Original article

Kinetics of particulate and solute marker passage in sheep supplemented with cationomycin and lasalocid antibiotics. Comparisons among methods for calculating mean retention time

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Summary — Passage of particulate and solute markers in the digestive tract was studied in sheep fed a roughage-pelleted diet supplemented or not with ionophore antibiotics. Methods of marker administration (continuous infusion *vs* pulse-dose) and mathematical treatment of data were investigated. Antibiotic supplementation did not affect markers' mean retention time *(MRT)* significantly, regardless of sampling site, technique of marker administration or *MRT* calculation methods used. The pulse dose technique led to 20–30% higher estimate of particle markers *MRT* in the entire gut and stomachs of sheep than did the continuous infusion method. Similar results were obtained between these methods for solute markers *MRT* at both sampling sites. Total *MRT* in the digestive tract could be partitioned among compartments using a deterministic model when applied to pulse–dose kinetics. Such a partitioning appeared unsatisfactory with continuous-infusion data. Estimations of particle or solute markers *MRT* in the rumen from duodenal and faecal marker kinetics were significantly different and rarely correlated.

antibiotic / marker / model / transit / sheep

Résumé — Cinétique du transit des marqueurs des particules et des liquides chez le mouton supplémenté en antibiotiques catiomycine et lasalocide. Comparaison entre les méthodes de calcul du temps moyen de rétention. *Le transit des marqueurs des particules et des liquides dans le tube digestif a été étudié chez des moutons recevant une ration de fourrage compacté supplémentée ou non par des antibiotiques ionophores. Des méthodes d'administration des marqueurs (arrêt d'infusion continue* vs *dose unique) et de calcul du temps de séjour moyen (TSM) ont été comparées. La supplémentation en antibiotiques n'a pas significativement affecté le transit, quels que soient le marqueur, la méthode d'administration des marqueurs ou de calcul du TSM considérés. La*

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technique de dose unique a surestimé le TSM *des marqueurs de particules de 20–30% par rapport à* l'arrêt d'infusion. Des résultats voisins entre ces techniques ont été obtenus pour les marqueurs des liquides. Le TSM *total a pu être réparti en* TSM *compartimentaux par un modèle déterministe, dans le* cas de le dose unique. Cette répartition est apparue peu satisfaisante pour l'arrêt d'infusion. Les esti-mations duodénale et fécale du TSM *dans le rumen ont été significativement différentes et rarement* corrélées.

antibiotique / marqueur / modèle / mouton / transit

INTRODUCTION

The time feeds are retained in the diges-tive tract and particularly in the stomachs is an important factor of their digestion by ruminants (Evans, 1981a,b; Warner, 1981; Faichney, 1986). Feed efficiency can be improved through ration supplementation using ionophore antibiotics, an effect which may be explained mainly by a shift in digestion from rumen to intestines with or without apparent effects on digestibility of nutrients in the whole tract (Ricke *et al,* 1984; Darden *et al,* 1985; Spears, 1990). However, the mean retention time *(MRT)* of particles and liquid in various parts of the gut does not always reflect such changes. For instance, monensin has been reported to increase solute and par-ticulate markers *MRT* in the rumen (Leme-nager *et al,* 1978; Allen and Harrison, 1979; Adams *et al,* 1981; Leng *et al,* 1984; Van Haecke *et al,* 1985; Ward *et al,* 1990a, b). However, nil or opposite effects have also been observed (Van Nevel and Demeyer, 1979; Delaney and Ellis, 1983; Arndt and Richardson, 1985; Faulkner *et al,* 1985), suggesting that antibiotic action may be more complex depending on the particular dietary situation.

The present results deal with the effect on *MRT* of less commonly employed iono-phore antibiotics, cationomycin and lasa-locid, which were used as feed additives in a study of digestion in sheep (Bogaërt *et al,* 1991; Gomez *et al,* 1991). Taking ad-vantage of this experiment, particulate and solute markers *MRT* measurements were also carried out simultaneously by: 1) ter-minating a continuous rumen infusion of markers; and 2) administering a pulse dose of markers into the rumen, and then in both situations following changes with time in the amount of marker excreted and/or marker concentration in duodenal diges-ta and faeces according to Faichney (1975). Some aspects of mathematical treatment of marker concentration patterns were also considered using algebraic and modelling techniques. Comparisons be-tween deterministic and stochastic models were not investigated in the present study, for the former have generally proved satis-factory (Quiroz *et al,* 1988), although small but systematic deviations from reference values have been reported (Faichney and Boston, 1983). A comprehensive compari-son of models has also been published re-cently (Lallès *et al,* 1991).

