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ORIGINAL ARTICLE

Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*)

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Summary

We performed intake, digestibility and ingesta passage studies in 11 Indian rhinoceroses (*Rhinoceros unicornis*) from four zoological institutions, using total faecal collection for the quantification of faecal output. The regularly fed zoo ration of roughage and concentrates (ration RC) and a roughage-only ration (ration R) were used; the roughage source differed between the facilities and comprised grass hay, grass silage, straw and lucerne hay. Dry matter intake ranged between 0.8 and 1.3% of body weight on ration RC and 0.5–1.2% on ration R. Digestibility coefficients achieved were similar to those reported for horses on diets of comparable composition. Endogenous losses as determined by linear regression analysis were within the range reported for horses. Measurements of faecal volatile fatty acids, faecal lactate and faecal pH also showed similarity to similar measurements in horses. The mean retention times of fluids (Co-EDTA) and particles (Cr-mordanted fibre <2 mm) in the whole gastrointestinal tract averaged 42 and 61 h, respectively, and were the longest ever recorded in a monogastric ungulate with this marker system. The results suggest that the horse is a useful model animal for designing diets for Indian rhinoceroses. Why digestive parameters are similar between these species in spite of enormous differences in body weight and retention times remains to be answered.

Introduction

The Indian rhinoceros is, after the elephant, the second largest extant mammalian herbivore (Owen-Smith, 1988). Its natural diet consists mainly of grasses (Brahmachary et al., 1971, 1974; Laurie, 1982; Dinerstein, 1989; Dinerstein and Price, 1991). As would be expected of a very large herbivore, the main diet item of the Indian rhinoceros, the grass *Saccharum spontaneum*, is reported to be of a high crude fibre (40% DM) and a low crude protein (5.4% DM) content (Duke and Atchley, 1986).

For large hindgut fermenters such as elephants or rhinoceroses, the horse has been propagated as the appropriate model when designing diets for captive animals (Oftedal et al., 1996). However, nutritional studies with elephants showed that the horse is not a suitable model for elephant digestion (Clauss et al.,

2003). We therefore intended to generate more data to facilitate a comprehensive comparison between the digestive physiology of Indian rhinoceroses, horses, and other hindgut fermenters.

Animals, materials and methods

Eleven Indian rhinoceroses from four zoological institutions were used. The animals were either actually weighed, or their body weights were estimated, using the weighed animals as comparison (Table 1). Animals had regular access to outside enclosures which were cleared of any potential food items. For the trial period, the animals were kept separately to allow individual recording of food intake and faecal excretion. Only two females at zoo C were allowed to access their outside enclosure together, and the correct allocation of faeces voided during this period was assured by constant observation.

At zoos A, B and D, two rations were fed to the animals – the one regularly fed at the respective zoo (i.e. a mixture of roughage and concentrates, ration RC), and another one consisting of the roughage feed only (ration R) after an adaptation period of 7 days. At zoo C, only the regularly fed diet was used. The roughage source was grass hay at zoo A, a combination of grass hay and grass silage at zoo B, straw at zoo C and a mixture of grass and lucerne hay at zoo D. Food intake was measured by weighing the food offered and the food left over at the next feeding time for 7 days; faeces were collected and weighed *in toto* for 5 days. For the estimation of mean ingesta retention times, cobalt EDTA as a fluid and chromium-mordanted fibre (<2 mm) as a particle marker prepared as in Behrend (2000) were fed to some of the animals. Faeces from these animals were collected, after each defecation, around the clock for the first 72 hafter marker feeding, and during the day for the rest of the trial; faeces voided at night after 72 h were treated as one defecation unit, with an assumed average defecation time.

Table 1 Indian rhinoceroses used in this study. Body weights represent either actual weights or estimates (°)

No.	Studbook No.	Sex	Age (years)	BW (kg)	Facility
1	152	m	13	(2300)°	A
2	193	f	12	(1950)°	A
3	135	m	15	(2200)°	B
4	195	f	10	(1900)°	B
5	220	m	8	(2100)°	C
6	110	f	20	(2000)°	C
7	210	f	8	(1900)°	C
8	53	m	31	1821	D
9	139	f	15	1989	D
10	223	f	8	1864	D
11	66	f	29	1833	D

The outer layer of dung balls was removed to avoid contamination of the sample. The rest of the material was thoroughly mixed, and a subsample representing 10% of the whole sample was taken and frozen at −20 °C. A subsample of fresh faecal water (gained by centrifugation of fresh faeces mixed with tridistilled water) preserved in orthophosphoric acid was used for the determination of faecal volatile fatty acid (VFA) content; another subsample preserved in perchloric acid was used to the determination of L-lactate. At zoo D, pH was measured in fresh faeces (dilution with water: 2:1) with an electric pH-meter.

