



**University of
Zurich** UZH

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2013

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

Müller, Dennis W H ; Codron, Daryl ; Meloro, Carlo ; Munn, Adam ; Schwarm, Angela ; Hummel, Jürgen ;
Clauss, Marcus

DOI: <https://doi.org/10.1016/j.cbpa.2012.09.018>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-67071>

Journal Article

Accepted Version

Originally published at:

Müller, Dennis W H; Codron, Daryl; Meloro, Carlo; Munn, Adam; Schwarm, Angela; Hummel, Jürgen; Clauss, Marcus (2013). Assessing the Jarman–Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology Part A: Molecular Integrative Physiology*, 164(1):129-140.

DOI: <https://doi.org/10.1016/j.cbpa.2012.09.018>

1 **Assessing the Jarman-Bell Principle: scaling of intake, digestibility, retention time and**
2 **gut fill with body mass in mammalian herbivores**

3
4 Dennis W.H. Müller^{1,2}, Daryl Codron^{1,3}, Carlo Meloro⁴, Adam Munn⁵, Angela Schwarm⁶,
5 Jürgen Hummel⁷, Marcus Clauss^{1*}

6
7 ¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260,
8 8057 Zurich, Switzerland, dcodron@vetclinics.uzh.ch, mclauss@vetclinics.uzh.ch

9 ²National Park 'Bavarian Forest', Freyungerstr. 2, 94481 Grafenau, Germany, dennis.mueller@npv-
10 bw.bayern.de

11 ³Florisbad Quaternary Research, National Museum, Bloemfontein, 9300, RSA

12 ⁴Center for Anatomical and Human Science, Hull York Medical School, University of Hull, Cottingham Road,
13 Hull HU6 3RX, UK, carlo.meloro@hyms.ac.uk

14 ⁵Institute for Conservation Biology and Environmental Management, School of Biological Sciences, The
15 University of Wollongong, New South Wales 2522 Australia, amunn@uow.edu.au

16 ⁶Research Unit Nutritional Physiology 'Oskar Kellner', Leibniz Institute for Farm Animal Biology (FBN),
17 Wilhelm-Stahl-Allee 2, 18196 Dummerstorf, Germany, schwarm@fbn-dummerstorf.de

18 ⁷Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany, jhum@itw.uni-
19 bonn.de

20
21
22 *to whom correspondence should be addressed

23
24 Running head: Herbivore digestive allometry

25

26 **Abstract**

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

55

56 Key words: Jarman-Bell Principle; herbivory; body size; diet quality; digestion; allometry;
57 feeding ecology; digestive physiology

58

59 **Introduction**

60 *The Jarman-Bell Principle*

61 The scaling relationships of digestive features with body mass (BM) in herbivores are a
62 fundamental part of our interpretation of herbivore feeding ecology, interspecific niche
63 differentiation and intraspecific niche segregation due to sexual dimorphism. Geist (1974)
64 explained how two PhD studies, which resulted in two publications (Bell, 1971; Jarman,
65 1974), crystallized an understanding of the ways in which BM affects the ecology of
66 ungulates of the African savannahs. These studies have become the springboard for most
67 analyses of mammal herbivore ecological interactions that include a range of BM (du Toit,
68 2005). The so-called 'Jarman-Bell Principle' (JBP) (Geist, 1974) has been applied to other
69 animal groups such as primates (Gaulin, 1979), fruit bats (Fleming, 1991) or baleen whales
70 (Tershy, 1992), and predicts that BM constrains nutritional ecology – in terms of the diet
71 quality that larger animals can or must tolerate, as well as their digestive efficiency. That
72 larger animals commonly ingest diets of lower quality has been demonstrated repeatedly (e.g.
73 Owen-Smith, 1988; Codron et al., 2007), and that they often must tolerate poor-quality foods
74 is usually not an issue of debate. This is considered a consequence of large animals' higher
75 absolute food requirements that prevent them from foraging selectively in terms of time
76 constraints, and also a consequence of larger, more 'clumsy' feeding apparatus that again
77 prevents them from foraging selectively in terms of picking out individual food items or plant
78 parts (Owen-Smith, 1988; Shipley, 2007).

79
80 A fact often used to explain the increased dietary tolerance (measured as the range in fibre
81 and/or protein content of the diet the animal can tolerate) of larger species are the decreased
82 mass-specific metabolic demands - because the daily requirements for energy (Nagy et al.,
83 1999), nitrogen (Robbins, 1993) and even minerals (Rucker and Storms, 2002) scale to
84 metabolic body mass ($BM^{0.75}$). This scaling effect means that small-bodied species require
85 more energy and nutrients per day and per unit of BM than do large-bodied forms (Geist,
86 1974). However, without information about the scaling of energy/nutrient intake, knowledge
87 about the scaling of requirements allows no further insight. Concepts about niche
88 diversification along a BM gradient must make an assumption about the difference in scaling
89 between requirement and intake. Given that larger animals ingest lower-quality diets, a
90 similar scaling of intake and requirements would make it necessary that digestive efficiency
91 has a positive scaling, i.e. it should increase with BM. This could be achieved either by
92 selecting a more digestible diet (which violates the assumption of decreasing diet quality), or

93 by measures of digestive physiology that increase digestive efficiency, such as prolonged
94 digesta retention. In contrast, if we postulate that there is no scaling of digestive efficiency
95 with BM, then intake would have to scale to BM at a higher exponent than requirements, in
96 order to compensate for the lower diet quality in larger animals. Historically, the JBP has
97 more often been linked to variation in digestive efficiency than to variation in intake levels.
98

99 When developing this approach of the JBP, food intake was, without empirical testing,
100 assumed to scale to body mass in a similar way as animal metabolism (explicitly in Demment,
101 1983; implicitly in Demment and Van Soest, 1985; note that Van Soest, 1994 does not make
102 an explicit assumption about intake scaling but rests his argument on the scaling of gut fill
103 only). In large datasets, food intake (measured as dry matter intake, DMI, or as gross energy
104 intake) was actually often found to scale to $BM^{0.75}$ across a wide range of mammalian species
105 (reviewed in Clauss et al., 2007a; Meyer et al., 2010), and thus resembles the scaling of
106 metabolism and requirements. Therefore, the approach that focuses on scaling effects on
107 digestive physiology appears as the logical next step. Including gut fill in these considerations
108 has extended the JBP to specifically comprise not only metabolic scaling, but also digestive
109 physiology. Gut fill (measured as wet matter content, WMC) or dry matter content (DMC)
110 has been suggested to be a constant fraction of BM in herbivores (Parra, 1978; Demment and
111 Van Soest, 1985; Illius and Gordon, 1992; Justice and Smith, 1992; Clauss et al., 2007a). If
112 gut fill actually scales to $BM^{1.00}$, and food intake scales to $BM^{0.75}$, these different scaling
113 effects result in a larger gut fill per unit food intake with increasing BM. This should in theory
114 lead to an increase in the time digesta is retained in the gastrointestinal tract (measured as
115 mean retention time, MRT) with increasing BM (Demment and Van Soest, 1985; Illius and
116 Gordon, 1992; Robbins, 1993; McNab, 2002). Explicitly, it is thought that MRT should scale
117 to $BM^{(1.00-0.75)} = BM^{0.25}$. Because MRT is positively linked to the digestive efficiency of a
118 herbivore (Foose, 1982; Udén and Van Soest, 1982; Clauss et al., 2007b), this concept has
119 been invoked to postulate that larger herbivores can use food of a lower quality *due to a*
120 *hypothetical capacity for more efficient digestion* (Demment and Van Soest, 1985; Illius and
121 Gordon, 1992; Gordon and Illius, 1996). In this way, the JBP delivers an elegant explanation
122 (higher digestive efficiency in larger animals) for a common observation (lower diet quality in
123 larger animals), and represents what may be the most prominent set of allometric
124 considerations in large animal ecology, including theoretical approaches to understanding
125 intraspecific size dimorphism (Short, 1963; Prins and Geelen, 1971; Sinclair, 1977; Hanley

126 and Hanley, 1980; Hanley, 1982; Barboza and Bowyer, 2000; du Toit, 2005; Shannon et al.,
127 2006; Woolley et al., 2011).

128

129 Empirical evidence for the physiological predictions of the JBP, however, is scarce. While the
130 findings that wet gut contents scale to $BM^{1.00}$ and food intake scales to $BM^{0.75}$ are mostly
131 undisputed, digesta retention has repeatedly been shown, in various datasets, *not* to scale to
132 $BM^{0.25}$ (Clauss et al., 2007a; Clauss et al., 2009; Franz et al., 2011a; Müller et al., 2011;
133 Steuer et al., 2011), with the exception of mammalian caecum fermenters (Clauss et al.,
134 2007a, but see the results of phylogenetically informed statistics in this study down below).
135 Additionally, there is little indication for an increase in digestive efficiency with BM (Justice
136 and Smith, 1992; Wenninger and Shipley, 2000; Pérez-Barbería et al., 2004; Clauss et al.,
137 2009; Steuer et al., 2012). These findings represent a serious conceptual problem for
138 herbivore digestive physiology, because the link between gut fill, food intake and digesta
139 retention is mathematically sound.

140

141 *Linking digesta retention to gut capacity, food intake and digestibility*

142 Holleman & White (1989) provided the underlying equation to this problem, based on the
143 ‘Stewart-Hamilton Principle’ or the ‘Occupancy Principle’ (Steele, 1971; Shipley and Clark,
144 1972), where

$$145 \quad \text{indDMC [kg]} = \text{faecal output [kg/h]} * \text{MRT}_{\text{particleGIT}} [\text{h}] \quad (1)$$

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

$$151 \quad \text{faecal output [kg/h]} = \text{DMI [kg/h]} * (\text{aID DM}) \quad (2)$$

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

$$153 \quad \text{indDMC [kg]} = \text{DMI [kg/h]} * \text{aID DM} * \text{MRT}_{\text{particleGIT}} [\text{h}] \quad (3)$$

154 Solving this equation for MRT yields

$$155 \quad \text{MRT}_{\text{particleGIT}} [\text{h}] = \text{indDMC [kg]} / (\text{DMI [kg/h]} * \text{aID DM}) \quad (4)$$

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

$$158 \quad \text{MRT}_{\text{particleGIT}} \sim \text{BM}^a / (\text{BM}^b * \text{BM}^c) \text{ or } \text{MRT}_{\text{particleGIT}} \sim \text{BM}^{a-(b+c)} \quad (5)$$

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

168
 169 The calculation of gut fill can be expanded to include not only indigestible gut fill, but also
 170 total gut fill (dry matter contents DMC) (Holleman and White, 1989). For that, the digestible
 171 portion of DMC (dDMC) has to be added to indDMC. To do so, one has to make an
 172 assumption regarding the course of digestion. If one assumes digestion to be exponential over
 173 MRT (with most of digestion occurring at the beginning of MRT and slowly ‘fading out’),
 174 then the estimated dDMC in the total GIT will be less than if one assumes digestion to be
 175 linear across MRT. Holleman and White (1989) and Munn et al. (2012) showed that assuming
 176 a linear course of digestion across MRT yields better results when validated against empirical
 177 measures in slaughtered animals, albeit using small sample sizes. Because assuming a linear
 178 course of digestion across MRT means that dDMC is assumed to be present in the GIT during
 179 half of MRT, it follows that

$$180 \quad dDMC [kg] = DMI [kg/h] * aD DM * (MRT_{particleGIT} [h] / 2) \quad (6).$$

181 Combining equation (3) and (6) to calculate total DMC yields,

$$182 \quad DMC [kg] = DMI [kg/h] * MRT_{particleGIT} [h] * (aID DM + 0.5 aD DM) \quad (7)$$

183 Solving the equation for $MRT_{particleGIT}$ [h] yields

$$184 \quad MRT_{particleGIT} [h] = DMC [kg] / DMI [kg/h] * (1 / (aID DM + 0.5 aD DM)) \quad (8)$$

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

$$187 \quad MRT_{particleGIT} \sim BM^d / BM^b * (1 / (BM^{-c} + 0.5 BM^c)) \text{ or } MRT_{particleGIT} \sim BM^{d-b+c} \quad (9)$$

189 Assuming that DMC scales similar as wet matter contents, i.e. to $BM^{1.00}$, and DMI scales to
 190 $BM^{0.75}$, we can thus again assume that $MRT_{particleGIT}$ should scale to $BM^{0.25}$ *if digestive*
 191 *efficiency does not change with BM*. Note that again, an increase in digestibility with BM
 192 (i.e., a positive c) would lead to a higher scaling exponent for $MRT_{particleGIT}$, and a decrease

193 in digestibility with BM would lead to a lower scaling exponent for $MRT_{particleGIT}$. One
194 important conclusion from these derivations is that if one uses the scaling of intake and gut
195 fill to make any conclusions about digesta retention, one must not use the result to make
196 inferences about digestive efficiency - because an assumption about the scaling of
197 digestibility is made already (explicitly or implicitly) to derive the scaling of digesta
198 retention. Deriving a scaling for digesta retention in this way and then using it to explain a
199 pattern of digestive efficiency with body mass amounts to circular reasoning.

