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Absorption of major minerals in the small and large intestines of the ruminant

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There is no reason to suppose that the intestines of ruminants differ basically from those of most non-ruminants in the way in which they handle minerals. Special factors peculiar to ruminants are most likely to be found in the nature of their diet and the modifying effects of the alimentary tract before the abomasum on that diet.

Exchange of sodium, potassium and chloride in the intestines and the regulation of water content of the digesta

Sodium and potassium contents of digesta entering the duodenum of non-ruminants, including non-ruminating calves, are influenced both by the diet and by endogenous factors. Passage of digesta down the small intestine of non-ruminating calves leads to a regulation of Na to K ratio so that in the ileum it depends upon the Na-K status of the animal and little or not at all upon the immediately preceding Na or K intake. Calves fed successively on Na-deficient and K-deficient synthetic milks showed marked changes in ileal Na and K concentrations only after 1 or 2 days on the new diet, when adaptation had taken place. Values for ileal Na to K mole ratio then varied from about 0.3 to 13 for Na-deficient and K-deficient diets respectively compared with normal values of about 3-7 (Smith, 1966). Similar adaptation to a low Na intake has been shown for the dog (Field, Swell, Dailey, Trout & Boyd, 1955).

The amounts of Na and K reaching the ileum are the final result of net secretion of Na into the duodenum and subsequent net absorption of Na and K in the rest of the small intestine (Mylrea, 1966 and Fig. 1). K absorption is probably passive (Donnet, Jacquin & Fondarai, 1963; Gilman, Koelle & Ritchie, 1963) but for the calf is none the less very efficient, at least with diets containing as much K as does milk (Smith, 1962; Mylrea, 1966). It has frequently been demonstrated that Na is actively absorbed (Parsons, 1967) and, although the mechanism is unclear, it

seems probable that Na, K exchange is controlled by hormones of the adrenal cortex (Levitan & Ingelfinger, 1965; Shields, Mulholland & Elmslie, 1966; Moll, 1967).

