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Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates

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Abstract

The relation between body mass (BM) and digesta mean retention time (MRT) in herbivores was the focus of several studies in recent years. It was assumed that MRT scaled with $BM^{0.25}$ based on the isometric scaling of gut capacity ($BM^{1.0}$) and allometric scaling of energy intake ($BM^{0.75}$). Literature studies that tested this hypothesis produced conflicting results, arriving sometimes at higher or lower exponents than the postulated 0.25. This study was conducted with 8 ruminants (n = 2-6 per species) and 6 hindgut fermenting species/breeds (n = 2-6, warthog n = 1) with a BM range of 60-4000 kg. All animals received a ration of 100% grass hay with ad libitum access. Dry matter intake was measured and the MRT was estimated by the use of a solute and a particle (1-2 mm) marker. No significant scaling of $MRT_{particle}$ with BM was observed for all herbivores (32 $BM^{0.04}$, p = 0.518) and hindgut fermenters (32 $BM^{0.00}$, p = 1.00). The scaling exponent for ruminants only showed a tendency towards significance (29 $BM^{0.12}$, p = 0.071). Ruminants on average had a $MRT_{particle}$ 1.61-fold longer than hindgut fermenters. Whereas an exponent of 0.25 is reasonable from theoretical considerations, much lower exponents were found in this and other studies. The energetic benefit of increasing MRT is by no means continuous, since the energy released from a given food unit via digestion decreases over time. The low and non-significant scaling factors for both digestion types suggest that in ungulates, MRT is less influenced by BM (maximal allometric exponent ≤ 0.1) than often reported.

Keywords: allometry, passage, ruminants, hindgut fermenters, scaling

1. Introduction

1.1. Mean retention time and body mass

Due to the low degradation rates (%/h) of cell walls, mean retention time (MRT) of food in the digestive tract is a factor that determines the digestive efficiency of herbivores (Udén et al., 1982; Owen-Smith, 1988; Van Soest, 1994; Hummel et al., 2006). In combination with intake capacity, MRT may reflect the separation of nutritional niches within herbivore communities. Digesta retention time is considered to be influenced by body mass (BM), and a positive correlation of BM with MRT has been proposed repeatedly (Demment, 1983; Demment and Van Soest, 1983; Illius and Gordon, 1992; Robbins, 1993; Gordon and Illius, 1994). This is based on the reasoning that the volume of the gastrointestinal tract (GIT) in herbivorous animals increases in proportion to $BM^{1.0}$ (Parra, 1978; Demment and Van Soest, 1985), while the energy requirements of an animal scale only to $BM^{0.75}$ (Kleiber, 1932). As a result, larger animals have larger fermentation capacities than smaller animals in relation to their energy needs. This effect is at the core of the so-called Jarman-Bell principle (Geist, 1974). Accordingly, the MRT of the ingesta should scale to $BM^{0.25}$, and larger animals should have capacities to digest food longer and more extensively and can therefore handle food of lower quality (i. e., forage with a high fibre content) (Owen-Smith, 1988; McNab, 2002).

Based on considerations estimates have been derived for the relationship of BM and MRT by Demment (1983) $\left(MRT\left[h\right]=0.69\times D\,DM\left[\%\right]\times BM^{\,0.30}\right)$ and Demment and Van Soest (1983) $\left(MRT\left[h\right]=0.59\times D\,DM\left[\%\right]\times BM^{\,0.28}\right)$ (D = digestibility, DM = dry matter).

Since then, several studies have related measured MRT data to BM; results like that of Gross et al. (1996) (longer MRT of 57 h in male Nubian ibex (60 kg BM) compared to females (23 kg BM) with 35 h) are only based on the comparison of 2 size classes. Several studies approached the problem with a collection of MRT literature data, for example, Illius and Gordon (1992) found a scaling of MRT for both digestion types (MRT = 9.4 $BM^{0.26}$ for

58 hindgut fermenters and MRT = 15.3 $BM^{0.25}$ for ruminants). In an expanded data collection,
59 Gordon and Illius (1994) found a correlation of MRT to $BM^{0.22}$ in ruminants. Robbins (1993)
60 found a scaling to $BM^{0.28}$ for ruminants. Because of the assumed positive correlation of
61 retention time and BM, Demment and Van Soest (1983) argued that BM in ruminants is
62 limited at a point where any further corresponding increase in MRT no longer pays or
63 becomes a constraint due to excessive methane losses.
64 However, a scaling exponent of approximately 0.25 or higher has not been generally
65 accepted. Other studies found considerably lower scaling exponents for hindgut fermenters
66 (32.0 $BM^{0.08}$) and perissodactyls (22.8 $BM^{0.14}$) (Owen-Smith, 1988), or even no significant
67 scaling in ruminants (Duncan et al., 1990), or in data collections combining all ungulates
68 (Owen-Smith, 1988; Clauss et al., 2009). These evaluations relied basically on the
69 comprehensive data set of Foose (1982). In a recent re-evaluation of the problem, based on an
70 comprehensive literature review excluding the Foose data set, Clauss et al. (2007a) found a
71 non-significant scaling of MRT in colon fermenters ($BM^{0.04}$), non-ruminant foregut
72 fermenters ($BM^{0.08}$) and in browsing ($BM^{0.06}$) and grazing ($BM^{0.04}$) ruminants. Only for
73 caecum fermenters did they find a significant scaling of MRT with $BM^{0.24}$, implying that in
74 mammalian herbivores, the assumed $BM^{0.25}$ scaling applied only to the low end of the BM
75 spectrum, below a certain threshold.

76 *1.2. Digestive strategies*

77 Animals ingesting forage with high fibre contents can be ranked along a continuum regarding
78 their retention times. Long MRT/low intake, and in consequence, relatively high digestibility
79 are a typical strategy of ruminants, while the other extreme (high intake, short MRT, lower
80 digestibility) is found in equids and elephants (Foose, 1982; Owen-Smith, 1988; Duncan et
81 al., 1990). Differences in chewing efficiency will additionally modify these relationships
82 (Clauss et al., 2009); for example, equids achieve a particularly high degree of particle size

reduction (compared to other non-ruminants) and can therefore attain higher digestibilities in spite of their comparatively short MRT. It should not be forgotten that the hindgut fermentation system can also allow a strategy of food intake and MRT closer to ruminants, as evident in rhinoceroses and perhaps, also in tapirs (Clauss et al., 2010b; Meyer et al., 2010; Steuer et al., 2010).

Aims of this study

To date, results on the influence of BM on MRT can be considered equivocal to some extent. Since other studies were mainly based on the data set of Foose (1982) and/or a summary of results of different trials from literature, this study, with an independent data set derived from relatively uniform conditions, aimed at evaluating the influence of BM (and the digestion type) on food intake, and particularly the MRT. By measuring intake and MRT in a variety of uniformly fed ungulate species ranging in average BM from 60-4000 kg, the following questions should be answered:

1. How does DM intake (DMI) scale with BM?
2. Is there an influence of BM on the MRT in ungulates?
3. To what extent do hindgut fermenters have shorter MRT and higher intake levels than ruminants?

