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ORIGINAL ARTICLE

Digestion coefficients achieved by the black rhinoceros (*Diceros bicornis*), a large browsing hindgut fermenter

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Summary

In contrast to the grazing white (*C. simum*) and Indian (*R. unicornis*) rhinoceros, the black rhinoceros (*D. bicornis*) is an exclusive browser. Due to the particular fermentation characteristics of browse, one would expect browsers to display both shorter ingesta retention times and lower digestion coefficients on comparable diets than grazers. In order to generate a database to test this hypothesis, we performed digestibility studies in eight black rhinoceroses (*D. bicornis*) from three zoological institutions, using total faecal collection for the quantification of faecal output. One to three regularly fed zoo rations of roughage, concentrates and varying proportions of browse material were used per animal. Additional data was taken from three hitherto unpublished studies as well as several published sources. When compared with horses on similar rations, black rhinoceroses achieved lower digestion coefficients for organic matter and CF. In general, an increase in dietary CF content led to a steeper decrease in organic matter and GE digestibility in black rhinoceroses than in horses. When comparing available data for rhinoceroses, browsing species showed a steeper decrease in organic matter digestibility than grazing species with increasing dietary cell wall content. Endogenous losses as determined by linear regression analysis were within the range reported for horses and Indian rhinoceroses. The results suggest that the horse is not a useful model animal for evaluating diets for black rhinoceroses energetically. In general, diets fed to captive black rhinoceroses seem to include higher proportions of concentrates than diets for other rhinoceros species, and an increase in browse or roughage would reduce digestion coefficients to levels observed in animals fed natural forage.

Introduction

For large hindgut fermenters such as elephants or rhinoceroses, the horse has been proposed as the appropriate model when designing diets for captive animals (Oftedal et al., 1996). While this assumption could be confirmed in feeding trials with white rhinoceroses (*Ceratotherium simum*, Kiefer, 2002) and Indian rhinoceroses (*Rhinoceros unicornis*, Clauss et al., 2005b), it was demonstrated that the horse is

Table 1 Diet composition (fresh matter) in free-ranging black rhinoceroses (*Diceros bicornis*)

Proportion of ingested diet (%)			
Shrubs and trees	Herbs	Grass	Source
87–95	5–13	0 (one observation)	Joubert and Eloff (1971)
54–81	18–41	0	Mukinya (1977)
81–94	6–19	0	Hall-Martin et al. (1982)
47–93	5–51	0	Oloo et al. (1994)
93–95	3–5	1	Atkinson (1995)
56–76	1–11	0–1	Pole (1995)
69	31	0	Hennig and Gindrig (2001)

not an adequate model for digestion in elephants (Clauss et al., 2003). The third rhinoceros species commonly represented in zoological gardens, the black rhinoceros (*Diceros bicornis*), has not been investigated in this respect so far.

In contrast to the other two rhinoceros species mentioned, which are both grazers (Foster, 1960; Dinerstein, 1989), the black rhinoceros has been shown to be a strict browser by both qualitative (Goddard, 1968, 1970; Schenkel and Schenkel-Hullinger, 1969; Loutit et al., 1987; Emslie and Adcock, 1994) and quantitative observations (cf. Table 1). The relevance of this fact lies in a fundamental difference in fermentation characteristics between browse and grass: in comparison, browse has a faster fermentation rate and soon reaches its maximum of fermentative energy release, whereas grass has a slow fermentation rate and still yields fermentative energy even after a longer period of time (Short et al., 1974; Hummel et al., 2005). Therefore, one would expect the process of evolutionary adaptation to have resulted in comparatively shorter ingesta retention times in browsing than in grazing herbivores, and corresponding, comparatively lower digestion coefficients in browsers than in grazers on comparable diets.

The black rhinoceros has recently been demonstrated to display shorter ingesta retention times than expected (Clauss et al., 2005a). In this study, we present data on digestion coefficients in black rhinoceroses to facilitate a comprehensive comparison between this species and horses, and between grazing and browsing hindgut fermenters.

Animals, materials and methods

Eight black rhinoceroses from three zoological institutions were used. The animals were either weighed or their body weights estimated using the weighed animals as a comparison (Table 2). Animals had regular access to outside enclosures that 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.

