sucrose was almost entirely due to bacterial utilization in the caecum and large intestine.

Lactose

While the relevance of the capacity to digest lactose in the small intestine may be limited after milk feeding has been terminated, preliminary observations on intestinal lactase show that the sheep apparently retain a considerable capacity. The total lactase activity in the small intestine determined in six-month-old sheep would theoretically enable them to digest 4-500 g/24 h regardless of whether lactose had been fed via the oesophageal groove for the whole period or only as part of the milk during the two months rearing period.

Capacity for removal of glucose from the small intestine

The capacity to remove glucose from the small intestine in mature sheep was investigated by infusion of glucose via the abomasum in amounts increasing by 20 g/day (Orskov, Mayes & Penn, 1971). When more than 300 g/day was infused most of the increments passed the terminal ileum and at about 400 g/day glucose appeared in the faeces, which became increasingly fluid and acid owing to extensive fermentation and inefficient absorption of the end-products. Comparisons between the absorptive capacity of rat and sheep small intestine have also shown the sheep to be inferior in this respect (White, Williams & Morris, 1971).

Glucose utilization

In the foregoing we have briefly discussed the capacity of the ruminant to digest crlinked glucose polymers and to absorb glucose and in this respect the ruminant is relatively ill-equipped. While glucose infused via the abomasum (Armstrong, Blaxter & Graham, 1960) has been shown to be efficiently utilized, it has been shown to alter the partition of energy in the lactating cow so that more energy is retained as fat in adipose tissue rather than being secreted in the milk (McClymont & Vallance, 1962) an effect similar to that of propionic acid (Rook & Balch, 1961). We have recently (E.R. Ørskov & C. Fraser, unpublished), carried out an experiment with lactating goats receiving a basal diet consisting of a 70:30 ratio of concentrate to hay. When 21% of the metabolizable energy from the concentrate was substituted by either acetic acid mixed with the feed or glucose sucked from a bottle the effect on the yield of milk fat is illustrated in Figure 1. The mean daily yield of milk fat were for the control, glucose and acetic acid treatments respectively 105, 74

and 142 g/day. The effect of small amounts of carbohydrates absorbed postruminally on the utilization of roughage feeds needs to be investigated.

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