Assessing the Jarman–Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores

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ABSTRACT

Differences in allometric scaling of physiological characters have the appeal to explain species diversification and niche differentiation along a body mass (BM) gradient — because they lead to different combinations of physiological properties, and thus may facilitate different adaptive strategies. An important argument in physiological ecology is built on the allometries of gut fill (assumed to scale to $BM^{1.0}$) and energy requirements/intake (assumed to scale to $BM^{0.75}$) in mammalian herbivores. From the difference in exponents, it has been postulated that the mean retention time (MRT) of digesta should scale to $BM^{1.0-0.75} = BM^{0.25}$. This has been used to argue that larger animals have an advantage in digestive efficiency and hence can tolerate lower-quality diets. However, empirical data does not support the $BM^{0.25}$ scaling of MRT, and the deduction of MRT scaling implies, according to physical principles, no scaling of digestibility; basing assumptions on digestive efficiency on the thus-derived MRT scaling amounts to circular reasoning. An alternative explanation considers a higher scaling exponent for food intake than for metabolism, allowing larger animals to eat more of a lower quality food without having to increase digestive efficiency; to date, this concept has only been explored in ruminants. Here, using data for 77 species in which intake, digestibility and MRT were measured (allowing the calculation of the dry matter gut contents (DMC)), we show that the unexpected shallow scaling of MRT is common in herbivores and may result from deviations of other scaling exponents from expectations. Notably, DMC have a lower scaling exponent than 1.0, and the 95% confidence intervals of the scaling exponents for intake and DMC generally overlap. Differences in the scaling of wet gut contents and dry matter gut contents confirm a previous finding that the dry matter concentration of gut contents decreases with body mass, possibly compensating for the less favorable volume–surface ratio in the guts of larger organisms. These findings suggest that traditional explanations for herbivore niche differentiation along a BM gradient should not be based on allometries of digestive physiology. In contrast, they support the recent interpretation that larger species can tolerate lower-quality diets because their intake has a higher allometric scaling than their basal metabolism, allowing them to eat relatively more of a lower quality food without having to increase digestive efficiency.

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1. Introduction

1.1. The Jarman–Bell Principle

The scaling relationships of digestive features with body mass (BM) in herbivores are a fundamental part of our interpretation of herbivore feeding ecology, interspecific niche differentiation and intraspecific niche segregation due to sexual dimorphism. Geist (1974) explained how two PhD studies, which resulted in two publications (Bell, 1971; Jarman, 1974), crystallized an understanding of the ways in which BM affects the ecology of ungulates of the African savannahs. These studies have become the springboard for most analyses of mammal herbivore ecological interactions that include a range of BM (du Toit, 2005). The so-called 'Jarman–Bell Principle' (JBP) (Geist, 1974) has been applied to other animal groups such as primates (Gaulin, 1979), fruit bats (Fleming, 1991) or baleen whales (Tershy, 1992), and predicts that BM constrains nutritional ecology

— in terms of the diet quality that larger animals can or must tolerate, as well as their digestive efficiency. That larger animals commonly ingest diets of lower quality has been demonstrated repeatedly (e.g. Owen-Smith, 1988; Codron et al., 2007), and that they often must tolerate poor-quality foods is usually not an issue of debate. This is considered a consequence of large animals' higher absolute food requirements that prevent them from foraging selectively in terms of time constraints, and also a consequence of larger, more 'clumsy' feeding apparatus that again prevents them from foraging selectively in terms of picking out individual food items or plant parts (Owen-Smith, 1988; Shipley, 2007).

A fact often used to explain the increased dietary tolerance (measured as the range in fiber and/or protein content of the diet the animal can tolerate) of larger species is the decreased mass-specific metabolic demands — because the daily requirements for energy (Nagy et al., 1999), nitrogen (Robbins, 1993) and even minerals (Rucker and Storms, 2002) scale to metabolic body mass ($BM^{0.75}$). This scaling effect means that small-bodied species require more energy and nutrients per day and per unit of BM than do large-bodied forms (Geist, 1974). However, without information about the scaling of energy/nutrient intake, knowledge about the scaling of requirements allows no further insight. Concepts about niche diversification along a BM gradient must make an assumption about the difference in scaling between requirement and intake. Given that larger animals ingest lower-quality diets, a similar scaling of intake and requirements would make it necessary that digestive efficiency has a positive scaling, i.e. it should increase with BM. This could be achieved either by selecting a more digestible diet (which violates the assumption of decreasing diet quality), or by measures of digestive physiology that increase digestive efficiency, such as prolonged digesta retention. In contrast, if we postulate that there is no scaling of digestive efficiency with BM, then intake would have to scale to BM at a higher exponent than requirements, in order to compensate for the lower diet quality in larger animals. Historically, the JBP has more often been linked to variation in digestive efficiency than to variation in intake levels.

When developing this approach of the JBP, food intake was, without empirical testing, assumed to scale to body mass in a similar way as animal metabolism (explicitly in Demment, 1983; implicitly in Demment and Van Soest, 1985; note that Van Soest, 1994 does not make an explicit assumption about intake scaling but rests his argument on the scaling of gut fill only). In large datasets, food intake (measured as dry matter intake, DMI, or as gross energy intake) was actually often found to scale to $BM^{0.75}$ across a wide range of mammalian species (reviewed in Clauss et al., 2007a; Meyer et al., 2010), and thus resembles the scaling of metabolism and requirements. Therefore, the approach that focuses on scaling effects on digestive physiology appears as the logical next step. Including gut fill in these considerations has extended the JBP to specifically comprise not only metabolic scaling, but also digestive physiology. Gut fill (measured as wet matter content, WMC) or dry matter content (DMC) has been suggested to be a constant fraction of BM in herbivores (Parra, 1978; Demment and Van Soest, 1985; Illius and Gordon, 1992; Justice and Smith, 1992; Clauss et al., 2007a). If gut fill actually scales to $BM^{1.00}$, and food intake scales to $BM^{0.75}$, these different scaling effects result in a larger gut fill per unit food intake with increasing BM. This should in theory lead to an increase in the time digesta is retained in the gastrointestinal tract (measured as mean retention time, MRT) with increasing BM (Demment and Van Soest, 1985; Illius and Gordon, 1992; Robbins, 1993; McNab, 2002). Explicitly, it is thought that MRT should scale to $BM^{(1.00-0.75)} = BM^{0.25}$. Because MRT is positively linked to the digestive efficiency of a herbivore (Foose, 1982; Udén and Van Soest, 1982; Clauss et al., 2007b), this concept has been invoked to postulate that larger herbivores can use food of a lower quality *due to a hypothetical capacity for more efficient digestion* (Demment and Van Soest, 1985; Illius and Gordon, 1992; Gordon and Illius, 1996). In this way, the JBP delivers an elegant explanation (higher digestive efficiency in larger animals) for a common observation (lower

diet quality in larger animals), and represents what may be the most prominent set of allometric considerations in large animal ecology, including theoretical approaches to understanding intraspecific size dimorphism (Short, 1963; Prins and Geelen, 1971; Sinclair, 1977; Hanley and Hanley, 1980; Hanley, 1982; Barboza and Bowyer, 2000; du Toit, 2005; Shannon et al., 2006; Woolley et al., 2011).

Empirical evidence for the physiological predictions of the JBP, however, is scarce. While the findings that wet gut contents scale to $BM^{1.00}$ and food intake scales to $BM^{0.75}$ are mostly undisputed, digesta retention has repeatedly been shown, in various datasets, *not* to scale to $BM^{0.25}$ (Clauss et al., 2007a, 2009; Franz et al., 2011a; Müller et al., 2011; Steuer et al., 2011), with the exception of mammalian caecum fermenters (Clauss et al., 2007a, but see the results of phylogenetically informed statistics in this study down below). Additionally, there is little indication for an increase in digestive efficiency with BM (Justice and Smith, 1992; Wenninger and Shipley, 2000; Pérez-Barbería et al., 2004; Clauss et al., 2009; Steuer et al., in press). These findings represent a serious conceptual problem for herbivore digestive physiology, because the link between gut fill, food intake and digesta retention is mathematically sound.

