British Journal of Nutrition (1992), **67**, 319–336

Studies of method of conserving grass herbage and frequency of feeding in cattle

2. Eating behaviour, rumen motility and rumen fill

BY L. R. L. THIAGO*, M. GILL† AND J. W. SISSONS‡

AFRC Institute for Grassland and Animal Production, Hurley, Maidenhead, Berkshire SL6 5LR

(*Received 4 October 1990 – Accepted 19 June 1991*)

The influence of the method of conserving grass herbage and the frequency of feeding on eating behaviour, rumen motility and rumen fill was studied in growing steers. Silage and hay were offered to twelve rumen-cannulated Friesian steers (average initial live weight (LW) 128 kg) at a restricted level of intake (20 g dry matter (DM)/kg LW) either once or eight times daily. With once daily feeding, the daily intake of hay was consumed in a single large meal which lasted about 2 h, while silage was eaten in many small meals throughout the day. The proportion of the day spent ruminating was higher (0·39) for steers offered hay once daily than for those offered silage (0·28) or hay eight times per day (0·29). There was little effect of conservation method on frequency of rumen contraction, but contractile intensity (integration of frequency and amplitude) increased during the second half of the 24 h feeding cycle in steers offered hay either once daily or eight times daily, while the same effect was only observed when silage was offered once daily. Total daily contractile activity (the integration of the frequency and duration of myoelectric spike bursts) was significantly ($P < 0·05$) higher in steers offered hay, compared with silage, once daily. The mean weight of organic matter in the reticulo-rumen of steers offered hay was significantly higher than for silage both with once (1593 *v*. 1326 g organic matter (OM)/100 kg LW, $P < 0·01$) and eight (1367 *v*. 1160 g OM/100 kg LW, $P < 0·05$) times daily feeding. The proportion of the particulate pool which was present as small (< 1·2 mm) particles was always greater than 0·60.

Grass herbage conservation: Feeding frequency: Eating behaviour: Rumen motility and fill: Steer

The total amount of feed eaten by a ruminant in a given period of time depends on the number of meals eaten in that time, the length of each meal and the rate of eating during each meal (Bines, 1976). Each of these processes is the result of the interaction between the metabolism of the animal and the physical and chemical properties of the diet stimulating receptors to signal the start and end of a meal. Rumen fill can be an important factor influencing the voluntary intake of forages by ruminants (Campling & Balch, 1961), and digestion and passage are the major processes for alleviating fill (Blaxter *et al.* 1956). Thus, forages with different rates of digestion and passage may induce different patterns of eating behaviour and differences in daily intake. Thiago *et al.* (1992) reported a higher daily intake of hay compared with silage made from the same crop. The eating behaviour of cattle offered these feeds, together with the pattern of motility of the reticulo-rumen and the weight of digesta in the reticulo-rumen at specific times within a 24 h feeding cycle, is

* Present address: EMBRAPA/CNPGC, Cx. Postal 154, 79.100, Campo Grande, MS, Brazil.
† Present address: Natural Resources Institute, Central Avenue, Chatham Maritime, Chatham, Kent ME4 4TB.
‡ Present address: Protein Technologies International, Checkerboard Square, St Louis, MO 63164, USA.

reported here. Preliminary results of some of the present work have been reported (Sissons *et al.* 1986; Thiago & Gill, 1986).

EXPERIMENTAL

Dietary treatments and animals

The procedures described in the present paper formed part of the same experiment described by Thiago *et al.* (1992). That is, twelve Friesian steers (average initial live weight (LW) 128 kg) were offered 20 g dry matter (DM)/kg LW of either hay or silage, once or eight times daily. Eight of the steers (two per treatment) were fitted with wire electrodes for recording myoelectric activity of the dorsal rumen. Pattern of consumption was measured (using load cells) only in steers fed once daily (two animals per treatment), while jaw movements were recorded (using elastic nose bands) with ten steers in period 1 and nine in period 2. Rumen fill was measured in nine steers in period 1 and eleven in period 2.

Experimental procedure

Animals were randomly allocated to either hay or silage given either once or eight times daily. After the first period of 6 weeks (2 weeks for adaptation and 4 weeks for measurement) the animals changed diet for a second period of 6 weeks. Rumen motility, pattern of consumption and jaw movements were recorded simultaneously during the second week of the measurement period, while the rumens were emptied to determine the total weight of contents during the last 2 weeks of each period.

Eating and ruminating behaviour

Jaw movements were monitored over a 24 h feeding cycle by means of a transducer, built up on an elastic nose band, which was placed around the jaws of each animal at least 1 h before offering fresh feed (Penning, 1983). Signals were recorded using a miniature cassette recorder and stored data were later processed using a microprocessor which determined each minute whether the animal was eating, ruminating or idling.

The pattern of feed consumption throughout the day was recorded using a load cell from which the feed container was suspended. Signals were stored on diskettes using a BBC microcomputer programmed to record the weight of the feed remaining at 1 min intervals. These data were subsequently processed on the mainframe computer to give the weight of feed consumed at 1 min intervals from time 0 until 24 h after feeding. It was not possible with this program to adjust for the high weights recorded when the animal had his head in the feed bin; thus, some degree of scatter representing these anomalies is apparent in Fig. 1.

Rumen motility

Stainless-steel wires were implanted on the dorsal surface of the rumen (Ruckebusch, 1970), and changes in electrical potential occurring at the electrode site were recorded over a 24 h feeding cycle using an electromyographic recorder (Grass model 7: Grass Instruments Co., Quincy, MA, USA) set to measure fast AC potentials in the range of 10–35 Hz. The total activity of these potentials was measured by passing the signals through a summating integrator. Recordings of fast potentials (or spike burst activity) and integrated myoelectric activity were made on an ink-writing oscillograph.

Rumen fill

The total weight of rumen contents was measured by manually emptying the rumen, weighing, mixing and subsampling the contents and returning the remainder to the rumen; the whole process took approximately 30 min per animal. Five subsamples, each

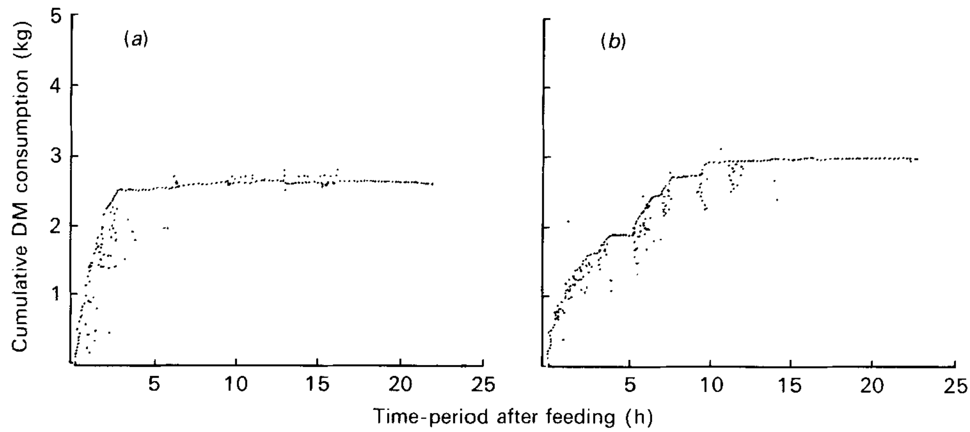

Fig. 1. Eating pattern for steers offered 20 g ryegrass (*Lolium perenne* cv. Endura) dry matter (DM)/kg live weight as recorded using load-cells for hay (*a*) or silage (*b*) offered once daily. For details of diets and procedures, see p. 320.

approximately 500 g fresh weight, were taken. Three of these were oven-dried at 100° for 48 h for DM determination, while the fourth was freeze-dried before organic matter (OM) and neutral-detergent fibre (NDF) analysis; the fifth was stored frozen for subsequent particle size and indigestible OM and NDF determinations. Samples of masticated feed (for particle size determination) were obtained by offering hay or silage to the animal during the time the rumen was empty and collecting samples by hand at the cardia.

