

## The influence of density and size of particles on rumination and passage from the reticulo-rumen of sheep

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Plastic particles with different densities (0.92, 1.03, 1.22 and 1.44 g/ml) and sizes (1, 10 and 20 mm) were introduced into the rumen of fistulated sheep kept on a roughage diet. The forestomach was emptied 12 and 24 h after the introduction of the particles, and the contents were replaced by the same amount of rumen contents without plastic particles. The proportions of particles which left the reticulo-rumen (RR) during the experimental period were determined by collecting the faeces during the following 5 d. Non-ruminated particles were separated from the dried RR contents and from the faeces. Large particles were ruminated independently of particle size and density within the investigated range. After 12 and 24 h, 59 and 81% respectively of the particles initially introduced were comminuted due to rumination. During the 12 h period about four times as many particles with a density of 1.44 g/ml passed from the RR into the omasum compared with particles with a density of 0.92 or 1.03 g/ml. Three to ten times more 1 mm particles were excreted than originally-large particles (10 and 20 mm). Particles introduced with an original size of 10 or 20 mm were recovered mostly comminuted in the faeces. In a further experiment the rumens of eight sheep were emptied and filled with a buffer solution. Plastic particles (10 g) of each length (1, 5, 10 and 20 mm; all with a density of 1.03 g/ml) were introduced into the ventral rumen. Sedimentation of particles was prevented by gassing the solution in the RR. Of the initially introduced particles, 31.9, 25.4, 12.7 and 1.5% of the 1, 5, 10 and 20 mm long particles respectively left the RR within 4 h. It is concluded that rumination of particles is independent of particle density and size within the tested range. The probability of particles leaving the RR increases with the higher particle density and with the smaller size. If particle sedimentation is prevented in the RR even 10 mm long particles can leave the RR in considerable amounts.

Particle size: Particle density: Passage: Rumination: Sheep

Feed intake of ruminants fed on a roughage diet is limited by the rate of passage of digesta from the reticulo-rumen (RR) into the lower gut (Balch & Campling, 1962; Hidari, 1984). The mechanisms by which the passage of feed particles into the omasum is controlled are not well understood.

Sieve experiments have suggested that there is a critical size for particles leaving the RR, with most particles being smaller than 1–2 mm in sheep and 2–3 mm in cattle (Troelsen & Campbell, 1968; Reid *et al.* 1977; Poppi *et al.* 1980; Welch, 1982; Kennedy & Poppi, 1984). Reduction of particle size is regarded as a prerequisite for passage (Ulyatt, 1983), but particle density is also an important factor affecting the rate of passage out of the RR. By measuring the faecal excretion of plastic particles or stained feed particles it has been shown that particles with a density of 1.2–1.4 g/ml have a considerably higher probability

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of leaving the RR than less dense particles in cattle (Campling & Freer, 1962; Durkwa, 1983; desBordes & Welch, 1984; Ehle, 1984; Ehle & Stern, 1986; Welch, 1986), sheep (Lindberg, 1985; Kaske, 1987) and goats (Katoh *et al.* 1988). In sheep rate of passage of particles is influenced even more by particle density than particle size (Kaske & Engelhardt, 1990).

Plastic particles are useful for studying factors affecting the rate of passage although care should be taken in applying findings gained from such experiments to the passage of feed particles. The density of natural feed particles changes during retention in the RR. Most of the feed particles entering the forestomach have a density below 1.0 g/ml because of their air-filled interiors (Evans *et al.* 1973; Van Soest, 1975, 1982; Sutherland, 1988). During their stay in the RR, particle density increases slowly due to hydration, ion-exchange and destruction of cellular space, the highest density of about 1.4 g/ml being reached after approximately 60 h (Hooper & Welch, 1985; Nocek & Kohn, 1987). On the other hand, particle size decreases mainly due to rumination, although it is not understood whether rumination is dependent on particle density or size.

The objectives of the present study were (a) to determine the influence of particle density and size on breakdown of large particles due to rumination, and (b) to investigate the influence of particle size on the outflow of particles from the RR when particle sedimentation was prevented.

## MATERIALS AND METHODS

### *Plastic particles*

Plastic particles with densities of 0.92, 1.03, 1.22 and 1.44 g/ml and lengths of 1, 5, 10 and 20 mm were produced by mixing different portions of polyethylene and barium sulphate according to Kaske & Engelhardt (1990). The flexible filaments were cylindrical with a diameter of 0.75 mm. Each length and density had a different colour. Plastic particles could be comminuted during chewing by the animals independent of their density.

