Rate of passage of digesta in sheep

5.* Theoretical considerations based on a physical model and computer simulation

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1. A simple two-compartment physical model was assembled with the aim of simulating passage of marker through the reticulo-rumen, small intestine, and caecum and proximal colon of sheep. Passage of marker through the whole digestive tract and the hind-gut were also simulated with a computer and methods of describing such results were compared.

2. The same mathematical equation applied equally well to the passage of a single injection of marker through the model and whole digestive tract of sheep. The magnitude of a rate-constant, reflecting in theory the retention time of marker in the caecum and proximal colon, was accurate for the model but larger than expected for the sheep. Modifications of the model are discussed which might account for the greater complexity in the biological system.

3. The average time available for digestion in the entire gut can be described with R or $\bar{t}$ and that for the intestinal tract distal to the abomasum with R_i or with a similar measurement $\bar{t}_i$. The magnitudes of these values and of rate-constants and a transit time of marker in the intestines, derived from the concentration curve of marker excretion in faeces, are closely related. The times for peak concentration of marker in faeces, for 5 and 50% excretion and the 80–5% excretion time were found to be of limited usefulness in describing the results of rate of passage experiments with sheep.

Simulation experiments are reported in this paper to show the interactions between mathematical measurements that could be used in describing the rate of passage of marker through the alimentary tracts of sheep. The mathematical formulation was basically that given by Blaxter, Graham & Wainman (1956) and Brandt & Thacker (1958). Three of the four mathematical measurements used in describing the concentration curve of marker excretion in sheep have been related to specific aspects of gut function (Grovum & Williams, 1973*c*). The equations pertaining to the cumulative percentage recovery curve of marker have been developed to explain the theory of marker excretion and to evaluate methods of analysing marker excretion results obtained for ruminants.

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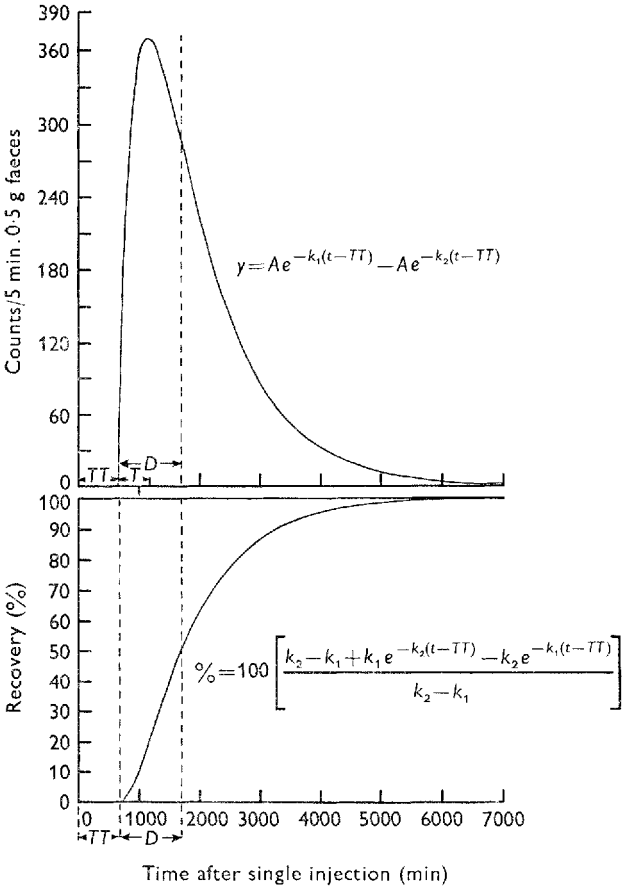

Fig. 1. Simulated marker excretion curves such as occur in faeces when a single injection of reference material is given into the reticulo-rumen of sheep. Upper graph, a marker concentration curve; lower graph, a cumulative percentage recovery curve.

EXPERIMENTAL

Description of marker excretion curves

The upper graph of Fig. 1 is characteristic of the changes which occur in marker concentration in faeces after a single injection into the reticulo-rumen of sheep. Equation (1), which is similar to equation (4) of Blaxter *et al.* (1956), was used by Grovum & Williams (1973*c*) to describe this pattern of excretion.

$$\left.\begin{aligned} y &= Ae^{-k_1(t-TT)} - Ae^{-k_2(t-TT)} \quad \text{for} \quad t \geqslant TT; \\ y &= 0 \quad \text{for} \quad t < TT, \end{aligned}\right\} \qquad (1)$$

where y and A are marker concentrations in faecal dry matter, k_1 and k_2 are rate-constants associated with the kinetics of marker in the reticulo-rumen and the hind-gut respectively and t is the sample time. Half-time ($0{\cdot}693/k$) has been notated $T_{\frac{1}{2}}$, and $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ are defined as $0{\cdot}693/k_1$ and $0{\cdot}693/k_2$ respectively. TT, the transit

time of the marker through the intestines of the sheep, was calculated from equation (2):

$$TT = \frac{\ln A_2 - \ln A_1}{k_2 - k_1}, \tag{2}$$

where A_1 and A_2 are intercept values for marker concentration in faecal dry matter (Grovum & Williams, 1973*c*) and k_1 and k_2 are defined above. Generally, TT may be thought of as the shortest time required for a particle of marker to pass from the site of injection to the site of sampling. Graphically, it is the time at which marker concentrations first increase from zero values on the time axis to form a distribution curve, as shown in the upper graph in Fig. 1.