The total of six emptyings (period 1) and seven emptyings (period 2) were conducted on each animal receiving feed once daily, and a total of six for each animal receiving feed eight times daily. The specific times were as follows:

(1) Animals offered feed once daily: just before the first meal (BM); at the time after feeding equal to half the length of the first meal (HM); at the end of the first meal (EM; average time of 115 min after feeding for hay, 75 min for silage), and at approximately 15.00 (T6), 20.00 (T11), 01.00 (T16) and 05.00 (T20) hours. Samples at T11 were taken only during the second experimental period.

(2) Animals offered feed eight times daily: samples were taken both during the day (d) and during the night (n). Before a meal (BMd, 13.30 hours and BMn, 01.00 hours); between meals (BeMd, 09.30 hours and BeMn, 21.30 hours); and at the end of a meal (EMd, 11.30 hours and EMn, 23.30 hours).

There was an interval of 2 d between emptyings from any individual steer to overcome the effects of emptying on the repeatability of the measurements (Aitchison, 1985).

Particle size

The particle size distributions of feed, masticated feed, rumen digesta and faeces were determined using a wet-sieving apparatus (Turner & Newall Limited, Trafford Park, Manchester) as described by Evans *et al.* (1973). Sieve sizes were chosen in a geometric progression (Kennedy, 1984), being of 2·40, 1·20, 0·60, 0·30 and 0·15 mm (length of side of square hole). The dry weight of the material retained on each sieve was expressed as a percentage of the total DM in the sample sieved, and the percentage of large particles (> 1·2 mm) was assumed to be the sum of particulate DM retained on sieves 2·40 and 1·20 mm.

Chemical analyses

OM and NDF contents of rumen digesta were determined as described previously for the feed samples (Thiago *et al.* 1992). The potentially indigestible fractions of OM (IOM) and NDF (INDF) of the feed and rumen contents were determined as the OM and NDF contents of the residues from samples incubated in Dacron bags in the rumen for 96 h. Samples of rumen contents were thawed, mixed and homogenized in size (using scissors), and about 30–40 g fresh weight (approximately 5 g DM) were put into bags and suspended in the rumen of steers (two animals per sample) offered the same forage as that from which the samples originated. Dried bag residues were ground and analysed for ash and NDF.

Calculations

Rumen fill variables

The mean rumen pool sizes were calculated by plotting the weights of OM, NDF, IOM and INDF *v.* time and integrating the area under the curve. For animals offered feed once daily the curves were fitted to an equation of the type:

$$Y = (B+Ct)e^{-kt},$$

thus assuming first-order kinetics. Fractional rates of disappearance (k_d) were calculated by plotting total digesta, DM, OM and NDF *v.* time. Rates of passage (k_p) of DM and NDF were calculated from the previously-mentioned equation applied to data on changes in the pool size of potentially indigestible DM (IDM) and INDF with time. These calculations were made using the Maximum Likelihood Programme (MLP; Ross, 1980).

The rates of disappearance and passage for cattle offered feed both once and eight times daily were also calculated as the reciprocal of the mean retention time (MRT) of total and potentially indigestible components respectively, where MRT was calculated as suggested by Minson (1966).

$$\text{MRT (h)} = \frac{\text{average weight of component in the rumen (g)}}{\text{weight of component eaten (g/h)}}$$

Particle kinetics

The retention time of large particles (RLP) in the rumen was calculated as suggested by Poppi *et al.* (1981*b*):

$$\text{RLP} = \frac{\text{total rumen content of large particles (g DM)}}{\text{input of large particles to the rumen (g DM/h)}},$$

where total rumen content of large particles was determined as the mean of rumen pool sizes during the 24 h feeding cycle, whereas input of large particles into the rumen was estimated from mean DM intake (g/d) and the percentage of large particles found in masticated feed.

Proportion of large particle breakdown in the rumen (BLP) was also calculated as suggested by Poppi *et al.* (1981*b*):

$$\text{BLP} = (I-F)/I,$$

where I is the mean amount of large particles entering the rumen per hour; and F is the mean amount of large particles excreted in the faeces each hour. It was assumed that little breakdown of large particles occurs after the rumen (Poppi *et al.* 1980).

Table 1. *Percentage of the day spent eating (E), ruminating (R) and idling (I) by steers offered 20 g ryegrass* (Lolium perenne *cv. Endura) hay (H) or silage (S) dry matter/kg live weight once (1 ×) or eight times (8 ×) daily* †

Feed pattern	Variable	H	S	SEM‡	Statistical significance H *v*. S
1 ×	E	9·6	30·8	1·43	**
	R	39·0	28·5	1·35	*
	I	51·4	40·7	2·75	NS
8 ×	E	21·6	21·0	1·76	NS
	R	29·0	28·2	1·16	NS
	I	49·4	50·7	2·92	NS

NS, not significant ($P > 0·05$).
* $P < 0·05$, ** $P < 0·01$.
† For details of diets and procedures, see p. 320.
‡ 3 df for 1 ×, 1 df for 8 × due to missing samples.

Statistical analysis

Analysis of variance was conducted using the GENSTAT (1977) statistical package. Statistical comparisons between rumen pool sizes at time of sampling T11 were not possible due to the low number of observations, since rumen pool sizes at this time were measured only during the second experimental period.

RESULTS

Eating and ruminating behaviour

Steers offered hay once daily spent less time eating ($P < 0·01$) and more time ruminating ($P < 0·05$) than did those offered silage, with no significant difference between diets in time spent idling (Table 1). When feed was offered eight times daily the time spent eating hay increased compared with once daily feeding, while that spent eating silage decreased such that no difference was observed between animals offered hay or silage.

Examples of the pattern of consumption of hay and silage for an individual animal offered feed once daily are shown in Fig. 1. Steers fed on hay once daily ate the total amount offered in a large single meal of about 2 h duration at an average rate of 18 g DM/min. Silage was eaten in many small meals at a reduced average eating rate of 6 g DM/min, and it took up to 10 h for the daily ration to be consumed completely.

The pattern of rumination throughout the day for steers fed once daily is shown in Fig. 2. There appeared to be a longer lag before the start of rumination but a more uniform distribution of this activity throughout the remainder of the day for steers eating silage compared with hay. However, for both diets a decline in rumination was observed during the 3 h period preceding the time when fresh feed was given. When feed was offered eight times daily, rumination activity appeared to increase during the early hours of the morning, particularly with hay (Fig. 3).

