

Fluid and particle retention times in the black rhinoceros *Diceros bicornis*, a large hindgut-fermenting browser

Marcus CLAUSS*, Tanja FROESCHLE, Johanna CASTELL, Jean-Michel HATT*,
Sylvia ORTMANN, W. Jürgen STREICH and Jürgen HUMMEL*

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The mean retention time (MRT) of ingesta in the gastrointestinal tract is one of the major determinants of herbivore digestive physiology. We examined MRTs of fluids and particles in the gastrointestinal tract of six adult captive black rhinoceroses *Diceros bicornis* on conventional zoo diets. Fluid MRT ranged from 25–45 h and averaged 31 h. Particle MRT ranged from 28–59 h and averaged 38 h. In the six animals, both fluid and particle MRT declined as relative dry matter intake (g/kg metabolic body mass) increased. Black rhinoceroses, which are large hindgut-fermenting browsers, retained ingesta for a shorter period relative to their body size than grazing equids or grazing rhinoceros species. Our findings support the hypothesis that browsing hindgut fermenters have relatively shorter MRTs than grazing hindgut fermenters.

Institute of Animal Physiology, Physiological Chemistry and Animal Nutrition, Schoenleutner Str. 8, 85764 Oberschleissheim, Germany (MC, TF, JC, JH); Division of Zoo Animals and Exotic Pets, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland (J-MH); Institute of Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany (SO, WJS); Zoological Garden of Cologne, Riehler Str. 173, 50735 Cologne, Germany (JH)

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Introduction

There is an ongoing debate as to whether documented differences between grass (monocots) and browse (dicots) plant species has led to differing adaptations of digestive physiology in grazing and browsing herbivorous mammals (eg Owen-Smith 1982, Clauss *et al.* 2003, Gordon 2003, Pérez-Barbería *et al.* 2004). Grass and browse vary in several chemical and physical characteristics – for example, browse generally has a higher proportion of lignin in its fibre fraction (Owen-Smith 1982), and grasses have a higher relative cell wall thickness

* Present address: Division of Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland, e-mail: mclauss@vetclinics.unizh.ch (MC); Institute of Animal Science, Department of Animal Nutrition, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany (JH)

(Spalinger *et al.* 1986). These factors might, amongst others, account for the fact that browse is usually characterized by a fast fermentation soon reaching its maximum, whereas grass is characterized by a slower fermentation that still yields energy after a longer period of time (Short *et al.* 1974). Thus, browsing herbivores should not retain ingesta in their gut for as long as grazers.

For ruminants, it has been suggested that browsers should have shorter mean retention times (MRTs) than grazers of comparable size (Kay 1987, Hofmann 1989). Data collections have been compiled to address this hypothesis (Gordon and Illius 1994, Robbins *et al.* 1995, Clauss and Lechner-Doll 2001), however most of the data cannot be compared directly due to differences in the methodologies used to measure ingesta retention (Clauss and Lechner-Doll 2001). Nevertheless, a recent comparison of the ability to digest fibre material between grazers and browsers indicates that grazers achieve higher digestion coefficients for fibre than browsers (Pérez-Barbería *et al.* 2004), supporting the hypothesis of a longer MRT and hence more thorough fibre digestion in grazers.

A comprehensive comparison of aspects of digestive physiology has not yet been conducted between browsing and grazing species of hindgut-fermenting herbivores. A major problem in this respect is the paucity of extant browsing species among the large hindgut fermenters. To date, the only comparative study in this respect is the thesis of Hackenberger (1987), who demonstrated that African elephants *Loxodonta africana* have shorter MRTs than Asian elephants *Elephas maximus* of comparable body mass, when both are eating grass hay. He interpreted this as an adaptation to the respective natural diet of the species. African elephants naturally ingest larger proportions of browse forage than Asian elephants (Cerling *et al.* 1999). Foose (1982) measured digestibilities and ingesta retention times in a large number of captive ungulates to compare the digestive physiology of hindgut versus foregut fermenters. Due to the large number of species and individuals investigated, it was only possible to calculate MRT for each individual by the use of one or two pooled faecal samples per day (Foose 1982). Thus, MRTs from that study are generally overestimated compared to those calculated from more faecal samples per day in other studies, and differences in the MRT between species that are smaller than the scope of days (ie, hours) might be overlooked (Clauss *et al.* 2003). Foose (1982) himself did not perform a comparison of ingesta retention between browsers and grazers with his own data.

