Voluntary intake, digestion, rate of passage, amount of material in the alimentary tract and behaviour in cows receiving complete diets containing straw and concentrates in different proportions

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1. Pelleted diets containing concentrates and 0, 20, 40 or 60% chopped straw were fed *ad lib.* for 5 h daily to four cows. Voluntary intake, digestion and rate of passage of these diets were examined, and also the behaviour of the cows and the amount of material in the rumen before and after feeding.

2. Least dry matter (7·5 kg) was consumed when there was no roughage in the diet. When roughage was present, its level had no effect on dry-matter intakes, which were 10·7, 11·3 and 10·7 kg for 20, 40 and 60% roughage respectively. Digestible energy intakes were greatest with diets containing 20 or 40% roughage.

3. The digestibilities of the dry matter of the four diets were 81, 69, 59 and 55% in increasing order of roughage content. The proportion of total digestion which occurred in the rumen decreased as the roughage content of the ration increased. The rate of breakdown of cotton threads in the rumen increased as the roughage content of the diet increased.

4. Rates of passage varied greatly between cows and there were no differences between treatments in passage rates through the entire alimentary tract. The diets on which the cows consumed the largest amounts of digestible energy (20 and 40% roughage) passed through the rumen more slowly, and through the hind gut more quickly, than the other diets.

5. The times spent daily eating and ruminating both increased as the proportion of roughage in the diet was increased, but in relation to the amount of dry matter eaten, eating times were lowest with diets containing 20 or 40% roughage. Time spent ruminating per kg straw eaten decreased with increasing straw content of the diet. Rumen contraction rate during eating was greatest when dry-matter intake was greatest, but during rumination it was similar with all three levels of roughage.

6. Before and after feeding, the amount of digesta and digesta dry matter in the rumen increased as the proportion of roughage in the diet increased. After feeding, there was a highly significant linear relationship between the amount of digesta in the rumen and the digestibility of the diet.

7. In a second experiment, similar diets containing 0 or 50% roughage were given to two cows for 5 or 24 h daily. The 24 h intake expressed as a percentage of 5 h intake was 148% for the 0% roughage diet, but only 105% when the diet contained 50% roughage.

8. The results of these experiments are interpreted as indicating a declining importance of physical factors in the regulation of the intake by cows of a range of diets of increasing digestibility.

There is a need to investigate further the factors that regulate voluntary intake in ruminants so that intake can be predicted over a wide range of food and, on occasions, increased consumption can be obtained. This knowledge would lead to the more efficient production of milk and meat.

Many workers (e.g. Balch & Campling, 1962; Blaxter, Wainman & Wilson, 1961) have concluded that, when roughages are eaten, physical distension of the reticulo-rumen is an important factor regulating food intake in ruminants. The results obtained by Ulyatt, Blaxter & McDonald (1967) support the hypothesis that sheep voluntarily

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consume roughages of different qualities to achieve constant fill of the rumen. Blaxter (1950–1) made the generalization that the amount of food dry matter consumed increased with increasing concentration of the ration expressed as net energy per unit of dry matter.

In contrast, from the results of experiments in which diets containing different proportions of lucerne and maize were given to heifers and lambs, Montgomery & Baumgardt (1965) concluded that ruminants will adjust voluntary food intake in relation to the physiological demand for energy if fill or rumen load does not limit their consumption. According to their views, energy intake would be expected to rise with increasing nutritive value of the diet, becoming constant at a level which met the animal's physiological demand for energy. Once this level was reached, the intake of dry matter would decline as the nutritive value of the diet was further increased in order to maintain a constant energy intake. This theory implies that, with diets of high nutrient value, intake would be regulated by chemostatic or thermostatic mechanisms.

In our study physical and chemical changes associated with food intake have been examined simultaneously. Diets with a wide range of digestibility were used and physical changes, such as the amount of material in different parts of the gut and rate of passage of food residues, were measured as well as changes in the levels of various metabolites in the rumen and blood. It was considered necessary to cover digestibilities from 55 to 80%, as this range includes the digestibilities of most diets for dairy cows in this country. This was achieved by preparing four diets containing different proportions of straw and concentrate; the diets were pelleted to prevent selection of individual components by the cows. The use of straw rather than hay permitted a reduction in the range of roughage:concentrate ratios required, thus facilitating quick changes from one diet to another during the experiment. It was considered important to use chopped rather than ground straw and to include in the measurements an assessment of the possible contribution of fill in the intestine to the control of intake of the complete diets. Distension of the intestine has been implicated (Campling & Freer, 1966) in the regulation of intake of ground roughages, although this is not thought to be of any importance in the control of concentrate intake (Freer & Campling, 1963). This paper deals with the physical measurements; concentrations of energy-yielding metabolites in the rumen and in blood will be dealt with subsequently.