Rumen motility

From myoelectric recordings made at the dorsal surface of the rumen it is possible to distinguish two types of activity referred to as A and B sequences (see Fig. 4). These sequences correspond to aboral and oral movements of the muscle wall. The diurnal

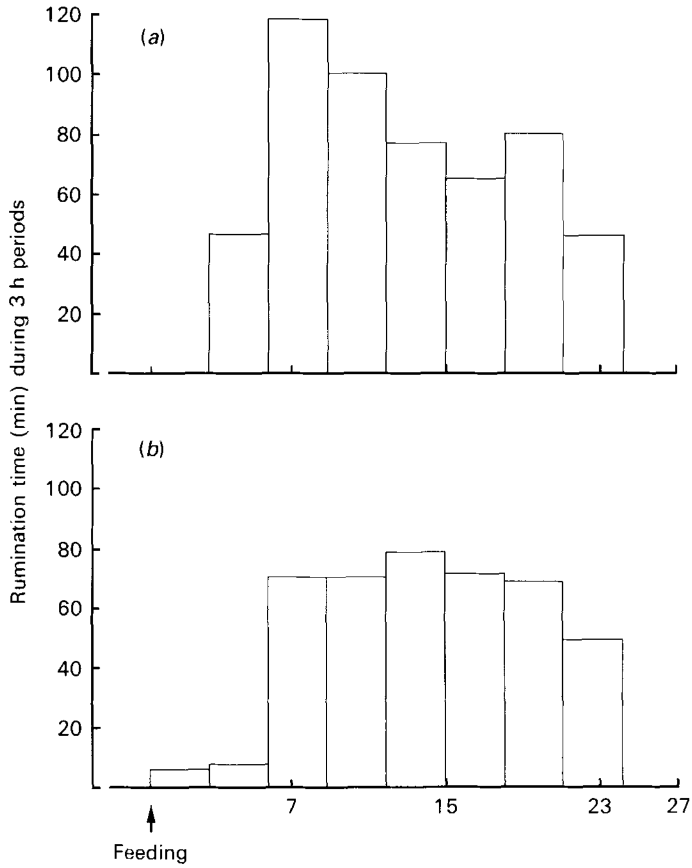

Fig. 2. Daily pattern of rumination for steers offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight once daily at 09.00 hours (↑). For details of diets and procedures, see p. 320.

patterns of A and B sequence contraction frequency for hay and silage offered once daily showed that the frequency of both sequences increased during eating, and then remained fairly uniform throughout the day (Fig. 4). There appeared to be little effect of conservation method on the frequency of rumen contractions.

Integration of total activity/unit time throughout the 24 h recording period takes account of both frequency and amplitude, and patterns for cattle offered feed both once and eight times daily are shown in Figs. 5 and 6. In steers offered hay once daily the contraction frequency decreased post feeding, also contributing to an observed decrease in intensity. However, after remaining low for 7 h contractile intensity began to increase, reaching a maximum about 13 h after feeding. In animals offered silage the effect of feeding was less obvious, but maximal activity was again observed to occur during the second half of the feeding cycle. Total myoelectric activity in steers offered hay once daily was higher than in those eating silage once daily (Table 2), but there was a significant ($P < 0.01$) interaction between feed type and feeding frequency, with no significant difference in myoelectric activity between animals offered hay or silage eight times daily.

In animals fed eight times daily the increase in contractile intensity in response to feeding was well characterized but, in addition, an increase in rumen contractile intensity was

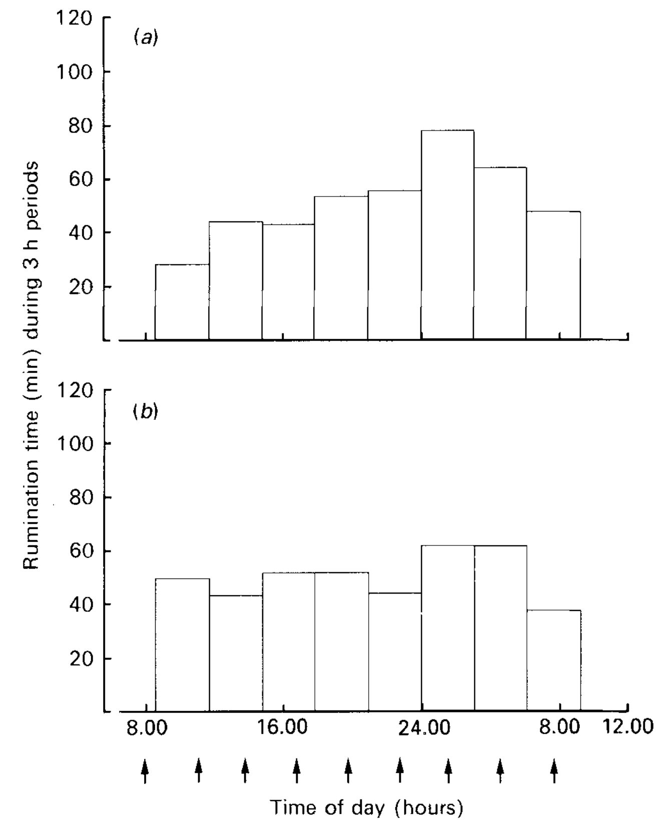

Fig. 3. Daily pattern of rumination for steers offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight eight times daily starting at 08.00 hours. ↑, Feeding. For details of diets and procedures, see p. 320.

observed during the second half of the 24 h feeding cycle when hay was fed. This was associated with an increase in rumination activity over the same period (Fig. 2).

Rumen fill

Removal of indigestible material from the rumen can only occur through onward propulsion of digesta into the omasum; thus changes in pool size of indigestible components should reflect changes in outflow rates. The weights of IOM and INDF in the rumen at different time-intervals after feeding are shown in Table 3. The main outflow of indigestible material appeared to occur in the second half of the feeding cycle at a time when the intensity of rumen motility was elevated (Fig. 7).

The effect of the different patterns of eating hay and silage on the change in rumen pool sizes with time is shown in Table 4. In cattle consuming hay the weight of rumen contents reached a maximum at the end of the first meal, while with silage maximum weights were not observed until 6 h after feed was offered. Hence, steers eating hay showed consistently higher ($P < 0{\cdot}05$) rumen pool sizes of total digesta, OM and NDF, at sampling during eating (HM and EM) than those offered silage, except for total digesta pools measured at HM when no significant ($P > 0{\cdot}05$) difference was observed between diets. By 20 h after offering the feed there was no difference in digesta weights between cattle offered hay or

