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The effects of phosphorus depletion, and of calcium and phosphorus intake, on the endogenous excretion of these elements by sheep

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1. Injections of ^{32}P and ^{45}Ca were used to study the influence of phosphorus depletion and repletion on the rates of endogenous calcium and P excretion in fifteen P-depleted and eighteen control sheep. 2. When given adequate P, there was a marked increase in the rate of excretion of metabolic faecal P in sheep which previously had been depleted. In control sheep a decrease was found in metabolic faecal P excretion with a diet deficient in P. 3. From the values for metabolic faecal P an indirect estimate of total intestinal secretion was made. The estimate was found to be in approximate agreement with values derived from published values for total daily digestive secretions in sheep. 4. The estimated rates of secretion of intestinal P suggest that after the addition of P to the diet the changes in the rate of excretion of metabolic faecal P in P-depleted sheep were the result of a decreased reabsorption of intestinally secreted P rather than of a change in the rate of secretion into the intestine. After a diet low in this element the decrease in metabolic faecal P excretion by control sheep appeared to be the result of a decreased rate of intestinal P secretion. 5. The possible significance of changes in metabolic faecal P excretion in relation to body P homoeostasis in the ruminant animal is discussed.

The physiological significance of endogenous faecal calcium and phosphorus excretion is not clear. Moreover, the question of whether there is a controlled secretion of these elements into the intestinal tract, regulating their concentration in the body, has been disputed for years. The current general consensus, as indicated in recent reviews (Hill, 1963; Irving, 1964), is that the excretions of Ca and P are not controlled, but instead represent a loss of these elements in the digestive juices and turnover of the intestinal mucosa.

However, metabolic faecal Ca and P excretions may result from different processes in the animal body. The metabolic faecal Ca loss in man (Blau, Spencer, Swernov, Greenberg & Laszlo, 1957), in rats (Hansard & Plumlee, 1954), and in ruminants (Visek, Monroe, Swanson & Comar, 1953; Lueker & Lofgreen, 1961) does not vary with current intake, suggesting that secretion of Ca into the intestinal tract is constant over varying Ca intakes. In contrast, the limited values available for metabolic faecal P excretion suggest that it varies with the level of P intake. This had been shown by Lueker & Lofgreen (1961) and by Preston & Pfander (1964) in the ruminant and, earlier, by Kjerulf-Jensen (1941–2) in rats.

Since the absorption of dietary P appears to occur by means of a passive diffusion process (McHardy & Parsons, 1956) in contrast to Ca, which appears to be actively absorbed (Bronner, 1964), it is possible that the intestinal secretion of P plays a

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regulatory role in the maintenance of body P homoeostasis. The more rapid rate of metabolic faecal P excretion with increased P intake may reflect an accelerated rate of intestinal secretion.

A further fact which might implicate intestinal secretion as a control site in the maintenance of body P homoeostasis is that the rate of urinary P excretion in ruminant animals is generally low (Hill, 1963). This may not be so in simple-stomached animals, however, since the kidney plays an important part in P metabolism in these species. It appears that more information about the rate of metabolic faecal P excretion in ruminant animals under various conditions of Ca and P nutrition is required before its possible physiological significance can be evaluated.

During the course of an investigation on the influence of P depletion and of the dietary Ca:P ratio on absorption of these elements in sheep (Young, Richards, Lofgreen & Luick, 1966) we also examined the effects of P depletion and repletion on the rates of excretion of endogenous faecal and urinary P and Ca. Metabolic faecal P excretion varied with P intake in contrast to metabolic faecal Ca excretion, which did not vary with changes in Ca intake over short periods. The rate of metabolic faecal P excretion increased in P-depleted sheep when they were fed on a diet adequate in P.

EXPERIMENTAL

Details of the experimental conditions and analytical techniques are described in previous papers (Young, Richards *et al.* 1966; Young, Luick & Lofgreen, 1966). After a P depletion period of 134 or 142 days, during which 4- to 6-month-old wether lambs were fed on a diet deficient in P and adequate in Ca (0·073 % P, 0·38–0·40 % Ca) or adequate in both (0·38–0·40 % P, 0·40 % Ca), a 21-day metabolism study was conducted in which each sheep received a subcutaneous injection of ^{45}Ca and ^{32}P.

