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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

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1. Eight wether sheep were offered a diet of perennial ryegrass (*Lolium perenne* cv. Endura) hay once daily at two levels of intake (11 and 16·5 g dry matter (DM)/kg live weight (LW)) with or without maize starch (175 g DM/kg hay DM). The experiment consisted of four periods, each lasting 32 d. Rates of digestion of the hay were measured by incubation in dacron bags and rates of passage using chromium-mordanted hay. Rumen pool sizes of DM, organic matter and fibre were measured by emptying the rumen.

2. The inclusion of starch in the diet appeared to increase significantly ($P < 0·01$) the lag phase before the start of fibre digestion, as observed both in the dacron bag studies and in the slower initial disappearance of digestible neutral-detergent fibre (NDF) from the rumen recorded by emptying of rumen contents. However, there was no significant effect of starch on apparent digestibility of fibre in the whole tract.

3. The main effect of increasing the level of feeding was to increase the rate of passage with a consequent decrease in overall digestibility. The fractional rate of passage increased from 0·0318 to 0·0400 as the level of feeding increased, while apparent digestibility of NDF decreased from 0·755 to 0·724.

4. On all treatments the weight of indigestible fibre in the rumen remained more or less constant between 5, 10 and 15 h after feeding, but was significantly lower at 24 h. These results suggest that a high proportion of the outflow of material from the rumen not associated with feeding appears to occur during the second half of the feeding cycle.

The quantity of digesta present in the rumen can be an important factor in influencing the voluntary intake of roughage diets by ruminants (Balch & Campling, 1969). Roughages contain a high level of fibre and since the rate of digestion of fibre is slower than that of other fractions (Van Soest, 1975), factors affecting this rate may thus be implicated in intake control. The effect of soluble carbohydrates in depressing cellulolysis is well documented (El-Shazly *et al.* 1961; Terry *et al.* 1969; Mertens & Loften, 1980) and often leads to a depression in voluntary intake. However, the relation between this depression and rumen volume has not been studied in detail.

The relation between rumen pool sizes and intake level has been studied by a number of workers, mainly with diets of oat straw (Pearce, 1967) or forages (Moseley & Jones, 1984; Ulyatt *et al.* 1984). The increase in rumen pool size has generally been less than the increase in intake, presumably due to the increase in rate of passage as intake level increased. The effect of concentrate:forage on the rate of passage is not clear, since Uden (1984) observed no effect of an increased ratio while Colucci *et al.* (1982) reported higher rates of passage with high-forage diets compared with low-forage diets.

The experiment reported here was designed to study the effects of supplementation of a forage diet with starch and to see how the responses obtained were influenced by level of feeding. The responses measured were the rates of digestion and passage from the rumen and their effects on rumen pool sizes. Maize starch was used to provide a high-energy supplement without adding fibre to the diet.

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MATERIALS AND METHODS

Animals

Eight Scottish half-bred wether sheep, weighing between 45 and 65 kg were used. Five were 1 year old, the remaining three were 2 years old. Each had been fitted with a rumen cannula (80 mm in diameter, Moseley & Jones, 1979) at least 3 months before the start of the experiment. The animals were housed in individual pens with peat bedding, except during faecal collection periods, when they were kept in individual metabolism crates. They had free access to water and a mineral block at all times.

Experimental treatments

The basal diet used was a sun-cured hay prepared from a sward of perennial ryegrass (*Lolium perenne* cv. Endura) cut on 7 June 1981. Before feeding, the hay was chopped to a length of 30–50 mm. Maize starch in the ground form was used as the supplementary feed (Globe Maize Starch UK Ltd).

The four treatments in the experiment comprised two levels of hay, offered with or without the maize starch as follows: L, hay fed at 11 g dry matter (DM)/kg live weight (LW); LS, hay fed at 11 g DM/kg LW + starch; H, hay fed at 16·5 g DM/kg LW; HS, hay fed at 16·5 g DM/kg LW + starch. The starch was included in the ration at 175 g starch DM/kg hay DM offered, at a level approaching the maximum at which hay intake was not depressed. The higher level of hay intake was set such that the daily allocation would be consumed within 5 h.