In this study, we examined the MRT of fluids and particles in a large, strictly browsing hindgut fermenter, the black rhinoceros *Diceros bicornis* Linné, 1758 (Goddard 1968, 1970, Mukinya 1977, Oloo *et al.* 1994). In theory, if a relatively short MRT is assumed to be an evolutionary adaptation to a browse-based diet, we would expect such short MRT in the black rhinoceros. To test this hypothesis, we compared the data gained in this study to published data on equids and grazing rhinoceros species gained in MRT trials with frequent faecal sampling.

Material and methods

Feeding trials were performed in six adult, captive black rhinoceroses at three zoological institutions. The animals had either been weighed recently at their respective institutions or their body masses were estimated, using the weighed animals as a comparison (Table 1). Animals had regular access to outside enclosures which were cleared of any potential food items before the study. For the trial period, the animals were kept separately to allow individual recording of food intake and faecal excretion. All animals received their regular zoo diet which consisted of grass hay as the staple diet item, and different proportions of lucerne hay, produce, concentrates (pelleted food), bread, and – in one case – browse (Table 1). Unfortunately, it was not possible to standardize the diet between facilities, or to conduct experiments with the same animals on different food rations. In particular, it was not possible to offer the animals browse ad libitum. Food intake was measured by weighing the food offered and the food left over at the next feeding time for seven days. For the estimation of mean ingesta retention times, cobalt (Co)-EDTA (Co) as a fluid marker and chromium-mordanted fibre (Cr; < 2 mm) as a particle marker were prepared according to Udén *et al.* (1980), and fed to the animals. These markers were chosen to allow direct comparisons with other data on large herbivore ingesta retention in the literature. Faeces were sampled after each defecation for the first 72 hours after marker feeding (ie, animals were observed day and night), 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 (the mean between the last check in the evening and the first check in the morning). The number of defecations during the first 72 hours was used to calculate the average number of defecations per day. 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 was taken and frozen at -20°C. Samples of feedstuffs were analysed for dry matter (DM) content by drying at 103°C to constant weight. Passage marker concentration in the faecal samples was measured after wet microwave ashing by atomic absorption spectroscopy (3300 AAS, Perkin Elmer) according to Behrend *et al.* (2004). Transit time (TT) is the time that passed until the first marker appearance; t_{max} is the time of the last observed marker excretion. The marker was assumed to have been passed completely once the faecal Co and Cr content equalled that before marker application. Mean retention times (MRT) were calculated according to Thielemans *et al.* (1978) as

$$MRT = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i}$$

where C_i = marker concentration in the faecal sample at time t_i (hours after marker administration) and dt_i = the interval (hours) of the respective sample

Table 1. Actual or estimated (°) body mass (BM) of the black rhinoceroses used in this study and the proportions of different feeds (on a dry matter basis) in their respective diets.

Animal	BM (kg)	Proportion of the diet (%)				
		Grass hay	Lucerne hay	Browse	Concentrates (pellets, cereals, bread, incl. vitamin supplements)	Fruits/vegetables
1	1160	44	–	–	47	9
2	1200	48	16	–	33	3
3	1200°	41	18	22	14	5
4	1200	47	20	–	29	4
5	1200°	76	–	–	10	14
6	1200°	76	–	–	9	15

Table 2. Literature data on body mass (BM, kg), dry matter intake (DMI, g/kg metabolic body mass), the proportion of structured roughage in the diet fed (% on a dry matter basis), the particle marker used and particle mean retention time (MRT, h) for other large hindgut fermenters used for the comparison with the data of black rhinoceroses of this study (cf Fig. 2).