### *Experimental design*

Experiments were carried out with eight rumen-fistulated 2–5-year-old Blackhead sheep weighing 62–85 kg (four females, four wethers). The animals had been adapted over several months to an *ad lib.* diet of medium-quality hay (g/kg dry matter: crude fibre 370 (Weender analysis; Nehring, 1960), crude protein (nitrogen  $\times$  6.25) 136, ash 90). Water and mineralized salt licks were accessible at all times.

### *Expt 1*

Four sheep were kept in metabolism crates. They were fed three times daily (08.00, 13.00 and 17.00 hours) with 800 g hay/meal. The previous feed refusal was weighed and removed before each feed. The adaptation period before each experiment was at least 5 d. Before feeding at 08.00 hours of day 1, the plastic particles were introduced through the fistula into the digesta of the dorsal rumen and distributed roughly by hand. Large particles (500) of each size (10 and 20 mm) and of each density (0.92, 1.03, 1.22 and 1.44 g/ml) were used (total 4000 particles). Additionally, 2000 small particles (1 mm) of each density were added. Therefore, a total of 12000 plastic particles were introduced as a mixture into the RR.

The animals were observed continuously during the following 12 h period. The time-period during which each animal ruminated was recorded. At 12 h after the introduction of the plastic particles (at 20.00 hours of day 1) the RR of the sheep was emptied

completely. The contents were replaced by a comparable amount of rumen contents from a fistulated, hay-fed cow. The rumen contents of the sheep were weighed and dried at a temperature of 105°. To avoid difficulties in the interpretation of the results related to uneven distribution of the particles in the RR, all the contents was analysed. Plastic particles which were found with their original length of 10 and 20 mm respectively were separated by hand; these particles had not been ruminated. For each particle size and for each density the separated non-ruminated particles were weighed. Thereby, the percentage of non-ruminated long particles in the RR relative to the total number of added particles could be calculated for each size and density. The ruminated long plastic particles in the RR were comminuted to a length of 0.5–5 mm and it was, therefore, not possible to make a total separation of all ruminated plastic particles from rumen contents.

To measure the non-ruminated particles (10 and 20 mm) which left the RR during the 12 h experimental period the faeces of the sheep were collected for 5 d. A subsample of one-third was taken from the faeces and dried at 105° for 24 h. The subsamples from each animal were ground for 45 s using a coffee grinder (K 6, Bosch, Stuttgart). Preliminary studies had indicated that this did not change the size of the plastic particles (Kaske, 1987). Ground subsamples were sieved through a 500  $\mu\text{m}$  wire-mesh sieve (Retsch, Haan). The chewed and unchewed plastic particles were manually separated on the sieve from the remaining faecal particles and sorted according to their density and original size by colour. The non-ruminated and ruminated long plastic particles were weighed and the percentages of the total particles added were calculated for each size and density.

The percentage of the introduced particles which were ruminated during the 12 h period was calculated as  $100 - (\text{RR}_{\text{nr}} + F_{\text{nr}})$ , where  $\text{RR}_{\text{nr}}$  is the percentage of added particles which were found non-ruminated in the RR contents and  $F_{\text{nr}}$  is the percentage of the added particles which were recovered non-ruminated in the faeces. The percentage of particles of each size and density which had left the RR during the 12 h period ( $F_{\text{total}}$ ) was calculated as  $F_{\text{total}} = F_{\text{nr}} + F_{\text{r}}$ , where  $F_{\text{r}}$  is the percentage of the particles added which were found comminuted in the faeces and  $F_{\text{nr}}$  is the percentage of the introduced particles which were found non-ruminated in the faeces.

For the second part of the present experiment the same four sheep were used. The experimental procedure was similar, but only 10 and 20 mm particles of each density were applied. During the 24 h period after the introduction of the plastic particles into the rumen (08.00 hours of day 1) rumination behaviour was recorded. At 08.00 hours of day 2 the RR was emptied and faeces were collected for the following 5 d. Analysis of RR contents and faeces was carried out as described previously.