MATERIAL AND METHODS

Animals, diets and experimental design

The animals, diets and experimental design were those used in a concurrent study of the ef-fet of 2 ionophore antibiotics, cationomycin and lasalocid, on ruminal digestion (Bogaërt *et al,* 1991; Gomez *et al,* 1991). Briefly, 6 adult Texel sheep (average body weight 67 kg) were fitted with rumen and duodenal simple cannulae. A

pelleted, roughage-based diet (intake: 1 060 g DM/d) supplemented (33 ppm) or not with antibiotics was fed in 8 equal meals/d to the sheep, as presented elsewhere (Bogaërt *et al*, 1991). While sheep were kept in metabolism cages, particulate and solute digesta markers, ytterbium (Yb) chloride and chromium (Cr)-EDTA respectively, were continuously and separately infused in the rumen at rates of 130 mg Yb and 140 mg Cr/d. Each experimental period was organized as follows: 21 d adaptation to diets with the last 5 d for adaptation to cages and infusion, 6 d digestibility and 2 d digesta flow trial. After sheep under continuous marker infusion had rested from digesta collection for 3 d, samples for MRT measurements were taken over 6 d.

Marker administration, duodenal digesta and faeces sampling

At the beginning of *MRT* measurements, flow marker (Yb and Cr-EDTA) infusion in the rumen was stopped (zero time) and the decline in marker concentration was followed in duodenal digesta and in faeces as described by Faichney (1975). At zero time, sheep were also dosed with a second set of markers, europium (Eu) and polyethylene glycol (PEG). The former, obtained as the chloride, had previously been attached to cell wall constituents of a fraction of the experimental feed according to a competitive binding procedure (Ellis and Beever, 1984). Sodium citrate was used as the ligand and immersion took place at pH 2.0. Twenty-nine percent of the labelled particles were retained on a 1-mm screen by wet sieving, the remainder being entirely recovered on the 0.8–0.16 mm sieves. The resulting mean particle size calculated as the screen size of the sieve on which half of particles in weight would be collected was 0.9 mm. A dose of 30 g DM oven-dried labelled feed (5 mg Eu/g DM) was offered to the sheep at the beginning of a meal. At the same time, 10 g PEG in 50 ml of water was given into the rumen through the cannula.

Duodenal digesta were collected manually every 2 h for the first 12 h, every 5 h from 13 to 42 h and then at 7 h intervals from 43 to 84 h post-dosing. Faeces were collected automatically every 3 h between 6 and 36 h, every 6 h from 37 to 72 h and then at 12 h intervals from 73 to 144 h post-dosing. Subsamples were prepared

after homogenization of duodenal digesta and faeces, and frozen (–20 °C) until analysed.

Marker analysis

The markers Yb, Cr and Eu were assayed after freeze-dried digesta samples had been ashed at 550 °C for 5 h. Markers were extracted from ash in a hot sulfuric/phosphoric acid solution as described for Cr by Siddons *et al* (1985) and then modified for simultaneous extraction of Cr and Yb by Lallès and Poncet (1990a). They were assayed using atomic absorption spectrophotometry (Perkin–Elmer 2380) in a nitrous oxide/acetylene flame for Yb (wavelength (τ) = 398.8 nm) and Eu (τ = 459.4 nm), and in an air/acetylene flame for Cr (τ = 357.9 nm), following manufacturer's recommendations. Blank samples of digesta and faeces were used to prepare respective standards in a similar way.

PEG was assayed in the liquid phase of undiluted digesta and aqueous extract (5/1 v/v) of thawed faeces by turbidimetry according to Hydén (1955) as modified by Malawer and Powell (1967).

MRT *estimation and statistical analysis*

The *MRT* of particulate (Eu) and solute (PEG) markers given as a single dose were calculated using numerical (algebraic) integration (eq [8] of Faichney, 1975) applied to faecal data (table I). However, this method of reference could not be applied to duodenal marker patterns as total digesta flow cannot be measured directly using simple cannulae (Faichney, 1975). The "method of the moments" considered to be an approximation of markers *MRT* (Thielemans *et al*, 1978; table I) was applied to faecal and duodenal data. At the latter sampling site, this equation was preferred to that (eq [9]) proposed by Faichney (1975) since digesta sampling took place at irregular (increasing) time intervals. In oder to provide a more thorough comparison of *MRT* calculation methods, faecal and duodenal marker patterns were then fitted to the most commonly used deterministic model of Grovum and Williams (1973). Following administration of a pulse dose of marker, changes in concentration over time at a given sampling site are related to initial marker concen-

Table I. Techniques of marker administration, markers, digesta sampling sites, models and equations used to determine the mean retention time (MRT) of particulate and solute markers in sheep.

Administration of marker	Marker	Sampling site	Model	Equation[1]	Ref
Pulse dose (PD)	Eu + PEG	Faeces (total collection)	Fa1	$MRT = \sum_{i=1}^{n} t_i \cdot M_i$	Faichney (1975) (eq [8])
		Faeces + duodenum (concentration)	Th	$MRT = \dfrac{\sum\limits_{i=1}^{n} c_i \cdot \delta t_i \cdot t_i}{\sum\limits_{i=1}^{n} c_i \cdot \delta t_i}$	Thielemans et al (1978)
		Faeces + duodenum (concentration)	Gw1	$Y = A\,(e^{-k_1(t-TT)} - e^{-k_2(t-TT)})$ $t < TT;\ (Y = 0 \text{ for } t < TT)$ $MRT = 1/k_1 + 1/k_2 + TT$	Grovum and Williams (1973)
Post-infusion (PI)	Yb + Cr-EDTA	Faeces + duodenum (concentration)	Fa2	$MRT = t_1 + \sum_{i=1}^{n} A_i \cdot (t_{i+1} - t_i)$	Faichney (1975) (eq [6])
		Faeces + duodenum (concentration)	Gw2	$Y = A\,(k_2 . e^{-k_1(t-TT)} - k_1 . e^{-k_2(t-TT)})$ $MRT = 1/k_1 + 1/k_2 + TT$	Derived from Grovum and Williams (1973) (eq of desaturation)

[1] For details, see text.

tration in the first pool assuming instantaneous mixing, turnover rates (k_1 and k_2) in mixing compartments and a time delay *(TT)* before marker appearance at the duodenum or in faeces.