Species	<i>n</i>	BM	DMI	Proportion of roughage	Marker used	MRT	Source
Donkey <i>Equus asinus</i>	4	178–197	55–100	100	Cr-mordanted fibre particles	33–44	Pearson <i>et al.</i> 2001
Domestic horse <i>Equus caballus</i>	6	197	72–84	0	Hay particles dyed with brilliant green	28–30	Wolter <i>et al.</i> 1976
	8	210–232	79–112	0	Ruthenium phenanthroline	23–29	Orton <i>et al.</i> 1985a, b
	4	508	71–86	33–55	Ytterbium chloride	32–42	Pagan <i>et al.</i> 1998
	4	241–266	68–155	100	Cr-mordanted fibre particles	21–36	Pearson <i>et al.</i> 2001
	4	300	56–62	100	Ytterbium-labelled chopped roughage	25–27	Moore-Colyer <i>et al.</i> 2003
White rhinoceros <i>Ceratotherium simum</i>	2	900/1600	90–100	85	Chromium oxide	49/53	Kiefer 2002
Indian rhinoceros <i>Rhinoceros unicornis</i>	6	1950–2300	59–90	73–100	Cr-mordanted fibre particles	57–66	Clauss <i>et al.</i> 2005

$$dt_i = \frac{(t_{i-1} - t_i) + (t_i - t_{i-1})}{2}$$

Pearson's correlation coefficients between pairs of variables were used to test for linear interdependencies. To compare the MRTs measured in black rhinoceroses with values measured in grazing rhinoceroses and equids in relation to body mass, we collated data on particle MRT from different literature sources (Table 2). Only data that had been gained by frequent daily faecal sampling was used.

In order to test whether the black rhino's MRT values fit the general trend between body mass and MRT for perissodactyls, we calculated a regression line between the species averages of body mass and MRT and determined the distance (MRT residual) to the regression line for each individual MRT value. ANOVA and simple contrasts (Tabachnick and Fidell 2001) were used to compare the black rhinoceros' residuals with those of each other species included. All statistical calculations were performed using the SPSS 11.0 (SPSS Inc., Chicago, Illinois, USA) statistical software package. The significance level was set at $p < 0.05$.

Results

The absolute dry matter intake (DMI) of the individual rhinoceroses varied from 11.5–19.3 kg/day, with a relative DMI of 58–95 g/kg^{0.75} metabolic body mass (MBM) (Table 3). The excretion of the fluid and particle markers followed a typical

curve with a steep increase and a longer reclining phase (Fig. 1). Fluid MRT ranged from 25–45 and averaged 31 h; particle MRT ranged from 28–59 and averaged 38 h. As DMI increased, MRT tended to decline (fluid MRT: $r = -0.782$, $p = 0.066$, particle MRT: $r = -0.807$, $p = 0.052$). MRT also declined as the number of daily defecations increased (fluid MRT: $r = -0.842$, $p = 0.036$, particle MRT: $r = -0.853$, $p = 0.031$). Fluids were excreted faster than the marked particles (mean fluid MRT = 31.5 ± 7.6 SD, mean particle MRT = 37.9 ± 12.0 SD, $t = 3.5$, $p = 0.016$, Table 3). The quotient of particle MRT : fluid MRT averaged 1.19 (range 1.10–1.33) and was negatively correlated with relative DMI ($r = -0.871$, $p = 0.024$). MRT was not correlated to TT (fluid: $r = 0.633$, $p = 0.177$, particle: $r = 0.554$, $p = 0.254$), and neither was DMI and TT (fluid TT: $r = -0.733$, $p = 0.098$, particle TT: $r = -0.619$, $p = 0.190$).

Table 3. Average dry matter intake (DMI, per metabolic body mass MBM), average number of defecations per day, time of first (TT: transit time) and last appearance (t_{max}) and mean retention time (MRT) of a fluid (Co-EDTA) and a particle (Cr-mordanted fibre < 2 mm) marker in captive black rhinoceroses. Time in hours.

