Factors Affecting the Utilization of Food by Dairy Cows

6. The Rate of Contraction of the Reticulum

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In an earlier communication (Balch, Kelly & Heim, 1951) the influence of the reticulo-omasal orifice on the retention of food in the reticulo-rumen was considered. Data there presented showed that the closing of the orifice and the cycle of pressure changes in the omasum took place at the same rate as the contractions of the reticulum, irrespective of the activity of the cow. It is likely that the co-ordinated action of these three parts is largely responsible for the transfer of digesta from the reticulum to the omasum and for preventing backflow of digesta from the omasum to the reticulum. Phillipson (1939) reviewed the literature dealing with movements in the reticulo-rumen and then showed that although the contraction of the reticulum is usually part of a co-ordinated cycle of movements in all parts of the reticulo-rumen, variations occur in the part played by the rumen in this cycle, but only in some exceptional instances is the reticular contraction absent. Schalk & Amadon (1928) showed how these movements of the reticulo-rumen affected the arrangement and movement of digesta within it. The importance of the specific gravity of particles of food in determining the arrangement of digesta in the rumen was considered by Schalk & Amadon and by Balch & Kelly (1950). From these various investigations it is clear that the movement of digesta in and from the reticulo-rumen is determined by the movements of the walls of the two compartments and the nature of the food.

Schalk & Amadon (1928) stated that the rate of reticulo-ruminal activity was fastest during eating and slowest during rumination, with an intermediate rate when the animal was neither eating nor ruminating, merely 'resting'.

Earlier parts of the present investigation have shown that the efficiency of break-down of food may be affected by the time the food remains in the reticulo-rumen (Balch, 1950) and the position it occupies (Balch & Johnson, 1950). An attempt was made, therefore, to find what variation occurred in rates of reticular contraction in cows receiving some of the diets used in our earlier investigations. The rate of contraction of the reticulum was determined during five types of activity: eating, standing ruminating, standing resting, lying ruminating and lying resting. It was thought that an investigation of this type would show whether variations in reticulo-ruminal motility, resulting from the different diets, were likely to change the arrangement of digesta within, or the rate of flow of digesta from, the reticulo-rumen. The rate of reticular contraction was used as an index of reticulo-ruminal motility.

METHODS

Cows and their treatment. Observations were made on two Dairy Shorthorn cows in which large rumen fistulas had been established; these cows had been used in previous experiments (Balch, 1950; Balch & Johnson, 1950; Balch & Kelly, 1950). The diets were similar to those used by these authors and also by Balch, Balch, Bartlett, Johnson & Rowland (1952). The concentrates were a mixture in the proportions of ground dredge corn (oats and barley) 100, linseed cake 50, weatings 25, undecorticated groundnut cake 25, decorticated groundnut meal 25, limestone flour 2 and common salt 1, parts. The thyroxine was given in four cubes mixed with the concentrate mixture, or eaten from the hand, two cubes twice daily. This dose supplied 100 mg L-thyroxine (see Balch *et al.* 1952).

Recording of reticular contractions. The activity of the reticulum was recorded by means of small toy balloons held in place by brass weights of about 750 g. From the balloons, pressure tubing passed through the fistulas to the tambours placed vertically in an Evershed and Vignole recorder. The tambours were fitted with pens which provided a continuous record, at 0·5 in. (12·7 mm)/min, of pressure changes in the reticulum for periods of up to 26 h. A more detailed description of this recorder has already been given by Balch & Kelly (1950).

The rumen fistulas were closed by means of the cannula and bung described by Balch & Johnson (1948); the bung used during the recording had a special opening through which the pressure tube passed.

Recording of jaw movements. While the cows were receiving diets in which all the hay was ground, and in a few instances while they were receiving other diets, the movements of the lower jaws were recorded. For this purpose the cows wore a leather head stall with a strip of lightly inflated bicycle inner tube fixed inside the muzzle strap. When the jaws opened the air pressure inside the tube increased, operating a small electrical switch clamped to the head stall and controlling the flow of current in a 4 V circuit which included a solenoid operating a pen in the recorder. Since these observations were made this system has been found less satisfactory than a tambour operated by a balloon on the muzzle-strap.