Experimental procedure

The experiment consisted of four periods, each lasting 32 d and divided into a 10 d adaptation period followed by 22 d experimental measurements. Four total emptyings of the rumen were carried out over a period of 14 d. During this time, dacron-bag and behaviour-study measurements were also carried out, but at least 1 d after each emptying was allowed before any other measurements took place. The sheep were transferred from the individual pens to the metabolism crates 2 d before the start of the faecal collection and rate of passage measurement.

Considerable difficulties were encountered before the start of the experiment in achieving the desired level of starch intake, presumably related to the dry, unpalatable nature of the supplement. Hence it was found necessary to administer the starch supplement through the rumen fistula. The starch supplement was contained on filter paper, the weight of which averaged 4 g, but this was considered to make a negligible contribution to the total rumen 'fibre' content. The starch was added to the rumen at 08.30 hours and the hay was offered at 09.00 hours.

The animals were weighed on two successive days at the beginning of each period, and the mean LW was used to calculate the levels of intake of the hay and therefore of the starch.

Details of the experimental methods, chemical analyses, and mathematical treatment of results have been described fully by Aitchison *et al.* (1986). Thus, only a summary of the methods is presented here.

Rumen contents. The total weight of rumen contents was measured by manual emptying of the rumen of each sheep at 5, 10, 15 and 24 h after the hay was offered. Samples were taken for subsequent analysis of DM, organic matter (OM) and fibre content, and the remainder was returned to the rumen within 20 min.

Rates of digestion. Dacron bags were used to estimate rates of digestion of the hay, by incubating pairs of bags for 6, 12, 18, 24, 48 or 72 h in the rumen of the sheep on each

treatment. A '0 h wash' value was also determined on one pair of bags. The residues were freeze-dried for determination of DM and neutral-detergent fibre (NDF) loss from the bag. The rates of digestion were calculated using the model of Ørskov & McDonald (1979).

Digestibility. A 7 d collection of total faeces production was undertaken for digestibility determinations. Faeces were collected daily and stored frozen. The bulk collection over 7 d for each sheep was then thawed, weighed and subsampled, for subsequent analysis for DM, ash, NDF and acid-detergent fibre (ADF) content.

Rates of passage. Estimates of the rate of passage of material from the rumen were made using chromium-mordanted hay. Samples of the chopped hay on offer to the sheep were mordanted with sodium dichromate (Uden *et al.* 1980) and portions (50 g DM) were administered to the sheep via the fistula immediately before feeding the hay on day 1 of the digestibility measurements. Samples of 15–20 g DM were taken from the rumen digesta and from the faeces four times during the first 15 h after dosing, then three times daily for the next 4 (digesta) or 6 (faeces) d. The samples were dried at 100° for 24 h, and analysed for Cr concentration. The rate of removal of the marked material from the rumen was estimated by fitting a single exponential curve to the decrease with time in Cr concentration in rumen digesta. However, there was a high random variability in concentration between samples, presumably due to sampling problems, which resulted in a high error associated with the estimates for individual animals. Use of the model by Blaxter *et al.* (1956) to determine rate constants (k_1 and k_2) from the faecal excretion data produced rate constants with lower errors and thus the constants derived from rumen samples were only used as a comparison to assign rumen outflow rate to the rate constant which agreed more closely (k_1). The model of Blaxter *et al.* (1956) was used as it was found to fit all of the data sets satisfactorily.

Behaviour study. On 1 d during each period, when no other experimental measurements were being taken, the sheep were fitted with jaw recorders (Penning, 1983), to record automatically each animal's chewing and ruminating activity throughout one 24 h period. The recorders were fixed to the sheep at least 30 min before the starch was administered, and were removed 24 h later. Miniature cassette tapes recorded each animal's behaviour during the day, and the stored data were processed using a microprocessor which determined each minute whether the animal was eating (E), ruminating (R) or idling (I), and also summarized the observations to give the total length of time spent on each activity during the day.

Statistical analysis

The experimental design was in the form of two concurrent 4×4 Latin squares, balanced for the residual effects of treatments. Because of the large variation in animal LW (45–65 kg before the start of the experiment), the animals were allocated to either of the squares according to body-weight, with the four heavier animals in one square and the four lighter ones in the other. Within the squares, animals were allocated at random to the treatments. Differences between squares were included as part of the between-animal variation (7 df). The statistical package GENSTAT was used to perform analysis of variance in which animal, period and treatment effects were estimated leaving eighteen residual error degrees of freedom. The maximum likelihood program MLP (Ross, 1980) was used in the estimation of rates of digestion and passage.