Animal	DMI kg/day	DMI g/kg MBM	Defecations No/day	Fluid			Particles		
				TT	MRT	t_{max}	TT	MRT	t_{max}
1	11.5	58	2.2	24	45	110	24	59	164
2	14.0	69	3.2	14	33	87	14	40	87
3	17.3	85	3.1	12	34	108	12	41	94
4	15.1	74	3.7	4	26	90	4	31	190
5	19.3	95	4.0	16	26	70	19	29	70
6	18.9	93	5.4	7	25	64	7	28	64

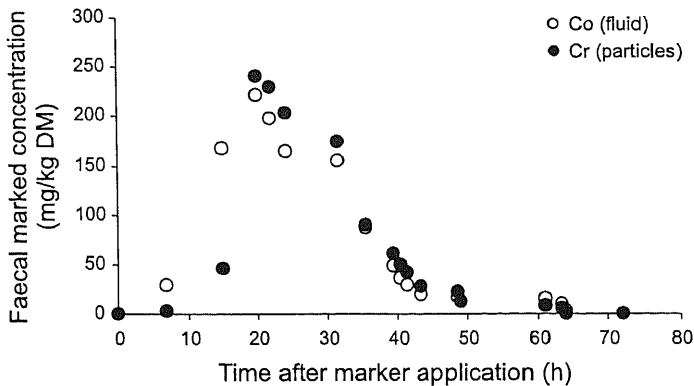


Fig. 1. Typical marker excretion pattern for a fluid (Co-EDTA) and a particle (Cr-mordanted fibre < 2 mm) marker in a black rhinoceros. Data from animal 6.

Particle MRT residuals differed among the species for which data was available ($F_{4, 30} = 4.8, p = 0.004$). Significant contrasts (donkey: $p = 0.022$, horse: $p = 0.001$; Indian rhinoceros: $p < 0.001$; white rhinoceros: $p = 0.015$) showed that the black rhinoceroses' average MRT deviated significantly more from the common regression line (meaning that black rhinoceroses had a shorter average particle MRT) than those of the four other species.

Discussion

The results of this study support the hypothesis that the black rhinoceros has a relatively short MRT for its body size when compared to grazing hindgut fermenters. Therefore the results support the notion that browsers should, in general, have shorter MRTs than grazers of comparable size and digestive anatomy.

Illius and Gordon (1992) derived allometric equations for the estimation of MRT from body mass based on a compilation of literature data, mainly from Foose (1982). Clauss and Lechner-Doll (2001) showed that, for ruminants, their equation tended to give realistic results for grazers but overestimated MRT in browsers, when compared to actual measurements from other studies. If Illius and Gordon's (1992) equation for hindgut fermenters of $MRT (h) = 9.4 \text{ body mass}^{0.255}$ is applied for average values for the Indian (2125 kg), white (1250 kg) and black rhinoceroses (1193 kg) from Fig. 2, the calculated MRT values (66 h, 58 h and 57 h, respectively) are all overestimations compared to the averages of actual measurements (60 h, 51 h, 38 h) as would be expected if mostly data from Foose (1982) is used for

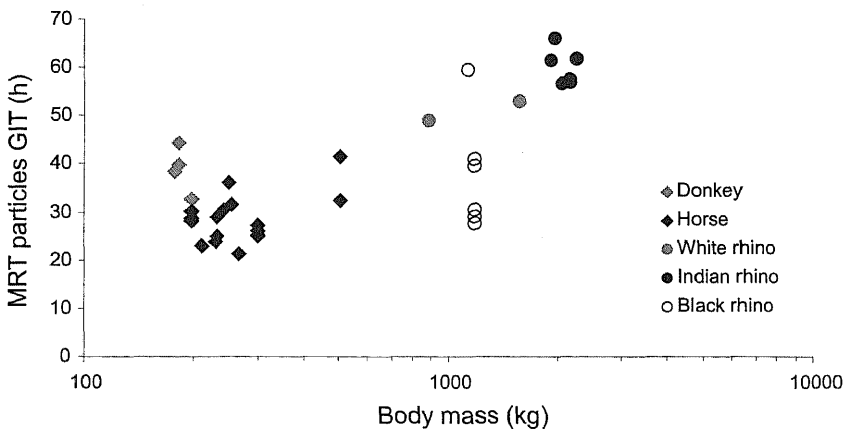


Fig. 2. A comparison of mean retention times (MRT) of particles in the gastrointestinal tract (GIT) of black rhinoceroses with donkeys (Pearson *et al.* 2001), horses (Wolter *et al.* 1976, Orton *et al.* 1985a, b, Pagan *et al.* 1998, Pearson *et al.* 2001, Moore-Colyer *et al.* 2003), white rhinoceroses (Kiefer 2002), and Indian rhinoceroses (Clauss *et al.* 2005).