1.2. Linking digesta retention to gut capacity, food intake and digestibility

Holleman and White (1989) provided the underlying equation to this problem, based on the 'Stewart–Hamilton Principle' or the 'Occupancy Principle' (Steele, 1971; Shipley and Clark, 1972), where

$$\text{indDMC } [\text{kg}] = \text{fecal output } [\text{kg/h}] * \text{MRT}_{\text{particle}}\text{GIT } [\text{h}] \qquad (1)$$

with indDMC being the indigestible (or undigested) DM content of the whole gastrointestinal tract (GIT), and $\text{MRT}_{\text{particle}}\text{GIT}$ the mean retention time of an indigestible particle marker in the whole GIT. Because fecal output is a function of food intake (measured as dry matter intake DMI) and apparent digestibility of dry matter (aD DM) or, in other terms, DMI and the apparent indigestibility of DM (aID DM), we get

$$\text{fecal output } [\text{kg/h}] = \text{DMI } [\text{kg/h}] * (\text{aID DM}) \qquad (2)$$

and thus gut fill, food intake and retention time are closely linked as

$$\text{indDMC } [\text{kg}] = \text{DMI } [\text{kg/h}] * \text{aID DM} * \text{MRT}_{\text{particle}}\text{GIT } [\text{h}]. \qquad (3)$$

Solving this equation for MRT yields

$$\text{MRT}_{\text{particle}}\text{GIT } [\text{h}] = \text{indDMC } [\text{kg}]/(\text{DMI } [\text{kg/h}] * \text{aID DM}). \qquad (4)$$

Assuming scaling laws for indDMC, DMI and aID DM with body mass with the exponents a, b and c, respectively, it follows that

$$\text{MRT}_{\text{particle}}\text{GIT} \sim BM^a/\left(BM^b * BM^c\right) \text{ or } \text{MRT}_{\text{particle}}\text{GIT} \sim BM^{a-(b+c)}. \qquad (5)$$

Under the assumption that indDMC scales as does wet matter contents, i.e. to $BM^{1.00}$, and DMI scales to $BM^{0.75}$, we can thus assume that $\text{MRT}_{\text{particle}}\text{GIT}$ should scale to $BM^{0.25}$ *if digestive efficiency does not change with BM*. Note that an increase in digestibility with increasing BM (i.e., a decrease in indigestibility, or a negative exponent c) would lead to a higher scaling exponent for $\text{MRT}_{\text{particle}}\text{GIT}$, and a decrease in digestibility with increasing BM would lead to a lower scaling exponent for $\text{MRT}_{\text{particle}}\text{GIT}$. This is because a lower digestibility would result in more material in the GIT that is pushed along due to the continuous food intake, and hence make any particular portion of the indigestible digesta be excreted relatively sooner (Hummel and Clauss, 2011).

The calculation of gut fill can be expanded to include not only indigestible gut fill, but also total gut fill (dry matter contents (DMC)) (Holleman and White, 1989). For that, the digestible portion of DMC

(dDMC) has to be added to indDMC. To do so, one has to make an assumption regarding the course of digestion. If one assumes digestion to be exponential over MRT (with most of digestion occurring at the beginning of MRT and slowly 'fading out'), then the estimated dDMC in the total GIT will be less than if one assumes digestion to be linear across MRT. Holleman and White (1989) and Munn et al. (2012) showed that assuming a linear course of digestion across MRT yields better results when validated against empirical measures in slaughtered animals, albeit using small sample sizes. Because assuming a linear course of digestion across MRT means that dDMC is assumed to be present in the GIT during half of MRT, it follows that

$$\text{dDMC [kg]} = \text{DMI [kg/h]} * \text{aD DM} * \left(\text{MRT}_{\text{particle}}\text{GIT [h]}/2\right). \quad (6)$$

Combining Eqs. (3) and (6) to calculate total DMC yields,

$$\text{DMC [kg]} = \text{DMI [kg/h]} * \text{MRT}_{\text{particle}}\text{GIT [h]} * (\text{aID DM} + 0.5 \text{ aD DM}). \quad (7)$$

Solving the equation for $\text{MRT}_{\text{particle}}\text{GIT [h]}$ yields

$$\text{MRT}_{\text{particle}}\text{GIT [h]} = \text{DMC [kg]}/\text{DMI [kg/h]} * (1/(\text{aID DM} + 0.5 \text{ aD DM})). \quad (8)$$

Assuming scaling laws for DMC, DMI and aD DM with body mass with the exponents d, b and c, respectively, it follows that

$$\text{MRT}_{\text{particle}}\text{GIT} \sim \text{BM}^d/\text{BM}^b * (1/(\text{BM}^{-c} + 0.5 \text{ BM}^c)) \text{ or} \quad (9)$$
$$\text{MRT}_{\text{particle}}\text{GIT} \sim \text{BM}^{d-b+c}.$$

Assuming that DMC scales similar as wet matter contents, i.e. to $\text{BM}^{1.00}$, and DMI scales to $\text{BM}^{0.75}$, we can thus again assume that $\text{MRT}_{\text{particle}}\text{GIT}$ should scale to $\text{BM}^{0.25}$ *if digestive efficiency does not change with BM*. Note that again, an increase in digestibility with BM (i.e., a positive c) would lead to a higher scaling exponent for $\text{MRT}_{\text{particle}}\text{GIT}$, and a decrease in digestibility with BM would lead to a lower scaling exponent for $\text{MRT}_{\text{particle}}\text{GIT}$. One important conclusion from these derivations is that if one uses the scaling of intake and gut fill to make any conclusions about digesta retention, one must not use the result to make inferences about digestive efficiency — because an assumption about the scaling of digestibility is made already (explicitly or implicitly) to derive the scaling of digesta retention. Deriving a scaling for digesta retention in this way and then using it to explain a pattern of digestive efficiency with body mass amounts to circular reasoning.

1.3. Re-assessing data from herbivore feeding trials

Given these considerations, a discrepancy in the scaling of gut contents, food intake, and digesta retention, as indicated by empirical data, warrants a re-assessment of both empirical datasets and, potentially, a revision of our understanding of herbivore digestive allometry. An intuitive reason for this discrepancy might be that whereas it is common practice to measure both food intake and digesta retention in the same experiment, gut fill is usually not measured simultaneously, as most experiments do not include the dissection of the experimental animals. The discrepancy of the scaling exponents therefore might simply result from the fact that different datasets have been used to generate these allometries (Clauss et al., 2007a); nevertheless, the discrepancy requires further explanation. If in addition to measures of food intake and digesta retention, the apparent digestibility of dry matter is also measured in the same feeding trial, the derivation of indigestible and complete gut fill (as DMC) as indicated in the equations above is possible. Although this has been done repeatedly in individual studies to compare selected species, or make intraspecific or inter-clade comparisons (Baker and Hobbs, 1987; Gross et al., 1996; Behrend et al., 2004; Munn and Dawson, 2006; Munn and Barboza, 2008; Schwarm et al., 2009a; Clauss et al., 2010b; Franz et al., 2011b; Sawada et al., 2011; Fritz et al., 2012; Munn et al., 2012), a large-scale comparison of mammalian herbivore gut fill has not been performed so far. Therefore, it was the aim of this study to explore the scaling of food intake, digesta retention, apparent digestibility and the calculated gut fill in mammalian herbivores, using available literature data. Because these variables are used to calculate gut fill according to the principles outlined above, we expected that their scaling relationships also follow these principles.

The following hypotheses guided our investigation:

(i) Across the whole mammal body size range, food intake measured as dry matter intake (DMI) has a scaling exponent close to $\text{BM}^{0.75}$ (reviewed in Clauss et al., 2007a).

(ii) Apparent digestibility generally does not scale with body mass (i.e. to $\text{BM}^{0.00}$) (Justice and Smith, 1992; Wenninger and Shipley, 2000; Pérez-Barbería et al., 2004; Clauss et al., 2009; Steuer et al., in press), and therefore the scaling exponents of gut fill (BM^a), food intake (BM^b) and digesta retention (BM^d) are associated according to $d = a − b$. It should be noted, however, that any conclusions concerning the apparent digestibility must be considered in the context of the food sources that were used across experiments. When collating data for a large variety of species from the literature, as we do here, it is highly likely that data on smaller species, which are often kept on artificial feeds for experimental purposes, is combined with data on larger species, which are more often kept on roughage-only diets that are generally less digestible. Thus, a putative negative allometry of digestibility (a decrease with body mass) would be an indication of this uneven distribution of diet quality. How close this potential decrease in diet quality with body size in the dataset actually might resemble the general decrease of diet quality with body size that is supposed to occur in the wild is difficult to judge. Therefore, if scaling is detected between body mass and digestibility, then the scaling exponents of gut fill (BM^a), food intake (BM^b), digestibility (BM^c) and digesta retention (BM^d) are associated according to $d = a − b + c$.

(iii) The low empirical overall scaling exponent for digesta retention (Clauss et al., 2007a, 2009; Müller et al., 2011; Steuer et al., 2011) results from the fact that gut fill, measured as dry matter contents (DMC), does *not* scale to $\text{BM}^{1.00}$ but to a lower exponent.