T in Fig. 1 is the time for marker concentration to increase from 0 to a maximum, and it can be calculated from equation (3).

$$T = \frac{\ln (k_2) - \ln (k_1)}{k_2 - k_1}. \tag{3}$$

The lower graph in Fig. 1 was defined by equation (4). It is similar to equation (3) given by Blaxter *et al.* (1956).

$$PC = 100\left[\frac{k_2 - k_1 + k_1 e^{-k_2(t-TT)} - k_2 e^{-k_1(t-TT)}}{k_2 - k_1}\right] \quad \text{for} \quad t \geqslant TT. \tag{4}$$

PC is the percentage marker recovery and the remaining symbols were defined for equation (1). $PC = 0$ for $t < TT$. When $k_1 = k_2$, equations (1) and (4) cannot be used to predict the concentration and cumulative curves of marker excretion. However, they can be described with equations given by Grovum & Williams (1973*c*) and Blaxter *et al.* (1956, bottom of page 76) respectively.

In Fig. 1, D is the time for 50% excretion $- TT$. Theoretically, the general shape of the cumulative excretion curve after first appearance of marker in faeces is entirely dependent upon the magnitudes of k_1 and k_2, which can be calculated from the marker concentration curve in faeces. Equation (4) was developed by integrating equation (1) between the times TT and FT (finite time), multiplying the result by 100 and dividing the product by the integral for the total area under the concentration curve for times ranging from TT to $+\infty$.

Precise estimates of D can be obtained from k_1 and k_2 by the iterative procedure of Newton-Raphson, described by McCracken & Dorn (1964). This method has been applied to the cumulative curve of marker excretion as follows: the absolute values of the rate-constants k_1 and k_2 from the experimental results and a crude estimate of D ($D = T_{\frac{1}{2}k_1} + T_{\frac{1}{2}k_2}$) were used in equations (5) and (6) to estimate $F(D)$ and $F^1(D)$ respectively:

$$F(D) = \left[\frac{k_2 - k_1 + k_1 e^{-k_2 D} - k_2 e^{-k_1 D}}{k_2 - k_1}\right] - 0{\cdot}5; \tag{5}$$

$$F^1(D) = \frac{(k_1 k_2)(e^{-k_1 D} - e^{-k_2 D})}{k_2 - k_1}. \tag{6}$$

The estimated value of D and $F(D)$ and $F^1(D)$ were then substituted into equation (7) to calculate ND, the first new value of D:

$$ND = D - \frac{F(D)}{F^1(D)}. \quad (7)$$

The initial estimate of D was then replaced with the value of ND, and $F(ND)$ and $F^1(ND)$ were calculated. ND was also used for D in equation (7) to calculate the second ND. Only three to four iterations were required to calculate a value for ND which was accurate within 1 min. With further iterations, ND would become a progressively better estimate of the true value of D. For example, when $T_{\frac{1}{2}k_1} = 700$ min and $T_{\frac{1}{2}k_2} = 600$, then successive values of D, $F(D) \times 10^4$, $F^1(D) \times 10^4$ and ND are 1300, −959·10, 3·69 and 1559·65 for iteration 1, 1559·65, −41·87, 3·35 and 1572·12 for iteration 2 and 1572·12, −0·12, 3·33 and 1572·15 for iteration 3 respectively.

Any percentage recovery time may be estimated with this method by replacing 0·5 in equation (5) with the appropriate decimal fraction (substitute 0·05 to estimate the time for 5% excretion minus transit time).

Experiment 1

The aim was to determine experimentally whether or not $T_{\frac{1}{2}k_2}$ obtained from the rising and peak portions of marker concentration curves in faeces (Grovum & Williams, 1973*c*) was independent of the kinetics of marker in the reticulo-rumen.

A physical model of the sheep digestive tract was assembled (Pl. 1). Infusion lines were calibrated and then grouped into three pairs. Distilled water was pumped at the rate of 6·78 ml/min from a reservoir through two mixing pools in series and finally into a waste container. The tubing connecting the two pools, a model small intestine, was inserted to create a numerical value for TT in equation (1). The volume of the model caecum and proximal colon was held constant at 200 ml. The pool size of the model rumen was 800 ml in part A and 400 ml in part B of the experiment to effect a change in its marker kinetics.

A single injection of $^{51}CrCl_3$ (supplied by the Australian Atomic Energy Commission, Lucas Heights, NSW, Australia) was placed into the model rumen in parts A and B and duplicate 0·2 ml samples were withdrawn from the two pools in the system. The half-time of marker in the model rumen was calculated direct from the regression coefficient (b) relating the natural logarithms of marker concentration and the time of sampling ($T_{\frac{1}{2}} = -0{\cdot}693/b$). The changes in marker concentration in the model caecum and proximal colon were analysed for TT, $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ with the methods presented by Grovum & Williams (1973*c*).

Experiment 2

The possible interactions between T, $T_{\frac{1}{2}k_1}$, $T_{\frac{1}{2}k_2}$ and D within the biological system were evaluated. The values $T + TT$ (time of peak concentration) and $D + TT$ (time for 50% excretion) are often used to describe marker excretion results.

A digital computer was used to calculate y and PC values from equations (1) and (4) respectively for times from $t = TT$ to $t = 10000$ min and for sets of $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$

with $T_{\frac{1}{2}k_1}$ ranging from 100 to 1600 min and $T_{\frac{1}{2}k_2}$ ranging from 5 to 1000 min. A and TT were held constant. D was read from the computer print-out and equation 3 was used to calculate T.

