

Factors affecting the voluntary intake of food by cows

5.* The relationship between the voluntary intake of food, the amount of digesta in the reticulo-rumen and the rate of disappearance of digesta from the alimentary tract with diets of hay, dried grass or concentrates

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Earlier experiments in this series (Campling, Freer & Balch, 1961, 1962) provided direct evidence that the voluntary intake by cows of hay, oat straw or oat straw with urea was related to the relative rates of disappearance from the reticulo-rumen of digesta derived from these foods. We suggested that this relationship was regulated in such a way that there was a critical amount of digesta in the reticulo-rumen at some time in relation to the time of feeding. We observed in our experiments that when the cows ceased eating different roughages, there were different amounts of digesta in the reticulo-rumen but that these amounts were such that they were reduced to about the same level immediately before the next meal. In this respect our results differed from the general concept of Blaxter, Wainman & Wilson (1961) of the regulation of the intake of roughages, which was based on estimates showing that the amount of digesta in the digestive tract after feeding was the same with different roughages offered *ad lib*.

However, it is possible that the voluntary intake of some roughages might be regulated more by the limited capacity of the reticulo-rumen during a meal than by their rate of disappearance from this organ. The situation might be expected to occur with roughages having a faster mean rate of disappearance from the reticulo-rumen than those used in our earlier experiments. Measurements of fill with such foods might, therefore, be more in agreement with the suggestions of Blaxter *et al.* (1961). In the work described here we have examined this possibility by comparing hay and artificially dried grass with respect to the relationship between the voluntary intake of food, the amount of digesta in the reticulo-rumen and the rate of disappearance of the digesta.

We have studied this relationship also with a diet of concentrates alone to provide comparative measurements with a food which, although disappearing rapidly from the alimentary tract, is probably not limited in its intake by the physical capacity of the reticulo-rumen.

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EXPERIMENTAL

The experiment was made with three cows. The experimental treatments, which were applied according to a Latin square design, were: (1) hay *ad lib.*, (2) dried grass *ad lib.*, (3) concentrates *ad lib.* All the foods were given once daily at 10.00 h.

Treatment periods. The treatment periods lasted approximately 7 weeks to allow sufficient time with treatment 3 for the change to a diet of concentrates alone. Each period consisted of about 5 weeks of preliminary feeding, a collection period of 12 days and a period of 2 days in which the amount of the contents of the reticulo-rumen was determined.

Cows and housing. Adult non-lactating, non-pregnant Friesian and Shorthorn cows were used. Each cow had a permanent rumen fistula which was closed by a rubber cannula and pneumatic bung. The cows were in standings that prevented food being stolen or wasted. Water and salt licks containing trace minerals were accessible at all times.

Foods. The hay was predominantly ryegrass cut on 22 June 1960. The dried grass was prepared by cutting ryegrass from the sward by cylinder mower in the autumn and drying it in a commercial grass-drying plant (Nottingham Crop Dryers Ltd). The concentrates were a dairy concentrate cube composed of barley 17, maize 20, wheat bran 20, decorticated groundnut meal 15, copra cake 10, palm-kernel cake 5, molasses 10, dicalcium phosphate 1, calcium carbonate 1 and salt 1%, with 5×10^6 i.u. vitamin A and 1×10^6 i.u. vitamin D added per ton. The composition of the foods is given in Table 1. When given hay or dried grass each cow received daily 40 g of a proprietary mineral mixture (Churn 105; British Glues and Chemicals Ltd) together with a weekly supplement of a concentrate of vitamins A and D (Drivite; Boots Pure Drug Company Ltd).

Table 1. *Chemical composition of the foods*

Food	Dry matter (%)	Crude protein	Ether extract	Crude fibre	Nitrogen-free extract	Ash
Hay	83.8	8.4	4.2	33.2	46.3	7.9
Dried grass	84.8	19.7	2.5	18.6	45.3	13.9
Concentrates	87.0	19.8	3.2	6.4	63.1	7.5

Determination of voluntary food intake. The daily allowance of food was offered in one meal for 5 h and the uneaten food was then removed and weighed. The amount offered was adjusted daily so that the uneaten food was about 10% of the amount offered.

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 food in the reticulo-rumen was estimated, in each cow once in every period, by application of the lignin-ratio technique (Balch, 1957) to bulked samples of digesta taken from close beside

the reticulo-omasal orifice. Details of this method and of the analyses used were given by Campling *et al.* (1961).