After thawing, the faeces of the whole collection period were pooled for each animal and mixed. Samples of feedstuffs and faeces were analysed for dry matter (DM), crude protein (CP), crude ash (CA), crude fibre (CF) and ether extract (EE) according to Naumann and Bassler (1988) and for neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) according to Van Soest (1967), using freeze-dried material for all analyses except for DM. Nitrogen-free extracts (NfE) was calculated as 100-CP-CA-CF-EE, organic matter (OM) as 100-CA, hemicelluloses (HC) as NDF-ADF and cellulose (C) as ADF-ADL. In order to measure metabolic faecal nitrogen (MFN), the protein content in the faecal NDF residue was determined according to Mason and Frederiksen (1979). Gross energy (GE) was determined by bomb calorimetry using an IKA-Calorimeter C 4000 adiabatic (Janke & Kunkel, Staufen, Germany). Passage marker concentration was measured after wet microwave ashing by atomic absorption spectroscopy (3300 AAS; Perkin Elmer, Überlingen, Germany) according to Behrend (2000). L-lactate was determined by enzymatic reaction and photometric measuring of the resulting $NADH/H^+$. The total VFA concentration was determined by gas chromatography (Perkin Elmer Auto System, glass column length 30 m, 25 mm diameter, column 150 °C, detector and injection block 300 °C, filling 'Crossbond Carbowax-PEG', carrier gas pressure 160 kPA). Results for L-lactate, VFA and pH represent the average of 6–10 individual measurements per animal and ration.

The apparent digestibilities (aD) of nutrients (N) were calculated as:

$$\mathrm{aD}_N(\%) = \frac{N_{\mathrm{feed}} - N_{\mathrm{faeces}}}{N_{\mathrm{feed}}} \times 100$$

According to Mason and Frederiksen (1979), true protein digestibility (TPD) was calculated as

$$\mathrm{TPD}(\%) = \frac{\mathrm{CP_{feed}} - \mathrm{CP_{faecal\,NDF}}}{\mathrm{CP_{feed}}} \times 100$$

Mean retention times were calculated according to Thielemans et al. (1978). The Spearman Correlation Coefficient (SCC) was used to test different nutrients and digestibilities for monotonous association. The *U*-test and the Wilcoxon-test were applied to compare different facilities or different diets, respectively. Linear regression analysis served to establish linear relationships. The significance level was set to 5%. All statistical analyses were performed using the SPSS 9.0 (SPSS Inc., Chicago, IL, USA) statistical software package.

Results

The general health of the animals during the study period did not seem to be compromised. Judged by external appearance, no animal seemed to lose weight during the study period. Animal 2 came into heat during the second trial period, when her food intake was particularly low, as well as that of the bull of the same facility (animal 1).

The dry matter intakes (DMI) and the ration compositions of the individual animals are recorded in Table 2. Total DMI was generally higher on RC rations with the exception of two animals at facility D. Rations R generally contained higher contents of fibre and lower contents of protein and NfE.

The corresponding digestibility coefficients are given in Table 3. In general, digestibility coefficients were lower for diet R at facilities A and D, but not at facility B. Whereas the apparent protein digestibilities ranged between 41 and 66%, the true protein digestibility varied between 85 and 94% (Table 3). Both parameters were significantly correlated (SCC = 0.69, p = 0.001). There was no correlation between DMI (% BW basis) and DM digestibility (SCC = 0.16, p = 0.519). Neither cell wall (NDF) nor lignin content were significantly correlated to DM digestibility (NDF: SCC = −0.29, p = 0.229; ADL: SCC = −0.17, p = 0.480). A linear regression analysis of the dietary crude fibre content (in% DM) and the apparent digestibility coefficients for OM results in the equation:

$$\mathrm{aD\ OM}(\%) = 80 - 0.81\mathrm{CF}(r^2 = 0.18, n = 19, \mathrm{p} = 0.069)$$

Therelationship, however, only tends towards significance. Linear regression analyses of nutrient ingested vs. nutrient absorbed (on a dry matter or a body weight basis, respectively), yielded the equations recorded in Table 4.