Experiment 3

The methods most often used to analyse marker excretion patterns in faeces were critically evaluated and compared. A digital computer was used to simulate results with equations 1 and 4, from which it was possible to calculate values for 80–5% excretion time (Balch, 1950), for R (Castle, 1956*a*) and for the mean time $\bar{t}$ for the entire gut used by Blaxter *et al.* (1956), Graham & Williams (1962) and Weston (1968). A and TT in equations (1) and (4) were assigned arbitrary numbers and $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ in min were changed systematically over biologically meaningful ranges for sheep. The theoretical sample times (t) were spaced at intervals of 1 or 10 min between the limits of 676 and 15000 min.

Part 1. A, TT and $T_{\frac{1}{2}k_1}$ were held constant at 10^6, 676 and 700 respectively and $T_{\frac{1}{2}k_2}$ was increased from 100 to 500 in increments of 100.

Part 2. A, TT and $T_{\frac{1}{2}k_2}$ were held constant at 10^6, 676 and 300 respectively and $T_{\frac{1}{2}k_1}$ was increased from 400 to 1200 in increments of 200.

Part 3. A, TT, D and the time for 50% excretion were held constant at 10^6, 676, 1500 and 2176 respectively and $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ were changed in opposite directions. The following sets of $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$, selected from Fig. 3 (Expt 2), were used: 1425, 50; 1270, 150; 1104, 250; 950, 350 and 880, 400.

Part 4. The total mean retention time (TMRT) of marker in the gut was calculated by a new method (equation 8) which utilizes values of TT, k_1 and k_2 described in relation to equation (1).

$$\text{TMRT} = TT + \frac{1}{k_1} + \frac{1}{k_2}. \tag{8}$$

The values of $1/k_1$ and $1/k_2$ in min are average times of marker retention in pools of digesta in the gut. Thus TMRT also equals $TT + 1{\cdot}443\ (T_{\frac{1}{2}k_1} + T_{\frac{1}{2}k_2})$.

A, TT and TMRT were held constant at 10^6, 676 and 2841 respectively and $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ were changed in opposite directions as follows: 1400, 100; 1300, 200; 1200, 300; 1000, 500 and 900, 600.

The times for 5, 15, 25, 35, 45, 55, 65, 75, 80, 85 and 95% excretion were obtained for each of the sets of half-times given. The mean times $\bar{t}$ were calculated from equation (9) (Graham & Williams, 1962):

$$\bar{t} = \frac{1}{N} \Sigma \frac{n(t + t^1)}{2}, \tag{9}$$

where the letters t and t^1 are successive times of sampling and n is the quantity of marker excreted between t and t^1. N is the total quantity of marker excreted. In this work, the partial areas under the concentration curve between successive times of sampling (differences between two finite integrals of equation 1) were used as values of n. The total area under the concentration curve was used as N.

The passage of marker through the intestinal tract distal to the duodenum, a system

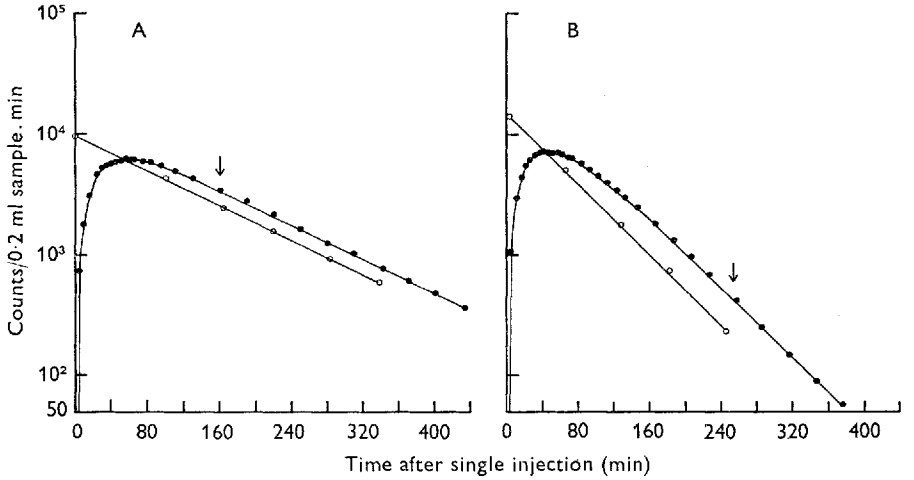

Fig. 2. Marker-concentration curves obtained from a physical model of the digestive tract of the sheep. A single injection of marker was given into the model rumen and samples were collected from the model rumen (○) and the model caecum and proximal colon (●). The solid lines through the open circles are least-square fits and the solid lines through the closed circles were fits obtained using the method described by Grovum & Williams (1973*c*). The arrows indicate the first point used in the regression analysis to calculate $T_{\frac{1}{2}k_1}$. A, model rumen 800 ml, model caecum and proximal colon 200 ml; B, model rumen 400 ml, model caecum and proximal colon 200 ml.

containing one mixing pool of digesta, was also simulated to calculate retention times for marker represented by R_i (Castle, 1956*b*) and $\bar{t}_i$ (Coombe & Kay, 1965; Weston, 1968). Grovum & Williams (1973*c*) reported that a half-time of ^{51}Cr EDTA in the hind-gut ($T_{\frac{1}{2}k_2}$), obtained by injecting the marker into the reticulo-rumen and sampling faeces, was about 66% of another half-time, $T_{\frac{1}{2}\mathrm{CPC}}$ obtained by injecting the marker into the abomasum and collecting faeces. The simulated results, based on values for k_2, apply to an ideal model in which $T_{\frac{1}{2}k_2}$ equals $T_{\frac{1}{2}\mathrm{CPC}}$. The problem of relating $T_{\frac{1}{2}k_2}$ and $T_{\frac{1}{2}\mathrm{CPC}}$, $\bar{t}_i$ and R_i in vivo is discussed on page 389. The concentration curve of marker excretion in faeces was simulated with equation (10),

$$y = Ae^{-k_2(t-TT')} \quad \text{for} \quad t \geqslant TT, \tag{10}$$

and the cumulative curve of marker excretion with equation (11),

$$PC = 100\,(1-e^{-k_2(t-TT')}) \quad \text{for} \quad t \geqslant TT. \tag{11}$$

