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Passage and rumination of inert particles varying in size and specific gravity as determined from analysis of faecal appearance using multicompartment models

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Plastic particles of defined length (2, 5 mm) and specific gravity (sp.gr. 1·10, 1·34, 1·77) were administered just before feeding into the reticulo-rumen of four cattle and four swamp buffaloes given a diet predominantly of rice straw *ad lib*. Simultaneously, doses of ground rice straw marked with Cr and Yb were likewise given. Plastic particles were recovered from faeces for 12 d after dosing, and divided into non-ruminated (NR) and ruminated (R) particles. Excretion data of plastic particles were interpreted using a four-pool model incorporating passage of NR (k_p) and R from the reticulo-rumen, post-ruminal passage, rate of chewing (k_r) and two lag times. An inverse relationship was found between k_r and sp.gr. The k_r was higher for 5 mm than that for 2 mm particles. In contrast, k_p was greatest for particles of sp.gr. 1·34, with higher k_p for 2 mm than for 5 mm particles. Rates of passage and rumination (k_p, k_r) were higher for buffaloes than for cattle. Rumination time was related to k_r, most highly (r^2 0·96) with k_r of 2 mm, 1·10 sp.gr. particles. Fragmentation of 5 mm particles by rumination tended to increase the rate of passage from the rumen. Ruminal passage rates of Yb and Cr markers were poorly correlated with each other and with k_p of any of the plastic markers. Reanalysis of published data from plastic particle studies supported the relationships between sp.gr., size, k_p and k_r. In view of the additional information (k_r) obtained using plastic particles, we suggest their use may be appropriate in studies which investigate specific differences in digestive function, while being less suitable for investigating differences between diets.

Plastic particle markers: Rumination rates: Specific gravity: Cow: Buffalo

Studies of ruminant digestion often include determination of mean retention time of particulate material in the rumen in order to calculate the amount of digestion from the rate of digestion, commonly estimated using the synthetic fibre bag technique. Mean retention time is estimated by dosing with particulate markers and either following their disappearance from the rumen or their appearance in the faeces. However, available markers suffer from non-ideal properties (Warner, 1981) such as migration between particles, variable inhibition of microbial activity (Evans *et al.* 1977) and variations in properties of size and specific gravity (sp.gr.) which may reduce their ability to move with digesta. Various inert materials have been used to study the effects of particle size and specific gravity on passage (King & Moore, 1957; Campling & Freer, 1962; desBordes & Welch, 1984); however, there has not been enough information available from which to recommend a size and sp.gr. combination that mimics passage of digesta particles from the rumen. As part of a study of factors which affect roughage intake, we wished to investigate whether the reputed superior ability of a ruminant species (swamp buffalo) to utilize fibrous diets was reflected in differences in passage behaviour of plastic particles of defined length

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and sp.gr. through the gut. In particular, we wished to determine the relative efficiency of chewing during rumination by swamp buffalo and cattle, in view of the proposed importance of rumination in the removal of undigested fibre from the rumen (e.g. Welch, 1986).

Plastic particles recovered from faeces after intra-ruminal dosing can be separated into ruminated and non-ruminated fractions based on the presence or absence of teeth marks respectively (desBordes & Welch, 1984). This characteristic provided an opportunity to obtain data about mechanisms involved in selecting particles for rumination and regulating digesta passage from the reticulo-rumen, important areas needing more quantitative information (Reid, 1984). Fractional passage rate (FPR) of digesta from the rumen is considered a major determinant of both digestion in this compartment and voluntary feed consumption.

MATERIALS AND METHODS

Four castrate male swamp buffaloes and four ovariectomized zebu crossbred cattle, aged 2·5 years, weighing 225–280 kg and equipped with simple rumen and simple abomasal fistulae, were fed *ad lib.* on a mixture (95:5, w/w) of rice straw (*Oryza sativa*, 660 g cell wall constituents (CWC, method of Van Soest & Wine, 1967) and 4·6 g N/kg dry matter (DM)) and leucaena leaf (*Leucaena leucocephala*, 398 g CWC and 34·1 g N/kg DM), together with a mineral mix (100 g/d, Siebert & Kennedy, 1972). Feed was offered once daily at 1·2 times consumption during the previous day. After 2 weeks of adaptation to the diet, doses (4000 particles, 1·0–1·3 mm diameter cylinders) of colour-coded plastic particles of three specific gravities (1·10, 1·34, 1·77 sp.gr.) and two lengths (2 or 5 mm) were administered into the ventral rumen at 08.00 hours; i.e. just before fresh feed was given. In addition, animals were dosed with labelled feed particles of rice straw which had been previously ground through a 1 mm screen and extracted with sodium lauryl sulphate (100°, 18 h). Particles were labelled by immersion in a solution of hydrated Yb-acetate (100 g/l, Research Chemicals, Phoenix, Arizona, USA) at pH 5·5 and washed as described by Mader *et al.* (1984), or were mordanted with Cr as described by Uden *et al.* (1980).