Table 2 Black rhinoceroses (*Diceros bicornis*) used for digestion trials

Animal no.	Studbook no.	Sex	Age (years)	BM (kg)	Diets fed	Study
1	451	F	10	1000/1065	N1, N2	Woodfine (unpublished data), this study
2	430	M	11	1093/1133	N1, N2	Woodfine (unpublished data), this study
3	533	M	6	1000°	N	This study
4	532	F	7	1000°	N	This study
5*	150	F	31	762	N1, N2	This study
6	217	F	*c.* 30†	1000°	N1, N2	This study
7	318	M	19	1200°	N, B1, B2	This study
8	662	F	5	900°	N, B1, B2	This study
9	428	F	10	1200°	N1, N2	Froeschle and Clauss (unpublished data)
10	610	M	4	1200°	N1, N2	Froeschle and Clauss (unpublished data)
11	240	F	27	1160	N1, N2	Froeschle and Clauss (unpublished data)
12	438	M	9	1200°	N1, N2	Froeschle and Clauss (unpublished data)
13	437	F	9	1200°	N1, N2	Froeschle and Clauss (unpublished data)
14	376	M	12	1100	N	Paros and Dierenfeld (unpublished data)
15	396	F	11	1200	N	Paros and Dierenfeld (unpublished data)

Body weights (BM) represent either actual weights or estimates (°). Diets used were conventional zoo diets with hay and concentrates (N) and zoo diets supplemented with different proportions of browse (B).

*Animal had an oral abscess and received a particular diet (Hatt et al., 2004).

†Exact age was unknown as animal was caught from the wild.

The diets used for these feeding trials were the regular diets used at the respective zoological institution (cf. Table 3). One animal (no. 5) had difficulties in ingesting roughage material because of an oral abscess (Hatt et al., 2004) and received a special diet with a high proportion of green meal pellets. Unfortunately, the feeding of a roughage-only diet was not possible. The measurement of food intake and total faecal excretion, as well as the sampling procedure, the laboratory analyses and the calculations followed the same protocol as outlined for Indian rhinoceroses in Clauss et al. (2005b). Analyses included dry matter (DM), crude protein (CP), crude ash, crude fibre (CF) and ether extract (EE), neutral detergent fibre (NDF), acid detergent fibre and acid detergent lignin, gross energy (GE), and non-dietary faecal nitrogen (NDFN) according to the protocol developed by Mason and Frederiksen (1979) for domestic sheep.

Additional data were available from the literature, and from three hitherto unpublished studies by T. Woodfine, D. Paros and E.S. Dierenfeld (Marwell Preservation Trust, Winchester, Hampshire, UK and St Louis Zoo, St Louis, MO, USA), and T. Froeschle and M. Clauss (University of Zurich, Zurich, Switzerland). The set up of these studies and the analytical procedures were identical to this study; however, the chemical analyses were performed by other laboratories. These additional data are added to the tables and the calculations where appropriate.

Hypothetical endogenous faecal losses of CP and EE were calculated using the Lucas test by plotting nutrient content of the diet against its digestible nutrient content; the slope of the regression line corresponds to the 'true' digestibility of the nutrient, and the intercept represents the endogenous losses per 100 g DM intake (Robbins, 1993). Digestibility coefficients of black rhinoceroses were compared with data from domestic horses in two different ways: (i) horse data were collected from the literature where diets of similar ingredient composition, of similar CF and similar CP content had been used; the maximum deviation of CF and CP content from the rhinoceros diets allowed was 2% points, and a maximum of two horse data points were allowed per black rhinoceros data point; (ii) the complete data set on domestic horse digestibility coefficients from Fehrle (1999) was compared against the complete rhinoceros data set. Additionally, we compared data on digestibility in grazing rhinoceros species – Indian and white rhinoceros – from the literature against coefficients measured in browsing rhinoceros species – Sumatran (*Dicerorhinus sumatrensis*) and black rhinoceros – from both the literature and this study.

The Spearman correlation coefficient (SCC) was used to test different nutrients and digestibilities for monotonous association. Analysis of covariance served to compare the slopes and intercepts of regression lines between nutrient and digestible nutrient content of rations. The significance level was set to 5%. All statistical analyses were performed using the SPSS 11.0 (SPSS, Chicago, IL, USA) statistical software package.

Results

With the exception of animal 5, 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.