The total amount of VFAs decreased, and the acetate:propionate ratio increased on diet R compared with diet RC (Table 5). The content of endogenous faecal nitrogen (measured as non-NDF-N in faeces) was positively correlated to the faecal VFA concentration (SCC = 0.85, p < 0.001; Fig. 1); this correlation was independent from the faecal water content as neither parameter was correlated to faecal dry matter (VFA: SCC = 0.37, p = 0.236; non-

Table 2 Total dry matter intake (DMI, kg), and ration nutrient (% DM) and GE (MJ/kg DM) content in the Indian rhinoceroses studied

Animal	Ration	DMI	OS	CP	EE	CF	NfE	NDF	ADF	ADL	HC	C	GE
1	RC	23.4	93.1	9.1	1.5	26.0	56.5	52.0	27.9	3.5	24.1	24.4	18.1
1	R	16.3	94.6	8.5	1.2	35.2	49.8	71.3	37.6	3.8	33.7	33.8	18.8
2	RC	17.2	92.6	9.3	1.5	25.3	56.6	50.4	27.3	3.7	23.1	23.6	18.1
2	R	8.8	94.6	8.5	1.2	35.2	49.8	71.3	37.6	3.8	33.7	33.8	18.8
3	RC	28.8	91.3	9.7	2.3	31.3	48.1	64.0	34.5	4.2	29.6	30.3	18.3
3	R	20.3	92.1	8.0	1.7	36.9	45.5	73.2	40.5	4.0	32.6	36.6	18.2
4	RC	22.3	91.0	11.1	2.2	28.9	48.8	60.1	31.5	3.8	28.6	27.7	18.2
4	R	15.4	91.8	8.1	1.8	36.8	45.1	73.6	40.5	3.8	33.1	36.7	18.2
5	RC	22.6	94.6	9.0	1.6	29.2	54.8	56.7	34.3	4.9	22.4	29.4	18.5
6	RC	20.4	94.7	8.3	1.5	30.3	54.5	58.4	35.6	5.0	22.8	30.6	18.5
7	RC	15.7	94.9	8.2	1.4	29.9	55.5	57.6	35.2	5.0	22.4	30.2	18.5
8	RC	20.8	93.7	9.2	3.4	32.4	48.7	56.9	35.7	7.1	21.2	28.6	19.7
8	R	22.2	93.8	7.3	1.9	36.0	48.5	65.7	40.4	6.7	25.3	33.7	19.4
9	RC	24.1	93.9	8.7	3.3	33.4	48.6	58.0	36.6	7.2	21.4	29.4	19.7
9	R	13.7	93.8	7.3	1.9	36.0	48.5	65.7	40.4	6.7	25.3	33.7	19.4
10	RC	17.7	93.9	8.6	3.3	33.5	48.6	58.2	36.8	7.3	21.4	29.6	19.7
10	R	18.3	93.8	7.3	1.9	36.0	48.5	65.7	40.4	6.7	25.3	33.7	19.4
11	RC	20.3	93.5	10.0	3.7	31.0	48.8	55.3	34.3	6.8	21.1	27.5	19.6
11	R	13.3	93.8	7.3	1.9	36.0	48.5	65.7	40.4	6.7	25.3	33.7	19.4

Table 3 Apparent digestibility coefficients for nutrients and gross energy, 'true protein digestibility' (TPD) and metabolic faecal nitrogen (MFN, in% of total faecal nitrogen) in the Indian rhinoceroses studied