Jaw movements were detected by the extension of an electrically semi-conductive silicone rubber tube placed under the jaw of the animal (see Penning, 1983).

The functional sp.gr. of labelled materials was measured in pycnometers as described by Hooper & Welch (1985); fibre labelled with Yb had a sp.gr. of 1·56 whereas that labelled with Cr was 1·37. Measured by an adaptation of the technique of Evans *et al.* (1973) of density gradient centrifugation in a linear ethanol to carbon tetrachloride mixture (10000 ***g***, 15 min, 4°), their sp.gr. was $> 1{\cdot}47$ and $> 1{\cdot}50$ respectively. The poor agreement between techniques for particles labelled with Cr was attributed to greater displacement by ethanol/CCl_4 of gas trapped within the fibre matrix.

Faeces were collected quantitatively at intervals of 12 h for 5 d, thereafter at 24 h intervals for 7 d. After subsampling (1–3 % of total) faeces for Yb and Cr analysis, plastic particles were recovered by hosing remaining faeces through a large screen, followed by separation of the dried residue using a vibrating seed separator. Particles were identified, counted, and separated manually into non-ruminated (NR) and ruminated (R) particles, according to the absence or presence of teeth marks. Recovery of particles broken during rumination was determined by weighing the resulting fragments.

Cr in faeces was analysed by the method of Williams *et al.* (1962). Yb concentration was determined by the method of Hart & Polan (1984) with use of a carbon furnace and detection by atomic emission.

Least-squares estimates of model parameters were made using the 1981 version of a

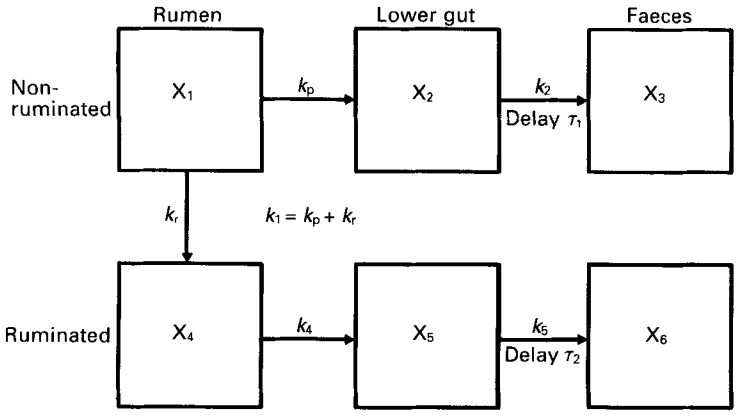

Fig. 1. Model chosen to represent rumination and passage of non-ruminated and ruminated plastic particles varying in specific gravity and length.

derivative-free non-linear regression technique (Ralston, 1979). The program was implemented on a DEC System-10 computer.

Choice of model

Passage and rumination of NR particles was envisaged as analogous to a three compartment model (X_1, X_2 and X_3) containing an accumulation compartment, as described by Atkins (1969) but with a discrete lag between the last two pools (Blaxter *et al.* 1956; Grovum & Williams, 1973; see Fig. 1). The model, shown in the top half of Fig. 1, was fitted to ln (faecal concentration of NR particles) *v.* time data to estimate k_1, k_2 (the fractional passage rate of NR particles from the lower gut) and τ_1. In this scheme, rate constant k_1 of the pool as a whole actually represented the sum of k_p (the fractional passage rate of NR particles) and k_r (the fractional rumination rate of NR particles) since these were the only possible routes of exit from the pool. By fitting ln (concentration) it was possible to stabilize the variance and obtain a uniform distribution of residuals similar to that described by Dhanoa *et al.* (1985). The fact that cumulative faecal output of NR particles reached a plateau by 12 d postdosing allowed k_p and k_r to be determined based on the assumption that only R particles would appear after that time; i.e. since flow of NR $= k_p \times$ pool and total flow $= k_1 \times$ pool, then k_p/k_1 was equated to the ultimate recovery of NR as a proportion of the dose. An underlying assumption of our proposed model was that NR particles selected for passage or rumination can be considered to be from the same pool, or from subpools in rapid equilibrium compared with the time for appreciable passage or rumination. From available information and given the relatively frequent mixing contractions of the reticulo-rumen, the latter concept is more defensible. Recently, Dardillat (1987) suggested that both resting and rumination contractions are associated with forward and backward movement of digesta through the reticulo-omasal orifice. Accordingly, regurgitated and passed digesta may conceivably be selected from the same pool. Passage of R particles was viewed as a four compartment model (X_1, X_4, X_5 and X_6), also with an accumulation compartment and discrete lag between the last two pools; however, prior estimation of k_1 for NR particles meant that only k_4 (the fractional passage rate of R particles from the rumen), k_5 (the fractional passage rate of R particles from the lower gut) and τ_2 needed to be determined using ln (faecal concentration of R particles) over time data.