The variables involved were defined for equations (1) and (4). y and PC equal zero for $t < TT$. TT and A were held constant at 676 and 10^6 and results were obtained for all the values of k_2 referred to in parts 1–4 ($k_2 = 0{\cdot}693/T_{\frac{1}{2}k_2}$). The retention time $\bar{t}_i$ was calculated using equation (9), but in this instance the values of n were differences between two finite integrals of equation (10).

Table 1. *Effect on TT and* $T_{\frac{1}{2}k_2}$ *of changing marker kinetics in the model sheep rumen (all times in min)*

		$T_{\frac{1}{2}}$ model rumen		$T_{\frac{1}{2}}$ model caecum and proximal colon	
Expt	*TT**	Direct	$T_{\frac{1}{2}k_1}$*	Calculated†	$T_{\frac{1}{2}k_2}$*
1A	2·8	83·9	84·1	20·4	20·2
1B	3·0	41·2	42·0	20·4	19·7

* Calculated from marker concentration changes in the model caecum and proximal colon with the methods described by Grovum & Williams (1973*c*).

† $T_{\frac{1}{2}}$ water (min) $= \frac{0{\cdot}693 \text{ (volume)}}{\text{flow-rate}} = \frac{0{\cdot}693 \text{ (200)}}{6{\cdot}78}$.

RESULTS

Expt 1. *The model digestive tract*

The concentration changes of ^{51}Cr in the model rumen and model caecum and proximal colon obtained in parts A and B are shown in Fig. 2. There was good agreement between $T_{\frac{1}{2}k_1}$ and the half-time of ^{51}Cr in the model rumen and between $T_{\frac{1}{2}k_2}$ and the calculated half-time of marker in the model caecum and proximal colon in both parts of the experiment (Table 1). *TT* and $T_{\frac{1}{2}k_2}$ were influenced relatively little by a marked change in $T_{\frac{1}{2}k_1}$ between parts *A* and *B*. TT was close to the time required for dyed water to pass through the model small intestine and first appear in the model caecum and proximal colon (2·7 min).

Expt 2. Interactions between T, $T_{\frac{1}{2}k_2}$, $T_{\frac{1}{2}k_1}$ *and D*

The relationships among *D*, *T*, $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ are presented in Fig. 3. A point on the interior of the graph can be located for each experimental set of $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$, using the internal vertical and diagonal axes respectively. Values for *D* and *T* can then be read off the external vertical and horizontal axes respectively (for example, when $T_{\frac{1}{2}k_1} = 1104$ and $T_{\frac{1}{2}k_2} = 250$, $D = 1500$ and $T = 693$). The relationship between *D* and the two half-times $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ is curvilinear. The value of *D* is always larger than the sum of the half-times, provided that neither is zero. It is seen that *D* approaches $T_{\frac{1}{2}k_1}$ as $T_{\frac{1}{2}k_2}$ approaches 0. Thus $T_{\frac{1}{2}}$ may also be thought of as the time required for 50% of the marker present in a pool at any time to be eliminated. *T* is most responsive to changes in $T_{\frac{1}{2}k_2}$ when $T_{\frac{1}{2}k_1}$ is large and $T_{\frac{1}{2}k_2}$ is small.

There are infinite sets of $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ that produce either constant values of *D* and variable values of *T* or constant values of *T* and variable values of *D*. Three cumulative excretion curves are shown in Fig. 4 which have a constant value for *D* of 1500 min. *TT* was constant at 676 min. The cumulative curves crossed over at the time for 50% excretion, but there were marked differences in their shapes as well as in the shapes of corresponding marker concentration curves. There were marked changes in the time of peak counts. This situation apparently arises only when the half-times are changed in opposite directions from one set of $T_{\frac{1}{2}k_1}$, $T_{\frac{1}{2}k}$ to another, as shown in Table 2, part 3.