2. Materials and methods

2.1. Animals and feeding

Food intake and MRT were measured for 8 ruminants: domestic goat (*Capra aegagrus hircus)*, domestic sheep (*Ovis orientalis aries),* blue wildebeest (*Connochaetes taurinus)*, oryx antelope *(Oryx gazella)*, sable antelope *(Hippotragus niger)*, waterbuck (*Kobus ellipsiprymnus)*, forest buffalo (*Syncerus caffer nanus)*, domestic cattle *(Bos primigenius*

106 *taurus*), and 6 hindgut fermenting species/breeds[1]: warthog *(Phacochoerus africanus)*,
107 domestic pony (*Equus ferus caballus)*, Grevy's zebra (*Equus grevyi)*, domestic horse *(Equus*
108 *ferus caballus)*, white rhinoceros *(Ceratotherium simum)* and African elephant *(Loxodonta*
109 *africana).* Trials were conducted in the winter seasons 2008 and 2009. All animals were adult
110 and not pregnant or lactating during the trials except the sable antelopes, which were in the
111 first stage of pregnancy (1-2 month). Species were chosen that were known to readily accept a
112 grass hay only diet. Due to inevitable logistical limitations when working with non-domestic
113 animals in a zoo, in some instances only a limited (< 3) number of individuals could be
114 measured. Only species means are used in the calculation of the final results (Table 1). All
115 animals were kept separately during the collection period. Exceptions were the African
116 elephants, which as a group had access to an outside enclosure for 4-6 hours a day. They were
117 constantly monitored to ascribe defecations to the correct individuals. The BM of the animals
118 ranged from 49 kg (a domestic goat) up to 6500 kg (an African elephant) (Table 1). Cattle,
119 goats, sheep, horses, ponies and a warthog were weighed; BM of the other zoo animals were
120 derived from estimations by zoo keepers, zoo veterinarians and the first author, based on
121 literature data and personal experiences. For an adaptation period of 14 days and a collection
122 period of at least 6 days for zoo animals (African elephants: 5 days) and 8 days for farm
123 animals, all animals had ad libitum access to a 100% grass hay ration.
124 The range of the neutral detergent fibre (NDF) content of the grass hay fed at different
125 feeding places was 64.2-75.8% organic matter (OM), for acid detergent fibre (ADF) 30.0-
126 43.1% OM, for acid detergent lignin (ADL) 3.1-7.8% OM and for crude protein (CP) 6.8-
127 12.1% OM (Table 2). Because of the large amount of grass hay that was needed, delivery in
128 three batches was necessary. While some variation of hay quality was present, no unbalanced
129 distribution of hay quality with respect to BM or digestion type was evident.

[1] While a plethora of mammalian herbivores belong to the group of hindgut fermenters, ungulates are at the centre of interest of this contribution. For the sake of simplicity, the term "hindgut fermenters" refers to ungulate hindgut fermenters (such as equids, rhinoceroses and elephants) in this study.

All boxes and stables were covered with material the animals did not feed on (saw dust, rubber mats or bare floor). For all animals, daily food intake was measured during the collection period. Every morning, the leftover grass hay from the previous day was quantified and fresh hay was offered. For most of the animals it was possible to collect the leftovers twice a day (exceptions were the African elephants and the warthog). Several times a day the animals received additional hay to ensure ad libitum access at all times.

2.2. Nutrient analysis

The grass hay (as offered and left-overs) was analyzed for DM during the sampling periods. For further analysis, food samples were ground through a 1 mm sieve. The DM and ash were analyzed according to VDLUFA[2] (2007; method 8.1). Grass hay and faeces were analyzed sequentially with the Gerhardt fibre bag system (Gerhardt, Königswinter, Germany) for NDF, ADF and ADL in accordance with Van Soest and Robertson (1985). The NDF and ADF were corrected for ash using the insoluble ash after ADL determination. Solutions were produced according to Van Soest and Robertson (1985). The N content of the grass hay was analysed by the Dumas method (Instrument FP-328, Leco, St. Joseph, USA) and CP expressed as N x 6.25.

2.3. Mean retention time

To estimate the MRT, two passage markers were fed to the animals in a single pulse dose at the beginning of the collection period. Cobalt-EDTA was used as a marker for the solute phase of the ingesta and chromium-mordanted fibre (1-2 mm particle size, made of grass hay) as a marker for the particle phase. The preparation was done according to Udén et al. (1980). Chromium content of the chromium-mordanted fibre was 1.9% DM. Faecal samples from zoo animals were collected at particular intervals (see below for details), dried at 103 °C and ground through a 1 mm sieve. Marker concentration was measured after wet ashing,

[2]Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten

154 according to Behrend et al. (2004) with atomic absorption spectroscopy (Perkin-Elmer 1100
155 B, Perkin Elmer, Wellesley, USA).
156 Faeces were sampled twice during the day (one pool sample for the morning, one for the
157 afternoon), and one pool sample was taken for the night for a minimum of 6 days (3
158 samples/24 h). In case of the African elephants, where video surveillance was used to
159 determine defecation time at night, each dropping was sampled over 5 days. From cattle,
160 sheep, goat, horse and pony samples were taken from pooled faeces every 4 h (day 1-2), 6 h
161 (day 3-4), 8 h (day 5-6) and 12 h (day 7-8).
162 Because of the difference in sampling intervals between the domestic animals and the
163 elephants and all other zoo animals, the MRT of domestic animals was further calculated to
164 assume only three collection times per 24 h (see below for details on the MRT calculation). A
165 linear regression of original MRT averages and those of the MRT values calculated based on
166 a less frequent sampling regime yielded the equations:
167 $MRT_{particle}$ 'corrected' = 0.97 *(95% CI 0.89, 1.04)* $MRT_{particle}$ + 1.79 *(95% CI -1.65, 5.21)*
168 MRT_{solute} 'corrected' = 0.98 *(95% CI 0.68, 1.27)* MRT_{solute} + 1.65 *(95% CI -6.96, 10.27)*
169 In other words, a slope of one and an intercept of zero were statistically not excluded in either
170 case, indicating no systematic difference between the two sampling schemes. Only data
171 calculated from all available sampling intervals are presented in the discussion.
172 The MRT for the whole gastrointestinal tract (GIT) was calculated according to Thielemans et
173 al. (1978):
174 $$MRT = \sum (ci \cdot dt \cdot ti) / \sum (ci \cdot dt)$$
175 (MRT = mean retention time [h]; ci = marker concentration in the faeces at time i [mg/kg
176 DM]; dt = length of time interval which represents the marker concentration ci [h]; ti = time
177 after marker application (middle of time interval which represents the marker concentration
178 ci) [h])

As an estimate of the ability to retain particles selectively in the GIT, the selectivity factor (SF) was calculated as $MRT_{particle}/MRT_{solute}$ (Lechner-Doll et al., 1990).

2.4. Statistics

All statistical comparisons were performed with species' means. In order to account for ancestry-based correlations in the data sets (i.e., finding a significant result simply because similar species are closely related) (Felsenstein, 1985; Pagel, 1999), the data was controlled for phylogenetic influences using the "Phylogenetic Generalized Least-Squares" method (PGLS; Martins and Hansen, 1997; Rohlf, 2001). This procedure estimates a covariance matrix of the species due to their ancestral roots and includes these interrelationships in a generalized least squares algorithm to determine the model parameters. The phylogenetic trees for the two data sets were derived by pruning the mammalian supertree from Bininda-Emonds et al. (2007) to include only the species of concern for our study, using Mesquite (Maddison and Maddison, 2006). The two different domestic horse breeds were represented as direct relatives in the tree. Because the resulting trees were not based on our own calculations of branch lengths with consistently the same characters, we used trees without branch lengths. The respective phylogenetic tree is shown in Fig. 1. When analysing ruminants or hindgut fermenters separately, the corresponding trees were derived as described above.