The rate of rumination of particles was calculated assuming an exponential decrease in the percentage of large plastic particles in the RR. An exponential equation was fitted to the disappearance of large particles:  $c_{(t)} = c_0 e^{-k \cdot t}$ , where  $c_{(t)}$  is the percentage of the added particles which were non-ruminated at sample time  $t$  ( $\text{RR}_{\text{nr}} + F_{\text{nr}}$ ),  $c_0$  is the initial amount of large particles in the RR (100%) and  $k$  is the rate-constant representing the portion of particles which were ruminated per hour. The value of  $k$  may be limited by the fact that only three data-points were available (0, 12 and 24 h after the introduction of the large particles).

### Expt 2

The outflow from the RR of plastic particles of various lengths was studied when the sedimentation of particles was prevented.

Rumen contents of eight sheep were removed and weighed. The RR was washed several times with a buffer solution (mmol/l: sodium 117, potassium 40, bicarbonate 25, chloride 13, hydrogen phosphate 32, dihydrogen phosphate 10, acetate 45, propionate 15, butyrate

15; pH 6.6; 300 mosm/l). Warm buffer solution (85% of the weight of the removed contents) was introduced into the rumen together with plastic particles with a density of 1.03 g/ml and lengths of 1, 5, 10 and 20 mm (each 10 g). Two 30 mm long gas frits (Felke, Greding) anchored with lead weights were placed in the ventral rumen. These frits were connected via plastic tubes to a bottle of carbon dioxide. During the experimental period of 4 h the buffer solution was gassed with CO<sub>2</sub> (approximately 800 ml/min) to prevent the sedimentation of the plastic particles. After 4 h the rumen was emptied. All particles were removed from the RR by washing the rumen with buffer solution several times. The particles were dried, separated according to their length and weighed. Thereby, the percentage of the particles of each size which left the RR during the 4 h period could be calculated. The original rumen contents which had been stored at 38° were transferred back into the RR of the animals after the experiment.

In preliminary experiments it was confirmed that rumen motility was not affected by these artificial conditions and that the outflow of fluid was within the range of hay-fed sheep. Rumen motility was recorded using air-filled latex balloons placed in the reticulum and the ventral rumen sac. The balloons were connected via polyethylene tubes with pressure transducers (Statham P 23 Db; H. Sachs, Freiburg). The pressure was recorded simultaneously by a recorder (Watanable WR 3310; H. Sachs, Freiburg). About 50 rumen contractions per h were recorded when the rumen was filled with buffer solution; this was comparable with the pattern of motility when the RR was filled with normal digesta. The rumen fluid outflow rate under the experimental conditions was 767 (SE 39) ml/h ( $n = 5$ ), estimated by measuring the dilution of polyethylene glycol (PEG) in the rumen fluid after a single PEG injection. Changes in RR fluid volume were less than 10% during a 4 h period. The animals showed no signs of concern or uneasiness during the experiment; their behaviour did not differ from that of sheep with normally-filled RR except that sheep did not ruminate during the 4 h period when the RR was filled with the solution; therefore, particles that left the RR still had their original lengths.

In four of the eight sheep the outflow of plastic particles from the RR within 4 h was compared with the appearance of plastic particles in the faeces during the following 2 d. Sheep were put in metabolism crates. Hay, water and salt licks were freely available. A 100 g/kg subsample of the faeces was separated and the weights of particles in each sample were determined as described previously. The weights of the particles found in the faeces were compared with those that had been calculated to have left the RR within 4 h. Faecal recoveries for particles with a length of 1, 5, 10 and 20 mm were 92.6 (SE 6.5), 87.9 (SE 4.4), 69.8 (SE 20.0) and 75.4 (SE 17.5)% respectively of the values calculated from the disappearance from the RR. The large standard errors may be explained by the small size of the subsample and the small number, particularly of large particles, which left the RR during the 4 h.

#### *Statistical analysis*

The effects of particle length and particle density on the proportion of particles which left the RR during the experimental period were evaluated by using a block analysis of variance with a blocking factor of sheep and the treatment factors of particle density and particle length (Winer, 1971). Results are given as means with their standard errors.

Differences between the outflow rates of particles in Expt 2 were tested by two-way analysis of variance (Winer, 1971), with animal and particle length being the independent variables.