RESULTS

Faecal appearance of plastic particles

Cumulative recoveries of NR and R particles are summarized for each species in Tables 1 and 2, respectively. Recovery of 2 mm particles (NR plus R) from cattle over 12 d declined from 80 to 72% of particles dosed, as sp.gr. increased from 1·10 to 1·77, but recovery for buffaloes increased from 82% of dose to 91%. In contrast, recovery of 5 mm (NR plus R) particles was poor (26–36%) for 1·10 sp.gr. but increased to 63–89% for the heavier particles. Plateau excretion of NR 2 mm particles was reached earlier for buffaloes than for cattle, with recovery after 12 d from buffaloes achieving 75, 93 and 148% of cattle values for 1·10, 1·34 and 1·77 sp.gr. (Table 1). After 12 d, fewer 5 mm than 2 mm particles were recovered unruminated, with the differences being inversely related to specific gravity.

Buffaloes excreted more R particles than did cattle (Table 2). There was an inverse relationship between proportion of the dose excreted over 12 d and specific gravity of 2 mm particles, but the relationship was curvilinear for 5 mm particles. The collection period of 12 d was insufficient to achieve plateau excretion of R particles except for 2 mm, 1·34 sp.gr. particles in buffaloes.

Fractional rates of passage and rumination

Estimates of k_p and k_r for each sp.gr. and length combination were obtained for all buffaloes but for only two of the four cattle. Low recovery of particles was associated with an inability to derive rate constants. Recovery of NR particles of 1·77 sp.gr. after 12 d was close to, but not at, plateau. To the extent that NR had not reached plateau, the estimate of k_p would be underestimated, and k_r overestimated to the same extent, without affecting the derived value for k_1. For both species and particle lengths, maximum values of k_p and k_r occurred at 1·34 and 1·10 sp.gr. respectively (Fig. 2*a*, *b*). Time (mean (SEM)) spent ruminating by buffaloes and cattle (635 (SEM 24) *v.* 452 (SEM 15) min/d respectively; McSweeney & Kennedy, 1987) was closely correlated with k_r for 2 mm 1·10 sp.gr. particles (r 0·98; $P < 0·01$); when k_r was expressed on the basis of rumination time, the rate at which teeth marks appeared on these particles was 0·070 (SEM 0·0022) *v.* 0·105 (SEM 0·0015) per h of rumination for cattle and buffaloes respectively. Time spent ruminating was also correlated with k_r for 2 mm 1·34 sp.gr., and 5 mm 1·10 sp.gr. particles, if values from one buffalo were excluded (r^2 0·67, 0·69 respectively, $P < 0·05$). Apparently, this buffalo was unable to ruminate efficiently the latter particles, and during a subsequent period of restricted intake, produced 43% fewer fine digesta particles (those passing a screen with 150 μm pores) per minute of rumination (Kennedy *et al.* 1987).

The mean (SEM) k_1 for Yb-labelled particles was 0·033 (SEM 0·0019)/h in cattle and 0·044 (SEM 0·0047)/h for buffaloes ($P > 0·05$). For Cr-mordanted fibre, k_1 averaged 0·020 (SEM 0·0005)/h and 0·023 (SEM 0·0006)/h in cattle and buffaloes respectively ($P < 0·05$). FPR (i.e. k_1 values) of the two markers were not significantly correlated with each other or to k_p for any of the plastic markers but that for Yb-particles was correlated (r^2 0·75; $P < 0·05$) with duration of rumination.