(iv) In parallel to observations on the scaling of mammalian basal metabolic rate (BMR) that does not follow a single exponent across the whole BM range (Clarke et al., 2010; Isaac and Carbone, 2010; Kolokotrones et al., 2010; Müller et al., 2012), we expect that DMI also does not follow one single exponent across the whole BM range. In fact, variation in the scaling of DMI across the BM range could be responsible for the observation that digesta retention scales differently in different digestion types, which are distributed unevenly across the BM range (Clauss et al., 2007a). In accord with Packard (2012), we do not follow the argument that a curvature (or 'quadratic scaling') in double-logarithmic space represents a true mechanistic pattern (Kolokotrones et al., 2010), but assume that it is the effect of combined simple scaling patterns in the overall dataset and can be used as a test for such scaling combinations (Müller et al., 2012). A test for such a curvature effect is then followed by analysis of scaling patterns within subsets of the data. In particular, following the dichotomy in metabolism scaling between animals with one and with more than one offspring per litter (Müller et al., 2012), we expect that food intake has a lower scaling exponent in herbivores that represent the majority of the lower BM range (especially caecum fermenters), and a higher scaling exponent in herbivores that represent the majority of

the higher BM range (i.e. non-coprophageous hindgut fermenters, nonruminant foregut fermenters and ruminants), resulting in a typical curvature shape in double-logarithmic space, or when plotting body mass-residuals of DMI against body mass. An important question when assessing the individual scaling relationships of intake in different groups will be whether the scaling exponent is similar to that of metabolism, or whether it is actually higher (Hackmann and Spain, 2010).

(v) Differences in the scaling of wet matter gut contents (WMC) and dry matter gut contents (DMC) with BM reflect the finding of Justice and Smith (1992) that larger animals have a higher digesta moisture content; when using the WMC and DMC allometries to calculate the allometry of the dry matter concentration of the GIT contents, the result should be close to that of Justice and Smith (1992) where DM concentration in the contents of the fermentation chamber scales to $22 \, BM^{-0.08}$.

(vi) Species with a relatively higher food intake have a relatively shorter retention time (Clauss et al., 2007a; Müller et al., 2011). Based on Eq. (6), this could in theory lead to relatively lower calculated dry matter gut contents. On the other hand, higher food intake itself should lead to higher calculated gut contents based on the same equation (Eq. (6)). We aim to characterize these interdependencies in our analysis. A longer relative retention time should be related to a higher relative digestibility (Udén et al., 1982; Clauss et al., 2007b).

Because one of the largest existing datasets on the digestive physiology of large herbivores (Foose, 1982) is basically incompatible with other published data (Clauss et al., 2007a, 2010b), we performed the same analyses for both the Foose (1982) dataset and an independent collation of literature data. With the limitation that the Foose (1982) dataset comprises only comparatively large species, this allows a corroboration of results from one dataset with the other.

2. Methods

The datasets used in this study are

a) Foose (1982), comprising 26 species of large (>100 kg) herbivores from the Artiodactyla, Perissodactyla and Proboscidea, which received two standardized diets (grass and lucerne hay); in this dataset, the unit of reference is organic matter rather than dry matter; and

b) the data collation of Clauss et al. (2007a) that was supplemented with additional sources, and pruned according to the following selection criteria. Only sources were used which gave body mass (BM), dry matter intake (DMI), particle mean retention time in the whole gastrointestinal tract ($MRT_{particle}GIT$,) and the apparent digestibility of dry matter (aD DM) from the same experiment (in some cases, this information had to be collected from several publications reporting on the same experiment). From these data, dry matter content (DMC) of the GIT was calculated as outlined in the Introduction. 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 in which small particles (generally <2 mm; as opposed to whole forages) were labeled were included. 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. Ideally, a data collection with a standardized diet (such as in Foose, 1982; Steuer et al., 2011, in press) or with diets representing the natural diets of the species would be preferable, but are not available at a larger scale and over a wide body mass range. With regard 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 in which coprophagy was not prevented by the study design were used. For each species, one average value for BM, DMI, $MRT_{particle}GIT$, aD DM and DMC was calculated using all available data from the cited publications. The data for the resulting 77 mammalian species and its sources are summarized in the Appendix.

c) To compare the relationship of wet matter contents (WMC) of the GIT with the dry matter contents, the data collection on WMC collated in Clauss et al. (2007a; n = 72 species) was used.

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). Additionally, species were allocated to litter size classes (one or more than one offspring per litter) (Müller et al., 2012) and body size classes (<10 kg, >10 kg). In order to account for ancestry-biased correlations in the datasets (i.e., significant associations in interspecific datasets might be due to the fact that phylogenetically related species exhibit similar eco-physiological traits; Harvey and Pagel, 1991), the data were 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 as error term in a generalized least squares algorithm to determine the model parameters. The phylogenetic trees for the two datasets were derived by pruning the mammal supertree from Bininda-Emonds et al. (2007, 2008) of those species not represented in the datasets.

Allometric regressions were performed as linear regressions on log-transformed data, with digestive parameters (DMI, $MRT_{particle}GIT$, aD DM, DMC) as the respective dependent variables, and with log-transformed BM as the independent variable. Tests for a 'curvature' in double-logarithmic space were made using quadratic regressions. Statistical analyses were performed without (ordinary least squares regressions: OLS) and with accounting for phylogeny (PGLS), in PASW 18.0 (SPSS Inc., Chicago, IL) and in *R* 2.15.0 (Team, 2011) with the ape and caper packages. The significance level was set to α = 0.05.

3. Results

3.1. Foose (1982) dataset

Variables scaled as: food intake (as organic matter intake, OMI) with $BM^{0.76}$, apparent digestibility (of organic matter) with $BM^{0.02}$, organic matter gut contents (OMC) with $BM^{0.82}$, and digesta retention with $BM^{0.07}$, which matches the predicted relationships of $0.07 \sim [0.82 - 0.76 + 0.02]$ (Table 1). Notably, the 95% confidence interval for the scaling of OMC did not include 1.00 (Table 1). Results were similar in PGLS. Similar patterns were evident within the hindgut fermenters and the ruminants only (Table 1). Both digesta retention and gut fill had a scaling exponent lower than expected.

Within the body mass residuals, intake was negatively correlated with digesta retention in the whole dataset in OLS but not in PGLS (Table 2), indicating that certain taxonomic groups (notably the ruminants) did not follow this pattern (Fig. 1a). Intake was positively correlated with gut fill in both OLS and PGLS (Table 2, Fig. 1b). There was a positive correlation between digesta retention and digestibility in OLS but not in PGLS (Table 2), because these two residuals showed a clear dichotomy between ruminants and colon fermenters (Fig. 1c). Digesta retention was not correlated with gut fill in OLS but it was in PGLS (Table 2), indicating that the relationship only existed within more closely related groups (Fig. 1d).

3.2. Our dataset

Variables scaled as: food intake (as dry matter intake, DMI) with $BM^{0.76}$ (Fig. 2a), apparent digestibility (of dry matter, aD DM) with

Table 1
Scaling relationships of parameters of digestive physiology with body mass (BM) in the Foose (1982) dataset using OLS and PGLS statistics according to $y = a\,BM^b$.

y	Stats	a	95%CI	b	95%CI	r^2	p
All species (n = 26)							
OMI	OLS	0.064	0.027–0.153	0.759	0.621–0.897	0.843	<0.001
aDOM		53.6	40.6–70.6	0.015	−0.029–0.059	0.020	0.494
OMC		0.074	0.038–0.147	0.819	0.710–0.927	0.910	<0.001
MRT		38.2	22.2–65.6	0.065	−0.020–0.151	0.094	0.128
OMI	PGLS	0.052	0.024–0.114	0.792	0.690–0.895	0.905	<0.001
aDOM		45.7	34.7–60.2	0.033	−0.004–0.069	0.115	0.062
OMC		0.063	0.025–0.161	0.842	0.719–0.964	0.883	<0.001
MRT		37.3	21.6–64.5	0.062	−0.010–0.134	0.107	0.075
Hindgut fermenter (n = 11)							
OMI	OLS	0.097	0.034–0.281	0.726	0.564–0.888	0.920	<0.001
aDOM		46.5	36.1–59.7	0.024	−0.015–0.062	0.180	0.194
OMC		0.085	0.037–0.196	0.809	0.681–0.937	0.958	<0.001
MRT		27.1	16.9–43.6	0.092	0.019–0.164	0.477	0.019
OMI	PGLS	0.083	0.029–0.242	0.748	0.597–0.899	0.913	<0.001
aDOM		37.1	26.9–51.3	0.054	0.008–0.099	0.375	0.029
OMC		0.074	0.026–0.208	0.824	0.679–0.970	0.932	<0.001
MRT		25.2	14.9–42.8	0.098	0.023–0.172	0.425	0.017
Ruminant (n = 13)							
OMI	OLS	0.104	0.029–0.372	0.664	0.452–0.875	0.813	<0.001
aDOM		52.1	33.8–80.2	0.031	−0.040–0.103	0.079	0.353
OMC		0.126	0.028–0.581	0.728	0.476–0.980	0.786	<0.001
MRT		39.3	17.1–89.7	0.079	−0.058–0.216	0.128	0.231
OMI	PGLS	0.099	0.034–0.283	0.665	0.504–0.825	0.857	<0.001
aDOM		67.2	43.8–103.0	−0.010	−0.075–0.055	0.008	0.911
OMC		0.165	0.037–0.737	0.687	0.460–0.915	0.761	<0.001
MRT		61.0	23.7–156.9	0.016	−0.128–0.160	0.004	0.954

Organic matter intake (OMI in kg d^{-1}); apparent digestibility of organic matter (aDOM in %); organic matter gut contents (OMC in kg); particle mean retention time (MRT in h).