Rate of disappearance of cotton thread in the rumen. The cotton-thread technique described by Campling *et al.* (1961) was used to obtain an index of the rate of digestion of cellulose in the rumen. Pairs of coils of cotton thread were removed after 12, 24, 28 and 32 h with diets of hay or dried grass and at intervals of 24 h when the cows received diets of concentrates alone.

Mean time of retention of food residues in the alimentary tract. On the 2nd day of each collection period about 4% of the daily intake of food was given as food stained with magenta and the stained particles in subsequent samples of faeces were counted (Balch, 1950). The mean time of retention of stained particles in the gut was calculated by the method of Castle (1956).

Amount of digesta in the reticulo-rumen. The weight of digesta in the reticulo-rumen was measured directly by manually emptying the reticulo-rumen and weighing, sampling and returning the contents before and after feeding on 2 successive days at the end of each treatment period.

pH of rumen liquor. Samples of digesta taken from beside the reticulo-omasal orifice at intervals of $\frac{1}{2}$, 1, 2, 3, 5, 8, 12, 24 h after feeding were strained through cotton gauze and the pH of the liquor was measured by glass electrode. The dry-matter content of duplicate samples of digesta was also measured.

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

Table 2. *Mean daily voluntary intake of food, time required for 25% loss in weight of cotton threads suspended in the rumen and mean time of retention of stained food particles in the alimentary tracts of the three cows*

Food	Mean daily intake of food (lb)	Time for 25% loss in weight of cotton threads (h)	Mean time of retention of food in the alimentary tract (h)
Hay	20.9	22	73
Dried grass	28.2	25	56
Concentrates	18.8	—*	60
SE of difference between two means	± 1.30	—	± 10.5

* With this diet cotton threads had lost no weight after 240 h.

RESULTS

Voluntary intake of food. The mean daily voluntary intake of each food during the 12-day collection periods is shown in Table 2. With each food the voluntary intake of the individual cows decreased in the order A, B, C, except that cows A and B ate about the same amount of dried grass.

Digestibility. The mean apparent digestibility coefficients for each food are shown in Table 3. Estimates of the disappearance of the foods by digestion in the reticulo-

rumen, obtained by the lignin-ratio technique, are shown in Table 4 and, by subtraction, the extent of disappearance in the remainder of the alimentary tract. The mean proportions of the total digestible organic matter and crude fibre which disappeared in the reticulo-rumen were 55 and 73 % respectively for hay and 57 and 65 % respectively for dried grass. With the diet of concentrates there were large differences between the cows in these values; 47 and 7 % respectively for cow A, 75 and 83 % for cow B and 18 and 11 % for cow C.

Table 3. *Mean apparent digestibility (%) of hay, dried grass and concentrates by three cows*

Food	Dry matter	Organic matter	Crude protein	Ether extract	Crude fibre	Nitrogen-free extract	Ash
Hay	54.6	55.4	45.8	78.7	60.2	50.9	48.6
Dried grass	66.1	71.6	69.5	54.1	69.3	74.2	33.3
Concentrates	80.9	82.9	80.0	91.5	34.6	88.0	55.8
SE of difference between two means	± 0.64	± 0.56	± 0.81	± 0.29	± 2.20	± 1.09	± 3.10

Table 4. *Mean apparent digestibility (%) of hay, dried grass and concentrates in the reticulo-rumen and in the remainder of the alimentary tract of three cows*

Food	Digestibility in reticulo-rumen			Digestibility in remainder of alimentary tract		
	Organic matter	Crude fibre	Nitrogen-free extract	Organic matter	Crude fibre	Nitrogen-free extract
Hay	30.6	43.8	28.8	24.8	16.4	22.1
Dried grass	40.6	45.1	43.4	31.0	24.2	30.8
Concentrates	38.6	11.2	60.0	44.3	23.4	28.0
SE of difference between two means	± 12.4	± 9.6	± 10.9			

Rate of disappearance of cotton thread in the rumen. The mean time required with each diet for the weight of cotton threads suspended in the rumen to be reduced by 25 % is shown in Table 2. Cotton threads disappeared slightly but consistently faster with hay than with dried grass. With the diet of concentrates, cotton threads were unchanged in weight when removed from the rumen after periods of up to 240 h.

Pairs of weighed coils of cotton thread were also placed in the rumen on successive days immediately after each change from a diet of concentrates to one of hay, and the loss of weight of each pair of threads in 24 h was recorded. After about 5 days the threads disappeared at a rate typical of that found with a diet of hay.

Mean time of retention of food residues. The mean times of retention of stained food residues in the alimentary tract with each diet are shown in Table 2. With diets of hay and dried grass the mean retention times, for the three cows and for the individual cows, were inversely related to the amount of food voluntarily consumed. However, there were large differences between the cows in the mean retention times of concentrates in the alimentary tract, and these times were not related to the amounts eaten; they were 53, 81 and 47 h for cows A, B and C, respectively.