EXPERIMENTAL

Expt 1: *procedure*

A balanced 4 × 4 Latin square experiment was used to compare the following diets each given to four cows:

Diet	Barley straw (%)	Concentrate (%)
60R	60	40
40R	40	60
20R	20	80
0R	0	100

Each 5-week experimental period consisted of: 14 d for adjustment to the diet; 10 d during which voluntary food intake, digestibility in the reticulo-rumen and in the entire digestive tract, breakdown of cotton threads in the ventral sac of the rumen, and mean retention time of undigested feed residues in the hind gut and in the entire digestive tract were measured; 3 d during which blood and rumen samples were collected (the results obtained from these samples will be the subject of another paper); 3 d recovery; 3 d on which behaviour was recorded; 2 d on which the amount of material in the reticulo-rumen was measured and the cows were weighed, after feeding but with the rumen emptied.

Cows and housing

The cows were mature non-pregnant, non-lactating Friesians, each fitted with a permanent rumen fistula closed by a rubber cannula and bung. The cows were housed in individual standings in a metabolism house. Water and salt licks containing trace elements were available at all times. During the experiment, the mean live weight of the cows, with the rumen emptied, was 532 kg.

Foods

The barley straw was chopped to give particles with a mean length of 1·09 ± 0·021 cm. Particle length was determined by separating the straw content of the extruded complete diets by flotation in water. The straw particles were air-dried, mixed

Table 1. *Expt* 1. *Composition of the complete diets given to the cows*

Component		Diet 60R	Diet 40R	Diet 20R	Diet 0R
		Proportions* (% by weight)			
Chopped barley straw		60	40	20	0
Concentrate		27	47	67	87
Molasses		10	10	10	10
Sodium chloride		1·5	1·5	1·5	1·5
Dicalcium phosphate		1·5	1·5	1·5	1·5
		Chemical composition			
DM (%)		86·56	85·92	86·77	86·88
Organic matter	as % of DM	92·50	92·51	92·26	91·45
Crude protein	as % of DM	9·15	11·15	14·87	18·23
Ether extract	as % of DM	1·92	2·18	2·77	3·20
Cellulose†	as % of DM	32·47	25·24	16·22	8·05
Lignin	as % of DM	5·72	5·06	3·97	2·90
Ash	as % of DM	7·50	7·49	7·74	8·55
Calorific value (kcal/g DM)‡		4·35	4·40	4·41	4·44

DM, dry matter.

* In addition, the following were added to all diets (g/1000 kg): vitamins A, D_3 and E (potencies 50000, 10000 and 52·5 i.u./g respectively) 200, $CoSO_4.7H_2O$ 17, $FeSO_4.7H_2O$ 36, $MnSO_4.4H_2O$ 18, KI (90%) 2, and ZnO 20.

† Calculated as acid detergent fibre–lignin.

‡ 1 cal = 4·184 J.

thoroughly and subsampled by hand. One thousand individual particles were taken at random from the subsample, the length of each was measured on a linear scale and the distribution of particles over various sizes was determined; from this, the mean value

was calculated. The composition of the concentrate was (in parts): barley 20, maize 23, wheat bran 23, decorticated groundnut meal 17, copra cake 11 and palm-kernel cake 6. The straw and concentrate were mixed in the proportions shown in Table 1, and to the final diets were added: molasses at a rate of 10%; dicalcium phosphate and sodium chloride each at a rate of 1·5%; and vitamin and trace-element supplements. The diets were extruded through a 1·6 cm die to give pellets approximately 5 cm in length. The chemical compositions of the complete diets are shown in Table 1.

Determination of voluntary intake

The total daily allowance of each diet was offered in one meal at 10.00 hours. The uneaten food was removed and weighed after 5 h and its dry matter determined. The amount of food offered was adjusted so that the uneaten portion was about 10% of the amount offered. Water intakes were recorded daily.

Digestibility

The total digestibility of the diets was determined by collecting the faeces with the harness and equipment described by Balch, Bartlett & Johnson (1951). The net amount of digestion occurring in the reticulo-rumen was estimated by means of the lignin-ratio technique (Balch, 1957; Campling, Freer & Balch, 1961); samples of digesta were taken from a point close to the reticulo-omasal orifice, five times daily over a period of 5 d, and were bulked for analysis.

Digestion of cellulose 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.

Mean time of retention of undigested food residues in the alimentary tract

On the 3rd day of each collection period, about 4% of the daily intake of food, stained with magenta, was thoroughly mixed by hand into the rumen contents. At the same time, 50 g milled (0·9 mm screen) food stained with Brilliant Green were suspended in warm water and introduced into the abomasum through a rubber tube inserted through the rumen fistula and the reticulo-omasal orifice. The numbers of stained particles of each colour were counted in subsequent samples of faeces (Balch, 1950) and the mean times of retention of stained particles in the whole gut and in the abomasum and intestine (subsequently abbreviated to 'hind gut') were calculated by the method of Castle (1956).