To achieve normal distribution, data on BM was log-transformed. Therefore, a regression analysis of log-transformed measurements was used for the estimation of allometries. Statistical analyses were performed using ordinary least squares (OLS), which did not account for phylogeny and using phylogenetic least squares (PGLS). Except in cases where the results differed, only PGLS results are discussed. In addition, general linear models (GLM) were used; for food intake (DMI), the model was:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha \times \beta)_{ij} + \varepsilon_{ijk}$$

where

Y_{ijk} = the observed response (dry matter intake);

μ = the population constant, common to all observations;

α_i = the effect of BM (continuous variable);

β_j = the effect of digestion type j; j = 1-2 (hindgut fermenter or ruminant);

$(\alpha \times \beta)_{ij}$ = the effect of interaction between BM i and digestion type j;

ε_{ijk} = the residual error.

For the passage parameters ($MRT_{particle}$, MRT_{solute}, SF), the initial model was:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha \times \beta)_{ij} + (\beta \times \gamma)_{jk} + \varepsilon_{ijkl}$$

where

Y_{ijkl} = the observed response ($MRT_{particle}$, MRT_{solute} or SF);

μ = the population constant; common to all observations;

α_i = the effect of BM (continuous variable);

β_j = the effect of digestion type j; j = 1-2 (hindgut fermenter or ruminant); cofactor;

γ_k = the effect of rDMI (= relative dry matter intake [g/(kg $BM^{0.75}$*d)]; continuous variable);

$(\alpha \times \beta)_{ij}$ = the effect of interaction between BM i and digestion type j;

$(\beta \times \gamma)_{jk}$ = the effect of interaction between rDMI k and digestion type j;

ε_{ijkl} = the residual error.

After running the initial models as outlined above, in a second step models were reduced to those factors that have been shown to have a significant effect in the first run; the significances found in this second step are presented in the results. In a post-hoc analysis, differences between the digestion types (hindgut fermenters vs. ruminants) were tested by t-test. Dry matter intake related to metabolic body size (rDMI) [g/(kg $BM^{0.75}$*d)] was used for comparison of intake. The statistical calculations were performed with PASW 18.0 (SPSS

230 Inc., Chicago, IL) and COMPARE 4.6 (Martins, 2004). The significance level was set to
231 α=0.05. 95% confidence intervals were calculated for coefficients in allometric regressions.
232 For $0.1 > p > 0.05$, differences are regarded as a trend.

233 # 3. Results

234 *3.1. Food intake*

235 The DMI for each species are shown in Table 1. Across all species, DMI scaled to BM as
236 DMI (in kg/d) = 0.039 $BM^{0.83}$ using PGLS; the 95% CI of the intercept came very close to
237 both 0.75 and 1.00 (Table 3). In a GLM with DMI as the dependent variable, BM ($p<0.001$),
238 digestion type ($p=0.054$) and their interaction term (BM x digestion type) ($p=0.031$) had a
239 significant influence. Hindgut fermenters had a significantly higher rDMI ($p=0.008$).

240 *3.2. Passage characteristics*

241 Typical marker excretion curves for ruminants (forest buffalo) and hindgut fermenters
242 (domestic horse, African elephant, warthog) are presented in Fig. 3 (to our knowledge this
243 represents the first published MRT estimation for the warthog). The range of $MRT_{particle}$ for
244 ruminants was between 43 h (blue wildebeest) and 75 h (domestic cattle) (Table 4). For the
245 hindgut fermenters the range was between 26 h (Shetland pony) and 47 h (white rhinoceros).
246 The range for MRT_{solute} was between 23 h (forest buffalo) and 37 h (sable antelope) for
247 ruminants and between 20 h (domestic pony) and 34 h (warthog) for hindgut fermenters. On
248 average, equids and elephants had shorter $MRT_{particle}$ than ruminants, whereas the white
249 rhinoceros and warthog had $MRT_{particle}$ approaching the lower level of the ruminant range. In
250 contrast, MRT_{solute} was of a similar magnitude for both digestive groups (Table 4). Allometric
251 equations gave no indication for an increase of $MRT_{particle}$ with BM in the overall sample
252 ($BM^{0.04}$, $p=0.518$) and for hindgut fermenters ($BM^{0.00}$, $p=1.00$); for ruminants alone, only a
253 trend was present (ruminants = $BM^{0.12}$, $p=0.071$) (Table 3; Fig. 4). No significant allometric

relationships existed for MRT_{solute}, neither in the whole data set nor within the digestion types (Table 3).

When a GLM was performed with $MRT_{particle}$ as the dependent variable, rDMI ($p<0.001$), BM ($p=0.001$) and the digestion type*rDMI-interaction ($p=0.019$) were shown to have a significant influence, indicating that the decreasing influence of food intake on $MRT_{particle}$ varies between the digestion types (Fig. 5). When using MRT_{solute} as the dependent variable, no significant model remained. While $MRT_{particle}$ was shown to be significantly different between the digestion types ($p=0.007$), this was not the case for MRT_{solute} ($p=0.134$).

In the overall data set, and within the ruminants, the relationship was negative between $MRT_{particle}$ and rDMI, whereas no such relationship was evident in the hindgut fermenters (Table 5, Fig. 5). In contrast, there was no significant relationship between MRT_{solute} and rDMI (Table 5).

The selectivity factor (SF) [$MRT_{particle}/MRT_{solute}$] was, on average, higher in ruminants than in hindgut fermenters; among the hindgut fermenters, only white rhinoceros achieved values within the range of those observed in ruminants (Table 4). The SF did not vary with BM in the overall data set, but increased significantly with BM within the ruminants (Table 3). A negative relationship between rDMI and SF was observed in the overall data set; this relationship was also significant within the hindgut fermenters in OLS, but not when PGLS were used (Table 5). In a GLM with SF as the dependent variable, and BM, rDMI, digestion type and the interactions of digestion type with BM and rDMI as the independent variables, only the digestion type*BM-interaction remained after eliminating non-significant variables (PGLS: $p<0.001$), indicating that SF was distributed differently across the BM range in each digestion type. When means were compared, SF was shown to be higher for ruminants ($p=0.001$).

4. Discussion

4.1. General influence of BM on food intake

Various aspects of the biology of a species can be influenced by BM (Owen-Smith, 1988; Fa and Purvis, 1997; Simard et al., 2008). Among variables related to digestion, absolute food intake [kg DM/d] is among the most obvious. It can be hypothesised that scaling of intake to $BM^{0.75}$ indicates an energetic regulation of food intake, while a scaling to $BM^{1.0}$ points to a regulation by mainly gut fill. Based on the allometric exponent found for DMI (Fig. 2) in this study, food intake of the animals of the complete data set and for hindgut fermenters alone could be interpreted to have been regulated by both energy needs and gut fill constraints. However, when looking at ruminants alone, the scaling to $BM^{0.69}$ would indicate a regulation by energy requirements alone; this is in contrast to the general view of intake limitation via gut fill being less significant in hindgut fermenters than in ruminants and implies some caution in the interpretation of scaling exponents in this way.

In the wild, the quality of the ingested food is a variable that changes significantly with BM in herbivores (Owen-Smith, 1988; Codron et al., 2007). Larger herbivores may eat the same daily amount of metabolizable energy per kg $BM^{0.75}$, but due to lower diet quality, they require larger amounts of food.