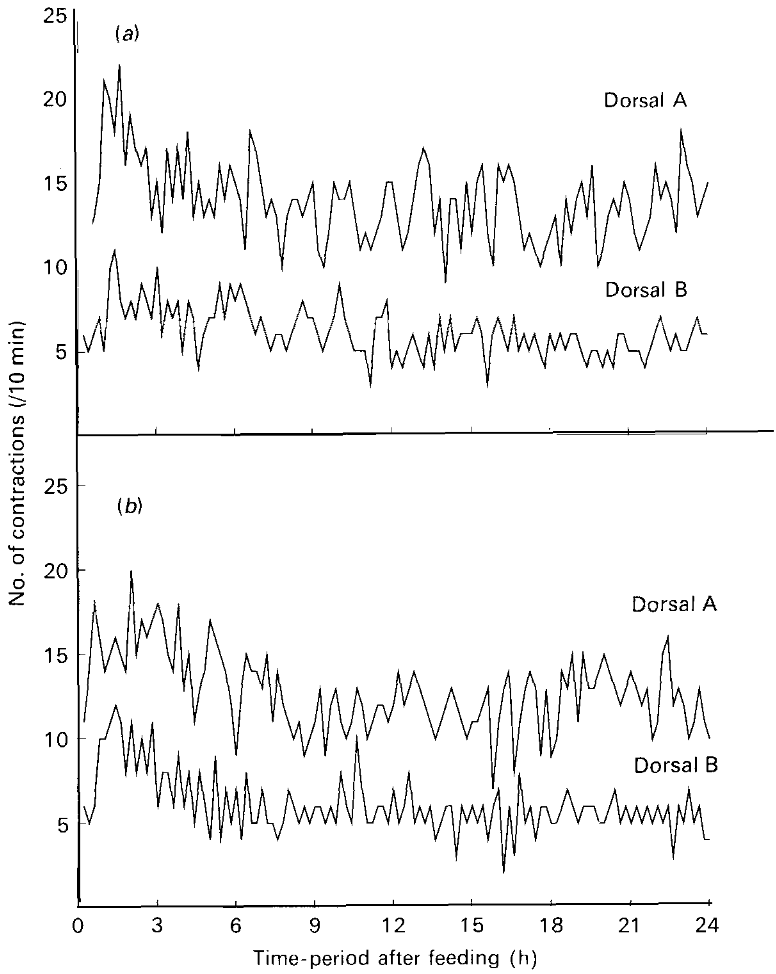

Fig. 4. Myoelectric patterns of A and B sequence spike bursts for an individual steer offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight once daily. For details of diets and procedures, see p. 320.

silage and minimum pool sizes were reached immediately before offering fresh feed. Rumen OM pools at this time were equivalent to 42 and 38% of the daily OM intake of hay and silage respectively, whereas the corresponding values for the IOM pool sizes were 195 and 214% of the respective daily IOM intakes of hay and silage.

The weighted means of the weights of individual components of rumen digesta in cattle offered feed once daily showed similar trends to the means for cattle offered feed eight times daily (Table 5). Mean weights for total digesta OM and NDF were significantly higher for cattle offered hay compared with silage, but there was no difference between diets for IOM and INDF.

Estimates of fractional rates of disappearance (k_d) and passage (k_p), based respectively on the digestible DM and NDF and IDM and INDF fractions of the rumen contents, and calculated by fitting rumen pool *v.* time curves (method 1) or as the reciprocal of MRT (average weight in the rumen divided by mean hourly intake; method 2), were obtained for steers offered feed once daily (Table 6). The fractional rate of disappearance from the

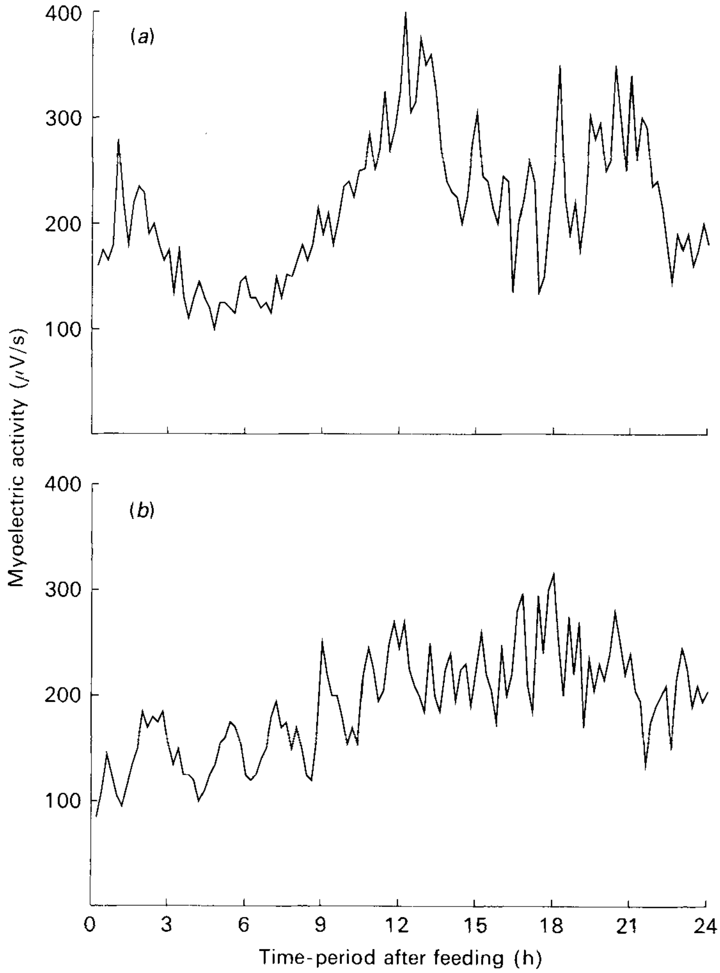

Fig. 5. Pattern of total myoelectric activity of the rumen for an individual steer offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight once daily. For details of diets and procedures, see p. 320.

rumen was significantly faster for silage than hay (except for the NDF content based on method 1), but no significant ($P > 0{\cdot}05$) effect of conservation method on passage rates was found. The fractional rates of passage measured assuming first-order kinetics (method 1) were consistently much higher than those rates based on rumen pools/hourly intake (method 2), while there was little difference between fractional rates calculated from mean pool sizes for cattle offered feed once or eight times daily.

Particle size

The distribution of faecal DM on sieves of various sizes showed that the threshold size in delineating large and small particles was 1·2 mm. Therefore, large particles were defined as those retained on sieves of 2·4 and 1·2 mm. A comparison between amounts of large and small particles in the rumen with time after once daily feeding is shown in Fig. 8. For both forages, rumen pools of small particles were consistently higher than the corresponding pool of large particles.

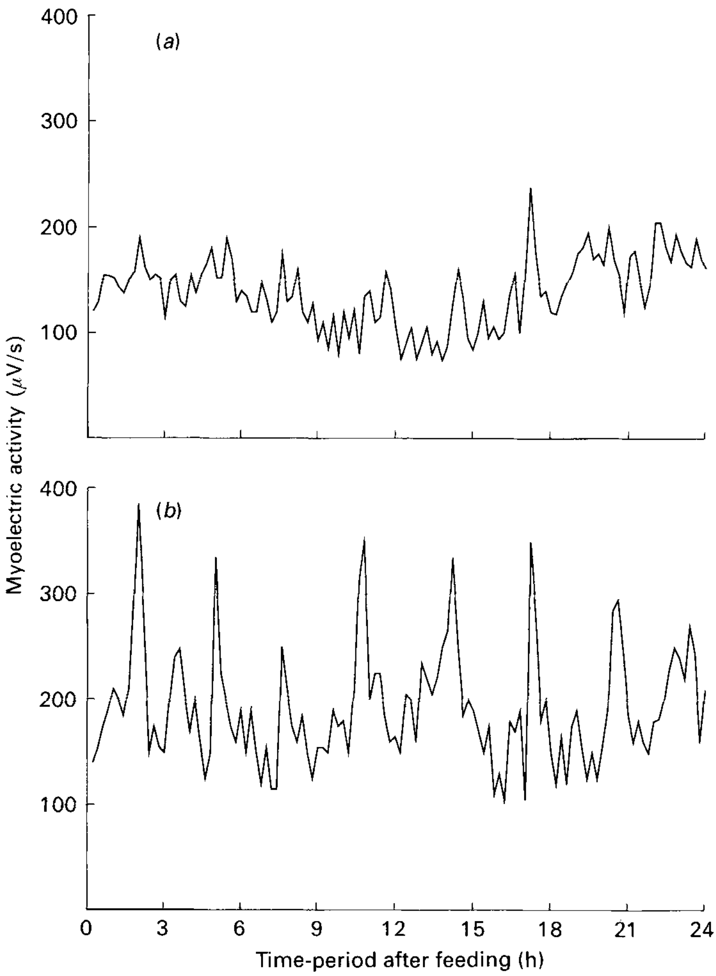

Fig. 6. Pattern of total myoelectric activity of the rumen for an individual steer offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight eight times daily. For details of diets and procedures, see p. 320.