Amount of digesta in the gastro-intestinal tract

The total weight of digesta and the amount of digesta dry matter in the reticulo-rumen were determined by manually emptying that organ and weighing, sampling and returning the contents before and after feeding on 2 consecutive days at the end of each treatment period. Total gut fill was calculated by the method of Baumgardt (1965). To find, by this method, the weight of dry matter contained in the digestive

tract at a given time, previous intakes of food are summed after being weighted by the fraction of the undigested residue still in the tract and the fraction of the meal not digested. The numerical values of these two weighting factors are determined by the time that has elapsed between the ingestion of each meal and the time at which fill is to be calculated. To make the calculation, it is necessary that the animals are fed at equal intervals of time, and the value is made more accurate if individual daily values for food intake are used. Fill, calculated in this way, assumes instantaneous intake.

An estimate was obtained, by difference between the calculated amount of material in the whole gut and the measured amount in the reticulo-rumen, of the amount of dry matter in the omasum and hind gut.

Behaviour

The times spent eating, ruminating and resting, and the motility of the reticulum, were recorded as described by Campling & Freer (1966), during periods of 72 h.

Chemical methods

Dried samples of feeds, faeces and rumen digesta were bulked and analysed for ash and ether extract (Association of Official Agricultural Chemists, 1965), and for lignin and acid detergent fibre by the method of Van Soest (1963). Cellulose was calculated as the difference between acid detergent fibre and lignin (Colburn & Evans, 1965). Crude protein was determined in dried feed samples, and in faeces and rumen digesta stored under acid (Association of Official Agricultural Chemists, 1965). The calorific values of dried foods and faeces were determined in an adiabatic bomb calorimeter.

Statistical analyses

Statistical analyses of the results were based on methods described by Snedecor (1956). A multiple range test (Duncan, 1955) was used to compare treatment means.

Expt 2

The influence of time of access to food on voluntary intake of complete diets was measured in a simple experiment with two of the cows previously used in Expt 1. The diets used were 0R and a mixture (50R) of equal parts of diets 40R and 60R used in Expt 1. Voluntary intakes of each diet by each cow were determined during 10 d periods with 5 h access, as in Expt 1, and when the cows were fed twice daily, in two equal parts at 06.00 and 18.00 hours, with 24 h access. When the cows had 24 h access, uneaten food was removed immediately before the 18.00 feed. The amount of food offered was adjusted so that the uneaten portion was about 10% of the amount given. No other measurements were made.

RESULTS

Voluntary intake

The mean daily intakes of water, dry matter, digestible organic matter and digestible energy by the four cows in Expt 1 are shown in Table 2.

There were no significant differences in dry-matter intake between the three diets containing roughage. These diets were all eaten in significantly ($P < 0.01$) greater amounts than the all-concentrate diet. Digestible organic matter and digestible energy intakes were significantly ($P < 0.05$) higher for diets 20R and 40R than for diets 0R and 60R. The intake of water was significantly ($P < 0.05$) less when diet 60R was

Table 2. *Expt* 1. *Mean daily intakes of water, dry matter, digestible organic matter and digestible energy by four cows offered* ad lib. *complete diets containing different proportions of straw and concentrate*

	Mean daily intake			
Diet (see Table 1)	Water (kg)	Dry matter (kg)	Digestible organic matter (kg)	Digestible energy (Mcal)*
60R	35.9^{a}	10.73^{A}	5.56^{a}	26.2^{a}
40R	42.3^{b}	11.25^{A}	6.32^{ab}	29.3^{ab}
20R	42.5^{b}	10.71^{A}	6.94^{b}	32.3^{b}
0R	38.2^{ab}	7.47^{B}	5.61^{a}	26.2^{a}
SE of difference between two means	2.10	0.63	0.41	2.08

Means in the same column with different superscripts are significantly different: ^{A}, ^{B}, $P < 0.01$; ^{a}, ^{b}, $P < 0.05$.
* 1 cal = 4.184 J.

Table 3. *Expt* 2. *Mean voluntary intake of complete diets containing* 50 *or* 0% *roughage, available to two cows for* 5 *or* 24 *h daily*

		Voluntary intake (kg dry matter/d)			
Diet (see p. 1017)	Time of access (h)	Cow G	Cow P	Mean	24 h value as % of 5 h value
50R	5	13.00	11.68	12.34	—
	24	13.82	12.07	12.95	105
0R	5	11.11	6.84	8.98	—
	24	14.04	12.57	13.31	148

given than when the animals received either of the other diets containing roughage. There were significant ($P < 0.05$) linear relationships between water intake and the intakes of dry matter ($r = 0.63$), digestible organic matter ($r = 0.66$) and digestible energy ($r = 0.63$); the regression coefficients were 1.59, 3.82 and 0.78 respectively.

When access to the complete diets was increased in the second experiment from 5 to 24 h, the intake (Table 3) of diet 50R increased to only 105% of that when the cows had 5 h access. However, with diet 0R the mean increase was to 148%, the 24 h intake being very similar to the 24 h intake of diet 50R.