Ruminal FPR (i.e. k_p) in buffaloes were higher by 40, 76 and 216% respectively for 2 mm particles of sp.gr. 1·10, 1·34 and 1·77 compared with cattle. Across species, k_p was poorly related to rumination time (r^2 0·02 to 0·30). On average k_p for 2 mm particles was 2·2 times k_p for 5 mm particles, with the latter being similar between species. The k_4 of R relative to k_p of NR 2 mm particles was dependent on sp.gr., with a ratio of R:NR of 0·77 (SEM 0·07):1, 0·97 (SEM 0·15):1 and 1·31 (SEM 0·29):1 for particles of sp.gr. 1·1, 1·34 and 1·77 respectively. In contrast, for 5 mm particles, which fragmented during chewing, rumination tended to increase passage rate from the rumen by 55 to 145%, with the increase largely

Table 1. *Cumulative recovery (percentage) of non-ruminated plastic particles*

(Mean values with their standard errors for four animals of each species except for cattle 1·34 and 1·77 particles where $n = 2$)

	Specific gravity																							
	1·10								1·34								1·77							
	Cattle				Buffaloes				Cattle				Buffaloes				Cattle				Buffaloes			
Length (mm)...	2		5		2		5		2		5		2		5		2		5		2		5	
Midpoint of interval (h)	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
6	0		0		0·4	0·4	0·1	0·1	0		0		0·1	0·1	0·1	0·1	0		0		0·1	0·2	0·1	0·1
18	0·3	0·3	0		6·4	2·5	1·4	0·6	0		0		5·9	3·7	2·5	1·6	0·2	0·2	0		1·8	1·0	0·9	0·5
30	8·1	2·7	1·5	0·5	15·4	2·8	3·0	0·9	1·4	1·4	2·4	1·7	10·1	4·6	3·7	2·0	3·9	2·7	2·0	1·3	2·8	1·6	1·6	1·0
42	17·0	3·2	3·3	0·6	22·8	4·2	5·1	1·3	9·9	5·5	4·0	2·7	19·7	5·5	7·9	2·3	5·0	3·9	2·6	1·9	6·3	2·9	3·7	1·6
54	22·2	2·3	4·9	0·5	25·4	4·1	6·0	1·6	21·2	0·1	10·7	0·1	34·0	8·4	14·8	4·7	13·6	2·2	9·9	3·2	17·6	8·0	11·2	5·6
66	26·8	2·0	6·2	0·7	26·3	4·1	6·3	1·6	28·2	2·5	14·5	0·8	40·6	7·8	18·5	5·1	15·7	3·0	11·8	4·0	24·9	10·6	16·3	8·4
78	29·6	1·7	7·1	0·7	26·8	3·9	6·4	1·6	34·2	5·5	18·4	2·5	46·9	8·3	22·6	6·2	17·3	4·1	13·0	5·1	32·6	2·0	20·9	9·2
90	31·8	0·9	7·7	0·6	27·0	3·9	6·5	1·6	39·1	6·3	22·8	1·6	50·3	8·1	24·2	6·2	20·1	2·5	16·2	3·1	39·6	12·0	24·3	9·5
102	33·3	1·1	8·0	0·6	27·2	3·9	6·5	1·6	44·9	7·2	27·1	1·4	52·2	7·3	25·0	5·8	24·2	1·9	20·2	2·7	45·0	10·0	27·1	9·1
114	34·1	1·1	8·3	0·6	27·2	3·9	6·5	1·6	49·1	8·7	29·4	0·9	53·2	6·6	25·5	5·5	25·4	1·4	21·2	2·3	49·8	8·0	28·8	8·3
132	36·2	1·8	8·5	0·6	27·2	3·9	6·5	1·6	55·5	6·0	33·4	1·3	54·7	7·0	26·0	5·6	31·4	4·2	23·9	4·5	56·7	6·4	33·7	8·8
156	36·4	1·8	8·6	0·6	27·2	3·9	6·5	1·6	57·4	6·9	34·3	1·7	55·2	6·9	26·3	5·5	35·2	4·7	29·5	7·1	65·4	4·9	37·4	9·2
180	36·5	1·8	8·6	0·6	27·3	3·9	6·5	1·6	58·6	7·5	34·9	2·0	56·6	7·9	26·4	5·5	40·6	2·6	33·5	5·3	69·3	4·6	39·0	8·8
204	36·6	1·8	8·6	0·6	27·3	3·9	6·5	1·6	59·8	8·5	35·4	2·3	56·6	7·9	26·4	5·5	44·0	4·9	36·6	6·1	71·6	4·4	40·1	8·7
228	36·6	1·8	8·6	0·6	27·3	3·9	6·5	1·6	60·4	9·0	35·7	2·6	56·6	7·9	26·4	5·5	47·7	5·4	38·5	6·0	73·5	3·8	40·8	8·5
252	36·6	1·8	8·6	0·6	27·3	3·9	6·5	1·6	60·6	9·0	35·8	2·7	56·6	7·9	26·4	5·5	49·7	6·1	41·0	7·7	74·6	3·4	41·2	8·4
276	36·6	1·8	8·6	0·6	27·3	3·9	6·5	1·6	60·7	9·1	35·9	2·7	56·6	7·9	26·4	5·5	51·5	7·3	41·2	7·6	76·4	4·0	42·1	8·3