Similarly, the *MRT* of particulate (Yb) and solute (Cr-EDTA) markers administered by continuous rumen infusion was first calculated using numerical integration (eq [6] of Faichney, 1975; table I) applied to faecal and duodenal marker concentration patterns. The *MRT* of markers was also calculated at both sites using an equation (table I; last eq) derived from that of Grovum and Williams (1973) to describe the "desaturation" curve of a marker administered in a 2-mixing compartment plus time delay system. In other words, it would represent the amount of marker remaining in the system at time *t*.

Respective models were fitted to individual sets of marker concentration data at duodenal and faecal sites using a computer programme for non-linear regression analysis (Snedecor and Cochran, 1971) based on a Marquardt least-square iteration procedure. Fits were considered to be satisfactory when 2–3 successive sets of different initial parameters led to very close parameter estimates. Final results retained were those which provided lowest overall residual standard errors and lowest standard deviations on each estimated parameter (coefficient of variation below 5–10%). Data were treated by analysis of variance according to the statistical model of 2 Latin inverse squares (Gill, 1978) as described by Bogaërt *et al* (1991). As antibiotics were shown to have no significant (*P* ≥ 0.05) effect on digesta markers *MRT* (see *Results*), data were pooled across treatments and comparisons between marker administration techniques and among *MRT* calculation methods were carried out using Student paired *t*-test and linear regression analysis (Snedecor and Cochran, 1971).

RESULTS

For reasons of clarity, results dealing with: 1) antibiotic effects on marker retention, and 2) comparisons among marker and MRT methods have been presented separately.

Ionophore antibiotics and transit of particulate and solute digesta markers

Results are presented in table II. Addition of cationomycin or lasalocid to the basal diet had no significant effect (*P* ≥ 0.05) on particulate and solute digesta markers *MRT* in the entire gut and stomachs of sheep regardless of marker administration procedure and *MRT* calculation methods used. Considering the algebraic methods, *MRT* of particle and solute markers in the whole tract was 55 and 39 h respectively. Approximately half of this time was spent in the stomachs (27 and 17 h respectively) leading to fairly close absolute *MRT* values (28 *vs* 22 h) in the post-stomach sections of the gut. Differences between marker administration techniques and among *MRT* calculation methods were nevertheless apparent from results in table II. They are detailed in the following section.

Marker administration techniques and MRT calculation methods

Quality of data fitting using models

Both models led to a better fit of faecal than duodenal marker kinetics (table III). This may be attributed mainly to the generally accepted observation that when sampling duodenal digesta, the delay of marker appearance or concentration decrease is rather short, the number of data points is limited in the first part of curves whatever their shape, and changes in marker concentration are rather large shortly after zero time. This latter problem may be related to marker heterogeneity within the rumen soon after dosing and/or sampling bias through the duodenal cannula. Considering the method of marker administration/modelling,

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Table II. Influence of antibiotic supplementation on *MRT* of particulate and solute markers in the whole digestive tract, the stomachs and subcompartments in sheep.