4.2. Influence of BM on MRT

Physiologically, an increase of MRT with BM is beneficial if one assumes an increase of dietary cell wall content (Demment and Van Soest, 1983) or digesta particle size with BM (Fritz et al., 2009). However, studies find scaling exponents close to and considerably lower than the postulated 0.25 (Table 6). Our data fits with the idea that MRT is less influenced by BM than assumed from theoretical considerations. The scaling exponent b was not significant (Table 3), indicating that an influence of body mass on MRT is not the dominant factor. Regarding the non-significant, but rather low p-value for the scaling of MRT with BM in

303 ruminants in this context, an influence of BM on MRT in this group can be less safely
304 excluded than for hindgut fermenters or the whole sample. A part of an explanation for that
305 may lie in be particularly and surprisingly low rDMI in the ruminant BM extreme (cattle) in
306 this study. While no explanation is evident for the low intake, the resulting particularly high
307 $MRT_{particle}$ in the largest ruminant will surely influence the scaling exponent disproportionally,
308 leading to a tendency of an increase of $MRT_{particle}$ with BM. It should also not be forgotten
309 that the GLM detected a significant influence of BM within the data set. However, it can be
310 stated that applying the statistical approach consistently used by other contributions on the
311 topic (allometric regression) did not result in a significant ($p<0.05$) indication for an increase
312 of $MRT_{particle}$ with BM this study.
313 Interestingly, Clauss et al. (2007a) found comparable low scaling factors for BM and MRT
314 ($BM^{0.13}$ ruminants; $BM^{0.04}$ colon fermenters, the former exponent significantly > 0) as in this
315 study ($BM^{0.12}$, $BM^{0.00}$ in PGLS). When Clauss et al. (2007a) split the ruminant group into
316 grazers and browsers, this resulted in lower (non-significant) scaling exponents (grazers:
317 $BM^{0.04}$; browsers: $BM^{0.06}$). This implies that the inhomogeneous BM distribution of ruminant
318 feeding types (grazers being on average heavier than browsers), in connection with a tendency
319 for longer retention times in grazers, has some potential to influence the estimated scaling
320 factor. In other words, a scaling with $BM^{0.25}$ is too steep to represent the empirical data.
321 Considerations arriving at an explicit relationship of MRT to $BM^{0.25}$ often do not take into
322 account the significantly lower degree in selectivity that can be safely assumed for larger
323 animals (Owen-Smith, 1988). In the wild, one should expect at least a part of the "spare gut
324 capacity" of large animals to be used up by the lower quality of a less digestible diet
325 (Hummel and Clauss 2010). Presumably, such differences in diet selectivity, and therefore
326 quality are also reflected in regular zoo diets. The proportions of coarse forage are regularly
327 higher in diets of large herbivores like bovinae, white rhinos or elephants than in those of
328 small antelopes. The larger the differences are in diet quality, the lower a potential increase in

329 MRT with BM can be expected. On the other hand, if one assumes an allometric increase of
330 MRT with BM, this scaling should be particularly evident if the diet of all animals is
331 comparable. The approach of this study should therefore have resulted in an overestimation
332 rather than an underestimation of the scaling factor compared to the wild situation, which
333 makes the finding of an absence of BM-scaling of MRT all the more robust.
334 Clauss et al. (2007a) found a significant increase of MRT with $BM^{0.24}$ for caecum fermenters,
335 implying that an increase of MRT coinciding with an increase in BM is only beneficial for
336 efficiency of the digestive process up to a certain body size limit. Demment and Van Soest
337 (1985) state that disadvantages will dominate advantages above a certain threshold for
338 retention times. An endless prolongation of the MRT also makes little sense because energy
339 gained from a given amount of food per unit time decreases over the digestion process, and
340 the probability of excessive methane losses is considered to increase, especially for ruminants
341 (Van Soest, 1994). The degree to which prolonged retention benefits an herbivore ingesting a
342 diet higher in fibre will finally depend on the extent of lignified or unlignified fibre. The
343 former will not be degradable, irrespective of the duration of exposure to microbial
344 fermentation; the latter will be digested to a higher degree the longer it is retained.
345 The type of relationship between BM and MRT is also of interest in a fascinating chapter of
346 herbivore digestive physiology: How should we speculate on the digestive physiology of
347 extraordinarily large dinosaurs, particularly on the sauropods who push the BM envelope to
348 50 t or even more, and for which extrapolations based on high scaling factors simply result in
349 “an improbability” (Van Soest, 1994)? Based on the results of this study and other recent
350 studies (Clauss et al., 2007a), guesses on sauropod retention times cause less problems than
351 may have been expected, because an increase of BM is by no means inherent with a
352 continuous increase in MRT beyond the scope of a plausible range. Besides this, elephants are
353 the best example for an animal contradicting any automatism of an increase of MRT with BM

354 (Foose, 1982; Clauss et al., 2003 and this study). Much more than BM, the assumed level of
355 metabolism gives a better estimation of MRT (Farlow, 1987).

356 *4.3. Differences between MRT of ruminants and hindgut fermenters*

357 While BM was shown to have only limited, if any, influence on MRT, digestive strategy is
358 important. In this respect, a fundamental difference between ungulate hindgut fermenters and
359 ruminants is accepted since the seminal contributions of Janis (1976) and Foose (1982). These
360 differences, however, mostly refer to comparisons between ruminants and equids and need
361 not necessarily be transferrable to all other hindgut fermenters.

362 Foose (1982) and Sponheimer et al. (2003) as well as our study found that some hindgut
363 fermenters achieve higher rDMI than ruminants. The ability of ruminants to withhold
364 particles in their fermentation chamber to elongate the digestion time for the rumen microbes
365 (Udén et al., 1982; Demment and Van Soest, 1985; Renecker and Hudson, 1990; Gordon and
366 Illius, 1994), allows them to achieve longer $MRT_{particle}$ than some hindgut fermenting species
367 (Parra, 1978; Foose, 1982; Udén et al., 1982 and the present study). In this study, ruminants
368 on average had a $MRT_{particle}$ 1.61 fold longer than hindgut fermenters, a value close to the
369 1.50 found in Foose (1982) for grazing ruminants compared to grazing hindgut fermenters.
370 Similarly the rDMI was 1.58 fold higher for hindgut fermenters than for ruminants in this
371 study and 1.55 fold higher in Foose (1982) (calculated with rOMI). A potential, important
372 shortcoming in summarizing data appears to be the creation of a uniform 'hindgut fermenter'
373 category. Generally, the hindgut fermenter system allows a broad spectrum of digestive
374 strategies (Clauss et al., 2010). Therefore, while grazing ruminants can be considered to have
375 a relatively uniform digestive strategy (as far as intakes and MRT are concerned), this is the
376 case to a lesser extent for the more variable (and phylogenetically much more heterogeneous)
377 group of hindgut fermenters (e.g. Foose, 1982). While both equids and elephants follow a
378 strategy of high rDMI/low MRT, the white rhino and at least the one warthog of this study

379 appear to have some traits closer to ruminants. This also points to some potential difficulties
380 in the establishment of allometric relations. A significant allometry could be considered
381 regarding the increase of MRT with BM from equids to rhinos (and elephants as outliers).
382 When the focus is on the data of equids and elephants, and rhinos are considered as deviating
383 from this rule, then there is no increase of MRT with BM. Corresponding to the heterogeneity
384 of strategies within the hindgut fermenters, differences between the digestive types were
385 evident in this study, in particular, in the interaction in the GLM.
386 As mentioned above, the white rhinoceros differs from the other hindgut fermenters. Its SF of
387 1.5 is comparable to the SF of the sable antelope (1.5) and the wildebeest (1.4). In contrast,
388 the warthog, the other hindgut fermenter with a comparatively low rDMI, fits well within the
389 other hindgut fermenters with a SF of 1.3. With a mean SF of 1.0, the African elephant was at
390 the lowest end of the SF range of this study. Hence also the SF data of the different hindgut
391 fermenter species shows the variety of digestive strategies within this group.
392 In general, a negative correlation can be expected for rDMI and MRT. Such a significant
393 negative correlation was only found for ruminants, but not for hindgut fermenters. In Foose
394 (1982) the opposite was found, while Lechner-Doll et al. (1990) and Pearson et al. (2001)
395 found negative correlations for ruminants and equids, respectively. Clauss et al. (2007a)
396 found for their entire data set (caecum, colon, non-ruminant and ruminant foregut fermenters)
397 a low ($r^2 = 0.12$) but significant ($p = 0.001$) negative correlation between rDMI and MRT. An
398 insensitivity of MRT to an increase in intake has been considered as a major trait in digestive
399 strategies of herbivores (Clauss et al., 2007b), as appears evident in the group of equids and
400 elephants in this study (Fig. 5). This result would be in line with the general view of some
401 hindgut fermenters as being able to maintain high DMI more easily than ruminants when diet
402 quality decreases. If MRT is less influenced by DMI in some hindgut fermenters, this would
403 facilitate a strategy where higher intakes could attenuate the negative effects of increased
404 intakes. However, empirical data does not support the notion that the food intake of hindgut