Three test diets were fed to the sheep during the metabolism study: diet 1—Ca:P = 10·4:1, 0·076 % P; diet 2—Ca:P = 1·9:1, 0·248 % P; diet 3—Ca:P = 9·9:1, 0·264 % P. Eighteen depleted and eighteen control sheep, randomly chosen from their respective groups, were studied in two trials, each consisting of nine depleted and nine control sheep. During the second trial three depleted sheep failed to eat their total allotment; hence, results from these sheep are not included. Each 21-day trial was divided into two collection periods; period 1 covered days 4–10·5 (trial 1) and 4–11·5 (trial 2) following feeding of the test diets and period 2 covered days 14–21. Results from both trials were similar and the results were combined.

Two methods for the calculation of metabolic faecal Ca and P excretion were adopted. For period 1 the method used was based on the kinetic analysis of Aubert, Bronner & Richelle (1963) and described by Young, Luick & Lofgreen (1966). For the first trial metabolic faecal Ca and P excretion was determined from urinary and faecal radiochemical excretion during a 150 h period following injection of ^{45}Ca and ^{32}P; in the second trial it was determined for a 180 h period following injection.

For period 2 it was necessary to adopt a slightly different method since the urinary ^{32}P and ^{45}Ca activities during this time were below reliable limits of detection by the analytical methods employed. Hence, calculations were based upon the isotope dilution principle which has been adequately described by Kleiber, Smith, Ralston & Black (1951) and by Thompson (1965). The formula used to calculate metabolic faecal excretion is as follows:

$$s = f\,\theta/\pi,$$

where s = rate of metabolic faecal Ca or P excretion, f = rate of total faecal Ca or P excretion, θ = average specific activity of faecal Ca or P and π = average specific activity of serum Ca or P.

The major assumption made when these techniques are used is that the specific activity of the secreted element is the same as that of the plasma (or serum). The available evidence (Kjerulf-Jensen, 1941–2; Bronner, 1964; Fuchs & Fuchs, 1953–4) suggests that this assumption usually holds true, although Giese & Comar (1964) showed that under conditions of starvation the specific activities of urinary and serum Ca did not correspond.

Table 1. *Mean values with their standard errors for phosphorus intake and for faecal and urinary P excretion by five P-depleted and six control sheep fed on diets in which the Ca:P ratio and P contents varied*

Diet no.	Ca:P ratio	P status	P intake (g/week)	Metabolic faecal P (g/week)	Total faecal P (g/week)	Urinary P (g/week)	Cumulative ^{32}P excretion in faeces (% injected dose)
				Period 1			
1	10·4:1	Depleted	3·0 ± 0·38	2·8 ± 0·28	3·7 ± 0·47	0·06 ± 0·006	13·8
		Control	3·6 ± 0·36	4·4 ± 0·82	5·7 ± 0·69	0·10 ± 0·017	17·9
2	1·9:1	Depleted	9·5 ± 0·63	2·8 ± 0·43	4·0 ± 0·96	0·08 ± 0·009	11·0
		Control	12·7 ± 1·08	5·5 ± 0·96	11·1 ± 1·03	1·01 ± 0·568*	27·1
3	9·9:1	Depleted	10·4 ± 0·73	2·4 ± 0·35	3·2 ± 0·26	0·11 ± 0·046	9·4
		Control	14·8 ± 1·01	6·0 ± 0·59	10·1 ± 0·86	0·15 ± 0·028	22·8
				Period 2			
1	10·4:1	Depleted	3·0 ± 0·37	2·4 ± 0·15	3·8 ± 0·23	0·04 ± 0·006	—
		Control	3·6 ± 0·36	3·2 ± 0·36	4·5 ± 0·53	0·09 ± 0·011	—
2	1·9:1	Depleted	9·5 ± 0·63	4·7 ± 0·62	7·0 ± 1·07	0·12 ± 0·051	—
		Control	13·2 ± 0·82	6·9 ± 0·78	10·6 ± 1·24	1·38 ± 1·041*	—
3	9·9:1	Depleted	10·2 ± 0·77	4·7 ± 0·46	6·8 ± 1·03	0·21 ± 0·398	—
		Control	14·8 ± 1·01	6·6 ± 0·24	10·9 ± 1·03	0·22 ± 0·130	—

* Two sheep had a high urinary P excretion. Values without these are 0·19 ± 0·053 and 0·10 ± 0·008 for periods 1 and 2 respectively.