$BM^{-0.03}$ (Fig. 2c), dry matter gut contents (DMC) with $BM^{0.93}$ (Fig. 2e), and digesta retention with $BM^{0.16}$ (Fig. 2g) (all in OLS), which matches the predicted relationships of $0.16 \sim [0.93 - 0.76 + (-0.03)]$. Notably, the 95% confidence interval for the scaling of DMC did not include 1.00 (Table 3). Results for PGLS were similar; notably, the scaling exponent for MRT was lower than in OLS at $BM^{0.12}$.

When testing for a curvature effect in the overall dataset in OLS, such a curvature (visible when plotting body mass residuals against body mass) was evident for dry matter intake (Fig. 2b) and for digesta retention (Fig. 2h), but not for digestibility (Fig. 2d) or gut contents (Fig. 2f). The full term describing the curvature was significant, with 95% confidence intervals that did not include zero for the quadratic term, for intake and digesta retention only (Table 4); the exponent of the quadratic term had a similar magnitude but a different sign for these two measurements (intake: 0.053, retention: −0.057). In PGLS, these quadratic terms were not significant (Table 4), indicating that the effect of the curvature was caused by the phylogenetic structure of the dataset.

Table 2
Correlations between body mass residuals of parameters of digestive physiology in all species of the Foose (1982) dataset analyzed by OLS and PGLS statistics (differences indicated by gray shading).

	Stats	Residual aDOM	Residual OMC	Residual MRT
Residual OMI	OLS	R=−0.137, p=0.505	R=0.841, p<0.001	R=−0.557, p=0.002
	PGLS	R=−0.300, p=0.114	R=0.828, p<0.001	R=0.033, p=0.975
Residual aDOM	OSL		R=0.173, p=0.398	R=0.654, p<0.001
	PSLG		R=0.297, p=0.120	R=0.293, p=0.126
Residual OMC	OSL			R=−0.055, p=0.790
	PSLG			R=0.575, p<0.001

Organic matter intake (OMI in kg d$_{-1}$); apparent digestibility of organic matter (aDOM in %); organic matter gut contents (OMC in kg); particle mean retention time (MRT in h).

Splitting the overall dataset led to different scaling exponents for the various subsets (Table 5). The scaling of food intake had a lower exponent among species that produce more than one offspring per litter or that are below a 10 kg threshold (95%CI 0.57–0.70 in OLS and 0.64–0.81 in PGLS), as opposed to species with one offspring per litter or above the 10 kg threshold (95%CI 0.82–0.96 in OLS and 0.74–0.95 in PGLS). The scaling of dry gut contents was similar among these groups (0.91–0.94 in OLS and 0.84–0.96 in PGLS; never including 1.00 in the 95%CI in OLS but for the larger animals in PGLS). In OLS, there was a difference in the scaling of digesta retention between these groups, with a significant scaling exponent in animals with more than one offspring per litter or below the 10 kg threshold, in contrast to no significant scaling (95% confidence interval for the exponent included zero) in animals above the 10 kg threshold (Table 5). In PGLS, the exponent of the MRT scaling in the animals with more than one offspring per litter/below the 10 kg threshold was distinctively lower than in OLS, with 95%CI approaching or including zero (Table 5) and thus making the scaling in this group similar to the scaling in the group of animals with one offspring per litter/more than 10 kg. Notably, the 95%CI of the scaling exponent of intake and dry gut contents overlapped in animals with a single offspring/animals > 10 kg in OLS, and for all herbivores in PGLS.

Splitting the species into the four digestion types resulted in similar patterns, with a lower scaling exponent for intake, and a higher one for digesta retention, in the (small) caecum fermenters as compared to the other groups in OLS (Table 6). In PGLS, these differences were not evident; in particular, the scaling exponent for MRT in caecum fermenters was much lower in PGLS at 0.14 than in OLS at 0.27, suggesting that the high scaling previously reported in caecum fermenters of 0.25 (Clauss et al., 2007a) was due to an uneven distribution of phylogenetically distant species within this data subset (Table 6). A scaling exponent of 1.00 for gut fill was only included in the confidence interval for ruminants in OLS, and for colon fermenters and ruminants in PGLS. The 95% CI of the scaling exponent overlapped for intake and gut fill in all but the caecum fermenters in OLS, and in all four groups in PGLS (Table 6).

Within the body mass residuals of the whole dataset (Table 7), intake was negatively correlated with digesta retention (Fig. 3a) and positively with gut fill (Fig. 3b) in both OLS and PGLS. Although digestibility was negatively related to intake and positively related to digesta retention (Fig. 3c) in OLS, these relationships were not significant in PGLS (Table 7), i.e. they do not occur within more closely related taxa. By contrast, digestibility was negatively related to gut fill in PGLS, indicating that among more closely related species, those with a higher gut fill had lower digestibilities. Gut fill was positively related to digesta retention in both OLS and PGLS (Table 7, Fig. 3d).

3.3. Wet gut contents

When testing for a scaling curvature in the dataset on wet gut contents, the quadratic term was not significant (OLS p = 0.706; PGLS p = 0.463). Wet gut contents scaled to 0.108 (0.095–0.123) $BM^{1.062(1.029–1.094)}$ ($R^2 = 0.984$, p<0.001) in OLS and 0.109 (0.036–0.332) $BM^{1.086(1.004–1.167)}$ ($R^2 = 0.907$, p<0.001) in PGLS. Thus, when comparing the scaling of wet gut contents and of dry matter gut contents, the difference between the two increases with body mass (Fig. 4); from the comparison of the two scaling exponents (OLS 0.93 and 1.06; PGLS 0.92 and 1.09), the dry matter concentration of gut contents should theoretically scale to $BM^{-0.13}$ or $BM^{-0.17}$.

