Getting it out of the (digestive) system: hindgut fermenters and calcium

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Introduction

Ruminants, omnivorous rodents, pigs and humans, dogs, cats and other carnivores (e.g., sea lions), and lizards regulate their calcium (Ca) metabolism at the site of absorption in the gut, absorbing only the amount necessary to meet their requirements. In dairy cattle, the apparent digestibility of Ca averages, independent of the composition of the diet, app. 30 %. (Khorasani et al., 1997) In contrast, horses absorb the majority of ingested Ca in the gut and excrete surplus Ca in the urine. (Schryver et al., 1974) Thus, horses achieve apparent digestibility coefficients for Ca of up to 70 % and more. The majority of the Ca is absorbed in the small intestine. (Schryver et al., 1970) Ca apparent digestibility increases with increasing dietary Ca content in horses, both when roughage-only diets are investigated (Cymbaluk, 1990) or concentrate diets that only differ in their Ca and phosphorus (P) content. (Nielsen et al., 1998) A similar Ca metabolism with increased gastrointestinal absorption and urinary excretion has been observed in rabbits. (Chapin et al., 1967, Cheeke et al., 1973, Kamphues et al., 1986) In veterinary medicine, the horse and the rabbit are usually considered as peculiar in this respect. The tendency to excrete Ca via urine is frequently the cause of uroliths in rabbits (Kamphues, 1991) that often require surgical intervention. Even in horses, Ca-containing uroliths are observed, (Neumann et al., 1994) although the size of the anatomical structures of the urinary tract will make clinical problems much less likely than in rabbits. Interestingly, Ippen & Henne (Ippen et al., 1991) also report a particularly high incidence of renal diseases with kidney stones in captive wild equids.

However, a comparison with other, less well-studied species shows that horses and rabbits are no outliers; rather, the strategy to absorb a majority of the dietary Ca from the gut and excrete any surplus in the urine seems to occur in most hindgut-fermenting herbivores, such as wild equids, tapirs, rhinoceroses, elephants, (Clauss et al., 2007; Clauss et al., 2003; Clauss et al., 2005; Hintz et al., 1976; Schryver et al., 1983) in hyraxes (Leon et al., 1979) and herbivorous rodents (Kaufman et al.; 1976, Shirley et al., 1967; Shore et al., 1992) as well as in subterranean herbivores such as naked mole rats, (Buffenstein et al., 1991; Pitcher et al., 1994; Pitcher et al., 1992; Skinner et al., 1991) and also in herbivorous tortoises. (Liesegang et al., 2001)

The evolutionary background for this fundamental difference in Ca absorption between hindgut fermenters and other animals, and its adaptive significance for hindgut fermenters, has received little attention to date (but see (Leon et al., 1979). To our knowledge, two different reasons for the observed peculiarity of hindgut fermenters have been proposed.
1. Pitcher and Buffenstein (Pitcher et al., 1994) speculate that the adaptation of absorbing large amounts of Ca could be accounted for by the fact that, in plant material, Ca is bound to the cell wall fraction and can only be dissociated slowly and incompletely. Hindgut fermenters, in which the cell wall fraction is not digested prior to the Ca absorption sites in the small intestine, therefore should have evolved particularly effective Ca absorption mechanisms or, in other words, would not have needed to evolve a protection mechanism against the absorption of too much Ca.

2. Clauss et al. (Clauss et al., 2007) speculate that Ca needs to be channelled around the site of fermentation so that the bacterial microflora can make use of ingesta P that is not complexed by Ca.

Here, we address the merits of each of these hypotheses, hoping to stimulate further research into this interesting phenomenon.

1. High absorptive capacity as a consequence of low dietary Ca availability in plant material

This concept is supported by several in vitro-trials on the availability of Ca from, or its ligation to, the cell wall fraction of plant material. (Ibrahim et al., 1990) Additionally, the cell wall fraction of plant material sequesters Ca in the small intestine, thus probably reducing its availability even further. (Emanuele et al., 1991) This would mean that hindgut-fermenting herbivores did not have to face, in the course of evolution, a situation of high Ca availability in the intestine, in contrast to omnivores, carnivores, and foregut-fermenting herbivores. In the latter, cell wall-bound Ca would be released to a large extent in the foregut due to microbial fermentation activity. Thus, there should have been no danger for hindgut fermenters to overcharge their urinary excretion system with Ca; (Leon et al., 1979) other animals, however, had to evolve a feedback mechanism that prevented the readily available Ca to accumulate in urine and precipitate as uroliths. Such a feedback mechanism would probably be the well-known vitamin D-dependent absorption of Ca from the intestine. In horses, rabbits and mole rats, vitamin D has little importance or influence on Ca absorption from the gut.