Table 1. *Relative amounts (%) of plastic particles varying in density and size in the contents of the reticulo-rumen (RR) 12 h after the single dose of the particles into the RR\**

(The whole contents of the RR were removed after 12 h and replaced by the same amount of RR contents of a cow. Particles which left the RR during the 12 h experimental period were estimated by analysing the faeces during the following 5 d. Mean values with their standard errors for four sheep)

Particle density (g/ml)	Particle length (mm)	Particles (% of the introduced wt)									
		Non-ruminated in the RR within 12 h (RR <sub>nr</sub> )		Non-ruminated in faeces (F <sub>nr</sub> )		Ruminated in faeces (F <sub>r</sub> )		Faeces total (F <sub>total</sub> = F <sub>nr</sub> + F <sub>r</sub> )		Ruminated particles within 12 h (100 - (RR <sub>nr</sub> + F <sub>nr</sub> ))	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0.92	1	nd		nd		nd		18.5	4.8	nd	
0.92	10	33.1	4.8	2.4	1.0	2.1	1.0	4.5	1.3	64.5	4.8
0.92	20	46.5	7.5	0.5	0.3	2.8	0.8	3.3	0.8	53.0	7.5
1.03	1	nd		nd		nd		15.1	1.6	nd	
1.03	10	44.4	5.7	0.8	0.4	2.8	0.3	3.6	0.6	54.8	5.5
1.03	20	45.9	6.4	npf		2.1	0.6	2.1	0.6	54.1	6.4
1.22	1	nd		nd		nd		51.6	8.4	nd	
1.22	10	40.6	5.5	2.0	0.3	5.0	1.3	7.0	1.4	57.4	5.3
1.22	20	44.1	5.7	0.2	0.2	5.0	1.5	5.2	1.5	55.7	5.7
1.44	1	nd		nd		nd		64.5	7.5	nd	
1.44	10	17.5	3.6	8.2	2.2	9.6	3.2	17.8	4.3	74.3	1.8
1.44	20	41.8	7.1	0.6	0.4	12.3	3.0	12.9	2.9	57.6	6.9

nd, not determined;

npf, no non-ruminated particles found in the faeces.

\* For details of procedures, see pp. 236–237.

## RESULTS

### *Expt 1*

#### *Feed intake and rumination time*

In both parts of the experiment the sheep consumed their feed mostly during the day. In the 12 h period they consumed 1769 (SE 68) g and in the 24 h period 1778 (SE 80) g. Rumination began in both experiments about 1 h after feeding at 08.00 hours. Rumination activity was almost regularly distributed throughout the day and night with an average of 23 min/h. This led to a total rumination activity of 4.2 (SE 0.5) h during the 12 h period and 9.5 (SE 0.3) h during the 24 h period.

#### *Rumination and particle density*

The plastic particles with a length of 10 and 20 mm were ruminated independently of their density (Tables 1 and 2,  $(100 - (RR_{nr} + F_{nr}))$ ). The rather low percentages of non-ruminated 10 mm particles with densities of 0.92 and 1.44 g/ml (Table 1, RR<sub>nr</sub>) may be due to the colour of these particles; they were grey and white respectively which made it more difficult to find them in RR contents. No significant differences were found between the number of non-ruminated 10 and 20 mm particles in the RR (Tables 1 and 2). Thus the rate of rumination was calculated for all plastic particles, independent of size and of density. At 12 h after the introduction of particles into the RR, 58.9 (SE 2.1)% of the plastic particles had been ruminated (Table 1). After 24 h the mean value had increased to 81.3 (SE 1.0)%

Table 2. *Relative amounts (%) of plastic particles varying in density and size in the contents of the reticulo-rumen (RR) 24 h after the single dose of the particles into the RR\**

(The whole contents of the RR were removed after 24 h and replaced by the same amount of RR contents of a cow. Particles which left the RR during the 24 h experimental period were estimated by analysing the faeces during the following 5 d. Mean values with their standard errors for four sheep)

		Particles (% of the introduced wt)									
Particle density (g/ml)	Particle length (mm)	Non-ruminated in the RR within 24 h (RR <sub>nr</sub> )		Non-ruminated in faeces (F <sub>nr</sub> )		Ruminated in faeces (F <sub>r</sub> )		Faeces total (F <sub>total</sub> = F <sub>nr</sub> + F <sub>r</sub> )		Ruminated particles within 24 h (100 - (RR <sub>nr</sub> + F <sub>nr</sub> ))	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0.92	10	14.8	2.1	0.6	0.3	5.0	0.7	5.6	1.1	84.6	1.8
0.92	20	19.5	2.6	npf		5.3	1.0	5.3	1.0	80.5	2.6
1.03	10	19.8	2.1	1.5	0.8	5.5	1.0	7.0	0.5	78.7	2.1
1.03	20	18.6	3.2	0.2	0.2	5.9	1.0	6.1	1.0	81.2	3.8
1.22	10	18.0	3.3	0.5	0.3	9.3	1.7	9.8	1.9	81.5	3.6
1.22	20	19.3	4.3	npf		8.2	1.8	8.2	1.8	80.7	4.4
1.44	10	12.2	3.6	6.7	1.7	13.4	2.5	20.1	3.8	81.1	3.6
1.44	20	18.3	3.8	npf		15.1	3.5	15.1	3.5	81.7	3.8

npf no non-ruminated particles found in the faeces.