RESULTS AND DISCUSSION

Total and metabolic faecal P

In sheep given adequate P after a period of depletion (diets 2 and 3) total faecal P increased markedly between the two periods (Table 1). These increases were largely due to the increases in metabolic faecal P shown by these sheep. In the control sheep fed on these diets there was a relatively constant total faecal P excretion but they excreted 10–20% less metabolic faecal P during period 1 than in period 2. In the control sheep fed at a deficient level of P intake (diet 1) there was a decrease in the rate of metabolic faecal P excretion during the second period. This change accounts for the decreased total faecal P excretion by this group during the second period. In contrast to the change noted for faecal P excretion there was relatively little change in the rate for faecal Ca excretion during the same periods (see Table 5).

Fig. 1 shows the relationship between the rate of P absorption and metabolic faecal P excretion during period 2. Mean values for metabolic faecal P during both periods are summarized in Table 1. Metabolic faecal P excretion was positively correlated with P absorption ($r = 0{\cdot}859$, $P < 0{\cdot}01$ for period 2). These findings agree with those of earlier workers (Lueker & Lofgreen, 1961; Preston & Pfander, 1964) and suggest, furthermore, that the use of a regression analysis of total faecal P excretion on P intake for estimation of metabolic faecal P excretion is of questionable value.

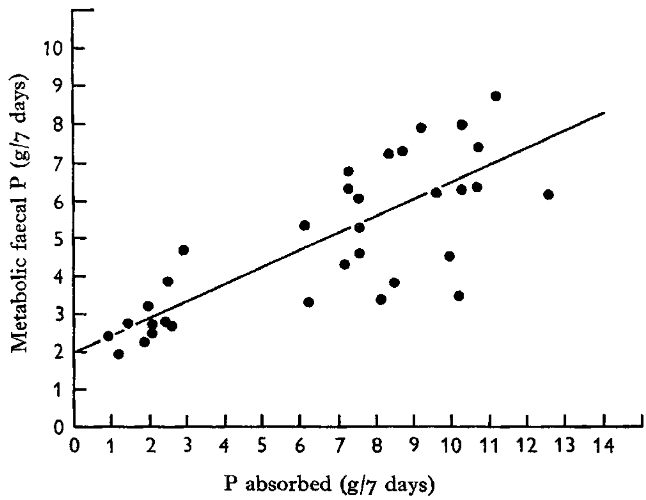

Fig. 1. Relationship between metabolic faecal phosphorus excretion by sheep and the amount of P absorbed. Values for P absorption were taken from the previous paper in this series (Young, Richards *et al.* 1966). The regression line was fitted by the method of least squares analysis.

Total intestinal P secretion

The rate of metabolic faecal P excretion given in Table 1 is a net rate and is not the rate of total P secretion into the digestive tract. Undoubtedly, part of the total secretion is reabsorbed and the quantity found in the faeces is the unabsorbed residue of the total intestinal secretion. To determine whether the changes in metabolic faecal P reflect a change in total secretion, an indirect estimate of the total rate of intestinal secretion was made by the method proposed by Blau *et al.* (1957) for Ca; the results are summarized in Table 2. The validity of this method depends upon certain assumptions, the most important of which is that there is complete mixing of the endogenously secreted pool with P of dietary origin before absorption and reabsorption occur. If this assumption holds true it might be expected that the specific activities of the soluble and insoluble fractions of the faecal P would be the same. This hypothesis was tested and the results obtained from one sheep fed on diet 3 are given in Table 3. Both fractions of faecal P had identical specific activities, a finding which supports the assumption and therefore adds validity to the method for estimating intestinal P secretion. The marked differences between the soluble and insoluble fractions of faecal Ca will be discussed below. Table 2 suggests that considerable recycling of endogenously secreted P occurred, varying between 16 and 22 g/week for the sheep with an adequate intake. In all instances the amounts of endogenous P recycled were greater than the quantity of P ingested during the same interval of time.