Sampling site	Administration /marker [2]	Model [3]	Transit parameter [4]	Treatment [1]			SEM	Effect [5]
				C	L	Ca		
Faeces	PD/Eu	Gw1	MRTC1	25.9	27.2	25.5	1.9	NS
			TT	19.0	19.0	18.0	2.6	NS
			MRTC2	13.3	15.4	15.4	2.0	NS
			MRTWT	58.1	61.6	58.9	1.9	NS
		Fa1	MRTWT	53.8	56.4	53.8	1.9	NS
		Th	MRTWT	54.0	56.6	53.8	1.8	NS
	PI/Yb	Gw2	MRTC1	25.5	24.6	23.3	2.2	NS
			TT	20.9	22.0	21.2	2.8	NS
			MRTC2	0.1	0.1	0.1	0.1	NS
			MRTWT	46.5	46.7	44.5	3.6	NS
		Fa2	MRTWT	45.9	45.5	43.5	3.6	NS
	PD/PEG	Gw1	MRTC1	15.9	17.0	16.9	2.2	NS
			TT	16.6	17.4	17.2	1.1	NS
			MRTC2	8.9	8.2	9.1	1.1	NS
			MRTWT	41.3	42.5	41.3	2.5	NS
		Fa1	MRTWT	38.9	40.1	37.8	2.0	NS
		Th	MRTWT	39.1	40.2	37.6	2.0	NS
	PI/Cr-EDTA	Gw2	MRTC1	21.9	23.6	22.9	2.6	NS
			TT	18.5	18.6	16.4	1.3	NS
			MRTC2	0.8	0.4	0.1	0.0	NS
			MRTWT	41.8	42.4	39.4	3.4	NS
		Fa2	MRTWT	40.6	39.6	38.4	3.4	NS
Duodenum	PD/Eu	Gw1	MRTC1	22.1	23.1	21.7	2.1	NS
			TT	1.8	2.4	2.4	1.0	NS
			MRTC2	4.9	6.2	6.1	2.4	NS
			MRTST	30.0	32.6	33.4	3.4	NS
		Th	MRTST	26.1	27.5	27.7	1.7	NS
	PI/Yb	Gw2	MRTC1	21.5	20.4	20.0	1.4	NS
			TT	1.4	1.2	1.4	1.2	NS
			MRTC2	0.6	0.1	0.4	0.4	NS
			MRTST	23.4	21.7	21.8	1.3	NS
		Fa2	MRTST	25.1	23.4	22.1	1.3	NS
	PD/PEG	Gw1	MRTC1	9.8	9.1	7.7	2.4	NS
			TT	0.2	0.3	0.2	0.4	NS
			MRTC2	4.9	6.2	6.1	2.4	NS
			MRTST	14.5	16.3	12.8	2.6	NS
		Th	MRTST	16.4	18.3	16.2	1.3	NS
	PI/Cr-EDTA	Gw2	MRTC1	14.6	14.7	12.2	2.6	NS
			TT	2.3	1.4	1.4	0.9	NS
			MRTC2	0.0	0.2	0.3	0.1	NS
			MRTST	15.4	16.2	14.2	2.2	NS
		Fa2	MRTST	15.9	18.3	17.9	3.1	NS

[1] C, control; L, lasalocid; Ca, cationomycin; [2, 3, 4] for details, see text and table I; [5] NS, not significant ($P \geq 0.05$).

Table III. Quality of curve fitting using models applied to faecal and duodenal marker concentration kinetics.

Administration / marker [2]	Model [3]	Proportion of variance (SD) [1]	
		Faeces	Duodenum
PD/Eu	Gw1	97.8 (2.73)	94.0 (4.53)
PI/Yb	Gw2	98.9 (0.66)	98.0 (1.06)
PD/PEG	Gw1	96.2 (2.47)	89.5 (8.59)PI/Cr-EDTA
	Gw2	96.5 (2.86)	94.6 (10.7)

[1] Proportion of variance accounted for by models (% total variance SD : standard deviation); [2, 3] for details, see text.

equation Gw2 tended to provide better fits than equation Gw1, as judged by respective proportions of variance accounted for by models (table III). However, these differences were not significant ($P \geq 0.05$). The visual analysis of the distribution of residuals did not reveal any significant bias in data fits.

MRT in the whole tract (MRTWT) and stomachs (MRTST)

A comparison of the various methods is presented in table IV. MRTWT was estimated for the particulate marker Eu (55 h) given by pulse dose in a similar way ($P \geq 0.05$) using both algebraic methods which were highly correlated ($r > 0.98$; slope 0.98; intercept < 1 h). The model Gw1 overestimated these values by 11% ($MRT = 60$ h). In post-infusion situations, MRTWT calculated using Fa2 and Gw2 models was 15% lower than that obtained for Eu given as a single dose of labelled feed (45–46 vs 55–60 h). Differences between calculation methods were much lower for the solute markers and generally not significant ($P \geq 0.05$), except for Gw1 and Gw2 ($P < 0.05$). They overestimated MRT

by 4–7% when compared with the respective reference methods of Faichney (1975).

At the duodenal level, modelling methods provided respectively higher (Gw1; 32.5 h) and lower (Gw2; 22.3 h) estimates of particulate markers MRT than the corresponding algebraic methods (Th 27.1 h; Fa2 23.5 h). Correlations between calculation methods were high within- and low between marker administration techniques. An important bias ($P < 0.01$) was observed between Th and Gw1 methods, the latter underestimating MRT at low values and overestimating it at high values. Similar conclusions can be drawn from table IV for solute markers MRT, although, in both cases of marker administration, modelling methods led to lower ($P < 0.05$) MRT estimates than those obtained by algebraic calculations; a significant bias ($P < 0.01$) was observed between Fa2 and Gw2.

Partition of total tract and stomachs MRT into partial MRTs

The 2-mixing-compartment-one-delay model of Grovum and Williams (1973) as fitted to pulse dose (Gw1) and post-infusion (Gw2) marker kinetics, was applied to all data sets and parameters related to MRT

Table IV. Influence of calculation method on *MRT* estimates of particulate and solute markers in the whole digestive tract of sheep.