The digestion coefficients achieved by the black rhinoceroses, as well as true protein digestibility and NDFN as derived by analysing CP content in the NDF residue according to Mason and Frederiksen (1979), are recorded in Table 4. There was a significant negative correlation between the CF content of the diet and the apparent digestibility (aD) of both dry and organic matter (DM: SCC = −0.705, $p < 0.001$; organic matter: SCC = −0.701, $p < 0.001$) (cf. Table 5). Accordingly, an increase in the proportion of browse in the diet led to a reduction in digestive efficiency, thus approaching magnitudes observed in free-ranging animals (Fig. 1). True protein digestibility was significantly correlated to apparent protein digestibility (SCC = 0.842, $p < 0.001$). Endogenous faecal losses and true digestibilities of CP and EEs calculated by regression analysis are given in Table 6.

When comparing horse and black rhinoceros data, obtained on comparable diets, black rhinoceroses achieved significantly lower organic matter (ANCOVA: $F(1,33) = 24.5$, $p < 0.001$) and CF digestibilities (ANCOVA: $F(1,33) = 46.0$, $p < 0.001$) (Fig. 2). In relation to the complete data set from horses from Fehrle (1999), black rhinoceroses had a significantly steeper negative slope in the regression of aD GE (comparison of slopes: $p = 0.020$) and at least an analogous tendency in the regression of aD OM (comparison of slopes: $p = 0.062$) against dietary CF content. In the interspecific rhinoceros comparison, the browsing black and Sumatran rhinoceros had a significantly steeper slope in the regression of aD OM against dietary NDF content than the grazing

Table 3 Ration composition (both in terms of ingredients and nutrients) of rations fed to black rhinoceroses (*Diceros bicornis*) in digestion trials