\* For details of procedures, see pp. 236-237.

Table 2). Using the exponential equation described on p. 237 it was calculated that the large plastic particles in the RR were comminuted at a rate of 0.07 /h by rumination.

#### *Faecal excretion of particles*

Both particle size and particle density influenced significantly ( $P < 0.001$ ) the number of particles that left the RR during the 12 h period (Table 1, F<sub>total</sub>). Small (1 mm) particles with a density of 1.44 g/ml were found in the faeces at a level of 3.8 times that of particles with a density of 0.92 and 1.03 g/ml. The 1 mm particles with a density of 1.22 g/ml left the RR 3.1 times faster than particles with the lower density. Also the total amount of ruminated and non-ruminated long particles found in the faeces was about three times higher for particles with a density of 1.44 and 1.22 g/ml compared with the less dense particles.

Markedly fewer particles with a size of 10 or 20 mm left the RR during the 12 h period compared with the 1 mm particles of corresponding density (Table 1, F<sub>total</sub>). The differences between the 1 mm particles and the originally 10 or 20 mm particles were significant ( $P < 0.001$ ) for all four densities. The originally 10 and 20 mm plastic particles with a high density (1.44 g/ml) were found in faeces after the 12 h period in the same proportions as small particles (1 mm) with a low density (0.92 and 1.03 g/ml; Table 1, F<sub>total</sub>); this also indicates the strong influence of particle density on rates of passage. Most of the originally long particles were found comminuted due to rumination to 0.5-4 mm in the faeces. The originally 10 mm particles tended to be excreted in higher proportions than particles introduced with a size of 20 mm, but differences were not significant.

It was an interesting observation that 8.2 (SE 2.2) % of the originally 10 mm particles with a density of 1.44 g/ml left the RR during the 12 h period with their original length; i.e. these particles had not been ruminated (Table 1, F<sub>nr</sub>). These unchewed particles in the faeces (F<sub>nr</sub>) represented 45 % of the total weight of particles excreted (F<sub>total</sub>); i.e. only 55 % of the

Table 3. *Outflow from the reticulo-rumen of sheep (% of the initially introduced weight during 4 h) of plastic particles (density 1.03 g/ml) of four different sizes*

(During the experiment the rumen was filled with buffer solution and sedimentation of particles was prevented by gassing the solution. Mean values with their standard errors for eight sheep)

Particle length (mm)	Outflow from the reticulo-rumen in 4 h during prevented sedimentation* (% of the introduced weight)	
	Mean	SE
1	31.9	8.8
5	25.4	7.2
10	12.7	4.9
20	1.5	1.0

\* For details of procedures, see pp. 236–237.

10 mm particles (1.44 g/ml) had been ruminated before they left the RR within the 12 h period. The same tendency was observed in the 24 h experiment where 33 % of the 10 mm particles (1.44 g/ml) left the RR with their original length ( $F_{nr}$  6.7 %;  $F_{total}$  20.1 %; Table 2).

#### *Expt 2*

When particle sedimentation in the RR was prevented by gassing the fluid in the forestomach the outflow of particles from the RR decreased significantly ( $P < 0.001$ ) with increasing particle size (Table 3). However, even 10 mm particles left the RR in an amount which represented about 40 % of the outflow of 1 mm particles, whereas particles with a length of 20 mm were retained almost totally in the RR.

The high variation of the individual results may be explained by the position of the frits in the ventral rumen. Endoscopic observation showed that particle sedimentation was effectively prevented only if the frits were positioned at the deepest point of the ventral rumen. Due to rumen motility and movements of sheep the frits changed their position in the rumen. Sedimentation of particles obviously had, therefore, not been prevented totally during certain periods. However, apart from the highly variable results, the relation between the outflow of the different particle sizes was comparable for all eight animals.