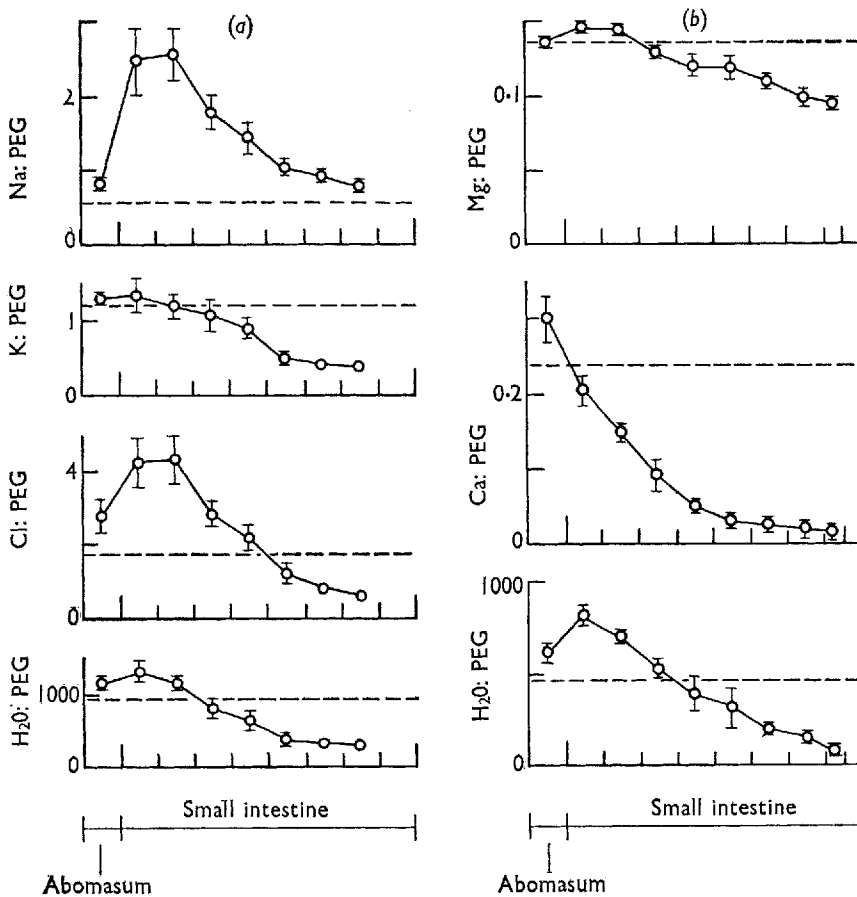


Fig. 1. Ratios of diet constituents to marker (polyethylene glycol (PEG)) (g/g) along the abomasum and small intestine of the non-ruminating calf. (a) Mean results with their standard errors for Na, K, Cl and water for five calves slaughtered 0.5-1.5 h after feeding with a fat-free synthetic milk containing PEG. Results were obtained only up to the marker front which travelled further in some calves than in others, so that fewer results were obtained for the more distal intestine. (b) Mean results with their standard errors for Ca, Mg and water for four calves slaughtered 2.5-3 h after feeding with a solution containing 5% glucose, 0.013 M-MgCl₂, 0.013 M-CaCl₂ and PEG. Ratios in the diets are shown by horizontal broken lines.

In ruminants the pattern of Na secretion into the duodenum and net absorption of Na and K in the rest of the small intestine appears to be qualitatively similar to that shown by non-ruminants (van Weerden, 1961; Pfeffer, Bertzbach & Lenkeit, 1967). The situation is, however, modified by the large amounts of saliva, with an Na to K ratio depending upon the Na-K status of the animal (Kay, 1960), added to the digesta and by absorption of Na and K before the abomasum (Scott, 1967). The Na and K concentrations in digesta entering the duodenum are therefore mainly

controlled by endogenous factors. In six calves fed a normal hay and concentrate diet containing about 0.25 g Na and 1.2 g K per 100 g dry matter we found that the mean Na to K mole ratios in the proximal duodenum and distal ileum respectively were 2.2 ± 0.2 and 3.2 ± 0.3 . When the calves were put on to pasture containing about 0.09 g Na and 2.3 g K per 100 g dry matter these ratios changed over a period of 1-2 weeks to 0.5 ± 0.1 and 0.4 ± 0.1 respectively. Similar, though less consistent, changes in the faeces were found, and this has also been shown for sheep (Devlin & Roberts, 1963) and cows (Renkema, Senshu, Gaillard & Brouwer, 1962). Adaptation to low Na intakes seems therefore to be a characteristic of ruminants as well as non-ruminants although the process can sometimes be confused, in the short term, by changes in the volume and composition of rumen fluid causing Na to be temporarily retained in or released from this compartment (Dobson, Scott & Bruce, 1966). Nevertheless, adaptation is normally so efficient that cattle can have very low Na intakes for long periods without showing obvious clinical signs of Na deficiency although milk yield may be depressed (McDonald, 1968). It should perhaps be borne in mind, however, that low levels of Na in the gut can lead to impaired utilization of other nutrients, particularly glucose and amino acids (Nelson & Beargie, 1965; Rosenberg, Coleman & Rosenberg, 1965), and this does not seem to have been investigated in ruminants.