No.	Diet	Lucerne hay	Grass hay	Browse	Conc.	Fruits and vegetables	CA	CP	EE	CF	NDF	ADF	ADL	GE	Source
1	N1	34	–	–	39	27	7.1	13.1	NA	NA	37.8	25.9	3.8	NA	Woodfine (unpublished data)
1	N2	25	–	–	69	6	7.5	15.1	2.8	23.6	44.6	29.3	6.0	18.3	This study
2	N1	55	–	–	29	16	7.5	12.4	NA	NA	46.9	33.5	4.9	NA	Woodfine (unpublished data)
2	N2	40	–	–	55	4	7.3	15.1	2.4	26.8	49.1	33.6	6.8	18.3	This study
3	N	–	70	5*	18	6	7.8	12.2	4.8	24.3	50.0	26.5	2.2	18.7	This study
4	N	–	68	6*	19	7	7.8	12.3	4.8	23.9	49.3	26.2	2.2	18.6	This study
5	N1	22	12	–	54	11	7.0	13.1	2.0	17.0	34.1	19.7	3.1	18.1	This study
5	N2	–	2	–	91†	7	9.5	14.6	2.4	13.6	31.6	16.4	2.6	17.6	This study
6	N1	13	28	–	47	12	6.4	11.3	1.9	19.1	38.6	22.3	3.1	18.1	This study
6	N2	–	43	–	50	7	6.5	9.4	1.5	20.8	40.7	23.8	2.7	18.0	This study
7	B1	–	48	18‡	30	4	6.3	8.1	1.3	27.2	50.7	31.5	4.9	18.2	This study
7	B2	18	41	22§	14	5	6.3	8.1	1.6	31.7	60.9	39.0	6.6	18.4	This study
7	N	24	39	–	29	8	6.6	11.4	1.7	22.5	43.3	26.1	3.7	18.1	This study
8	B1	–	40	13‡	41	5	6.3	8.9	1.5	23.8	45.3	27.5	4.1	18.1	This study
8	B2	19	39	21§	15	6	6.5	8.1	1.7	31.1	60.5	38.6	6.6	18.4	This study
8	N	19	17	–	52	12	6.7	12.6	1.9	17.0	34.0	19.7	3.0	18.1	This study
9	N1	17	48	–	32	3	6.4	12.0	NA	29.7	46.2	24.8	5.7	18.7	Froeschle and Clauss (unpublished data)
9	N2	–	91¶	–	–	9	8.4	16.4	NA	28.3	42.5	25.7	4.6	19.3	Froeschle and Clauss (unpublished data)
10	N1	19	47	–	30	4	6.4	12.1	NA	30.1	46.4	25.3	5.8	18.7	Froeschle and Clauss (unpublished data)
10	N2	–	91¶	–	–	9	8.7	16.7	NA	28.3	42.5	25.6	4.5	19.2	Froeschle and Clauss (unpublished data)
11	N1	–	44	–	46	10	6.6	11.2	NA	24.0	42.6	21.1	4.1	18.6	Froeschle and Clauss (unpublished data)
11	N2	–	91¶	–	–	9	8.7	16.7	NA	28.3	42.5	25.6	4.5	19.2	Froeschle and Clauss (unpublished data)
12	N1	–	76	–	10	14	9.6	8.9	NA	25.6	46.2	25.8	3.4	17.8	Froeschle and Clauss (unpublished data)
12	N2	–	90¶	–	10	–	11.3	18.7	NA	23.7	NA	NA	NA	17.8	Froeschle and Clauss (unpublished data)
13	N1	–	76	–	9	15	9.6	8.8	NA	25.5	46.0	25.8	3.4	17.8	Froeschle and Clauss (unpublished data)
13	N2	–	89¶	–	11	–	11.2	18.6	NA	23.6	NA	NA	NA	17.9	Froeschle and Clauss (unpublished data)
14	N	70	–	–	30	–	9.3	20.5	2.7	NA	38.9	28.8	7.7	NA	Paros and Dierenfeld (unpublished data)
15	N	66	3	–	31	–	9.2	20.1	2.7	NA	39.4	29.1	7.6	NA	Paros and Dierenfeld (unpublished data)
16		NR	NR	NR	NR	NR	9.1	6.8	NA	NA	49.0	37.8	NA	NA	Hamilton (1999)
17		–	82	–	18	–	7.5	10.9	2.3	29.0	NA	NA	NA	16.4	Spala and Hradecky (1993)
18		–	78	–	22	–	7.4	11.0	2.5	28.0	NA	NA	NA	16.4	Spala and Hradecky (1993)
19		–	76	–	24	–	7.4	11.0	2.5	27.6	NA	NA	NA	16.5	Spala and Hradecky (1993)
17		–	83	–	17	–	7.8	12.6	2.3	27.8	NA	NA	NA	16.3	Spala and Hradecky (1993)
18		–	83	–	17	–	7.8	12.6	2.3	27.6	NA	NA	NA	16.3	Spala and Hradecky (1993)
19		–	83	–	17	–	7.8	12.6	2.3	27.7	NA	NA	NA	16.3	Spala and Hradecky (1993)
20		–	100	–	–	–	NA	8.0	NA	NA	66.0	44.0	NA	17.6	Ullrey et al. (1979)

Table 3 (Continued.)

No.	Diet	Lucerne hay	Grass hay	Browse	Conc.	Fruits and vegetables	CA	CP	EE	CF	NDF	ADF	ADL	GE	Source
21		–	100	–	–	–	5.3	4.5	NA	NA	72.9	43.3	6.6	NA	Foose (1982)
21		100	–	–	–	–	9.4	20.0	NA	NA	37.8	30.8	6.5	NA	Foose (1982)
22		–	–	100**	–	–	4.8	10.5	NA	NA	54.1	42	10.6	NA	Atkinson (1995)
23		–	–	100**	–	–	4.4	10.4	NA	NA	56.8	45	11.1	NA	Atkinson (1995)
24		–	–	100**	–	–	3.9	10.1	NA	NA	54.9	42	10.9	NA	Atkinson (1995)
25		–	–	100**	–	–	2.7	9.6	NA	NA	56.0	45	10.3	NA	Atkinson (1995)
26		–	–	100††	–	–	6.8	15.1	3.2	44.4	66.4	NA	9.0	18.2	Clemens and Maloiy (1982)

GE in MJ/kg dry matter (DM), all other values in % DM; Conc., concentrates (including grains and bread); CA, crude ash; CP, crude protein; EE, crude fat; CF, crude fibre; NDF, neutral detergent fibre/cell walls; ADF, acid detergent fibre; ADL, acid detergent lignin; GE, gross energy; NA, not analysed; NR, not reported. For coding of diets see Table 2.

*Dried temperate browse.

†Fresh temperate browse.

‡Temperate browse silage and fresh temperate browse.