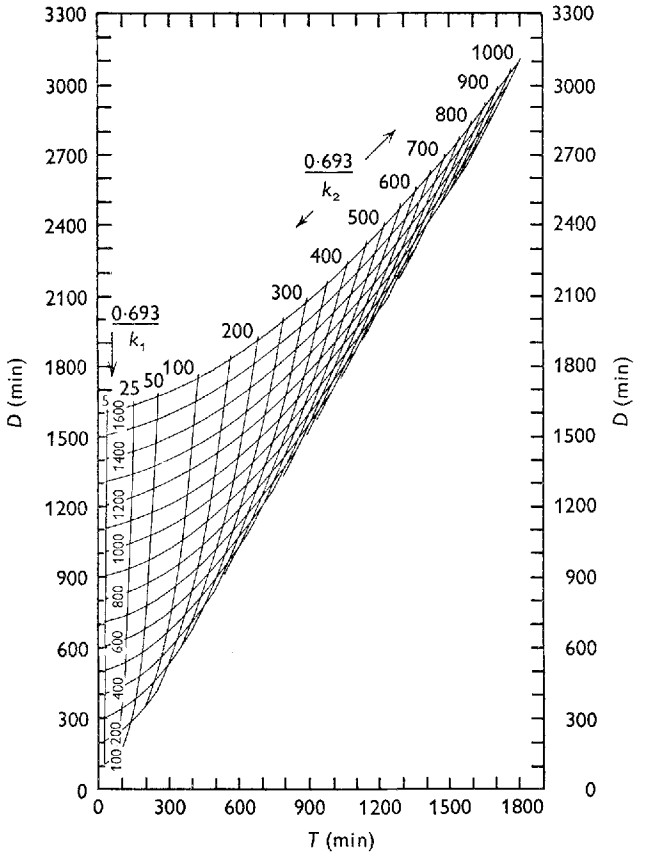

Fig. 3. Interactions between the measurements used to describe the patterns of marker excretion in sheep when the reference material is given as a single injection into the reticulorumen. *TT*, calculated time for first appearance of marker in the faeces; *D*, time for 50% excretion $-TT$; $T_{\frac{1}{2}k_1}$, half-time in the terminal portion of the marker-concentration curve in faecal dry matter; $T_{\frac{1}{2}k_2}$, half-time obtained from the rising and peak portion of the marker-concentration curve in faecal dry matter; *T*, time of peak marker concentration $-TT$.

Expt 3. Evaluation of methods used to analyse marker excretion results

The values of R, $\bar{t}$ and TMRT were always larger than the time for 50% excretion (Table 2). The magnitudes of $\bar{t}$ were only slightly smaller than those of TMRT. The discrepancy was greatest for large values of $T_{\frac{1}{2}k_1}$ in parts 3 and 4, which were associated with protracted excretion patterns and theoretical recoveries of marker between 99·8 and 100%. Thus $\bar{t}$ was underestimated slightly because the terminal sample times in the simulation experiment were limited to 15000 min. When the recovery of marker is 100%, $\bar{t}$ = TMRT = $TT + 1{\cdot}443\ (T_{\frac{1}{2}k_1} + T_{\frac{1}{2}k_2})$. Similarly, $\bar{t}_i = TT + 1{\cdot}443\ (T_{\frac{1}{2}k_2})$. The values of R were 1–2% smaller than those of $\bar{t}$. This similarity in magnitude of R and $\bar{t}$ has been recognized previously and substantiated with experimental results (Phillips, unpublished). The magnitudes of R and TMRT were essentially identical when the 95% excretion time used to calculate R was replaced by the 96·4% time. The magnitude of R_i was also close to that of $\bar{t}_i$.

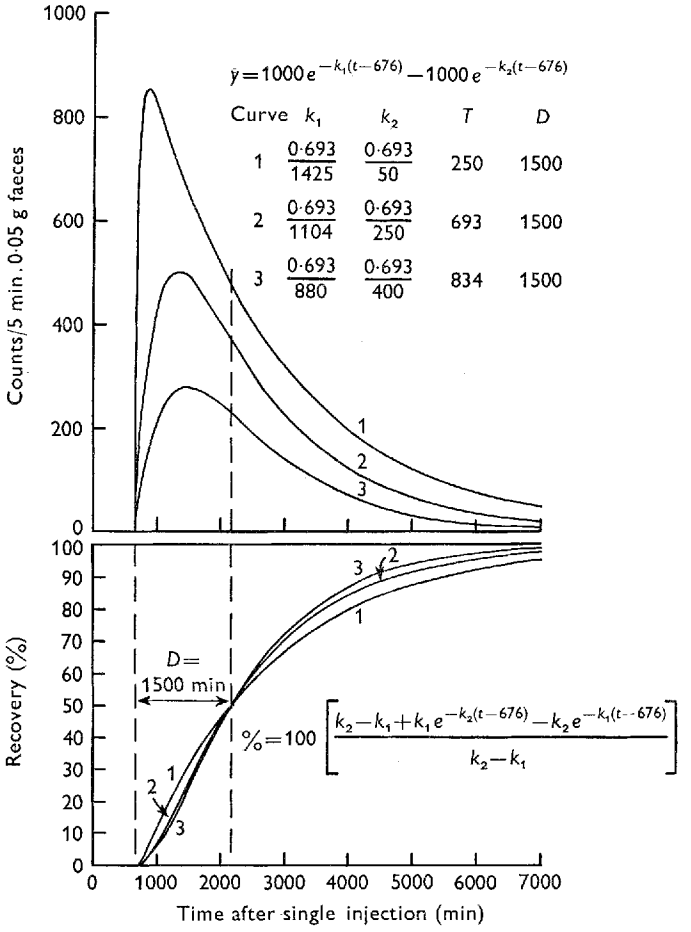

Fig. 4. Simulated marker-concentration curves (upper graph) associated with recovery curves in the lower graph that cross over at a common time for 50% excretion.

The 50% excretion time showed trends similar to those of R, $\bar{t}$ and TMRT in parts 1 and 2 but not in parts 3 and 4. The 50% time is therefore of little use in describing the results of marker-excretion experiments. The changes in rate of passage simulated in part 4 would not be detected with $\bar{t}$ or R. However, such results should be interpreted correctly when any of the following sets of measurements are used: $T_{\frac{1}{2}k_1}$, $T_{\frac{1}{2}k_2}$ and TT; $\bar{t}$, $\bar{t}_i$ and a time similar to TT; R, R_i and a time similar to TT.

The 80–5% time responded to changes in $T_{\frac{1}{2}k_2}$ and $T_{\frac{1}{2}k_1}$ in parts 1 and 2, indicating that it is not entirely an index of marker retention time in the reticulo-rumen. The 5% time was influenced by changes in $T_{\frac{1}{2}k_1}$, so it is not solely a measure of the time of passage of digesta through the hind-gut. Also, it was a relatively poor measure of the time of marker retention in the hind-gut (part 1) compared with $T_{\frac{1}{2}k_2}$, $\bar{t}_i$ or R_i. The 80–5% time was either greater or less than the 50% time, R and $\bar{t}$.