Most evidence suggests that water exchange in the small intestine is passive (Parsons, 1967). In the non-ruminating calf (Smith, 1966) and other non-ruminants (cf. Kalser, Williams, Peterson & Smitherman, 1964) digesta are nearly isotonic by the time they reach the ileum and this is true also in sheep (Care, Vowles, Mann & Ross, 1967), ruminating calves (Smith, unpublished data) and adult cows (van Weerden, 1961). It appears that most absorption of water in the small intestine occurs secondarily to the absorption of osmotically active solutes. Some water is absorbed with low-molecular weight organic solutes but for much of the small intestine it is clear that absorption of Na and K (with associated anions) is the main governing factor. The amount of water remaining with the digesta at the ileum is usually closely related to the amounts of Na and K (and to a lesser extent magnesium) remaining at this site (Smith, 1966). In general, in our experiments with calves, changes in Na to K ratio have not been accompanied by consistent changes in the total moles of (Na+K) or water passing the ileum in unit time (Smith, 1966, and unpublished data). Much information about ileal flow has been obtained by studying human subjects with ileostomies. In such patients it has usually been found that the amounts of water in digesta leaving the ileum in unit time are fairly constant for most diets (e.g. Kramer, Kearney & Ingelfinger, 1962). Factors influencing ileal flow in non-ruminating calves have been discussed by Smith (1966), but for normal animals fed on milk the amounts of water passing the distal ileum were similar to those shown by human subjects. Ruminating calves and sheep, however, showed much greater amounts (Table 1), and human subjects eating diets containing much indigestible roughage also showed a small increase (Kramer *et al.* 1962). These greater flows of water, associated with greater amounts of (Na+K), are clearly necessary to maintain the additional insoluble matter in a mobile condi-

Table 1. Mean amounts of water and of (Na+K) passing the distal ileum of different animals in unit time

Animal	No.	Body-weight (kg)	Diet	Digesta passing distal ileum*			Reference
				Water (g/h)	Na+K (m-moles/h)		
Man	7	60	Normal mixed	19	2.8		Kramer <i>et al.</i> (1962)
Non-ruminant calf	5	55-75	Milk	21-36†	3.0		Smith (1966)
Ruminant calf	3	70-100	Hay + concentrates or grass	230	31		Smith (unpublished results)
Sheep	2	32-43	Hay + concentrates	110	17		Goodall & Kay (1965)

*In all animals the flow was, to a greater or lesser extent, intermittent. Mean hourly values are given for collections made over much longer periods and do not necessarily imply a consistent flow from hour to hour.

†Variation produced by the cyclic arrival of residual dietary magnesium at the ileum.

Table 2. Percentage net absorption of minerals and water between proximal duodenum and distal ileum of calves aged 3-5 months

(Calves were fistulated at the two sites. Polyethylene glycol was given with the diet for two or three feeds and then a sample taken from the duodenum. At the same time phenol red was injected into the duodenum and effluent from the distal ileum examined until the dye appeared. An ileal sample was then taken and its composition compared with the duodenal sample)

Diet	No. of calves	Mean concentration in proximal duodenum (m-moles/l.)						Mean net absorption in small intestine (%)						
		Na	K	Cl	Ca	Mg	PO ₄	Water	Na	K	Cl	Ca	Mg	PO ₄
Hay, concentrates	3	54	38	130	11	3.8	16	75 ± 3	63 ± 7	73 ± 3	94 ± 1	59 ± 6	6 ± 9	88 ± 4
Pasture	2	33	57	130	7.4	3.7	11	82 ± 3	77 ± 1	73 ± 2	95 ± 2	82 ± 1	18 ± 10	72 ± 4

tion, but it is not clear how the control is exercised. The effect is to reduce net Na and K absorption up to the ileum in the ruminant, compared with the non-ruminant, and to lead to greater dilution of other solutes in the digesta at this site. This has particular significance for Mg and will be discussed later.

Evidence obtained with non-ruminating calves (Smith, 1962), ruminating calves (Table 2), cows (van Weerden, 1961) and sheep (Pfeffer *et al.* 1967) shows that chloride is normally the major anion present in material entering the duodenum but is absorbed more effectively than (Na+K) in the small intestine where it is partly replaced by bicarbonate.

Sodium and chloride are very effectively absorbed in the large intestine of ruminants (van Weerden, 1961; Goodall & Kay, 1965; Pfeffer *et al.* 1967) and non-ruminating calves (Smith, 1962). Potassium is also absorbed but somewhat less efficiently so that the Na to K ratio always decreases between ileal contents and faeces. In the non-ruminating calf absorption of K and chloride in the large intestine is of little importance as only small amounts leave the distal ileum. Greater amounts of Na enter the large intestine but, even so, milk-fed calves may be kept with a discharging ileotomy for many weeks without serious effect (Smith, 1966). Similar considerations probably apply to non-ruminants in general, and human subjects with ileotomies live for many years without ill effects or any need for drastic mineral supplementation (cf. Kramer *et al.* 1962). However, with the large volume of digesta leaving the ileum in ruminants (Table 1), the large intestine may be of vital importance. Goodall & Kay (1965), for example, have shown that sheep on some diets pass more Na and chloride from the ileum than they ingest.