Table 2. *Cumulative recovery (percentage) of ruminated plastic particles*

(Mean values with their standard errors for four animals of each species except for cattle 1·34 and 1·77 particles)

	Specific gravity																			
	1·10								1·34								1·77			
	Cattle				Buffaloes				Cattle				Buffaloes				Cattle				Buffaloes			
Length (mm)...	2		5		2		5		2		5		2		5		2		5		2		5	
Midpoint of interval (h)	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
6	0		0		0		0		0		0		0		0		0		0		0·1	0·1	0·1	0·1
18	0·1	0·1	0		0·8	0·5	0·4	0·3	0		0		4·2	3·2	0·7	0·7	0·1	0·1	0·1	0·1	0·6	0·6	0·5	0·5
30	0·6	0·2	0		2·6	0·5	0·9	0·3	0·4	0·3	0·2	0·1	5·2	3·3	0·7	0·7	0·3	0·3	0·9	0·9	0·6	0·6	0·6	0·5
42	3·8	0·7	0·6	0·3	9·5	0·6	2·3	0·4	0·9	0·5	0·7	0·4	8·5	3·7	2·3	0·7	0·4	0·3	1·3	1·2	0·8	0·7	1·0	0·5
54	6·5	0·0	1·1	0·2	16·9	2·2	3·7	0·7	2·5	0·3	2·7	0·3	13·1	5·3	7·3	1·8	0·7	0·2	2·3	0·9	1·6	0·9	2·6	1·1
66	11·5	1·1	1·9	0·3	22·6	2·8	4·9	0·8	3·7	0·7	4·6	0·2	16·9	5·4	11·5	2·4	0·8	0·2	2·8	0·9	2·4	1·0	4·4	1·3
78	16·1	1·1	2·6	0·3	28·3	2·9	5·9	1·8	5·8	1·5	7·7	0·7	21·7	6·4	16·9	3·7	0·9	0·1	3·5	0·4	3·3	1·2	9·3	3·0
90	21·3	1·8	3·3	0·4	32·6	2·8	7·1	0·8	8·9	1·3	13·0	0·5	25·4	7·5	20·7	3·0	1·4	0·3	5·6	1·5	5·0	1·2	13·0	2·8
102	23·3	2·3	4·5	0·7	36·4	2·9	8·2	0·9	11·2	2·5	17·4	0·1	27·9	8·6	24·5	1·7	1·9	0·4	7·6	1·6	6·6	2·2	16·1	1·5
114	27·2	2·6	5·3	0·8	39·4	2·9	9·3	0·8	12·8	2·9	22·4	0·2	30·1	9·8	27·6	1·4	2·0	0·6	8·2	1·9	8·4	3·5	19·2	2·0
132	30·0	2·8	7·4	1·0	43·5	2·9	11·8	1·0	16·2	3·8	31·9	2·2	33·0	9·6	38·7	3·8	2·7	0·3	12·2	1·0	10·0	4·8	25·1	2·3
156	33·9	3·0	8·6	0·9	46·1	2·9	13·8	1·2	17·1	3·6	35·5	2·5	33·9	9·8	44·5	4·4	3·1	0·3	14·3	1·7	11·7	5·2	32·4	3·5
180	36·9	2·9	9·8	0·7	48·4	2·9	15·6	1·2	18·1	3·1	38·8	1·9	34·3	9·8	48·5	3·8	3·5	0·5	16·2	1·7	12·4	5·1	35·9	3·9
204	39·3	2·9	11·2	0·6	50·5	2·9	20·1	3·1	18·9	2·6	42·8	0·1	34·3	9·8	52·0	4·1	4·0	0·4	18·3	3·0	13·4	5·2	39·6	5·0
228	40·8	2·9	13·1	1·1	51·6	2·9	21·9	2·6	19·1	2·3	44·8	1·0	34·4	9·8	52·8	3·9	4·4	0·3	19·5	3·8	13·9	5·4	42·3	5·9
252	42·1	2·6	14·8	1·8	52·9	3·0	26·4	3·4	19·3	2·2	45·8	1·5	34·5	9·9	54·1	3·5	4·5	0·3	21·0	3·7	14·1	5·5	44·6	6·5
276	43·3	1·6	17·2	1·7	54·3	3·4	29·6	3·2	19·4	2·2	46·8	1·6	34·5	9·9	55·4	3·2	4·7	0·1	21·6	4·1	14·6	5·7	47·1	7·6