200

201 *Re-assessing data from herbivore feeding trials*

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

223

224 The following hypotheses guided our investigation:

- 225 (i) Across the whole mammal body size range, food intake measured as dry matter
226 intake (DMI) has a scaling exponent close to $BM^{0.75}$ (reviewed in Clauss et al.,
227 2007a).
- 228 (ii) Apparent digestibility generally does not scale with body mass (i.e. to $BM^{0.00}$)
229 (Justice and Smith, 1992; Wenninger and Shipley, 2000; Pérez-Barbería et al.,
230 2004; Clauss et al., 2009; Steuer et al., 2012), and therefore the scaling exponents
231 of gut fill (BM^a), food intake (BM^b) and digesta retention (BM^d) are associated
232 according to $d = a - b$. It should be noted, however, that any conclusions concerning
233 the apparent digestibility must be considered in the context of the food sources that
234 were used across experiments. When collating data for a large variety of species
235 from the literature, as we do here, it is highly likely that data from smaller species,
236 which are often kept on artificial feeds for experimental purposes, is combined
237 with data from larger species, which are more often kept on roughage-only diets
238 that are generally less digestible. Thus, a putative negative allometry of
239 digestibility (a decrease with body mass) would be an indication of this uneven
240 distribution of diet quality. How close this potential decrease in diet quality with
241 body size in the dataset actually might resemble the general decrease of diet
242 quality with body size that is supposed to occur in the wild is difficult to judge.
243 Therefore, if scaling is detected between body mass and digestibility, then the
244 scaling exponents of gut fill (BM^a), food intake (BM^b), digestibility (BM^c) and
245 digesta retention (BM^d) are associated according to $d = a - b + c$.
- 246 (iii) The low empirical overall scaling exponent for digesta retention (Clauss et al.,
247 2007a; Clauss et al., 2009; Müller et al., 2011; Steuer et al., 2011) results from the
248 fact that gut fill, measured as dry matter contents (DMC), does *not* scale to $BM^{1.00}$
249 but to a lower exponent.
- 250 (iv) In parallel to observations on the scaling of mammalian basal metabolic rate
251 (BMR) that does not follow a single exponent across the whole BM range (Clarke
252 et al., 2010; Isaac and Carbone, 2010; Kolokotronis et al., 2010; Müller et al.,
253 2012), we expect that DMI also does not follow one single exponent across the
254 whole BM range. In fact, variation in the scaling of DMI across the BM range
255 could be responsible for the observation that digesta retention scales differently in
256 different digestion types, which are distributed unevenly across the BM range
257 (Clauss et al., 2007a). In accord with Packard (2012), we do not follow the
258 argument that a curvature (or ‘quadratic scaling’) in double-logarithmic space

259 represents a true mechanistic pattern (Kolokotronis et al., 2010), but assume that it
260 is the effect of combined simple scaling patterns in the overall dataset and can be
261 used as a test for such scaling combinations (Müller et al., 2012). A test for such a
262 curvature effect is then followed by analysis of scaling patterns within subsets of
263 the data. In particular, following the dichotomy in metabolism scaling between
264 animals with one and with more than one offspring per litter (Müller et al., 2012),
265 we expect that food intake has a lower scaling exponent in herbivores that
266 represent the majority of the lower BM range (especially caecum fermenters), and
267 a higher scaling exponent in herbivores that represent the majority of the higher
268 BM range (i.e. non-coprophageous hindgut fermenters, nonruminant foregut
269 fermenters and ruminants), resulting in a typical curvature shape in double-
270 logarithmic space, or when plotting body mass-residuals of DMI against body
271 mass. An important question when assessing the individual scaling relationships of
272 intake in different groups will be whether the scaling exponent is similar to that of
273 metabolism, or whether it is actually higher (Hackmann and Spain, 2010).

274 (v) Differences in the scaling of wet matter gut contents (WMC) and dry matter gut
275 contents (DMC) with BM reflect the finding of Justice and Smith (1992) that
276 larger animals have a higher digesta moisture content; when using the WMC and
277 DMC allometries to calculate the allometry of the dry matter concentration of the
278 GIT contents, the result should be close to that of Justice and Smith (1992) where
279 DM concentration in the contents of the fermentation chamber scales to $22 \text{ BM}^{0.08}$.
280

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

288 Because one of the largest existing datasets on the digestive physiology of large herbivores
289 (Foose, 1982) is basically incompatible with other published data (Clauss et al., 2007a; Clauss
290 et al., 2010b), we performed the same analyses for both the Foose (1982) dataset and an
291 independent collation of literature data. With the limitation that the Foose (1982) dataset

292 comprises only comparatively large species, this allows a corroboration of results from one
293 dataset with the other.

294

295 **Methods**

296 The datasets used in this study are

- 297 a) Foose (1982), comprising 26 species of large (>100 kg) herbivores from the
298 Artiodactyla, Perissodactyla and Proboscidea, which received two standardized diets
299 (grass and lucerne hay); in this dataset, the unit of reference is organic matter rather
300 than dry matter; and
- 301 b) the data collation of Clauss et al. (2007a) that was supplemented with additional
302 sources, and pruned according to the following selection criteria. Only sources were
303 used which gave body mass (BM), dry matter intake (DMI), particle mean retention
304 time in the whole gastrointestinal tract ($MRT_{\text{particleGIT}}$) and the apparent digestibility
305 of dry matter (aD DM) from the same experiment (in some cases, this information had
306 to be collected from several publications reporting on the same experiment). From
307 these data, dry matter content (DMC) of the GIT was calculated as outlined in the
308 Introduction. For the sake of a large data collection, we did not select publications
309 according to the passage markers used. Therefore, any particle marker was accepted;
310 however, only studies in which small particles (generally < 2 mm; as opposed to
311 whole forages) were labelled were included. Similarly, we did not select publications
312 according to the type of food offered; therefore, the data collection comprises animals
313 fed on a complete, pelleted diet, animals on mixtures of roughages and concentrates,
314 as well as animals on roughage-only diets. Ideally, a data collection with a
315 standardized diet (such as in Foose, 1982; Steuer et al., 2011; 2012) or with diets
316 representing the natural diets of the species would be preferable, but are not available
317 at a larger scale and over a wide body mass range. With regards to some domestic
318 species (rabbits, horse, goats, sheep, cattle), no attempt was made to collate all
319 published data. For lagomorphs and rodents, only data from trials in which
320 coprophagy was not prevented by the study design were used. For each species, one
321 average value for BM, DMI, $MRT_{\text{particleGIT}}$, aD DM and DMC was calculated using
322 all available data from the cited publications. The data for the resulting 77 mammalian
323 species and its sources are summarized in the Appendix.

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

327 Species were allocated, according to Stevens and Hume (1995), to one of the following
328 categories: caecum fermenters, colon fermenters, non-ruminant foregut fermenters, and
329 ruminants (Appendix). Additionally, species were allocated to litter size classes (one or more
330 than one offspring per litter) and body size classes (<10 kg, >10 kg). In order to account for
331 ancestry-biased correlations in the datasets (i.e., significant associations in interspecific
332 datasets might be due to the fact that phylogenetically related species exhibit similar eco-
333 physiological traits; Harvey and Pagel, 1991), the data were controlled for phylogenetic
334 influences using the “Phylogenetic Generalized Least-Squares” method (PGLS; Martins and
335 Hansen, 1997; Rohlf, 2001). This procedure estimates a covariance matrix of the species due
336 to their ancestral roots and includes these interrelationships as error term in a generalized least
337 squares algorithm to determine the model parameters. The phylogenetic trees for the two
338 datasets were derived by pruning the mammal supertree from Bininda-Emonds et al. (2007,
339 2008) of those species not represented in the datasets.

340
341 Allometric regressions were performed as linear regressions on log-transformed data, with
342 digestive parameters (DMI, $MRT_{particleGIT}$, aD DM, DMC) as the respective dependent
343 variables, and with log-transformed BM as the independent variable. Tests for a ‘curvature’ in
344 double-logarithmic space were made using quadratic regressions. Statistical analyses were
345 performed without (ordinary least squares regressions: OLS) and with accounting for
346 phylogeny (PGLS), in PASW 18.0 (SPSS Inc., Chicago, IL) and in R 2.15.0 (Team, 2011)
347 with the caper package. The significance level was set to $\alpha=0.05$.

348

349 **Results**

350 *Foose (1982) dataset*

351 Variables scaled as: Food intake (as organic matter intake, OMI) with $BM^{0.76}$, apparent
352 digestibility (of organic matter) with $BM^{0.02}$, organic matter gut contents (OMC) with $BM^{0.82}$,
353 and digesta retention with $BM^{0.07}$, which matches the predicted relationships of $0.07 \sim [0.82 -$
354 $0.76 + 0.02]$ (Table 1). Notably, the 95% confidence interval for the scaling of OMC did not
355 include 1.00 (Table 1). Results were similar in PGLS. Similar patterns were evident within
356 the hindgut fermenters and the ruminants only (Table 1). Both digesta retention and gut fill
357 had a scaling exponent lower than expected.

358

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

367

368 *Our dataset*

369 Variables scaled as: Food intake (as dry matter intake, DMI) with $BM^{0.76}$ (Fig. 2a), apparent
370 digestibility (of dry matter, aD DM) with $BM^{0.03}$ (Fig. 2c), dry matter gut contents (DMC)
371 with $BM^{0.93}$ (Fig. 2e), and digesta retention with $BM^{0.16}$ (Fig. 2g) (all in OLS), which matches
372 the predicted relationships of $0.16 \sim [0.93 - 0.76 + (-0.03)]$. Notably, the 95% confidence
373 interval for the scaling of DMC did not include 1.00 (Table 3). Results for PGLS were
374 similar; notably, the scaling exponent for MRT was lower than in OLS at $BM^{0.12}$.

375

376 When testing for a curvature effect in the overall dataset in OLS, such a curvature (visible
377 when plotting body mass residuals against body mass) was evident for dry matter intake (Fig.
378 2b) and for digesta retention (Fig. 2h), but not for digestibility (Fig. 2d) or gut contents (Fig.
379 2f). The full term describing the curvature was significant, with 95% confidence intervals that
380 did not include zero for the quadratic term, for intake and digesta retention only (Table 4); the
381 exponent of the quadratic term had a similar magnitude but a different sign for these two
382 measurements (intake: 0.053, retention: -0.057). In PGLS, these quadratic terms were not
383 significant (Table 4), indicating that the effect of the curvature was caused by the
384 phylogenetic structure of the dataset.