fermenters decreases less in response to a decrease in diet quality than that of ruminants (Meyer et al., 2010), leaving this speculation unresolved. When testing, the influence of rDMI and BM on MRT was significant, just as the interaction between digestion type and rDMI was significant, which indicates rDMI affects the digestion types differently. However, whatever the effect of BM on MRT may be, it cannot be expressed in terms of a simple allometric function (Table 3).

5. Conclusions

- The influence of BM on DMI between $BM^{0.75}$ and $BM^{1.00}$ was in the expected range and indicates that the food intake of the animals in this study was restricted by both energy needs and gut fill.
- The results of this study indicate little influence of BM on MRT; if there is any influence at all, it will be on the size of $BM^{0.1}$ maximally.
- Digestion type (ruminant or hindgut fermenter) had a significant effect on MRT, whether in its interaction with BM or in its interaction with rDMI.
- Within the hindgut fermenters, there seems to be a wider spectrum of digestive strategies than in the ruminants, making the validity of generalized conclusions in terms of 'ruminants vs. hindgut fermenters' questionable.

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525 **Table 1** Mean body mass (BM) [kg], dry matter intake (DMI) [kg/d] and DMI related to metabolic body size (rDMI)
526 [g/(kg $BM^{0.75}$*d)] (± standard deviation (SD) or individual values when n = 2)

	n	Sex [m/f]	BM [kg]	SD	DMI [kg/d]	SD	rDMI [g/(kg $BM^{0.75}$*d)]	SD
Ruminants								
Domestic goat[a]	6	6[1]/0	58	4.7	1.1	0.15	51.5	5.50
Domestic sheep[b]	3	0/3	94	4.2	1.2	0.31	39.7	9.54
Blue wildebeest[c]	4	0/4	160*	0.0	3.4	0.25	74.5	5.59
Oryx antelope[c]	3	2/1	170*	17.3	2.0	0.20	43.3	5.17
Sable antelope[c]	3	0/3	170*	17.3	2.0	0.22	41.9	7.38
Waterbuck[c]	2	2/0	210*	180/240	2.4	2.1/2.6	43.9	52.9/34.9
Forest buffalo[c]	2	0/2	350*	350/350	5.1	4.7/5.5	63.3	68.3/58.3
Domestic cattle[a]	3	3[1]/0	1287	25.2	8.0	1.15	37.3	4.99
Mean							**49.4**	**13.05**
Hindgut fermenters								
Warthog[c]	1	1/0	77	--	1.5	--	57.0	--
Domestic pony[b]	3	0/3	97	6.1	2.2	0.60	71.7	15.95
Grevy´s zebra[c]	4	1/3	390*	20.0	8.1	2.61	91.5	25.77
Domestic horse[d]	6	5[1]/1	564	49.2	9.8	2.26	82.8	16.75
White rhinoceros[c]	2	2/0	1750*	1500/2000	18.6	17.2/20.0	68.4	67.0/69.8
African elephant[c]	6	1/5	4000*	1300	51.0	13.33	103.1	24.94
Mean							**79.1**	**16.79**

527 *BM were estimated; [a]University of Bonn, Germany; [b]University and ETH Zurich, Switzerland; [c]Safari
528 Park Beekse Bergen, Netherlands; [d]Riding stable Lückerath, Germany; [1]males were castrated

529 **Table 2** Chemical composition of the grass hay of the different trials (± standard deviation
530 (SD))

Species	NDF	ADF	ADL	CP
		[% OM]		
Warthog	75.8	41.6	4.6	12.1
Oryx antelope and blue wildebeest	70.7	39.1	4.1	11.8
African elephant	71.0	39.5	4.6	10.4
Forest buffalo and waterbuck	73.4	42.0	7.8	10.9
Grevy´s zebra and sable antelope	74.6	39.5	6.4	11.3
White rhinoceros	64.2	34.3	5.9	11.7
Domestic sheep and Domestic pony	71.0	39.4	5.7	7.0
Domestic horse	66.9	30.0	3.1	9.5
Domestic cattle	73.6	38.9	3.9	9.5
Domestic goat	74.6	43.1	6.9	7.7
Mean ± SD	**71.5 ± 3.55**	**38.8 ± 3.71**	**5.3 ± 1.42**	**10.2 ± 1.76**

531 (NDF = neutral detergent fibre, ADF = acid detergent fibre, ADL = acid detergent lignin, CP = crude
532 protein, NDF and ADF were corrected for ash using the insoluble ash after lignin
533 determination)

534 **Table 3** Estimated constants of allometric equations for DMI, $MRT_{particle}$, MRT_{solute} and SF (variable = a BM^b)

Variable	Group	Statistics	*a* (95%CI)	p	*b* (95%CI)	p	R2
DMI	all	OLS	0.033 (0.014, 0.079)	<0.001	0.85 (0.70, 1.01)	<0.001	0.93
		PGLS	0.039 (0.017, 0.087)	<0.001	0.83 (0.69, 0.97)	<0.001	0.92
	rum	OLS	0.066 (0.016, 0.265)	0.003	0.69 (0.43, 0.95)	0.001	0.88
		PGLS	0.068 (0.022, 0.209)	0.001	0.69 (0.47, 0.91)	<0.001	0.87
	hf	OLS	0.045 (0.019, 0.110)	0.001	0.84 (0.70, 0.98)	<0.001	0.99
		PGLS	0.045 (0.024, 0.083)	0.001	0.84 (0.74, 0.94)	<0.001	0.99
$MRT_{particle}$	all	OLS	53 (16, 135)	<0.001	-0.04 (-0.20, 0.13)	0.649	0.02
		PGLS	32 (13, 74)	<0.001	0.04 (-0.08, 0.16)	0.518	0.04
	rum	OLS	29 (14, 59)	<0.001	0.12 (-0.02, 0.25)	0.073	0.44
		PGLS	29 (16, 51)	<0.001	0.12 (0.00, 0.24)	0.071	0.43
	hf	OLS	31 (7, 137)	0.003	0.01 (-0.23, 0.24)	0.927	0.00
		PGLS	32 (12, 87)	0.001	0.00 (-0.16, 0.16)	1.00	0.00
MRT_{solute}	all	OLS	30 (17, 51)	<0.001	-0.00 (-0.10, 0.09)	0.935	0.00
		PGLS	25 (15, 42)	<0.001	0.02 (-0.06, 0.10)	0.626	0.03
	rum	OLS	34 (14, 84)	<0.001	-0.02 (-0.19, 0.15)	0.766	0.02
		PGLS	33 (16, 68)	<0.001	-0.01 (-0.15, 0.13)	0.889	0.01
	hf	OLS	21 (7, 65)	0.002	0.04 (-0.14, 0.22)	0.574	0.09
		PGLS	23 (11, 47)	0.001	0.03 (-0.07, 0.13)	0.581	0.05
SF	all	OLS	1.84 (0.92, 3.66)	0.079	-0.03 (-0.15, 0.09)	0.545	0.03
		PGLS	1.51 (0.81, 2.82)	0.221	0.00 (-0.1, 0.1)	1.000	0.00
	rum	OLS	0.88 (0.43, 1.78)	0.671	0.13 (0.00, 0.27)	0.048	0.50
		PGLS	0.87 (0.49, 1.55)	0.653	0.13 (0.03, 0.23)	0.025	0.50
	hf	OLS	1.49 (0.78, 2.83)	0.162	-0.03 (-0.13, 0.07)	0.437	0.16
		PGLS	1.48 (0.93, 2.34)	0.164	-0.03 (-0.11, 0.05)	0.495	0.15