Table 2. *Integrated myoelectric activity*† *recorded from the dorsal sac of steers offered 20 g ryegrass* (Lolium perenne *cv. Endura*) *hay* (*H*) *or silage* (*S*) *dry matter/kg live weight once* (*1* ×) *or eight* (*8* ×) *times daily.*

				Statistical significance		
Variable	H	S	SEM	H *v*. S	1 × *v*. 8 ×	Interaction
1 ×	32475	21248	1224·6	*	**	**
8 ×	20044	21937				

* $P < 0.05$, ** $P < 0.01$.

† One unit of integration is equivalent to a standard potential of 500 μV occurring in a frequency range of 10–35 Hz (−3 dB).

‡ For details of diets and procedures, see p. 320.

Table 3. *Rumen pools of potentially indigestible organic matter (IOM) and neutral-detergent fibre (INDF) (g/100 kg live weight (LW)) at specific times of a 24 h feeding cycle and intake (g/100 kg LW) for steers offered 20 g ryegrass (*Lolium perenne *cv. Endura) hay (H) or silage (S) dry matter/kg LW once daily*†

Variables	H	S	SEM‡	Statistical significance H *v*. S
IOM				
HM	378	358	5·7	NS
EM	447	367	13·2	NS
T_6	428	402	11·9	NS
T_{16}	385	416	19·8	NS
T_{20}	342	313	8·8	NS
BM	299	321	23·7	NS
Intake	153	150	4·9	
INDF				
HM	292	267	3·4	*
EM	348	263	10·7	*
T_6	329	298	11·1	NS
T_{16}	297	303	13·8	NS
T_{20}	252	224	6·2	NS
BM	215	220	16·0	NS
Intake	121	105	0·9	

HM, half-way through the first meal; EM, end of the first meal; T_6, T_{16} and T_{20}, approximately 6, 16 and 20 h after feeding; BM, before feeding; NS not significant ($P > 0·05$).

* $P < 0·05$

† For details of diets and procedures, see p. 320–321.

‡ 2 df due to missing samples.

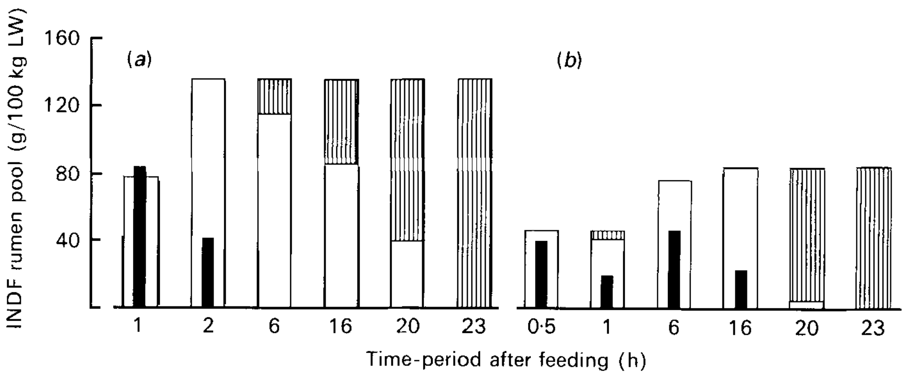

Fig. 7. Disappearance of rumen indigestible neutral-detergent fibre (INDF) content with time-period after feeding (▥) from the potentially removable INDF pool (□) and INDF intake (■) in steers offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight (LW).

Table 7 shows the mean dry weight of large particles, the retention time of these particles and the proportion broken down in the rumen of steers. As observed for total DM, the weight of large particle DM pools in the rumen was consistently higher ($P < 0·05$) for hay than silage when offered either once or eight times daily. Thus, large particles tended to be retained longer in the rumen of steers eating hay than those eating silage, although a significant difference was only observed in those animals offered feed once daily. Most large

Table 4. *Weights of fresh organic matter (OM) and neutral-detergent fibre (NDF) contents in the rumen (g/100 kg live weight (LW)) at specific times of a 24 h feeding cycle and intake (g/100 kg LW per d) of steers offered 20 g ryegrass (*Lolium perenne *cv. Endura) hay (H) or silage (S) dry matter/kg LW once daily*†

Sampling times	H	S	SEM‡	Statistical significance H *v.* S
Total weight of digesta				
HM	16551	13318	589·4	NS
EM	20950	14712	299·8	**
T_6	19620	14622	317·6	**
T_{16}	15060	13245	282·8	*
T_{20}	12561	10165	139·9	NS
BM	11020	9652	808·1	NS
Intake	2384	9698	16·7	
OM				
HM	1866	1295	33·9	**
EM	2265	1265	41·7	***
T_6	1968	1734	24·4	*
T_{16}	1331	1274	30·5	NS
T_{20}	996	864	22·7	NS
BM	777	728	28·7	NS
Intake	1835	1912	3·1	
NDF				
HM	1097	743	35·8	**
EM	1331	739	35·8	**
T_6	1210	1063	25·7	NS
T_{16}	727	757	21·1	NS
T_{20}	539	505	8·9	NS
BM	437	429	20·2	NS
Intake	1040	946	1·9	

HM, half the length of the first meal; EM, end of first meal, T_6, T_{16} and T_{20}, approximately 6, 16 and 20 h after feeding; BM, before feeding; NS, not significant ($P > 0·05$).

* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

† For details of diets and procedures, see p. 320–321.

‡ 2 df due to missing samples.

particles were broken down before leaving the rumen with both diets, but a consistently larger proportion of breakdown occurred with silage.

DISCUSSION

Eating and ruminating behaviour

Results reported previously (Thiago *et al.* 1992) for the effect of conservation method on intake showed that the voluntary intake of this particular silage was 17% lower than that of the hay made from the same crop. The main difference in digestion variables at restricted intakes was a greater initial solubility of the silage, while overall digestibility remained similar (Thiago *et al.* 1992). This increased solubility and more rapid fall in pH may explain the difference in eating pattern between hay and silage shown in Fig. 1. When offered once daily, hay was eaten in one single large meal while silage was eaten in many small meals over a much longer time. However, it is important to note the high digestibility of this silage and, while similar patterns were observed when silage of high digestibility was offered to

Table 5. *Mean† rumen pool sizes (g/100 kg live weight (LW)) of total, organic matter (OM), neutral-detergent fibre (NDF) and potentially indigestible OM (IOM) and NDF (INDF) contents for steers offered 20 g ryegrass* (Lolium perenne *cv. Endura) hay (H) or silage (S) dry matter/kg LW once (1 ×) or eight times (8 ×) daily‡*

Variables	H	S	SEM§	Statistical significance H *v.* S
1 × : Total	16764	13688	236·3	**
OM	1593	1326	11·1	**
NDF	922	793	12·9	*
IOM	399	379	12·2	NS
INDF	306	273	9·3	NS
8 × : Total	14039	11547	140·2	**
OM	1367	1160	24·3	*
NDF	779	679	6·3	**
IOM	361	348	12·3	NS
INDF	275	255	10·2	NS