385

386 Splitting the overall dataset led to different scaling exponents for the various subsets (Table
387 5). The scaling of food intake had a lower exponent among species that produce more than
388 one offspring per litter or that are below a 10 kg threshold (95%CI 0.57-0.70 in OLS and
389 0.64-0.81 in PGLS), as opposed to species with one offspring per litter or above the 10 kg
390 threshold (95%CI 0.82-0.96 in OLS and 0.74-0.95 in PGLS). The scaling of dry gut contents
391 was similar among these groups (0.91-0.94 in OLS and 0.84-0.96 in PGLS; never including

392 1.00 in the 95%CI in OLS but for the larger animals in PGLS). In OLS, there was a difference
393 in the scaling of digesta retention between these groups, with a significant scaling exponent in
394 animals with more than one offspring per litter or below the 10 kg threshold, in contrast to no
395 significant scaling (95% confidence interval for the exponent included zero) in animals above
396 the 10 kg threshold (Table 5). In PGLS, the exponent of the MRT scaling in the animals with
397 more than one offspring per litter/below the 10 kg threshold was distinctively lower than in
398 OLS, with 95%CI approaching or including zero (Table 5) and thus making the scaling in this
399 group similar to the scaling in the group of animals with one offspring per litter/more than 10
400 kg. Notably, the 95%CI of the scaling exponent of intake and dry gut contents overlapped in
401 animals with a single offspring/animals >10 kg in OLS, and for all herbivores in PGLS.

402
403 Splitting the species into the four digestion types resulted in similar patterns, with a lower
404 scaling exponent for intake, and a higher one for digesta retention, in the (small) caecum
405 fermenters as compared to the other groups in OLS (Table 6). In PGLS, these differences
406 were not evident; in particular, the scaling exponent for MRT in caecum fermenters was much
407 lower in PGLS at 0.14 than in OLS at 0.27, suggesting the high scaling previously reported in
408 caecum fermenters of 0.25 (Clauss et al., 2007a) was due to an uneven distribution of
409 phylogenetically distant species within this data subset (Table 6). A scaling exponent of 1.00
410 for gut fill was only included in the confidence interval for ruminants in OLS, and for colon
411 fermenters and ruminants in PGLS. The 95% CI of the scaling exponent overlapped for intake
412 and gut fill in all but the caecum fermenters in OLS, and in all four groups in PGLS (Table 6).

413
414 Within the body mass residuals of the whole dataset (Table 7), intake was negatively
415 correlated with digesta retention (Fig. 3a) and positively with gut fill (Fig. 3b) in both OLS
416 and PGLS. Although digestibility was negatively related to intake and positively related to
417 digesta retention (Fig. 3c) in OLS, these relationships were not significant in PGLS (Table 7),
418 i.e. they do not occur within more closely related taxa. By contrast, digestibility was
419 negatively related to gut fill in PGLS, indicating that among more closely related species,
420 those with a higher gut fill had lower digestibilities. Gut fill was positively related to digesta
421 retention in both OLS and PGLS (Table 7, Fig. 3d).

422 423 *Wet gut contents*

424 When testing for a scaling curvature in the dataset on wet gut contents, the quadratic term was
425 not significant (OLS $p=0.706$; PGLS $p=0.463$). Wet gut contents scaled to 0.108 (0.095-

426 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) $BM^{1.086(1.004-$
427 $1.167)}$ ($R^2=0.907$, $p<0.001$) in PGLS. Thus, when comparing the scaling of wet gut contents
428 and of dry matter gut contents, the difference between the two increases with body mass (Fig.
429 4); from the comparison of the two scaling exponents (OLS 0.93 and 1.06; PGLS 0.92 and
430 1.09), the dry matter concentration of gut contents should theoretically scale to $BM^{-0.13}$ or
431 $BM^{-0.17}$.

432

433 **Discussion**

434 The aim of this study was to test whether empirical data allow evoking differences in the
435 allometric scaling between physiological characteristics, to explain species diversification and
436 niche differentiation along a body size gradient in herbivores. Two effects have previously
437 been associated with body size-driven diversification in mammalian herbivores, namely a
438 higher scaling of food intake as compared to the scaling of metabolism (Hackmann and Spain,
439 2010), and a distinct difference in the scaling of food intake and gut fill, leading to a positive
440 scaling of digesta retention time (Demment and Van Soest, 1985). If we assume that the
441 results of controlled feeding studies are indeed representative of the digestive physiology of
442 the animals investigated, then the results indicate that from these two effects, the former
443 represents the more promising approach, in particular for larger herbivores.

444

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

460 exponent of retention time (see Introduction). The ultimate reason why digesta retention
461 shows a low scaling with body mass in herbivores might stem from the fact that from a
462 certain body size upwards, a further increase in retention time will not, on average, convey
463 additional advantages, principally because the additional gain from exposing digesta to the
464 digestive process for a longer time is lower than the gain from additional food intake
465 (Hummel et al., 2006).

466
467 Several arguments can be put forward to support the validity of our findings. The below-
468 linear scaling of gut contents was present in both of the datasets investigated (Tables 1 and 3).
469 The assumption that gut contents (as a proxy for gut capacity) scale linearly with body mass
470 was originally derived from datasets that related wet gut content mass to body mass (Parra,
471 1978; Demment and Van Soest, 1985; Justice and Smith, 1992; Clauss et al., 2007a; Illius and
472 Gordon 1992 is the only publication that uses dry matter gut contents and also arrives at linear
473 scaling, but the dataset comprised only 16 species). If one assumes that this finding translates
474 directly into a similar scaling for that unit of gut fill related to food intake (i.e. dry matter),
475 then one makes the silent assumption that the proportion of moisture in gut contents is similar
476 across all body sizes (as done by Demment, 1983). However, Justice and Smith (1992)
477 reported that the DM concentration of the contents of the fermentation chamber scales to $BM^{0.08}$
478 – in other words, the contents of this part of the gut becomes more watery in larger
479 animals. Their finding is corroborated by our comparison of the scaling of total wet and dry
480 matter gut contents, which yields a similar negative scaling at $BM^{-0.13}$ to $BM^{-0.17}$. Similarly,
481 Müller et al. (2011) found, in a comparative analysis of mean retention times of particle and
482 solute (fluid) markers, that the difference between these two digesta phases tends to increase
483 with body mass – not necessarily because particles are retained longer in larger animals, but
484 also because fluids are passed through their digestive system at a higher rate. One non-
485 exclusive ultimate reason for this might be the fact that in the larger guts of larger animals,
486 diffusion distances from within the digesta to the sites of absorption in the gut wall are
487 increased (Clauss and Hummel, 2005), a problem that could be solved by a more fluid digesta
488 (Lentle et al., 2006). Thus, we suggest that the assumption that that part of gut fill relevant to
489 food intake and digestibility (i.e. the dry matter gut fill) scales linearly with body mass cannot
490 be defended until more data become available.

491
492 The other important assumption that is challenged by our findings is that food intake scales
493 uniformly to $BM^{0.75}$. Unfortunately, a direct inclusion of data on basal metabolic rate (BMR)

494 in our study is not feasible; although BMR has been measured in a large variety of
495 mammalian species (McNab, 2008), the large animals that form a majority of our dataset are
496 not included in the available BMR data pool. Therefore, we need to refer to comparisons of
497 our findings to those from BMR studies, inherently with a distinct difference in the species
498 sets investigated. In the debate on the scaling of basal metabolic rate, it has been found
499 repeatedly that across the whole mammalian body mass range, a single allometric exponent
500 does not represent the data very precisely, but that either a curvature in log-log space, or a
501 combination of different scaling relationships of subgroups provides a better fit (Hayssen and
502 Lacy, 1985; Clarke et al., 2010; Isaac and Carbone, 2010; Kolokotronis et al., 2010; Müller et
503 al., 2012). The magnitude of an overall mammalian scaling exponent will therefore depend
504 either on the body mass range included in the analysis (Lovegrove, 2000; Dodds et al., 2001;
505 Glazier, 2005; White and Seymour, 2005), the taxonomic composition of the sample
506 (Hayssen and Lacy, 1985; Sieg et al., 2009; White et al., 2009; Capellini et al., 2010), or on
507 the inclusion of animals according to certain biological characteristics (McNab, 2008; Müller
508 et al., 2012). Although our species sample of mammalian herbivores is lower than the datasets
509 used to investigate the scaling of metabolism, a similar ‘curvature effect’ is evident in the
510 intake and retention data (Fig. 2ab and 2gh). Our findings thus provide further support to
511 these previous studies that scaling exponents are not necessarily a universal characteristic for
512 the whole mammalian clade, but may differ either between different groups, or vary across
513 the body mass range. In particular, the results indicate that the group of mammals that can be
514 classified as either small, giving birth to multiple young at a time, or being caecum fermenters
515 has a generally lower scaling of food intake than animals classified as larger, giving birth to a
516 single offspring, or being colon fermenters, nonruminant foregut fermenters or ruminants.
517 Which of these classifications is biologically relevant for the difference in scaling, or whether
518 they are all proxies for a yet undefined functional subdivision of mammals, remains to be
519 investigated. Because a similar ‘curvature effect’ is evident in the scaling of metabolic rate,
520 where not only herbivores but also other feeding types were included in the dataset
521 (Kolokotronis et al., 2010; Müller et al., 2012), we suggest that digestive strategy is unlikely
522 to be the relevant proxy. Regardless, our study suggests that the use of one single exponent to
523 describe relative metabolic rates or relative food intakes may be convenient, but should not be
524 the basis for biological models.

525

526 Within one notable subset of large herbivores, the ruminants, the assumption that food intake
527 scales to $BM^{0.75}$ has previously been refuted based either on conceptual approaches or

528 collections of empirical data: Mertens (1994) and Südekum (2002) explain that for low-
529 quality forages, relating food intake in domestic ruminants to body mass may be more
530 appropriate than using metabolic body mass as the basis. Hackman and Spain (2010) collated
531 data on the voluntary food intake (VFI) in domestic and wild ruminant species in a dataset
532 more comprehensive than ours (that was limited to studies that also measured digestibility and
533 retention), and concluded that VFI scaled to $BM^{0.9}$, which was similar to that described in
534 previous studies on domestic ruminants (Graham, 1972; Minson, 1990; Reid et al., 1990). The
535 authors concluded that the intermediate scaling between metabolism (0.75) and gut fill (1.0)
536 indicated that both metabolic and physical constraints determine food intake; they also
537 conclude that the putative difference between the scaling of metabolism (0.75) and the scaling
538 of intake (0.9) allows larger animals to ingest lower-quality food and still meet their energetic
539 requirements. Note that this interpretation of scaling differences does not draw on an alleged
540 scaling of digestion efficiency and retention times.

541
542 The assumption that intake might scale to a higher exponent than basal metabolic rate is
543 supported when comparing the intake scaling exponent of large herbivores/herbivores with
544 one offspring of this study (0.81-0.89, Table 5) with that of the BMR in mammals with one
545 offspring (0.76; Müller et al. 2012). In contrast, for the small herbivores/herbivores with more
546 than one offspring, such a difference is not evident at 0.62-0.72 for the intake scaling
547 exponent in this study and 0.69 for that of BMR (Müller et al. 2012). To explain body size
548 effects in this group, factors such as variation in feeding selectivity and caecotroph use via
549 coprophagy must be further investigated (Justice and Smith, 1992; Franz et al., 2011b). In
550 particular, it remains unknown whether the proportion of intake achieved via coprophagy
551 varies systematically with body mass. Preliminary results indicate that this proportion
552 increases with increasing dietary fibre content (Takahashi and Sakaguchi, 1998). If we
553 assume that compared to smaller species, larger caecum fermenters are adapted to lower-
554 quality diets (i.e. diets higher in fibre), and should therefore be generally adapted to a higher
555 proportion of intake via coprophagy, this might help explain the lower scaling of intake via
556 food (as measured in the digestion experiments collated in this study) in this group. Further
557 studies that assess the contribution of coprophagy over a wide range of body sizes are
558 required to explore this possibility.

