

Factors affecting the voluntary intake of food by cows

2.* The relationship between the voluntary intake of roughages, the amount of digesta in the reticulo-rumen and the rate of disappearance of digesta from the alimentary tract

BY R. C. CAMPLING, M. FREER AND C. C. BALCH

National Institute for Research in Dairying, Shinfield, Reading

(Received 8 February 1961—Revised 28 June 1961)

It has often been supposed that the amount of roughage cows will voluntarily consume at any one meal is largely determined by the effect of that meal in filling the reticulo-rumen and giving rise to a feeling of satiety (cf. Kruger & Müller, 1955; Mäkelä, 1956). Earlier experiments (Campling & Balch, 1961) provided direct evidence of a relationship between the amount of the contents of the reticulo-rumen and the voluntary intake of hay. There have, however, been few measurements of the amount of digesta in the reticulo-rumen of cattle receiving roughages *ad lib.*

It is clearly important to know whether, in individual cows, the voluntary intake of roughages offered *ad lib.* ceases when the amount of digesta in the reticulo-rumen reaches some critical level. We interpreted our earlier experiments as evidence for the existence of such a critical level. We have now attempted, therefore, to find whether this level is determined by the capacity of the reticulo-rumen or whether it is fixed in relation to the amount of digesta in the reticulo-rumen at some time of the day other than during a meal. In the latter event it would be expected that the critical level would differ with different roughages. We have also considered factors influencing the rate of breakdown of roughages in the reticulo-rumen and the time of retention of residues in the reticulo-rumen, since they influence the amount of the reticulo-ruminal contents during a meal and determine the decrease between meals. Blaxter, Graham & Wainman (1956) and Crampton (1957) stressed the probable importance of the rate of disappearance of digesta from the reticulo-rumen in determining the voluntary intake of roughages.

EXPERIMENTAL

The experiment was made with four cows, two of which (E and F) were known to have a greater voluntary intake of food than the other two (G and H).

The experimental treatments were: (1) hay *ad lib.*, (2) straw *ad lib.*, (3) 10 lb hay daily, (4) 10 lb straw daily, (5) 15 lb hay providing about 4 lb faecal dry matter daily, (6) 10 lb straw providing about 4 lb faecal dry matter daily. All foods were given once daily at 10.00 h.

The most important observations were made while the cows were receiving hay or

* Paper no. 1: *Brit. J. Nutr.* (1961), 15, 523.

straw *ad lib*. They included estimates of the contents of the reticulo-rumen before and after meals, the mean time of retention of food residues, the rate of digestion in the reticulo-rumen and the extent of digestion in the reticulo-rumen and in the whole gut. All these estimates are known, however, to be partly dependent on the amount of food consumed. Treatments 3-6 were included accordingly to permit repetition of the observations at comparable levels of intake. It was considered that with these treatments individual differences, for example in the mean time of retention of food residues or in the rate of digestion in the reticulo-rumen, would be apparent.

Treatment periods. The six treatments were each given in turn for a period of 33 days to the four cows. The periods were arranged so that at any one time two cows were receiving hay and two straw. The periods consisted of 18 days of preliminary feeding, a collection period of 12 days and a period of 3 days in which the amount of the contents of the reticulo-rumen was determined.

Cows and housing. The cows were adult non-lactating, non-pregnant Shorthorns in each of which a permanent rumen fistula had long been established. The fistulas were closed by our usual rubber cannula and bung (Balch & Johnson, 1948). The cows were housed in standings which prevented food being stolen or wasted.

Foods. The hay was a mixture of perennial rye-grass and a little white clover, cut on 16 June 1959. The oat straw was bought locally and was unweathered and bright in colour. The chemical composition of the foods is given in Table 1. Each cow received daily 40 g of a proprietary mineral mixture (Churn 105, British Glues & Chemicals Ltd) together with a weekly supplement of a concentrate of vitamins A and D (Drivite, Boots Pure Drug Company Ltd) and free access was allowed to salt blocks containing trace minerals.

