

Review

A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores[☆]

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Abstract

As gut capacity is assumed to scale linearly to body mass (BM), and dry matter intake (DMI) to metabolic body weight ($BM^{0.75}$), it has been proposed that ingesta mean retention time (MRT) should scale to $BM^{0.25}$ in herbivorous mammals. We test these assumptions with the most comprehensive literature data collations ($n=74$ species for gut capacity, $n=93$ species for DMI and MRT) to date. For MRT, only data from studies was used during which DMI was also recorded. Gut capacity scaled to $BM^{1.06}$. In spite of large differences in feeding regimes, absolute DMI (kg/d) scaled to $BM^{0.76}$ across all species tested. Regardless of this allometry inherent in the dataset, there was only a very low allometric scaling of MRT with $BM^{0.14}$ across all species. If species were divided according to the morphophysiological design of their digestive tract, there was non-significant scaling of MRT with $BM^{0.04}$ in colon fermenters, $BM^{0.08}$ in non-ruminant foregut fermenters, $BM^{0.06}$ in browsing and $BM^{0.04}$ in grazing ruminants. In contrast, MRT significantly scaled to $BM^{0.24}$ (CI 0.16–0.33) in the caecum fermenters. The results suggest that below a certain body size, long MRTs cannot be achieved even though coprophagy is performed; this supports the assumption of a potential body size limitation for herbivory on the lower end of the body size range. However, above a 500 g-threshold, there is no indication of a substantial *general* increase of MRT with BM. We therefore consider ingesta retention in mammalian herbivores an example of a biological, time-dependent variable that can, on an interspecific level, be dissociated from a supposed obligatory allometric scaling by the morphophysiological design of the digestive tract. We propose that very large body size does not automatically imply a digestive advantage, because long MRTs do not seem to be a characteristic of very large species only. A comparison of the relative DMI ($g/kg^{0.75}$) with MRT indicates that, on an interspecific level, higher intakes are correlated to shorter MRTs in caecum, colon and non-ruminant foregut fermenters; in contrast, no significant correlation between relative DMI and MRT is evident in ruminants.

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[☆] This contribution is dedicated to the memory of Thomas J. Foose (1945–2006), author of what could be the most comprehensive experimental large herbivore digestion study of all time.

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1. Introduction

In broad general terms, digestive efficiency in mammalian herbivores for a given food source can be modelled as the result of the interplay of three major variables — gut contents mass, food intake, and ingesta passage (Clauss et al., 2007b). If gut capacity is considered as a fixed variable, then an increase in food intake should lead to a faster ingesta passage; if, in contrast, ingesta passage is considered as a fixed variable, then an increase in food intake should lead to an increase in gut contents (which is often termed “gut capacity”). In herbivores, the efficiency of digestion of plant material is a function of the time available for this process (the shorter the ingesta retention, the lower the digestive efficiency; cf. Fig. 3 in Udén et al., 1982; Clauss et al., 2007b). The rate of digestion is a factor basically determined by properties of the ingested forage (Smith et al., 1971; Smith et al., 1972; Waldo et al., 1972; Short et al., 1974; Wofford and Holechek, 1982; Wilman and Riley, 1993; Hummel et al., 2006) and potentially also by the masticatory efficiency of a species (as smaller particle size enhances digestion rate, Fadlalla et al., 1987; Gerson et al., 1988; Bjorndal et al., 1990; Udén, 1992; Bowman and Firkins, 1993; Ellis et al., 2005). In contrast, gut capacity, food intake and ingesta passage can be considered pure “animal factors”, the interplay of which characterizes the digestive adaptation of a particular (group of) species.

Traditionally, these three “animal factors” have been considered as being allometrically related to, and therefore determined by, body mass (BM). The question whether certain morphophysiological subgroups differ in the correlation between any of these parameters has been a point of contention, in particular with respect to the differentiation of ruminants into the grazer, mixed feeder, and browser feeding types [gut capacity: Gordon and Illius (1994) and Clauss et al. (2003b); ingesta passage: Gordon and Illius, (1994) and Clauss et al. (2006a), Hummel et al. (2006); food intake: see Clauss and Lechner-Doll, (2001), Hummel et al. (2006)]. However, when considering this debate, which has been bluntly summarized as a question of “body mass versus morphology”, it should be considered that even the most prominent supporters of a

feeding type-independent, body mass-only oriented approach intuitively calculated different regression equations for the relationship between body mass and ingesta passage for ruminants on the one hand and hindgut fermenters on the other hand (Illius and Gordon, 1992), based on the silent, preconceived assumption that gross morphological differences will overrule allometric effects. Actually, the a priori exclusion of omnivores, carnivores, piscivores and insectivores from such calculations is another manifestation of a reasonable, preconceived assumption that certain gross eco-morphological borders exist and that, depending on the questions asked, it may not make sense to cross these borders. Therefore, we limit the scope of this contribution to herbivorous mammals only and analyse for potential differences between the four major morphophysiological groups — the (mostly coprophageous) caecum fermenters, the (non-coprophageous) colon fermenters, the non-ruminating foregut fermenters and the ruminating foregut fermenters.

1.1. Gut capacity

In his historical paper, Parra (1978) prepared a data collection demonstrating that in herbivores, gut capacity, measured as total gastrointestinal tract wet contents, scales nearly isometrically with body mass ($BM^{1.08}$). This data collection was specifically extended by Demment and Van Soest (1985) who confirmed Parra’s finding; the most evident outlier species to this pattern, the elephant, was later shown to probably also follow the general pattern (Clauss et al., 2005d). Although systematic variation in gut capacity within species as a reaction to diet quality have been reported in numerous publications (Gross et al., 1985a; Hammond and Wunder, 1991; Dykstra and Karasov, 1992; Foley and Cork, 1992; Cork et al., 1999; Starck, 1999; Pei et al., 2001a; Pei et al., 2001b; Munn et al., 2006), the general validity of Parra’s finding on an interspecies level has remained unchallenged, and has been the basis for important further assumptions in relation to consequences of body size increase in herbivores (Demment and Van Soest, 1985; Illius and Gordon, 1992; Clauss and Hummel, 2005).

1.2. Food intake

Food intake is generally considered to be directly related to the energy requirement (Parra, 1978; Demment and Van Soest, 1985; Illius and Gordon, 1992), which is broadly assumed to scale to metabolic body weight ($BM^{0.75}$). In general, empirical data confirms this assumption. The absolute dry matter intake (aDMI, per day) in mammals was shown to scale between $BM^{0.84}$ and $BM^{0.72}$ in 12 herbivorous and 12 carnivorous species, respectively (Bourlière, 1975), and organic matter intake in 26 ungulate species from Foose (1982) scaled to $BM^{0.77}$. Energy intake was shown to scale to $BM^{0.75}$ in a collection of 120 species of zoo mammals (Evans and Miller, 1968). Similarly, Farlow (1976) found, in 98 mammalian and avian herbivores, a relation of energy intake with $BM^{0.72}$, and with $BM^{0.69}$ in 111 mammalian and avian carnivore species. Kirkwood (1983) found maximum energy intake to scale to $BM^{0.72}$ in a combined data collection of 8 mammal and 11 bird species. Shifting the resolution of the intake rate, from dry matter per day to dry matter per minute, Shipley et al. (1994) found that maximum dry matter intake scaled to $BM^{0.71}$ in a dataset of 23 herbivore species. A potential source of error in the perceived relevance of the scaling factor for energy requirements and hence food intake was presented by Nagy (1987) with data that indicated that mammalian field metabolic rate (23 eutherian species), in contrast to maintenance energy requirements, scaled to $BM^{0.81}$; however, in a larger dataset, it was subsequently concluded that field metabolic rate of terrestrial mammals (79 species) also scaled to $BM^{0.73}$ (Nagy et al., 1999). In the course of a more recent discussion on the scaling of metabolic rate, White and Seymour (2005) showed that the exponent describing the relationship between mammalian metabolic rate and BM is 0.68–0.69, rather than the 0.75 claimed by Savage et al. (2004) and many other authors earlier on. Thus, the White and Seymour (2005) data support the assumption that the major determinant of metabolic rate in mammals at rest is heat loss (Glazier, 2005), which in turn is a function of surface, in contrast to any of the more recent explanatory theories that account for a quarter-power scaling. White and Seymour (2005) convincingly demonstrate that an increase of the exponent from 0.68 towards 0.75 is an effect of the inclusion of data from large herbivores in the data set: large herbivores can hardly be assessed for metabolic rate in a post-absorptive state due to the presence of an active microbial fauna in their gut, even after a prolonged fast. Similarly, Glazier (2005) demonstrated a higher scaling exponent in larger versus smaller rodents, and collated a list of publications that also found a general increase in the scaling exponent with body mass range in mammals. The results of White and Seymour (2005) have enormous relevance for the discussion about the determinants of metabolic rate. However, for the purpose of our study, which is concerned with digestive physiology in herbivores, including large ones, their results emphasize that we should expect food intake – which is a function of the metabolic unit of the herbivore and its symbiotic microbes – to scale to $BM^{0.75}$ in an interspecific comparison.