Examination of recorder charts. In summarizing the data collected, the paper charts from the recorder were examined in lengths representing 20 min of recording. The easily distinguished double contractions of the reticulum were counted as one, and the records were used to find how long the animal spent eating, resting or ruminating and whether she was standing or lying. During eating, the jaw movements were recorded as a long period of movement with few pauses, and there was a highly characteristic rapid rate of contraction of the reticulum. Rumination was shown as periods of regular jaw movement broken up by short pauses at regular intervals (Fig. 1) and by an extra contraction of the reticulum immediately preceding the normal double contraction and the start of each period of chewing. When the cows lay down there was a rise in the basal pressure in the reticulum, and the respiratory movements became more regular and prominent. Throughout the periods of recording, notes on the activity of the cows were added to the charts to provide a check on the interpretation of the records.

RESULTS

Details of the rate of contraction of the reticulum were collected during various types of activity while the cows were receiving three different diets. These diets will be considered separately.

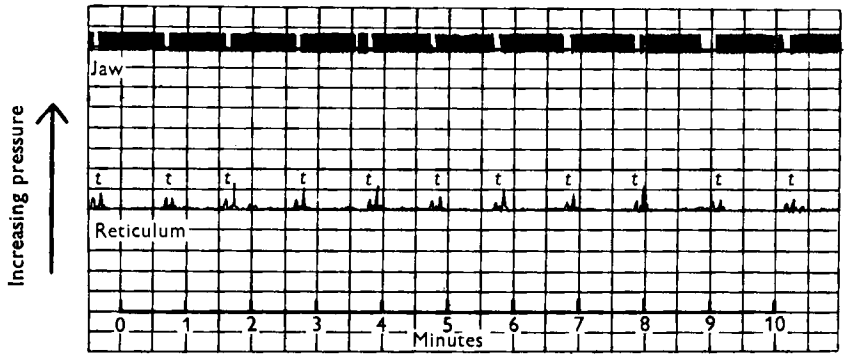

Fig. 1. Long-hay diet. Movements of the jaw, and pressure changes in the reticulum of cow Y standing ruminating. The triple contraction of the reticulum (*t*) is shown.

Table 1. *Numbers of reticular contractions and amounts of rumination in cows receiving long hay*

Cow	No. of recording	Daily diet: Hay (kg)	Daily diet: Concentrates (kg)	Period of recording (min)	Total reticular contractions: Per period	Total reticular contractions: Per h	Time spent ruminating (min)
W	1	8·2	—	1380	1469	64	584
	2	8·2	—	1380	1528	67	785
	3	8·2	—	740	843	68	254
		Total	—	3500	3840	—	1623
		Daily mean	—	—	1580	66	668
Y	1	9·1	4·5	880	1019	70	383
	2	8·2	8·6	1400	1626	70	676
	3	8·2	8·6	840	932	67	334
		Total	—	3120	3577	—	1393
		Daily mean	—	—	1651	69	643

Long hay. Typical values for the total contractions of the reticulum of cows receiving normal diets, containing unground hay, are given in Table 1. The reticulum contracted at an average rate of 66/h in cow W and 69/h in cow Y. Both cows ruminated daily for about 11 h. The rate of contraction was fastest during eating (Table 2) and slowest during either resting or ruminating when the cows were lying down. When she was standing ruminating the mean rate of contraction in cow W was faster than when resting in either position. However, with this exception, possibly a false effect due to the small number of 20 min periods in which cow W was resting, the rate of contraction was slower during rumination than during resting.

On any one day the rates of contraction during different activities tended to be related; thus, if the rate of contraction was above the mean value for, say, eating it also was above the mean value for the other activities. The most constant rates of activity were observed during periods when the cows were lying ruminating. Variation in the rate of contraction while the cows were standing resting may have been partly due to the cows' eating during some periods small amounts of food remaining from the main meal. Since the jaw movements were not regularly recorded while the cows were receiving long hay, such spasmodic eating may have passed unobserved.

Table 2. *Mean rates of contraction of the reticulum, and heart rates of cows receiving long hay*

		Mean no. of reticular contractions/20 min* during					
			Resting		Ruminating		
Cow	No. of recording	Eating	Standing	Lying	Standing	Lying	Heart rate (beats/min)
W	1	26·0 (8)	21·0 (5)	18·4 (7)	24·4 (17)	18·3 (17)	Not recorded
	2	27·6 (15)	—	22·3 (7)	21·5 (4)	19·7 (27)	54
	Mean†	27·0	21·0	20·3	23·8	19·2	—
Y	1	30·4 (8)	27·0 (7)	23·7 (4)	19·5 (4)	18·7 (9)	Not recorded
	2	29·1 (16)	24·3 (9)	22·5 (4)	20·7 (15)	18·0 (23)	68
	Mean†	29·5	25·5	23·1	20·4	18·2	—

* Values in parentheses show the number of 20 min periods in which only the specified activity was recorded.