Digestibility

The digestibilities of the diets when offered *ad lib.* in Expt 1 are shown in Table 4. The values for digestibility in the hind gut were calculated as the differences between the digestibilities in the whole gut and in the reticulo-rumen. The differences between all diets were significant ($P < 0.01$) but the increases in digestibility with each reduction in straw content of the diet were not equal. Digestibility of the dry matter in the reticulo-rumen followed a similar pattern. On all diets, the greater part of the

Table 4. *Expt* 1. *Mean apparent digestibilities* (%) *in the whole gut, reticulo-rumen and hind gut of dry matter, organic matter, cellulose, crude protein and lignin in complete diets containing different proportions of straw and concentrate, offered* ad lib. *to four cows*

Diet (see Table 1)	Dry matter	Organic matter	Cellulose	Crude protein	Lignin
		Digestibility in whole gut			
60R	55.1^{A}	56.4^{A}	49.9^{b}	51.6^{A}	−4·4
40R	59.1^{B}	60.8^{B}	47.1^{ab}	56.9^{A}	0·7
20R	69.1^{C}	70.6^{C}	42.9^{a}	72.6^{B}	7·2
0R	80.6^{D}	82.6^{D}	58.5^{c}	78.3^{B}	10·5
SE of difference between two means	0·34	0·83	2·27	2·14	—
		Digestibility in reticulo-rumen			
60R	33.3^{A}	35.6^{A}	28.6^{B}	20.1^{a}	—
40R	40.8^{B}	42.6^{B}	26.8^{B}	30.6^{b}	—
20R	51.4^{C}	52.5^{C}	12.2^{A}	42.5^{c}	—
0R	65.0^{D}	67.8^{D}	50.4^{C}	41.2^{c}	—
SE of difference between two means	1·39	1·42	3·03	3·56	—
		Digestibility in hind gut (by difference)			
60R	21.8^{a}	20.8^{a}	21.3^{B}	31.5^{ab}	—
40R	18.3^{ab}	18.2^{ab}	20.3^{B}	26.3^{a}	—
20R	17.7^{b}	18.1^{ab}	30.7^{A}	30.1^{ab}	—
0R	15.6^{b}	14.8^{b}	8.1^{C}	37.1^{b}	—
SE of difference between two means	1·58	1·53	1·76	2·90	—

Means in the same column with different superscripts are significantly different: ^{A}, ^{B}, ^{C}, ^{D}, $P < 0.01$; ^{a}, ^{b}, ^{c}, ^{d}, $P < 0.05$.

digestible dry matter disappeared in the reticulo-rumen, the proportion increasing with decreasing straw content of the diet from 60% on diet 60R to 80% on diet 0R. In the hind gut there was a decline in the amount of the total dry matter digested as the proportion of straw in the diet declined, but the variation between diets was much less than in the reticulo-rumen. Significantly ($P < 0.05$) more of the dry matter of diet 60R than of 20R or 0R was digested in the hind gut; no other differences between diets were significant. The digestibility of the organic matter of the four diets closely paralleled that of the dry matter in all parts of the alimentary tract.

With diets 40R and 60R, about half the cellulose consumed was digested, slightly more disappearing in the reticulo-rumen than in the hind gut. The total digestibility

of the cellulose of diet 20R was only a little less than that of the two high-roughage diets. However, the digestion of cellulose in the reticulo-rumen was severely depressed in comparison with that in the two high-roughage diets, and this difference was significant ($P < 0.01$). In contrast, the disappearance of digestible cellulose in the hind gut was significantly ($P < 0.01$) greater than when diet 60R or 40R was given. Nearly 60% of the cellulose of the all-concentrate diet was digested; this was significantly ($P < 0.01$) more than with any of the diets containing straw. Most of this digestion took place in the reticulo-rumen, where the cellulose digestibility was significantly ($P < 0.01$) higher than with any of the roughage diets.

Significantly ($P < 0.05$) more nitrogen of diet 40R than of diet 60R disappeared from the reticulo-rumen. The total digestibility of the crude protein of diets 0R and 20R was significantly ($P < 0.01$) greater than that of the two high-roughage diets, owing mainly to a significantly ($P < 0.05$) greater digestibility in the reticulo-rumen. When diet 0R was given, the digestibility of crude protein in the hind gut was also significantly ($P < 0.05$) greater than that of diet 40R.

The digestibility of lignin ranged from −4% to +11%; thus faecal recoveries of lignin were very close to the range 90–110% considered necessary for accurate application of the lignin-ratio technique (Balch, 1957).