559
560 Apart from the logical issue with drawing conclusions on the scaling of digestibility from the
561 scaling of digesta retention explained in the Introduction, our data collection yields some

562 further insights concerning correlates and effects of digesta retention. As reported previously
563 in inter- and intraspecific analyses (Clauss et al., 2007a; Clauss et al., 2007b; Müller et al.,
564 2011; Steuer et al., 2011), species with a higher relative food intake have comparatively
565 shorter retention times (Fig. 3a). Langer and Snipes (1991) suggested that interspecifically,
566 animals achieve longer digesta retention by higher gut capacities, a concept supported by our
567 findings (Fig. 3b). Additionally, capacity for a higher gut fill will allow a higher food intake
568 (Fig. 3d).

569

570 Although increasing retention times may be associated with higher general digestive
571 efficiencies in intraspecific studies (Clauss et al., 2007b), this effect is most evident in
572 interspecific comparisons in relation to the digestibility of the fibre component of the food
573 (Udén and Van Soest, 1982; Clauss et al., 2009). When comparing the overall diet
574 digestibility, as in this study, where we collated data on the dry matter or organic matter
575 digestibility but not the fibre digestibility, no significant effect of digesta retention on
576 digestibility is evident when accounting for the phylogenetic structure of the data (Table 3 and
577 7). In other words, although larger clades differ systematically in retention and digestibility,
578 such as the colon fermenters and ruminants in Fig. 1c, the effect is not evident among more
579 closely related species – in the case of the Foose (1982) dataset even though consistent diets
580 were used. One potential reason is that digesta retention is not the only determinant of
581 digestibility, but acts together with digesta particle size reduction, either compensating for
582 poor chewing efficiency (as for example in hippopotamuses) or reinforcing a high chewing
583 efficiency (as in the ruminants) (Clauss et al., 2009). Another potential reason is that overall
584 dry matter digestibility does not necessarily reflect fibre digestibility. A small-scale data
585 collection in Clauss and Hummel (2005) suggested that fibre digestibility may vary more
586 across a large herbivore body mass range than does overall diet digestibility, which remained
587 rather constant (as in this study). The authors summarized concepts that interpret these data as
588 indication for a better utilization of non-fibrous food components in smaller animals,
589 including the segregation of bacterial protein during caecotroph formation by the colonic
590 separation mechanism (Björnhag, 1987; Franz et al., 2011b). Understanding how bacterial
591 nitrogen utilization and endogenous/metabolic nitrogen losses vary with body mass and
592 between the different herbivore digestive strategies remains one of the major challenges in
593 studying herbivore digestive physiology (Schwarm et al., 2009b).

594

595 Herbivores will maximize energy intake if they maximize feeding selectivity, food intake and
596 digesta retention (by increasing gut fill), particle size reduction (by more elaborate cranio-
597 dental designs and by sorting mechanisms in ruminants that increase chewing efficiency), and
598 minimize endogenous/metabolic faecal losses. The major dilemma in this array of factors is
599 that increasing food intake is usually associated with a lower feeding selectivity, shorter
600 digesta retention and reduced particle size reduction (Clauss et al., 2010a). It is commonly
601 assumed that the different herbivore species or groups represent different, equally successful
602 'digestive strategies' to solve this dilemma, varying in the emphasis of the individual
603 interrelated factors (Hume, 2005). Alternatively, one can hypothesize that the sequence of
604 radiation events in herbivores indicates different levels of optimization of the overall interplay
605 of these factors (Fritz et al., 2009). For example, bovid ruminants, as the most recently
606 radiated large herbivore group, potentially represent the hitherto most sophisticated design
607 that combines high food intakes, long retention times and high chewing efficiency with a very
608 efficient use of the symbiotic microflora (Clauss et al., 2010a; Müller et al., 2011). How
609 species that use similar niches with different digestive strategies can persist then requires
610 different explanations. Such a view shifts the focus in tracing niche differentiation and species
611 diversification from simple allometric considerations to more complex aspects of variation in
612 organismal design.

613

614 **Acknowledgements**

615 This work was supported by DFG grants CL 182/3-1, 5-1 and 6-1. This is contribution no.
616 119 of the DFG Research Group 533 Biology of the Sauropod Dinosaurs: The Evolution of
617 Gigantism.

618

619 **References**

- 620 Baker, D.L., Hobbs, N.T., 1987. Strategies of digestion: digestive efficiency and retention
621 times of forage diets in montane ungulates. *Can. J. Zool.* 65, 1978-1984.
- 622 Barboza, P.S., Bowyer, R.T., 2000. Sexual segregation in dimorphic deer: a new gastrocentric
623 hypothesis. *J. Mammal.* 81, 473-489.
- 624 Behrend, A., Lechner-Doll, M., Streich, W.J., Clauss, M., 2004. Seasonal faecal excretion,
625 gut fill, liquid and particle marker retention in mouflon (*Ovis ammon musimon*), and a
626 comparison with roe deer (*Capreolus capreolus*). *Acta Theriol.* 49, 503-515.
- 627 Bell, R.H.V., 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* 225, 86-93.
- 628 Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D.,
629 Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2007. The delayed rise of
630 present-day mammals. *Nature* 446, 507-512.

631 Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D.,
632 Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2008. Corrigendum: The
633 delayed rise of present-day mammals. *Nature* 456, 274.

634 Björnhag, G., 1987. Comparative aspects of digestion in the hindgut of mammals. The
635 colonic separation mechanism. *Dt. tierärztl. Wschr.* 94, 33-36.

636 Brown, J.H., Sibly, R.M., Kodric-Brown, A., 2012. Introduction: metabolism as the basis for
637 a theoretical unification of ecology, in: R.M. Sibly, J.H. Brown, A. Kodric-Brown (Eds.),
638 *Metabolic ecology. A scaling approach.* Wiley-Blackwell, Chichester, UK, 1-6.

639 Capellini, I., Venditti, C., Barton, R.A., 2010. Phylogeny and metabolic scaling in mammals.
640 *Ecology* 91, 2783–2793.

641 Clarke, A., Rothery, P., Isaac, N.J.B., 2010. Scaling of basal metabolic rate with body mass
642 and temperature in mammals. *J. Anim. Ecol.* 79, 610-619.

643 Clauss, M., Hummel, J., 2005. The digestive performance of mammalian herbivores: why big
644 may not be *that* much better. *Mammal Rev.* 35, 174-187.

645 Clauss, M., Schwarm, A., Ortmann, S., Streich, W.J., Hummel, J., 2007a. A case of non-
646 scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta
647 passage in mammalian herbivores. *Comp. Biochem. Physiol. A* 148, 249-265.

648 Clauss, M., Streich, W.J., Schwarm, A., Ortmann, S., Hummel, J., 2007b. The relationship of
649 food intake and ingesta passage predicts feeding ecology in two different megaherbivore
650 groups. *Oikos* 116, 209-216.

651 Clauss, M., Nunn, C., Fritz, J., Hummel, J., 2009. Evidence for a tradeoff between retention
652 time and chewing efficiency in large mammalian herbivores. *Comp. Biochem. Physiol. A*
653 154, 376-382.

654 Clauss, M., Hume, I.D., Hummel, J., 2010a. Evolutionary adaptations of ruminants and their
655 potential relevance for modern production systems. *Animal* 4, 979-992.

656 Clauss, M., Lang-Deuerling, S., Müller, D.W.H., Kienzle, E., Steuer, P., Hummel, J., 2010b.
657 Retention of fluid and particles in captive tapirs (*Tapirus* spp.). *Comp. Biochem. Physiol.*
658 *A* 157, 95–101.

659 Codron, D., Lee-Thorp, J.A., Sponheimer, M., Codron, J., de Ruiter, D., Brink, J.S., 2007.
660 Significance of diet type and diet quality for ecological diversity of African ungulates. *J.*
661 *Anim. Ecol.* 76, 526-537.

662 Demment, M.W., 1983. Feeding ecology and the evolution of body size of baboons. *Afr. J.*
663 *Ecol.* 21, 219-233.

664 Demment, M.W., Van Soest, P.J., 1985. A nutritional explanation for body size patterns of
665 ruminant and nonruminant herbivores. *Am. Nat.* 125, 641-672.

666 Dodds, P.S., Rothman, D.H., Weitz, J.S., 2001. Re-examination of the "3/4-law" of
667 metabolism. *J. Theor. Biol.* 209, 9-27.

668 du Toit, J.T., 2005. Sex differences in the foraging ecology of large mammalian herbivores,
669 in: K.E. Ruckstuhl, P. Neuhaus (Eds.), *Sexual segregation in vertebrates: ecology of the*
670 *two sexes.* Cambridge University Press, New York, 35-52.

671 Fleming, T.H., 1991. The relationship between body size, diet, and habitat use in frugivorous
672 bats, Genus *Carollia* (Phyllostomidae). *J. Mammal.* 72, 493-501.

673 Foote, T.J., 1982. *Trophic strategies of ruminant versus nonruminant ungulates.* University of
674 Chicago, Chicago.

675 Franz, R., Hummel, J., Müller, D.W.H., Bauert, M., Hatt, J.-M., Clauss, M., 2011a.
676 Herbivorous reptiles and body mass: effects on food intake, digesta retention, digestibility
677 and gut capacity, and a comparison with mammals. *Comp. Biochem. Physiol. A* 158, 94-
678 101.

679 Franz, R., Kreuzer, M., Hummel, J., Hatt, J.-M., Clauss, M., 2011b. Intake, selection, digesta
680 retention, digestion and gut fill of two coprophageous species, rabbits (*Oryctolagus*

681 *cuniculus*) and guinea pigs (*Cavia porcellus*), on a hay-only diet. J. Anim. Physiol. Anim.
682 Nutr. 95, 564–570.

683 Fritz, J., Hummel, J., Kienzle, E., Arnold, C., Nunn, C., Clauss, M., 2009. Comparative
684 chewing efficiency in mammalian herbivores. Oikos 118, 1623-1632.

685 Fritz, J., Hammer, S., Hebel, C., Arif, A., Michalke, B., Dittmann, M.T., Müller, D.W.H.,
686 Clauss, M., 2012. Retention of solutes and different-sized particles in the digestive tract of
687 the ostrich (*Struthio camelus massaicus*), and a comparison with mammals and reptiles.
688 Comp. Biochem. Physiol. A 163, 56–65.

689 Gaulin, S.J.C., 1979. A Jarman-Bell model of primate feeding niches. Human Ecology 7, 1-
690 20.

691 Geist, V., 1974. On the relationship of social evolution and ecology in ungulates. American
692 Zoology 14, 205-220.

693 Glazier, D.S., 2005. Beyond the '3/4-power law': variation in the intra- and interspecific
694 scaling of metabolic rate in animals. Biol. Rev. 80, 1-52.

695 Gordon, I.J., Illius, A.W., 1996. The nutritional ecology of African ruminants: a
696 reinterpretation. J. Anim. Ecol. 65, 18-28.

697 Graham, N.M., 1972. Units of metabolic body size for comparisons amongst adult sheep and
698 cattle. Proceedings of the Australian Society of Animal Production 9, 352-355.

699 Gross, J.E., Alkon, P.U., Demment, M.W., 1996. Nutritional ecology of dimorphic
700 herbivores: digestion and passage rates in Nubian ibex. Oecologia 107, 170-178.

701 Hackmann, T.J., Spain, J.N., 2010. Ruminant ecology and evolution: Perspectives useful to
702 ruminant livestock research and production. J. Dairy Sci. 93, 1320–1334.

703 Hanley, T.A., Hanley, K.A., 1980. Food resource partitioning by sympatric ungulates on
704 Great Basin rangeland. J. Range Manage. 35, 152-158.

705 Hanley, T.A., 1982. The nutritional basis for food selection by ungulates. J. Range Manage.
706 35, 146-151.

707 Harvey, P.H., Pagel, M.D., 1991. The comparative method in evolutionary biology. Oxford
708 University Press, Oxford.