Sampling site	Administration /marker [2]	Model [3]	Mean [4] SD	Regression parameters [1]					
				X	Y	Slope	Intercept	Syx	r
Faeces	PD/Eu	Fa1	54.7 (7.49) [a]	Fa1	Th	0.98	0.97	1.03	0.991
		Th	54.8 (7.44) [a]	Fa1	Gw1	1.11	-1.08	1.32	0.988
		Gw1	59.5 (8.40) [b]	Fa1	Fa2	1.04	-11.9	3.91	0.899
				Fa1	Gw2	1.07	-12.7	3.70	0.913
	Pl/Yb	Fa2	45.0 (8.66) [c]	Th	Gw1	1.12*	-2.00	0.90	0.995
		Gw2	45.9 (8.80) [d]	Th	Fa2	1.03	-11.5	4.14	0.886
				Th	Gw2	1.06	-12.1	4.04	0.895
				Gw1	Fa2	0.91	-9.49	4.12	0.887
				Gw1	Gw2	0.94	-9.77	4.09	0.893
				Fa2	Gw2	1.01	0.59	1.16	0.992
	PD/PEG	Fa1	38.9 (5.55) [a]	Fa1	Th	0.99	0.62	1.01	0.984
		Th	39.0 (5.55) [a]	Fa1	Gw1	1.02	1.87	1.52	0.968
		Gw1	41.7 (5.87) [b]	Fa1	Fa2	1.09	-2.99	3.97	0.844
				Fa1	Gw2	1.05	0.20	3.37	0.872
	Pl/Cr-EDTA	Fa2	39.5 (7.18) [a]	Th	Gw1	1.01	2.43	1.81	0.954
		Gw2	41.0 (6.66) [b]	Th	Fa2	1.07	-2.07	4.18	0.825
				Th	Gw2	1.01	1.54	3.70	0.843
				Gw1	Fa2	1.11	-6.64	3.16	0.904
				Gw1	Gw2	1.02	1.35	3.09	0.893
				Fa2	Gw2	0.87	6.60	2.40	0.937
Duodenum	PD/Ei	Th	27.1 (2.57) [a]	Th	Gw1	1.99**	-21.5*	3.42	0.839
		Gw1	32.5 (6.11) [b]	Th	Fa2				0.456
				Th	Gw2				0.436
	Pl/Yb	Fa2	23.5 (5.09) [c]	Gw1	Fa2	0.42	9.89	4.54	0.503
		Gw2	22.3 (5.11) [d]	Gw1	Gw2	0.42	8.69	4.56	0.500
				Fa2	Gw2	0.98	-0.79	1.11	0.978
	PD/PEG	TH	17.0 (2.85) [ac]	Th	Gw1	1.27	-7.10	2.43	0.839
		Gw1	14.5 (4.33) [b]	Th	Fa2				0.392
				Th	Gw2	0.68	3.67	3.65	0.481
	Pl/Cr-EDTA	Fa2	17.4 (4.94) [a]	Gw1	Fa2				0.401
		Gw2	15.2 (4.04) [bc]	Gw1	Gw2	0.46	8.62	3.64	0.488
				Fa2	Gw2	0.73**	2.53	1.87	0.894

[1] Slope and intercept different from 1 and 0 respectively (* $P < 0.05$; ** $P < 0.01$) Syx : residual SD; r correlation coefficient; [2], [3] for details see text; 4 for a given sampling site and type of marker (particulate or solute), means with different superscripts (a, b, c) are different ($P < 0.05$).

Table V. Influence of modelling method on partial MRTs of particulate and solute markers estimated from faecal and duodenal marker kinetics.

Sampling site	Administration / marker[2]	Model[3]	Partial MRT[4]	Mean (SD)[5]	Regression parameters[1]					
					X	Y	Slope	Intercept	Syx	r
Faeces	PD/Eu	Gw1	C1	26.2 (4.23)	Gw1	Gw2	0.73	5.25	4.07	0.617
	Pl/Yb	Gw2	C1	24.5 (5.02)						
			TT	18.6 (4.12)a	Gw1	Gw2	0.81	6.19	3.91	0.659
			TT	21.2 (5.04)b						
			C2	14.7 (2.77)a	Gw1	Gw2				-0.178
			C2	0.1 (0.08)b						
	PD/PEG	Gw1	C1	16.6 (2.88)a	Gw1	Gw2	1.22	2.62	3.46	0.464
	Pl/Cr-EDTA	Gw2	C1	22.8 (4.85)b						
			TT	16.4 (3.35)a	Gw1	Gw2	0.52**	9.27**	1.82	0.704
			TT	17.8 (2.49)b						
			C2	8.7 (1.83)a	Gw1	Gw2				0.299
			C2	0.35 (0.42)b						
Duodenum	PD/Eu	Gw1	C1	22.5 (5.45)	Gw1	Gw2	0.46*	10.2	4.24	0.524
	Pl/Yb	Gw2	C1	20.6 (4.83)						
			TT	2.23 (1.34)	Gw1	Gw2				0.000
			TT	1.33 (1.41)						
			C2	8.01 (1.73)a	Gw1	Gw2				0.000
			C2	0.35 (0.39)b						
	PD/PEG	Gw1	C1	8.86 (3.24)a	Gw1	Gw2				0.000
	Pl/Cr-EDTA	Gw2	C1	13.3 (3.70)b						
			TT	0.3 (0.48)a	Gw1	Gw2				0.000
			TT	1.7 (1.89)b						
			C2	5.73 (3.36)a	Gw1	Gw2	0.09	-0.18	0.30	0.741
			C2	0.36 (0.43)b						