4. Discussion

The aim of this study was to test whether empirical data allow evoking differences in the allometric scaling between physiological characteristics, to explain species diversification and niche differentiation along a body size gradient in herbivores. Two effects have
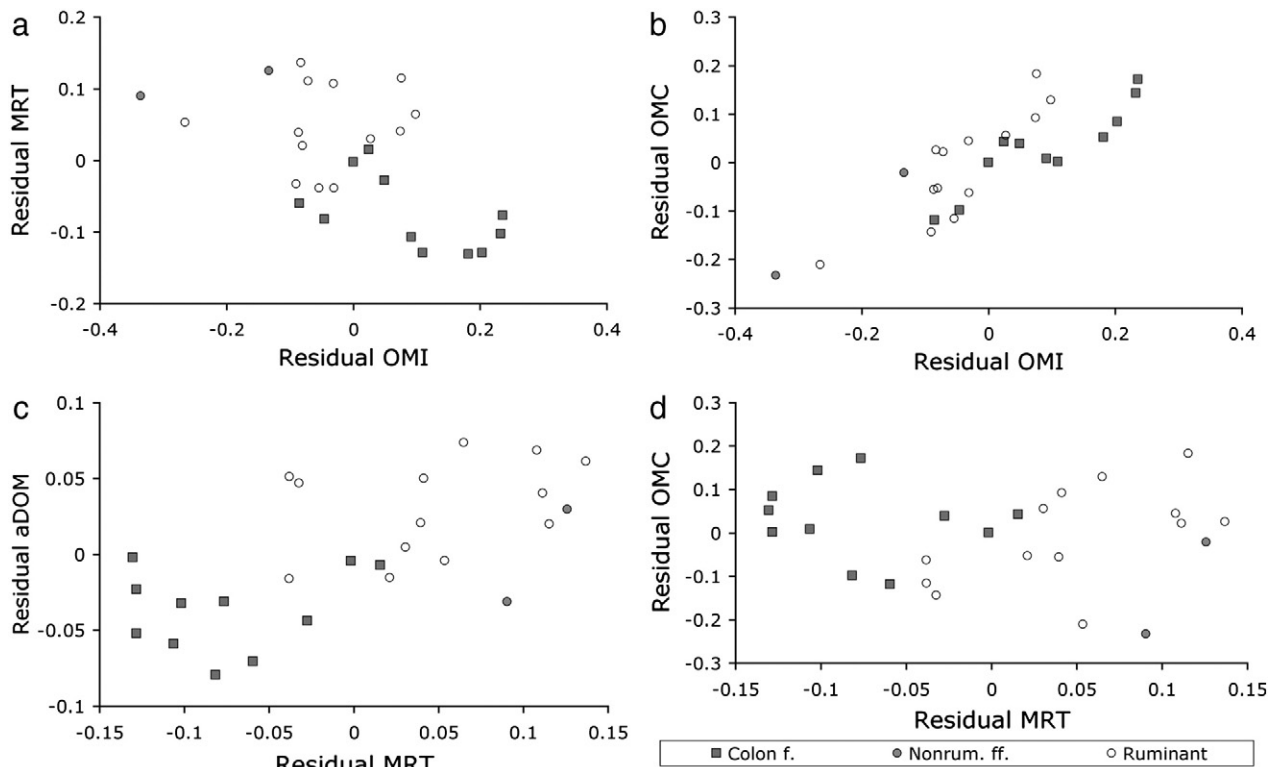
Fig. 1. Relationships between body mass residuals of different parameters of digestive physiology (organic matter intake (OMI in kg d^{-1}); particle mean retention time (MRT in h); organic matter gut contents (OMC in kg), apparent organic matter digestibility (aDOM in %)) in large mammalian herbivores of different digestion types (colon fermenters, nonruminant foregut fermenters, ruminants) in the dataset of Foose (1982). a) OMI and MRT; b) OMI and OMC; c) MRT and aDOM; d) MRT and OMC. For statistics, see Table 2.

previously been associated with body size-driven diversification in mammalian herbivores, namely a higher scaling of food intake as compared to the scaling of metabolism (Hackmann and Spain, 2010), and a distinct difference in the scaling of food intake and gut fill, leading to a positive scaling of digesta retention time (Demment and Van Soest, 1985). If we assume that the results of controlled feeding studies are indeed representative of the digestive physiology of the animals investigated, then the results indicate that from these two effects, the former represents the more promising approach, in particular for larger herbivores.

We suggest several reasons for the fact that the concept of an increasing difference between intake and gut fill, and hence increasing digesta retention time with body size, does not apply to herbivores to the extent previously suggested. Indeed, the concept has been questioned repeatedly based on the empirical finding that the expected scaling of digesta retention with body mass cannot be demonstrated (see Introduction). Similarly, the results of our study demonstrate that any scaling of digesta retention, though principally existent, is below the quarter-power scaling often associated with biological times (Illius and Gordon, 1992; Brown et al., 2012). Because of the mathematical relationships between intake, digestibility, retention and gut fill, this translates into the following deviations from the original concept: gut fill does not scale linearly with body mass, but to a slightly lower exponent (the 95%CI often did not include 1.0); on the other hand, intake scales to an exponent higher than 0.75 in large herbivores. Therefore, the difference between the two scaling exponents is lower than assumed when interpreting the Jarman–Bell Principle in terms of digestive physiology, with confidence intervals overlapping in many datasets. Additionally, there is a slight negative scaling of digestibility with body mass across these experiments, which also reduces the scaling exponent of retention time (see Introduction). The ultimate reason why digesta retention shows a low scaling with body mass in herbivores might stem from the fact that from a certain

body size upwards, a further increase in retention time will not, on average, convey additional advantages, principally because the additional gain from exposing digesta to the digestive process for a longer time is lower than the gain from additional food intake (Hummel et al., 2006).

Several arguments can be put forward to support the validity of our findings. The below-linear scaling of gut contents was present in both of the datasets investigated (Tables 1 and 3). The assumption that gut contents (as a proxy for gut capacity) scale linearly with body mass was originally derived from datasets that related wet gut content mass to body mass (Parra, 1978; Demment and Van Soest, 1985; Justice and Smith, 1992; Clauss et al., 2007a; Illius and Gordon, 1992 is the only publication that uses dry matter gut contents and also arrives at linear scaling, but the dataset comprised only 16 species). If one assumes that this finding translates directly into a similar scaling for that unit of gut fill related to food intake (i.e. dry matter), then one makes the silent assumption that the proportion of moisture in gut contents is similar across all body sizes (as done by Demment, 1983). However, Justice and Smith (1992) reported that the DM concentration of the contents of the fermentation chamber scales to BM$^{-0.08}$ — in other words, the contents of this part of the gut become more watery in larger animals. Their finding is corroborated by our comparison of the scaling of total wet and dry matter gut contents, which yields a similar negative scaling at BM$^{-0.13}$ to BM$^{-0.17}$. Similarly, Müller et al. (2011) found, in a comparative analysis of mean retention times of particle and solute (fluid) markers, that the difference between these two digesta phases tends to increase with body mass — not necessarily because particles are retained longer in larger animals, but also because fluids are passed through their digestive system at a higher rate. One non-exclusive ultimate reason for this might be the fact that in the larger guts of larger animals, diffusion distances from within the digesta to the sites of absorption in the gut wall are increased (Clauss and Hummel, 2005), a problem that could be solved by a more fluid digesta (Lentle et al., 2006). Thus, we suggest
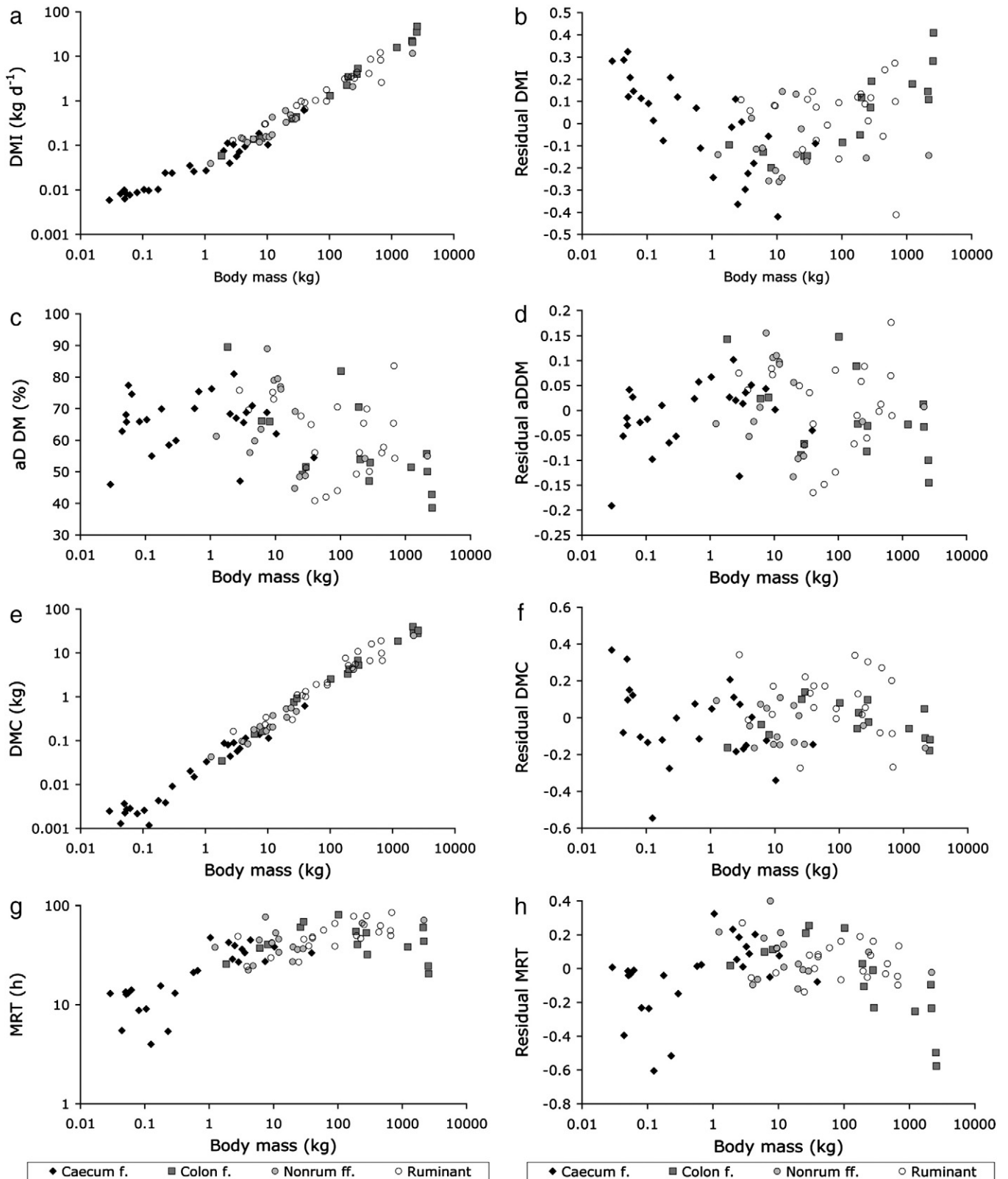
Fig. 2. Scaling relationships between body mass (BM) and parameters of digestive physiology (left side) and plots of body mass-residuals of these parameters against body mass to visualize patterns of quadratic scaling (curvatures) (right side) in mammalian herbivores of different digestion types (caecum fermenters, colon fermenters, nonruminant foregut fermenters, ruminants). a,b) dry matter intake (DMI) c,d) apparent digestibility of dry matter (aD DM) e,f) dry matter gut contents (DMC) g,h) particle mean retention time (MRT). For statistics, see Tables 3–6.