NS, not significant ($P > 0·05$).
* $P < 0·05$, ** $P < 0·001$.
† These means were calculated from the area under the curve of rumen pools *v.* time.
‡ For details of diets and procedures, see pp. 320–321.
§ 2 df for 1 ×, 3 df for 8 × and 5 df for between frequency comparisons.

dairy cows as the only feed (Gill *et al.* 1987), cows offered low-digestibility silage tended to eat larger and fewer meals. These results suggest that rapid solubilization of highly-digestible silages may lead to a rise in concentration of metabolites in the rumen which stimulates chemo-receptors to inhibit further intake. Evidence for the existence of chemo-receptors sensitive to, for example, the concentration of acetic acid in the rumen has been reported previously (Martin & Baile, 1972). There is also evidence that oro-pharyngeal receptors can participate in the control of intake in ruminants (Greenhalgh & Reid, 1967). However, the relative importance of these receptors in the control of silage intake is unclear. Buchanan-Smith (1989) reported a negative effect of acetate on intake which appeared to be mediated through oro-pharyngeal receptors; however, the effect was neutralized by high levels of other acids.

The rate of consumption of hay DM during the single meal was much higher than the average rate of consumption of silage DM (18 *v.* 6 g/min). Since the cattle were offered the same amounts of DM as either hay or silage, time spent eating was apparently much higher for the silage (Table 1). Reasons for this difference are unclear but may be due either to the wetter or more acidic nature of the silage. However, the cattle offered hay spent more time ruminating since the fast rate of consuming hay DM may have decreased forage comminution (Reid, 1984; Ulyatt *et al.* 1986) and consequently have increased rumination time (Kennedy & Milligan, 1984).

The total time spent chewing did not differ between hay and silage, which supports the conclusion of McLeod (1986) that the amount of chewing varies according to the fibre content of the forage. In the present study the cell wall content of the hay and silage were very similar since they were conserved from herbage from the same field.

The daily pattern of rumination activity showed inhibition of rumination in all cattle at about 08.00 hours with the highest peak of rumination activity occurring 6–9 h after offering hay once daily. This appeared to be earlier than the peak rumination observed by Ulyatt *et al.* (1984) and Aitchison (1985) in sheep offered hay.

Table 6. *Fractional rate of dry matter (DM) and neutral-detergent fibre (NDF) disappearance* (k_d/h) *and passage* (k_p/h) *out of the rumen for steers offered 20 g ryegrass* (Lolium perenne *cv. Endura) hay (H) or silage (S) dry weight/kg live weight either once or eight times daily*†

Variables	H	S	SEM‡	Statistical significance H *v.* S
Once daily				
Method 1: DM: k_d	0·102	0·116	0·0018	*
k_p	0·059	0·061	0·0016	NS
NDF: k_d	0·118	0·122	0·0027	NS
k_p	0·071	0·069	0·0014	NS
Method 2: DM: k_d	0·048	0·063	0·0001	***
k_p	0·016	0·016	0·0008	NS
NDF: k_d	0·048	0·054	0·0005	*
k_p	0·017	0·016	0·0006	NS
Eight times daily				
Method 2: DM: k_d	0·052	0·062	0·0007	**
k_p	0·016	0·017	0·0008	NS
NDF: k_d	0·053	0·055	0·0009	NS
k_p	0·016	0·018	0·0004	*

Method 1, by fitting rumen pool *v.* time curves to the equation:

$$Y = (B + Ct)^{e^{-Kt}};$$

Method 2, reciprocal of mean retention time (MRT) calculated as:

$$\text{MRT} = \frac{\text{average mass in the rumen}}{\text{mean hourly intake}}$$

NS, not significant ($P > 0·05$).
* $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† For details of diets and procedures, see pp. 320–322.
‡ 2 df for 1 ×, 3 df for 8 × due to missing samples.

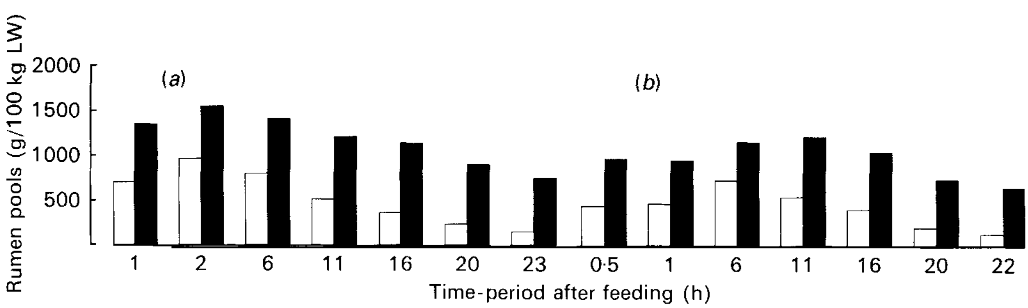

Fig. 8. Mean rumen pool (g/100 kg LW) of large (> 1·2 mm; □) and small (< 1·2 mm; ■) particles for steers offered 20 g ryegrass (*Lolium perenne* cv. Endura) hay (*a*) or silage (*b*) dry matter/kg live weight (LW) once daily. Sampling times: half the length of the first meal; end of the first meal; T_6, T_{11}, T_{16} and T_{20}, approximately 6, 11, 16 and 20 h after feeding.

Motility

Recordings of A and B sequences of spike bursts from the dorsal rumen surface indicated that the oral and aboral contractions were closely associated with eating behaviour, as noted also by other workers (Freer *et al.* 1962; Reid, 1963; Waghorn & Reid, 1983). Thus,

Table 7. *Mean quantity of large particles (> 1·2 mm; QLP), time-period they are retained (TLP) and the proportion broken down (BLP) in the rumen of steers offered 20 g ryegrass (*Lolium perenne *cv. Endura) hay (H) or silage (S) dry matter (DM)/kg live weight once (1 ×) or eight times (8 ×) daily*†

Variables	H	S	SEM‡	Statistical significance H *v.* S
1 × : QLP (g DM)	737	527	14·2	**
TLP (h)	11·1	8·1	0·40	*
BLP (g/g)	0·991	0·998	0·0009	*
8 × : QLP (g DM)	671	437	40·3	*
TLP (h)	9·3	7·9	0·34	NS
BLP (g/g)	0·992	0·994	0·0005	*

NS, not significant ($P > 0.05$).
* $P < 0.05$, ** $P < 0.01$.
† For details of diets and procedures, see pp. 320–322.
‡ 2 df for 1 × and 3 df for 8 ×.

an elevation in the frequency of both A and B sequences can be seen at times of feeding, especially in those steers fed eight times daily (Fig. 6). Diet had only a minor effect on diurnal patterns of A and B sequences, as also observed by Waghorn & Reid (1983).

With steers offered forage once daily, intensity of rumen contractions was found to be minimal for the first 9 h after feeding but thereafter an increase was observed with both hay and silage. The period of maximal activity was less pronounced for silage than hay, which contributed to a higher total myoelectric activity during the day for hay compared with silage. The higher activity in the second half of the 24 h feeding cycle suggests that greater disappearance of digesta from the rumen may have occurred during this period, particularly for the hay diet.