Table 1. *Chemical composition of the foods*

Food	Dry matter (%)	Crude protein	Ether extract	Crude fibre	Nitrogen-free extract	Ash
		(As percentage of dry matter)				
Hay	83.0	8.7	1.8	31.1	52.1	6.3
Straw	84.6	2.9	2.2	40.6	48.9	5.4

Determination of voluntary food intake. The complete daily allowance of food was offered in one meal, the amounts offered being adjusted daily until the uneaten food remaining when the cows stopped eating was about 10% of the amount offered. Cows were judged to have stopped eating when they either lay down or began to ruminate, usually after 3-4 h of eating. Uneaten food was then removed and weighed. Access to water was allowed only during the period when food was available each day.

Digestibility. The digestibility of the foods was determined in the usual way with the harness and equipment described by Balch, Bartlett & Johnson (1951).

Digestibility in the reticulo-rumen. The extent of digestion of the foods in the reticulo-rumen was estimated with treatments 1, 2, 5 and 6 by the technique described by Balch (1957). This method involves application of the lignin-ratio technique to bulked samples of digesta taken from close beside the reticulo-omasal orifice. We consider

that such samples are representative of the digesta passing through the orifice during the sampling period. The samples were taken six times daily on 6 days in the collection period. The frequency of sampling during eating was twice that during the remainder of the 24 h to allow for the increased flow of digesta from the reticulo-rumen during eating (Balch, 1958).

Proximate analyses of the foods, faeces and digesta were made by standard procedures after the samples had been dried at 100°; nitrogen was determined in faeces stored under acid and in dried digesta. Lignin was determined by the method of Armitage, Ashworth & Ferguson (1948) on the dried samples.

Rate of breakdown of cotton thread in the reticulo-rumen. A cotton-thread technique similar to that described by Balch & Johnson (1950) was used to obtain an index of the rate of breakdown of cellulose in the reticulo-rumen. The method was modified as follows, according to suggestions by R. J. Moir (1959, personal communication). Air-dried coils of washed cotton thread were trimmed to the same weight as an air-dried standard coil known to contain 250 mg dry matter. After removal from the rumen, the cotton loops were washed, stored in 95% alcohol and then allowed to dry in air before they were weighed against the standard coil. Duplicate coils of cotton thread were tied to a 1 kg brass weight which lay in the ventral sac of the rumen. When the cows were receiving hay, pairs of coils were removed after 12, 24, 30 and 36 h on two occasions in each collection period. When the cows received straw, only one series of measurements was made during each collection period, and pairs of coils were withdrawn at 24 h intervals for 240 h. Estimates of the rate of digestion of cotton thread were expressed as the time (h) taken for the weight of a coil to be reduced by 25%.

Time of retention of undigested residues. The time of retention of undigested residues in the alimentary tract of the cow was measured by giving 0.25 lb of food stained with magenta on the 2nd day of each collection period and counting the number of stained particles in subsequent samples of faeces (Balch, 1950). In counting the stained particles the faeces were washed over a double thickness of cotton gauze. The mean time of retention of stained particles in the gut was expressed in the way suggested by Castle (1956). On several occasions the time of retention of food residues in the lower gut was measured by introducing milled stained food particles into the abomasum through the rumen fistula at the same time as stained food was given by mouth.

Amount of digesta in the reticulo-rumen. The combined effect of the extent of digestion in, and the rate of passage of the digesta from, the reticulo-rumen was measured directly by manually emptying, weighing and sampling the digesta in the reticulo-rumen. The total weight of digesta and amount of digesta dry matter were determined before and after feeding on 3 days at the end of each treatment period. On several occasions the apparent density of the digesta was estimated by measuring the volume of a known weight of digesta held in steel buckets with parallel sides. The digesta were returned to the rumen immediately after sampling.

The motility of the reticulum was also recorded with each treatment, but the results will be reported separately.