1.3. Ingesta passage

When comparing digestive strategies of different species, the ingesta passage time or mean retention time (MRT)¹ has traditionally been understood as a species-specific parameter that is determined by the species-specific body mass (Demment and Van Soest, 1985; Illius and Gordon, 1992; Robbins, 1993) and/or by the species-specific volume of the gastrointestinal fermentation chamber (Langer and Snipes, 1991). It seems intuitively evident that larger animals, with larger guts, should have longer ingesta retention times. A certain amount of material (per unit time, e.g. kg/d) needs twice the time to pass through a tube of a given volume (length \times diameter) as it takes for the same amount to pass through a tube of half that volume. However, a doubling in BM will also result in an increase in food intake. If this increase were linear to BM as well, MRT would not change. But if it is assumed, as explained above, that food intake scales to $BM^{0.75}$, the following simple consideration is evident (following Calder, 1984, p. 126; Illius and Gordon, 1992; McNab, 2002). If gut capacity (the volume of the tube) effectively scales to $BM^{1.00}$, and food intake (the amount of material per unit time) scales to $BM^{0.75}$, then the time required for the material to pass through the tube should scale to $BM^{0.25}$, in a similar manner as many other biological time-related variables (Peters, 1983; Calder, 1984). In correspondence to these considerations, Illius and Gordon (1992) demonstrated, using data collections on ruminant and hindgut-fermenting mammals, that the respective MRTs scaled to $BM^{0.25}$ and $BM^{0.26}$. For ruminants and macropods combined, Robbins (1993) found a similar scaling of MRT to $BM^{0.28}$ – $BM^{0.31}$. Apart from ungulates (mainly from Foose 1982), the data collection of Illius and Gordon (1992) included only two hindgut fermenters below 100 kg. In another data collection of MRTs in eutherian hindgut fermenters, Robbins (1993) found a correlation with $BM^{0.13}$. Cork et al. (1999, footnote on p. 243) expanded the data collection on hindgut fermenters and found a relationship with $BM^{0.19}$. This data set included more measurements on smaller species, especially rodents and marsupials. It should be noted that for their digestion model, these latter authors used a food intake scaling of $BM^{0.81}$ according to Nagy (1987). Even more recently, White and Seymour (2005, Fig. 2 of their publication) presented a data collection on herbivore retention times (foregut and hindgut fermenters combined) and found a correlation with $BM^{0.17}$. In short, it seems that, as more data are collected, the scaling exponent is reduced further away from the originally postulated 0.25 value.

Regardless of these considerations of scaling factor, depending on the data used for comparison or verification, the concept of increasing MRT with increasing BM does not automatically explain obvious deviations from the pattern. Playing the devil's advocate: if, among the hindgut fermenters, a 7 kg-koala

¹ Note that the unit for passage time or MRT is time (e.g., minutes, hours or days); the unit of “passage rate” is, as the word “rate” implies, a mass, volume or fraction per unit time (e.g. % per hour). Data that gives a time in hours should therefore not be referred to as “passage rate”.

(*Phascolarctos cinereus*, Cork and Warner, 1983) has a longer particle MRT than a 30 kg-wombat (*Vombatus ursinus*, Barboza, 1993), which has a longer particle MRT than a 90 kg-orang utan (*Pongo pygmaeus*, Caton et al., 1999), which has a longer particle MRT than a 1200 kg-black rhinoceros (*Diceros bicornis*, Clauss et al., 2005a), which has a longer particle MRT than a 3000 kg-Asian elephant (*Elephas maximus*, Hackenberger, 1987); or if, among the foregut fermenters, a 2.5 kg-sloth (*Bradypus tridactylus*, Foley et al., 1995) has a longer particle MRT than a 230 kg-pygmy hippopotamus (*Hexaprotodon liberiensis*, Clauss et al., 2004), which has a longer particle MRT than a 400 kg-water buffalo (*Bubalus bubalis*, Bartocci et al., 1997), which has a longer particle MRT than a 1200 kg-giraffe (*Giraffa camelopardalis*, Clauss et al., 1998), then an interspecific concept of increasing MRT with increasing BM, as a natural law overruling other aspects of adaptations related to nutritional ecology, seems difficult to accept.

Actually, numerous authors have commented on the discrepancy of their own findings to the assumption that MRT should increase with increasing BM: Van Soest et al. (1995) did not find a correlation between BM and MRT in three very small ruminant species; similarly, Wenninger and Shipley (2000) did not find differences in MRT in ruminants ranging from 2–100 kg. Clauss et al. (2006a) analysed available standardized data on the MRT in the reticulorumen (RR) of ruminants and stated that the available data (10 species) did not allow the conclusion that $MRT_{particle,RR}$ was a function of BM, neither in inter- nor in intraspecific comparisons. Like Robbins et al. (1995) before, these authors could not find a correlation between body weight and $MRT_{fluid,RR}$ in their dataset. Felicetti et al. (2000) remarked that porcupines had a distinctively longer MRT than expected on the basis of their body weight. As several authors before them, Loehlein et al. (2003) noted that elephants have surprisingly short ingesta MRTs for their enormous body size. In a study on transit time (the time until the first marker appearance) in primate species, Milton (1984) found notable exceptions to the general rule of longer transit times with increasing BM. Similarly, Lambert (1998) found, in a data collection on the transit time in primates, that the larger species do not necessarily have the longer transit times.² Caton and Hume (1996) did not find a correlation between BM and MRT in small New World primates, and Nijboer et al. (2006) did not find a correlation between BM and MRT in foregut-fermenting primates. Clauss et al. (2004) found identical ranges of particle MRT in pygmy hippos and common hippos (*Hippopotamus amphibius*) in spite of a tenfold difference in BM between these species. Stevens and Hume (1998) stated that there seemed to be no consistent correlation between BM and MRT in their collection of data on 27 herbivore species.

Many authors have noted a negative correlation between food intake and MRT, not only in herbivorous species [e.g. for pigs (Parker and Clawson, 1967); for geese (Halse, 1984); for sharks (Wetherbee and Gruber, 1990); for ruminants (Lechner-

Doll et al., 1991); for beavers (Fryxell et al., 1994); for deer mice (Reid and Brooks, 1994); for camels (Cahill and McBride, 1995); for bandicoots (McClelland et al., 1999); for equids (Pearson et al., 2001); for hippos (Clauss et al., 2004); for black rhinoceros (Clauss and Hummel, 2005)]. In this contribution, we want to adopt the corresponding interpretation of measured ingesta retention times, which we do not consider to be so much dependent on BM, but rather on the relative dry matter intake (rDMI, in $g/kg^{0.75}$ metabolic body weight per day). We suspected that this interpretation would lead to more instructive results and correspond to the simple mechanistic model outlined above: animal species with a higher rDMI will have a shorter MRT than animals with a low rDMI. Our point can be illustrated using the data from Foose (1982) on hindgut-fermenting ungulates, which allows two different interpretative approaches: if MRT data are plotted against body weight (Fig. 1a), either one assumes that MRT increases with BM, and elephants deviate from the common pattern; alternatively, one could assume that MRT is constant over a large range of BM, with rhinoceroses as an exception to this pattern. If, on the other hand, MRT data are plotted against the relative food intake (in the case of Foose, 1982, this is expressed as organic matter), it seems that

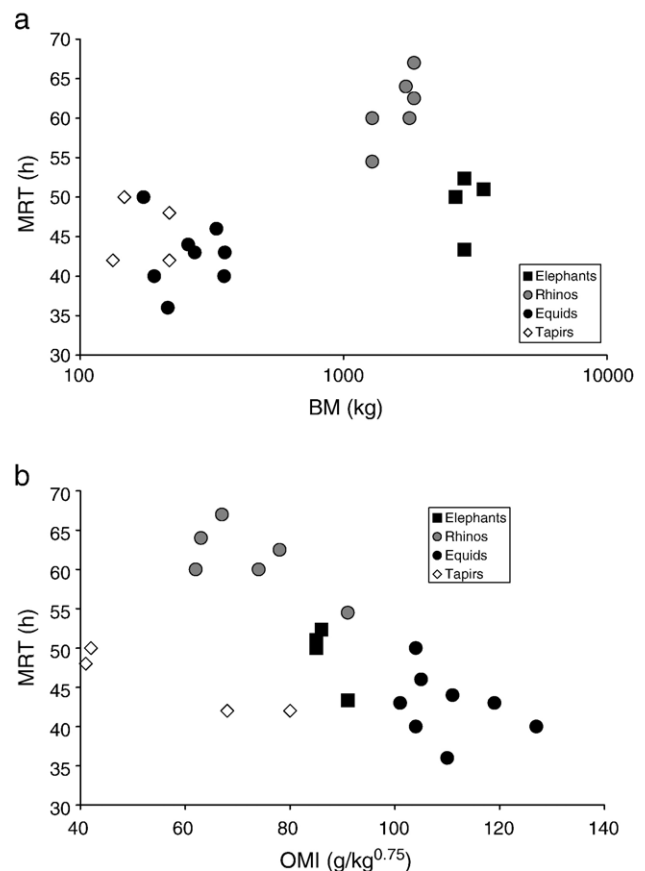


Fig. 1. Data on the mean retention time (MRT) in the total digestive tract of non-ruminant ungulates (Asian and African elephants, Indian, white and black rhinoceroses, Asian and American tapirs, zebras and wild asses; 2 measurements per species) from Foose (1982). MRT determined by analysing one or two pooled faecal samples per day, plotted against (a) body mass (BM, kg) or (b) relative organic matter intake (OMI, in $g/kg^{0.75}$).