Animal	Ration	DM	OS	CP	EE	CF	NfE	NDF	ADF	ADL	HC	C	GE	TPD	MFN
1	RC	56	56	53	15	40	65	41	36	−1	47	41	52	88	74
1	R	41	42	41	−6	37	47	39	34	−7	45	39	39	85	74
2	RC	59	60	52	17	42	70	45	41	−2	48	48	56	90	80
2	R	49	49	56	12	38	57	43	38	3	50	42	47	91	79
3	RC	56	56	51	30	51	61	52	51	17	54	56	52	91	82
3	R	57	57	46	−2	60	59	60	59	18	60	64	53	91	83
4	RC	59	59	57	12	53	66	55	52	13	58	57	56	93	84
4	R	61	62	47	0	67	63	64	66	42	62	68	58	91	83
5	RC	53	54	55	38	39	62	40	38	18	44	41	50	88	74
6	RC	53	54	51	40	41	63	42	41	21	45	44	50	88	76
7	RC	58	59	56	22	45	68	48	48	29	49	51	52	88	73
8	RC	56	57	62	30	45	66	48	47	35	51	50	50	93	82
8	R	47	47	57	−41	33	59	41	36	10	49	41	43	90	78
9	RC	53	54	52	48	41	63	45	42	30	48	46	48	91	81
9	R	49	49	58	−4	38	58	43	38	13	50	43	45	92	80
10	RC	63	63	66	36	53	72	55	53	44	59	56	59	94	82
10	R	53	53	57	−35	43	59	47	43	19	54	48	49	92	80
11	RC	55	55	63	44	40	64	43	39	25	50	43	53	92	80
11	R	35	35	43	−33	20	47	29	23	−17	39	31	29	88	79

Table 4 Linear regression analysis for nutrient intake (x) vs. digestible nutrient intake (y) on a dry matter or a (metabolic) body weight basis, according to the equation $y = ax + b$

Nutrient	a	b	r^2	p
Crude protein (g/100 g DM)	0.71	−1.47	0.61	<0.001
Crude protein (g/kg$^{0.75}$ MBW)	0.61	−0.38	0.88	<0.001
Crude fat (g/100 g DM)	0.62	−0.94	0.49	0.001
Crude fat (mg/kg BW)	0.51	−69	0.54	<0.001
NfE (g/kg DM)	0.95	−16.6	0.56	<0.001

NDF-N: SCC = 0.34, p = 0.28). The measured amounts of faecal L-lactate were negligible and did not show a pattern according to the ration used (Table 5). Faecal pH values for the animals from facility D averaged 6.3 (±0.1) on ration RC and 6.5 (±0.1) on ration R. The difference tended towards significance (Wilcoxon test, p = 0.063). The lack of significance might be the result of the small data set (four pairs) causing a low power of the test.

The mean retention times of the fluid and the particle marker are given in Table 6. On average, the particles were retained 1.4 times longer than the fluids. A typical excretion curve is shown as Fig. 2. In the one animal (animal 3) in which the retention was quantified on both rations, no difference between the rations was evident. There was no evident correlation between the ingesta MRT and the dry matter intake or the dry matter or a fibre digestibility.

Table 5 Content and proportions of volatile fatty acids, and of l-lactate, in faecal water of the Indian rhinoceroses studied. Values represent averages of 6–10 measurements per animal and ration

Animal	Ration	C2 (mmol/l)	C3 (mmol/l)	C4 (mmol/l)	Sum (C2,C3,C4) (mmol/l)	C2 (%)	C3 (%)	C4 (%)	C2:C3	l-lactate (mmol/l)
2	RC	43.6	7.6	3.3	55	80	14	6	5.7	1.7
2	R	17.8	1.8	1.1	21	86	9	6	9.8	1.4
3	RC	37.1	6.0	2.4	45	81	13	5	6.2	2.2
3	R	26.4	2.6	1.7	31	87	8	5	10.2	3.6
4	RC	36.7	5.6	2.3	45	82	13	5	6.5	1.9
4	R	31.0	4.5	2.2	38	83	12	6	6.8	2.7
5	RC	19.9	4.9	1.2	26	77	19	5	4.0	2.4
5	R	17.3	2.3	1.0	21	84	11	5	7.7	1.1
6	RC	22.9	4.6	2.3	30	77	14	9	5.0	1.8
6	R	16.6	2.2	1.0	20	84	10	5	7.5	1.2
7	RC	28.7	5.3	1.8	36	80	15	5	5.4	1.9
7	R	18.8	2.7	1.0	23	85	11	5	7.1	2.2

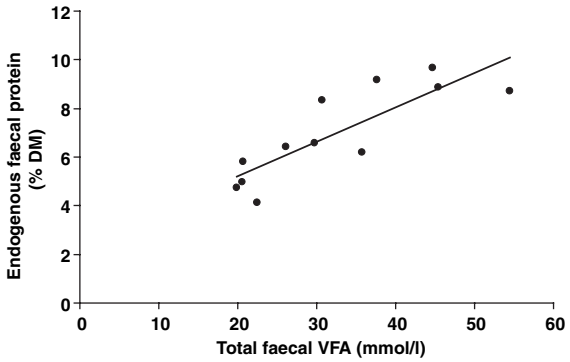

Fig. 1 Correlation between the 'endogenous faecal protein' in % faecal dry matter and the volatile fatty acid content of faecal water.