Rumen fill

The higher intensity of contractile activity observed on the hay diet did not appear to result in higher fractional rates of passage of fibre from the rumen, either as reported by Thiago *et al.* (1992) or as calculated from the weight of INDF in the rumen (Table 6). However, it was associated both with a greater proportion of the day spent ruminating and with a greater mean weight of contents in the rumen in cattle offered hay, compared with silage, once daily.

The link between motility and rumination, however, was not as clear when comparing diurnal patterns (Figs. 2 and 5), but the association with passage of material out of the rumen is more apparent. Indigestible material can only leave the rumen by passage down the gastrointestinal tract and, thus, a study of the changes in IOM and INDF content of the rumen with time after feeding should give an indication of the period of greatest outflow. The findings in Table 3 and Fig. 6 suggest peak outflow occurred between 16 and 20 h after feeding, which corresponds approximately with peak contractile activity in animals offered feed once daily. Similar observations were made from rumen emptying data obtained with sheep offered hay once daily by Aitchison *et al.* (1986*a*, *b*), and can be seen in the data of Moseley & Jones (1984). Studies based on duodenal flow measurements have also demonstrated an increased flow during the second half of the feeding cycle (Harris & Phillipson, 1962, Phillips & Dyck, 1964). However, the mechanism whereby contractile activity is increased is as yet unknown, although it should be noted that it was amplitude rather than frequency which changed, as suggested by Ulyatt *et al.* (1986).

This uneven diurnal pattern of flow suggests that within a day, flow of material out of the rumen cannot be considered to follow first-order kinetics, i.e. that rumen pool sizes decline exponentially, as suggested by Alexander *et al.* (1969). Thus, when passage rates based on the INDF rumen pool sizes were calculated assuming first-order kinetics (method 1) values were consistently much higher than those estimated from 1/MRT (method 2; Table 6). A third estimate of passage rate obtained using chromium-mordanted feed, as reported by Thiago *et al.* (1992), gave intermediate values, although they agreed more closely with those derived by method 2. Taken together, this indicates that instantaneous outflow of NDF from the rumen does not obey the principles of first-order kinetics when measured over short time-periods.

The diurnal variation in the total amount of OM in the rumen of steers offered hay once daily was considerably greater (777–2265 g/100 kg LW or 292%) than in those offered silage (728–1734 g/100 kg LW or 238%). A similar magnitude of variation was observed in sheep fed once daily at a restricted level of lucerne (*Medicago sativa*) hay (268%) (Ulyatt *et al.* 1984), in sheep offered ryegrass (221%) and clover (*Trifolium repens*) hay (270%) (Aitchison, 1985), and in cattle fed on grass hay (204%) (Campling & Balch, 1961).

By feeding once daily, rumen pools of steers eating silage increased more slowly and reached a lower maximum pool size than did those of hay-fed steers. This reflects first, the longer time taken to eat the daily ration of silage than hay (approximately 12 and 2 h respectively), and second, it may be a result of the more rapid initial digestion of the silage (Thiago *et al.* 1992) resulting in a faster rate of DM, OM and NDF disappearance from the rumen. This again suggests that the cessation of eating the first meal of silage is more likely to be related to the soluble nature of the silage than to the degree of rumen fill. Similar observations of pool sizes at the end of a meal being less than maximum have been made for other rapidly digested feeds such as legume hays (Ingalls *et al.* 1966; Aitchison *et al.* 1986*b*) or concentrates (Freer & Campling, 1963).

Rumen pool sizes of steers fed eight times daily were fairly uniform throughout a 24 h feeding cycle, e.g. mean rumen OM pools were 1377 (SE 80·7) and 1193 (SE 120·1) g/100 kg LW with hay and silage respectively. A similar lack of variation in rumen pool size in hourly-fed sheep was also observed by Ulyatt *et al.* (1984). However, average rumen pool sizes in steers consuming hay were consistently higher than in those steers eating silage.

Particle size and passage rates

Although there does appear to be a critical size above which particles have a low probability of leaving the rumen (Poppi *et al.* 1980), particle size *per se* does not seem to be the first limiting factor to passage of digesta out of the rumen at least on chopped or ground diets (Poppi *et al.* 1981*b*). The findings reported here (Fig. 8), in agreement with the results of e.g. Leibholz (1984) and Moseley & Jones (1984), support this suggestion since at all times the proportion of particles $< 1·2$ mm length was greater than the proportion of particles $> 1·2$ mm. Observations of this nature have led to the suggestion that the movement of particles out of the rumen is restricted by the existence of a raft of particles which traps small particles thus reducing their rate of escape from the rumen (Sutherland, 1987). This raft might be expected to have a greater effect immediately after feeding. Hence Pond (as cited by Kennedy & Milligan, 1984) observed that passage of labelled particles dosed into the rumen of cattle at the end of a meal was 42% lower than those inserted at the beginning of the meal. In the present experiment, as also observed by Campling (1966), silage produced a much more compact and closely interwoven particulate rumen mass than in the cattle eating hay, which could be hypothesized to increase the entrapment of small particles in the rumen (Welch, 1982). In fact, the percentage of rumen particulate DM retained on the 0·15 mm sieve (the size which discriminates the particulate from the nonparticulate phase, as recommended in Kennedy, 1984) was significantly higher for silage than hay, except at 20 h after feeding when no difference between diets was found. This was also the time when passage of INDF appeared to start in those animals eating silage (Fig. 6).

Although the passage of INDF out of the rumen appeared to start earlier for hay compared with silage, it was still later than observed by Aitchison (1985) with sheep. Since a tendency for sheep to have higher passage rates of particulate mass out of the rumen has been reported (Thomas & Campling, 1977; Poppi *et al.* 1981 *a*), this may indicate a different type of raft structure, or at least a different ability to trap particles, between species.

In conclusion, therefore, the soluble nature of the silage, rather than the degree of rumen fill, appears likely to be the main factor contributing to the smaller first meal of silage compared with hay. However, since rumen motility increased during the second half of the feeding cycle, rumen distension or the need to remove large quantities of fibrous material from the rumen may be a more important factor in intake control during this part of the feeding cycle in an *ad lib.* feeding situation.

L.R.L.T. acknowledges financial support from EMBRAPA (Brazilian Agricultural Research Organization). The authors would like to thank Messrs P. England and K. Hill for technical support. The Institute for Grassland and Animal Production was financed by the AFRC; the work was in part commissioned by the Ministry of Agriculture, Fisheries and Food.

REFERENCES

Aitchison, E. M. (1985). A study of the removal of fibre from the rumen and voluntary intake of sheep eating hay diets. PhD Thesis, University of Reading.

Aitchison, E. M., Gill, M., Dhanoa, M. S. & Osbourn, D. F. (1986*a*). The effect of digestibility of forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. *British Journal of Nutrition* **56**, 463–476.

Aitchison, E. M., Gill, M. & Osbourn, D. F. (1986*b*). The effect of supplementation with maize starch and level of intake of perennial ryegrass (*Lolium perenne* cv. Endura) hay on the removal of digesta from the rumen of sheep. *British Journal of Nutrition* **56**, 477–486.

Alexander, C. L., Meyer, R. M. & Bartley, E. E. (1969). Rumen removal rates of some chemically defined fractions of ^{14}-C labelled alfalfa. *Journal of Animal Science* **29**, 746–756.

Bines, J. A. (1976). Regulation of food intake in dairy cows in relation to milk production. *Livestock Production Science* **3**, 115–128.

Blaxter, K. L., Graham, McC. & Wainman, F. W. (1956). Some observations on the digestibility of food by sheep and on related problems. *British Journal of Nutrition* **10**, 69–91.