² Note that in these primate data collections, not only strict herbivores but also frugivores and omnivores were included.

elephants, rhinoceroses and equids follow a similar pattern, with tapirs being the exception (Fig. 1b).³

Starting from this, we collated data on BM and gut capacity (total gut contents wet weight), and BM, MRT and DMI from the literature to look for patterns emerging from an analysis based on a large number of herbivore species of various gastrointestinal designs. We specifically predicted that

- i) gut capacity scales linearly with BM
- ii) absolute daily food intake scales allometrically to BM with an exponent close to 0.75,
- iii) there is no consistent relationship between MRT and BM,
- iv) MRT can be better explained by the level of rDMI than by BM.

Additionally, systematic differences between the four major digestion strategies (the mostly coprophageous caecum fermenters, the non-coprophageous colon fermenters, the non-ruminating foregut fermenters and the ruminating foregut fermenters) in these relationships were investigated without specific hypotheses as a preliminary, exploratory analysis.

2. Methods

Ideally, all parameters — gut capacity, food intake, and mean retention time, should be taken from trials where these parameters were all measured in the same animals. However, the number of studies where all three parameters were measured is very small. Therefore, we collated data on BM and gut capacity on the one hand, and data on BM, DMI and MRT on the other hand. As the retention of ingesta particles, not fluids, is the biologically more relevant parameter (reflecting the time available for particle fermentation), we limit our presentation to particle MRT data; henceforward, “MRT” denotes particle MRT in the total digestive tract unless otherwise identified. Only sources were used which gave BM, DMI and MRT together, thus omitting publications which gave BM and MRT measurements but that did not measure food intake in their animals. The only exception to this rule were Sakaguchi et al. (1991), who gave rDMI and MRT for their adult langur monkeys (*Semnopithecus cristatus*) but no BM; in this case, BM was taken from Silva and Downing (1995) for *Presbytis* (= *Semnopithecus*) *cristata*. Additionally, in three cases, the data originated from two publications describing the same study (Udén et al., 1982; Udén and Van Soest, 1982; Orton et al., 1985b; Orton et al., 1985a; Cherney et al., 1990; Cherney et al., 1991). In the case of the koala, data on mean DMI was taken from Cork et al. (1983) and linked to the MRT data from Cork and Warner (1983); similarly, data for two marsupials was combined from Foley and Hume (1987b,a). For some species, data were used that is currently being prepared for publications.

³ However, as captive tapirs mostly only defecate once or twice per day (Clauss, pers. obs.), the actual retention times of tapirs might have been accurately measured in that study (only one or two pooled faecal samples per animal and day were analysed for the determination of MRT), whereas that of the other species is likely to have been overestimated due to this infrequent sampling pattern (see footnote 5).

For the sake of a large data collection, we did not select publications according to the passage markers used. Therefore, any particle marker was accepted; however, only studies were accepted in which small particles were labelled; studies in which whole forages were labelled were not included in this collation, excluding the data from Foose (1982). There is reason to believe that an inclusion of the Foose (1982) dataset in a comparative database would lead to a bias in longer MRTs in larger animals, as this dataset comprises only ungulates (Clauss et al., 2003a; see also footnote e). In addition, an exclusion of these data allows their use as a comparative dataset that may or may not produce similar patterns as the dataset of this study. The exclusion of labelled whole forage was mainly done due to the known large differences in the retention of fine particles (that do not require rumination) as compared to large particles (that are even more selectively retained) in ruminants (Lechner-Doll et al., 1991). Studies in which ¹⁰³Ru–Phe was used as a particle marker were accepted, as this marker is prone to bind to the fine particle fraction (Cork and Warner, 1983). Similarly, we did not select publications according to the type of food offered; therefore, the data collection comprises animals fed on a complete, pelleted diet, animals on mixtures of roughages and concentrates, as well as animals on roughage-only diets. With regards to some domestic species (rabbits, horse, goats, sheep, cattle), no attempt was made to collate all published data. For lagomorphs and rodents, only data from trials was used during which coprophagy was not prevented by the study design. For each species, one average value for BM and gut capacity, and for BM, MRT and DMI was calculated using all available data from the cited publications, without weighing the data from the individual studies (e.g. not multiplying by the number of animals of a group if a publications gave only a group average, or not controlling for the fact that in other studies, repeated measurements in the same animals were given). The data and its sources for the two data collections are summarized in Appendix Tables 1 and 2.

Species were allocated, according to Stevens and Hume (1995), to one of the following categories: caecum fermenters, colon fermenters, non-ruminant foregut fermenters, and ruminants (Appendix Tables 1 and 2). In addition, the true ruminants were classified according to Hofmann (1988, 1991) into grazers, intermediate feeders and browsers (Appendix Table 2). This was necessary to control for an effect of the different representation of the feeding types, which most likely differ systematically in MRT (Clauss et al., 2006a; Hummel et al., 2006), across the BM range. Although it would be desirable to apply a similar, niche-based classification to other groups that are represented by a large number of species, such as the primates or the rodents, no according, easily available classification is known to us that could be similarly applied.

Linear regression analysis between MRT and rDMI (as the independent variable), and allometric regression (i.e., linear regression between the logarithmic values) between DMI and BM (independent) or MRT and BM (independent), respectively, was performed for diverse groups of animals. The resulting coefficients in allometric or linear equations are always given with their 95% confidence intervals in brackets. These analysis

were performed without phylogenetic control, assuming that the results of simple regression analyses are similar in conventional and phylogenetically controlled statistics (Ricklefs and Starck, 1996). Digestion parameters (MRT, DMI) for groups of species with different digestion type were compared using Analysis of Covariance (ANCOVA) with BM as covariate, sometimes followed by pair-wise post hoc tests. Due to the absence of phylogenetic control, the results of these tests must be considered exploratory (Ricklefs and Starck, 1996). All statistical calculations were performed with the SPSS 12.0 statistical package (SPSS Inc., Chicago, Illinois, USA). The significance level was set at $\alpha=0.05$.

3. Results

There was a clear demarcation in BM in the hindgut fermenters for which data were available; there were no caecum fermenters above 45 kg, and no colon fermenters below 1.6 kg. Non-ruminant and ruminant foregut fermenters had a similar lower body weight limit of approximately 1 kg; non-ruminant foregut fermenters were mostly limited to a weight range of up to 40 kg, whereas ruminants covered a broader spectrum of up to 700 kg. Only the hippopotamuses represented large non-ruminant foregut fermenters within the weight range covered by the larger ruminants (in the case of the pygmy hippopotamus) or exceeding it (in the case of the common hippopotamus).

