

A pilot study on dietary and faecal calcium/phosphorus ratios in different types of captive ruminating herbivores

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Abstract

Quantitative differences in calcium and phosphorus metabolism between domestic species exist and can be visualised using data on calcium and phosphorus intake and faecal excretion. The parameter for analysing the results was defined as Δ = dietary calcium/phosphorus (Ca/P) ratio – faecal Ca/P ratio. In previous studies, hindgut fermenters had significantly higher Δ values than ruminants (sheep, cattle, goats), which was explained by the high calcium digestibilities in hindgut fermenters in contrast to highly efficient phosphorus recycling in ruminants. The first hypothesis of the present study was that different types of ruminants (grazer, browser, intermediate feeder) would show differences in Δ as a proxy for quantitative calcium and phosphorus metabolism. The second hypothesis was that camelids as functional, but not taxonomic ruminants would show Δ values similar to ruminants. We used herbivorous zoo animals (17 species, hindgut and foregut fermenters), which were kept on their regular diet without variation for 1 week. Then, faecal samples were obtained from the individual animals. Feed items and faecal samples were analysed for calcium and phosphorus, and dietary and faecal Ca/P ratios as well as Δ were calculated. A comparison of the species groups (one-way ANOVA on ranks, $p < 0.05$) showed that zoo hindgut fermenters had significantly higher Δ values (0.67 ± 0.34) than camelids and zoo ruminants (-1.07 ± 0.35 and -1.87 ± 1.56). There was no significant difference between camelids, grazers (-1.49 ± 1.31), browsers (-1.63 ± 0.88) and intermediate feeders (-2.11 ± 1.76). The ruminant species from this study had markedly lower Δ than domestic ruminants from literature data. Especially intermediate feeders had low Δ , possibly due to more efficient phosphorus recycling than the domestic ruminants.

KEYWORDS

antelope, digestive physiology, intermediate feeder, minerals, nutrition

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1 | INTRODUCTION

Calcium and phosphorus homeostasis is highly complex. In many species, intestinal absorption of calcium occurs mainly via passive, paracellular uptake during adequate or high supply, while in a phase of low calcium supply or elevated requirement, active vitamin D-mediated uptake takes place (Horst et al., 1994; Perez et al., 2008). Phosphorus is transported across the intestinal mucosa via sodium-dependent transporters. It is known that species differences in the importance of absorption and excretory pathways for both minerals and their regulation exist (Böswald et al., 2018; Breves & Schröder, 1991; Ichida et al., 2020; Stanik, 2006).

Those species differences in quantitative calcium and phosphorus homeostasis could be shown by comparing dietary and faecal calcium/phosphorus (Ca/P) ratios between species groups (Böswald et al., 2018). As a parameter to display these results, Δ was calculated as the difference dietary Ca/P ratio – faecal Ca/P ratio. Figure 1 shows a schematic overview of changes in dietary and faecal Ca and P that affect the Δ parameter. Literature data showed significantly higher Δ values for hindgut fermenting species [Black rhino (*Diceros bicornis*), Sumatran rhino (*Dicerorhinus sumatrensis*), Indian rhino (*Rhinoceros unicornis*), horse (*Equus caballus*), lowland tapir (*Tapirus terrestris*), Malayan tapir (*Tapirus indicus*), Asian elephant (*Elephas maximus*), rabbit (*Oryctolagus cuniculus*), guinea pig (*Cavia porcellus*), long-tailed chinchilla (*Chinchilla lanigera*), degu (*Octodon degus*)] than for domestic ruminants [cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra capra*)] (cattle, sheep, goat; Böswald et al., 2017). A possible explanation for the hindgut fermenters' high calcium absorption is that these species 'remove' excess calcium from the small intestine in order to make phosphorus available for microbial fermentation in the hindgut (Clauss & Hummel, 2008). The main regulation and excretory route of calcium in hindgut fermenters is urine (Cheeke & Amberg, 1973; Clauss & Hummel, 2008;

Schryver et al., 1983; Whiting & Quamme, 1984), in contrast to other species groups (Stanik, 2006). Ruminants do not need to adopt a kind of 'by pass mechanism' for calcium because fermentation takes place in their foregut and phosphorus is efficiently recycled and secreted into the rumen via saliva.