709 Hayssen, V., Lacy, R.C., 1985. Basal metabolic rates in mammals: taxonomic differences in
710 the allometry of BMR and body mass. Comp. Biochem. Physiol. A 81, 741-754.

711 Holleman, D.F., White, R.G., 1989. Determination of digesta fill and passage rate from non
712 absorbed particulate phase markers using the single dosing method. Can. J. Zool. 67, 488-
713 494.

714 Hume, I.D., 2005. Concepts of digestive efficiency, in: J.M. Starck, T. Wang (Eds.),
715 Physiological and ecological adaptations to feeding in vertebrates. Science Publishers,
716 Enfield NH, 43-58.

717 Hummel, J., Südekum, K.-H., Streich, W.J., Clauss, M., 2006. Forage fermentation patterns
718 and their implications for herbivore ingesta retention times. Funct. Ecol. 20, 989-1002.

719 Hummel, J., Clauss, M., 2011. Feeding and digestive physiology, in: N. Klein, K. Remes,
720 C.T. Gee, M. Sander (Eds.), Understanding the life of giants. The biology of the sauropod
721 dinosaurs. Indiana University Press, Bloomington, 11-33.

722 Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores:
723 evolution of body size and competitive interactions. Oecologia 89, 428-434.

724 Isaac, N.J.B., Carbone, C., 2010. Why are metabolic scaling exponents so controversial?
725 Quantifying variance and testing hypotheses. Ecol. Lett. 13, 728-735.

726 Jarman, P.J., 1974. The social organization of antelope in relation to their ecology. Behaviour
727 48, 215-266.

728 Justice, K.E., Smith, F.A., 1992. A model of dietary fiber utilization by small mammalian
729 herbivores, with empirical results for *Neotoma*. Am. Nat. 139, 398-416.

730 Kolokotronis, T., Savage, V.M., Deeds, E.J., Fontana, W., 2010. Curvature in metabolic
731 scaling. Nature 464, 753-756.

- 732 Langer, P., Snipes, R.L., 1991. Adaptations of gut structure to function in herbivores, in: T.
733 Tsuda, Y. Sasaki, R. Kawashima (Eds.), *Physiological aspects of digestion and metabolism*
734 *in ruminants*. Academic Press, San Diego, 349-384.
- 735 Lentle, R., Hemar, Y., Hall, C., 2006. Viscoelastic behaviour aids extrusion from and
736 reabsorption of the liquid phase into the digesta plug: creep rheometry of hindgut digesta
737 in the common brushtail possum *Trichosurus vulpecula*. *J. Comp. Physiol. B* 176, 469-
738 475.
- 739 Lovegrove, B.G., 2000. The zoogeography of mammalian basal metabolic rate. *Am. Nat.* 156,
740 201-219.
- 741 Martins, E.P., Hansen, T.F., 1997. Phylogenies and the comparative method: a general
742 approach to incorporating phylogenetic information into analysis of interspecific data. *Am.*
743 *Nat.* 149, 646-667.
- 744 McNab, B.K., 2002. *The physiological ecology of vertebrates. A view from energetics.*
745 Cornell University Press, Ithaca & London.
- 746 McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of
747 mammalian BMR. *Comp. Biochem. Physiol. A* 151, 5-28.
- 748 Mertens, D.R., 1994. Regulation of forage intake, in: G.C. Fahey, M. Collins, D.R. Mertens,
749 L.E. Moser (Eds.), *Forage quality, evaluation, and utilization*. American Society of
750 Agronomy, Madison, WI, 450-493.
- 751 Meyer, K., Hummel, J., Clauss, M., 2010. The relationship between forage cell wall content
752 and voluntary food intake in mammalian herbivores. *Mammal Rev.* 40, 221-245.
- 753 Minson, D.J., 1990. *Forage in ruminant nutrition*. Academic Press, London.
- 754 Müller, D.W.H., Caton, J., Codron, D., Schwarm, A., Lentle, R., Streich, W.J., Hummel, J.,
755 Clauss, M., 2011. Phylogenetic constraints on digesta separation: variation in fluid
756 throughput in the digestive tract in mammalian herbivores. *Comp. Biochem. Physiol. A*
757 160, 207–220.
- 758 Müller, D.W.H., Codron, D., Werner, J., Fritz, J., Hummel, J., Griebeler, E.M., Clauss, M.,
759 2012. Dichotomy of eutherian reproduction and metabolism. *Oikos* 121, 102-115.
- 760 Munn, A.J., Dawson, T.J., 2006. Forage fibre digestion, rates of feed passage and gut fill in
761 juvenile and adult red kangaroos (*Macropus rufus*): why body size matters. *J. Exp. Biol.*
762 209, 1535-1547.
- 763 Munn, A.J., Barboza, P.S., 2008. Could a big gut be too costly for muskoxen (*Ovibos*
764 *moschatus*) in their first winter? *Zoology* 111, 350-362.
- 765 Munn, A.J., Tomlinson, S., Savage, T., Clauss, M., 2012. Retention of different-sized
766 particles and derived gut fill estimate in tammar wallabies (*Macropus eugenii*):
767 physiological and methodological considerations. *Comp. Biochem. Physiol. A* 161, 243–
768 249.
- 769 Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles,
770 and birds. *Ann. Rev. Nutr.* 19, 247-277.
- 771 Owen-Smith, N., 1988. *Megaherbivores - the influence of very large body size on ecology.*
772 Cambridge University Press, Cambridge.
- 773 Packard, G.C., 2012. Is non-loglinear allometry a statistical artifact? *Biol. J. Linn. Soc.*
774 (online).
- 775 Parra, R., 1978. Comparison of foregut and hindgut fermentation in herbivores, in: G.G.
776 Montgomery (Ed.), *The ecology of arboreal folivores*. Smithsonian Institution Press,
777 Washington DC, 205-229.
- 778 Pérez-Barbería, F.J., Elston, D.A., Gordon, I.J., Illius, A.W., 2004. The evolution of
779 phylogenetic differences in the efficiency of digestion in ruminants. *Proc. R. Soc. B* 271,
780 1081-1090.
- 781 Prins, R.A., Geelen, M.J.H., 1971. Rumen characteristics of red deer, fallow deer and roe
782 deer. *J. Wildl. Manage.* 35, 673-680.

783 Reid, R.L., Jung, G.A., Cox-Ganser, J.M., Rybeck, B.F., Townsend, E.C., 1990. Comparative
784 utilization of warm-and cool-season forages by cattle, sheep and goats. *J. Anim. Sci.* 68,
785 2986–2994.

786 Robbins, C.T., 1993. *Wildlife feeding and nutrition*. Academic Press, San Diego.

787 Rohlf, F., 2001. Comparative methods for the analysis of continuous variables: geometric
788 interpretations. *Evolution* 55, 2143-2160.

789 Rucker, R., Storms, D., 2002. Interspecies comparisons of micronutrient requirements:
790 metabolic vs. absolute body size. *J. Nutr.* 132, 2999-3000.

791 Sawada, A., Sakaguchi, E., Hanya, G., 2011. Digesta passage time, digestibility, and total gut
792 fill in captive Japanese macaques (*Macaca fuscata*): effects food type and food intake
793 level. *Int. J. Primatol.* 32, 390-405.

794 Schwarm, A., Ortmann, S., Wolf, C., Streich, W.J., Clauss, M., 2009a. More efficient
795 mastication allows increasing intake without compromising digestibility or necessitating a
796 larger gut: comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus
797 (*Hexaprotodon liberiensis*). *Comp. Biochem. Physiol. A* 152, 504-512.

798 Schwarm, A., Schweigert, M., Ortmann, S., Hummel, J., Janssens, G., Streich, W.J., Clauss,
799 M., 2009b. No easy solution for the fractionation of faecal nitrogen in captive wild
800 herbivores: results of a pilot study. *J. Anim. Physiol. Anim. Nutr.* 93, 596–605.

801 Shannon, G., Page, B., Duffy, K., Slotow, R., 2006. The role of foraging behaviour in the
802 sexual segregation of the African elephant. *Oecologia* 150, 344-354.

803 Shipley, L.A., 2007. The influence of bite size on foraging at larger spatial and temporal
804 scales by mammalian herbivores. *Oikos* 116, 1964-1974.

805 Shipley, R.A., Clark, R.E., 1972. *Tracer methods for in vivo kinetics*. Academic Press, New
806 York.

807 Short, H.L., 1963. Rumen fermentation and energy relationships in the white-tailed deer. *J.*
808 *Wildl. Manage.* 28, 445-458.

809 Sieg, A.E., O'Connor, M.P., McNair, J.N., Grant, B.W., Agosta, S.J., Dunham, A.E., 2009.
810 Mammalian metabolic allometry: do intraspecific variation, phylogeny, and regression
811 models matter? *Am. Nat.* 174, 720-733.

812 Sinclair, A.R.E., 1977. *The African buffalo: a study of resource limitation of populations*.
813 University of Chicago Press, Chicago.

814 Steele, R., 1971. *Tracer probes in steady state systems*. Charles C. Thomas Publisher,
815 Springfield IL.

816 Steuer, P., Südekum, K.-H., Müller, D.W.H., Franz, R., Kaandorp, J., Clauss, M., Hummel, J.,
817 2011. Is there an influence of body mass on digesta mean retention time in herbivores? A
818 comparative study on ungulates. *Comp. Biochem. Physiol. A* 160, 355-364.

819 Steuer, P., Südekum, K.-H., Müller, D.W.H., Kaandorp, J., Clauss, M., Hummel, J., 2012.
820 Fibre digestibility in large herbivores as related to digestion type and body mass - an in
821 vitro approach. (submitted).

822 Stevens, C.E., Hume, I.D., 1995. *Comparative physiology of the vertebrate digestive system*.
823 Cambridge University Press, New York.

824 Südekum, K.-H., 2002. Technical basis of international feed evaluation systems for dairy
825 cows and future prospects for the German recommendations (energy, protein and amino
826 acids). *Übersichten Tierernährung* 30, 135-162.

827 Takahashi, T., Sakaguchi, E., 1998. Behaviors and nutritional importance of coprophagy in
828 captive adult and young nutrias (*Myocastor coypus*). *J. Comp. Physiol. B* 168, 281-288.

829 Team, R.D.C., 2011. *R: A language and environment for statistical computing*. R Foundation
830 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)
831 [project.org/](http://www.R-project.org/).