3.1. Gut capacity

Data were collated on 40 hindgut fermenter (30 caecum and 10 colon fermenter) and 34 foregut fermenter species (11 non-ruminants and 23 ruminants; c.f. Appendix Table 1). There was a close correlation of BM and gut capacity (Fig. 2). Gut capacity scaled to $BM^{1.06}$ (95% CI 1.03–1.10, $r^2=0.98$, $p<0.001$) across all species [caecum fermenters: $BM^{1.05}$ (0.93–1.16, $r^2=0.93$, $p<0.001$), colon fermenters: $BM^{1.03}$ (0.94–1.13, $r^2=0.99$, $p<0.001$), non-ruminant foregut fermenters: $BM^{1.11}$ (0.91–1.30, $r^2=0.95$, $p<0.001$), ruminant foregut

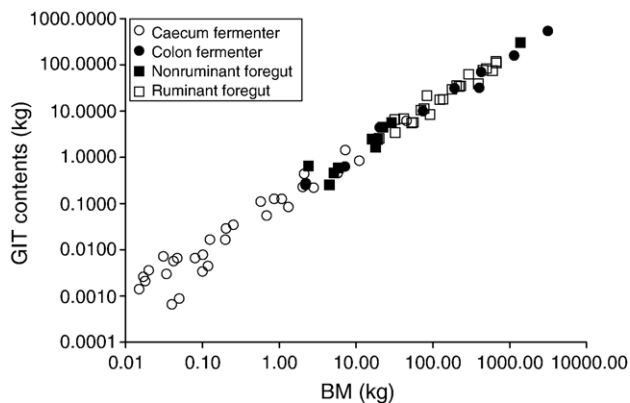


Fig. 2. Correlation of body mass (BM) and the mass of the gastrointestinal (GIT) contents (measured as wet weight, kg). Data from Appendix Table 1. The overall allometric regression equation is $y=0.107x^{1.06}$ (caecum fermenters: $y=0.102x^{1.05}$; colon fermenters: $y=0.117x^{1.03}$; non-ruminant foregut fermenters: $y=0.100x^{1.11}$; ruminant foregut fermenters: $y=0.114x^{1.05}$).

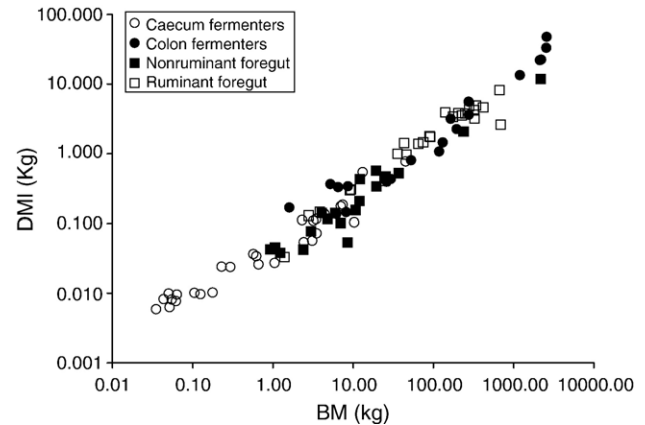


Fig. 3. Correlation of body mass (BM) and absolute dry matter intake (DMI, measured as kg per day). Data from Appendix Table 2. The overall allometric regression equation is $y=0.047x^{0.76}$ (caecum fermenters: $y=0.046x^{0.64}$; colon fermenters: $y=0.049x^{0.79}$; non-ruminant foregut fermenters: $y=0.034x^{0.76}$; ruminant foregut fermenters: $y=0.050x^{0.77}$).

fermenters: $BM^{1.05}$ (0.94–1.16, $r^2=0.95$, $p<0.001$)]. There were no significant differences between the digestion types in the scaling factor or in the absolute values (intercepts).

3.2. Food intake and ingesta passage

Data were collated on 49 hindgut fermenter (29 caecum and 20 colon fermenter) and 46 foregut fermenter species (19 non-ruminants and 25 ruminants; cf. Appendix Table 2). For some species, a large range of DMI was available; for some species, only one value was found.

In spite of the variety and the obvious differences in the energy density of feeds offered to the different species, there was a close correlation of aDMI and BM (Fig. 3). aDMI scaled to $BM^{0.76}$ (0.73–0.79, $r^2=0.96$, $p<0.001$) across all species [caecum fermenters: $BM^{0.64}$ (0.57–0.70, $r^2=0.94$, $p<0.001$), colon fermenters: $BM^{0.79}$ (0.69–0.89, $r^2=0.94$, $p<0.001$), non-ruminant foregut fermenters: $BM^{0.76}$ (0.65–0.87, $r^2=0.93$, $p<0.001$), ruminant foregut fermenters: $BM^{0.77}$ (0.69–0.86, $r^2=0.94$, $p<0.001$)]. Due to the difference in slope, a comparison of the digestion types had to exclude the caecum fermenters. ANCOVA revealed a significant difference in the BM–aDMI relationship (intercepts) between colon fermenters and non-ruminant foregut fermenters ($p=0.005$), ruminants and non-ruminant foregut fermenters ($p=0.008$) but not between colon fermenters and ruminants ($p=1.0$), with non-ruminant foregut fermenters displaying lower aDMI values.

For all herbivorous species combined, there was a weak correlation between BM and MRT (Fig. 4). MRT scaled to $BM^{0.14}$ (0.10–0.17, $r^2=0.42$, $p<0.001$) across all species [caecum fermenters: $BM^{0.24}$ (0.16–0.33, $r^2=0.57$, $p<0.001$), colon fermenters: $BM^{0.04}$ (–0.07–0.14, $r^2=0.03$, $p=0.455$), non-ruminant foregut fermenters: $BM^{0.08}$ (–0.03–0.19, $r^2=0.13$, $p=0.137$), ruminant foregut fermenters: $BM^{0.13}$ (0.06–0.21, $r^2=0.37$, $p=0.001$)]. Due to the difference in slope, a comparison of the digestion types had to exclude the caecum fermenters. ANCOVA revealed no significant differences between the BM–MRT relationship of colon fermenters,

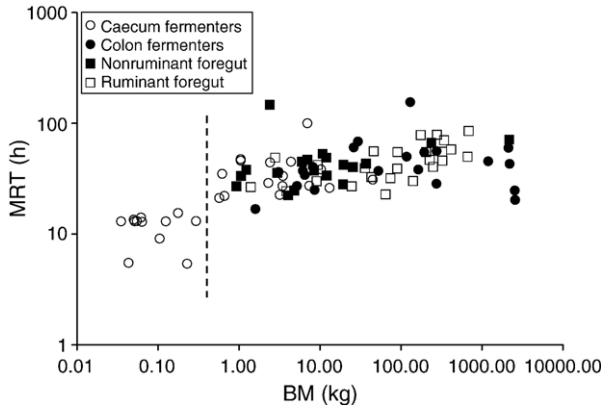


Fig. 4. Correlation of body mass (BM) and particle mean retention time (MRT) in the whole gastrointestinal tract. Data from Appendix Table 2. The overall allometric regression equation is $y = 24.4x^{0.14}$ (caecum fermenters: $y = 23.6x^{0.24}$; colon fermenters [not significant]: $y = 34.2x^{0.04}$; non-ruminant foregut fermenters [not significant]: $y = 34.7x^{0.08}$; ruminant foregut fermenters: $y = 24.7x^{0.13}$). When only species >0.5 kg BM are considered, the overall regression is $y = 32.8x^{0.07}$.

non-ruminant foregut fermenters and ruminants. If, triggered by the visual pattern, data for all species was restricted to animals above 500 g only ($n=81$), there was an even lower overall scaling of MRT with $BM^{0.07}$ ($0.03–0.10$, $r^2=0.12$, $p=0.001$). Above this threshold, three particular outliers are evident in Fig. 4, representing the koala (caecum fermenter), the dugong (*Dugong dugon*, colon fermenter) and the sloth (non-ruminant foregut fermenter); these species were excluded from the subsequent analyses where indicated.

As it was suspected that the allometric exponent for the ruminants was influenced by an uneven distribution of grazing and browsing species in the dataset, these feeding types were analysed individually (Fig. 5). The allometric exponent of either feeding type was low and included 0 in the 95% CI [browsers: $BM^{0.06}$ ($-0.07–0.19$, $r^2=0.14$, $p=0.314$); grazers: $BM^{0.04}$ ($-0.22–0.30$, $r^2=0.02$, $p=0.727$)].

For the complete data set, there was a significant, negative correlation between rDMI and MRT, but r^2 was very low (all

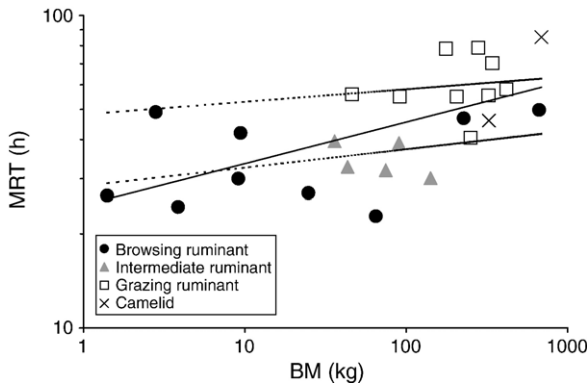


Fig. 5. Correlation of body mass (BM) and particle mean retention time (MRT) in the whole gastrointestinal tract of ruminant foregut fermenters. Data from Appendix Table 2. The overall allometric regression equation for all data points is $y = 24.7x^{0.13}$ (solid line). When grazing and browsing ruminants are considered individually, the resulting non-significant equations are $y = 48.2x^{0.04}$ for grazers (upper dashed line) and $y = 28.4x^{0.06}$ for browsers (lower dashed line).