Absorption of calcium and phosphate

For several non-ruminant animals, *in vitro* experiments with everted sacs of intestine and perfusion experiments *in vivo* have shown that (a) Ca is actively absorbed from the small intestine with the absorption approaching a maximum rate with increasing concentration, (b) the process is most efficient in the proximal duodenum, (c) absorption is influenced by vitamin D (Schachter & Rosen, 1959; Wasserman, Kallfelz & Comar, 1961; Cramer & Dueck, 1962; Schachter, Kowarski & Finkelstein, 1964; Krawitt & Schedl, 1968). Absorption is also controlled by endogenous factors and improves with Ca depletion (e.g. Hansard, Comar & Plumlee, 1951). Parathyroid hormone may be responsible for governing this adaptation (Shah & Draper, 1966). Efficiency of Ca absorption also decreases with increasing age (Hansard & Crowder, 1957) and is affected by other endogenous (e.g. oestrogens and thyroxine) and dietary (e.g. lactose and certain amino acids) factors. It may be depressed by gut stasis, and Moodie & Robertson (1962) have suggested that this may be a contributory factor in clinical hypocalcaemia at parturition (milk fever). The controversial subject of Ca-Mg interrelationships is discussed in the next section.

Absorption of Ca by ruminants appears to follow a general pattern similar to that shown by non-ruminants. Thus, for example, it is influenced by vitamin D (Wallis, Palmer & Gullickson, 1935; Conrad, Hansard & Hibbs, 1956), by Ca status of the animal (Manston, 1967) and by age (Hansard, Comar & Plumlee, 1954).

In the milk-fed calf, absorption of Ca was very effective in the proximal small intestine (Fig. 1) as would be expected from the general findings for non-ruminants described above. It is not clear whether the finding of Phillipson & Storry (1965) that net absorption of Ca occurred only below the bile duct in sheep represents a real difference for this animal or a more precise location of the site studied. It may be related to the effect of bile salts on Ca absorption reported by Webbling & Holdsworth (1966).

Absorption of Ca in the non-ruminant can be depressed by dietary factors, such as phytate, which precipitate or bind Ca in the small intestine. In the ruminant such substances may be destroyed in the rumen but others may be elaborated. Storry (1961*b*) showed that abomasal digesta of sheep contain materials which bind Ca above pH 5. Nucleic acids which are formed in the rumen and pass largely unchanged to the duodenum (Smith, McAllan & Hill, 1968) are potent Ca-binding agents down to about pH 5 (Chang & Carr, 1968) and were presumably in part responsible for this binding. Other Ca-binding agents have been demonstrated in the calf ileum (Smith & McAllen, 1966). It seems that the poorer net absorption of Ca in the small intestine shown by ruminating calves (Table 2) compared with milk-fed calves (Smith, 1962) and the poorer overall Ca absorption which they show (Lengemann, Comar & Wasserman, 1957) is due, at least partly, to these binding materials.

There is no evidence to show that Ca is absorbed appreciably in the large intestine, and in the milk-fed calf there was virtually no net exchange of Ca between ileal contents and faeces (Smith, 1962).

With different animals, excessive amounts of either Ca or phosphate in the diet have sometimes been found to interfere with absorption of the other ion (O'Dell, Morris, Pickett & Hogan, 1957; Compère, 1965), presumably, in part, by leading to precipitation of insoluble calcium phosphate. Cattle and sheep, however, appear able to tolerate quite a wide range of Ca to P ratios in their diet without any serious interference in the utilization of either (Bohstedt, 1942; Young, Richards, Lofgreen & Luick, 1966). Precipitation of calcium phosphate certainly occurs in the small intestine of ruminating and non-ruminating calves even with normal intakes (Smith & McAllan, 1966), but only where the pH exceeds about 6.5 and not therefore in the middle and upper small intestine where most absorption of Ca and probably phosphate occurs.