## DISCUSSION

### *Rumination and particle density*

The results of the present study indicate that, in sheep, the proportion of ruminated particles in the RR is not influenced by particle density within the tested range. In an earlier experiment we compared, in hay-fed sheep, the mean retention time (MRT) of plastic particles with two different sizes (1 and 10 mm) and four different densities (0.92, 1.03, 1.22 and 1.44 g/ml; Kaske & Engelhardt, 1990); the MRT of particles with a low density was about two to three times longer than that of particles with a high density (1.44 g/ml). However, the MRT of 1 and 10 mm long particles of each density were not significantly different (on average 22.7 h). These earlier results also indicated similar rumination rates for particles of the four different densities.

DesBordes & Welch (1984) and Murphy *et al.* (1989), on the other hand, observed in experiments with cows an inverse relationship between particle density and rumination

rate. Their results contrast with those of the present study and this may be due to species differences between sheep and cows. In cows the origin of the rejected bolus seems to be either from the dorsal region of the reticulum or from the cranial sac of the rumen; the proportion of large particles found in the rejected bolus of cows is higher than that in mixed rumen contents (Ulyatt *et al.* 1986); these larger feed particles mostly have a lower density than the smaller ones (Evans *et al.* 1973; Hooper & Welch, 1985). A higher proportion of particles with a lower density in the rejected bolus of cows may explain higher rumination rates of light particles. In sheep, on the other hand, radiological studies showed that the bolus is regurgitated from the more ventral region of the reticulum (Rousseau *et al.* 1982), and the proportion of large particles in the bolus of sheep is lower than that in mixed rumen contents (Ulyatt *et al.* 1986). This may explain why particles with a low density are not preferentially rejected and ruminated in sheep.

Conclusions by desBordes & Welch (1984) and Murphy *et al.* (1989) on rumination and passage were based exclusively on analysis of faeces. The chemical compositions of plastic particles in their studies were different, and it is not clear whether the comminution of these particles due to rumination was similar for particles of different densities. That is, however, a prerequisite if rumination rates are calculated from faecal analysis because the proportions of ruminated and non-ruminated particles in a faeces sample are influenced by both, i.e. breakdown rate due to rumination and rate of passage, depending on particle density.

#### *Effectiveness of particle breakdown*

Our experiments indicate that comminution of particles due to rumination is a comparatively fast process. 7.0% of the long particles per h were ruminated; this value is in good agreement with breakdown rates calculated from values of Ulyatt *et al.* (1986) and Faichney (1986) for long feed particles (0.07–0.083 /h). On the other hand, the increase in the density of feed particles in forestomach contents seems to be a slower process than particle breakdown. Rate-constants for density increase of 0.03–0.045 /h were estimated (M. Lechner-Doll, personal communication). The low rate-constant for density increase compared with the high particle breakdown rate may explain why very few larger feed particles with a high density were found in RR contents (Evans *et al.* 1973).

#### *Influence of particle size on rate of passage*

The probability of large particles leaving the RR is lower than that for smaller particles (Reid *et al.* 1977; Ulyatt, 1983). This is in agreement with our results (Tables 1 and 2). However, the diameter of the reticular-omasal orifice (ROO) (Bueno & Ruckebusch, 1974; McBride *et al.* 1983) is much larger than the 'critical particle size' and we may ask why only small particles leave the RR. The influence of particle size on passage had been overestimated in most of the earlier studies. When sedimentation of particles in the RR was prevented (Expt 2, Table 3) the outflow of 10 mm particles was about 40% of the outflow of the 1 mm particles. These results indicate that particles up to 10 mm are able to pass the ROO of sheep in considerable amounts if present in the reticulum when the RR opens. Most of the large feed particles in the RR have a low density due to the air-filled interior. These lighter particles are preferentially pushed into the caudo-dorsal regions of the forestomach by the reticular contractions, and when passage of digesta through the ROO occurs at the maximum of the second reticular contraction (Stevens *et al.* 1960; Ehrlein & Hill, 1969) only few particles with a low density are present in contents of the reticulum. Lighter particles, therefore, have a long MRT. Particles with a density of 1.3–1.4 g/ml, on the other hand, have a high probability of leaving the RR of sheep (Tables 1 and 2; Lindberg, 1985; Katoh *et al.* 1988) since these particles remain in the reticulum during the reticular contraction (Kaske, 1987); consequently, their MRT is comparatively short.



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