832 Tershy, B.R., 1992. Body size, diet, habitat use, and social behavior of balaenoptera whales in
833 the Gulf of California. *J. Mammal.* 73, 477-486

- 834 Udén, P., Rounsaville, T.R., Wiggans, G.R., Van Soest, P.J., 1982. The measurement of
835 liquid and solid digesta retention in ruminants, equines and rabbits given timothy (*Phleum*
836 *pratense*) hay. Br. J. Nutr. 48, 329-339.
- 837 Udén, P., Van Soest, P.J., 1982. Comparative digestion of timothy fiber by ruminants, equines
838 and rabbits. Br. J. Nutr. 47, 267-272.
- 839 Van Soest, P.J., 1994. Nutritional ecology of the ruminant, 2nd ed. Cornell University Press,
840 Ithaca.
- 841 Wenninger, P.S., Shipley, L.A., 2000. Harvesting, rumination, digestion, and passage of fruit
842 and leaf diets by a small ruminant, the blue duiker. Oecologia 123, 466-474.
- 843 White, C.R., Seymour, R.S., 2005. Allometric scaling of mammalian metabolism. J. Exp.
844 Biol. 208, 1611-1619.
- 845 White, C.R., Blackburn, T.M., Seymour, R.S., 2009. Phylogenetically informed analysis of
846 the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-
847 power scaling. Evolution 63, 2658-2667.
- 848 Woolley, L.-A., Page, B., Slotow, R., 2011. Foraging strategy within African elephant family
849 units: Why body size matters. Biotropica 43, 489-495.
- 850
- 851
- 852

853 Table 1. Scaling relationships of parameters of digestive physiology with body mass (BM) in
 854 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

855 organic matter intake (OMI in kg d⁻¹); apparent digestibility of organic matter (aDOM in %);
 856 organic matter gut contents (OMC in kg); particle mean retention time (MRT in h)

857
 858

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

	stats	Residual aDOM	Residual OMC	Residual MRT
Residual OMI	OLS	R=-0.137, p=0.505	R=0.841, p<0.001	R=-0.577, p=0.002
	PGLS	R=-0.300, p=0.114	R=0.828, p<0.001	R=0.033, p=0.975
Residual aDOM	OLS		R=0.173, p=0.398	R=0.654, p<0.001
	PGLS		R=0.297, p=0.120	R=0.293, p=0.126
Residual OMC	OLS			R=-0.055, p=0.790
	PGLS			R=0.575, p<0.001

862 organic matter intake (OMI in kg d⁻¹); apparent digestibility of organic matter (aDOM in %);
 863 organic matter gut contents (OMC in kg); particle mean retention time (MRT in h)

864
 865

866 Table 3. Scaling relationships of parameters of digestive physiology with body mass (BM) in
 867 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- -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- -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

868 dry matter intake (DMI in kg d⁻¹); apparent digestibility of dry matter (aDDM in %); dry
 869 matter gut contents (DMC in kg); particle mean retention time (MRT in h)

870
 871

872 Table 4. Evidence for quadratic scaling in parameters of digestive physiology with body mass
 873 (BM) in the dataset of this study (n=77) (OLS). Linear regression models according to
 874 $\log y = a + b1(\log BM) + b2((\log BM)^2)$ or $y = a BM^{(b1+b2(\log BM))}$

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--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--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--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

875 dry matter intake (DMI in kg d⁻¹); apparent digestibility of dry matter (aDDM in %); dry
 876 matter gut contents (DMC in kg); particle mean retention time (MRT in h)

877
 878

879 Table 5. Scaling relationships of parameters of digestive physiology with body mass (BM) in
 880 the dataset of this study in subsets according to litter size or a 10 kg body mass threshold
 881 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		62.230	57.4-67.3	-0.023	-0.054-0.008	0.095	0.142
DMC		0.027	0.022-0.034	0.905	0.825-0.986	0.961	<0.001
MRT		19.275	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		72.611	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		36.475	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		67.453	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		22.751	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		64.863	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		41.687	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

882 dry matter intake (DMI in kg d⁻¹); apparent digestibility of dry matter (aDDM in %); dry
 883 matter gut contents (DMC in kg); particle mean retention time (MRT in h)

884

885 Table 6. Scaling relationships of parameters of digestive physiology with body mass (BM) in
 886 the dataset of this study in subsets according to digestion types using OLS and PGLS statistics
 887 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

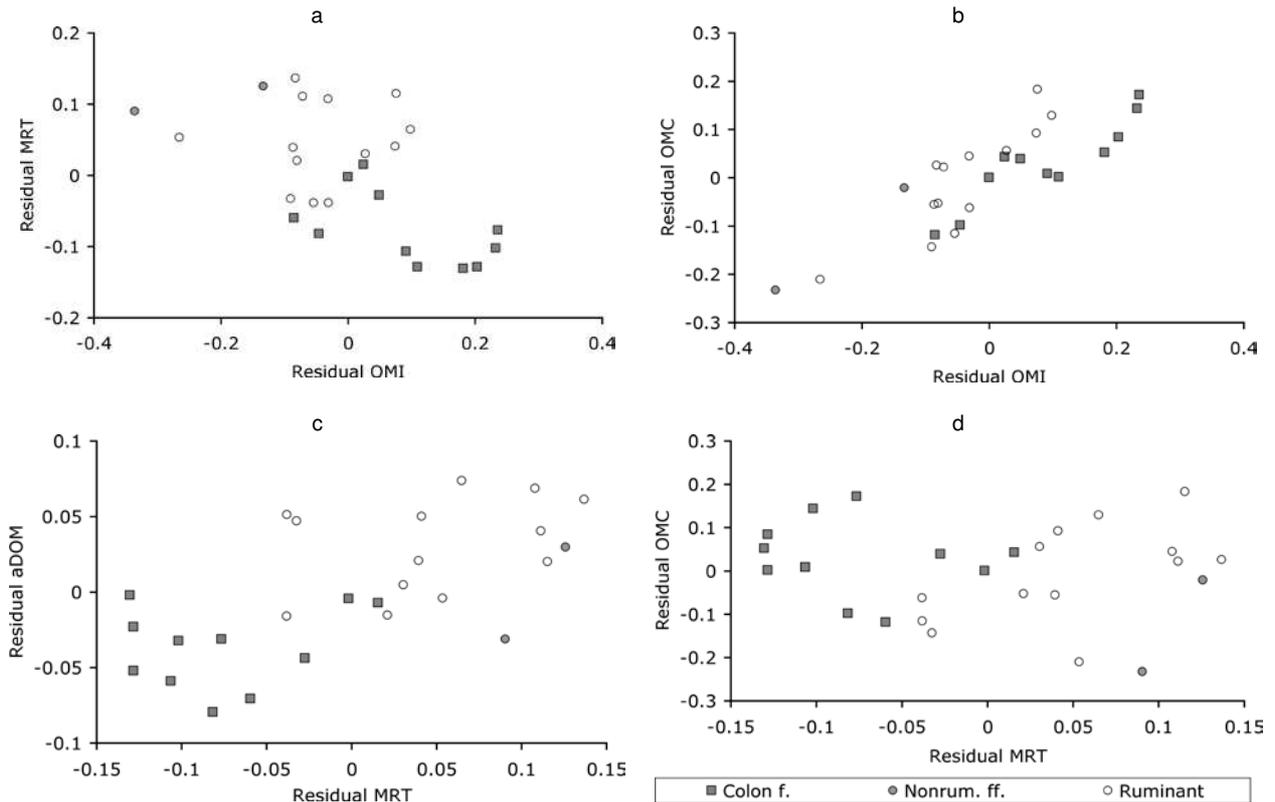
888 dry matter intake (DMI in kg d⁻¹); apparent digestibility of dry matter (aDDM in %); dry
 889 matter gut contents (DMC in kg); particle mean retention time (MRT in h)

890
 891
 892

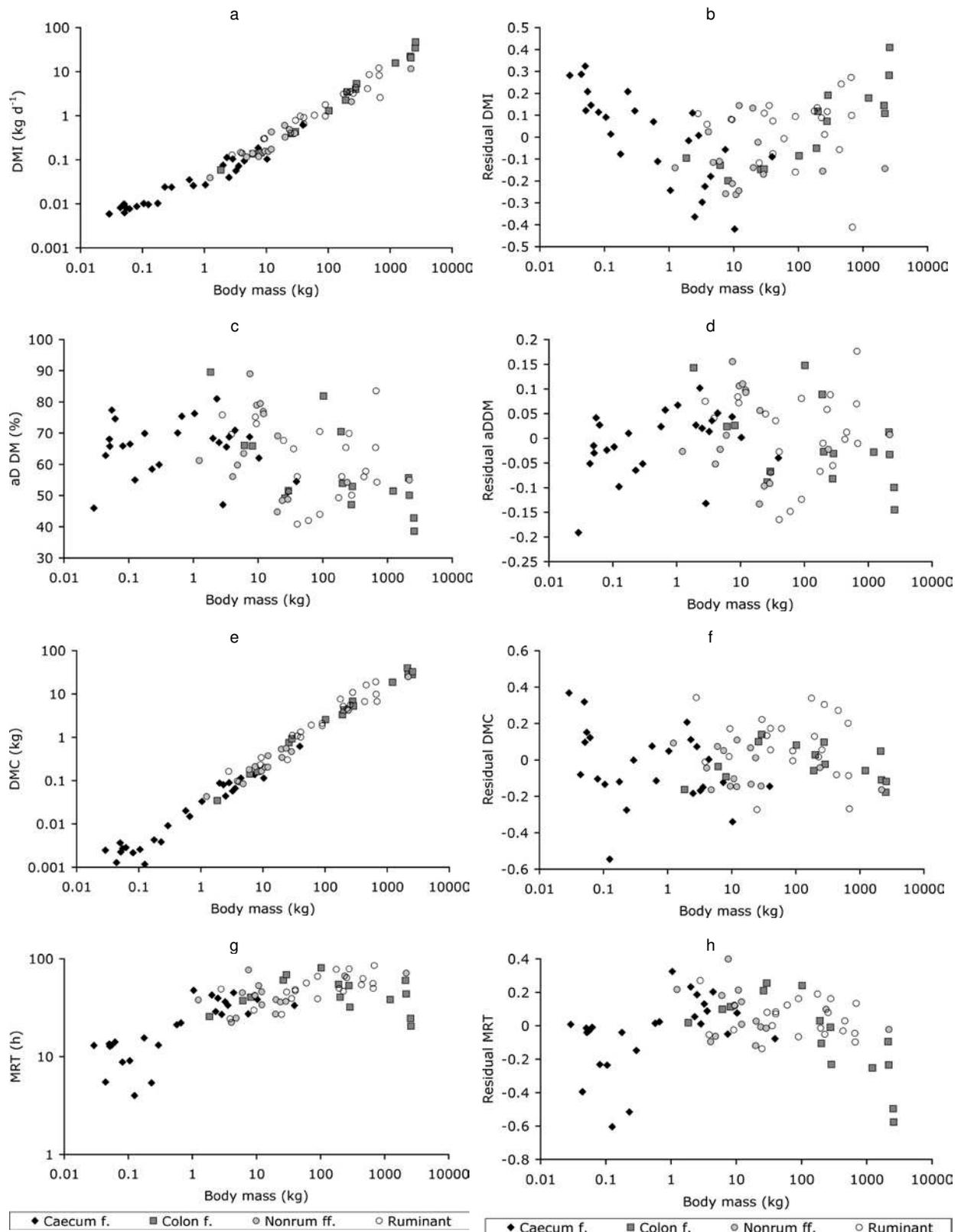
893 Table 7. Correlations between body mass residuals of parameters of digestive physiology in
 894 the dataset of this study (n=77) analysed by OLS and PGLS statistics (differences indicated
 895 by grey shading).