However, there are different types of ruminants: grazers, intermediate feeders and browsers (Hofmann, 1989; Hofmann & Stewart, 1972). They show many physioanatomical adaptations to their diets that range from the mouth opening to digesta retention times and fibre digestibility (Clauss et al., 2008). Saliva production also differs between ruminant types: browsers' saliva contains tannin-binding proteins (Austin et al., 1989; McArthur et al., 1995; Shimada, 2006) in order to minimise the negative effects of tannins on diet digestibility. Their salivary glands are bigger than those of grazing ruminants (Hofmann et al., 2008; Kay, 1987). Additionally, there are differences in the amount of produced saliva and in the salivary phosphorus content of different ruminants (Fickel et al., 1998). For example, sheep as grazers have a significantly lower salivary phosphorus content than goats as intermediate feeders (Wilkins et al., 2014). Possibly, intermediate feeders are more efficient in phosphorus recycling because they need to ensure high salivary phosphorus concentrations. Accordingly, if we assume a higher phosphorus digestibility as a mode for efficient phosphorus recycling, Δ would be lower in intermediate feeders than grazers (Böswald et al., 2019).

In regard of these differences, we aimed to investigate Δ as an approximate parameter for the quantitative gastrointestinal calcium and phosphorus homeostasis in zoo ruminant species and to compare them to domestic ruminant data. Further, we aimed to explore possible differences between grazers, intermediate feeders and browsers.

Most research on calcium and phosphorus homeostasis in ruminating species was performed on members of the suborder Ruminantia. Camelids (suborder Tylopoda) are also functional ruminants with a

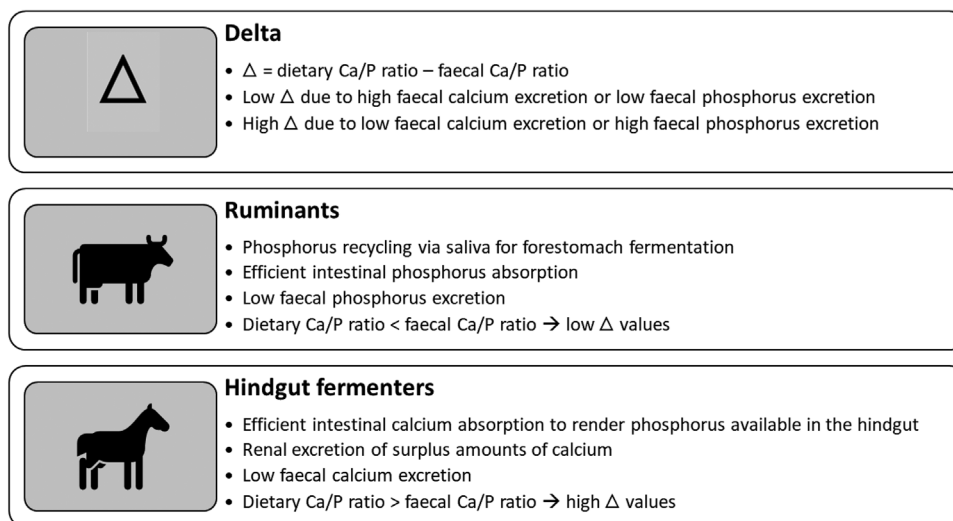


FIGURE 1 Overview of the parameter delta and how it may be affected by species-specific adaptation in calcium and phosphorus homeostasis. It is calculated as the difference between the dietary and faecal calcium to phosphorus (Ca/P) ratios and is used to demonstrate species differences in this study

complex forestomach (Stevens & Hume, 2004) that is the major site of microbial fermentation. Up to date, there is few data on camelid calcium and phosphorus metabolism (e.g. Schryver et al., 1983). Therefore, we included four camelid species into this study and compared them to the taxonomical ruminant species. The parameter Δ was used as a proxy to test our hypothesis that camelids show a similar quantitative calcium and phosphorus homeostasis as the other non-domestic ruminants investigated.