Table 2. *Expt* 3. *Simulated values for methods of describing marker excretion results*

$T_{\frac{1}{2}k_1}$	$T_{\frac{1}{2}k_2}$	TT	T	R_i*	$\bar{t}_i$†	5% time	80% time	80–5% time‡	R§	50% time	$\bar{t}$‖	TMRT¶
Part 1: fixed TT, A, k_1 and varied k_2												
700	100	676	328	815	820	821	2456	1635	1797	1531	1829	1830
700	200	676	506	955	964	873	2639	1766	1942	1693	1973	1975
700	300	676	642	1094	1108	914	2841	1927	2086	1845	2118	2119
700	400	676	754	1234	1253	949	3054	2105	2231	1986	2263	2263
700	500	676	850	1373	1397	980	3269	2289	2374	2120	2407	2408
Part 2: fixed TT, A, k_2 and varied k_1												
400	300	676	498	1094	1108	854	2188	1334	1669	1520	1686	1686
600	300	676	600	1094	1108	895	2623	1728	1947	1739	1975	1975
800	300	676	679	1094	1108	931	3063	2132	2227	1947	2262	2263
1000	300	676	745	1094	1108	963	3508	2545	2504	2156	2550	2552
1200	300	676	800	1094	1108	994	3961	2967	2784	2351	2834	2841
Part 3: fixed TT, A and varied k_1 and k_2 to hold the 50% time constant												
1425	50	676	251	746	748	848	4059	3211	2735	2176	2772	2804
1270	150	676	524	885	892	918	3856	2938	2664	2176	2717	2725
1104	250	676	693	1025	1036	957	3648	2691	2577	2176	2626	2630
950	350	676	799	1164	1180	976	3497	2521	2507	2176	2550	2552
880	400	676	834	1234	1253	984	3446	2462	2482	2176	2522	2523
Part 4: fixed TT, A and varied k_1 and k_2 to hold total retention (TMRT) constant												
1400	100	676	410	815	820	892	4081	3189	2772	2226	2825	2841
1300	200	676	638	955	964	953	4009	3056	2778	2286	2830	2841
1200	300	676	800	1094	1108	994	3960	2966	2784	2348	2834	2841
1000	500	676	1000	1373	1397	1041	3921	2880	2794	2448	2838	2841
900	600	676	1053	1512	1540	1054	3918	2864	2798	2476	2838	2841

* Castle (1956*b*).
† Coombe & Kay (1965) and Weston (1968).
‡ An index of marker retention time in the reticulo-rumen (Balch, 1950).
§ Castle (1956*a*).
‖ Blaxter, Graham & Wainman (1956).
¶ Total mean retention time (TMRT) = $TT + 1{\cdot}443\ (T_{\frac{1}{2}k_1} + T_{\frac{1}{2}k_2})$. The average time of retention of marker in a pool = $1/k$ or $1{\cdot}443\ (T_{\frac{1}{2}})$.

DISCUSSION

Expt 1. *Model digestive tract*

Equation (1) was used in previous work (Grovum & Williams, 1973*c*) to describe changes in concentrations of ^{144}Pr and ^{51}Cr EDTA in faeces. TT and $T_{\frac{1}{2}k_1}$ for ^{51}Cr EDTA were shown to be measures of the time of marker transit through the intestines and the rate of marker elimination from the reticulo-rumen respectively. However, $T_{\frac{1}{2}k_2}$ was on the average about 66% of a half-time $T_{\frac{1}{2}\mathrm{CPC}}$ obtained by injecting markers into the abomasum and collecting faeces. In the model, the mean $T_{\frac{1}{2}k_2}$ for Expt 1 (20·0 min) was close to the expected value of 20·4. This lends confidence to the method used in determining $T_{\frac{1}{2}k_2}$ but it neither accounts for the difference between $T_{\frac{1}{2}k_2}$ and $T_{\frac{1}{2}\mathrm{CPC}}$ in vivo nor establishes without doubt which is the correct indicator of time available for fermentation in the hind-gut. Either may prove to be satisfactory for reflecting changes in this time, as the ratio of the two half-times was relatively

constant even for marked changes in the level of food intake (Grovum & Williams, unpublished). The differences of magnitude between $T_{\frac{1}{2}k_2}$ and $T_{\frac{1}{2}CPC}$ in vivo may be due to imperfect mixing of digesta in the caecum and proximal colon of the sheep (Grovum & Hecker, 1973; Grovum & Williams, 1973*b*).

In Expt 1, $T_{\frac{1}{2}k_2}$ and TT were not greatly influenced by the rate of elimination of marker from the model reticulo-rumen, indicating that $T_{\frac{1}{2}k_1}$, $T_{\frac{1}{2}k_2}$ and TT were independent measurements in the model. The same should be true in the sheep, provided that $T_{\frac{1}{2}k_1}$ is not biased by counts near the peak of marker concentration in faecal dry matter. A tube simulating the distal large intestine was not included as a part of the physical model because of the ease of sampling the contents of the model caecum and proximal colon and because this part would only have increased the magnitude of TT if samples were obtained at its point of outflow.