	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 DMC	OLS			R=0.450, p<0.001
	PGLS			R=0.593, p<0.001

896 dry matter intake (DMI in kg d⁻¹); apparent digestibility of dry matter (aDDM in %); dry
 897 matter gut contents (DMC in kg); particle mean retention time (MRT in h)
 898



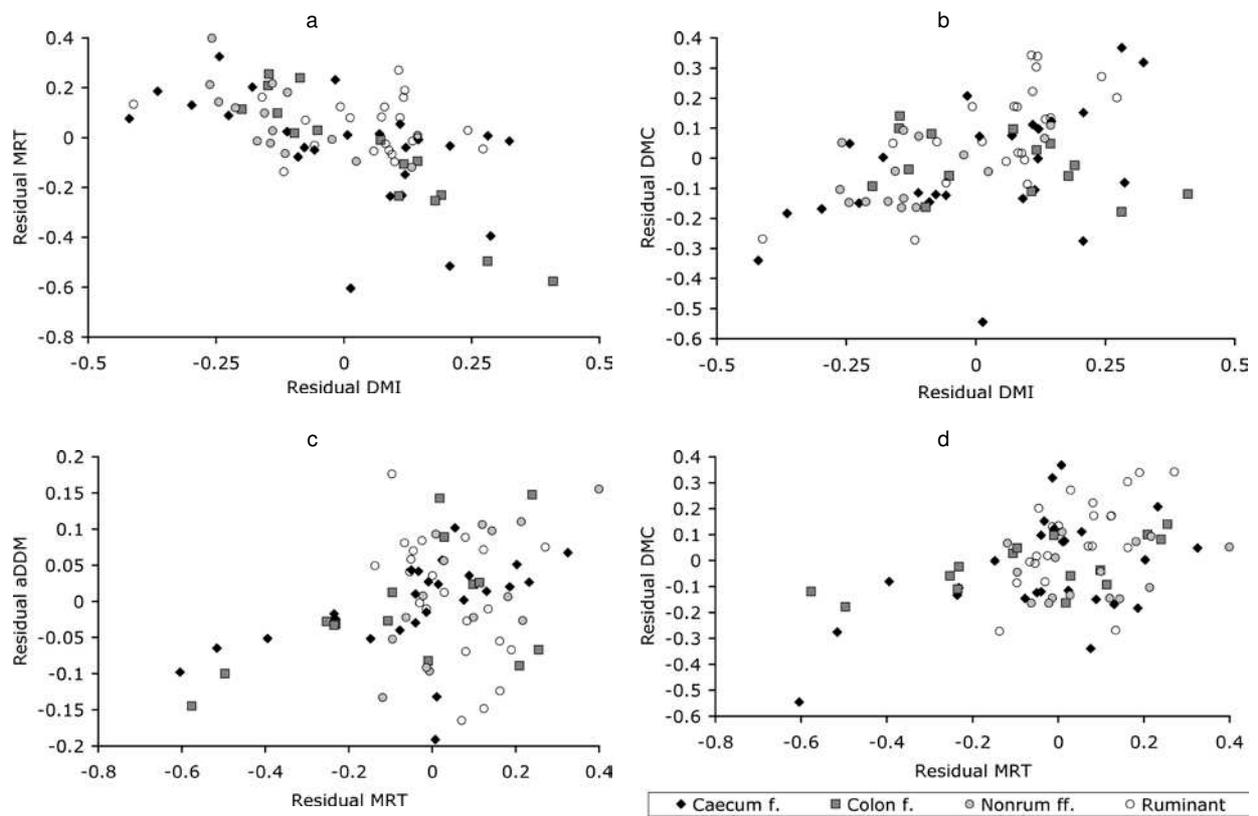
899 Fig. 1. Relationships between body mass residuals of different parameters of digestive
 900 physiology (organic matter intake OMI in kg d^{-1} ; particle mean retention time MRT in h;
 901 organic matter gut contents OMC in kg, apparent organic matter digestibility aDOM in %) in
 902 large mammalian herbivores of different digestion types (colon fermenters, nonruminant
 903 foregut fermenters, ruminants) in the dataset of Foose (1982). a) OMI and MRT; b) OMI and
 904 OMC; c) MRT and aDOM; d) MRT and OMC. For statistics, see Table 2.
 905



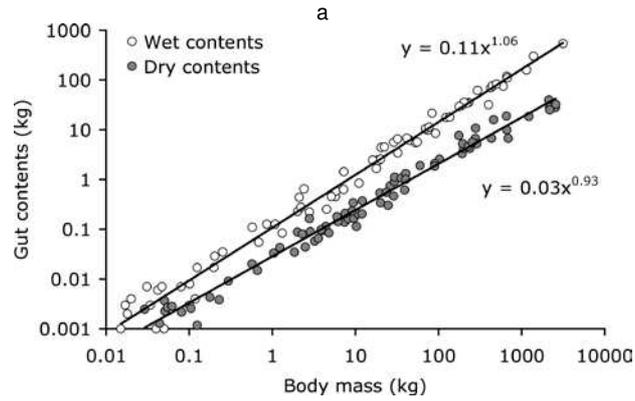
906
 907
 908
 909
 910
 911
 912
 913

Figure 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.

914
915



916 Fig. 3. Relationships between body mass residuals of different parameters of digestive
917 physiology (dry matter intake DMI in kg d^{-1} ; particle mean retention time MRT in h; dry
918 matter gut contents DMC in kg, apparent dry matter digestibility aDDM in %) in mammalian
919 herbivores of different digestion types (colon fermenters, nonruminant foregut fermenters,
920 ruminants) in the dataset of this study. a) DMI and MRT; b) DMI and DMC; c) MRT and
921 aDDM; d) MRT and DMC. For statistics, see Table 7.
922



924 Figure 4. Scaling of wet gut contents (open symbols, Clauss et al., 2007a) and
925 gut contents (closed symbols, this study) with body mass. Note the increasing difference between
926 the two with increasing body mass.
927

Assessing the Jarman-Bell-principle: scaling of intake, digestibility, retention time and gut capacity with body mass in mammalian herbivores

Dennis W.H. Müller^{1,2}, Daryl Codron^{1,3}, Carlo Meloro⁴, Adam Munn⁵, Angela Schwarm⁶, Jürgen Hummel⁷, Marcus Clauss^{1*}

¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland,, mclauss@vetclinics.uzh.ch

²National Park 'Bavarian Forest', Freyungerstr. 2, 94481 Grafenau, Germany

³Florisbad Quaternary Research, National Museum, Bloemfontein, 9300, RSA

⁴Center for Anatomical and Human Science, Hull York Medical School, University of Hull, Cottingham Road, Hull HU6 3RX, UK

⁵Institute for Conservation Biology and Environmental Management, School of Biological Sciences, The University of Wollongong, New South Wales 2522 Australia

⁶Research Unit Nutritional Physiology 'Oskar Kellner', Leibniz Institute for Farm Animal Biology (FBN), Wilhelm-Stahl-Allee 2, 18196 Dummerstorf, Germany

⁷Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany

Supplements

Table 1. Dataset from Foose (1982)

Gastrointestinal anatomy (GIT-Anatomy), mean of body mass (BM), organic matter intake (OMI), mean retention time of particle markers (different markers) through the whole gastrointestinal tract (MRT), apparent digestibility of organic matter (aD OM) and calculated mass of organic matter gastrointestinal tract content (OMC) of 26 herbivorous mammalian species for which all relevant data were measured on grass and lucerne hay diets

Species	GIT-Anatomy	BM (kg)	OM (kg/d)	MRT (h)	aD OM (%)	OMC (kg)
<i>Tapirus terrestris</i>	2	140	2.239	46	49.0	3.24
<i>Equus asinus</i>	2	183	5.747	45	53.8	7.86
<i>Boselaphus tragocamelus</i>	4	193	2.848	59	60.8	4.87
<i>Cervus duvaucelii</i>	4	193	2.822	50	64.5	3.98
<i>Hexaprotodon liberiensis</i>	3	200	1.649	67	53.9	3.34
<i>Oryx gazella</i>	4	204	4.318	71	60.7	8.84
<i>Kobus ellipsiprymus</i>	4	204	3.859	58	58.6	6.59
<i>Tapirus indicus</i>	2	218	3.432	45	48.3	4.88
<i>Equus zebra</i>	2	265	7.553	44	54.0	9.98
<i>Equus burchellii</i>	2	272	7.200	41	55.2	8.91
<i>Cervus elaphus</i>	4	284	3.874	58	56.2	6.73
<i>Syncerus caffer</i>	4	291	5.954	64	69.0	10.44
<i>Equus grevyi</i>	2	353	8.347	42	58.1	10.24
<i>Taurotragus oryx</i>	4	431	5.959	52	56.5	9.27
<i>Bison bison</i>	4	499	6.651	74	68.8	13.36
<i>Camelus bactrianus</i>	4	544	6.308	79	67.7	13.73
<i>Camelus dromedarius</i>	4	544	6.477	75	64.5	13.62
<i>Bos frontalis</i>	4	765	8.728	54	66.5	13.11
<i>Giraffa camelopardalis</i>	4	1153	7.321	69	58.9	14.74
<i>Bubalus bubalis</i>	4	1270	17.232	67	66.8	32.03
<i>Diceros bicornis</i>	2	1285	16.419	57	53.8	28.62
<i>Ceratotherium simum</i>	2	1752	18.550	62	59.2	33.73
<i>Rhinoceros unicornis</i>	2	1852	20.468	65	58.9	38.96
<i>Hippopotamus amphibius</i>	3	2240	16.443	85	64.3	39.28
<i>Loxodonta africana</i>	2	2873	34.729	48	53.4	50.72
<i>Elephas maximus</i>	2	3034	34.748	51	52.6	53.86

GIT-Anatomy = gastrointestinal tract anatomy: 2 = colon fermenter, 3 = nonruminant foregut fermenter, 4 = ruminant foregut fermenter

Table 2. Data collection of this study

Gastrointestinal anatomy (GIT-Anatomy), number of offspring per litter (Nos offspring) mean of body mass (BM), dry matter intake (DMI), mean retention time of particle markers (different markers) through the whole gastrointestinal tract (MRT), apparent digestibility of dry matter (aD DM) and calculated mass of dry matter gastrointestinal tract content (DMC) of 77 herbivorous mammalian species for which all relevant data were measured in individual studies

Species	GIT-Anatomy	Nos offspring	BM (kg)	DMI (kg/d)	MRT (h)	aD DM (%)	DMC (kg)	Source
<i>Mus musculus</i>	1	>1	0.03	0.006	13.0	46.0	0.002	(Karasov et al., 1986)
<i>Lasiopodomys brandtii</i>	1	>1	0.04	0.008	5.5	62.9	0.001	(Pei et al., 2001a)
<i>Meriones unguiculatus</i>	1	>1	0.05	0.006	12.8	65.8	0.002	(Pei et al., 2001b)
<i>Microtus ochrogaster</i>	1	>1	0.05	0.010	13.5	68.1	0.004	(Hammond and Wunder, 1991)
<i>Microtus townsendii</i>	1	>1	0.05	0.008	13.1	77.4	0.003	(Hume et al., 1993)
<i>Tamias amoenus</i>	1	>1	0.06	0.008	14.1	74.6	0.003	(Hume et al., 1993)
<i>Phyllotis darwini</i>	1	>1	0.08	0.009	8.8	65.9	0.002	(Sakaguchi and Ohmura, 1992)
<i>Cricetus cricetus</i>	1	>1	0.11	0.011	9.1	66.5	0.003	(Sakaguchi et al., 1987)
<i>Neotoma lepida</i>	1	>1	0.13	0.010	4.0	55.0	0.001	(Karasov et al., 1986)
<i>Octodon degus</i>	1	>1	0.18	0.010	15.5	69.9	0.004	(Sakaguchi and Ohmura, 1992)
<i>Arvicola terrestris</i>	1	>1	0.23	0.024	5.4	58.5	0.004	(Woodall, 1989)
<i>Rattus norvegicus</i>	1	>1	0.30	0.024	13.1	59.9	0.009	(Sakaguchi et al., 1987)
<i>Cavia porcellus</i>	1	>1	0.57	0.036	21.1	70.1	0.020	(Sakaguchi et al., 1987; Sakaguchi and Nabata, 1992; Sakaguchi et al., 1992b; Sakaguchi and Ohmura, 1992; Franz et al., 2011)
<i>Spermophilus columbianus</i>	1	>1	0.66	0.026	22.1	75.4	0.015	(Hume et al., 1993)
<i>Haplemur griseus</i>	1	1	1.04	0.027	47.5	76.3	0.033	(Campbell et al., 2004)
<i>Oryctolagus cuniculus</i>	1	>1	2.01	0.079	42.6	68.4	0.088	(Sakaguchi et al., 1987; Sakaguchi and Hume, 1990; Sakaguchi et al., 1992a; Franz et al., 2011)
<i>Marmota caligata</i>	1	>1	2.31	0.112	28.9	81.0	0.080	(Hume et al., 1993)
<i>Trichosurus vulpecula</i>	1	1	2.50	0.040	39.6	67.0	0.044	(Sakaguchi and Hume, 1990)
<i>Lagostomus maximus</i>	1	>1	2.86	0.105	27.0	47.0	0.090	(Besselmann, 2005; Clauss et al., 2007a)
<i>Propithecus tattersalli</i>	1	1	3.24	0.057	36.3	65.6	0.058	(Campbell et al., 1999)
<i>Propithecus verreauxi</i>	1	1	3.58	0.072	33.5	68.8	0.066	(Campbell et al., 1999; Campbell et al., 2004)
<i>Myocastor coypus</i>	1	>1	4.40	0.094	45.0	70.9	0.114	(Sakaguchi and Nabata, 1992)
<i>Dolichotis patagonum</i>	1	>1	7.40	0.185	27.3	68.8	0.138	(Sakaguchi et al., 1992b)
<i>Erethizon dorsatum</i>	1	1	10.3	0.103	38.4	62.0	0.114	(Felicetti et al., 2000)
<i>Hydrochaeris hydrochaeris</i>	1	>1	39.2	0.606	33.3	54.5	0.620	(A. Schwarm, S. Ortmann, M. Clauss pers. obs. 2010)