2 | ANIMALS, MATERIAL AND METHODS

2.1 | Animals

Adult healthy individuals of 17 herbivorous species kept in the Munich Zoo (Tierpark Hellabrunn) were used for the study. All animals were in maintenance metabolism, that is, not growing, in gestation or lactation. We grouped the species according to digestive physiology. Hindgut fermenter: Przewalski's horse (*Equus ferus przewalskii*, $n = 5$), tarpan crossbred (*Equus ferus ferus*, $n = 5$); camelids: Bactrian camel (*Camelus ferus*, $n = 5$), llama (*Lama glama*, $n = 3$), alpaca (*Vicugna pacos*, $n = 2$), vicuña (*Vicugna vicugna*, $n = 1$); browser: moose (*Alces alces*, $n = 3$), reticulated giraffe (*Giraffa camelopardalis reticulata*, $n = 4$); grazer: yak (*Bos mutus grunniens*, $n = 9$), Dahomey dwarf cattle (*Bos primigenius taurus*, $n = 5$), aurochs (*Bos primigenius primigenius*, $n = 4$); intermediate feeder: Lowland nyala (*Tragelaphus angasii*, $n = 8$), Girgentana goat (*Capra capra*, $n = 4$), Mhorr gazelle (*Nanger dama mhorr*, $n = 11$), banteng (*Bos javanicus*, $n = 8$), nilgai antelope (*Boselaphus tragocamelus*, $n = 5$), wood bison (*Bison bison athabasca*, $n = 6$). Ethical approval for the use of the animals was obtained from the ethical committee of the ethical committee of the Faculty of Veterinary Medicine, LMU München (reference no. 101-27-11-2017).

2.2 | Diets

The regular zoo diets were not changed during the study so that no adaptation period was necessary. For 1 week, the diet was kept as constant as possible and the usual variation of the diet plans, for example exchange of vegetables, was suspended for this period. We took samples of all feedstuffs and used average amounts weighed and reported by the zookeepers for ration calculation. Details of all rations are listed in Table 1.

2.3 | Faecal samples

We collected faecal spot samples once, following this week on a constant diet. In most species, it was possible to obtain one sample per animal, for example in case of single housing during the night from the clean ground of the enclosure. Each sample consisted of non-contaminated faeces, ranging from ca. 16 to 222 g fresh matter. Only in the group of nyalas, we were not able to take individual samples and

had to use a collective sample for the whole group of eight animals. We included aliquots of different faecal droppings to ensure a representative group sample in this case. Contamination by dirt, bedding material or feedstuff was avoided. Fresh faecal samples were frozen (-20°C) until further analysis.

2.4 | Analysis

Feed samples were dried at 103°C for at least 24 h; faecal samples were dried slowly over 3 days with increasing temperatures (60°C to 80°C to 100°C). Then, samples were ground (< 1 mm particle size) and prepared for further analysis by nitric acid digestion. Calcium was analysed by flame emission spectrography, phosphorus was determined photometrically with ammonium molybdate and ammonium vanadate in HNO_3 (Gericke & Kurmies, 1952). We did not analyse samples of feedstuffs like vegetables and fruit because contribution to the dietary calcium and phosphorus content can be considered low. Feedstuff table data was used for these ration components (Souci et al., 2000).

2.5 | Statistics

We calculated Ca/P ratios from diets and faecal samples. From these values, we calculated $\Delta = \text{dietary Ca/P ratio} - \text{faecal Ca/P ratio}$. The mean Δ values of all individuals in the respective species group were compared between the following groups: hindgut fermenters, camelids, ruminant browsers, ruminant grazers and ruminant intermediate feeders (Kruskal-Wallis test due to failed normality testing, SigmaPlot®, significance level: $p < 0.05$).

Statistical testing of all species individually would have been underpowered due to the low number in many species. To avoid this, we compared the sub-groups of foregut fermenters [domestic cattle, camelids (Bactrian camel, llama, alpaca, vicuña), wild cattle-type grazers (yak, Dahomey dwarf cattle, aurochs) and intermediate feeding antelopes (Mhorr gazelle, nilgai antelope, lowland nyala, banteng) in a Kruskal-Wallis test; significance level $p < 0.05$] without including the hindgut fermenters.

3 | RESULTS

Dietary Ca and P content calculated for the daily rations ranged from 3.72 to 14.80 g/kg dry matter (DM) and from 3.51 to 5.63 g/kg DM, respectively. Except for the hindgut fermenters, faecal Ca content was higher than dietary Ca concentration in all species (Table 2). The dietary Ca/P ratios ranged from 1.03/1 in llamas to 3.39/1 in reticulated giraffes. Faecal Ca/P ratios were lower in hindgut fermenters (Przewalski's horse: 0.72 ± 0.30 ; tarpan crossbred: 1.15/1) than in the ruminating species (range from 1.73/1 in bantengs to 5.87/1 in wood bison). This resulted in positive Δ values in these species, while the ruminating species had negative Δ values (Table 3).