Should the high intestinal Ca absorption in hindgut fermenters be a reaction to the low availability of Ca from plant material, then artificial diets with a high proportion of finely ground plant material and supplemented with non-cell wall-bound Ca from mineral premixes should lead to even higher apparent Ca digestion coefficients. However, it has been observed that in horses, Ca absorption is higher, not lower, on roughage diets as compared to diets consisting of mixed feeds/concentrates. (Stadermann et al., 1992) The same effect has been observed in hyraxes (Leon et al., 1979) and elephants. (Clauss et al., 2003) Nehring (Nehring, 1991) collated literature data for horses and found different correlations for Ca intake and Ca absorption between roughage-only diets and diets with concentrates. Fig. 1a, representing the data sources collated by Nehring (Nehring, 1991) supplemented with additional literature data, also demonstrates higher apparent Ca digestion coefficients for roughages than for mixed rations of similar Ca content. Therefore, a simply “unrefrained” Ca absorption in hindgut fermenters as an adaptation to low availability of this mineral in plant material appears unlikely. A conclusive test of this hypothesis would include the comparison of Ca absorption in horses on two dietary treatments, consisting of the same roughage, once given in its natural form (unchopped), and once finely ground.
2. High intestinal Ca absorption as a prerogative for microbial fermentation in the hindgut

An important prerogative for the growth of microorganisms that will finally ferment plant material - and thus allow herbivores to exploit their particular feeding niche - is the presence of sufficient amounts of phosphorus (P). Bacteria consist of only 0.1-0.3 g Ca/kg dry matter, (Durand et al., 1988) whereas their P content is between 6-19 g/kg dry matter; (Komisarczuk et al., 1987) this results in a Ca:P-ratio of about 1:100. Low levels of dietary P can reduce microbial growth, organic matter and cellulose digestibility, and the production volatile fatty acids – the main energy source of herbivores. (Breves et al., 1987, Komisarczuk et al., 1987) Ca can form insoluble complexes with P, thereby reducing its availability. In human patients with chronic renal failure, Ca carbonate (Slatopolsky et al., 1986) or Ca acetate (Mai et al., 1989) have been given as intestinal P binders to reduce the availability of dietary P. Therefore, it could be postulated that a prerogative for symbiotic, microbial digestion is that excess Ca be eliminated from the ingesta prior to the main fermentation chamber, in quantities that grant the microbial population a sufficient supply of available P. In hindgut fermenters, the dietary Ca:P-ratio should thus be an important determinant of the proportion of dietary Ca that is removed from the gastrointestinal tract, with higher Ca absorption at higher Ca:P-ratios. If the data on horses from Fig. 1a is plotted not according to dietary Ca content, but to dietary Ca:P-ratio, the difference between the different food types mostly vanishes (Fig. 1b). Higher apparent Ca digestion coefficients on forages are due to the high Ca:P-ratios in these feeds. In a similar manner, Ca absorption increased with increasing dietary Ca:P-ratio in Asian rhinoceroses. (Clauss et al., 2005)

If the hypothesis was valid that hindgut fermenters evolved a very effective Ca absorption as a response to the low availability of Ca in forages prior to bacterial fermentation, species adapted to forage of higher Ca content should display a less efficient Ca absorption than species adapted to forage of lower Ca content. If, however, hindgut fermenters evolved to shunt dietary Ca away from their bacterial symbionts, then we would expect that species adapted to forage of higher Ca content should display even more efficient Ca absorption than species adapted to forage of lower Ca content.

These conditions can be tentatively tested in large browsing and grazing hindgut fermenters. Because browse generally contains higher levels of Ca than grass (Clauss et al., 2006), one can collate literature data to test whether browsers actually have a higher or lower Ca absorption efficiency than grazers. According data for four large hindgut fermenters are presented in Fig. 2 – the browsers black rhinoceros (Diceros bicornis) and tapirs (Tapirus spp.), the mixed feeder Asian elephant (Elephas maximus), and the grazer white rhinoceros (Ceratotherium simum). Data is presented in comparison to the domestic horse, which is – like all equids – considered a grazer. Although more data appear warranted, these plots support the latter hypothesis, with browsers showing a particularly efficient Ca absorption.

Conclusion

These results suggest that the relevance of removing Ca from the gut for microbial fermentation should be further investigated. Interestingly, whereas in hindgut fermenters Ca is absorbed either in the small intestine (Schryver et al., 1970) or in the caecum, it is mainly absorbed directly in
the foregut in ruminants. (Khorasani et al., 1992, Schröder et al., 1997) But in ruminants, large amounts of P are secreted into the gastrointestinal tract by the salivary glands, (Breves et al., 1991) which might reduce the degree to which Ca must be absorbed. In particular, the mechanisms regulating Ca absorption in hindgut fermenters – especially potential feedback signals from the fermentation process – might be a promising area of future research.

Literature Cited


Figure 1. Apparent digestibility (aD) of calcium (Ca) in horses from different feeding regimes in relation to a) dietary Ca content and b) dietary Ca:Phosphorus ratio. Data collection from\textsuperscript{27} supplemented with horse data from\textsuperscript{3}.

Figure 2. The relationship of dietary digestible calcium (dCa) content to dietary calcium (Ca) content in a) black rhinoceros\textsuperscript{6}, b) tapir\textsuperscript{25}, c) Asian elephant\textsuperscript{6} and d) white rhinoceros\textsuperscript{13} as compared to the domestic horse\textsuperscript{6}.