§Including a high proportion of green meal pellets.

¶Fresh grass.

**Different indigenous browse species fed to boma animals in Zimbabwe.

††Browse consumed by a free-ranging animal.

Indian and white rhinoceros (comparison of slopes: $p < 0.001$) (Fig. 3).

Discussion

The results of this study confirm the hypothesis that black rhinoceroses achieve relatively low digestion coefficients when compared with species of similar gastrointestinal morphology and similar body size. This has already been indicated by data from single feeding trials in equids and rhinos by Foose (1982), and in white and black rhinoceroses by Ullrey et al. (1979) and Foose (1982). Ideally, this result should be confirmed by more comparative digestion trials using roughage-only diets. Whereas the Indian and white rhinoceros achieve digestion coefficients that are of the same scope as those of horses on similar diets (Foose, 1982; Frape et al., 1982; Kiefer, 2002; Clauss et al., 2005b), the black rhinoceros displays a lesser digestive efficiency. This lesser digestive efficiency is particularly evident on high-fibre diets, and could, in part, be explained by the comparatively short ingesta retention times observed in black rhinoceroses (Clauss et al., 2005a). Among wild ruminant species, it has been demonstrated that browsing species achieve lower coefficients for fibre digestion than grazing species (Iason and Van Wieren, 1999; Pérez-Barbería et al., 2004), and relatively shorter ingesta retention times have been suspected in browsing ruminants (Clauss and Lechner-Doll, 2001). For elephants, Hackenberger (1987) demonstrated that the African elephant (*Loxodonta africana*), which is thought to be adapted to a diet with a higher proportion of browse material than its Asian counterpart (Cerling et al., 1999), also displays both shorter retention times and lower digestibilities for grass hay than the Asian elephant (*Elephas maximus*). A digestive strategy of long retention times with high digestion coefficients is an evolutionary adaptation one would expect in grazing species, be they foregut or hindgut fermenters, because of the fermentation characteristics of grass material (cf. *Introduction*). In contrast, shorter retention times and lower digestion coefficients would be expected in browsing species. In theory, this should result in comparatively lower food intakes in the grazing species, as suggested by Owen-Smith (1982) or Prins and Kreulen (1991). Although comprehensive data collections to test this suspicion are missing, the intakes observed by Foose (1982) in rhinoceros and elephant species on a similar diet could be a first indication that this concept may be valid (organic matter intake in $g/kg^{0.75}$ metabolic body mass on lucerne hay: black rhino 91, white rhino 74, Indian rhino 78; African elephant 91, Asian elephant 85).

Comparing the calculated endogenous faecal losses of black rhinoceroses to other larger hindgut fermenters (Table 6) indicates similarities between species in these parameters. Additionally, the

Table 4 Apparent digestibility coefficients for nutrients and gross energy (GE), 'true protein digestibility' (TPD) and non-dietary faecal nitrogen (NDFN, in % of total faecal nitrogen) in black rhinoceroses (*Diceros bicornis*)