[1] Slope and intercept different from 1 and 0 respectively (* $P < 0.05$; ** $P < 0.01$). Syx residual SD; r correlation coefficient; [2,3,4] for details, see text; [5] within each partial MRT, means with different superscripts (a, b) are different ($P < 0.05$).

of markers in the compartments compared (table V). The most striking feature was that the latter model applied to kinetics obtained after cessation of marker infusion generated very low MRT attributed to compartment C2, regardless of sampling site and marker. For example, estimated retention of particulate markers from faecal data in the compartment C2 was 14.7 (Gw1) and 0.1 h (Gw2), probably representing problems of fit (see *Discussion*). The consequence was an increased TT and/or MRT in C1. At the faecal level, correlations between Gw1 and Gw2 models for TT and C1 MRT were moderate, suggesting that main parts of marker concentration curves partly described similar (integrated) phenomena. At the duodenum, differences between models were also apparent but values were generally not correlated ($P \geq 0.05$).

Influence of sampling site on estimation of *MRT* in mixing compartments

This set of comparisons was intended as MRT of digesta markers in the rumen (supposed to be represented by C1) may

be estimated from faecal curve modelling. Results in table VI show that MRT in the rumen was generally overestimated by 20–40% when faecal data were used. Furthermore, correlations were low and most often not significant ($P \geq 0.05$). Gw2 model was not considered here because of abnormally low C2 estimates.

Identification of mixing compartments from faecal data analysis

As suggested by Faichney and Boston (1983), if post-stomachal transit is similar for particulate and solute markers, their respective retention in the second mixing-compartment C2 should be the same. Data from table VII show they were different when considering the model Gw1. Values were moderately correlated ($r = 0.58$; slope 0.38 different from unity ($P < 0.01$)). This was observed even though particle and solute markers had effectively the same ($P \geq 0.05$) post-stomachal retention time (table VIII). This MRT was calculated directly by subtracting stomachs MRT from whole tract MRT. Differences between means, although slight, were most

Table VI. Influence of sampling site on particulate and solute markers *MRT* in the rumen estimated from faecal and duodenal marker kinetics.

Partial MRT [3]	Administration /marker [4]	Model [5]	Mean (SD) [1]		Regression parameters [2]					
			Faeces (F)	Duodenum (D)	X	Y	Slope	Intercept	Syx	r
C1	*PD*/Eu	Gw1	26.2 (4.23)[a]	22.5 (5.45)[b]	F	D				0.204
	PI/Yb	Gw2	24.5 (5.02)[a]	20.6 (4.83)[b]	F	D	0.597	6.0	3.9	0.622
C1	*PD*/PEG	Gw1	16.6 (2.88)[a]	8.9 (3.24)[b]	F	D				0.416
	PI/Cr-EDTA	Gw2	22.8 (4.85)[a]	13.3 (3.70)[b]	F	D				0.370

[1] Means in the same line with different superscripts (a, b) are different ($P < 0.05$); [2] Syx residual SD; *r* correlation coefficien ; [3, 4, 5] for details, see text.

Table VII. Comparisons between partial *MRT* of particulate (P) and solute (S) markers in mixing compartments (C1 and C2) obtained by modelling faecal marker kinetics.

Partial MRT [2]	Administration /marker [3]	Model [4]	Mean (SD) [5]	Regression parameters [1]					
				X	Y	Slope	Intercept	Syx	r
C1	PD/Eu	Gw1	26.2 (4.23) [a]	P	S	0.32	8.2	2.6	0.474
	PD/PEG	Gw1	16.6 (2.88) [b]						
C2	PD/Eu	Gw1	14.7 (2.77) [a]	P	S	0.37	3.1	1.58	0.580
	PD/PEG	Gw1	8.72 (1.83) [b]						

[1] Syx residual SD; r correlation coefficient; [2, 3, 4] for details, see text; [5] within the same partial *MRT*, means with different superscripts (a, b) are different (*P* < 0.05).

Table VIII. MRT of particulate (P) and solute (S) markers in the post-stomachal section of the digestive tract of sheep obtained by numerical integration and modelling faecal marker kinetics.

Administration /marker [2]	Model [3]	Mean (SD) [4]	Regression parameters [1]					
			X	Y	Slope	Intercept	Syx	r
PD/Eu	Th	27.7 (6.38) [a]	P	S	0.51 **	7.98 **	2.11	0.845
PD/PEG	Th	22.0 (3.83) [b]						
PD/Eu	Gw1	27.0 (7.77)	P	S	0.37 **	17.1 **	3.41	0.660
PD/PEG	Gw1	27.2 (4.40)						
PI/Yb	Fa2	22.1 (6.89) [a]	P	S	0.77	5.67	5.51	0.632
PI/Cr-EDTA	Fa2	21.5 (5.67) [b]						
PI/Yb	Gw2	23.6 (6.09) [a]	P	S	0.79	7.14	4.27	0.757
PI/Cr-EDTA	Gw2	25.7 (6.33) [b]						

[1] Slope and intercept different from 1 and 0 respectively (** *P* < 0.01); Syx residual SD; c correlation coefficient; [2, 3] for details, see text; [4] within the same model, r means with different superscripts (a, b) are different (*P* < 0.05).

often significant (*P* < 0.05). Correlations between particle and solute markers *MRT* in post-stomachal sections of the gut were significant (*P* < 0.01) within a given model but relationships were often highly biased (*P* < 0.01).