The model used in Expt 1 may be refined so that it simulates exactly the kinetics observed when a single injection of marker passes through the digestive tract of the sheep. The first step might be to insert a third small mixing pool to simulate the effect of the abomasum. Then a connecting tube, branched in the middle to provide a range of marker transit time, could be inserted between the model abomasum and the model caecum and proximal colon to simulate the effect of spread of a pulse of marker in the small intestine, as observed by Coombe & Kay (1965) in sheep. Finally sponges (A.C.I. Warner, personal communication) could be inserted into the model caecum and proximal colon or into the model rumen, or into both, to simulate the effect of inadequate mixing in the major pools of the digestive tract. King & Moore (1957) showed that mixing of digesta in the reticulo-rumen of cows was imperfect.

Expt 2. Interaction between T, $T_{\frac{1}{2}k_1}$, $T_{\frac{1}{2}k_2}$ and D

This experiment showed that infinite sets of $T_{\frac{1}{2}k_1}$ and $T_{\frac{1}{2}k_2}$ could produce constant values of either D or T. Also, the value of D was not equal to either the sum of half-times or the sum of average times ($1/k$) associated with k_1 and k_2.

Balch & Campling (1965) presented cumulative marker excretion curves for cattle fed *ad lib.* on long and pelleted hay, which crossed over near the time for 50% excretion. The R value of Castle (1956*a*) did not account for the difference in the shape of these curves. A similar effect has been simulated in Expt 3 by simultaneously decreasing $T_{\frac{1}{2}k_1}$ and increasing $T_{\frac{1}{2}k_2}$ (Table 2; Fig. 4). Thus R and $\bar{t}$ are good measures of average retention time of marker in the tract, but they do not account for the relative times of retention of marker in the reticulo-rumen and the hind-gut. Experiments should be conducted to determine whether feeding cattle *ad lib.* with pelleted hay causes $T_{\frac{1}{2}k_1}$ to decrease and $T_{\frac{1}{2}k_2}$ to increase relative to the results for long hay.

The cumulative excretion curve of marker has been described with a logistic function (Patton & Krause, 1972), knowing values for maximum slope of the cumulative excretion curve and the time for 50% of marker to be excreted in faeces. The biological usefulness of these values is yet to be proven but may be limited for reasons just discussed.

Expt 3. Evaluation of methods to analyse marker-excretion results

Putnam, Bond & Lehmann (1967) and Asplund & Harris (1970) were concerned about the confusion arising from the many methods and terms used in describing the rate of passage of digesta in ruminants. Controlled quantitative comparisons of the various methods have not been published, so it was not meaningful to relate results expressed in different ways. Equation (1) was used to evaluate other methods of analysing passage of marker through the ruminant digestive tract because it described the concentration curve of marker in the faeces of sheep (Grovum & Williams, 1973*c*). The use of equation (4) seemed justified because it was derived from equation (1) and because the times for 50% excretion of marker ($TT+D$), calculated from equations (2), (5), (6) and (7), were not significantly different from similar paired estimates obtained graphically from the experimental results (unpublished). The means were 1059 and 1074 min respectively ($n = 27$).

The $T_{\frac{1}{2}}$ of marker in the reticulo-rumen ($T_{\frac{1}{2}k_1}$) is not biased by marker kinetics in the hind-gut. Therefore it is preferable to the 80–5% time (Balch, 1950). The 5% excretion time was not a good measure of R_i, as has been suggested by Balch (1950) and Castle (1956*b*). The values $1/k_2$ and TT or either of $\bar{t}_i$ or R_i with the time for first appearance of marker in faeces are preferable to the 5% time as measures of the time of retention of digesta in the hind-gut. $T_{\frac{1}{2}k_2}$ and TT were not biased by changes in $T_{\frac{1}{2}k_1}$ (Expt 1), as was the 5% time (Expt 3).

There is difficulty in describing the rate of passage of marker through the digestive tract by means of one criterion such as the 50% time, R or $\bar{t}$ because the reticulo-rumen, caecum and proximal colon and the small and large intestines may not respond similarly to changes in ration or in food intake (Coombe & Kay, 1965; Grovum & Williams, 1973*a*, *c*; Grovum & Hecker, 1973). However, with one possible exception, mentioned below, the results of experiments on rate of passage can be described adequately with the use of either $\bar{t}$ and $\bar{t}_i$ or R and R_i along with the time for first appearance of marker in faeces. This would involve surgical interference with the gut of the sheep so that marker could be injected into the duodenum to obtain $\bar{t}_i$ or R_i. Two separate determinations of rate of passage would be needed and this could be managed by collecting either one or two lots of samples. However, TT, k_1 and k_2 can be determined without surgical intervention and with only one set of results. Values of R and $\bar{t}$ can be obtained for experiments on passage of marker with any species, but the original results cannot be predicted and the model that characterizes the excretion pattern is never investigated. However, a poor fit between the observed concentrations of marker and the predicted values from equation (1) may indicate that a model with two compartments is not descriptive of passage of marker through the gut. Thus, new models and new equations can be sought that are more appropriate. Expts 2 and 3 demonstrate the usefulness of equations and measurements such as TT, k_1 and k_2 in theoretical exercises such as computer simulation. TT, k_1 and k_2 would be difficult to calculate if computer facilities were not available.

The value $1/k$ or 1·443 ($T_{\frac{1}{2}}$) is the average time available for fermentation in a pool of digesta (Hungate, 1966). Thus, TT, k_1 and k_2 may be useful in assessing the

average times available for digestion in the intestines, reticulo-rumen and caecum and proximal colon of the sheep respectively (Grovum & Williams, 1973*c*). However, caution should be exercised in the interpretation of all the measurements presently available for assessing the average time available for digestion in the caecum and proximal colon of the sheep. It is not known whether the true average time in the sheep is represented by the value 1·443 ($T_{\frac{1}{2}k_2}$) or by other values such as 1·443 ($T_{\frac{1}{2}CPC}$), or $\bar{t}_i$ or R_i minus the time for first appearance of marker in faeces. The use of the measurement $1/k_2$ seems to be reasonable because the marker passed through the gut of the sheep as did the food, and the concentration curve of marker excretion in faeces was described in its entirety with equation (1) and numerical values of A, k_1, k_2 and TT (Grovum & Williams, 1973*c*).