Table 2. *Comparison of mean values (g/week) for total and net metabolic excretion of phosphorus and calcium by five P-depleted and six control sheep during period 2 (days 14–21) of the metabolism study*

Diet no.	P status	Net metabolic faecal P	Total metabolic P excretion*	Metabolic P re-absorbed	Net metabolic faecal Ca	Total metabolic Ca excretion*	Metabolic Ca re-absorbed
1	Depleted	2·4	5·8	3·4	5·4	6·5	1·1
	Control	3·2	9·6	6·4	4·5	5·5	0·9
2	Depleted	4·7	20·7	16·0	4·1	7·1	3·0
	Control	6·9	25·7	18·8	4·5	6·5	2·0
3	Depleted	4·7	26·2	21·5	3·8	4·8	1·1
	Control	6·6	25·0	18·4	5·3	6·4	1·0

* Calculated by method of Blau *et al.* (1957).

Table 3. *Specific activity of duplicate samples of soluble and insoluble faecal calcium and phosphorus for one control sheep fed on diet 3*

Fraction of faecal Ca or P	Count/min mg P	Count/min mg Ca
Soluble (*a*)	648	356
(*b*)	647	344
Insoluble (*a*)	656	< 1
(*b*)	645	< 1

The estimates of total intestinal P secretion may be compared with an estimate based on previously published values for total daily digestive secretions and their composition in various portions of the intestinal tract of sheep (Table 4). Storry (1961) has made a similar assessment of Ca and magnesium secretion by sheep and the estimates of the daily volume of the secretions were taken from the references referred to in the table. Unfortunately, there are fewer values for the P concentration in these secretions. Values given by Tribe & Peel (1963) were used to calculate the total salivary P secretion; those of Adams & Heath (1963) were used for the biliary contribution. Similar values were not found for the other secretions; but, from the earlier work done in this laboratory (Smith, Kleiber, Black & Baxter, 1955; Smith, Kleiber, Black & Lofgreen, 1956) using ^{32}P, it might be concluded that only small quantities of the element are secreted into the gastro-intestinal tract distal to the abomasum in the mature ruminant. This may contrast with the immature ruminant or young milk-fed calf, in which the small intestine plays a greater part in the total intestinal secretion (Lofgreen, Kleiber & Smith, 1952; Chandler & Cragle, 1962).

Table 4 shows that the estimated total rates of excretion derived by the two methods are closely similar, particularly since the range of P concentration in the salivary secretion may be large (Kay, 1960; Tribe & Peel, 1963).

Earlier work by Smith *et al.* (1956) showed that the predominant site of P secretion in the ruminant is proximal to the duodenum, and the comparison of our results with published data lends support to these findings. Further, the present results suggest that under the conditions of these experiments dietary P and endogenously secreted P were absorbed to the same extent. This might be predicted if the major site of P secretion is at the salivary level and salivary P occurs mainly as inorganic phosphate (Kay, 1960).

Hence, the salivary secretion of P appeared to be reduced by a diet deficient in P (Table 2). Direct studies have not been made under these conditions; but our results are supported by those of Preston & Pfander (1964), who recently showed that the level of endogenous P in the rumen of lambs decreased with an inadequate P intake. Dobson (1961) has shown that the ruminal epithelium is relatively impermeable to P, which again suggests that most of the endogenous P present in the rumen is derived from salivary secretions.

Table 4. *Total daily digestive secretion of phosphorus in the sheep*

Secretion	Daily volume of secretion: Value (l.)	Daily volume of secretion: Reference*	Daily P secretion: Value (mg)	Daily P secretion: Reference*
Parotid saliva	5	1	2268	5
Submaxillary saliva	0·5	1	—	—
Residual saliva	5	1	2225	5
Gastric juice	4	2	—	—
Bile	1	3	550	6
Pancreatic juice	0·3	3	—	—
Brünner's glands	0·6	4	—	—
Caecum	0·2	3	—	—
Total	16·6	—	5043	—
Total secretion as estimated by method of Blau *et al.* (1957)			3500† (2500–4560)	

Values for the P content of the other digestive secretions are not available.
* References: 1, Kay (1960); 2, Masson & Phillipson (1952); 3, Storry (1961); 4, Harrison & Hill (1962); 5, Tribe & Peel (1963); 6, Adams & Heath (1963).
† Mean for control sheep fed on diets 2 and 3. Range given in parentheses.

Total and metabolic faecal Ca

In contrast to the results obtained for metabolic faecal P excretion, the rate of metabolic faecal Ca excretion did not correlate with intake or absorption of the element (Table 5) and intake of P did not appear to influence the rate significantly. However, under our conditions a slightly though not significantly ($P > 0·1$) higher rate of Ca excretion was noted for sheep fed on diet 1; the rate was consistently lower in all groups during period 1 than in period 2. This finding may reflect the fact that the values derived from periods 1 and 2 depended upon different methods of calculation. However, since Ca intakes of the sheep were higher during the metabolism study than during the depletion period, the possibility that the increase between the periods reflects a higher intake cannot be discarded.