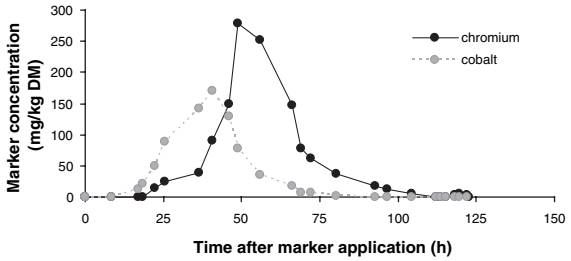

Fig. 2 Typical excretion pattern of fluid and particle markers in an Indian rhinoceros (animal 5).

Discussion

At facilities A, C and D, higher digestibility coefficients were observed on ration RC than on ration R; similarly, an addition of concentrates to a roughage ration increases the digestive efficiency in domestic horses (Kienzle et al., 2002). At facility B, an increase in the proportion of grass silage in ration R led to higher digestibility coefficients than on diet RC. Such an effect has also been reported in domestic horses fed silage instead of hay (Moore-Colyer and Longland, 2000). The apparent DM digestibilities on the regular zoo diets (ration RC) did not differ considerably in spite of different roughages used (grass hay, grass silage, alfalfa/grass hay, straw); although the DM digestibility of diet RC on a straw basis at facility C (average: 55%) was slightly lower than the averages of the other facilities (range 57–58%), the difference was not significant (*U*-test A/D vs. C, $p = 0.291$). In domestic horses, the digestive efficiency on a ration of high-quality straw and mixed feed can approximate that of a hay-mixed feed ration (Kienzle et al., 2002). On rations R, there was no significant difference between the DM digestive efficiency of the grass hay and the lucerne hay/grass hay mix (average 45–46%). In the only other study that measured the digestive efficiency of Indian rhinoceroses, Foose (1982) found OM digestibility coefficients of 52% for a grass hay of similar nutrient and fibre composition and 65% for lucerne hay, and higher fibre digestibilities. The digestive efficiency of white rhinoceroses (*Ceratotherum simum*) in that study resembles that of the Indian rhinoceroses. The digestibility coefficients in white rhinoceroses measured by Frape et al. (1982) and Kiefer (2002) resemble the values determined in our study, for mixed rations and roughage only rations, respectively.

The digestibility coefficients determined in our study for Indian rhinoceroses generally also resemble those of domestic horses on comparable diets. For hays of similar nutrient composition from Cymbaluk (1990) and Moore-Colyer et al. (2003), aD of DM (horses: 42–48%; Indian rhinoceroses from A and D: 35–53%), CP (horses: 29–59%; Indian rhinoceroses from A and D: 43–58%) and ADF (horses: 26–40%; Indian rhinoceroses from A and D: 23–43%) were of the same scope as the values determined in this study. On ration R from facility B, consisting mainly of grass silage, DM digestibilities of 57–61% were achieved, which resembles the results of 61% in domestic horses on a silage of similar composition from Moore-Colyer and Longland (2000). On rations RC with a crude fibre content of 25.6 and 30.1% DM, respectively, DM digestibilities were 41 and 45%. In domestic horses, Schmidt (1980) and

Table 6 First (transit time, TT) and last marker excretion and mean retention time (MRT) for Co-EDTA (fluid) and Cr-mordanted fibre (particles < 2 mm). Measurements in hours (h)

		Fluid marker			Particle marker		
Animal	Ration	TT	Last excretion	MRT	TT	Last excretion	MRT
1	RC	18.6	96.2	45.4	23.7	96.2	61.7
2	RC	17.3	94.1	45.3	17.3	94.1	61.5
3	RC	11.0	81.5	36.4	11.0	95.8	57.5
3	R	10.0	96.8	38.7	10.0	96.8	57.0
5	RC	17.0	80.3	39.7	22.3	122.0	56.6
6	RC	22.0	105.2	42.8	22.0	114.8	66.0