Measurement of rumen contents at 5 h after feeding was not possible in two instances due to inappetance, and consequently these missing values were estimated by the GENSTAT analysis of variance algorithm. Values for the concentrations of volatile fatty acids (VFA) in the rumen fluid were not available for the fourth period; values from periods 1–3 were therefore analysed using a Youden square design.

Table 1. *Fractional rates of digestion (/h) of dry matter (DM) and neutral-detergent fibre (NDF), estimates of NDF lag-time* (t_0, *h), and fractional rates of passage (/h) from the rumen* (k_p) *in sheep fed on perennial ryegrass* (Lolium perenne *cv. Endura*) *hay at two levels of feeding (high (H) and low (L)) with (S) or without maize starch as supplement*

(Mean values for eight sheep per treatment)

	Treatment					Statistical significance of effect of:	
	H	HS	L	LS	SEM	Level	Starch
DM	0·0292	0·0243	0·0307	0·0323	0·00331	NS	NS
NDF	0·0384	0·0333	0·0390	0·0410	0·00270	NS	NS
NDF t_0	5·21	6·86	5·12	6·40	0·464	NS	**
k_p	0·0401	0·0398	0·0323	0·0313	0·00265	**	NS

NS, not significant. ** $P < 0·01$.

Table 2. *Apparent digestibility coefficients of dry matter (DM), organic matter (OM), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF), for sheep eating perennial ryegrass* (Lolium perenne *cv. Endura*) *hay at two levels of feeding (high (H) and low (L)) with (S) or without maize starch as supplement*

(Mean values for eight sheep per treatment)

	Treatment					Statistical significance of effect of:	
	H	HS	L	LS	SEM	Level	Starch
DM	0·696	0·716	0·716	0·752	0·00649	***	***
OM	0·700	0·723	0·722	0·758	0·00627	***	***
NDF	0·736	0·713	0·756	0·754	0·00762	***	NS
ADF	0·734	0·712	0·761	0·757	0·00664	***	NS

NS, not significant. *** $P < 0·001$.

In the statistical analysis of the data, the interaction term level × starch did not achieve significance at ($P > 0·05$); it has therefore not been included in the column summarizing the significant effects in the tables.

RESULTS

Diet composition. The perennial ryegrass hay offered had a DM content of 874 g/kg fresh weight, and had the following chemical composition (g/kg DM): OM 911, nitrogen 18, water-soluble carbohydrate 85, NDF 619, ADF 332, indigestible NDF (INDF) 159, indigestible ADF (IADF) 51. The maize starch contained 990 g OM/kg DM and 2 g N/kg DM with a DM content of 883 g/kg fresh weight. It contained a negligible amount of NDF.

Rates of digestion and passage. Fractional rates of digestion of DM and NDF from the dacron bags are shown in Table 1; addition of starch appeared to reduce the rate of digestion at the H level of feeding but no effect was observed at the L feeding level.

Table 3. *Mean rumen pool sizes (g) at four sampling times after feeding, treatment means (g) and intake (g/d) of total wet weight of digesta dry matter (DM) and organic matter (OM) of sheep eating perennial ryegrass* (Lolium perenne *cv. Endura*) *hay fed once daily at two levels of feeding (high (H) and Low (L)) with (S) or without maize starch as supplement*

(Mean values for eight sheep per treatment)

Period after feeding (h)	Treatment				SEM	Statistical significance of effect of:	
	H	HS	L	LS		Level	Starch
			Wet weight of digesta				
5	12553	13805	10855	11339	432·8	***	NS
10	12694	12753	10154	10621	310·1	***	NS
15	11696	11131	9016	9557	414·1	***	NS
24	8983	9233	8392	8876	460·4	NS	NS
Mean	11481	11768	9604	10098	231·0	***	NS
			DM				
5	1121	1251	890	960	46·8	***	*
10	1056	1016	719	815	37·5	***	NS
15	872	886	634	690	31·1	***	NS
24	578	561	483	466	28·7	**	NS
Mean	907	938	682	733	29·8	***	NS
Intake	889	1040	594	698			
			OM				
5	965	1094	754	830	41·1	***	*
10	908	883	608	700	35·3	***	NS
15	750	769	534	594	28·2	***	NS
24	485	472	402	388	25·1	**	NS
Mean	777	787	575	628	26·6	***	NS
Intake	810	959	540	642			

NS, not significant. * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

However, neither this apparent interaction nor the difference in rate constants were significant ($P > 0·05$), although analysis of the percentage loss of DM at specific times (12, 18 and 24 h) was significantly ($P < 0·05$) less in the starch-supplemented sheep.