Total intestinal Ca secretion

Table 3 shows that the dietary Ca did not equilibrate with the endogenously secreted element. Had a soluble Ca supplement been used in the diets, different results might have been obtained. However, the rates of total intestinal Ca secretion were again calculated by the method of Blau *et al.* (1957) and are recorded in Table 2. In view of the results shown in Table 3 the values given in Table 2 probably represent overestimates of total intestinal Ca secretion. The estimated rate of intestinal Ca secretion appears to be less than 1000 mg/day, which is considerably lower than the rate of P secretion. Storry (1961) estimated that the total Ca flux into the intestine of sheep was approximately 540 mg/day, with which our results are in reasonable agreement.

Table 5. *Mean values with their standard errors for calcium intake and for faecal and urinary Ca excretion by five phosphorus-depleted and six control sheep fed on diets varying in Ca:P ratio and in P content*

Diet no.	Ca:P ratio	P status	Ca intake (g/week)	Metabolic faecal Ca (g/week)	Total faecal Ca (g/week)	Urinary Ca (g/week)	Cumulative ^{45}Ca excretion in faeces (% injected dose)*
				Period 1			
1	10·4:1	Depleted	31·1 ± 3·41	5·1 ± 0·95	29·4 ± 3·91	0·92 ± 0·295	17·4
		Control	38·1 ± 2·98	4·03 ± 0·64	34·2 ± 4·13	1·36 ± 0·289	
2	1·9:1	Depleted	18·8 ± 2·18	3·1 ± 0·60	14·9 ± 3·03	0·14 ± 0·008	12·2
		Control	23·5 ± 2·07	3·5 ± 0·46	20·1 ± 1·64	0·14 ± 0·017	
3	9·9:1	Depleted	104·9 ± 10·24	3·2 ± 0·25	77·2 ± 8·99	0·22 ± 0·025	11·2
		Control	142·3 ± 12·13	3·5 ± 0·43	125·5 ± 11·27	0·50 ± 0·111	
				Period 2			
1	10·4:1	Depleted	30·8 ± 3·50	5·4 ± 0·52	31·1 ± 2·87	1·05 ± 0·322	—
		Control	38·1 ± 2·98	4·5 ± 0·33	36·1 ± 2·81	1·21 ± 0·273	
2	1·9:1	Depleted	18·8 ± 2·18	4·1 ± 0·42	15·2 ± 2·26	0·16 ± 0·044	—
		Control	24·4 ± 1·63	4·5 ± 0·64	22·2 ± 0·96	0·15 ± 0·033	
3	9·9:1	Depleted	105·3 ± 10·20	3·8 ± 0·28	85·5 ± 8·55	0·17 ± 0·067	—
		Control	142·3 ± 12·13	5·3 ± 0·62	123·6 ± 10·35	0·43 ± 0·053	

* Dietary means.

^{32}P and ^{45}Ca elimination in faeces

The cumulative faecal excretions of ^{32}P and ^{45}Ca are shown in Figs. 2 and 3 respectively. P-depleted sheep excreted significantly less ^{32}P than did the controls during the same period (Table 1). Apparently, body P was more efficiently retained by the depleted sheep. On the other hand, ^{45}Ca excretion was not significantly different between P-depleted and control sheep. However, as summarized in Table 5, the excretion of ^{45}Ca was slightly higher in the group fed on the diet deficient in P, which in part reflects a slightly higher rate of metabolic faecal Ca excretion. This excretion rate may also reflect the higher specific activity of serum Ca in these sheep (Young, unpublished results).