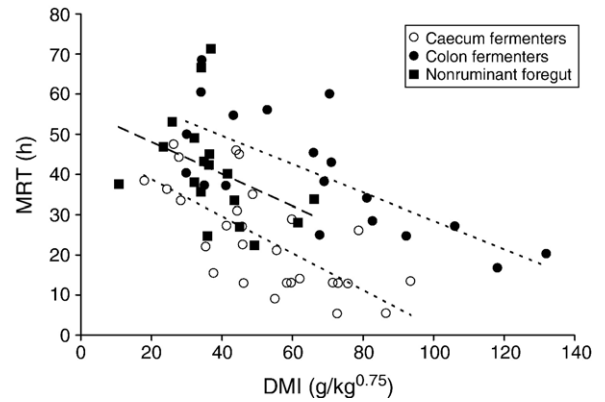


Fig. 6. Correlation of relative dry matter intake (DMI, measured as $g/kg^{0.75}$ per day) and particle mean retention time (MRT) in the whole gastrointestinal tract. Data from Appendix Table 2. The linear regression equation is $y = 48.1 - 0.46x$ for caecum fermenters ($r^2=0.49$; without the koala; lower dashed line), $y = 63.8 - 0.35x$ for colon fermenters ($r^2=0.53$; without the dugong, upper dashed line) and $y = 56.1 - 0.40x$ for non-ruminant foregut fermenters ($r^2=0.15$; without the sloth, middle interrupted line).

species: $MRT = 60.5 - 0.38 \text{ rDMI}$, $r^2=0.12$, $p=0.001$; caecum fermenters: $MRT = 54.4 - 0.54 \text{ rDMI}$, $r^2=0.30$, $p=0.002$; colon fermenters: $MRT = 79.6 - 0.52 \text{ rDMI}$, $r^2=0.28$, $p=0.016$; non-ruminant foregut fermenters: $MRT = 79.6 - 0.89 \text{ rDMI}$, $r^2=0.18$, $p=0.072$; ruminant foregut fermenters: $MRT = 52.2 - 0.09 \text{ rDMI}$, $r^2=0.01$, $p=0.693$). ANCOVA revealed significant differences in the rDMI-MRT relationship between the caecum fermenters and the colon fermenters ($p<0.001$) and the caecum fermenters and the ruminants ($p<0.001$) but not between any other groups. Within the hindgut fermenters, there was a similar decline in MRT with increasing rDMI in caecum fermenters as compared to colon fermenters (with or without the dugong), with a difference in the respective intercepts (Fig. 6). There was a steeper decline in MRT with increasing rDMI in non-ruminating foregut fermenters (with or without the sloth) than in ruminants; this difference between these groups, however, only became significant if both the sloth and the hippos were excluded from the non-ruminant foregut fermenters. Thus, the slope of the rDMI-MRT relationship was similar in the interspecific comparison between caecum, colon and non-ruminating foregut

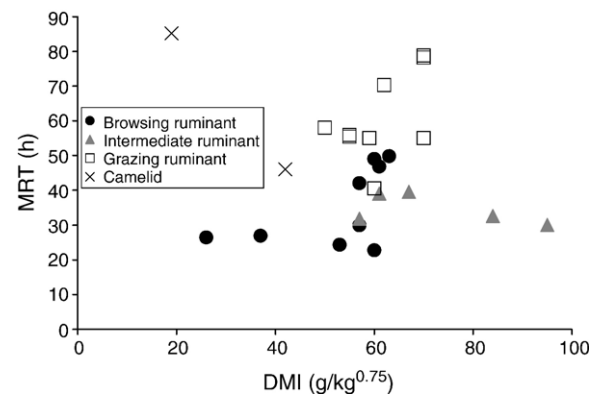


Fig. 7. Correlation of relative dry matter intake (DMI, measured as $g/kg^{0.75}$ per day) and particle mean retention time (MRT) in the whole gastrointestinal tract of ruminant foregut fermenters. Data from Appendix Table 2.

fermenters (Fig. 6), whereas for the ruminants, no slope in the rDMI-MRT relationship could be demonstrated (Fig. 7). Apart from the sloth, the dugong and the hippos, the ruminants were outstanding insofar as many ruminant species (in particular the grazing ones) attained, on intermediate rDMI levels, very high MRTs.

4. Discussion

4.1. Gut capacity

As predicted, the results of our expanded dataset confirm the previous findings mentioned in the introduction that gut capacity scales nearly isometrically with BM. The 95% confidence interval did not exclude unity (an exponent of 1.0) for any digestion type. Thus, in the interspecific comparison, gut capacity could represent a constant proportion of the overall body mass and should, therefore, not pose in itself a limit to any increase in body mass. The finding that overall gut capacity remains relatively constant supports the argument that a disproportional increase in capacity of one gut compartment should result in a disproportional decrease of the capacity of another (Clauss et al., 2003a). This interspecific linearity does not exclude sometimes enormous, relevant, intraspecific, variation in gut capacity (as measured in different individuals, see references in Introduction; and as extrapolated for individual “spare capacity” of the digestive tract, Clauss et al., 2007b).

4.2. Food intake and ingesta passage

4.2.1. Validity of results

Several issues need to be mentioned that could possibly reduce the validity of our findings. Although the scope of the data set is relatively large, individual additions or omissions still have a drastic effect on the statistical evaluation. If, e.g., for the lesser mousedeer from Morat and Nordin (1978), not the average values of rDMI 25.6 g/kg^{0.75}, MRT 27 h, measured by chromium oxide, but the average values of rDMI 23.0 g/kg^{0.75}, MRT 53 h, measured with stained sorghum grains, was used, then the allometric relation between BM and MRT would become even less distinctive for ruminants in general. The allocation of certain primate and marsupial species to either the caecum or the colon fermenters – a seemingly arbitrary decision in several cases – influences the slope of the rDMI-MRT relationship of these groups. Therefore, the interpretation of the data focuses on the meaning of potential patterns, without claiming universal validity of the analyses performed. The choice to use only publications that give data on all three measurements – BM, MRT and DMI – limits the number of data points available for an evaluation of the relationship between BM and MRT. Nevertheless, the data set covers a large body size range without evident gaps.

The decision to include only publications that also give the DMI makes an important control possible — whether an expected allometric relationship (aDMI to BM) can be observed in the data set at all. As this allometric scaling is observed, the validity of the result, based on data from the same investiga-

tions, that there is a less than expected scaling between MRT and BM, is increased.

A more critical issue might be the inclusion of data gained by the use of different particle markers. A close inspection of the data on ruminants, e.g., shows that the Cr-mordanted fibres mostly tend to yield longer MRT measurements than other methods. Therefore, for a more specialized investigation on MRT characteristics in certain animal taxa, the use of a database derived from one marker system is to be preferred (Clauss et al., 2006a). A systematic underestimation of particle MRT of large species in our dataset can be excluded, since most data for these species were measured using Cr-mordants. Although, for the elephants, the data given by Hackenberger (1987) for the appearance of rubber rings in the faeces were used to calculate the individual MRTs of the trial animals, it had been demonstrated by the author in pilot trials that no statistical difference existed in the excretion pattern of the rubber rings and Cr-mordanted fibre.

Another problem in choosing a particulate marker is the fact that ingesta particle size is very likely to depend on BM, even if this has not been demonstrated empirically on a larger scale (Clauss and Hummel, 2005). The fact that larger animals from primates (Caton et al., 1999) to equids (Björnhag et al., 1984) and ruminants (Lechner-Doll et al., 1991) retain “small” particles selectively is reflected in the finding that Cr-mordanted fibres (<2 mm) are generally retained longer than associated fluid markers. On the other hand, the same particulate marker may represent those “large” particles that are selectively expelled in the smaller caecum fermenters (Foley and Hume, 1987b; Hume and Sakaguchi, 1991). The question of marker particle size will be particularly relevant in a comparison of ruminants and other herbivores. Functional ruminants (the Ruminantia and the Tylopoda) are the only mammal species in which the selective retention of larger particles has so far been demonstrated [camelids (Heller, 1986; Heller et al., 1986); ruminants (reviewed by Lechner-Doll et al., 1991); in contrast, non-ruminant foregut fermenters could be suspected to pass larger particles either at the same rate or faster than small particles (Clauss, 2004; Clauss et al., 2004)]. Using particles <2 mm when comparing ruminants and equids, e.g., will reduce differences, as these comparatively small particles are among the first to pass the GIT of ruminants (Lechner-Doll et al., 1991) but are probably retained in horses (Björnhag et al., 1984). If, in contrast, a larger particle size would be chosen for the measurement of MRT, the difference between the two groups would increase, as longer particles remain in the forestomach of ruminants or camelids until further ruminated upon, but pass quickly through the GIT of equids. Any conclusions derived from the data collection in this study, therefore, do not intend to contradict this difference between ruminants and non-ruminants, but refers to broad generalized patterns of body size and its consequences on mammalian herbivore physiology.