535 (BM = body mass, all = ruminants + hindgut fermenters, rum = ruminants, hf = hindgut fermenters, DMI = dry matter intake,
536 MRT = mean retention time, SF = selectivity factor, OLS = Ordinary Least Squares, PGLS = Phylogenetic
537 Generalized Least-Squares, CI = confidence interval)

538 **Table 4** Mean retention time of particles ($MRT_{particle}$) and solute (MRT_{solute}) and
539 selectivity factor (SF) ($MRT_{particle}/MRT_{solute}$) for the whole gastrointestinal tract
540 (± standard deviation (SD) or individual values when n = 2)

	$MRT_{particle}$ [h]	**SD**	**MRT_{solute} [h]**	**SD**	**SF ($MRT_{particle}/MRT_{solute}$)**	**SD**
Ruminants						
Domestic goat	50	5.2	32	3.3	1.6	0.21
Domestic sheep	54	4.2	34	1.8	1.6	0.19
Blue wildebeest	43	4.9	32	8.7	1.4	0.33
Oryx antelope	59	7.8	30	4.5	2.0	0.21
Sable antelope	54	15.0	37	13.1	1.5	0.33
Waterbuck	52	42/61	27	19/34	2.0	1.81/2.19
Forest buffalo	49	48/51	23	21/24	2.2	1.98/2.39
Domestic cattle	75	5.0	34	0.6	2.2	0.17
Mean	**55**	**9.5**	**31**	**4.5**	**1.8**	**0.31**
Hindgut fermenters						
Warthog	44	--	34	--	1.3	--
Domestic pony	26	1.0	20	1.2	1.3	0.11
Grevy´s zebra	28	7.2	25	8.5	1.2	0.20
Domestic horse	29	5.6	25	6.5	1.2	0.15
White rhinoceros	47	43/50	32	30/34	1.5	1.44/1.45
African elephant	30	5.2	30	4.0	1.0	0.10
Mean	**34**	**9.1**	**28**	**5.2**	**1.3**	**0.16**

Table 5 The linear regression with rDMI of different parameters (variable = *a* + *b* rDMI) for the different groups in this study

Variable	Group	Statistics	*a* (95%CI)	p	*b* (95%CI)	p	R2
$MRT_{particle}$	all	OLS	82 (67, 96)	<0.001	-0.58 (-0.80, -0.36)	<0.001	0.74
		PGLS	80 (67, 94)	<0.001	-0.55 (-0.75, -0.35)	<0.001	0.71
	rum	OLS	81 (55, 106)	<0.001	-0.53 (-1.03, -0.03)	0.042	0.53
		PGLS	81 (62, 101)	<0.001	-0.54 (-0.93, -0.15)	0.021	0.56
	hf	OLS	62 (14, 110)	0.023	-0.36 (-0.95, 0.24)	0.173	0.41
		PGLS	61 (30, 91)	0.018	-0.34 (-0.71, 0.03)	0.148	0.45
MRT_{solute}	all	OLS	37 (28, 46)	<0.001	-0.12 (-0.26, 0.01)	0.074	0.24
		PGLS	37 (29, 45)	<0.001	-0.11 (-0.23, 0.01)	0.092	0.22
	rum	OLS	38 (22, 54)	0.001	-0.14 (-0.45, 0.17)	0.311	0.17
		PGLS	38 (25, 51)	<0.001	-0.14 (-0.39, 0.11)	0.305	0.17
	hf	OLS	34 (-1, 70)	0.054	-0.09 (-0.53, 0.35)	0.606	0.07
		PGLS	34 (14, 55)	0.031	-0.08 (-0.32, 0.16)	0.541	0.11
SF	all	OLS	2.40 (1.89, 2.92)	<0.001	-0.01 (-0.02, -0.01)	0.003	0.54
		PGLS	2.34 (1.85, 2.83)	<0.001	-0.01 (-0.02, 0.00)	0.028	0.48
	rum	OLS	2.11 (0.93, 3.28)	0.005	-0.01 (-0.03, 0.02)	0.539	0.07
		PGLS	2.11 (1.33, 2.89)	<0.001	-0.01 (-0.03, 0.01)	0.339	0.09
	hf	OLS	1.84 (1.32, 2.36)	0.001	-0.01 (-0.01, -0.00)	0.029	0.73
		PGLS	1.84 (1.47, 2.21)	0.001	-0.01 (-0.02, 0.00)	0.067	0.73

(rDMI = relative dry matter intake, all = ruminants + hindgut fermenters, rum = ruminants, hf = hindgut fermenters, MRT = mean retention time, SF = selectivity factor, OLS = Ordinary Least Squares, PGLS = Phylogenetic Generalized Least-Squares, CI = confidence interval)

Table 6 Literature data about allometric exponents for the relationship between body mass (BM) and $MRT_{particle}$, including: exponents, sample size (n), p-value, 95% confidence interval (CI) and digestion type of the sampled animals

Equation	n	p-value	CI	digestion type	Source
$BM^{0.30}$		-	-	all herbivores (based on theoretical calculations)	Demment (1983)
$BM^{0.28}$		-	-	all herbivores (based on theoretical calculations)	Demment and Van Soest (1983)
9.4 $BM^{0.26}$	40	-	-	hindgut fermenters	Illius and Gordon (1992)
15.3 $BM^{0.25}$	40	-	-	ruminants	
$BM^{0.22}$	45	-	-	ruminants	Gordon and Illius (1994)
15.9 $BM^{0.31}$	12	-	-	ruminants and macropods	Robbins (1993)
43.9 $BM^{0.41}$	5	-	-	hindgut fermenters (marsupials)	
15.4 $BM^{0.13}$	14	-	-	hindgut fermenters (eutherians)	
3.3 $BM^{0.24}$	6	-	-	carnivores and insects	
1.6 $BM^{0.33}$	13	-	-	birds	
32.0 $BM^{0.08}$	11	< 0.05	-	hindgut fermenters	Owen-Smith (1988)
22.8 $BM^{0.14}$	9	< 0.01	-	perissodactyls	
46.1 $BM^{0.05}$	26	n.s.	-	ungulates	
7.3 $BM^{0.17}$	60	-	-	foregut, hindgut and caecum fermenters	White and Seymour (2005)
23.6 $BM^{0.24}$	29	< 0.001	0.16 - 0.33	caecum fermenters	Clauss et al. (2007a)
34.2 $BM^{0.04}$	20	0.455	-0.07 - 0.14	colon fermenters	
34.7 $BM^{0.08}$	19	0.137	-0.03 - 0.19	non-ruminant foregut fermenters	
24.7 $BM^{0.13}$	25	0.001	0.06 - 0.21	ruminant foregut fermenters	
32.8 $BM^{0.07}$	81	0.001	0.03 - 0.10	all herbivores > 0.5 kg	
24.4 $BM^{0.14}$	93	< 0.001	0.10 - 0.17	all herbivores	
29.1 $BM^{0.12}$	8	0.0730	-0.02 - 0.25	ruminants	this study
31.0 $BM^{0.01}$	6	0.9120	-0.22 - 0.24	hindgut fermenters	