Buchanan-Smith, J. G. (1989). Effect of soluble constituents of silage on oro-pharyngeal intake response of sheep. *Animal Production* **48**, 638 Abstr.

Campling, R. C. (1966). The intake of hay and silage by cows. *Journal of the British Grassland Society* **21**, 41–48.

Campling, R. C. & Balch, C. C. (1961). Factors affecting the voluntary intake of food by cows. 1. Preliminary observations on the effect, on the voluntary intake of hay, of changes in the amount of the reticulo-rumen contents. *British Journal of Nutrition* **15**, 523–530.

Evans, E. W., Pearce, G. R., Burnett, J. & Pillinger, S. L. (1973). Changes in some physical characteristics of the digesta in the reticulo-rumen of cows fed once daily. *British Journal of Nutrition* **29**, 357–376.

Freer, M. & Campling, R. C. (1963). 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. *British Journal of Nutrition* **17**, 79–88.

Freer, M., Campling, R. C. & Balch, C. C. (1962). Factors affecting the voluntary intake of food by cows. 4. The behaviour and reticular motility of cows receiving diets of hay, oat straw and oat straw with urea. *British Journal of Nutrition* **16**, 279–295.

GENSTAT (1977). *A General Statistical Program*. Harpenden, Herts: Rothamsted Experimental Station.

Gill, M., Sargeant, A. & Evans, R. T. (1987). The effect of type of silage and level of concentrate on pattern of eating in dairy cows. In *Proceedings of the 8th Silage Conference*, pp. 63–64. Hurley: AFRC Institute for Grassland and Animal Production.

Greenhalgh, J. F. D., Reid, G. W. (1967). Separating the effects of digestibility and palatability on food intake in ruminant animals. *Nature* **214**, 744.

Harris, L. E. & Phillipson, A. T. (1962). The measurement of the flow of food to the duodenum of sheep. *Animal Production* **4**, 97–116.

Ingalls, J. R., Thomas, J. W., Tesar, M. B. & Carpente, D. L. (1966). Relations between *ad libitum* intake of several forage species and gut fill. *Journal of Animal Science* **25**, 283–289.

Kennedy, P. M. (1984). Summary and conclusions from discussion. In *Techniques in Particle Size Analysis of Feed and Digesta in Ruminants. Canadian Society of Animal Production. Occasional Publication* no. 1, pp. 184–186. Edmonton: Canadian Society of Animal Science.

Kennedy, P. M. & Milligan, L. P. (1984). Particle kinetics in the rumen: comminution and passage. Paper presented at the second research co-ordination meeting on 'Isotope-aided studies on the non-protein nitrogen and agro-industrial byproducts utilization by ruminants with particular reference to developing countries'. VIC Vienna, Austria.

Leibholz, J. (1984). Roughage intake comparisons between calves and adult cattle. *Canadian Journal of Animal Science* **64**, suppl., 154–155.

McLeod, M. N. (1986). Physical and biological factors controlling the reduction of feed particles in the ruminant. PhD Thesis, University of Queensland, Australia.

Martin, F. H. & Baile, C. A. (1972). Ruminal wall anaesthesia and feed intake of goats. *Journal of Animal Science* **31**, 248.

Minson, D. J. (1966). The apparent retention of food in the reticulo-rumen at two levels of feeding by means of an hourly feeding technique. *British Journal of Nutrition* **20**, 765–773.

Moseley, G. & Jones, J. R. (1984). The physical digestion of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in the foregut of sheep. *British Journal of Nutrition* **52**, 381–390.

Penning, P. D. (1983). A technique to record automatically some aspects of grazing and ruminating behaviour in sheep. *Grass and Forage Science* **38**, 89–96.

Phillips, G. D. & Dyck, G. W. (1964). The flow of digesta into the duodenum of sheep. *Canadian Journal of Animal Science* **44**, 220–227.

Poppi, D. P., Minson, D. J. & Ternouth, J. H. (1981 *a*). Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Australian Journal of Agricultural Research* **32**, 99–108.

Poppi, D. P., Minson, D. J. & Ternouth, J. H. (1981 *b*). Studies of cattle and sheep eating leaf and stem fractions of grasses. III. The retention time in the rumen of large feed particles. *Australian Journal of Agricultural Research* **32**, 123–137.

Poppi, D. P., Norton, B. W., Minson, D. J. & Hendricksen, R. E. (1980). The validity of the critical size theory for particles leaving the rumen. *Journal of Agricultural Science, Cambridge* **94**, 275–280.

Reid, C. S. W. (1963). Diet and motility of the forestomachs of the sheep. *Proceedings of the New Zealand Society of Animal Production* **23**, 169–188.

Reid, C. S. W. (1984). The progress of solid feed residues through the reticulo-rumen: the ins and outs of particles. In *Ruminant Physiology. Concepts and Consequences*, pp. 79–84 [S. K. Baker, J. M. Gawthorne, J. B. Macintosh and D. B. Purser, editors]. Perth: University of Western Australia.

Ross, G. J. S. (1980). *MLP: Maximum Likelihood Program*. Harpenden, Herts: Rothamsted Experimental Station.

Ruckebusch, Y. (1970). The electrical activity of the digestive tract of the sheep as an indication of the mechanical events in various regions. *Journal of Physiology* **210**, 857–882.

Sissons, J. W., Gill, M. & Thiago, L. R. S. (1986). Effect of conservation method and frequency of feeding on forestomach motility. *Proceedings of the Nutrition Society* **45**, 96A.

Sutherland, T. M. (1987). Particle separation in the forestomachs of sheep. In *Comparative Aspects of Physiology of Digestion in Ruminants*, pp. 43–73 [A. Dobson and M. J. Dobson, editors]. Ithaca: Cornell University Press.

Thiago, L. R. S. & Gill, M. (1986). Effect of conservation method and frequency of feeding on the removal of digesta from the rumen. *Proceedings of the Nutrition Society* **45**, 97A.

Thiago, L. R. S., Gill, M. & Dhanoa, M. S. (1992). Studies of method of conserving grass herbage and frequency of feeding in cattle. 1. Voluntary feed intake, digestion and rate of passage. *British Journal of Nutrition* **67**, 305–318.

Thomas, S. & Campling, R. C. (1977). Comparisons of some factors affecting digestibility in sheep and cows. *Journal of the British Grassland Society* **32**, 140–149.

Ulyatt, M. J., Dellow, D. W., John, A., Reid, C. S. W. & Waghorn, G. C. (1986). Contribution of chewing during eating and rumination to the clearance of digesta from the ruminoreticulum. In *Control of Digestion and Metabolism in Ruminants*, pp. 498–515 [L. P. Milligan, W. L. Grovum and A. Dobson, editors]. Reston, VA: Reston Publishing Co.

Ulyatt, M. J., Waghorn, G. C., John, A., Reid, C. S. W. & Monro, J. (1984). Effect of intake and feeding frequency on feeding behaviour and quantitative aspects of digestion in sheep fed chaffed lucerne hay. *Journal of Agricultural Science, Cambridge* **102**, 645–657.

Waghorn, G. C. & Reid, C. S. W. (1983). Rumen motility in sheep and cattle given different diets. *New Zealand Journal of Agricultural Research* **26**, 289–295.

Welch, J. G. (1982). Rumination, particle size and passage from the rumen. *Journal of Animal Science* **54**, 885–894.

Printed in Great Britain