that the assumption that that part of gut fill relevant to food intake and digestibility (i.e. the *dry* matter gut fill) scales linearly with body mass cannot be defended until more data become available.

The other important assumption that is challenged by our findings is that food intake scales uniformly to $BM^{0.75}$. Unfortunately, a direct inclusion of data on basal metabolic rate (BMR) in our study is not

Table 3

Scaling relationships of parameters of digestive physiology with body mass (BM) in the dataset of this study (n = 77) using OLS and PGLS statistics according to y = a BM^b.

y	stats	a	95%CI	b	95%CI	r^2	p
DMI	OLS	0.046	0.041–0.052	0.763	0.732–0.794	0.970	<0.001
aDDM		65.5	61.9–69.2	−0.025	−0.039 to −0.011	0.147	0.001
DMC		0.029	0.025–0.032	0.931	0.902–0.960	0.982	<0.001
MRT		22.3	19.5–25.5	0.158	0.124–0.191	0.540	<0.001
DMI	PGLS	0.039	0.017–0.089	0.773	0.720–0.825	0.916	<0.001
aDDM		67.8	42.3–108.6	−0.052	−0.082 to −0.021	0.130	<0.001
DMC		0.028	0.010–0.075	0.915	0.851–0.979	0.913	<0.001
MRT		26.1	11.639–58.4	0.120	0.068–0.172	0.214	<0.001

Dry matter intake (DMI in kg d^{-1}); apparent digestibility of dry matter (aDDM in %); dry matter gut contents (DMC in kg); particle mean retention time (MRT in h).

feasible; although BMR has been measured in a large variety of mammalian species (McNab, 2008), the large animals that form a majority of our dataset are not included in the available BMR data pool. Therefore, we need to refer to comparisons of our findings to those from BMR studies, inherently with a distinct difference in the species sets investigated. In the debate on the scaling of basal metabolic rate, it has been found repeatedly that across the whole mammalian body mass range, a single allometric exponent does not represent the data very precisely, but that either a curvature in log–log space, or a combination of different scaling relationships of subgroups, provide a better fit (Hayssen and Lacy, 1985; Clarke et al., 2010; Isaac and Carbone, 2010; Kolokotrones et al., 2010; Müller et al., 2012). The magnitude of an overall mammalian scaling exponent will therefore depend either on the body mass range included in the analysis (Lovegrove, 2000; Dodds et al., 2001; Glazier, 2005; White and Seymour, 2005), the taxonomic composition of the sample (Hayssen and Lacy, 1985; Sieg et al., 2009; White et al., 2009; Capellini et al., 2010), or on the inclusion of animals according to certain biological characteristics (McNab, 2008; Müller et al., 2012). Although our species sample of mammalian herbivores is lower than the datasets used to investigate the scaling of metabolism, a similar 'curvature effect' is evident in the intake and retention data (Fig. 2a–b and g–h). Our findings thus provide further support to these previous studies that scaling exponents are not necessarily a universal characteristic for the whole mammalian clade, but may differ either between different groups, or vary across the body mass range. In particular, the results indicate that the group of mammals that can be classified as either small, giving birth to multiple young at a time, or being caecum fermenters has a generally lower scaling of food intake than animals classified as larger, giving birth to a single offspring, or being colon fermenters, nonruminant foregut fermenters or ruminants. Which of these classifications is biologically relevant for the difference in scaling, or whether they are all proxies for a yet undefined functional subdivision of mammals, remains to be investigated. Because a similar 'curvature effect' is evident in the scaling of metabolic rate, where not only herbivores but also other feeding types were included in the dataset (Kolokotrones et al., 2010; Müller et al., 2012), we suggest that digestive strategy is unlikely to be the relevant proxy. Regardless,

Table 5

Scaling relationships of parameters of digestive physiology with body mass (BM) in the dataset of this study in subsets according to litter size or a 10 kg body mass threshold using OLS and PGLS statistics according to y = a BM^b.

y	Stats	a	95%CI	b	95%CI	r^2	p
Litter size > 1 (n = 24)							
DMI	OLS	0.050	0.046–0.055	0.663	0.626–0.701	0.984	<0.001
aDDM		62.2	57.4–67.3	−0.023	−0.054–0.008	0.095	0.142
DMC		0.027	0.024–0.030	0.905	0.825–0.986	0.961	<0.001
MRT		19.3	16.0–23.2	0.233	0.160–0.307	0.662	<0.001
DMI	PGLS	0.047	0.032–0.067	0.724	0.647–0.802	0.938	<0.001
aDDM		64.3	50.7–81.6	−0.015	−0.066–0.035	0.015	0.712
DMC		0.028	0.014–0.058	0.884	0.733–1.036	0.856	<0.001
MRT		21.8	12.6–37.9	0.153	0.036–0.270	0.230	0.006
Litter size = 1 (n = 53)							
DMI	OLS	0.029	0.024–0.036	0.864	0.818–0.910	0.966	<0.001
aDDM		72.6	65.9–80.0	−0.046	−0.067; −0.024	0.260	<0.001
DMC		0.028	0.023–0.035	0.935	0.891–0.978	0.973	<0.001
MRT		36.5	30.3–44.1	0.051	0.009–0.093	0.105	0.018
DMI	PGLS	0.030	0.013–0.074	0.814	0.747–0.881	0.917	<0.001
aDDM		67.0	45.0–99.8	−0.040	−0.071; −0.010	0.117	0.002
DMC		0.026	0.010–0.070	0.916	0.841–0.990	0.919	<0.001
MRT		31.5	14.1–70.2	0.084	0.023–0.145	0.125	0.002
<10 kg (n = 36)							
DMI	OLS	0.045	0.040–0.050	0.622	0.568–0.677	0.941	<0.001
aDDM		67.5	64.3–70.8	0.020	−0.005–0.045	0.070	0.119
DMC		0.028	0.024–0.032	0.909	0.834–0.984	0.947	<0.001
MRT		22.8	19.8–26.2	0.297	0.223–0.371	0.661	<0.001
DMI	PGLS	0.038	0.021–0.069	0.723	0.640–0.806	0.896	<0.001
aDDM		67.3	49.7–91.2	0.007	−0.036–0.050	0.003	0.896
DMC		0.029	0.011–0.074	0.840	0.707–0.973	0.819	<0.001
MRT		27.4	11.4–65.9	0.119	−0.005–0.243	0.095	0.040
> 10 kg (n = 41)							
DMI	OLS	0.026	0.018–0.037	0.885	0.815–0.955	0.944	<0.001
aDDM		64.9	53.6–78.5	−0.029	−0.066–0.009	0.058	0.129
DMC		0.030	0.021–0.043	0.924	0.854–0.993	0.948	<0.001
MRT		41.7	29.9–58.2	0.026	−0.038–0.091	0.017	0.414
DMI	PGLS	0.029	0.010–0.081	0.844	0.743–0.945	0.873	<0.001
aDDM		54.8	34.6–86.7	−0.003	−0.049–0.042	0.001	0.979
DMC		0.023	0.007–0.070	0.959	0.848–1.070	0.880	<0.001
MRT		26.3	12.1–57.5	0.114	0.037–0.190	0.176	0.001

Dry matter intake (DMI in kg d^{-1}); apparent digestibility of dry matter (aDDM in %); dry matter gut contents (DMC in kg); particle mean retention time (MRT in h).

our study suggests that the use of one single exponent to describe relative metabolic rates or relative food intakes may be convenient, but should not be the basis for biological models.