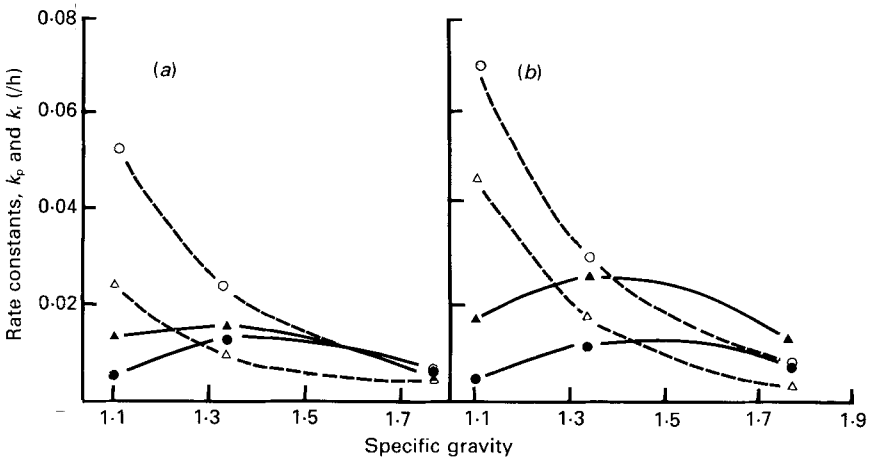

Fig. 2. Rates of rumination (k_r: 5 mm, ○; 2 mm, △) and passage from the rumen (k_p: 5 mm, ●; 2 mm, ▲) as affected by specific gravity and length of plastic particles (2 and 5 mm) in cattle (*a*) and buffaloes (*b*).

Table 3. *Correlation of rates of passage from the rumen* (k_p) *for plastic particles varying in specific gravity and length*

Specific gravity	Length (mm)...	Specific gravity: 1·10 — 2	1·10 — 5	1·34 — 2	1·34 — 5
1·34	2	0·754*	0·474*	—	—
	5	NS	0·875**	NS	—
1·77	2	NS	NS	0·813*	NS
	5	NS	NS	NS	0·833*

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

attributable to size reduction of the plastic marker. Correlations between k_p of particles differing in sp.gr. and size indicated that there was more consistency of movement of particles of the same size regardless of sp.gr. than of particles of the same sp.gr. regardless of size (Table 3).

Post-ruminal FPR for NR (k_2) and R (k_5) particles were similar ($P > 0·9$), averaging 0·044 (SEM 0·005) and 0·048 (SEM 0·008) (n 10) across species and lengths at a sp.gr. of 1·34. For other sp.gr., direct comparison was precluded by variation in k_2 and k_5, which resulted from poor definition of the early segment of faecal appearance curves due to relatively infrequent sampling.

DISCUSSION

Use of compartmental models to describe the flow of substances through the digestive tract of animals has been reviewed recently (France *et al.* 1985). It was concluded that the double-exponential model proposed by Dhanoa *et al.* (1985) appeared to have a wide range of practical applications. In its partly linearized form, obtained by logarithmic

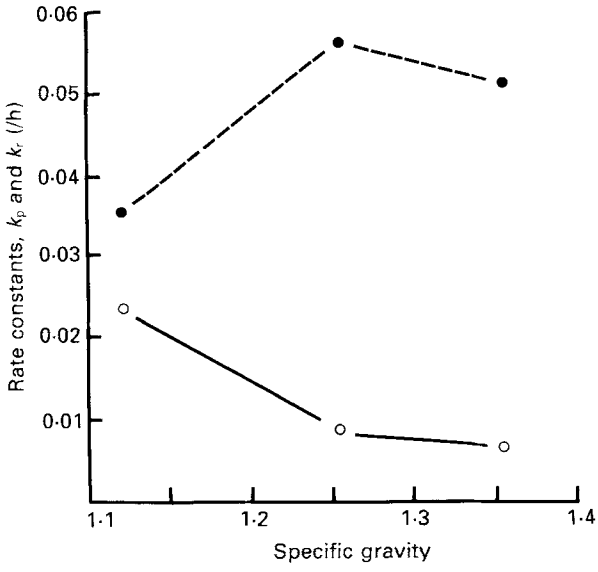

Fig. 3. Rates of rumination (k_r, ○) and passage from the rumen (k_p, ●) across particle length as affected by specific gravity of plastic particles for the data of Durkwa (1983).