R, $\bar{t}$ and the total mean retention time TMRT were similar in magnitude but were always larger than the 50% time and either greater or less than the 80–5% time in parts 1–4 of this experiment. Excluding mention of TMRT, these conclusions are generally substantiated by the experimental results of Shellenberger & Kesler (1961), Pieterse, Lesch & Van Schalkwyk (1963), Eng, Riewe, Craig & Smith (1964) and Stielau (1967). There is not sufficient justification for the continued use of the 80–5% time and the 5 and 50% excretion times in describing the results of experiments on the rate of passage of digesta. The 50% time was greater than the value of R for some sheep in the experiments of Asplund & Harris (1970), but the shape of their cumulative excretion curves for Sudan III dye differed from those in Figs. 1 and 4 and from those of Castle (1956*a*).

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EXPLANATION OF PLATE

A physical model of the sheep digestive tract. Distilled water was pumped (9) from a reservoir (1) into the model rumen (3) through two infusion lines (2) and the contents of this pool were mixed with a magnetic stirrer (11). Water was pumped through a model small intestine (4–6) into a model caecum and proximal colon (8). The contents of the pool were mixed (11) and pumped (9) through infusion lines (7) into a waste reservoir (10).

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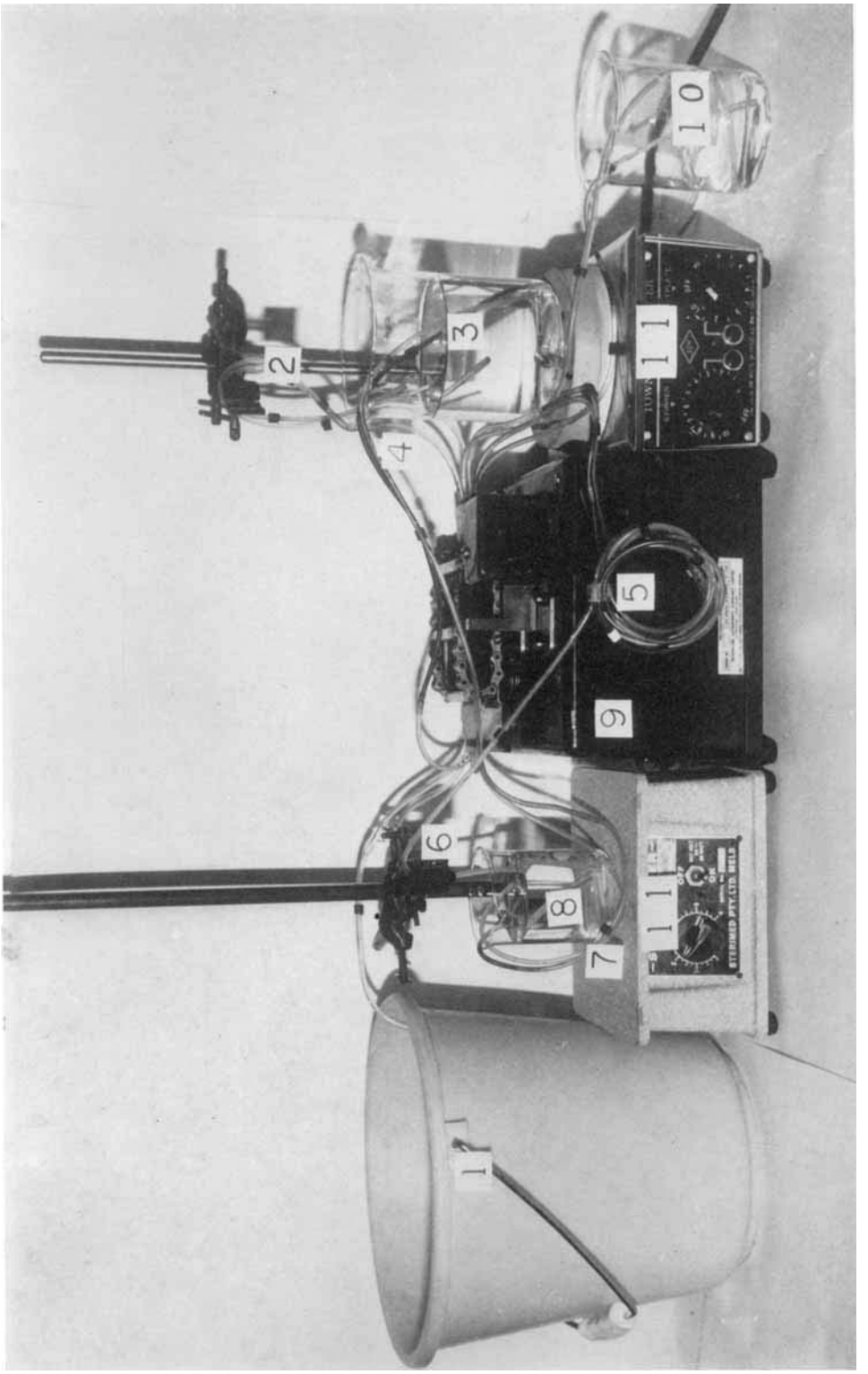

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