Amount of digesta in the reticulo-rumen. The mean amounts of digesta and dry matter in the reticulo-rumen before and after feeding are shown in Table 5. Immediately before feeding the reticulo-rumen contained 40% more digesta and 84% more dry matter with a diet of hay than with dried grass. Immediately after feeding these differences were much smaller (12 and 10%, respectively) and less consistent. With a diet of concentrates the reticulo-rumen contained about two-thirds the amount of digesta and half the amount of dry matter found with the diets of dried grass, both before and after feeding.

With diets of hay and dried grass, dry matter disappeared from the reticulo-rumen, by digestion and onward passage, slightly faster between meals than during them, whereas with concentrates dry matter disappeared from the reticulo-rumen nearly four times faster during a meal than between meals.

Table 5. Mean amount of total digesta and dry matter in the reticulo-rumen of three cows before and after feeding and rate of disappearance of dry matter from the reticulo-rumen

Food	Intake of dry matter (lb)	Amount of digesta in the reticulo-rumen				Rate of disappearance of dry matter	
		Before feeding		After feeding		During feeding (lb/100 min)	Between meals (lb/100 min)
		Total (lb)	Dry matter (lb)	Total (lb)	Dry matter (lb)		
Hay	18.1	188	20.9	256	35.6	0.97	1.36
Dried grass	24.6	133	11.4	228	32.4	1.47	1.75
Concentrates	15.7	87	6.3	133	14.6	2.61	0.72
SE of difference between two means	± 1.47	± 0.7	± 1.19	± 10.5	± 1.71	± 0.052	—

Dry-matter content of digesta leaving the reticulo-rumen. The mean dry-matter percentages, for each diet, of the samples of digesta taken at the reticulo-omasal orifice at intervals during the day are shown in Fig. 1. The patterns for hay and dried grass were similar, with little variation between cows. The dry-matter percentage of the digesta fell from about 6.5 immediately before feeding to about 4.0 within 1 or 2 h of the beginning of the meal; it changed little for the next 6 h and then increased slowly. The reverse of this pattern was observed with concentrates. A rapid rise, 5–6 percentage units of dry matter in the first 1–2 h of the meal, was followed by a gradual return to the initial level. With this diet the range of dry-matter percentages was from 5 to 10 for cow A, from 9 to 14 for cow B and from 2 to 8 for cow C.

pH of digesta. The mean pH, for each of the duplicate samples of digesta taken at the reticulo-omasal orifice, is shown in Fig. 1. With hay the pH fell by about 0.2 during the 5–10 h after feeding, with dried grass by about 0.4 during the first 2 h of a meal and with concentrates by about 2.0 within 1 or 2 h of feeding, to a mean minimum of 4.65. Although there was little variation between the cows, the pH of the digesta of cows A and C tended to rise more rapidly after feeding than that of the digesta of cow B.

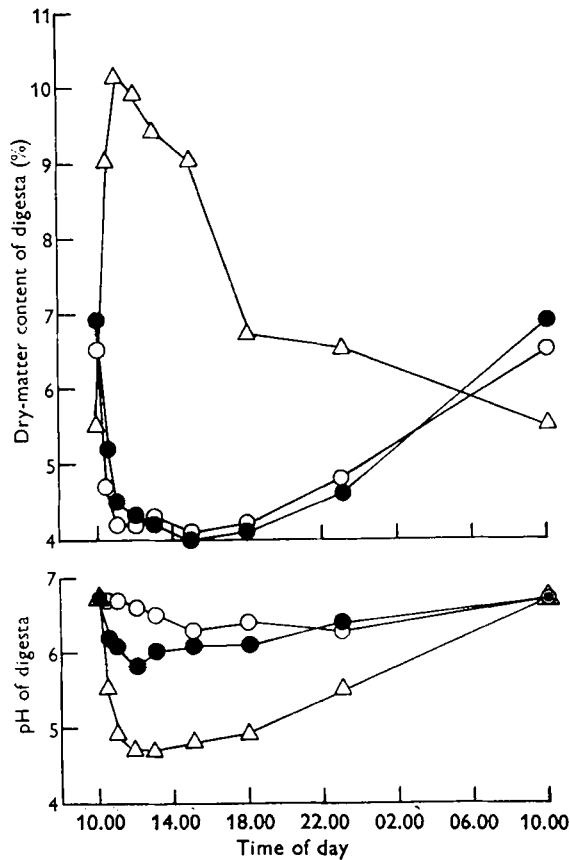


Fig. 1. Mean dry-matter content and pH of samples of digesta taken near the reticulo-omasal orifice at intervals during the day from three cows offered *ad lib.*: ○—○, hay; ●—●, dried grass; △—△, concentrates.