Inorganic phosphate is absorbed very efficiently in the small intestine of both the ruminating and non-ruminating calf (Smith, 1966, and Table 2). Little is known of the mechanism of absorption although the *in vitro* results of Harrison & Harrison (1961) suggest that active transport might be involved. Adaptation in net absorption efficiency with changing P intakes has been demonstrated in the sheep (Young, Lofgreen & Luick, 1966).

Absorption of magnesium

Up to about 1 month of age calves absorb Mg in the large as well as the small intestine (Smith, 1962), giving efficient overall net absorption (about 70–90% intake). This ability is lost with increasing age until by about 3–4 months the

small intestine is the only important absorption site. This also seems to be the main site of Mg absorption in adult sheep (Field, 1961), rabbits (Aikawa, 1959) and human subjects (Graham, Caesar & Burgen, 1960). In non-ruminating calves net Mg absorption appears to occur slowly over much of the small intestine (Fig. 1), is not very efficient even when milk or simple magnesium chloride solutions are fed (about 20–40% intake (Smith, 1962 and unpublished data)), and shows no tendency to adapt in Mg deficiency. Net absorption in the small intestine or whole alimentary tract of ruminating calves is however even less efficient (Smith, 1959 and Table 2) and a large loss of Mg in the faeces (usually about 70–95% intake) appears to be a characteristic of adult cattle and sheep (Rook & Storry, 1962; Field, 1962). Most of this faecal loss appears to consist of unabsorbed food Mg with normal intakes (Blaxter & McGill, 1956; Field, 1959).

Experiments to examine the possibility of competition between Mg and Ca for absorption in the gut, which might, if established, provide evidence of active Mg absorption, have given contradictory results. In experiments by different workers each of these elements has been shown to depress, have no effect upon or improve absorption of the other. In non-ruminating calves we found no effect. Some of these experiments have been discussed by Smith (1964*a*) and more recent work has not resolved the matter (Clark, 1965; Kessner & Epstein, 1966; Lifshitz, Harrison & Harrison, 1967). However, it appears that, at least in the calf, Mg absorption in the gut has quite a different pattern to that of Ca (Fig. 1) and is not appreciably influenced by vitamin D (Smith, 1958). Furthermore, no experiments have ever demonstrated transport of Mg across the gut wall against an electrochemical gradient. In fact, the low efficiency of Mg absorption and the apparently unlimited increase (unless diarrhoea occurred) in amounts absorbed with increasing intake shown by a number of animals (Smith, 1959, 1962; Graham *et al.* 1960; Heaton & Parsons, 1961; Chutkow, 1964) strongly suggest passive absorption. As would be expected, because high concentrations of Mg retain water osmotically in the gut (Smith, 1966), percentage absorption tended to decrease at high intakes but there was no indication of the absorption mechanism becoming saturated. Scott (1965) has calculated that, before passive diffusion from small intestine lumen to blood could occur, Mg concentrations in the digesta of above about 1.4–2.1 m-moles/l. would be necessary to overcome the fairly small electrical potential (7–15 mV, blood positive) across the wall of the small intestine of the sheep. Care & van't Klooster (1965) found that Mg absorption from ileal loops occurred only above about this concentration. Digesta from non-ruminating calves and ruminants normally contain appreciably higher total Mg concentrations than this, at least in the ileum (Smith, 1962; Smith & McAllan 1966; Storry, 1961*a*; and Table 2), but all the Mg is not necessarily in an available ionic form (see below).