Urinary P and partition of endogenous P loss

Urinary P excretion was low on all treatments (Table 1). Table 6 shows a comparison of the urinary contribution and the total rate of endogenous loss in period 2. Results for period 1 were similar to those given in Table 6, except that the P-depleted

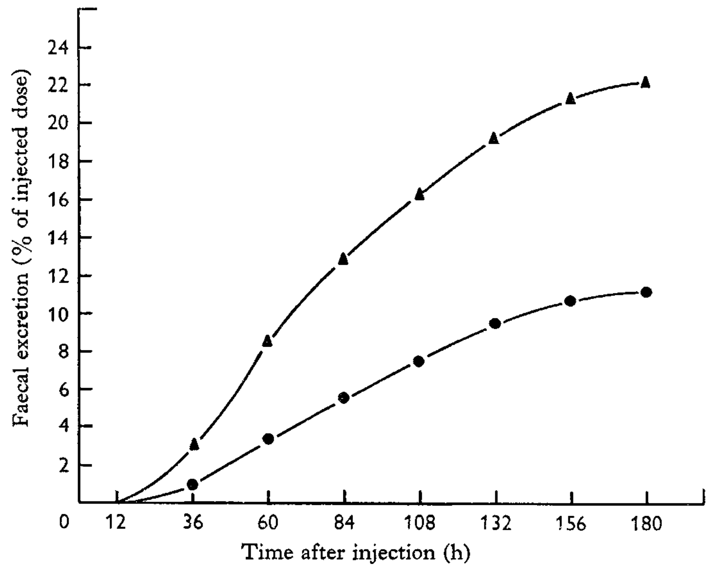

Fig. 2. Cumulative faecal excretion of ^{32}P (administered subcutaneously) by phosphorus-depleted and control sheep. Except for the 180 h value, which represents the mean for six depleted and nine control sheep, each point represents mean values for fifteen depleted and eighteen control sheep. ▲—▲, control sheep; ●—●, depleted sheep.

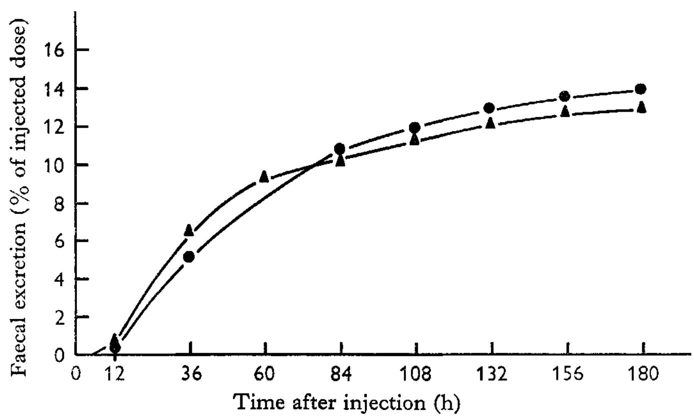

Fig. 3. Cumulative faecal excretion of ^{45}Ca (administered subcutaneously) by phosphorus-depleted and control sheep. Except for the 180 h value, which represents the mean for six depleted and nine control sheep, each point represents mean values for fifteen depleted and eighteen control sheep. ▲—▲, control sheep; ●—●, depleted sheep.

group fed on diet 3 excreted less P by the urinary route than during period 2; the equivalent value for period 1 was 4·4 %. In two control sheep fed on diet 2 extremely high values for urinary P excretion were observed. These were 1·45 and 6·45 g P per week, which were markedly higher than the values obtained for any of our other animals. No reasonable explanation can be offered for this finding. If these two sheep are discarded there is a close similarity between the results of all dietary treatments.

Table 6. *Percentage of total endogenous calcium and phosphorus losses in urine and faeces in five P-depleted and six control sheep during period 2*

Diet no.	P status	Ca Faeces	Ca Urine	P Faeces	P Urine
1	Depleted	83·6	16·4	98·4	1·6
	Control	78·9	21·1	97·2	2·8
2	Depleted	96·3	3·7	97·5	2·5
	Control	96·7	3·3	83·3*	16·7*
3	Depleted	95·6	4·4	88·6	11·4
	Control	92·5	7·5	96·8	3·2

* Two sheep gave high urinary P values. Without these, values would be 98·7 and 1·3 for faeces and urine respectively.

Urinary Ca and partition of endogenous Ca loss

Urinary Ca excretion, unlike P excretion, was influenced significantly ($P < 0{\cdot}01$) by current dietary treatment (Table 5). Urinary Ca was considerably higher in sheep fed on the P-deficient diet (diet 1) than in animals fed on the diets (diets 2 and 3) containing adequate P. As a result, the urinary contribution to total endogenous loss of Ca (Table 6) was low when the intake of P was adequate; it increased significantly when P intake was deficient. The results shown in Table 6 confirm the view expressed by Hill (1963) that urinary Ca accounts for a small proportion of the total endogenous loss under conditions of adequate Ca and P nutrition. These observations also tend to emphasize the difference between ruminants and man, since the urinary route of both Ca (Bronner, Richelle, Saville, Nicholas & Cobb, 1963) and P (Schofield & Morrell, 1960) appears to account for a greater percentage of the total endogenous loss in man than in sheep.