Amounts of digesta in the reticulo-rumen and hind gut

Before a meal, the amounts of wet digesta and digesta dry matter present in the reticulo-rumen were smallest in cows receiving diet 0R and 20R (Table 5). The greatest amounts were present when diet 60R was given, these being significantly

Table 5. *Expt* 1. *Mean amounts* (*kg*) *of digesta and digesta dry matter in the reticulo-rumen of four cows before and after feeding* ad lib. *on complete diets containing different proportions of straw and concentrate*

Diet (see Table 1)	Before feeding		After feeding	
	Total digesta	Digesta dry matter	Total digesta	Digesta dry matter
60R	64.0^{C}	6.78^{A}	92.9^{A}	13.95^{A}
40R	54.9^{BC}	5.64^{A}	86.3^{A}	12.82^{A}
20R	43.1^{A}	3.95^{B}	71.9^{B}	9.52^{B}
0R	45.9^{AB}	3.63^{B}	59.8^{C}	6.67^{C}
SE of difference between two means	2.84	0.42	3.09	0.66

Means in the same column with different superscripts are significantly different ($P < 0.01$).

($P < 0.01$) more than when 0R and 20R were given. In cows receiving diet 40R, there were significantly ($P < 0.01$) more digesta in the rumen than in cows receiving 20R and the amount of digesta dry matter was significantly ($P < 0.01$) greater than in cows receiving either of the low-roughage diets.

After a meal, there was a highly significant ($P < 0.001$) linear relationship ($r = -0.92$) between the total amount of digesta in the reticulo-rumen and the digestibility of the

diet (Fig. 1). There were significant ($P < 0.01$) differences between 40R and 20R, and between 20R and 0R, in the amounts of digesta and digesta dry matter in the reticulo-rumen.

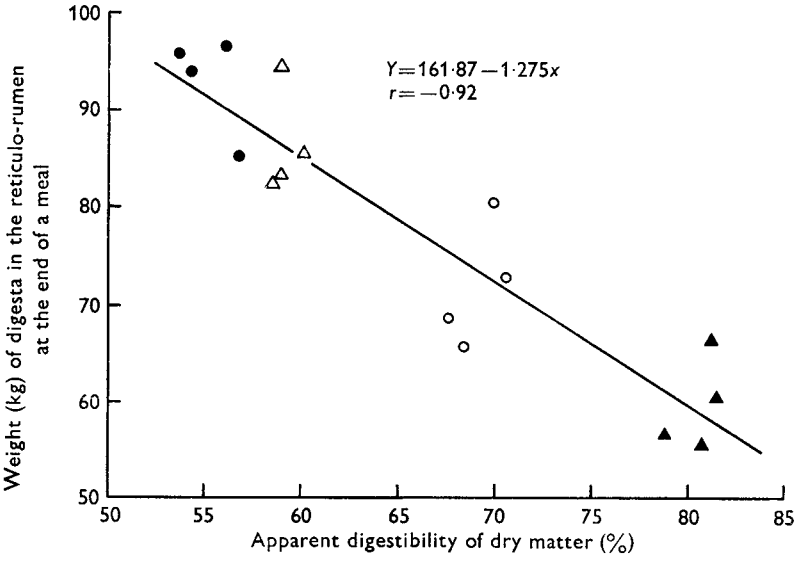

Fig. 1. The relationship between the weight of digesta in the reticulo-rumen at the end of a meal and the apparent digestibility of the dry matter of the diet when complete diets containing concentrates and 60% (●), 40% (△), 20% (○) or 0% (▲) barley straw were offered *ad lib.* to four cows.

Table 6. *Expt* 1. *Amount of dry matter (kg) in the reticulo-rumen of cows on the* 1*st day of rumen emptying together with the total amount of dry matter (kg) in the whole gut (calculated according to Baumgardt,* 1965*) and, by difference, the amount of dry matter (kg) in the gut distal to the reticulo-rumen*

Diet (see Table 1)	Dry matter in different parts of the alimentary canal		
	Total	Reticulo-rumen	Hind gut
60R	19·74^{bc}	13·84	5·90^{a}
40R	21·02^{c}	12·56	8·46^{b}
20R	18·98^{b}	9·59	9·39^{b}
0R	10·53^{a}	6·59	3·94^{a}

Means in the same column with different superscripts are significantly different ($P < 0.05$).

The calculated amounts of dry matter in the whole alimentary canal on the 1st day of rumen emptying are given in Table 6. The measured amounts of dry matter in the reticulo-rumen at the end of feeding are also given, together with the amount of dry matter in the omasum, abomasum and intestines, calculated as the difference between the above amounts. The contents of the whole gut were greatest when diet 40R was given, being significantly ($P < 0.05$) greater than when 0R or 20R was given. When

diet 0R was given, the contents of the whole gut were significantly ($P < 0.05$) less than when any of the other diets was given. In the gut distal to the reticulo-rumen, the greatest amount of material was found in cows receiving diet 20R. Cows receiving diet 0R or 60R had significantly ($P < 0.05$) less digesta in the hind gut than those receiving 20R or 40R.