A fundamental discrepancy between the data from most caecum fermenters and that of the other digestion types must also be stated. The MRT values of caecum fermenters represent, in most cases, more than one marker passage through the gastrointestinal tract, as passage markers are often recycled in these species as a side-effect of coprophagy (reviewed in Clauss

et al., 2007a). Any relationship between the reported DMI of coprophageous animals and another parameter must be interpreted with caution, because the true total dry matter intake, consisting of both food and faeces, is usually not measured in conventional digestion studies. In other words, the data on food intake in these animals will invariably underestimate their total DMI.

Although some key species are absent from our data collection, such as more grazing non-domesticated ruminants, or more herbivorous primate species, the pattern of BM and digestive anatomy found in our dataset is similar to that observed in other surveys on mammalian herbivory; e.g. Stevens (1998) observed body size ranges for caecum, colon and foregut fermenters principally identical to those of our dataset. Therefore, an under-representation of a certain body size group did not influence the outcome of our study.

4.2.2. Relationship between body mass and dry matter intake

As predicted, this data collection supports the general assumption that aDMI scales to $BM^{0.75}$ in herbivorous mammals. The exponent of the BM–aDMI relationship differed between the different morphophysiological digestive groups in our data set. In caecum fermenters, aDMI scaled to $BM^{0.64}$, which is in between the exponents of 0.62 and 0.71 determined by Glazier (2005) for small and large rodent metabolism, and closer to the allometric exponent of 0.68 determined by White and Seymour (2005) for mammal metabolism if large herbivores are excluded. The lower exponent of the BM–aDMI relationship in caecum fermenters (0.63 vs. 0.75 in other mammals) could thus be indicative of a lesser contribution of the symbiotic gut microflora to the overall metabolic rate of the animals. However, as stated above, DMI data for coprophageous animals must be interpreted with the reservation that the additional dry matter intake of faecal matter is not accounted for. The proportion of faecal matter in the total DMI will vary with the nutritional composition of the diet (Fekete and Bokori, 1985; Zucker and Flurer, 1989), but additional trends with BM can, so far, not be excluded. Should, e.g., the proportion of ingested faeces in the total DMI increase with increasing BM, the comparatively lower allometric exponent of the BM–aDMI relationship found in this study could be explained by this fact as well.

In spite of an allometric exponent of 0.76, the non-ruminating foregut fermenters had a significantly lower DMI than the other three digestion types. Interestingly, this digestion type comprises different herbivores which have been shown to have comparatively low metabolic rates or energy requirements, such as the sloth (McNab, 1978), the colobine monkeys (Ross, 1992), the macropods (McNab, 1986), peccaries (Zervanos and Day, 1977; Comizzoli et al., 1997)⁴ or the hippos (Schwarm et al., 2006). Although this coincidence of a digestion type and a low metabolic rate is suggestive, we do not think that the digestive anatomy of a foregut fermentation system necessitates

a lower metabolic rate. Such a causal relation could be construed if it was assumed that a foregut *in general* represents a factor that limits intake. This could be suggested in hippos (Clauss et al., 2007b), but has, e.g., been suspected to be explicitly *not* the case in macropods (Hume, 1999). Rather, it could be argued that the foregut-fermenting system implies other (yet to be determined) disadvantages that led, in general, to a replacement of hypothetical, foregut-fermenting species by hindgut fermenters with higher metabolic rates (in the sense of a metabolic rate-dependent competition, McNab, 2002), with extant foregut fermenters surviving in niches with little competitive challenge from other organisms (c.f. McNab, 2005) and/or with certain adaptations in lifestyle against predators (Lovegrove, 2001). The ruminants are the marked exception to this hypothetical pattern, with their high diversification and high metabolic rates that are also reflected in their high DMI level in our data collection. It seems that rumination allows the use of a foregut fermentation system at competitively high DMI levels/metabolic rates, and thus ruminants could participate in the evolutionary arms race of increasing running speed that is characteristic of unguligrade mammals (Lovegrove, 2004). Among the ruminating foregut fermenters, the Bactrian camel had a surprisingly low DMI. Although this species has not been investigated with respect to its energy metabolism to our knowledge, a close relative, the dromedary (*Camelus dromedarius*) shows a particularly low metabolic rate in comparative analyses (Williams et al., 2001; Lovegrove, 2004). Thus, the camelids represent species that combine the efficient ruminant digestive physiology with a conservative energy metabolism adapted to extreme habitats.

4.2.3. Relationship between body mass and particle retention

In contrast to the clear allometric relationship found between BM and aDMI in our dataset, there were few clear allometric relationships between BM and MRT. Only within the caecum fermenters did we find a clear allometric scaling relationship of MRT with BM, which was not significantly different from $BM^{0.25}$ (0.25 was included in the 95% confidence interval for the exponent), in accordance with theoretical assumptions (see Introduction). But the 95% confidence interval of the exponent of the BM–MRT relationship included 0 for both the colon and the non-ruminant foregut fermenters, and although it did not include 0 for all ruminant foregut fermenters combined, in separate analyses of the relationship for grazing and browsing ruminantia, respectively, 0 was included in the 95% confidence interval of the exponent in either case. For the ruminantia, this finding complements another data evaluation focussing on forestomach rather than total digestive tract MRT, in which also no significant correlation between BM and the retention parameters could be found (Clauss et al., 2006a). This finding might reflect a general adaptation in mammalian herbivores: above a certain BM range that is represented by mostly caecum fermenters, species can generally achieve MRTs that facilitate an efficient fermentation of plant material. Although comparative data evaluations are scarce, the fact that there is no clear increase in digestive efficiency with increasing BM in ungulates in general (Foote, 1982) or in ruminants in particular (Pérez-

⁴ These authors calculate a digestible energy requirement for peccaries of 340–440 kJ/kg^{0.75}/d, which contrasts to the usually accepted mammalian average of 490–660 kJ/kg^{0.75}/d (Schwarm et al., 2006).

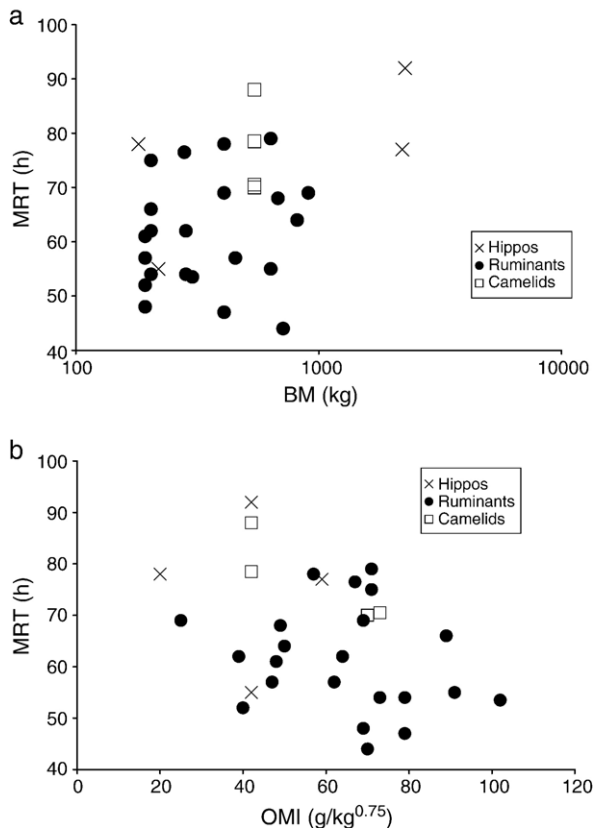


Fig. 8. Data on the mean retention time (MRT) in the total digestive tract of hippopotamidae and ruminant ungulates (camelids, giraffids, bovids and cervids; 2 measurements per species) from Foose (1982). MRT determined by analysing one or two pooled faecal samples per day, plotted against (a) body mass (BM, kg) or (b) relative organic matter intake (OMI, in $\text{g/kg}^{0.75}$).

Barbería et al., 2004) supports the finding that there is no strong correlation between BM and MRT.