RESULTS

Food intake. For treatments 1 and 2 the mean daily intakes of the cows during the 12-day collection periods are given in Table 2. The mean voluntary daily intake of hay with treatment 1 was 21.8 lb, cows E and F eating on average 3.8 lb more than cows G and H. The voluntary intake of straw proved to be little, if at all, above the arbitrary level of 10 lb chosen for treatments 4 and 6; cows E and F ate on average only 1.2 lb more than cows G and H. It was noticeable nevertheless that with both foods the voluntary intake of the cows decreased in the order E, F, G, H.

Table 2. *Mean daily voluntary intake (lb) of food by the four cows*

Food	Cow E	Cow F	Cow G	Cow H	Mean
Hay	24.1	23.3	21.0	18.7	21.8
Straw	11.0	10.1	9.6	9.1	10.0

Table 3. *Mean digestibility values (%) of the hay and straw in different treatments*

(Each value is a mean for four cows)

Treatment	Dry matter	Organic matter	Crude protein	Ether extract	Crude fibre	Nitrogen-free extract	Ash
10 lb hay	68.8	70.8	58.4	54.2	73.1	70.6	51.2
15 lb hay	67.3	69.4	57.2	49.6	72.1	69.1	48.8
Hay <i>ad lib.</i>	65.0	67.4	51.8	45.2	69.9	67.7	44.1
Mean for hay	67.0	69.2	55.8	49.7	71.7	69.1	48.0
Mean for straw*	45.0	45.8	-8.6	22.1	55.1	42.9	33.3

* Values for straw are means for three determinations with each cow with intakes of about 10 lb straw.

Digestibility. Mean apparent faecal digestibility coefficients for each food are given in Table 3. They show typical differences in the digestibility of the two foods; with straw the faeces usually contained more nitrogen than the food, giving rise to negative coefficients for crude protein. Variations in digestibility due to the amount of hay given were small but consistent. The digestibility of hay dry matter rose only from 65% with a mean *ad lib.* daily intake of 21.8 lb to 68.8% when the intake was restricted to 10 lb.

It was noticeable (Table 4) that cow E consistently digested hay and straw to about the same extent as cow F, whereas cow G consistently digested either food better than any of the other cows. Cow H gave results for hay similar to those given by cows E and F, but with straw gave results similar to those for cow G.

As Blaxter, Wainman & Wilson (1960) have pointed out, the effect on nutritive value of differences in the digestibility of individual roughages is magnified by parallel differences in voluntary intake. In the experiment now described the mean daily intake of digestible organic matter was 12.5 lb with hay *ad lib.* and 3.9 lb with straw *ad lib.* This difference was reflected in the mean daily change in the empty body-weight of the cows, +1.70 lb with hay *ad lib.* and -1.75 lb with straw. In calculating empty body-weight it was assumed that the contents of the reticulo-rumen represent 73% of the total contents of the gut (Mäkelä, 1956).

Digestion in the reticulo-rumen. Mean estimates of the extent of digestion in the reticulo-rumen obtained with the lignin-ratio technique in treatments 1, 2, 5 and 6 are given in Table 5. Some slight digestion of lignin was detected in the determinations of total (faecal) digestibility though it had little effect on values calculated by the method of Balch (1957). The negative values for the digestibility of crude protein in the reticulo-rumen (Table 5) presumably indicate that the addition of nitrogen to the rumen, mainly in saliva, exceeded any absorption from the rumen. Digestion in the reticulo-rumen accounted for 65% of the total digestible crude fibre in the hay and only 59% of that in the straw.

Table 4. Differences between individual cows in the digestibility (%) of the dry matter, organic matter and crude fibre of the hay and straw

Treatment	Food constituent	Cow E	Cow F	Cow G	Cow H
10 lb hay	Dry matter	66.4	67.8	72.2	68.8
	Organic matter	68.9	69.7	73.9	70.7
	Crude fibre	71.8	70.6	77.1	72.9
15 lb hay	Dry matter	67.1	68.3	68.2	65.5
	Organic matter	69.3	70.5	70.3	67.6
	Crude fibre	72.6	72.8	74.1	68.8
Hay <i>ad lib.</i>	Dry matter	64.7	64.5	67.4	63.4
	Organic matter	66.8	66.8	69.6	66.3
	Crude fibre	69.0	69.8	71.8	68.9
Straw*	Dry matter	40.4	40.9	49.6	49.0
	Organic matter	41.2	41.2	51.0	49.7
	Crude fibre	50.6	49.3	61.7	58.5

* Values for straw are means for three determinations with each cow with intakes of about 10 lb straw.