		Apparent digestibility (%)										
No.	Diet	DM	OM	CP	EE	CF	NDF	ADF	GE	TPD	NDFN	Source
1	N1	55	–	55	–	–	32	21	–	–	–	Woodfine (unpublished data)
1	N2	59	60	65	58	31	40	37	56	92	78	This study
2	N1	46	–	51	–	–	21	18	–	–	–	Woodfine (unpublished data)
2	N2	51	52	66	45	20	28	26	47	91	75	This study
3	N	46	47	55	55	28	26	22	45	90	77	This study
4	N	50	51	52	50	38	34	31	47	90	79	This study
5	N1	69	71	74	45	38	44	38	67	94	77	This study
5	N2	68	71	52	31	53	56	50	65	88	75	This study
6	N1	63	65	64	41	31	39	34	61	93	81	This study
6	N2	66	67	62	46	40	44	40	63	93	83	This study
7	B1	56	56	57	8	36	36	34	53	90	76	This study
7	B2	48	48	55	16	27	35	33	45	87	72	This study
7	N	62	63	72	48	32	38	34	61	93	76	This study
8	B1	62	63	60	36	40	44	41	59	93	81	This study
8	B2	36	36	43	16	12	20	17	32	87	77	This study
8	N	72	74	79	55	39	44	37	71	95	76	This study
9	N1	53	57	48	–	44	36	31	52	–	–	Froeschle and Clauss (unpublished data)
9	N2	53	59	54	–	60	43	47	52	–	–	Froeschle and Clauss (unpublished data)
10	N1	54	57	51	–	52	36	31	54	–	–	Froeschle and Clauss (unpublished data)
10	N2	53	59	61	–	60	45	48	52	–	–	Froeschle and Clauss (unpublished data)
11	N1	54	64	57	–	56	45	42	59	–	–	Froeschle and Clauss (unpublished data)
11	N2	57	59	62	–	59	47	49	52	–	–	Froeschle and Clauss (unpublished data)
12	N1	54	57	45	–	40	41	38	53	–	–	Froeschle and Clauss (unpublished data)
12	N2	63	65	77	–	49	–	–	59	–	–	Froeschle and Clauss (unpublished data)
13	N1	48	51	39	–	33	32	27	46	–	–	Froeschle and Clauss (unpublished data)
13	N2	62	64	76	–	41	–	–	59	–	–	Froeschle and Clauss (unpublished data)
14	N	65	66	78	31	–	49	34	–	–	–	Paros and Dierenfeld (unpublished data)
15	N	63	63	78	34	–	42	35	–	–	–	Paros and Dierenfeld (unpublished data)
16		50	55	26	–	–	27	42	56	–	–	Hamilton (1999)
17		46	47	50	29	35	–	–	46	–	–	Spala and Hradecky (1993)
18		55	56	54	22	49	–	–	55	–	–	Spala and Hradecky (1993)
19		60	61	58	28	56	–	–	60	–	–	Spala and Hradecky (1993)
17		63	65	51	60	57	–	–	65	–	–	Spala and Hradecky (1993)
18		43	44	35	45	22	–	–	44	–	–	Spala and Hradecky (1993)
19		44	45	36	38	26	–	–	47	–	–	Spala and Hradecky (1993)
20		–	–	30	–	–	33	22	34	–	–	Ullrey et al. (1979)
21		–	43	–	–	–	41	37	–	84	–	Foose (1982)
21		–	65	–	–	–	49	49	–	96	–	Foose (1982)
22		40	44	69	–	–	22	18	–	–	–	Atkinson (1995)*
23		40	45	57	–	–	27	26	–	–	–	Atkinson (1995)*
24		36	41	66	–	–	16	13	–	–	–	Atkinson (1995)*
25		43	49	69	–	–	26	30	–	–	–	Atkinson (1995)*
26		27	30	45	15	8	16	–	27	–	–	Clemens and Maloiy (1982)

For coding of diets see Table 2. DM, dry matter; OM, organic matter; CP, crude protein; EE, crude fat; CF, crude fibre; NDF, neutral detergent fibre; ADF, acid detergent fibre.

*Calculated from data on DM intake, DM digestibility and faeces composition from two different trial sets.

proportion of NDFN was of a similar scope in the black rhinoceroses of this study (72–83%) and in Indian rhinoceroses (73–84%; Clauss et al., 2005b), but somewhat lower in three Sumatran rhinoceroses (64–76%) studied by Dierenfeld et al. (2000). Whether this parameter can be used to identify species differences remains to be tested with further data. In contrast to a study on Indian rhinoceroses (Clauss

Table 5 Correlation between crude fibre content of the diet and the apparent digestibility (aD) of dry matter (DM) and organic matter (OM) in black rhinoceroses (*Diceros bicornis*), Indian rhinoceroses (*Rhinoceros unicornis*), elephants (*Elephas maximus*) and domestic horses, according to the equation aD = *a*CF + *b*

	a	*b*	R^2	*n*	Source
aD DM					
Black rhinoceros	−1.47	92.7	0.66	31	cf. Tables 3 and 4
Indian rhinoceros	−0.77	78.3	0.17	19	Clauss et al. (2005a)
Asian elephant	−1.18	81.9	0.35	31	Clauss et al. (2003)
aD OM					
Black rhinoceros	−1.45	94.4	0.63	31	cf. Tables 3 and 4
Indian rhinoceros	−0.82	80.3	0.18	19	Clauss et al. (2005a)
Horse	−1.07	88.6	0.79	95	Fehrle (1999)

et al., 2005b), the true protein digestibility in black rhinoceroses determined by regression analysis and by measuring faecal NDF-bound protein yielded comparable results. As in that study, there was a positive correlation between the true and the apparent protein digestibility. The fact that the true fat digestibility calculated for black and Indian rhinoceroses is distinctively lower than that calculated for domestic horses (Table 6), can probably be explained by the relatively small range of dietary fat contents used in the rhinoceros species. These considerations underline the difficulties in attempting to compare endogenous losses between species, which would necessitate more trials with a wider range of nutrient contents.