† Mean values have been weighted according to the number of 20 min periods used in arriving at the mean values for each period of recording.

Ground hay. When all the hay in the diet was finely ground the mean daily number of contractions of the reticulum was not markedly different from that observed with long hay. The average rate of contraction was 70/h in cow W and 68/h in cow Y (Table 3).

The ground-hay diet caused a marked decrease in the amount of true rumination. In cow W the triple contractions occurred, on the average, for only 63 min/day and in cow Y they were virtually absent. The typical pattern of reticular contractions and jaw movements found during the rumination of diets containing 16–20 lb. long hay (Fig. 1) was never normally observed while the cows were receiving the diets in which all the hay was ground. On the last day of recording with cow Y, true rumination was induced by placing a bristle brush in the reticulum (Fig. 2); the resulting periods of rumination occupied 28 min and involved twenty-eight triple contractions of the reticulum.

Although triple contractions of the reticulum were observed in cow W they were usually not accompanied by the periods of regular jaw movements found in true rumination. During the false rumination observed while this cow was receiving ground hay, the jaw movements were extremely irregular and bore little relationship

Table 3. *Numbers of reticular contractions and amounts of rumination and irregular jaw movements in cows receiving ground hay*

Cow	No. of recording	Daily diet: Ground hay (kg)	Daily diet: Concentrates (kg)	Period of recording (min)	Total reticular contractions: Per period	Total reticular contractions: Per h	Rumination: Time (min)	Rumination: Total triple contractions	Time spent in irregular jaw movements (min)
W	1	8·2	—	1480	1736	70	129	104	419
	2	8·2	—	940	1058	68	0	0	251
	3	8·2	—	940	1071	68	0	0	274
	4	8·2	—	640	764	71	45	49	178
		Total	—	4000	4629	—	174	153	1122
		Daily mean	—	—	1666	70	63	55	404
Y	1	9·1	4·5	1600	1792	67	0	0	90
	2	9·1	4·5	1320	1660	76	0	0	45
	3	9·1	4·5	1460	1618	67	0	0	36
	4	9·1	4·5	1800	1938	65	44*	38*	133
		Total	—	6180	7008	—	44	38	304
		Daily mean	—	—	1422	68	9	8	62

* In cow Y, rumination took place for 28 min including twenty-eight triple contractions, while a brush was in the reticulum (see p. 369).

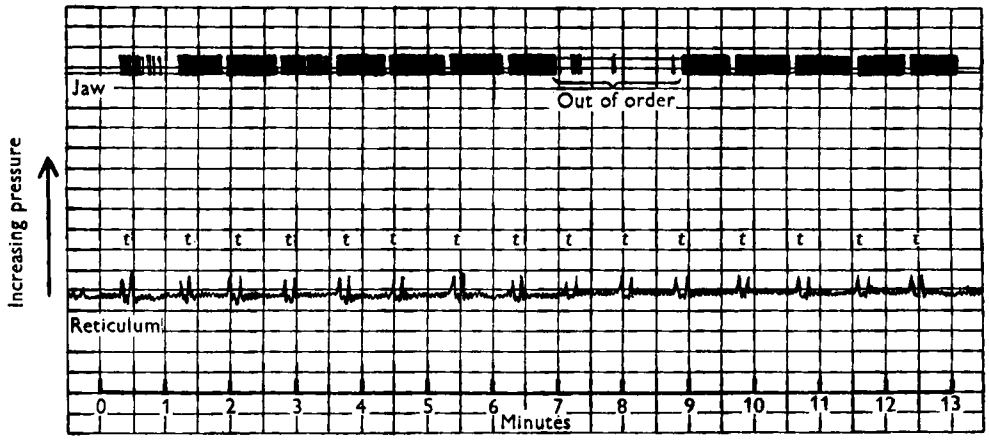

Fig. 2. Ground-hay diet. Movements of the jaw, and pressure changes in the reticulum of cow Y lying ruminating. This period of true rumination was induced by the presence of a brush in the reticulum. The triple contraction of the reticulum (*t*) is shown.