DISCUSSION

In this experiment the cows ate, on average, 35% more dried grass than hay. The dried grass was more digestible than the hay by 16 percentage units for the organic matter, and the mean retention time of the dried grass was 17 h less. The combined result was a more rapid disappearance of digesta from the alimentary tract with a diet of dried grass. However, this effect was not associated with an increase in the amount of digesta in the reticulo-rumen immediately after feeding to the extent required to maintain a uniform fill immediately before the next meal, as we found when comparing poorer-quality roughages (Campling *et al.* 1961, 1962). The situation we observed in the experiment here described approximated to that predicted by Blaxter *et al.* (1961), in that the cows ceased eating the hay and dried grass when the reticulo-rumen contained about the same amount of digesta.

It appears, therefore, that with the feeding régime used in this experiment, there were limiting values for the fill of the reticulo-rumen both before and after feeding, and that with the different roughages used these limits were approached at one or

other of these times. The amounts of digesta dry matter in the reticulo-rumen in this experiment, and in an earlier one (Campling *et al.* 1962) with the same cows, are shown in Fig. 2. When roughages having a mean rate of disappearance from the reticulo-rumen greater than 18 lb dry matter/day were offered *ad lib.*, eating ceased when the reticulo-rumen contained about 250 lb digesta or 35 lb dry matter. This limitation was probably set by the physical capacity of the reticulo-rumen. With roughages with a slower rate of disappearance, which would, if eaten to this same fill, be reduced to an amount greater than about 19 lb dry matter before the next meal, eating ceased when the reticulo-rumen contained less than 250 lb digesta, the amount present being that which would be reduced to about 19 lb dry matter immediately before the next meal.

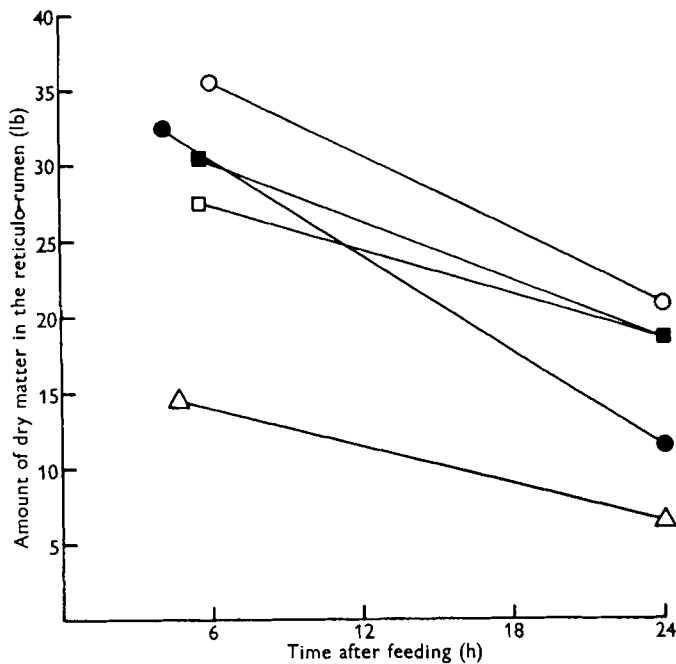


Fig. 2. Mean amounts of digesta dry matter in the reticulo-rumen immediately after feeding and before the next meal in three cows offered *ad lib.*: ○—○, hay; ●—●, dried grass; △—△, concentrates; □—□, oat straw; ■—■, oat straw with 150 g urea/day.

It is apparent from Fig. 2 that when concentrates were offered *ad lib.* the amount of digesta in the reticulo-rumen did not approach these limiting values either before or after feeding. Nor, considering the high digestibility of this food, does it seem possible that fill in the remainder of the alimentary tract could have limited intake.

It also seems unlikely that the energy intake of these animals was limited by their energy requirements, as would be expected in non-ruminants with similar diets (Kennedy, 1950). The amount of concentrates voluntarily consumed by our cows contained 21% less digestible organic matter than did their intake of dried grass. Also we have found in further experiments with diets of concentrates alone that the voluntary intake of concentrates to which access was available continuously was about 84% higher than the intake when access was restricted to 5 h/day, compared with

the corresponding increase of about 20% which we had found earlier with several roughage diets (Freer, Campling & Balch, 1962).