Within one notable subset of large herbivores, the ruminants, the assumption that food intake scales to BM$^{0.75}$ has previously been refuted based either on conceptual approaches or collections of empirical data: Mertens (1994) and Südekum (2002) explain that for low-quality forages, relating food intake in domestic ruminants to body mass may be more appropriate than using metabolic body mass as the

Table 4

Evidence for quadratic scaling in parameters of digestive physiology with body mass (BM) in the dataset of this study (n = 77) (OLS). Linear regression models according to log y = a + b1(logBM) + b2((logBM)^2) or y = a BM$^{(b1 + b2(logBM))}$. Equations with both b1 and b2 significant indicated in bold.

y	Stats	a	95%CI	b1	95%CI	b2	95%CI	R2 (adj.)	p
DMI	OLS	0.042	0.038–0.047	**0.659**	**0.616–0.702**	**0.053**	**0.035–0.070**	0.980 (0.979)	<0.001
aDDM		66.7	63.1–70.5	−0.004	−0.027–0.018	−0.010	−0.019 to −0.001	0.202 (0.181)	<0.001
DMC		0.028	0.025–0.032	0.930	0.881–0.979	0.001	−0.019–0.021	0.982 (0.981)	<0.001
MRT		24.7	22.0–27.7	**0.270**	**0.223–0.316**	**−0.057**	**−0.076 to −0.038**	0.692 (0.983)	<0.001
DMI	PGLS	0.039	0.018–0.088	0.706	0.617–0.795	0.026	−0.002–0.054	0.920 (0.918)	<0.001
aDDM		67.7	42.1–108.9	−0.056	−0.108 to −0.003	0.001	−0.015–0.018	0.130 (0.106)	0.002
DMC		0.028	0.010–0.074	0.851	0.743–0.959	0.025	−0.009–0.060	0.915 (0.913)	<0.001
MRT		26.1	11.6–58.7	0.121	0.032–0.211	−0.001	−0.029–0.028	0.214 (0.193)	<0.001

Dry matter intake (DMI in kg d^{-1}); apparent digestibility of dry matter (aDDM in %); dry matter gut contents (DMC in kg); particle mean retention time (MRT in h).

Table 6
Scaling relationships of parameters of digestive physiology with body mass (BM) in the dataset of this study in subsets according to digestion types using OLS and PGLS statistics according to $y = a\ BM^b$.

y	Stats	a	95%CI	b	95%CI	r^2	p
Caecum fermenter (n = 25)							
DMI	OLS	0.041	0.036–0.048	0.589	0.524–0.654	0.938	<0.001
aDDM		65.3	61.4–69.5	0.001	−0.029–0.031	0.000	0.950
DMC		0.025	0.021–0.031	0.860	0.767–0.954	0.940	<0.001
MRT		21.7	17.8–26.5	0.271	0.177–0.365	0.606	<0.001
DMI	PGLS	0.033	0.017–0.066	0.688	0.594–0.782	0.900	<0.001
aDDM		67.2	50.7–89.2	−0.003	−0.042–0.036	0.001	0.977
DMC		0.025	0.009–0.070	0.830	0.689–0.972	0.852	<0.001
MRT		27.4	11.5–65.1	0.140	0.021–0.258	0.187	0.013
Colon fermenter (n = 15)							
DMI	OLS	0.024	0.018–0.033	0.911	0.856–0.967	0.990	<0.001
aDDM		78.7	61.9–100.0	−0.066	−0.109; −0.023	0.459	0.006
DMC		0.029	0.021–0.040	0.919	0.861–0.977	0.989	<0.001
MRT		47.1	27.2–81.5	−0.021	−0.120–0.077	0.017	0.647
DMI	PGLS	0.031	0.016–0.058	0.852	0.757–0.947	0.960	<0.001
aDDM		75.7	49.3–116.1	−0.070	−0.134; −0.006	0.259	0.032
DMC		0.027	0.015–0.049	0.948	0.858–1.037	0.971	<0.001
MRT		34.4	14.3–82.6	0.061	−0.071–0.192	0.060	0.461
Nonruminant foregut fermenter (n = 15)							
DMI	OLS	0.036	0.026–0.051	0.755	0.655–0.855	0.953	<0.001
aDDM		69.8	56.0–87.3	−0.038	−0.105–0.030	0.102	0.246
DMC		0.030	0.023–0.038	0.881	0.806–0.957	0.980	<0.001
MRT		30.3	21.4–43.0	0.109	0.003–0.215	0.274	0.045
DMI	PGLS	0.031	0.009–0.113	0.812	0.659–0.965	0.893	<0.001
aDDM		75.1	46.7–120.9	−0.064	−0.120; −0.008	0.276	0.025
DMC		0.033	0.009–0.114	0.844	0.697–0.992	0.907	<0.001
MRT		40.2	11.1–145.1	0.006	−0.145–0.158	0.001	0.993
Ruminant (n = 22)							
DMI	OLS	0.054	0.035–0.083	0.752	0.659–0.845	0.934	<0.001
aDDM		66.7	51.6–86.3	−0.025	−0.080–0.030	0.044	0.347
DMC		0.041	0.024–0.067	0.897	0.788–1.005	0.937	<0.001
MRT		27.6	20.2–37.7	0.133	0.066–0.200	0.464	<0.001
DMI	PGLS	0.036	0.014–0.093	0.765	0.660–0.870	0.910	<0.001
aDDM		85.3	42.8–169.9	−0.072	−0.149; −0.005	0.144	0.055
DMC		0.024	0.007–0.078	0.973	0.841–1.104	0.913	<0.001
MRT		26.3	13.2–52.5	0.177	0.100–0.254	0.502	<0.001

Dry matter intake (DMI in kg d^{-1}); apparent digestibility of dry matter (aDDM in %); dry matter gut contents (DMC in kg); particle mean retention time (MRT in h).

basis. Hackmann and Spain (2010) collated data on the voluntary food intake (VFI) in domestic and wild ruminant species in a dataset more comprehensive than ours (that was limited to studies that also measured digestibility and retention), and concluded that VFI scaled to $BM^{0.9}$, which was similar to that described in previous studies on domestic ruminants (Graham, 1972; Minson, 1990; Reid et al., 1990). The authors concluded that the intermediate scaling between metabolism (0.75) and gut fill (1.0) indicated that both metabolic and physical constraints determine food intake; they also conclude that the

Table 7
Correlations between body mass residuals of parameters of digestive physiology in the dataset of this study (n = 77) analyzed by OLS and PGLS statistics (differences indicated by gray shading).

	Stats	Residual aD DM	Residual DMC	Residual MRT
Residual DMI	OLS	R=−0.254, p=0.026	R=0.444, p<0.001	R=−0.583, p<0.001
	PGLS	R=0.087, p=0.567	R=0.589, p<0.001	R=−0.270, p=0.004
Residual aD DM	OLS		R=−0.082, p=0.471	R=0.345, p=0.002
	PGLS		R=−0.200, p=0.050	R=−0.084, p=0.592
Residual CMD	OLS			R=0.450, p<0.001
	PGLS			R=0.593, p<0.001

Dry matter intake (DMI in kg d_{-1}); apparent digestibility of dry matter (aDDM in %); dry matter gut contents (DMC in kg); particle mean retention time (MRT in h).

putative difference between the scaling of metabolism (0.75) and the scaling of intake (0.9) allows larger animals to ingest lower-quality food and still meet their energetic requirements. Note that this interpretation of scaling differences does not draw on an alleged scaling of digestion efficiency and retention times.

The assumption that intake might scale to a higher exponent than basal metabolic rate is supported when comparing the intake scaling exponent of large herbivores/herbivores with one offspring of this study (0.81–0.89, Table 5) with that of the BMR in mammals with one offspring (0.76; Müller et al., 2012). In contrast, for the small herbivores/herbivores with more than one offspring, such a difference is not evident at 0.62–0.72 for the intake scaling exponent in this study and 0.69 for that of BMR (Müller et al., 2012). To explain body size effects in this group, factors such as variation in feeding selectivity and caecotroph use via coprophagy must be further investigated (Justice and Smith, 1992; Franz et al., 2011b). In particular, it remains unknown whether the proportion of intake achieved via coprophagy varies systematically with body mass. Preliminary results indicate that this proportion increases with increasing dietary fiber content (Takahashi and Sakaguchi, 1998). If we assume that compared to smaller species, larger caecum fermenters are adapted to lower-quality diets (i.e. diets higher in fiber), and should therefore be generally adapted to a higher proportion of intake via coprophagy, this might help explain the lower scaling of intake via food (as measured in the digestion experiments collated in this study) in this group. Further studies that assess the contribution of coprophagy over a wide range of body sizes are required to explore this possibility.