the derivation of the equation (cf Introduction). However, the deviation is most prominent in the black rhinoceros, whose measured MRT is drastically lower than the calculated value.

We propose that the significant deviation from the interspecific regression line in the black rhinoceroses investigated in this study, the more prominent overestimation of MRT in browsing ruminant and rhinoceros species and the difference in MRT patterns found in elephants by Hackenberger (1987), could be regarded as evidence for lower MRTs in browsers as compared to grazers – a pattern that can be observed in both hindgut fermenters and ruminants. This pattern can be best explained by the mentioned difference in fermentation characteristics between grass and browse. In ruminants, subtle differences in digestive morphology, such as the relative capacity of the forestomach (Hanley 1982, Owen-Smith 1982, Hofmann 1989, Van Soest *et al.* 1995, Clauss *et al.* 2003), have been linked to the postulated differences digestive physiology, and by analogy, a comparatively lesser hindgut capacity might be expected in black rhinoceroses or African elephants. Unfortunately, data on the comparative gastrointestinal morphology of large hindgut fermenters is far too scarce to allow any tests of this hypothesis (Clauss *et al.* 2003).

Regardless of potential, subtle differences in digestive anatomy, our results from the black rhinoceroses indicate that physiological ingesta retention mechanisms are broadly similar in the perissodactyla. The ratio of particle MRT : fluid MRT, ranging between 1.10–1.33 in the black rhinoceroses, has been reported to be 1.04–1.14 in horses and 1.13–1.30 in donkeys (Pearson *et al.* 2001), and 1.36–1.58 in Indian rhinoceroses (Clauss *et al.* 2005), indicating a certain degree of selective particle retention. In horses, a selective retention mechanism for small particles (in contrast to larger ones) was reported by Björnhag *et al.* (1984); these authors demonstrated differences in the ingesta particle size composition between the caecum and proximal colon on the one, and the distal colon on the other hand. Such a mechanism can be assumed to operate in other perissodactyla as well. As in ruminants (Shaver *et al.* 1988), it is to be expected that any selective retention is more prominent at lower intake levels. The results of this study, with an increasing particle MRT : fluid MRT ratio with decreasing food intake, support this prediction.

The frequency of defecation varied between the rhinoceroses of this study, and increased with increasing food intake. The sporadic nature of the defecation pattern of these large animals is in stark contrast to a much higher defecation frequency in large ruminants, camelids or horses. Because defecation of rhinoceroses is sporadic, transit time is not a useful measure to compare ingesta retention between species. TT varied by a six-fold magnitude, whereas MRT only varied two-fold. Additionally, TT did not correlate with dry matter intake. This indicates that the use of TT for comparative purposes should be limited to species with a relatively frequent and consistent defecation pattern, such as in the comparison of primate TT data from Lambert (1998). For more general com-

parisons, MRT data are to be preferred, especially in species with a digestive compartment where the ingesta is mixed (Warner 1981).

Unfortunately, it was not possible to use a standardized diet in the animals used for this study, or to measure MRTs on a variation of intake levels within the same animals. Ideally, studies on MRTs in herbivores should not only include a range of intake levels but also a range of different diets to facilitate a proper comparison with other studies. In addition, it would be useful to perform measurements in a larger number of animals and trials, as some of the observations made in this study only tended towards significance, most likely due to the low power of the statistical tests caused by the low number of measurements. As long as these data are lacking, conclusions based on a low number of trials such as used in this study must be considered preliminary.

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