This finding lends support to the possibility that it was the concentration of some products of digestion which, in this experiment, limited the intake of concentrates. However, individual differences in the site of digestion of organic matter and therefore, presumably, in the products of digestion, had little effect on the intake of concentrates. For example, in cow B 75% and in cow C only 18% of the total digestible organic matter disappeared in the reticulo-rumen, but their relative intakes of concentrates were similar to those of the roughages. Support for these individual differences in the site of digestion was provided by the apparently greater formation of foam in the reticulo-rumen in cow A and, particularly, in cow B during the 5 h feeding period than in cow C. These differences also make it unlikely that distension of the reticulo-rumen by foam limited the intake of concentrates.

Table 6. *Differences between individual cows in the voluntary intake of concentrates, amounts of digesta dry matter in the reticulo-rumen before and after feeding, percentage of total digestible organic matter digested in the reticulo-rumen and retention times of rubber particles (sp.gr. 1.21) in the reticulo-rumen*

Cow	Voluntary food intake (lb)	Digesta dry matter		Percentage of total digestible organic matter	Mean retention time of rubber particles* (h)
		Before feeding (lb)	After feeding (lb)		
A	20.2	7.41	17.06	47	18
B	18.4	8.99	16.04	75	110
C	17.7	2.46	10.81	18	9

* Taken from Campling & Freer (1962).

The estimated digestion of concentrates in the reticulo-rumen of the individual cows was directly related to the mean retention time of stained food in the alimentary tract (Table 6). Values presented earlier (Campling & Freer, 1962) for the mean time of retention of inert particles in the different portions of the alimentary tract of these cows suggest that the individual differences in the mean retention time of concentrates were restricted to the reticulo-rumen.

We have no evidence on the nature of the digestion products that might have limited the intake of concentrates. The pH of the rumen contents fell to the same level in all three cows within 1 or 2 h of the beginning of feeding but this cannot have had a direct effect since eating continued at intervals during the 5 h despite the low pH. No explanation can be offered for the fact that the rumen pH fell to the same value in all three cows although they were each digesting different amounts of concentrates in the reticulo-rumen. It was also observed, as will be reported later, that the motility of the reticulo-rumen was not depressed at a pH of about 4.6; in fact while the animals were eating, the frequency of reticular contraction was higher with a diet of concentrates than we have recorded for other diets.

The unexpectedly large between-cow differences in the site of digestion of concentrates observed in this experiment must be investigated further and confirmed before the implication of these differences can be considered.

SUMMARY

1. The relationship between the voluntary intake of food, the amount of digesta in the reticulo-rumen and the rate of disappearance of digesta from the alimentary tract with diets of hay, dried grass or concentrates was examined in a Latin square design with three adult non-lactating cows.

2. The mean voluntary intakes of food offered *ad lib.* for 5 h/day were 20.9 lb hay, 28.2 lb dried grass and 18.8 lb concentrates. The intakes of hay and dried grass were directly related to the digestibility of the foods in the whole alimentary tract and in the reticulo-rumen alone and inversely related to the mean retention time of residues in the alimentary tract.

3. The amount of digesta in the reticulo-rumen immediately after feeding was about the same with diets of hay as it was with diets of dried grass and was consequently much less with the diet of dried grass immediately before the next meal. With the feeding régime used in our experiments it is suggested that with different roughages having a mean daily rate of disappearance from the reticulo-rumen greater than about 18 lb dry matter, eating ceased when the reticulo-rumen contained the same amount of digesta, about 35 lb dry matter for our cows, a limit possibly set by the capacity of the organ. With roughages having a slower rate of disappearance it appears that eating ceased when the reticulo-rumen contained less digesta, the amount present being that which would be reduced to about 19 lb dry matter immediately before the next meal.

4. The voluntary intake of concentrates was not related in the same way to the digestibility of the food or its mean time of retention in the alimentary tract. The amount of digesta in the reticulo-rumen did not approach the amount found with the other foods, either before or after eating. It is suggested that the concentration of products of digestion of the concentrates may have limited their intake. The pH of rumen digesta fell to about 4.6 within 1 or 2 h of the beginning of feeding and remained at this level for from 3 to 6 h.

5. Individual differences in the voluntary intake of concentrates were similar to the individual differences between cows in the intake of the two roughages. Although there was little difference between the cows in the overall digestibility of the concentrates there were wide differences in the proportion of the disappearance by digestion which occurred in the reticulo-rumen and this was directly related to the mean retention time of food in that organ. In all cows cotton threads suspended in the rumen were not reduced in weight with a diet of concentrates, but when hay was given they disappeared within 5 days at a rate typical of a hay diet.

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