Change in total intestinal P secretion

A comparison of the total intestinal secretion of P during both periods was made by means of the formula proposed by Comar (1955); the results are recorded in Table 7. Whereas the rate of excretion of metabolic faecal P by the depleted sheep fed on diets 2 and 3 markedly increased during the two periods, it would appear that the rate of intestinal secretion did not increase during the same time. In fact, the depleted sheep fed on diet 3 appeared to secrete less P into the intestine during the second period. This suggests that the increase in excretion of metabolic faecal P was probably due to a decreased intestinal absorption during the second period, as described in the previous paper (Young, Richards *et al.* 1966). This finding shows that results based entirely upon the faecal elimination of radioisotopes must be interpreted with care. Although the total ^{32}P elimination in the faeces was lower in depleted than in control sheep, this may be the result of a greater reabsorption in the intestinal tract rather than of a lower rate of P entry into the intestine. However, from the standpoint of overall balance, body P was more efficiently retained by the depleted sheep. Control sheep fed on diet 2 showed a substantial change in total intestinal secretion between the periods. The reason for this change is not readily discernible. It may reflect the fact that these sheep absorbed less P during the first period, as previously described (Young, Richards *et al.* 1966).

Table 7. *A comparison of mean values (g/week) for the total intestinal phosphorus secretion and metabolic faecal P excretion in five P-depleted and six control sheep during both periods**

		Period 1		Period 2	
Diet no.	P status	Total intestinal P secretion†	Metabolic faecal P excretion	Total intestinal P secretion†	Metabolic faecal P excretion
1	Depleted	7·9	2·8	5·3	2·4
	Control	13·0	4·4	9·7	3·2
2	Depleted	20·8	2·8	19·7	4·7
	Control	12·9	5·5	25·0	6·9
3	Depleted	31·4	2·4	23·8	4·7
	Control	21·7	6·0	23·4	6·6

* Calculated from values in Table 1 and in a previous paper (Young, Richards *et al.* 1966).

† Total intestinal secretion $= \frac{\text{metabolic faecal P}}{1-(\text{net digestibility})/100}$ (from Comar, 1955).

The results given in Table 7 suggest that intestinal secretion of P was decreased after 4 days on a P-deficient diet and that a further decrease occurred during the second period. This may be due to the decrease in serum P concentration which occurred during the experimental period (Young, Richards *et al.* 1966) and suggests that serum P levels might influence the total rate of intestinal P secretion.

It should be emphasized that the estimates of total P secretion reported in this paper are indirect and the possibility remains that between periods 1 and 2 no change occurred in the extent to which the secreted P was absorbed. If there was no change in the extent to which secreted P was absorbed, the increased rate of metabolic faecal P excretion would reflect an increased rate of intestinal P secretion. This finding would add further support to the concept that intestinal secretion of P in the ruminant plays a major part in the maintenance of P homoeostasis.

In agreement with earlier work by Bronner (1964), it was found that metabolic faecal Ca excretion did not increase during short periods of high Ca intake. This fact supports the view of Hansard & Plumlee (1954) that metabolic faecal Ca reflects the Ca status of the animal more closely than it does the current Ca intake. During both periods the metabolic faecal Ca excretion by P-depleted sheep fed on diets 2 and 3 was slightly, although not significantly, lower than that for the control sheep.

Urinary Ca excretion increased as a result of deficient P intake, which agrees with earlier findings in rats (Carlsson, 1953; Henry & Kon, 1953). Copp, Hamilton, Jones, Thompson & Cramer (1951) suggested that renal clearance of Ca was increased in rats fed on a P-deficient diet and this might explain the present results. However, the mechanisms involved remain to be established.

Clearly, from these results there appears to be a difference in the metabolism of these elements by the tissues of the intestinal tract. The physiological significance of changes in metabolic faecal P excretion requires further study. Direct estimates of the rate of total intestinal P secretion in both ruminant and non-ruminant species should be made under differing dietary conditions before the role of intestinal P secretion in the maintenance of P homoeostasis can be fully ascertained.

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