TABLE 1 Diet composition calculated according to average amounts reported by the animal keepers

	Amount of feedstuffs (kg as fed/animal/day)													
	Hay	Alfalfa hay	Vegetables	Beetpulp flakes ^a	Moose pellets ^b	Grass cobs	Zoo pellets ^c	Muesli	Branches ^d	Mineral supplement ^e	Browser pellets ^f	Pellets ^g	Alfalfa pellets	Pressed oats
Przewalski's horse	4.25		0.3	0.1			0.4		0.05					
Tarpan crossbred	4.75			0.1		0.25			0.08					
Bactrian camel	6					0.2		0.5						
Llama	2						0.2							
Alpaca	1													
Vicuna	0.75						0.2							
Moose	4	1.5		0.35	3			4						
Reticulated giraffe	5	3						0.4	0.1	1.5	0.25	0.75		
Dahomey cattle	3	0.1		0.07			0.1		0.02					
Yak	3.5	0.9		0.08		0.35								
Aurochs	7			0.1		0.9			0.08					
Banteng	4	1.5		0.1		0.5			0.05					
Girgentana goat	1			0.04		0.08			0.005					
Mhorr gazelle		1.5		0.06			0.15		0.01					0.1
Nilgai antelope	1.5	0.1		0.25		0.4	0.2		0.03					
Lowland nyala	2	3.5		0.5		1.5	1.8	0.2						
Wood bison	8			0.1		0.9	0.5		0.08					

^aPavo SpeediBeet.^bMazuri UK Moose Pellets.^cZoo M1 standard pellets, Michael Hassel GmbH.^dWillow, hawthorn.^eHorse mineral/cattle mineral/Salvana Pansenaktiv/Mineral.^fBoskos Browser.^gMazuri UK Browser Pellets.

TABLE 2 Dietary and mean faecal Ca and P content (g/kg DM) of the species investigated

	n	Diet		Faeces	
		(g/kg DM)		(means, g/kg DM)	
		Ca	P	Ca	P
Przewalski's horse	5	7.10	5.20	4.08	5.72
Tarpan crossbred	5	8.36	4.58	5.09	4.45
Bactrian camel	5	4.57	4.81	16.99	7.78
Llama	3	5.49	5.31	14.07	6.22
Alpaca	2	6.30	5.37	13.58	7.26
Vicuña	1	5.96	4.41	12.37	5.99
Moose	3	8.03	4.60	46.32	11.58
Reticulated giraffe	4	14.80	4.36	36.30	8.27
Dahomey cattle	5	6.82	3.84	18.00	6.37
Yak	9	3.72	3.51	14.51	6.52
Aurochs	4	6.26	4.65	12.77	6.30
Banteng	8	7.64	5.63	10.47	6.08
Girgentana goat	4	6.27	5.20	14.41	5.75
Mhorr gazelle	11	12.89	5.06	32.58	9.73
Nilgai antelope	5	9.54	4.56	23.24	5.54
Lowland nyala	*	10.14	3.84	40.53	7.52
Wood bison	6	6.55	4.68	24.26	4.32

*1 group sample (8 animals in the group).

TABLE 3 Dietary and faecal Ca/P ratios and Δ values for all species investigated (means and standard deviation given)

	N	dietary Ca/P ratio	faecal Ca/P ratio		Δ = dietary - faecal Ca/P	
			Mean	SD	Mean	SD
			Przewalski's horse	5	1.37	0.72
Tarpan crossbred	5	1.83	1.15	0.39	0.68	0.39
Bactrian camel	5	0.95	2.20	0.29	-1.25	0.29
Llama	3	1.03	2.27	0.17	-1.24	0.17
Alpaca	2	1.17	1.89	0.39	-0.72	0.39
Vicuña	1	1.35	2.10		-0.75	
Moose	3	1.75	3.97	0.51	-2.22	0.51
Reticulated giraffe	4	3.39	4.42	0.81	-1.03	0.81
Dahomey cattle	5	1.78	2.89	0.95	-1.11	0.95
Yak	9	1.06	2.48	1.70	-1.42	1.70
Aurochs	4	1.35	2.04	0.28	-0.69	0.28
Banteng	8	1.36	1.73	0.14	-0.37	0.14
Girgentana goat	4	1.21	2.57	0.83	-1.36	0.83
Mhorr gazelle	11	2.64	3.55	1.30	-0.91	1.30
Nilgai antelope	5	2.09	4.44	2.08	-2.35	2.08
Lowland nyala	*	2.64	5.40		-2.76	
Wood bison	6	1.36	5.87	1.78	-4.51	1.79

*1 group sample (8 animals in the group).