Suttle & Field (1967) found that high K intakes depressed Mg absorption in the sheep although we have not found this to be so in non-ruminating calves (unpublished observation). The finding in sheep may be related to changes in aldosterone production since aldosterone infusion has been shown to depress plasma Mg in sheep (Care & Ross, 1963; Scott & Dobson, 1965) and apparent changes in aldo-

sterone status, as a result of changes in dietary K, have been related to falls in plasma Mg in sheep going on to pasture (Dobson, Scott & McDonald, 1966). The mechanism of these interactions is, however, not clear and the results do not provide evidence of interference with an active Mg absorption process. One possibility is that high K, low Na concentrations in the small intestine are associated with an increase in the electrical potential between digesta and blood, as they are in the sheep rumen (Sellers & Dobson, 1960) and rat colon (Edmonds, 1967).

If it is accepted that Mg moves passively across the wall of the small intestine then it appears that the only factors (apart from electrical potential) which are likely to be responsible for major differences in the efficiency of Mg absorption are the concentration of available Mg in the digesta and the time of contact between the digesta and the absorbing surface. The latter depends upon transit time through the small intestine and this has been shown to be related to the efficiency of Mg absorption in the non-ruminating calf (Smith, 1963). Transit time variation can be responsible for animal-to-animal variation in this efficiency but there is no evidence to show that it is responsible for differences between one ruminant diet and another (Smith, 1964*b*). Concentrations of Mg ions in the digesta in the small intestine of ruminants tend to be low because of the large amounts of water retained in the ileum (Table 1) and the presence in the digesta of materials able to bind Mg at intestinal pH. Such materials have been demonstrated in the abomasum of sheep (Storry, 1961*b*) and ileum of ruminating calves (Smith & McAllan, 1966). Lowering of ultrafiltrable Mg in the calf ileum was due partly to a variable precipitation with phosphate (usually as a mixed Ca-Mg phosphate rather than as $MgNH_4PO_4$ (Smith & McAllan, 1967)) and partly to binding independent of phosphate. The latter was estimated to account for 30-45% of the Mg in calf ileal contents but did not increase in calves put on to spring pasture.

Clinical hypomagnesaemia in cattle and sheep is usually associated with transferring the animals on to spring pasture. Grass causing the condition often has rather a low Mg content (Butler *et al.* 1963; Larvor & Guéguen, 1963) and dry-matter intakes may be low in animals when they are first put on to such pasture (Rohr & Kaufmann, 1967). These factors combined with the characteristically poor Mg absorption shown by ruminants are probably enough in themselves to cause clinical hypomagnesaemia in some animals. Nevertheless, it appears also that the efficiency of Mg absorption from a diet of spring grass is less than from most stall diets (Rook & Campling, 1962; L'Estrange, Owen & Wilman, 1967). Many theories have been put forward in attempts to account for this reduced absorption, mostly based on the presence of factors which might reduce Mg availability in the digesta. None offers an adequate explanation of the phenomenon, but the presence of certain organic acids in pasture grass which might chelate Mg in the gut (Burt & Thomas, 1961; Stout, Brownell & Burau, 1967) merits further investigation.

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Diarrhoea of nutritional origin

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Definition

For the purpose of this paper, diarrhoea will be defined as the condition in which faeces containing less than 12% dry matter are produced. It may be the result of poor absorption of water from, or increased secretion of water into, the alimentary tract, or in certain cases a reduced excretion of faecal dry matter.

Economic importance

The economic importance of diarrhoea in the ruminant animal is mainly of relevance in the nutrition at the pre-ruminant stage. In a recent survey of calf wastage (Leech, Macrae & Menzies, 1968) 8.9% of 40 000 calves were affected with diarrhoea on some occasion during the 1st year of life. The cause of death in 44.9% of 350 post-mortem examinations was classified as being due to gastro-intestinal disorders, with a further 24.8% resulting from septicaemia. Since an earlier survey of 2046 post-mortem examinations showed that *Escherichia coli* was associated with 46% of deaths up to 6 months of age and *Salmonella* with 24% (Veterinary Investigation Service, 1964), the great majority of the gastro-intestinal disorders are clearly associated with colibacillosis. Most of the mortality from diarrhoea occurs at a young age and, in the survey of Leech *et al.* (1968), the probability of death at any time in home-bred calves was about equal to the reciprocal of age, and percentage mortality up to age W (in weeks) was equal to $\log_e W + 1.72$.