Brehms (1983) measured, on mixed rations of a crude fibre content of 24.5 and 28.8% DM, DM digestibilities of 42%. The digestibilities on the straw-based ration RC at facility C (crude fibre 29.8% DM, crude protein 8.5% DM) for OM (54–59%) and crude fibre (39–45%) are slightly higher than those achieved by horses on a straw-mixed feed ration (crude fibre 29.7% DM, crude protein 9.3% DM) of 50% for OM and 27% for crude fibre (Güldenhaupt, 1979). Kiefer (2002) already noted that the white rhinoceroses of her study did not achieve higher digestive efficiencies than domestic horses on comparable diets; similarly, the Indian and white rhinoceroses investigated by Foose (1982) did not achieve significantly higher digestibilities for organic matter than the equids of the same study.

Fehrle (1999) found a relationship of the dietary crude fibre content (in% DM) and the apparent OM digestibility in horses of

$$\text{aD OM}(\%) = 88.6 - 1.07\text{CF}(n = 95, r^2 = 0.79).$$

The corresponding equation determined in this study resembles this one; however, it has a lower correlation coefficient, which could be the result of the lower number of animals and experiments, and the smaller range of dietary CF content.

In horses, endogenous protein losses between 2.17–3.30 g/100 g DM ingested feed have been determined by linear regression analysis (Fonnesbeck, 1969; Slade and Robinson, 1970; Cymbaluk, 1990; Zeyner and Kienzle, 2002). The slope of the regression line is commonly interpreted as the true protein digestibility, which ranges in horses from 80% (Slade and Robinson, 1970) to 92% (Zeyner and Kienzle, 2002). For Indian rhinoceroses, the corresponding values from the regression analysis are 1.47 g/100 g DM and 71%. Whereas these values are lower than those reported for horses, the endogenous protein losses, expressed on a metabolic body weight (MBW) basis of 376 mg/kg$^{0.75}$ MBW, are well within the range of 169–625 mg/kg$^{0.75}$ MBW reported for horses (Prior et al., 1974; Haverkamp, 1988; Gibbs et al., 1996; Olsman et al., 2003). If, in contrast, the endogenous protein losses (MFN) are estimated, according to Mason and Frederiksen (1979), by analysing the faecal N fraction not bound to NDF residue, a higher average true protein digestibility of 89% results, as well as calculated endogenous protein losses of 3.08 g/100 g DM ingested feed or 2020 mg/kg$^{0.75}$ MBW. Using the protein content of the faecal ADF residue, Foose (1982) determined metabolic protein losses of 3.30 g/100 g DM or 3600 mg/kg$^{0.75}$ MBW in ponies and 3.89 g/100 g DM or 4500 mg/kg$^{0.75}$ MBW in horses. These comparisons underline the difficulty in the exact determination of endogenous/metabolic losses, and of finding a reliable base for interspecific comparisons. The advantage of the method propagated by Mason and Frederiksen (1979) is that it allows an estimation of the metabolic protein losses for each individual feeding trial and does not depend, as does the linear regression method, on a larger number of trials. The fact that the 'metabolic' (i.e. non-NDF bound) protein content of the faeces correlates well with the faecal VFA content, which is an indicator of microbial activity, suggests that the use of the non-NDF bound protein fraction of the faeces as an indicator of the 'metabolic' (i.e. mostly bacterial) fraction is valid (Fig. 1).

As in digestion studies with Indian elephants (*Elephas maximus*, Clauss et al. 2003), negative fat digestibilities were measured in some Indian rhinoceroses, which is probably a combined effect of low dietary fat intake and endogenous losses via gut epithelium and bacteria. The endogenous fat losses, estimated by linear regression, were 0.94 g/100 g DM ingested feed in the Indian rhinoceroses or 69 mg/kg BW, which is comparable with values for domestic horses of 1.15 g/100 g DM (from Zeyner and Kienzle, 2002) or 50–100 mg/kg BW (Zeyner, 1995). Hypothetical endogenous losses of NfE in the Indian rhinoceroses of 16.6 g/100 g DM correspond to a value for horses derived from Zeyner and Kienzle (2002) of 15 g/100 g DM.