It has been suggested that the black rhinoceros might receive, in captivity, diets that are characterized by a comparatively low-fibre content and unnaturally high nutrient availabilities (Dierenfeld, 1995). The comparison of the diets used in the different rhinoceros species in Fig. 3 supports that suspicion. The addition of browse (cf. Fig. 1), but most likely any addition of roughage and restriction of concentrates will lead to digestion coefficients more similar to those achieved by animals consuming natural forages. Whether diets high in concentrates contribute to the uncommon disease phenomena observed in captive black rhinoceroses (Miller, 2003) remain to be demonstrated.

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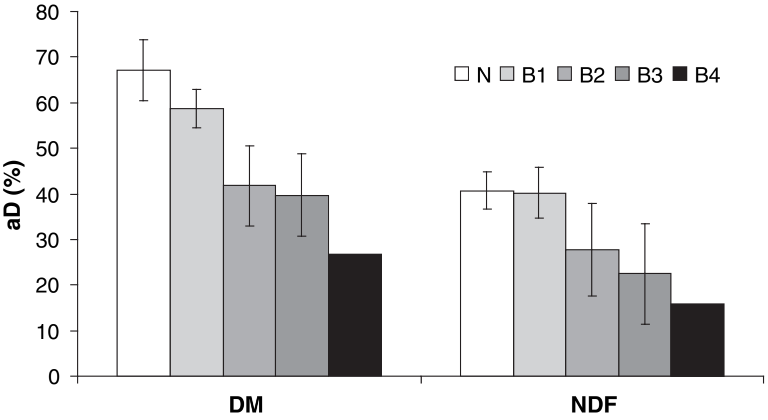

Fig. 1 Influence of an increasing proportion of browse on apparent digestibilities (aD) of dry matter (DM) and neutral detergent fibre (NDF) in black rhinoceroses (*Diceros bicornis*). Data represent conventional zoo rations (N, no browse; this study), with increasing amounts of browse (B1, 13–18% browse in DM; B2, 21–22% browse in DM; this study), animals fed natural browse only under boma conditions (B3, Atkinson, 1995) and free-ranging animals (B4, Clemens and Maloiy, 1982).

Table 6 Endogenous faecal losses of crude protein (CP) and crude fat (EE) in g/100 g dry matter intake and 'true digestibility' (tD) in percentage as calculated by regression analysis for black rhinoceroses (*Diceros bicornis*), Indian rhinoceroses (*Rhinoceros unicornis*) and domestic horses

	CP	tD CP	EE	tD EE	Source
Black rhinoceros	3.7	88	0.4	57	cf. Tables 3 and 4
Indian rhinoceros	1.5	71	1.0	62	Clauss et al. (2005a)
Horse	2.2–3.3	80–92	1.2	100	Fonnesbeck (1969); Slade and Robinson (1970); Cymbaluk (1990); Zeyner and Kienzle (2002)