($MRT_{particle}$ = mean retention time of particle)

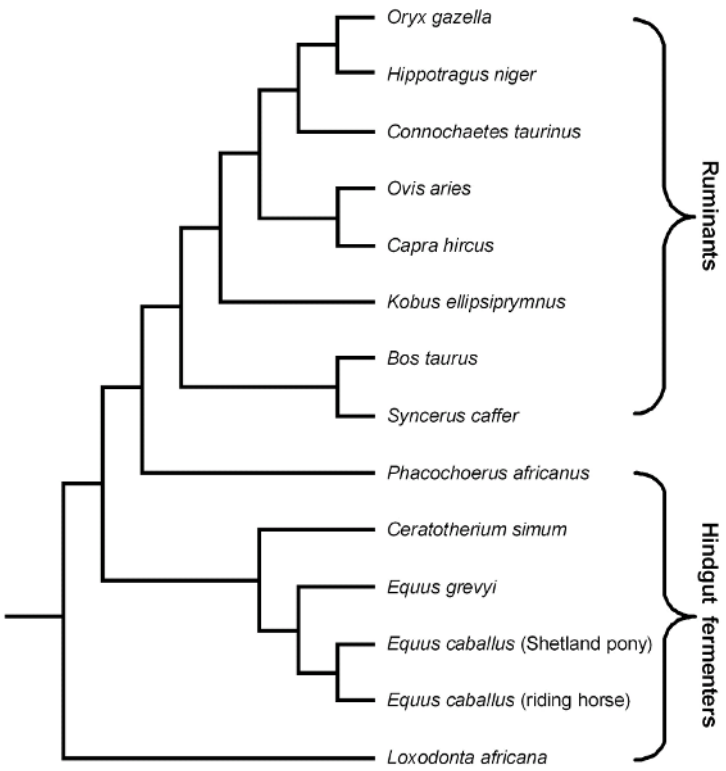
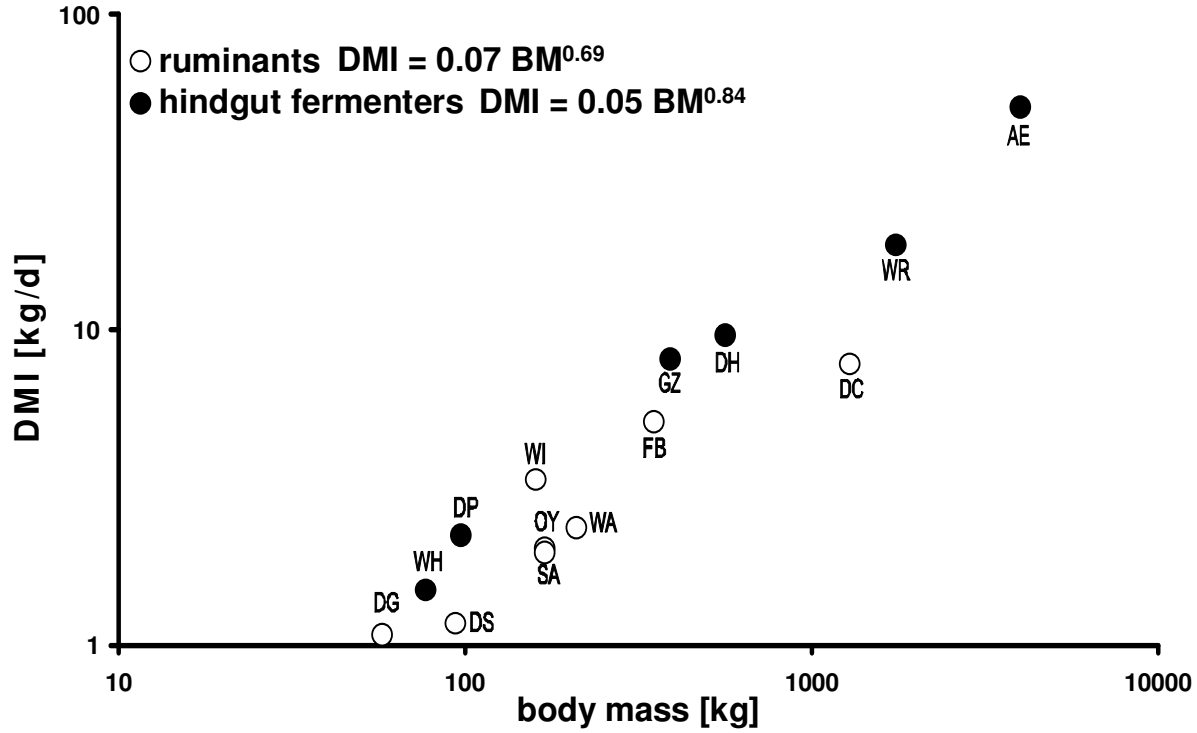
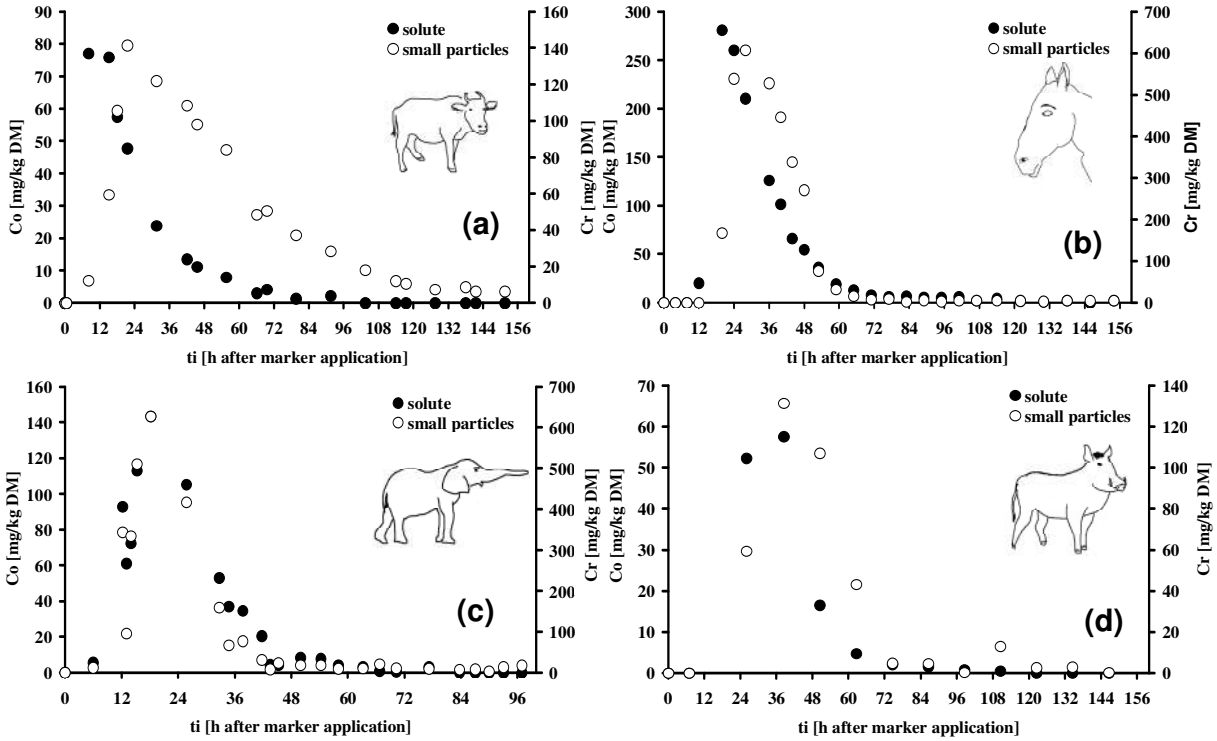