DISCUSSION

The time spent by feeds and digesta in the tract of ruminants may affect both rumen degradation and intestinal digestion and absorption functions. This *MRT* is difficult

to measure accurately, especially for particulate matter. This digesta phase is heterogeneous in physical features and chemical composition, and neither of the markers used in the present study can be considered to represent it. As a result, marker choice and labelling techniques are certainly more critical in estimating *MRT* and dynamics of solid digesta (Coleman *et al*, 1984; Ellis and Beever, 1984; Faichney, 1986; Faichney *et al*, 1989) than data analysis *per se*. There are, however, numerous techniques of marker administration and *MRT* (total or partial) calculation methods which may in turn affect the reliability of such results, as pointed out by Warner (1981). Besides methodological considerations, then appears the problem of sensitivity of transit measurement to dietary manipulations.

Antibiotic supplementation and transit of particulate and solute digesta markers

The influence of ionophore antibiotics on digesta transit in the gut and more precisely in the rumen still remains controversial, since significant effects on digesta flow could or could not be linked to changes in the retention of digesta (Spears, 1990). This would suggest the mode of antibiotic action on ruminal metabolism to be more complex than expected from known interrelationships between digesta turnover rate and microbial activity. Indeed, we found that microbial protein synthesis was greatly depressed by adding lasalocid or cationomycin to the basal diet but effects on the apparent digestion of nitrogen and plant cell walls in the rumen were not significant (Bogaërt *et al*, 1991; Gomez *et al*, 1991). Nevertheless, in our experimental conditions, neither marker administration techniques nor *MRT* calculation/partitioning methods

were able to detect any significant change with antibiotic supplementation in particle and solute markers *MRT* (table II).

Marker administration and MRT calculation methods

As previously noted (Lallès *et al*, 1988, 1991), both algebraic methods compared (Faichney, 1975; Thielemans *et al*, 1978) similarly estimated the total *MRT* of particle and solute markers. The faecal excretion which is basically discrete may be assumed to be a continuous process, provided steady-state conditions are observed and sampling interval is not too large. However, these *MRT* estimates differ consistently from those obtained following the post-infusion technique in the case of particulate markers.

These expected differences are primarily the consequence of the preferential labelling of small particles including microbes, and to the fact that a significant amount of the marker remains in solution when lanthanides are infused in the rumen. Seventeen percent of the marker ([169]Yb infused as chloride) was recovered in the supernatant after samples of rumen contents from sheep fed fresh forage or concentrate diets had been centrifuged at 40 000 *g* (Al Abd, 1986). Also in that experiment, the radioactivity concentrated in the particulate fraction not retained on a 0.16 mm sieve and precipitated at 500 *g*. That fraction is known to contain small feed particles and associated bacteria, free-floating bacteria, bacterial clumps and protozoa. It is noteworthy that radioactivity distribution among the different physical fractions of rumen contents paralleled that of microbial markers, DAPA (Legay-Carmier and Bauchart, 1989) or [15]N (Yang, 1991). When particles are labelled prior to introduction into the rumen using a

competitive procedure (Ellis and Beever, 1984) to bind the marker selectively on sites of strong affinity, its uneven distribution according to particle size is greatly reduced or even disappears (C Poncet, unpublished results).

The presence of lanthanides in solution in rumen liquid may be related to their affinity for soluble molecules like VFA, organic acids and various forms of nitrogen compounds (Teeter et al, 1984). Reasons for which lanthanides concentrate on small particle fraction in the rumen are not really understood, even if this has been reported frequently (Erdman and Smith, 1985; Siddons et al, 1985; Al Abd, 1986). It may be a passive surface phenomenon probably amplified by the fact that bacteria and perhaps protozoa are strongly labelled by lanthanides (Poncet, 1976; Combs et al, 1984) because of their size and/or ability to metabolize these markers (Johnson and Kyker, 1966). The role of microbes in marker migration generally evoked when discussing results obtained with rare earths (Poncet, 1976; Faichney and Griffiths, 1978; Hartnell and Satter, 1979; Crooker et al, 1982; Mader et al, 1984) is probably of prime importance. Migration may be preferentially directed towards small feed particles if they are more colonized by microbes than larger ones. Lanthanides infused as chloride or any other highly ionised form may precipitate as hydroxide at the rumen pH (Siddons et al, 1985). This would in turn increase the amount of particulate marker flowing in association with the liquid and small particle phase of digesta.

All these phenomena would tend to underestimate the actual MRT of particulate markers (Faichney, 1986). This was effectively observed in the present work when considering the low marker MRT values obtained after infusion arrest.