Table 1 also gives estimates of the lag time t_0 before the start of digestion of the NDF: for treatments with starch, estimates of t_0 were significantly greater ($P < 0·01$) than for treatments without starch.

Estimates of the rate of passage of Cr mordant from the rumen obtained from the decline in faecal concentration of Cr (k_p) are also shown in Table 1. There was a significant ($P < 0·01$) increase in k_p with increased level of feeding but no effect of starch.

Digestibility. Values for the in vivo apparent digestibility coefficients for DM, OM, NDF and ADF are given in Table 2. The higher level of feeding resulted in significantly ($P < 0·001$) reduced digestibilities of all fractions measured whilst, as expected, DM and OM digestibilities increased in response to starch supplementation.

Rumen pool sizes. Table 3 shows the mean digesta pool sizes in the rumen at 5, 10, 15 and 24 h after the hay was offered, for the total wet digesta content, digesta DM and OM, also the means of the four measurements within each treatment, and the daily intakes of DM and OM.

The increase in level of feeding resulted in significant increases ($P < 0·001$) in rumen pool

Table 4. *Mean rumen pool sizes (g) at four sampling times after feeding, treatment means (g) and intake (g/d) of fibre measured as dNDF, dADF, INDF and IADF of sheep eating perennial ryegrass* (Lolium perenne *cv. Endura*) *hay fed once daily at two levels of feeding (high (H) and low (L)) with (S) or without maize starch as supplement*

(Mean values for eight sheep per treatment)

	Period after feeding (h)	Treatment				SEM	Statistical significance of effect of:	
		H	HS	L	LS		Level	Starch
dNDF†	5	351	402	221	277	20·1	***	**
	10	252	286	170	203	12·5	***	*
	15	124	190	90	114	10·2	**	*
	24	38	62	21	32	6·4	NS	NS
	Mean	191	239	126	157	8·6	***	***
	Intake	393	391	262	262	8·4		
dADF‡	5	272	288	190	205	14·5	***	NS
	10	226	223	148	165	12·2	***	NS
	15	170	174	117	125	8·4	**	NS
	24	86	99	79	70	7·1	*	NS
	Mean	189	199	134	141	8·2	***	NS
	Intake	277	274	185	185	6·2		
INDF	5	311	301	280	262	16·7	*	NS
	10	337	291	234	245	15·9	***	NS
	15	339	287	253	251	16·9	**	NS
	24	271	241	231	209	13·0	*	NS
	Mean	315	283	250	242	11·7	***	NS
	Intake	158	157	105	105	3·4		
IADF	5	90	97	83	84	4·4	*	NS
	10	98	86	70	78	5·1	*	NS
	15	89	79	67	69	4·7	*	NS
	24	76	61	58	54	8·2	NS	NS
	Mean	88	82	69	71	4·3	**	NS
	Intake	51	51	34	34	1·1		

NDF, neutral-detergent fibre; ADF, acid-detergent fibre; dNDF, digestible NDF; dADF, digestible ADF; INDF, indigestible NDF; IADF, indigestible ADF; NS, not significant.

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

† Calculated as NDF − INDF.

‡ Calculated as ADF − IADF.

sizes for all constituents. Intake of DM and OM was higher on those treatments with starch than on those without, and gave rise to significant increases ($P < 0·05$) in rumen DM and OM contents at 5 h after feeding compared with those treatments without starch. These differences were no longer significant at the 10 h sampling time.

Mean digesta pool sizes in the rumen of the fibre components of the digesta at 5, 10, 15 and 24 h after feeding are presented in Table 4, together with treatment means and daily intakes. The fibre fractions presented are the indigestible fractions INDF and IADF, and the digestible NDF and ADF fractions (dNDF and dADF respectively), calculated as (NDF − INDF) and (ADF − IADF) respectively.