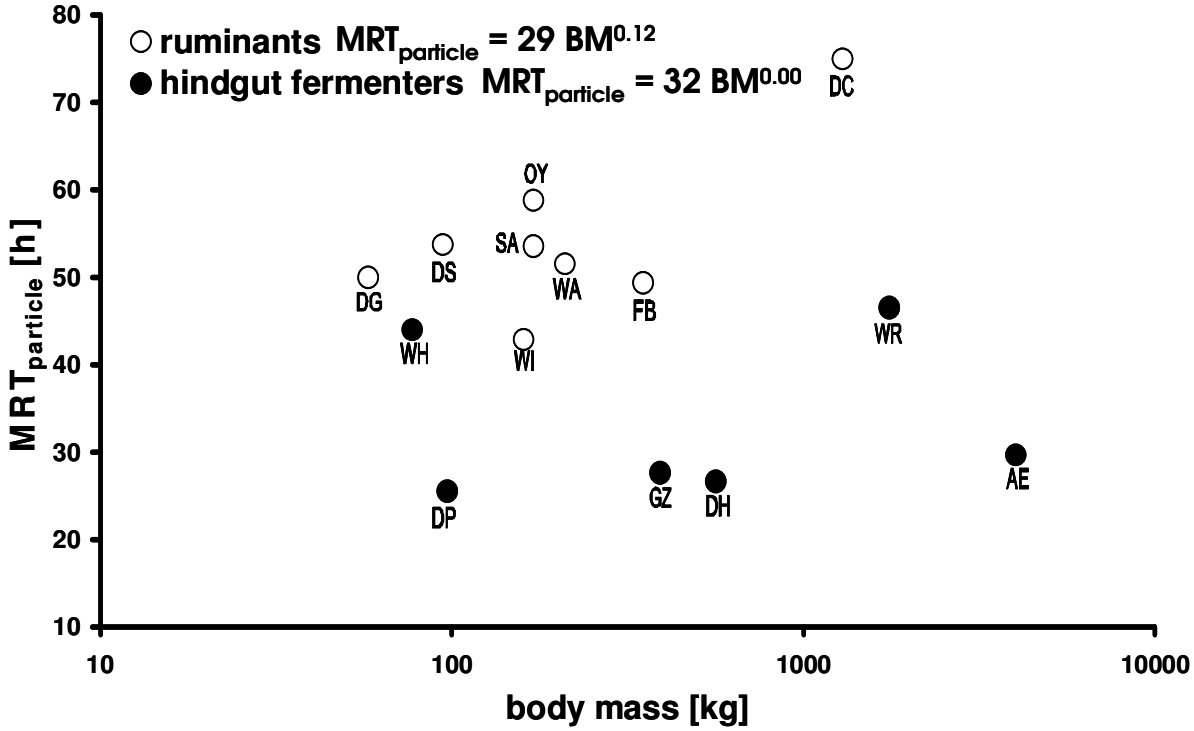
Fig. 1. Phylogenetic tree for the studied animals



578
579 **Fig. 2.** Relationship between dry matter intake (DMI) [kg/d] and body mass (BM) [kg] of all
580 species of this study. (**Abbreviations** are the same for all figures: AE = African elephant(n =
581 6), DC = domestic cattle (n = 3), DG = domestic goat (n = 6), DH = domestic horse (n = 6),
582 DP = domestic pony (n = 3), DS = domestic sheep (n = 3), FB = forest buffalo (n = 2), GZ =
583 Grevy's zebra (n = 4), OY = oryx antelope (n = 3), SA = sable antelope (n = 3), WA =
584 waterbuck (n = 2), WH = warthog (n = 1), WI = blue wildebeest (n = 4), WR = white
585 rhinoceros (n = 2))
586



587
588 **Fig. 3.** Marker excretion pattern of a forest buffalo (a), domestic horse (b), African elephant
589 (c) and warthog (d). Solute marker (Co-EDTA), small particles (Cr-mordanted fibre, < 2 mm)
590 (DM = dry matter)



591
592 **Fig. 4.** Relationship between $MRT_{particle}$ [h] and body mass (BM) [kg] of all species of this
593 study. (MRT = mean retention time) (For species abbreviations see Fig. 2)

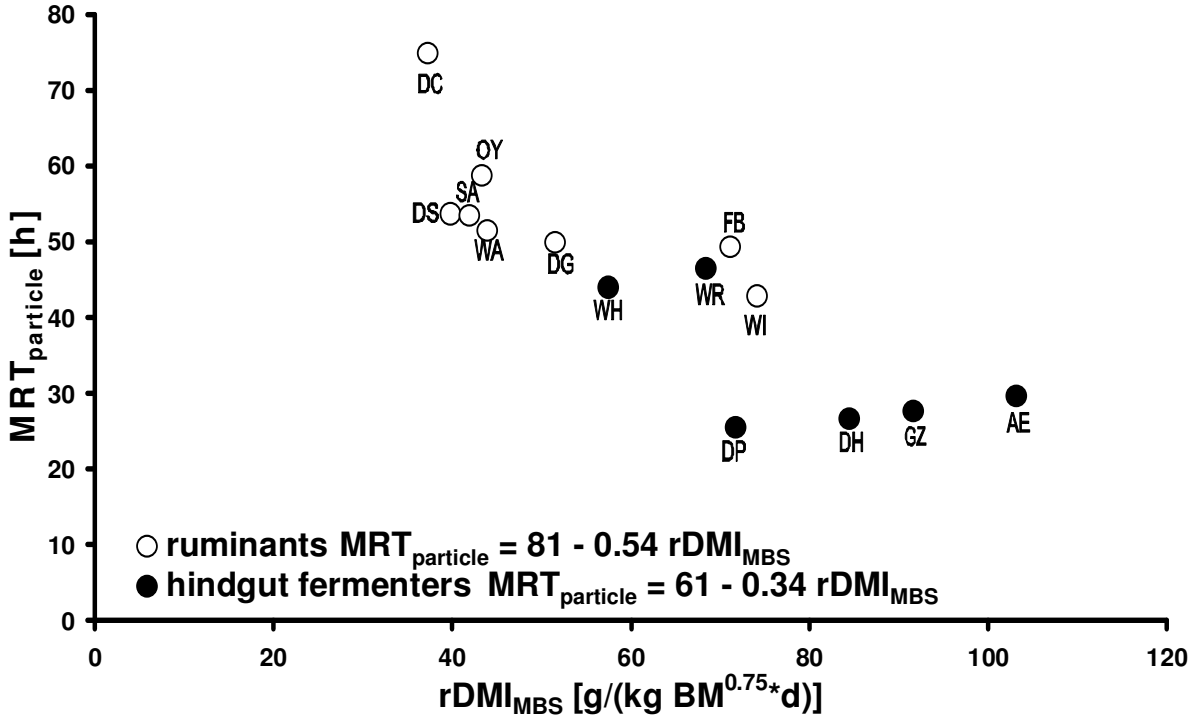


Fig. 5. Relationship between $MRT_{particle}$ [h] and rDMI [g/(kg $BM^{0.75}$*d)] of all species of this study. (MRT = mean retention time, rDMI = relative dry matter intake, MBS = metabolic body size, BM = body mass, DM = dry matter) (For species abbreviations see Fig. 2)