Digestion of cellulose in the rumen

The times taken for cotton threads placed in the ventral sac of the rumen to lose 25% of their weight were least in cows receiving diet 40R and 60R, there being no difference between the values with these diets (Table 7). On diet 20R, the time taken

Table 7. *Expt* 1. *Time for* 25% *loss of weight of cotton threads placed in the ventral sac of the rumen of four cows offered* ad lib. *complete diets containing different proportions of straw and concentrate*

Diet (see Table 1)	Time (h) for 25% loss of weight
60R	29·6
40R	28·5
20R	> 60
0R	> 120

Table 8. *Expt* 1. *Mean retention time in the whole gut, hind gut and reticulo-rumen of undigested residues of complete diets, containing different proportions of straw and concentrate, offered* ad lib. *to four cows*

Diet (see Table 1)	Mean retention time (h)		
	Whole gut	Hind gut	Reticulo-rumen (by difference)
60R	$61·2^{a}$	$16·7^{ab}$	$44·5^{a}$
40R	$59·0^{a}$	$12·2^{a}$	$46·8^{ab}$
20R	$69·7^{a}$	$13·3^{a}$	$56·4^{b}$
0R	$62·5^{a}$	$19·5^{b}$	$43·0^{a}$
SE of difference between two means	4·86	2·24	4·09

Means in the same column with different superscripts are significantly different ($P < 0.05$).

was in excess of 60 h, more than twice that taken on the two high-roughage diets. When the all-concentrate diet was given, there was no loss of weight of cotton threads after 5 d in three of the cows. In the fourth cow, cotton threads lost 25% of their weight after 47 h; during the experiment, this animal had received the diets in the order 60R, 40R, 20R and 0R.

Mean time of retention of undigested food residues in the alimentary tract

The mean time of retention in the gut of undigested residues of the four diets varied greatly between cows, so few of the observed differences were significant.

In the hind gut, residues of diet 0R were retained for a significantly ($P < 0.05$)

longer time than residues of diet 20R and 40R. In the reticulo-rumen, the longest retention time was for residues of diet 20R, being significantly ($P < 0.05$) greater than for those of diet 0R or 60R.

Behaviour

The behaviour of the cows in Expt 1 is shown in Table 9. In this table 'resting' refers to all activity other than eating or ruminating. The mean time spent daily eating the four diets declined as the percentage of roughage in the diet was reduced. In relation to the amount of dry matter consumed, cows receiving 0R spent the greatest amount of time eating, the time being significantly ($P < 0.05$) greater than in cows

Table 9. *Expt 1. Mean daily time spent eating, ruminating and resting, and the frequency of reticular contractions during each activity when complete diets, containing different proportions of straw and concentrate, were offered to four cows*

Diet (see Table 1)	Time (min)			Contractions/100 min			Time spent ruminating/kg straw DM eaten (min)	Time spent eating/kg total DM eaten (min)	Time between start of feeding and first rumination (min)
	Eating	Ruminating	Resting	Eating	Ruminating	Resting			
60R	198^{c}	468^{C}	774^{C}	177^{b}	103^{a}	122^{c}	72·6	$18{\cdot}4^{ab}$	163^{A}
40R	190^{bc}	409^{C}	841^{C}	184^{c}	102^{a}	118^{bc}	91·2	$17{\cdot}0^{a}$	184^{A}
20R	168^{ab}	218^{B}	1054^{B}	180^{bc}	107^{a}	105^{ab}	102·5	$15{\cdot}7^{a}$	541^{B}
0R	154^{a}	0^{A}	1286^{A}	168^{a}	—	102^{a}	—	$20{\cdot}8^{b}$	705^{*C}
SE of difference between two means	9·4	24·4	24·7	2·6	5·5	5·9	—	1·27	40·1

DM, dry matter.

Means in the same column with different superscripts are significantly different: ^{A}, ^{B}, ^{C}, $P < 0.01$; ^{a}, ^{b}, ^{c}, $P < 0.05$.

* First triple contractions of reticulo-rumen.

given 20R or 40R, but not significantly greater than 60R. The rate of reticular contractions during eating was greatest on 40R, the rate being significantly ($P < 0.05$) faster than on 0R or 60R. The rate recorded with 0R was significantly ($P < 0.05$) lower than with any of the other diets.

Similarly, the mean daily time spent ruminating decreased as the proportion of straw in the diet decreased. On 20R the time spent ruminating was significantly ($P < 0.01$) less than on 60R and 40R, and more than on 0R, when there was no true rumination at all. When diet 0R was given, periods of triple reticular contractions, without the corresponding jaw movements, were noted in all cows; they were similar to those observed by Freer & Campling (1965) in cows fed an all-concentrate diet. In relation to the amount of straw dry matter eaten, there was an increase in the daily time spent ruminating as the proportion of straw in the diet decreased. There were no differences between treatments in the rate of reticular contractions during rumination.

The time between the start of eating and the first subsequent period of rumination increased as the proportion of straw in the diet decreased. On both diets 60R and 40R there were up to three periods of rumination while the cows still had access to food.