transformation, this model was found by these authors to be particularly effective in describing digesta flow along the gastrointestinal tract of ruminants. However in view of (i) the simplified kinetics of plastic particle movement compared with rumen digesta which undergoes time-dependent changes in sp.gr. and size and (ii) differences in estimates of k_2 (attributable to marker excretion from the post-ruminal pool) derived from use of alternative models (Dhanoa *et al.* 1985; Beauchemin & Buchanan-Smith, 1987) we have described passage and rumination of plastic particles by reference to a simple three-compartment model with a discrete lag between the last two pools (Blaxter *et al.* 1956; Grovum & Williams, 1973).

The patterns of k_p and k_r with sp.gr. showed that maximum rates of rumination occurred at a lower sp.gr. than did maximum passage from the reticulo-rumen. Similar patterns were evident when the data of Durkwa (1983) and desBordes & Welch (1984) were reanalysed using the model shown in Fig. 1 (Figs 3 and 4). In addition, particle length affected k_p and k_r in cows (results of Durkwa, 1983; Fig. 5) with the major effects evident for particles 5 mm or greater in length. These findings are consistent with concepts of the importance of size and sp.gr. in contributing to the sorting of particles in the reticulo-rumen into dense small particles which tend to flow to the omasum and lighter, longer particles which tend to be aspirated into the mouth during rumination (Wyburn, 1980).

There was an apparent association of the greater force of reticular contractions of swamp buffaloes (McSweeney & Kennedy, 1987) with increased k_p of the 2 mm relative to 5 mm plastic particles. At the same time, retention of large plastic particles in the buffalo rumen was reduced by more prolonged rumination and higher k_r. In addition, in both cattle and buffaloes, data for NR (k_p) and R (k_4), 2 mm plastic particles indicated that the passage from the reticulo-rumen of heavy ($> 1{\cdot}4$ sp.gr.) particles was enhanced by rumination activity. This presumably resulted from dispersal of light particles away from the reticulo-omasal orifice after reswallowing of the chewed bolus, and would function in preferentially removing from the rumen digesta particles which had undergone extended digestion. For

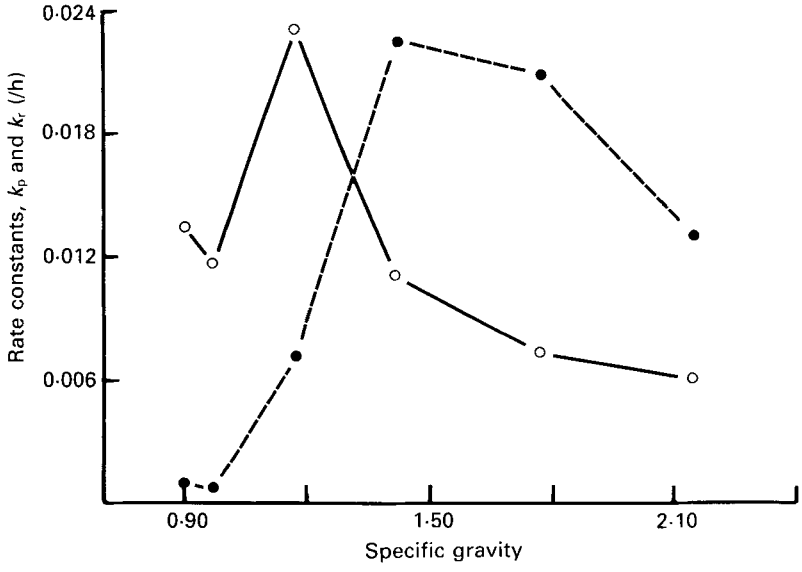

Fig. 4. Rates of rumination (k_r, ○) and passage from the rumen (k_p, ●) as affected by specific gravity of plastic particles for the data of desBordes & Welch (1984).