Table 5. Mean apparent digestibility (%) of the hay and straw in the reticulo-rumen of the four cows in treatments 1, 2, 5 and 6 (see p. 531)

Food	Organic matter	Crude protein	Crude fibre	Nitrogen-free extract
Hay	33.2	-25.3	46.6	34.2
Straw	22.7	-59.6	32.3	19.7

Rate of digestion. The mean time required for the weight of the cotton threads to be reduced by 25% in the rumen was 26 h with all the hay diets and 166 h with straw. The values varied little between cows given hay but, as shown in Fig. 1, there was a slight decrease in the rate of loss with increasing hay intakes. The main observation was that with hay the breakdown of cotton in the ventral sac of the rumen was about six times as fast as with straw.

Time of retention of undigested residues. The retention times of undigested residues of hay and straw in the gut are given in Table 6. There was considerable variation between the cows, the retention being consistently more prolonged in cows G and H than in cows E and F. The cows could be ranked in the same order of retention time with both foods and at all three levels of hay intake. The decreased time of retention

found with increasing hay intakes is in agreement with the results of Balch (1950), Mäkelä (1956) and Blaxter *et al.* (1956); the relationship does not appear to be linear.

Particles of straw were retained in the gut for a time about 25–30% longer than hay particles even when the intake of both foods was 10 lb daily.

The introduction of stained food particles into the abomasum gave values suggesting that the mean time of retention of hay in the lower gut was 23 h and of straw 27 h.

Amount of digesta in the reticulo-rumen. The amounts of digesta present in the reticulo-rumen before and after feeding are given in Table 7. When the foods were

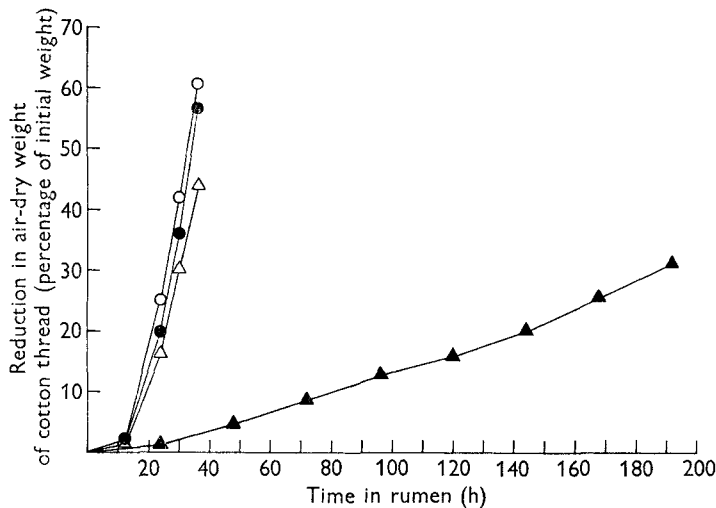


Fig. 1. Mean rate of loss of weight of cotton thread suspended in the ventral sac of the rumen of four cows on different diets. ○—○, 10 lb hay; ●—●, 15 lb hay; △—△, hay *ad lib.*; ▲—▲, straw *ad lib.*

Table 6. *Times of retention (h) of food residues in the alimentary tract of the four cows*