When diet 20 R was given, the first period of rumination did not start until 9 h after food was offered; this was significantly ($P < 0.01$) later than when 60 R or 40 R was given. In no instance did cows given diet 20 R ruminate while they still had access to food. In cows given diet 0 R, triple contractions of the reticulum were not seen until nearly 12 h after the food was first offered.

As the proportion of roughage in the diet decreased, the time spent daily in resting increased, being significantly ($P < 0.01$) less on 60 R and 40 R than on 20 R, and less on 20 R than on 0 R, and the rate of reticular contraction during resting decreased.

DISCUSSION

In Expt 1, cows were given *ad lib.* access to food for 5 h daily; under this regimen, dry-matter intakes did not increase with increasing digestibility of the diets containing roughage. Intakes of digestible energy were greatest when diet 20 R was given; there was a large fall in intake of both dry matter and digestible energy with the change from 20 R to 0 R. Thus, there was no evidence of an increase in dry-matter intake with increasing digestibility of the diets containing roughage, as has been observed by many workers, including Blaxter *et al.* (1961) and Ulyatt *et al.* (1967). Owing to the low intake of diet 0 R, there was also no evidence of a constant maximum level of energy intake being achieved as the proportion of roughage in the ration decreased, as was noted by Montgomery & Baumgardt (1965). However, Baumgardt (1970) has pointed out that energy intake is often less on diets of very high energy content than on diets that are moderately high in energy. Also, had the animals had access to food for 24 h daily, energy intake might have become more constant among diets as the intake in Expt 2 of diet 0 R increased by a much greater margin relative to the 5 h intake than did that of the diet of lower digestibility and higher roughage content (see Table 3). Freer & Campling (1963) have also observed this relative change in intakes of concentrates and roughages as the time of access is increased.

Consideration must be given to the extent to which intake may have been influenced by the decrease in crude-protein content of the rations as the proportion of roughage in the diet increased (Table 1). Elliott (1967*a*) pointed out that level of protein in the diet, below approximately 10% crude protein, affects voluntary intake by ruminants. He found that the concept of a positive correlation between intake and digestibility of a food was valid only when protein intake was at least 4 g digestible crude protein/kg $W^{0.73}$ per d. In the present work, diet 60 R contained 9·15% crude protein and supplied 5·2 g digestible crude protein/kg $W^{0.73}$ per d when eaten *ad lib.* Kay, Bowers & McKiddie (1968) in experiments with young, rapidly growing steers observed lowered intake and digestibility of a concentrate diet containing 11% crude protein when compared with diets containing 14 or 17% crude protein. However, it seems likely that the critical protein level would be lower in mature animals with a lower protein requirement. With sheep, crude protein contents near 8% have been found adequate to maximize intake (Elliott & Topps, 1963; Blaxter & Wilson, 1963), although Elliott (1967*b*) has suggested that cattle have higher protein requirements than sheep. It is thus possible that the intake of diet 60 R may have been marginally reduced owing to its low protein content,

but it seems unlikely that intakes of the other diets would have been influenced in this way. A decline in the intake of mixed diets of high roughage content was also observed by Swan & Lamming (1967) in an experiment in which the crude-protein content of all diets was standardized at 12%.

The differences in intake observed in the present study are, in effect, differences in intake at individual meals and reflect differences in the mechanism of regulation of intake of the different diets used. The cows did not eat to a constant fill of their rumen, as has been observed in sheep consuming roughages of different quality (Blaxter *et al.* 1961; Ulyatt *et al.* 1967). The high negative correlation between the amount of material in the reticulo-rumen at the end of a meal and the digestibility of the dry matter consumed in that meal (Fig. 1) indicates a steady decline in the importance of distension of the rumen in controlling intake, as digestibility increases. The total amounts of digesta in the reticulo-rumen at the end of the feeding period were of the same order for diets 40R and 60R, suggesting that the maximum fill of this organ was closely approached when these higher-roughage diets were given. However, the relatively high rates of passage and rapid rates of cellulose breakdown when these diets were given reduced the margins between these diets and diets 20R and 0R in the amount of material in the rumen before feeding; nevertheless, this margin was still significant, there being no tendency towards equality of rumen fill before feeding, as was observed by Campling, Freer & Balch (1962) when various roughages were given. This agrees with the finding of Freer & Campling (1963) that the amount of material in the rumen was less before a meal of concentrates than before a meal of roughage.

There was no evidence that distension of the hind gut limited intake of diet 0R because the calculated value for fill in the hind gut (Table 6) was lower for this diet than for any of the diets containing straw. Furthermore, it seems unlikely that the energy intake, when this diet was given, was limited by the energy requirements of the cows receiving the diet, since more energy was consumed with 20R or 40R than with 0R. Thus, it must be concluded that some product or products of digestion in some way limited the intake of the all-concentrate diet to a much greater extent than it limited the intake of the other diets. The nature of these products will be discussed in a later paper. Unlike the work of Freer & Campling (1963), only small differences between cows in the main site of digestion of the all-concentrate ration were observed. The amount of the total digestible organic matter disappearing in the rumen ranged only from 81·3 to 84·4% for the four cows given diet 0R; it is unlikely, therefore, that there were large differences in the proportions of food digested to volatile fatty acids and to monosaccharides.