Table 5. *Mean time (min/d) spent eating (E), ruminating (R) and idling (I) by sheep eating perennial ryegrass* (Lolium perenne *cv. Endura) hay at two levels of feeding (high (H) and low (L)) with (S) or without maize starch as supplement*

(Mean values for eight sheep per treatment)

	Treatment					Statistical significance of effect of:	
Activity	H	HS	L	LS	SEM	Level	Starch
E	201	228	161	167	16·1	**	NS
R	545	515	437	451	19·0	***	NS
I	694	697	842	822	20·5	***	NS
E+R	746	743	598	618	20·5	***	NS
/kg DM intake†	846	853	1020	1077	32·3	***	NS
/kg NDF intake	1367	1378	1644	1700	55·3	***	NS

DM, dry matter: NDF, neutral-detergent fibre; NS, not significant.
** $P < 0·01$, *** $P < 0·001$.
† Excluding starch intake.

As with the components shown in Table 3, significant increases in rumen fibre content were observed when the level of feeding was increased. Addition of starch resulted in significantly higher amounts of dNDF in the rumen, but while there were also higher quantities of dADF in the rumen this increase was not significant. The rumen contents of INDF and IADF did not change significantly with the addition of starch to the diet.

The proportion of the daily intake remaining after 24 h was considerably less for the digestible fractions of the fibre content of the diet than for the indigestible fractions. The quantity of dNDF present in the rumen at the 24 h sampling time averaged 0·12 of the daily dNDF intake, while the corresponding value for INDF was 1·9.

Within treatments, there were significant reductions in the rumen content of dNDF between each sampling interval from 5 to 24 h after feeding, both at the L ($P < 0·05$) and at the H ($P < 0·01$) levels of feeding, both with or without starch. The dADF fraction showed similar trends. In contrast, there were no significant decreases within treatments, between 5 and 15 h after feeding, for either the INDF or the IADF fractions. There was, however, a reduction in the rumen content of these fractions by the 24 h sample ($P < 0·05$).

Eating behaviour. Table 5 gives the total time (min/d) spent on each activity, E, R and I during the 24 h recording period, also the total time spent chewing (E+R) expressed in terms of the DM and NDF intake for each treatment. The increase in the quantity of feed offered resulted in a significant increase in the length of time occupied by E ($P < 0·01$) and R ($P < 0·001$), with a corresponding decrease in I time ($P < 0·001$). This increase in chewing time did not occur in proportion to the increase in hay intake: at the H feeding level, total chewing time expressed per kg DM or NDF intake was significantly ($P < 0·001$) reduced.

The presence of starch in the diet did not affect E or R significantly, but since the starch was added to the diet via the fistula, it was thought unlikely that eating time would be increased. The addition of starch to the diet was found to have no effect on total chewing time (i.e. E+R) per kg DM or NDF intake.

DISCUSSION

The dietary treatments were imposed to study the effect of starch supplementation on the removal of digesta from the rumen and to observe whether the effect was influenced by level of feeding. The statistical analysis did not show any significant interactions between changes in the level of feeding and the starch supplement and hence the effects of these two factors will be discussed separately.

Energy supplementation

The maize starch added to the basal hay diet provided a source of readily available energy which resulted in higher VFA concentrations and lower pH levels in the rumen fluid (Aitchison, 1985). Starch also resulted in the highest VFA concentrations and the lowest pH being recorded earlier than for the treatments without starch. This rapid initial digestion resulted in a significantly ($P < 0{\cdot}001$) longer lag time before the start of fibre digestion in animals receiving starch (Table 1). Other workers have also reported a prolonged lag phase in the presence of starch (e.g. Mertens & Loften, 1980) and El-Shazly *et al.* (1961) suggested that rumen micro-organisms preferentially utilize the starch before the structural carbohydrates of the diet. However, despite the increased lag time in this experiment, there was no effect of starch on the fractional rate of digestion measured by incubation of the hay in dacron bags over 72 h.

The presence of starch also had no effect on k_p using Cr-mordanted hay and thus there was no significant ($P < 0{\cdot}05$) effect of starch on the apparent digestibility of NDF or ADF (Table 2). However, there was a trend ($P < 0{\cdot}10$) for starch to decrease fibre digestion at the higher feeding level.