Treatment	Cow E	Cow F	Cow G	Cow H	Mean
10 lb hay	76	80	85	93	84
15 lb hay	71	74	75	81	75
Hay <i>ad lib.</i>	65	71	74	80	73
Straw <i>ad lib.</i>	92	93	106	110	100

given *ad lib.* the mean amounts of digesta in the reticulo-rumen before feeding were 165 lb (14.4 lb dry matter) and 128 lb (13.6 lb dry matter) with hay and straw respectively. Thus the difference in the weight of dry matter was only 6%. After feeding, the amounts were 250 lb (27.2 lb dry matter) with hay and 184 lb (20.2 lb dry matter) with straw. The difference in the weight of dry matter was thus 35%. This difference would have been larger if, during eating, the rate of disappearance of hay from the reticulo-rumen, 1.33 lb dry matter/h, had not been faster than the rate of disappearance of straw, 0.51 lb dry matter/h. During the period between meals the rate of loss was 0.64 lb dry matter/h with hay and 0.32 lb dry matter/h with straw.

The rate of loss of digesta during feeding was markedly influenced by the amount of

hay consumed. The mean rate with 10 lb and 15 lb hay was only 0.32 lb dry matter/h compared with 1.33 lb with hay *ad lib.* The mean rate of loss between meals was 0.45 lb dry matter/h with 10 lb and 15 lb hay compared with 0.64 lb with hay *ad lib.* It was not possible to partition these rates of loss between digestion and passage from the reticulo-rumen since we have no measure of the variation in the rate of digestion during the day.

No significant differences were detected in the apparent density of digesta derived from hay and from straw.

Table 7. Amount of digesta (lb) in the reticulo-rumen of the cows before and after feeding

Treatment	Cow E		Cow F		Cow G		Cow H		Mean	
	Total	Dry matter	Total	Dry matter	Total	Dry matter	Total	Dry matter	Total	Dry matter
	Before feeding									
10 lb hay	109.8	8.19	70.9	6.57	126.5	7.56	77.3	6.86	96.1	7.30
15 lb hay	119.9	9.08	109.7	9.51	150.7	9.56	131.8	11.32	128.1	9.87
Hay <i>ad lib.</i>	155.1	13.32	158.1	14.87	200.7	14.18	147.6	15.23	165.4	14.40
Straw <i>ad lib.</i>	138.6	13.76	106.3	13.26	135.8	12.34	129.8	15.03	127.6	13.60
	After feeding									
10 lb hay	175.4	13.37	142.2	13.71	214.1	17.98	130.4	14.96	165.5	15.01
15 lb hay	192.0	18.48	185.1	22.13	228.5	22.87	190.9	23.74	199.1	21.80
Hay <i>ad lib.</i>	251.8	26.28	239.1	26.29	274.8	28.65	234.3	27.55	250.0	27.20
Straw <i>ad lib.</i>	234.2	22.94	162.9	22.00	169.2	16.12	168.8	19.76	183.8	20.22

DISCUSSION

Our results will be discussed in relation to the hypothesis that the voluntary intake of roughage is in equilibrium with the rate of disappearance of digesta from the alimentary tract in such a way that a critical level of undigested food residues occurs in some region of the gut and at a certain time in relation to the time of feeding.

Evidence suggesting that the reticulo-rumen is the region of the gut in which the amount of undigested residues may regulate the intake of food was provided by the results of previous experiments showing that altering the amount of digesta in the reticulo-rumen immediately before feeding affected the mean voluntary intake of hay (Campling & Balch, 1961). However, although the differences observed by us in the experiment now described between the amounts voluntarily consumed of hay and of straw appear to be explicable in terms of changes within the reticulo-rumen alone, it is of course possible that conditions in the omasum, abomasum and intestine may influence the rate of disappearance of digesta from the reticulo-rumen.