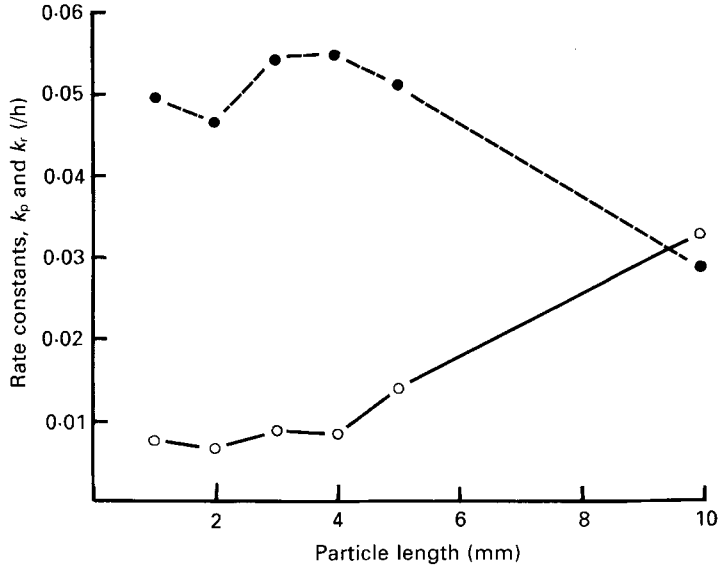

Fig. 5. Rates of rumination (k_r, ○) and passage from the rumen (k_p, ●) across specific gravity as affected by length of plastic particles for the data of Durkwa (1983).

swamp buffaloes given the rice straw-based diet used in the present experiment, the reduced time available for action of cellulolytic microbes depressed digestibility of cell wall constituents, but the consequent depression in digestible organic matter intake was compensated for by increased feed intake (Kennedy *et al.* 1987).

The effects of sp.gr. on the fate of particles in the reticulo-rumen is pertinent to the

accuracy with which markers adherent to particles requiring pretreatment with detergent to remove cell solubles may mimic the passage of digesta to the intestines. The poor correlations between FPR for Yb-labelled and Cr-mordanted fibre, and k_p of plastic particles indicates that such markers yield FPR estimates which may be of limited value. Others (Mader *et al.* 1984; Coleman *et al.* 1984; Smith *et al.* 1987; Cochran *et al.* 1987) have also reported that material labelled with Yb passed from the rumen quicker than that labelled with Cr; however, none have stated whether or not measurements within individual animals were correlated. Poncet & Al Abd (1984) explained differences between mean retention times in sheep of Cr-mordanted fibre and Yb marker as the result of altered digestion of the former, and adherence of the latter to the small particle fraction of rumen digesta. Moreover, Smith *et al.* (1987) found that fluid dilution in vitro influenced fractional passage rates of Cr and Yb markers. The fact that Yb- and Cr-labelled materials had such high sp.gr. in our experiment may have influenced their propensity to be comminuted during rumination and their FPR from the rumen. In addition, the effect of rumination in acceleration of passage of chewed relative to non-ruminated material of sp.gr. $> 1{\cdot}4$ may differentially affect dietary residues labelled with Yb or Cr. The bulk density of Cr-mordanted material has been shown to affect its FPR (Ehle *et al.* 1984). Although relative treatment comparisons may still be valid, the above results do not engender confidence in the accuracy with which these markers estimate FPR.

The agreement in FPR (k_2 and k_5, respectively) in the post-ruminal tract of NR and R particles is consistent with the conclusion of Siciliano-Jones & Murphy (1986) that length of inert particles, from 1 to 10 mm, did not affect post-ruminal passage in steers. Others (King & Moore, 1957; Campling & Freer, 1962; Siciliano-Jones & Murphy, 1986) have reported post-ruminal passage rate was maximized with particles having a sp.gr. of approximately 1·2; however, Campling & Freer (1962) found that the fractional passage rate of inert particles in the lower gut was inversely related to sp.gr. and slower than that from the reticulo-rumen within the range 1·12 to 1·40. Over this range the common assumption that the slowest FPR applies to the reticulo-rumen may be incorrect. To identify compartments correctly, Faichney & Boston (1983) suggested that liquid and particulate phase markers be used simultaneously (when unable to sample directly from the rumen) because these phases do not behave independently in the lower gut of ruminants. Although the closeness of k_1 (equal to $k_r + k_p$) and k_2 at a sp.gr. of 1·34 made these parameters computationally difficult to estimate in our study (see Atkins, 1969), it also made compartment identification less critical. Had the fractional passage rates differed substantially, it would have been difficult to assign them to a particular compartment without additional information.

Use of plastic particles of defined sp.gr. and length, although laborious, has yielded information concerning effectiveness of rumination and passage which is not available using other markers, and combined with estimates of digesta particle size, rumen fill and intake, offers the possibility of examining the differences between animals and species in their ability to utilize roughage diets. For the two large ruminant species used in this study, use of the plastic markers allowed us to conclude that faster passage of digesta through the reticulo-rumen of the swamp buffalo was attributable to more prolonged (and perhaps more efficient) rumination in conjunction with more effective propulsion of small digesta particles to the intestines.

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