Here, a closer look at the nature of the allometric exponent of the BM–MRT relationship is warranted. The concept that herbivore MRT should generally scale to $\text{BM}^{0.25}$ has been backed by an evaluation of empirical data from Warner (1981) and Foose (1982) by Illius and Gordon (1992). As mentioned in the Introduction, the data from Foose (1982), which in itself does not suggest a relationship between BM and MRT (Figs. 1a and 8a), will invariably be higher than data gained under similar conditions but (in ruminants) on the basis of small particle markers and (in all species) more frequent faecal sampling per day.⁵ As the data set of Foose (1982) comprises most of the very large herbivores represented in the data collections of Illius and Gordon (1992), this bias alone will lead to a seeming correlation between BM and MRT. Additionally, these data collections are marked by a paucity of data for the smaller body size ranges, and for hindgut

fermenters, no distinction is made between the caecum and the colon fermenters. According to the findings of our evaluation, combining the data of caecum fermenters with that of any other digestion type will automatically lead to more distinct BM–MRT relationship than if the other digestion type is analysed on its own.

The assumption that MRT scales to $\text{BM}^{0.25}$ has been declared central to digestion models used to explore the respective limitations of herbivory and body size in mammals (Illius and Gordon, 1992; Cork, 1996; Cork et al., 1999). Cork (1996) stated that the version of the digestion model he adapted from Illius and Gordon (1992) was most sensitive to changes in MRT, gut capacity, and energy requirement (a determinant of DMI), but relatively insensitive to the rate of digestion of the diet. This statement has two important implications, which can be addressed on the basis of our findings.

On the one hand, these three parameters were thus identified to be the ones by which evolutionary adaptation might offset the theoretical limits of body size implied by such models. The fact that MRT seems to be basically independent from BM in our study suggests that the leeway for adaptation outlined by those models is actually being used in extant herbivore species. As reviewed in other publications, adaptations on the level of gut capacity (Cork et al., 1999) and basal metabolic rates (McNab, 2002) are also observed that will both contribute to an efficient use of a herbivorous diet. In this respect, the three most extreme outliers of this data collection, the koala, the sloth and the sirenians, are usually named as outstanding examples, combining long ingesta retention (Cork and Warner, 1983; Lomolino and Ewel, 1984; Foley et al., 1995; Lanyon and Marsh, 1995), high to extraordinarily high gut capacity (Cork and Warner, 1983; Langer, 1988; Reynolds and Rommel, 1996) and low basal metabolic rates (McNab, 1978; Degabriele and Dawson, 1979; Gallivan and Best, 1980; Nagy and Martin, 1985; Miculka and Worthy, 1998). Moving the focus from outliers to general patterns, a major difference between the $\text{BM}^{0.25}$ -approach used in these models and the findings of our study lies

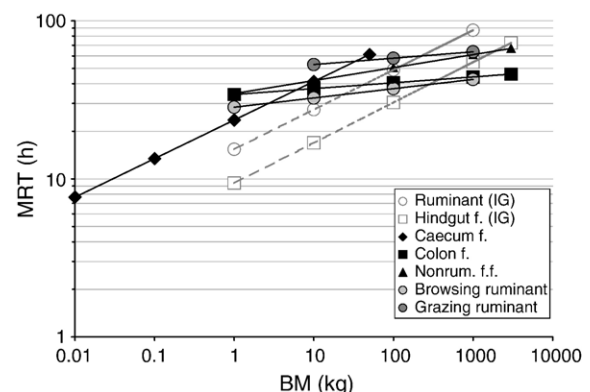


Fig. 9. Theoretical relationships of body mass (BM, kg) and particle mean retention time (MRT, h) in the total gastrointestinal tract in different herbivore groups. IG denotes equations from Illius and Gordon (1992) for ruminants and hindgut fermenters (caecum and colon fermenters combined) (open symbols); equations for caecum fermenters, colon fermenters, non-ruminant foregut fermenters and browsing and grazing ruminants are derived from this study. Note in particular the difference in the increase in MRT between 100 and 1000 kg BM in the IG relationship and those of this study.

⁵ Whether the frequency of faecal sampling per day will have an influence on the MRT as calculated depends on the equation actually used for that calculation (Van Weyenberg, et al., 2006. Passage rate of digesta through the equine gastrointestinal tract: a review. *Livestock Science* 99, 3–12.). The equation used by Foose (1982, p.80) is one demonstrated by Van Weyenberg et al. (2006) to be influenced by sampling frequency, with increasing calculated MRT values as the sampling interval increases. In studies that use a more frequent sampling regime, differences due to different ways of calculation will be minimized.

in the realisation that long MRTs, and hence efficient fibre digestion, occurs at much lower body weights in our dataset than suggested by the $BM^{0.25}$ -relationship (Fig. 9).

On the other hand, a close look at the quantitative implications of the BM–MRT relationships from Illius and Gordon (1992) and those presented in this study are interesting. Assuming an increase in BM from 100 to 1000 kg, the equations based on the 0.25 exponent result in an increase in MRT of 38 h (from 49 to 87 h) for ruminants and 25 h (from 30 to 55 h) for hindgut fermenters (Fig. 9). Regardless of individual outlier species, assuming such an enormous general increase in MRT with BM might not be meaningful in a physiological sense, since the complete fermentation of plant material occurs in *in vitro* studies within 30–50 h already (Hummel et al., 2006). In other words, it is difficult to conceive of a plant material that is of such a low quality as to make such drastic increases in MRT adaptive. Only if an increase in ingesta particle size with increasing BM could be demonstrated, with a correlating increase in the time necessary for fermentation, could such drastic increases in MRT be assumed to be adaptive; however, an according investigation in herbivores is still lacking (Clauss and Hummel, 2005). Given the assumption of such enormous MRTs in a general model, the statement recorded above that these models are relatively insensitive to changes in the assumed digestion rate of the forage become understandable. However, such a statement is at severe odds with well-recorded observations that different species feed in a selective manner, and that even so-called large unselective feeders as the giraffe or the buffaloes (c.f. Fig. 3.2 in Van Soest, 1994) have been shown to practice a certain degree of selectivity when feeding rather than indiscriminately ingesting whatever plant they come across (even if the supposed rules behind this selection have hardly been described in empirical, quantitative terms). When data for the fermentation characteristics of a certain group of forage are evaluated (e.g. Hummel et al., 2006), differences in MRT of the scope of several hours would be expected between animals selecting the less fibrous portions of these forages as compared to animals ingesting these forages less selectively. The increase in MRT between 100 and 1000 kg BM according to the non-significant allometric equations derived in this study are 4 h (from 41 to 44) for colon fermenters, 11 h (from 61 to 67) for non-ruminant foregut fermenters, 5 h (from 37 to 43) for browsing ruminants and 6 h (from 58 to 64) for grazing ruminants. Thus, the numerical increase in MRT according to the non-significant allometric relationships found in this study are of a scope that would explain both the fact that larger animals can ingest forage of a lower quality, and that they nevertheless cannot generally completely neglect the quality of their food. This scope of allometric MRT increase with BM has such a low exponent (between 0.04 and 0.08) that any attempt to prove its existence in statistical terms with data collected from different sources appears unlikely to be successful, and one would assume that a large number of very controlled MRT studies would have to be performed in order to exclude 0 from the 95% confidence interval.

Thus, the relationships between BM and MRT allow different conclusions from this dataset. We propose that, once the threshold limiting herbivores to the strategy of caecum fermentation has been surpassed, large body size does not

automatically imply a fundamental digestive advantage, because long MRTs do not seem to be a characteristic of very large species only; any potential advantage of large body size will be found in the fact that it allows the combination of a standard to extended MRT– and an according digestive efficiency– with other advantages, e.g. large home range sizes, predator avoidance, fasting endurance, resource competition, extended longevity, improved thermal efficiency, etc. (Hone and Benton, 2005). In contrast, the confounding MRT– $BM^{0.25}$ relationship was confirmed in our data collection for the caecum fermenters. Predictions about the evolution of *small* body size based on the models mentioned above may therefore be accurate. This general approach of looking at different groups, defined by their functional morphology and its evolutionary history, has recently been advocated for other physiological characteristics as well such as basal metabolic rate and locomotor mode (Lovegrove, 2000; Lovegrove and Haines, 2004).

Another argument to support a supposed allometric scaling of MRT to $BM^{0.25}$ is one of analogy; many other time-related biological variables show this scaling characteristic, as demonstrated e.g. by Peters (1983) or Calder (1984). However, we think that the fact that the MRT–BM relationship in larger herbivores does *not* follow this pattern, although gut capacity scales to BM^1 and aDMI scales to $BM^{0.75}$, is the most remarkable finding of our investigation. A parsimonious explanation for this discrepancy between theory and measured values is the influence of the morphophysiological adaptations displayed by the different herbivore species. Yet to be defined morphophysiological adaptations dissociate the BM–MRT relationship in larger mammals and make MRT an outstanding, non-scaling parameter. This finding does not *per se* exclude any potential allometric scaling relationships observed within certain species or groups of species; and we want to emphasize that the non-significant, but biologically relevant increase of MRT with BM in larger species should not be neglected for statistical reasons only. However, the results suggest that explanation models for the evolution of *large* body size based on supposed allometric relationships between BM and MRT (and hence digestibility) may not be exhaustive, but that the particular morphophysiological adaptations of the digestive tract of individual species or group of species must be considered.