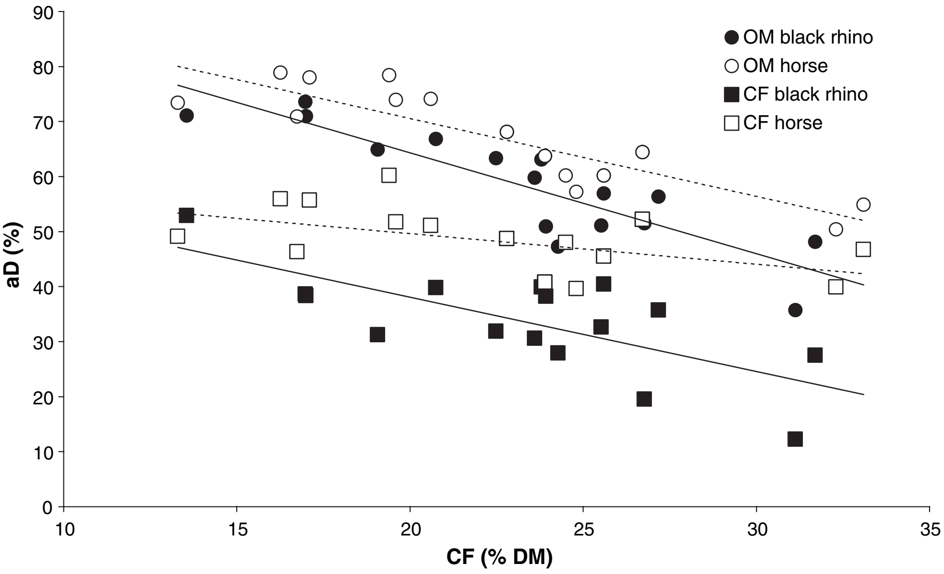

Fig. 2 Correlation of dietary crude fibre [(CF), in % dry matter (DM)] content and the apparent digestibility (aD) of organic matter (OM) and CF in black rhinoceroses (*Diceros bicornis*) and domestic horses on comparable diets (see *Methods* for choice of horse data). Data on black rhinoceroses from Tables 3 and 4, data on horses from Hoffmann et al. (1967); Ahlswede (1977); Güldenhaupt (1979); Schmid (1980); Schubert and Fuchs (1987); Faurie et al. (1992); Zeyner et al. (1992) and Fehrle (1999). Regression equations for black rhinoceroses (solid lines) aD OM $= -1.83x + 101$; $R^2 = 0.77$ (upper line), aD CF $= -1.35x + 65$; $R^2 = 0.51$ (lower line); for horses (dashed lines) aD OM $= -1.42x + 99$; $R^2 = 0.78$ (upper line), aD CF $= -0.56x + 61$; $R^2 = 0.23$ (lower line).

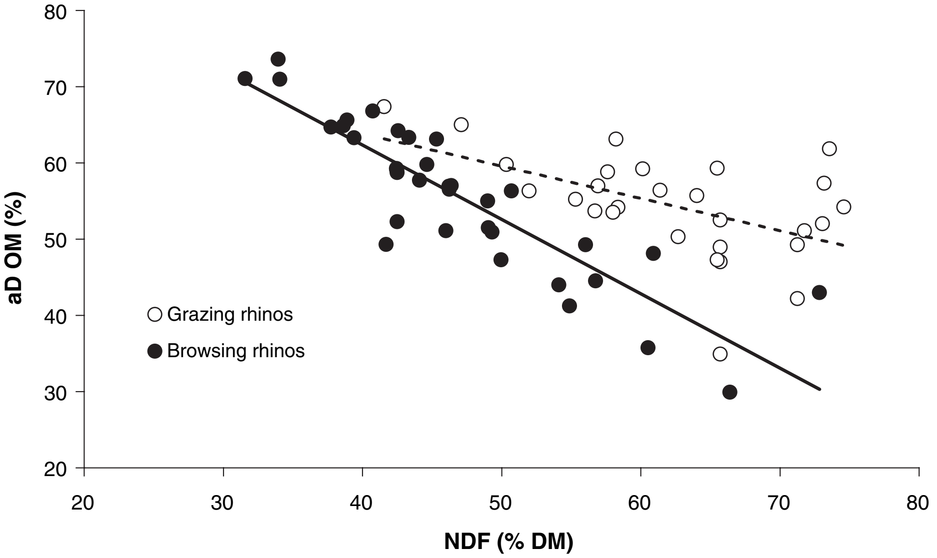

Fig. 3 Correlation of dietary cell wall [neutral detergent fibre (NDF), in % dry matter (DM)] content and the apparent digestibility (aD) of organic matter (OM) of grazing (Indian and white) and browsing (Sumatran and black) rhinoceros species. Data on black rhinoceroses from Tables 3 and 4, on Sumatran rhinoceroses from Dierenfeld et al. (2000), on white rhinoceroses from Foose (1982) and Kiefer (2002), on Indian rhinoceroses from Clauss et al. (2005a). Regression for browsing rhinoceroses (solid line): $y = -0.98x + 101$; $R^2 = 0.77$. Regression for grazing rhinoceroses (dashed line): $y = -0.42x + 81$; $R^2 = 0.28$.

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