to the contractions of the reticulum (Fig. 3). Cow W devoted an average of 404 min/day and cow Y of 62 min/day to irregular jaw movements; in most instances these movements were accompanied by, but were not related to, the normal double contraction of the reticulum and by irregular belching (Fig. 4); this type of activity followed the insertion of a brush into the reticulum of cow W. Digesta appeared to be raised to the mouth by the irregular belching. Incomplete rumination, possibly of a similar type but lacking the contraction of the reticulum, was observed by Wester (1926) following atropin administration.

The rate of contraction of the reticulum during eating and resting was not markedly changed by ground hay (Table 4). The rate of contraction was again slower while the cows were lying resting than when they were standing resting, and during eating the

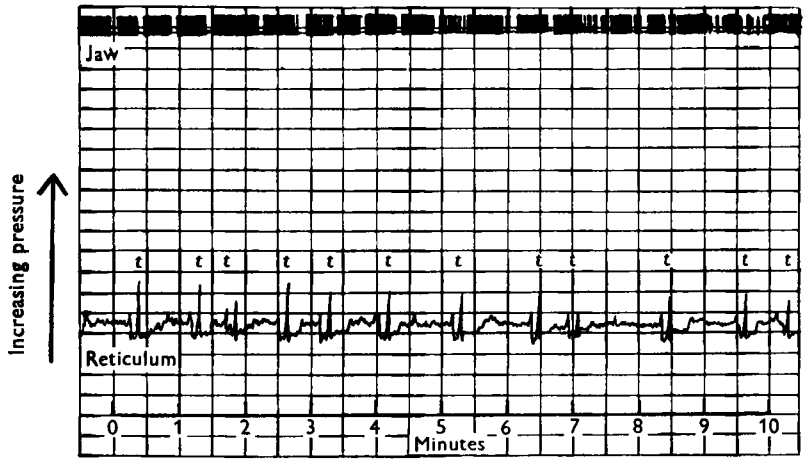

Fig. 3. Ground-hay diet. Movements of the jaw, and pressure changes in the reticulum of cow W standing attempting to ruminate. In this instance the reticulum had a type of triple contraction (*t*) but the periods of chewing were irregular.

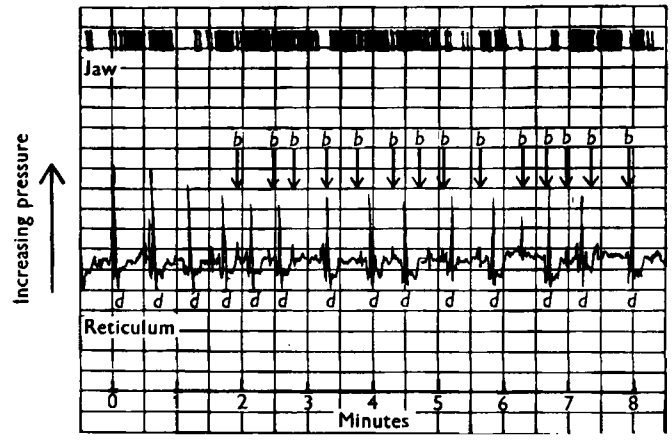

Fig. 4. Ground-hay diet. Movements of the jaw and pressure changes in the reticulum of cow W standing attempting to ruminate. This type of false rumination was characteristic of this cow with or without a brush in the reticulum (see p. 369). The double contraction of the reticulum (*d*) and the irregular belching (*b*) are shown.

rate of contraction was markedly faster than during resting; this was true not only for the mean values for each cow but also for seven of the eight separate periods of recording. The tendency for the rates of contraction during each type of activity to be all either fast or slow together on different days was again very noticeable.