The ingesta retention times of caecum fermenters represent a particular case among herbivorous mammals, because the values measured are the result of a repeated passage through the gastrointestinal tract, facilitated by coprophagy (Clauss et al., 2007a). The recycling of non-fibre material (especially nitrogen in the form of bacterial protein) might be an important reason why overall dry matter digestibility in caecum fermenters is not lower than in larger herbivores regardless of a comparatively lower fibre digestion (Clauss and Hummel, 2005). In small caecum fermenters, MRTs necessary for effective fibre fermentation might be difficult to achieve even with coprophagic recycling. The fact that the strategy of caecum fermentation/coprophagy is not continued above a BM threshold that seems to allow MRTs that are sufficient for efficient fibre fermentation could be an indication of potential disadvantages of coprophagy, such as the auto-infestation with endoparasites. Clauss and

Hummel (2005) suggested that with increasing body size, a shift in digestive strategy occurs from a low efficiency of fibre digestion, compensated by reduced metabolic losses (via coprophagy), towards a higher efficiency of fibre digestion that no longer needs to be compensated for by reduced metabolic losses. However, comparative studies on the metabolic losses of mammalian herbivores are lacking. Whether the absence of large caecum fermenters really indicates a fundamental, adaptive disadvantage of this digestion type remains to be demonstrated. In a similar, more definite way, another morphophysiological characteristic, the plantigrade locomotor mode, has been shown to represent a constraint on potential body size increase in mammals (Lovegrove, 2004; Lovegrove and Haines, 2004). A clear definition of caecum versus colon fermenters might be difficult; in terms of the scenario outlined above, the most useful distinction would be between species that do and do not practice coprophagy. However, as coprophagy can be regarded as a facultative strategy that need not be applied under all dietary conditions to the same extent (Fekete and Bokori, 1985; Zucker and Flurer, 1989), such a distinction may be hard to come by.

4.2.4. Relationship between relative dry matter intake and particle retention

The assumption that MRT decreases with increasing rDMI is an integral part of digestion theories, including those that model animal gut as chemical reactors (Sibly, 1981; Penry and Jumars, 1987; Jumars and Martinez del Rio, 1999; McWorther, 2005). In the interspecific comparisons in our data collection, this relationship was not as clear-cut as we had predicted based on the analysis of the findings of Foose (1982, c.f. Fig. 1b). As in the data of Foose (1982, Fig. 1b and 8b), only for the group of the colon fermenters did the interspecific rDMI–MRT relationship have distinctively higher explanatory power ($r^2=0.53$; excluding the dugong) than the BM–MRT relationship ($r^2=0.04$; excluding the dugong). In the data scatter, certain trends can be delineated: The slopes of the interspecific rDMI–MRT relationships of caecum fermenters (excluding the koala) and the colon fermenters (excluding the dugong) are similar, with little overlap between the two data clouds (Fig. 6). In addition, the slope of the non-ruminant foregut fermenters (excluding the sloth, including or excluding the hippos) is of similar scope as well: whereas the intercept (the hypothetical MRT at zero intake) is higher in colon fermenters (64 h, without the dugong) than in non-ruminant foregut fermenters (56 h without the sloth, 51 h without sloth and hippos) and in caecum fermenters (48 h without the koala), the slope of the respective regressions is -0.35 (colon fermenters without dugong), -0.40 or -0.35 (non-ruminant foregut fermenters without sloth and without sloth and hippo, respectively) and -0.46 (caecum fermenters without koala), indicating that on an interspecific level, the DMI–MRT pattern is relatively similar. If we assume these characteristics (intercept and slope) to be fixed determinants of the respective digestion types, then a calculation of the effect of a doubling of DMI on MRT shows that a DMI limit due to the accelerating effect on MRT is reached earlier in the caecum fermenters than in the non-ruminant foregut fermenters, and at even higher intakes in the colon fermenters (Fig. 10).

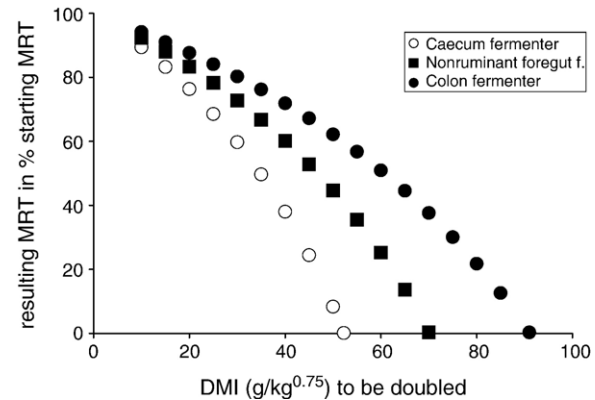


Fig. 10. Theoretical model of the percentage of the mean retention time (MRT), which results if dry matter intake (DMI, $\text{g/kg}^{0.75}$ per day) is doubled, from the MRT on the original DMI. Note that for any reduction step that might still be considered feasible, colon fermenters can operate at higher DMIs.

This could be an additional explanation why the colon fermenting strategy might be particularly favourable for very large herbivores that have to be adapted to very high food intakes (Clauss et al., 2003a, 2007b). As stated above, it must be remembered that for the coprophageous caecum fermenters, the actual DMI is underestimated if only data on food intake is used, as in our collection; however, the DMI–MRT-regression line of the caecum fermenters would only match the one of the colon fermenters if an additional faeces DMI of the same quantity as the food DMI was assumed, which can obviously be considered impossible.

Why there is, in contrast, no discernible relationship between DMI and MRT in the ruminants, remains a puzzling question. The similarity of the results of this study and those of Foose (1982), however, with no evident relationship between BM and MRT (Fig. 8a) and food intake and MRT (Fig. 8b), suggests that across ruminant species, the radiation of digestive adaptations has led to the disappearance of a clear interspecific pattern; in other words, ruminants have, as a group, achieved relative independence from both BM and DMI in terms of MRT and, probably, digestive efficiency. The rumen physiology, with its intricate particle retention mechanism, seems to offer the potential for effective forage digestion at varying levels of body size and food intake. On an intraspecific level, in contrast, clear DMI–MRT-relationships can be found in individual ruminant species as well (Clauss et al., 2007b).

5. Conclusions and outlook

This review rejects the traditional concept of generally increasing MRT with increasing BM and gives examples on potential differences in digestive strategies between different herbivore groups. Derived hypotheses on differences between digestive groups (with different fermentation sites and rumination), however, must be evaluated by phylogenetically controlled statistics. While digestive constraints in connection with MRTs might be responsible for the lower BM limit for herbivory, digestive advantages connected with long MRTs alone cannot be

considered to be the major evolutionary payoff of large body size (c.f. Bjørndal and Bolten, 1992). In a similar manner, other factors that have been cited as potential evolutionary drivers of body size increase, such as maximum running speed or fasting endurance, have been shown to be not consistently correlated to BM (Dunbrack and Ramsay, 1993; Lovegrove, 2004).

The lack of coherent associations between relative DMI and MRT, in the overall data set of this study, is probably partly due to the fact that animals of many different herbivorous feeding strategies – in terms of botanical and chemical composition of the diet – are lumped together, and that the experimental diets used were highly variable. More investigations among particular feeding groups (not only within the ruminants, but also in other groups such as primates or rodents) are likely to yield more consistent results. In this respect, the investigation of ingesta retention in more species should be linked with experimental setups that investigate the effect of food intake level and dietary parameters on MRT. It is in the comparison of these effects between species of digestive groups that revealing insights are to be expected. Karasov and McWilliams (2005) state that the magnitude of spare capacity of the digestive system is a key to understanding the evolutionary adaptations of mammals to varying ecological food niches. An important measure of this spare capacity is the DMI-MRT relationship, i.e. the answer to the question to what extent MRT is decreased by increasing DMI (Clauss et al., 2007b). MRT should always be considered in connection with DMI, and conclusions regarding any DMI-independent effect, e.g. of fibre level on MRT, must be validated by an experimental setup where fibre level is manipulated but DMI kept constant. In studies quantifying also digestibility (besides intake and MRT), it will be interesting to evaluate the influence of the indigestible fraction of DMI on MRT separately.

In particular, the digestive trade-offs of strategies including or excluding coprophagy will be revealing for the influence of BM on digestion. The quantification of the proportion of DMI that constitutes re-ingested faeces (coprophagy), and potential correlations not only with food quality but also BM, is a major challenge for future digestion studies. This work suggests that the body size range in which caecum fermenters and other digestion types overlap promises most insights into the trade-offs associated with herbivory and body size.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, doi:10.1016/j.cbpa.2007.05.024.

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