When a cow is established on any diet and routine of feeding the reticulo-rumen must contain about the same amount of digesta at any given time each day. If the voluntary intake of a roughage were limited by the capacity of the reticulo-rumen, and thus the amount of digesta in the reticulo-rumen at the end of a meal were the same when either hay or straw was offered *ad lib.*, it would be expected that immediately before the next meal a much greater amount of digesta would be found in the

reticulo-rumen of cows offered straw *ad lib.* than in those offered hay *ad lib.* As shown in Table 7, this was not the situation observed when our cows were receiving hay or straw *ad lib.* The situation we did observe approximated closely to that expected theoretically if the voluntary intake of such foods by the cows were so regulated that almost equal amounts of undigested food residues remained in the reticulo-rumen immediately before the next meal. Although this concept of the regulation of voluntary food intake is similar to that suggested by Blaxter *et al.* (1960) and Blaxter, Wainman & Wilson (1961), Blaxter *et al.* (1961) suggested that sheep eat to a constant distension of their digestive tracts at the end of a meal, as measured by the 'fill'. However, in our experiment when the cows were offered hay or straw *ad lib.* it was not so.

We have no evidence to suggest the mechanism by which the voluntary intake of the animal might be regulated in relation to the amount of food residues in the

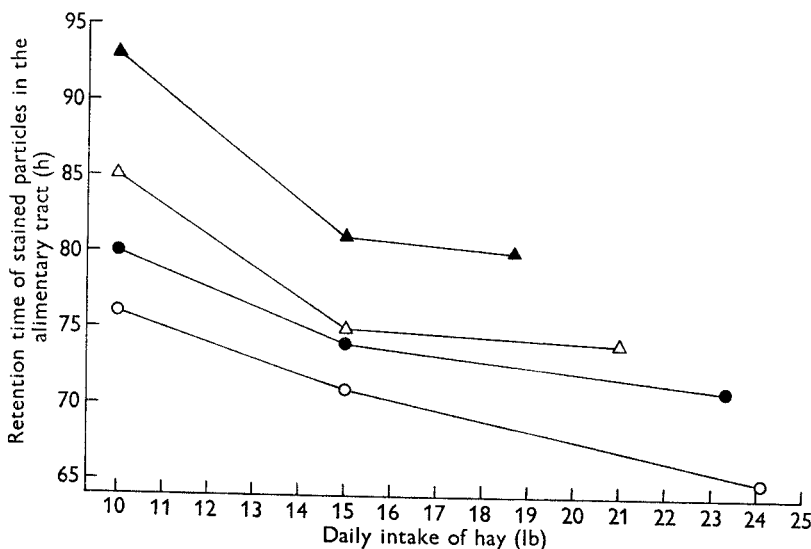


Fig. 2. Relationship between amount of hay eaten and the retention time of stained particles in the alimentary tract of individual cows. ○—○, cow E; ●—●, cow F; △—△, cow G; ▲—▲, cow H.

reticulo-rumen, but it must presumably involve the gradual development of an association between the degree of distension of the reticulo-rumen when a particular food is eaten and the subsequent rate of disappearance of that food.

It is suggested that the main reasons for the low intake of straw relative to hay are (a) its lower digestibility in the rumen, and (b) the longer mean time of retention of straw residues. The longer time of retention of straw residues could be due to (1) a slower breakdown of straw to an optimum particle size for passage from the rumen, associated with a slower rate of digestion, or (2) a metabolic effect of the diet on the motility of the alimentary tract. Although no decrease in the frequency of reticulum contractions was found with straw relative to hay, the size of these contractions was not measured. It is thought, however, that the slower rate of breakdown of particle size is the more probable explanation.

The voluntary intake of both hay and straw varied considerably between individual cows. The differences were most marked with hay, but the ranking of the four cows was the same with both roughages. As differences between cows in the extent of digestion of hay in the reticulo-rumen were either negligible or not directly related to food intake, the only factor that could alter the rate of disappearance of digesta was the time of retention of food residues. The results illustrated in Fig. 2 show that the voluntary intake of hay by each cow was inversely related to the time of retention of undigested residues in the whole gut when she received 10 or 15 lb of hay. Similar differences in retention times were found between the cows at all levels of intake. These results suggest that in cows with a characteristically longer retention time, a limiting retention time, setting a limit to the voluntary intake of food, is reached at a lower level of intake than in cows with a characteristically shorter retention time. Differences in retention times between cows could be due to (a) a more rapid reduction in particle size in the rumen, or (b) differences in the motility of the alimentary tract. The first cause seems unlikely, because the individual times of retention did not appear to be associated with differences either in the rate at which cotton thread was digested or in the amount of rumination per lb hay (Freer, Campling & Balch, unpublished). Although, as will be reported in a separate paper, we found no relationship between the frequency of reticulum contractions and the time of retention of food residues when comparing cows that were eating the same amount of hay, the size of the pressure changes in either the reticulo-rumen or the omasum may be of greater importance.