Diets containing L-*thyroxine*. When the cows received daily 100 mg L-thyroxine there was a distinct increase in heart rate and, in cow Y, in milk yield. There was,

Table 4. *Mean rates of contraction of the reticulum of cows receiving ground hay*

Cow	No. of recording	Mean no. of reticular contractions/20 min* during: Eating	Resting: Standing	Resting: Lying
W	1	30·2 (8)	26·7 (9)	22·5 (39)
	2	25·1 (4)	20·2 (5)	21·4 (22)
	3	34·5 (2)	25·3 (9)	21·4 (23)
	4	28·2 (6)	23·7 (4)	21·3 (14)
	Mean†	29·0	24·6	21·8
Y	1	28·7 (8)	23·1 (16)	20·3 (36)
	2	32·6 (5)	26·2 (6)	23·1 (33)
	3	31·3 (6)	21·4 (14)	20·6 (30)
	4	27·2 (8)	21·9 (14)	20·1 (38)
	Mean†	29·6	22·7	21·0

* Values in parentheses show the number of 20 min periods in which only the specified activity was recorded.

† Mean values have been weighted according to the number of 20 min periods used in arriving at the values for each period of recording.

Table 5. *Numbers of reticular contractions and amounts of rumination in cows receiving* L-*thyroxine*

Cow	No. of recording	Daily diet: Hay (kg)	Daily diet: Concentrates (kg)	Daily diet: Thyroxine (mg)	Period of recording (min)	Total reticular contractions: Per period	Total reticular contractions: Per h	Rumination: Time (min)	Rumination: Total triple contractions
W	1	8·2	—	100	1280	1388	65	530	534
	2	8·2	—	100	1200	1344	67	438	435
	3	8·2	—	100	1580	1922	73	531	556
	Total		—	—	4060	4654	—	1499	1525
	Daily mean		—	—	—	1651	69	532	541
Y	1	7·3	6·8	100	1160	1442	74	470	396
	2	7·3	6·8	100	1480	1885	76	481	401
	3	7·3	6·8	100	1560	1797	69	630	501
	Total		—	—	4200	5124	—	1581	1298
	Daily mean		—	—	—	1757	73	542	445

therefore, no reasonable doubt that the metabolism of both cows was considerably raised by the thyroxine. Recordings of reticular motility (Table 5), compared with those in Table 1, showed that the mean number of contractions rose by 3/h in cow W and 4/h in cow Y during thyroxine feeding. However, the considerable variation between values obtained in the different periods of recording suggested that these differences were not significant. This difference in the rate of contraction was due, apparently, to less time being spent ruminating, the reduction being 136 and 101 min/day in cows W and Y, respectively (cf. Tables 1 and 5), and also to a tendency for the rate of contraction to be more rapid during eating and resting (cf. Tables 2 and 6). However, in cow Y there was also a tendency for the reduced amount of rumination to take place with a slower rate of reticular contraction.

Table 6. *Mean rates of contraction of the reticulum and heart rates of cows receiving* L-*thyroxine*

Cow	No. of recording	Mean no. of reticular contractions/20 min* during: Eating	Resting: Standing	Resting: Lying	Ruminating: Standing	Ruminating: Lying	Heart rate (beats/min)
W	1	26·1 (11)	25·2 (2)	20·5 (6)	20·0 (1)	20·4 (13)	66
	2	27·6 (14)	—	21·7 (10)	—	20·3 (11)	66
	3	31·9 (7)	27·1 (8)	24·4 (8)	21·7 (6)	20·3 (3)	61
	Mean†	28·0	26·7	22·3	21·5	20·3	64
Y	1	32·9 (16)	20·0 (2)	22·0 (2)	17·0 (6)	15·9 (12)	74
	2	34·4 (18)	31·0 (1)	24·8 (4)	19·0 (4)	15·3 (9)	75
	3	32·1 (7)	29·9 (9)	24·0 (6)	16·6 (7)	15·0 (11)	80
	Mean†	33·4	28·3	23·9	17·1	15·4	76

* Values in parentheses show the number of 20 min periods in which only the specified activity was recorded.

† Mean values have been weighted according to the number of 20 min periods used in arriving at the mean values for each period of recording.

DISCUSSION

It is known that the feeding of ground hay reduces the time spent in rumination (Kick, Gerlaugh, Schalk & Silver, 1937). Observations made in the course of the present study have shown that the reduction in time spent ruminating is due to the absence, as a result of the grinding of the hay, of the stimulus necessary to initiate the regurgitation reflex, and the pattern of behaviour associated with the reflex, in true rumination. The study confirms the finding of Schalk & Amadon (1928) that the regurgitation reflex is initiated by the presence in the reticulum and anterior rumen of material such as hay, that scratches the mucosa lining the walls of those regions, particularly that surrounding the cardia. As a result of the removal of this stimulus, by grinding the hay, triple contractions of the reticulum were extremely rare, and even when they occurred the pattern of rumination was rarely complete.