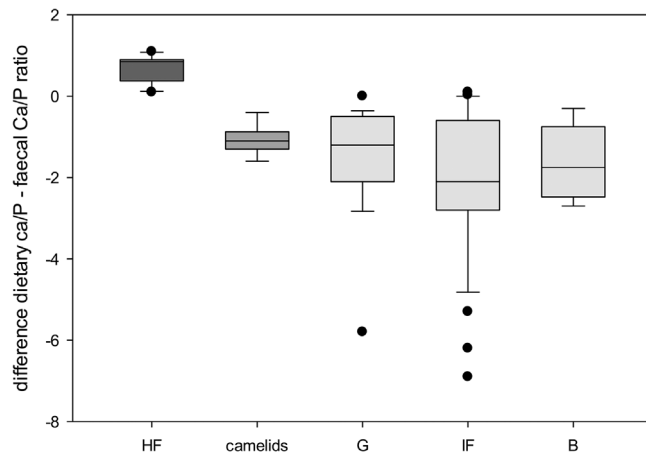


FIGURE 2 Box plot of Δ in hindgut fermenters (HF), camelids, grazers (G), intermediate feeders (IF) and browsers (B). There was a significant difference between hindgut fermenters and the groups of ruminating species ($p < 0.05$)

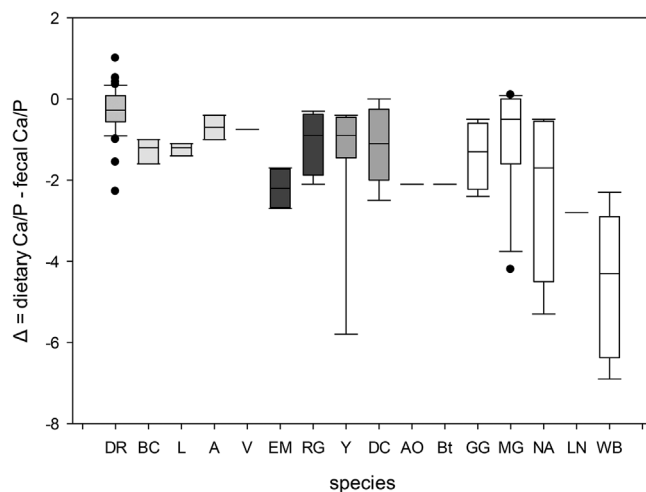


FIGURE 3 Box plot of Δ in domestic ruminants (cattle, sheep, goats) from literature data (Böswald et al., 2018) and the ruminating species investigated in this study. Species on the x-axis listed as follows: DR = domestic ruminants, BC = Bactrian camel, L = llama, A = alpaca, V = vicuña, EM = European moose, RG = reticulated giraffe, Y = yak, DC = Dahomey cattle, AO = aurochs, Bt = banteng, GG = Girgentana goat, MG = Mhorr gazelle, NA = nilgai antelope, LN = lowland nyala, WB = wood bison

When comparing hindgut fermenters, camelids, grazers, browsers and intermediate feeder, the camelids did not differ significantly from the taxonomic ruminant types in terms of Δ ($p > 0.05$, see Figure 2).

Compared to literature data on domestic ruminants (Böswald et al., 2018), all ruminant species investigated in this study had lower Δ values (Figure 3). The intermediate feeding species Girgentana goat, Mhorr gazelle, nilgai antelope, lowland nyala and wood bison showed very high variations and extremely negative Δ values.

There were significant differences between domestic ruminants from Böswald et al. (2018) and the wild cattle-type grazers ($p < 0.001$), the camelids ($p = 0.006$) and the intermediate feeding antelopes

($p = 0.011$). The three non-domestic subgroups used in this comparison did not differ significantly from each other ($p > 0.05$).

4 | DISCUSSION

In the present study, we reproduced the difference in Δ between hindgut and foregut fermenters (Böswald et al., 2018) in zoo animals. This finding suggests that the methods employed in this study were feasible to obtain valid results; 1 week of keeping the diets constant before taking faecal samples seemed to be sufficient to obtain results that are comparable to literature. Selective feed intake or unusual variations in feed intake, which would have influenced mineral intake in single individuals, were not observed throughout the study. High variations in dry matter intake may influence endogenous calcium losses in ruminants (Kamphues et al., 2014). The basic diet composition of roughage plus concentrates as necessary was similar between the species. This similarity in diet composition combined with the fact that all animals were in maintenance and not performing (e.g. lactation) makes extremely high or low dry matter intakes unlikely, so that endogenous calcium losses are not expected to be unusually high.