In conclusion, differences between cows in their voluntary intake of hay appeared to be explicable on the basis of the physical regulation of appetite. Differences in voluntary intake between the two widely different roughages, hay and straw, could also be explained on this basis without recourse to the concept of palatability.

SUMMARY

1. Hay or oat straw was offered *ad lib.* and at two controlled levels of intake to four dry Shorthorn cows with rumen fistulas. The cows received one meal daily.
2. The mean voluntary intake of hay was more than twice that of straw. The lower voluntary intake of straw was associated with a lower overall digestibility, and, in the reticulo-rumen, a lower digestibility of crude fibre, a slower rate of digestion of cotton thread and a longer time of retention of food residues.
3. Immediately after they had eaten food offered *ad lib.* the dry weight of digesta in the reticulo-rumen of cows offered hay was 35 % greater than in cows offered straw. However, as a result of the slower rate of disappearance of straw the difference was less than 6 % immediately before the next meal.
4. It is suggested that the voluntary intake of these two roughages was regulated in relation to their respective rates of disappearance from the alimentary tract in such a way as to maintain a constant amount of food residues in the reticulo-rumen immediately before feeding.
5. The voluntary intake of hay by individual cows was inversely related to the time of retention of food residues in the alimentary tract when the cows received 10 or 15 lb of hay.

We thank our colleagues Mr V. W. Johnson, Mr D. Godden and Mr H. S. Thornett for their help with the conduct of this experiment and also Mrs P. M. Christie and Miss L. H. M. Birch for the chemical analyses. We acknowledge the suggestions made by Mr R. J. Moir for the modification of the cotton-thread technique. One of us (M.F.) thanks the University of Melbourne and the Australian Dairy Produce Board for financial assistance.

REFERENCES

- Armitage, E. R., Ashworth, R. de B. & Ferguson, W. S. (1948). *J. Soc. chem. Ind., Lond.*, **67**, 241.
- Balch, C. C. (1950). *Brit. J. Nutr.* **4**, 361.
- Balch, C. C. (1957). *Brit. J. Nutr.* **11**, 213.
- Balch, C. C. (1958). *Brit. J. Nutr.* **12**, 330.
- Balch, C. C., Bartlett, S. & Johnson, V. W. (1951). *J. agric. Sci.* **41**, 98.
- Balch, C. C. & Johnson, V. W. (1948). *Vet. Rec.* **60**, 446.
- Balch, C. C. & Johnson, V. W. (1950). *Brit. J. Nutr.* **4**, 389.
- Blaxter, K. L., Graham, N. McC. & Wainman, F. W. (1956). *Brit. J. Nutr.* **10**, 69.
- Blaxter, K. L., Wainman, F. W. & Wilson, R. S. (1960). *Proc. Nutr. Soc.* **19**, xxx.
- Blaxter, K. L., Wainman, F. W. & Wilson, R. S. (1961). *Anim. Prod.* **3**, 51.
- Campling, R. C. & Balch, C. C. (1961). *Brit. J. Nutr.* **15**, 523.
- Castle, E. J. (1956). *Brit. J. Nutr.* **10**, 15.
- Crampton, E. W. (1957). *J. Anim. Sci.* **16**, 546.
- Kruger, L. & Müller, W. (1955). *Züchtungskunde*, **27**, 17.
- Mäkelä, A. (1956). *Suom. Maataloust. Seur. Julk.* no. 85.