When all the hay in the diet was ground there was no marked change in the average rate of contraction of the reticulum over periods of 24 h. The rate of contraction may have increased slightly during the administration of thyroxine. Apart from these slight differences the rate of contraction of the reticulum showed a considerable variation depending on the activity of the cow; mean values during the five major types of activity are given in Table 7.

If digesta tended to flow from the reticulum to the omasum at the time of each double or treble contraction of the reticulum (Wester, 1926; Schalk & Amadon, 1928; Phillipson, 1939; Balch *et al.* 1951) there is reason for supposing that the flow of digesta would be proportional to the rate of reticular contraction. This hypothesis therefore, would lead to the conclusion that the flow of digesta to the omasum was greatest during meals and least during rumination. Schalk & Amadon claimed to have detected, by palpation, a rapid transfer of concentrates to the omasum during the course of a meal, but no comparable transfer has yet been detected in the fistulated cows at this Institute. However, as boluses composed of concentrates tend

to disintegrate in the rumen more rapidly than boluses composed of hay (Schalk & Amadon, 1928) it is likely that newly ingested concentrates would arrive in the reticulum and the adjacent parts of the anterior rumen, and would be, therefore, in a favourable position for transfer to the omasum; such transfer would be likely to take place more rapidly than the transfer of hay eaten at about the same time.

Table 7. *Mean rates/h of contraction of the reticulum during various types of activity in two cows*

	Diet		
Type of activity	Long hay	Ground hay	Long hay and thyroxine
Eating	84·6	87·9	92·1
Standing resting	69·6	70·8	82·5
Lying resting	65·1	64·2	69·3
Standing ruminating	66·3	—	57·9
Lying ruminating	56·1	—	53·4

It was surprising to find that the rate of reticular contraction did not alter markedly during administration of thyroxine. The administration of thyroid-active materials is known to increase the rate of emptying of the stomach and intestinal motility in non-ruminants; this has been discussed previously (Balch *et al.* 1952). If the small increases in the rate of contraction of the reticulum, observed in the present experiments, indicated a slightly faster passage of digesta from the reticulo-rumen to the omasum, they would explain the slight increase in the index of the rate of passage of stained hay through the reticulo-rumen observed by Balch *et al.* (1952) in three out of four cows.

The frequency of the cycle of contractions in the reticulo-rumen, as indicated by the rate of contraction of the reticulum, was not markedly different for the three diets studied. It is unlikely that this factor alone could have caused any major change in the arrangement of digesta in the reticulo-rumen. The rate of contraction of the reticulum, unsupported by any index of the relative power of the contractions forming the whole cycle, gives little indication of the amount of mixing to which the reticulo-ruminal contents were subjected. Because of the absence of long particles from the digesta in the reticulo-rumen of cows getting only ground hay, these digesta could be very much more easily mixed (Balch, 1950), and since the rate of contraction varied little between diets containing either long or ground hay it is certain that the digesta were mixed more thoroughly when the hay was ground. This offers an explanation for the suggestion (Balch, 1950) that ground hay, from diets in which all the hay was ground, tended to be retained in the reticulo-rumen as long as, or longer than, unground hay.

SUMMARY

1. The rate of contraction of the reticulum was studied in two cows with rumen fistulas. Pressure changes in the reticulum were recorded continuously for periods of up to 30 h.

2. Grinding all the hay in the diet did not alter markedly the mean rate of contraction of the reticulum, but caused a great reduction in the amount of rumination.

This reduction was apparently due to the absence of the stimulus for the regurgitation reflex.

3. The rate of contraction of the reticulum was most rapid during eating and least rapid during rumination, with an intermediate rate during resting. When the cows were lying, the rate of contraction, during either resting or ruminating, was slower than when they were standing.

4. When the metabolism of the cows was raised by the addition to the daily diet of 100 mg L-thyroxine, there were only slight increases in the rate of contraction of the reticulum.

5. It is likely that the cycle of reticulo-ruminal contraction produced a more complete mixing of digesta in the reticulo-rumen when the cows were receiving a diet in which all the hay was ground than when the diet contained long hay.

I wish to thank Mr G. Heim and Mr V. W. Johnson for help during these experiments.

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