It is more difficult to determine the nature of the signal causing the cows to stop eating diet 20R. Distension of the reticulo-rumen is not likely to have exerted a major influence, the amount of digesta in this organ after a meal being substantially lower than when diet 40R or 60R was given. The amount of dry matter in the hind gut was greatest when 20R was given and may have exerted a physical effect restricting further intake. Intake of 20R may have been adequate to meet the energy requirements of the cows, in which event an accumulation of energy-yielding metabolites in the blood may have caused the cessation of eating.

The total digestibility of the cellulose of the three diets containing roughage declined as the proportion of concentrate in the diet increased. There was a parallel decline in the digestibility of cellulose in the reticulo-rumen and this corresponded to a decline in the rate of loss of weight of cotton threads. However, the cellulose of the all-concentrate diet was digested to a greater extent than that of any of the diets containing roughage. This high coefficient of digestion was almost entirely due to digestion of cellulose in the reticulo-rumen, yet in only one cow on this diet was there any measurable loss of weight of cotton threads in the rumen. The lower recovery of lignin from the faeces of cows given this diet (see Table 4) was not sufficient to account for a difference of this size. Nelson, Ellzey, Morgan & Allen (1968) have observed a similar elevated digestion of the cellulose of a mixed all-concentrate diet but have not partitioned this digestion between the rumen and the hind gut. No explanation is offered for this observation.

The total digestibility of dry matter (and of organic matter, which follows a similar pattern) of all four diets increased as the proportion of concentrates in the diet increased. The reticulo-rumen played an increasingly important part in the digestion of the dry matter as the proportion of concentrates in the diet increased, presumably owing to the increase in the proportion of readily fermentable constituents, and the net measurements available provided no evidence of any tendency for the more concentrated diets to escape rumen fermentation and to be digested extensively in the hind gut. The increasing digestibility of dry matter in the rumen with increasing proportion of concentrates in the diet was related to an increased retention time in the rumen for the diets containing roughage, but for diet 0R the highest digestibility in the reticulo-rumen occurred in conjunction with the lowest retention time. The absence of straw particles requiring physical diminution before passage through the reticulo-omasal orifice had apparently permitted a much reduced mean retention time in the rumen of undigested residues of this diet, the components of the concentrate mixture being digested to a much greater extent during their time in the rumen than were the constituents of the dry matter of the straw in the mixed diets. The increased digestibility in the rumen of the dry matter of diet 20R, relative to that of 40R and 60R, offers an explanation for the lower amount of dry matter in the rumen at the end of a meal of this diet, even though the intake was similar to that of diet 40R and 60R, and the mean retention time was longer.

Although, on all diets, substantially more of the total dry matter digested disappeared in the rumen than in the hind gut, on a net basis, the hind gut played a much greater part in the total apparent digestion of crude protein on all diets; with diet 60R it accounted for over 50% of the total protein digested. It is interesting to speculate on the extent to which this was due to an influx of endogenous nitrogen into the rumen, especially when the cows were receiving the diets of higher roughage content.

The straw used in the diets in the present experiment was chopped rather than ground in an attempt to avoid the various complications associated with the use of ground roughages; these complications include increased intake and rate of passage, decreased digestibility, absence of true rumination and a possible limiting effect of hind gut capacity on intake (Campling & Freer, 1966). It is difficult to estimate the

extent to which this attempt was successful in an experiment in which the straw was not given alone in any treatment. However, the information on behaviour (Table 9) provides good evidence that the chopped straw was as effective as long roughage in stimulating rumination in those animals that received it. On the highest roughage diet, the total time spent ruminating approached 8 h daily, or 72 min per kg straw dry matter consumed, which agrees well with the findings of Freer, Campling & Balch (1962) in cows fed on long oat straw with or without urea.

The reduced frequency of reticular contractions, together with the long period of time elapsing between the start of feeding and the onset of triple reticular contractions in cows receiving diet 0 R, suggest that the absence of roughage or low rumen pH may have partly inhibited the motility of the reticulo-rumen. However, the relatively small difference in these two measurements between diets 0 R and 20 R seems unlikely to have been a major contributory factor to the large difference in intake between these diets.

In conclusion, it can be stated that, as the proportion of roughage in the cow's diet is reduced, there is an obvious decline in the importance of distension of the reticulo-rumen in the regulation of food intake. On diets of lower roughage content, distension of the hind gut may assume some importance, but when roughage is excluded completely distension of neither the reticulo-rumen nor the hind gut appears to be of any significance in food intake regulation. When an all-concentrate diet is given, and possibly also with diets containing low proportions of roughage, it is necessary to seek other control mechanisms probably dependent upon concentrations of chemical substances within the gut or after absorption therefrom; this will be the subject of a subsequent paper.

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