Species were grouped according to their digestive physiology to allow for reasonable comparisons between species groups in spite of limited numbers of individuals per species. For hindgut fermenters, grazing and browsing ruminants, data distribution with a low variance shows that they can be appropriately grouped according to their feeding types. The same is true for camelids, where we even grouped old world and new world camelids together. In the intermediate feeders, however, a higher variation of Δ values may indicate that further differentiation (with a higher n) would be preferable to better understand the determinant for their variation in Δ .

It is a known limitation of working with zoo herbivores (especially when kept in herds) that it is difficult to conduct a complete balance trial with determination of the exact feed intake and collection of the total amount of faeces as this would mean single-housing for several days. The advantage of calculating the Ca/P ratios from diets and faeces is that a balance trial is not necessary. Usually, the informative value of data obtained with the method of grab samples is limited, but by comparing dietary and faecal Ca/P ratios or Δ , we can demonstrate species differences and similarities. This study design is practically non-invasive for the animals and still provides insights into comparative aspects of calcium and phosphorus homeostasis.

The parameter Δ may reach limitations if the dietary Ca/P ratio is strongly inverse or extremely high. In this study, however, the dietary Ca/P ratios were comparable, so that shifts in Δ will show species differences.

In accordance with the results from the previous meta-analysis (Böswald et al., 2017), hindgut fermenters showed positive Δ values that were significantly higher than the ruminating species' values. Hindgut fermenters are known to efficiently absorb calcium from the small intestine, excreting excess amounts via the urine (Cheeke & Amberg, 1973; Clauss & Hummel, 2008). With relatively low faecal Ca excretion, the resulting faecal Ca/P ratio is low. Given a dietary

Ca/P ratio in the usual range of herbivores, a low faecal Ca/P ratio results in high Δ values as seen in the present study and Böswald et al. (2017).

There was no significant difference between camelids and taxonomic ruminant species investigated in this study ($p > 0.05$). Both groups are foregut fermenters with microbial fermentation taking place in a more or less complex forestomach chamber (Dittmann et al., 2015; Stevens & Hume, 2004). The development of this digestive strategy took place independently, as shown by anatomic and histologic differences (Lechner-Doll et al., 1995).

Like in the data of domestic ruminants taken from literature (meta-analysis by Böswald et al., 2018), the foregut fermenting species investigated in this study had negative Δ values. However, when we take a closer look at the distribution across species, all non-domestic foregut fermenting species showed even lower Δ than the domestic ruminants (Figure 3). Using subgroups for statistical testing, the difference between domestic ruminants and the exotic species (camelids, wild cattle-type grazers and intermediate feeding antelopes) is significant. A very low Δ means that relative to the dietary Ca/P ratio, the faecal Ca/P ratio is much higher. Given an average faecal calcium excretion (Schryver et al., 1983), high faecal Ca/P ratios can be explained by efficient phosphorus absorption. Thus, the non-domestic foregut fermenters may be more efficient in intestinal phosphorus recycling than the domestic ruminants. It was noticeable that we found the lowest Δ values for the intermediate feeders, that is mostly antelopes. It has to be taken into account that captive intermediate feeders are fed a more grazer-like diet and can adapt to this rather well. Even under these circumstances, the intermediate feeding antelope species may have adapted to their natural habitats, that is Africa and India, where phosphorus is scarce (Alloway, 2008; MacDonald et al., 2011; Magnone et al., 2019). Historic reports of phosphorus deficiency resulting in osteophagia and botulism ('lamsiekte') show that domestic ruminants, mostly cattle, brought to Africa could not cope with the low phosphorus intake without supplementation (Bigalke, 2012; Green, 1949; Sigwart, 1929; Theiler, 1927). To our knowledge, there are no reports of phosphorus deficiency as a cause for botulism in intermediate feeders native to the low-phosphorus soil of Africa. This supports the interpretation of our results that intermediate feeders seem to be highly efficient in phosphorus absorption and recycling.

5 | CONCLUSION

The present study shows species differences in the relationship of dietary and faecal Ca/P ratios between ruminating herbivores of different feeding types that may be related to the respective physiological adaptations. Further research into this aspect of comparative mineral homeostasis is warranted.

AUTHOR CONTRIBUTIONS

LB originally formulated the idea, LB, EK and BD developed methodology, MK and CG conducted fieldwork, LB handled data and wrote the manuscript, EK and BD were involved in manuscript writing.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

ETHICAL APPROVAL

All applicable institutional and national guidelines for the care and use of animals were followed. Ethical approval by the Faculty of Veterinary Medicine, LMU München, was obtained (reference no. 101-27-11-2017).

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