Apart from the logical issue with drawing conclusions on the scaling of digestibility from the scaling of digesta retention explained in the Introduction, our data collection yields some further insights concerning correlates and effects of digesta retention. As reported previously in inter- and intraspecific analyses (Clauss et al., 2007a, 2007b; Müller et al., 2011; Steuer et al., 2011), species with a higher relative food intake have comparatively shorter retention times (Fig. 3a). Langer and Snipes (1991) suggested that interspecifically, animals achieve longer digesta retention by higher gut capacities, a concept supported by our findings (Fig. 3b). Additionally, capacity for a higher gut fill will allow a higher food intake (Fig. 3d).

Although increasing retention times may be associated with higher general digestive efficiencies in intraspecific studies (Clauss et al., 2007b), this effect is most evident in interspecific comparisons in relation to the digestibility of the fiber component of the food (Udén and Van Soest, 1982; Clauss et al., 2009). When comparing the overall diet digestibility, as in this study, where we collated data on the dry matter or organic matter digestibility but not the fiber digestibility, no significant effect of digesta retention on digestibility is evident when accounting for the phylogenetic structure of the data (Tables 3 and 7). In other words, although larger clades differ systematically in retention and digestibility, such as the colon fermenters and ruminants in Fig. 1c, the effect is not evident among more closely related species — in the case of the Foose (1982) dataset even though consistent diets were used. One potential reason is that digesta retention is not the only determinant of digestibility, but acts together with digesta particle size reduction, either compensating for poor chewing efficiency (as for example in hippopotamuses) or reinforcing a high chewing efficiency (as in the ruminants) (Clauss et al., 2009). Another potential reason is that overall dry matter digestibility does not necessarily reflect fiber digestibility. A small-scale data collection in Clauss and Hummel (2005) suggested that fiber digestibility may vary more across a large herbivore body mass range than does overall diet digestibility, which remained rather constant (as in this study). The authors summarized concepts that interpret these data as indication for a better utilization of non-fibrous food components in smaller animals, including the segregation of bacterial protein during caecotroph formation by the colonic separation mechanism (Björnhag, 1987; Franz et al., 2011b). Understanding how bacterial nitrogen utilization and
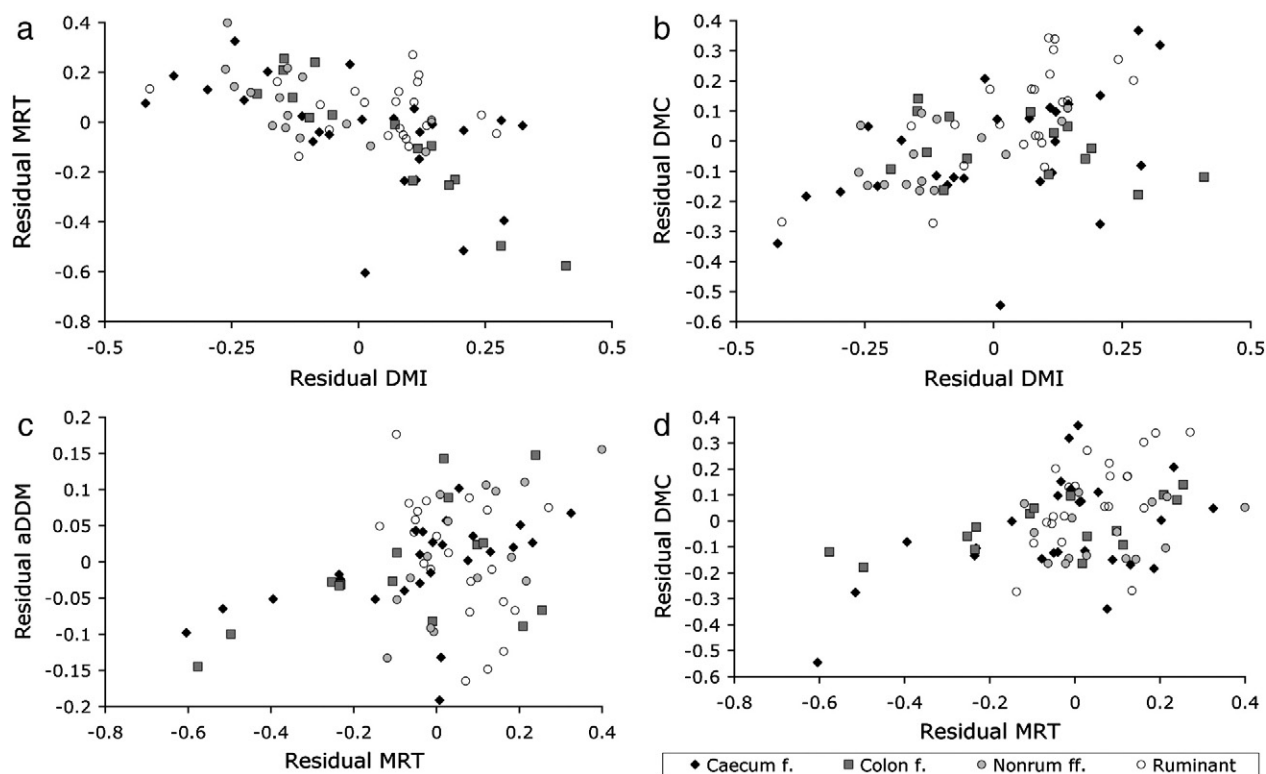
Fig. 3. Relationships between body mass residuals of different parameters of digestive physiology (dry matter intake (DMI in kg d^{-1}); particle mean retention time (MRT in h); dry matter gut contents (DMC in kg), apparent dry matter digestibility (aDDM in %)) in mammalian herbivores of different digestion types (colon fermenters, nonruminant foregut fermenters, ruminants) in the dataset of this study. a) DMI and MRT; b) DMI and DMC; c) MRT and aDDM; d) MRT and DMC. For statistics, see Table 7.

endogenous/metabolic nitrogen losses vary with body mass and between the different herbivore digestive strategies remains one of the major challenges in studying herbivore digestive physiology (Schwarm et al., 2009b).

Herbivores will maximize energy intake if they maximize feeding selectivity, food intake and digesta retention (by increasing gut fill), particle size reduction (by more elaborate cranio-dental designs and by sorting mechanisms in ruminants that increase chewing efficiency), and minimize endogenous/metabolic fecal losses. The major dilemma in this array of factors is that increasing food intake is usually associated with a lower feeding selectivity, shorter digesta retention and reduced particle size reduction (Clauss et al., 2010a). It is commonly assumed

that the different herbivore species or groups represent different, equally successful 'digestive strategies' to solve this dilemma, varying in the emphasis of the individual interrelated factors (Hume, 2005). Alternatively, one can hypothesize that the sequence of radiation events in herbivores indicates different levels of optimization of the overall interplay of these factors (Fritz et al., 2009). For example, bovid ruminants, as the most recently radiated large herbivore group, potentially represent the hitherto most sophisticated design that combines high food intakes, long retention times and high chewing efficiency with a very efficient use of the symbiotic microflora (Clauss et al., 2010a; Müller et al., 2011). How species that use similar niches with different digestive strategies can persist then requires different explanations. Such a view shifts the focus in tracing niche differentiation and species diversification from simple allometric considerations to more complex aspects of variation in organismal design.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.cbpa.2012.09.018.

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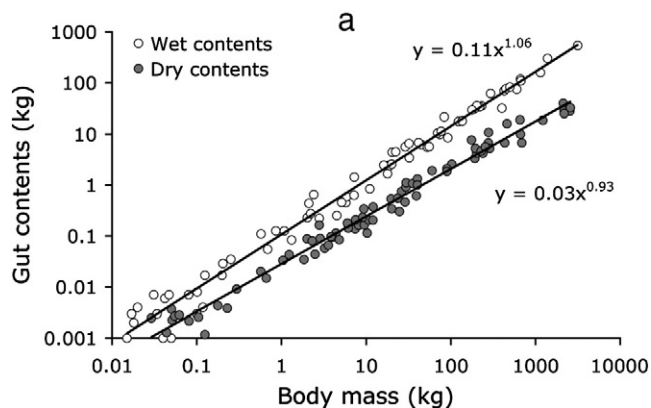

Fig. 4. Scaling of wet gut contents (open symbols, Clauss et al., 2007a) and dry matter gut contents (closed symbols, this study) with body mass. Note the increasing difference between the two with increasing body mass.

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