The pH of the Indian rhinoceros faeces at facility D was between 6.3 and 6.5. Clauss et al. (2003) reported an average value of 6.4 in Asian elephants; in horses, the faecal pH ranges between 5.6 and 6.5, depending on the feeding regime, but is mostly between 6.3 and 6.5 (Argenzio et al., 1974; Radicke, 1990; Zeyner et al., 1992). According to Radicke (1990), only negligible amounts of faecal lactate are to be expected when the faecal pH is only slightly acidic. The L-lactate concentration was between 1.0 and 3.1 mmol/l in the Indian rhinoceroses; in horses, values between 0.1 and 0.9 mmol/l are measured on roughage-only rations (Alexander and Davies, 1963) or up to 4 mmol/l on concentrate rations (Argenzio et al., 1974). Clemens and Maloiy (1982) measured values of 0.9 mmol/l in free-ranging black rhinoceroses (*Diceros bicornis*). The difference in faecal VFA content between the different rations follows the same pattern observed in horses and elephants (Zeyner et al., 1992; Clauss et al., 2003). However, the total VFA content in the Indian rhinoceroses was lower than that reported for

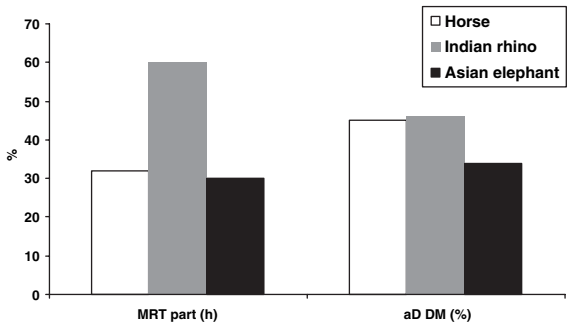

Fig. 3 Comparison of the mean particle retention time (MRT part, h) and the apparent dry matter digestibility (aD DM,%) of a hay-only diet in the domestic horse, the Indian rhinoceros and the Asian elephant. Data from Pagan et al. (1998)/Udén and Van Soest (1982) (horse); Loehlein et al. (2003)/Clauss et al. (2003) (elephant); and this study (rhinoceros).

horses (Argenzio et al., 1974; Drochner and Meyer, 1991; Zeyner et al., 1992). On the one hand, this could be the result of longer ingesta retention times with a more extended absorption of VFA in the distal colon; on the other hand, this could be a dilution effect caused by the higher faecal water content in the rhinoceroses (average 82% of wet weight) compared with horse values (e.g. 76% of wet weight, Fehrle, 1999).

The mean ingesta particle retention times of the Indian rhinoceroses were the longest ever measured with this marker system in a monogastric ungulate. Thus, the general pattern found by Foose (1982) was confirmed – in that study, the Indian rhinoceros also had the longest mean retention time of all hindgut fermenters. A general concept of the influence of body size on the digestion is that larger animals have a digestive advantage, as the increase in body size is accompanied by an increase in gut capacity (Parra, 1978) and ingesta retention time (Illius and Gordon, 1992); as the digestion of fibrous material depends on the time the substrate is submitted to bacterial fermentation, a longer retention time should result in higher digestion coefficients (Demment and Van Soest, 1985). A comparison of measured retention times and digestibility coefficients for hay-only diets in horses, Indian rhinoceroses and elephants, however, shows a different picture (Fig. 3): the Indian rhinoceros has a distinctively longer ingesta retention time than the horse, but achieves only a similar digestibility coefficient. The elephant, on the contrary, has a similar ingesta retention time as the horse, yet does not achieve a similar digestive efficiency, but distinctively lower coefficients. This comparison indicates that larger body size must infer a digestive disadvantage, which is compensated for in the Indian rhinoceros by the long retention time. Potential reasons for such a disadvantage have been proposed by Clauss and Hummel (in press) and comprise an increase in ingesta particle size, and a decrease in the ratio of absorptive gut surface:gut volume; however, the potential effects of these factors have not been quantified to date.

We conclude that the Indian rhinoceros resembles the domestic horse in most digestive characteristics, and the use of the domestic horse as a model animal in the diet design for captive Indian rhinoceroses (Oftedal et al., 1996) is justified. The question of why this resemblance is evident in spite of the immense body size difference between the species remains to be answered.

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