Starch had little effect on the pool sizes of DM and OM in the rumen except at 5 h after the feed was offered, when the amount present was increased. This may partly have resulted from the increased DM input contributed by the starch but was also contributed to by the increase ($P < 0{\cdot}01$) in the dNDF content. Maize starch contributed negligible amounts of fibre to the diet but the pool size of dNDF was significantly higher in starch-supplemented sheep, during the first 15 h after feeding. These differences could still be detected at the 24 h sampling time, but were no longer statistically significant. Comparing the percentage loss of dNDF during different periods, from 0 to 5 h, 20, 9, 23 and 6 of the dNDF in the rumen (calculated as the 24 h value+intake) were lost, for treatments H, HS, L and LS respectively, while for the period 5–10 h after feed was offered, these percentages were 28, 31, 24 and 26 respectively of the dNDF present at 5 h. While the presence of starch in samples is known to interfere with the analysis of NDF and thus analytical problems may have contributed to the increased dNDF with starch treatment, the biological significance of these findings is supported by the findings of a longer digestion lag with the starch treatment as observed in the dacron bags.

Level of feeding

The daily pattern of rumen fermentation did not appear to be altered by the change in intake level; similarly, the dacron bag studies were unable to detect any changes in the fractional rates of digestion of either the DM or the NDF of the hay (Table 1). Digestibility of DM, OM and the fibre fraction in the whole tract was significantly ($P < 0{\cdot}001$) reduced at higher intakes (Table 2) and this effect appeared to be more pronounced in the presence of starch. This decrease in digestibility was presumably due to the 26% increase in fractional outflow rate observed using Cr-mordanted hay (Table 1). Similar results have been reported by Hogan & Weston (1967), Osbourn *et al.* (1981) and Uden (1984).

Increased k_p from the rumen may be brought about by increased frequency of reticulum

contractions, increased flow from the rumen per contraction, or a combination of both (Wyburn, 1980), while the frequency of reticulum contractions is known to be greatest during eating (Poppi *et al.* 1981). In this experiment, the total time spent chewing/kg DM intake was reduced ($P < 0{\cdot}001$) at the higher intake level, although total time spent chewing was increased (Table 5). The increase observed in the k_p therefore does not appear to result from increased rumen contractions stimulated by chewing but may have been associated with a larger volume of digesta flowing per contraction (Ulyatt *et al.* 1984).

In consequence of the increased rate of passage, the increases in rumen pool sizes were proportionally less than the 50% increase in intake. The greatest percentage increases (33) were observed with the NDF and DM fractions of the digesta: with a 17% increase in wet weight of digesta. Similarly, Moseley & Jones (1984) found lower increases (9 and 16%) in the wet weight of digesta compared with increases of 29 and 42% of DM in the rumen for clover and grass diets respectively, when intake was increased from 300 to 600 g DM/d. Ulyatt *et al.* (1984) observed increases of 22, 40 and 42% for mean pool sizes of total wet weight, DM and fibre respectively for animals fed once daily when the level of feeding was increased by 50%.

The actual weights of DM and the fibre fractions in the rumen at the high level of feeding were slightly lower than those reported by Aitchison *et al.* (1986) for a grass hay of similar digestibility offered at a slightly higher level of feeding (18 *v.* 16·5 g DM/kg LW). The diurnal pattern of rumen fill, however, was similar. The percentage of DM intake that was lost from the rumen during the first 5 h after feeding was 39, 30, 31 and 29 for treatments H, HS, L and LS respectively, whereas during the next 5 h it was only 6, 21, 19 and 15 respectively. For the indigestible fractions of the digesta, the amounts removed during the initial 5 h were even greater: losses of INDF were 75, 54, 53 and 50% respectively during this period, whereas there were no significant decreases in the quantities of INDF present between 5 and 15 h after feeding. Significant decreases did occur, however, between 15 and 24 h post feeding, for the INDF fraction of the digesta, and these coincided with the peak periods of rumination activity. These observations are similar to those of Aitchison *et al.* (1986) and support their conclusions that, in sheep fed once daily, outflow of material from the rumen is closely related to chewing and ruminating behaviour, with a high proportion of the outflow that is not associated with eating occurring during the second half of the feeding cycle.

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