Secondly, the marker administration techniques compared do not exactly represent the same sum of basic events. Markers were dosed as a bolus in one case, whereas in the second case they were evenly distributed throughout the rumen at zero time. This difference in marker mixing could also explain part of the differences observed between pulse-dose and infusion-arrest techniques. This remark is supported by the results of Dehareng and Godeau (1989) who found no significant differences between these techniques in estimating ruminal solute marker turnover, and by the fact that such differences here are much lower for solute than for particulate markers.

Thirdly, different markers were used in each administration technique which may account for a presumably marginal part of the observed differences in markers MRT. Based on theoretical aspects, lanthanides Eu and Yb were assumed to exhibit similar affinities for plant cell walls, although some differences between them could be related to adsorption side-effects in the presence of metabolite molecules in the rumen (Allen and Van Soest, 1984; Ellis and Beever, 1984; Teeter et al, 1984). Nevertheless, direct comparisons suggest behaviour in ruminant digesta to be similar among rare-earths, but to differ from that of Ru-phenanthroline and of Cr-mordanted fibre (Ellis et al, 1980; Dixon et al, 1983; Goetsch and Galyean, 1983; Weiss and Martz, 1983; Al Abd, 1986; Gonzalez et al, 1987; Satter et al, 1987; Pond et al, 1989).

Regarding solute markers MRT in the entire tract, results in table IV showed that both markers led to similar MRT estimates regardless of marker administration technique. PEG and Cr-EDTA proved to behave similarly when used in digesta flow experiments (Downes and McDonald, 1964; Binnerts et al, 1968; Peyraud, 1983;

Al Abd, 1986; Poncet and Al Abd, 1987). When used as transit markers, PEG and metal-EDTA (Cr, Co) generated similar estimates of liquid *MRT* (Teeter and Owens, 1983; Doreau *et al*, 1987), although large but not systematic behavioural differences have been reported (Poncet and Al Abd, 1984). It may therefore be reasonably deduced from our observations that mixing of solute markers in the rumen of our sheep was practically instantaneous.

At the duodenum level, a fairly similar pattern has been observed (table IV). This would indicate that *MRT* differences between marker administration techniques arise from phenomena essentially located in the stomachs (rumen). However, *MRT* differences in the post-stomachal section of the gut are apparent (table VIII) and more difficult to interpret.

Modelling and MRT partitioning among compartments of models

As already observed in sheep (Faichney and Boston, 1983) and ruminant calves (Lallès *et al*, 1991), modelling faecal marker kinetics generally overestimates *MRT* calculated by numerical integration and may consequently limit the use of such models.

Two mathematical expressions of the functioning of a similar 2-mixing-compartment-one-delay deterministic system in which markers had been given using either a pulse dose or a post-infusion technique were compared. Beyond strict comparisons and differences, a sigmoid curve following marker infusion arrest and a "bell-shape" curve after single-dose administration of marker could be fitted satisfactorily using respective equations, as judged by the proportion of total variance

accounted for by models. However, *MRT* partitioning among 3 compartments appeared to raise specific problems with the S-shape kinetics. Indeed, partial *MRT* ascribed to the second mixing compartment C2 obviously was greatly underestimated (Grovum and Williams, 1973; Dixon *et al*, 1982). This may be related to variations with time in the initial marker concentration at the plateau, the vicinity and the quite undifferentiable shape of the curve portion underlying C2 *MRT* estimation. Undoubtedly, if *MRT* in C2 reflects retention in the caecum-proximal colon compartment (Grovum and Williams, 1973), the Gw2 model used in the present work was not adapted to estimate C2 *MRT*, and probably other partial *MRTs*. A simplified form may be derived to estimate only 2 transit components (*TT*+C2) and C1.

Rumen MRT estimated from faecal kinetic data

As already observed in our laboratory (Poncet and Al Abd, 1984; Lallès and Poncet, 1990b) and in agreement with other results (Faichney and Boston, 1983; Robinson and Sniffen, 1983; Goetsch and Owens, 1985; Cochran *et al*, 1986; Beauchemin and Buchanan-Smith, 1989; Cruickshank *et al*, 1989), the present study confirms that it could be hazardous to estimate ruminal *MRT* from faecal data. However, high correlations have been found between rumen or duodenal and faecal slopes of decreasing parts of marker concentration kinetics (Elimam and Ørskov, 1984; Ellis *et al*, 1984) suggesting such an approach may be satisfactory in dietary situations in which very long relative retention of digesta in the rumen occurs.

CONCLUSION

In conclusion, the addition of cationomycin and lasalocid to a roughage-based diet had no significant effect on the retention of solute and particulate markers in sheep regardless of sampling site, marker administration technique or MRT calculation used. Pulse-dose and post-infusion techniques led to differences which may be explained by the difference between ways of labelling rumen contents (infusion of a solution of marker vs pulse dose of pre-labelled feed particles) and the subsequent specific behaviour of markers in the digestive tract following their administration. Partitioning MRT among 3 partial MRTs using a deterministic model seemed to be difficult in the case of the post-infusion technique. More direct investigations are required to validate the estimation of markers MRT using models.

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