<i>Pithecia pithecia</i>	2	1	1.85	0.059	25.6	89.5	0.035	(Norconk et al., 2002)
<i>Alouatta pigra</i>	2	1	6.15	0.137	37.3	66.1	0.142	(Edwards and Ullrey, 1999)
<i>Alouatta seniculus</i>	2	1	8.18	0.144	40.4	65.9	0.163	(Edwards and Ullrey, 1999)
<i>Lasiorhinus latifrons</i>	2	1	26.2	0.394	60.5	49.2	0.750	(Barboza, 1993)
<i>Vombatus ursinus</i>	2	1	29.5	0.434	68.5	51.6	0.918	(Barboza, 1993)
<i>Gorilla gorilla</i>	2	1	102	1.267	80.6	81.9	2.560	(Remis and Dierenfeld, 2004)
<i>Tapirus terrestris</i>	2	1	192	2.247	54.7	70.5	3.320	(Clauss et al., 2010)
<i>Equus asinus</i>	2	1	202	3.445	40.5	53.9	4.250	(Pearson and Merritt, 1991; Pearson et al., 2001, 2006)
<i>Tapirus indicus</i>	2	1	278	3.945	53.1	47.1	6.720	(Clauss et al., 2010)
<i>Equus caballus</i>	2	1	287	5.416	32.0	52.9	5.250	(Pearson and Merritt, 1991; Pagan et al., 1998; Pearson et al., 2001; Moore-Colyer et al., 2003; Pearson et al., 2006)
<i>Diceros bicornis</i>	2	1	1222	15.700	38.3	51.4	18.614	(Clauss et al., 2005a; Clauss et al., 2006; Steuer et al., 2010)
<i>Rhinoceros unicornis</i>	2	1	2125	22.065	60.1	55.7	39.935	(Clauss et al., 2005b)
<i>Ceratotherium simum</i>	2	1	2175	20.781	43.8	50.1	28.286	(Steuer et al., 2010)
<i>Elephas maximus</i>	2	1	2547	33.874	24.5	42.8	27.998	(Hackenberger, 1987)
<i>Loxodonta africana</i>	2	1	2583	47.207	20.5	38.6	32.515	(Hackenberger, 1987)
<i>Lagorchestes hirsutus</i>	3	1	1.23	0.040	38.0	61.3	0.043	(Bridie et al., 1994)
<i>Thylogale thetis</i>	3	1	4.05	0.141	22.4	56.1	0.095	(Dellow, 1982; Dellow and Hume, 1982)
<i>Macropus eugenii</i>	3	1	4.80	0.117	24.8	59.8	0.084	(Dellow, 1982; Dellow and Hume, 1982)
<i>Trachypithecus auratus</i>	3	1	6.00	0.140	45.0	63.5	0.179	(Nijboer et al., 2007)
<i>Colobus angolensis</i>	3	1	7.50	0.118	77.0	89.0	0.210	(Schwarm et al., 2009a)
<i>Trachypithecus johnii</i>	3	1	9.50	0.157	42.0	79.0	0.166	(Comizzoli et al., 1997; Schwarm et al., 2009a)
<i>Colobus guereza</i>	3	1	10.8	0.154	53.1	79.5	0.206	(Edwards and Ullrey, 1999)
<i>Colobus polykomos</i>	3	1	12	0.174	46.0	77.0	0.205	(Schwarm et al., 2009a)
<i>Pygathrix nemaeus</i>	3	1	12.1	0.429	33.8	76.2	0.374	(Edwards and Ullrey, 1999)
<i>Macropus robustus</i>	3	1	19.8	0.608	27.2	44.7	0.534	(Freudenberger and Hume, 1992)
<i>Pecari tajacu</i>	3	>1	20.1	0.324	38.2	69.1	0.343	(Schwarm et al., 2009a)
<i>Macropus giganteus</i>	3	1	23.6	0.504	36.2	48.4	0.555	(Forbes and Tribe, 1970; Dellow, 1982; Dellow and Hume, 1982)
<i>Macropus rufus</i>	3	1	28.7	0.468	36.7	48.8	0.467	(Foot and Romberg, 1965; McIntosh, 1966; Forbes and Tribe, 1970; Dellow, 1982; Dellow and Hume, 1982; Munn and Dawson, 2006; Schwarm et al., 2009a)
<i>Hexaprotodon liberiensis</i>	3	1	238	2.067	66.5	54.3	4.215	(Clauss et al., 2004)
<i>Hippopotamus amphibius</i>	3	1	2175	11.733	71.4	55.0	25.011	(Clauss et al., 2004)
<i>Tragulus napu</i>	4	1	2.8	0.129	49.0	75.8	0.164	(Conklin and Dierenfeld, 1994)

<i>Cephalophus monticola</i>	4	1	3.85	0.146	24.4	69.6	0.098	(Luginbuhl et al., 1990)
<i>Pudu puda</i>	4	1	9.1	0.299	29.9	75.2	0.232	(Conklin-Brittain and Dierenfeld, 1996)
<i>Cephalophus maxwellii</i>	4	1	9.4	0.305	42.2	73.0	0.341	(Conklin-Brittain and Dierenfeld, 1996)
<i>Capreolus capreolus</i>	4	>1	24.7	0.405	27.0	67.7	0.302	(Holand, 1994)
<i>Capra hircus</i>	4	1	29.7	0.777	45.9	51.3	1.117	(Udén et al., 1982; Udén and Van Soest, 1982; Freudenberger and Hume, 1992; Kennedy et al., 1992)
<i>Capra ibex</i>	4	1	35.4	0.989	39.3	65.0	1.074	(Gross et al., 1996)
<i>Odocoileus virginianus</i>	4	>1	40.3	0.648	47.0	40.9	1.011	(Barnes et al., 1992)
<i>Ovis ammon</i>	4	1	40.3	0.914	48.4	56.1	1.325	(Foot and Romberg, 1965; McIntosh, 1966; Forbes and Tribe, 1970; Dellow, 1982; Dellow and Hume, 1982; Udén et al., 1982; Udén and Van Soest, 1982; Luginbuhl et al., 1990; Kennedy et al., 1992; Pearson et al., 2006)
<i>Odocoileus hemionus</i>	4	>1	60	1.028	56.7	42.0	1.918	(Baker and Hobbs, 1987)
<i>Bubalus depressicornis</i>	4	1	90	1.767	39.0	70.5	1.858	(Flores-Miyamoto et al., 2005)
<i>Ovis canadensis</i>	4	1	90	0.984	66.0	44.0	2.111	(Baker and Hobbs, 1987)
<i>Bos grunniens</i>	4	1	176	3.122	78.2	49.3	7.663	(Schaefer et al., 1978)
<i>Cervus elaphus</i>	4	1	196	3.763	49.7	56.1	5.226	(Baker and Hobbs, 1987; Jiang and Hudson, 1996)
<i>Okapia johnstoni</i>	4	1	227	3.531	46.8	65.4	4.626	(Hummel et al., 2005; Hummel et al., 2006)
<i>Ovibos moschatus</i>	4	1	254	3.223	64.2	69.9	5.623	(Adamczewski et al., 1993; Barboza et al., 2006)
<i>Bison bison</i>	4	1	279	4.410	78.8	50.1	10.852	(Schaefer et al., 1978)
<i>Bos javanicus</i>	4	1	432	4.654	54.2	56.0	6.711	(Schwarm et al., 2008, 2009b)
<i>Bos taurus</i>	4	1	460	7.357	62.8	57.8	16.052	(Schaefer et al., 1978; Colucci et al., 1982; Udén et al., 1982; Udén and Van Soest, 1982; Mathers et al., 1989; Luginbuhl et al., 1994; Burns et al., 1997; Whetsell et al., 2004; Pearson et al., 2006)
<i>Bubalus bubalis</i>	4	1	656	12.120	56.0	65.4	19.037	(Mathers et al., 1989)
<i>Giraffa camelopardalis</i>	4	1	665	8.224	49.8	83.5	9.942	(Schaub, 2005)
<i>Camelus bactrianus</i>	4	1	687	2.601	85.2	54.3	6.724	(Cahill and McBride, 1995)

GIT-Anatomy = gastrointestinal tract anatomy: 1 = caecum fermenter, 2 = colon fermenter, 3 = nonruminant foregut fermenter, 4 = ruminant foregut fermenter; BM = body mass; DMI = dry matter intake; MRT = mean retention time of particle markers (different markers) through the whole gastrointestinal tract; aD DM = apparent dry matter digestibility; DMC= mass of dry matter gastrointestinal tract content calculated according to Holleman and White (1989; for equations see the main text)

Table 3. Data collection of wet gut contents

This dataset is given as the supplement to Clauss et al. (2007b).

References

- Adamczewski, J.Z., Chapin, R.E., Schaefer, J.A., Flood, P.F., 1993. Intake, digestibility and passage rate of a supplemented hay diet in captive muskoxen. *Rangifer* 13, 57-60.
- Baker, D.L., Hobbs, N.T., 1987. Strategies of digestion: digestive efficiency and retention times of forage diets in montane ungulates. *Can. J. Zool.* 65, 1978-1984.
- Barboza, P.S., 1993. Digestive strategies of the wombats: feed intake, fiber digestion, and digesta passage in two grazing marsupials with hindgut fermentation. *Physiol. Zool.* 66, 983-999.
- Barboza, P.S., Peltier, T.C., Forster, R.J., 2006. Ruminal fermentation and fill change with season in an Arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). *Physiol. Biochem. Zool.* 79, 497-513.
- Barnes, T.G., Varner, L.W., blankenship, L.H., Gallagher, J.F., 1992. Indigestible particulate passage in white-tailed deer, in: R. Brown (Ed.), *The biology of deer*. Springer Verlag, New York, 436-442.
- Besselmann, D., 2005. Untersuchungen zur Anatomie und Verdauungsphysiologie des Flachland-Viscachas (*Lagostomus maximus*). Diss. thesis, University of Zurich.
- Bridie, A., Hume, I.D., Hill, D.M., 1994. Digestive tract function and energy requirements of the rufous hare-wallaby (*Lagorchestes hirsutus*). *Aust. J. Zool.* 42, 761-774.
- Burns, J.C., Pond, K.R., Fisher, D.S., Luginbuhl, J.M., 1997. Changes in forage quality, ingestive mastication, and digesta kinetics resulting from switchgrass maturity. *J. Anim. Sci.* 75, 1368-1379.
- Cahill, L.W., McBride, B.W., 1995. Effect of level of intake on digestion, rate of passage and chewing dynamics in hay-fed Bactrian camels. *Proceedings of the Nutrition Advisory Group* 1, 3-35.
- Campbell, J.L., Eisemann, J.H., Glander, K.E., Crissey, S.D., 1999. Intake, digestibility, and passage of a commercially designed diet by two propithecus species. *Am. J. Primatol.* 48, 237-246.
- Campbell, J.L., Williams, C.V., Eisemann, J.H., 2004. Use of total dietary fiber across four lemur species (*Propithecus cerreauxi coquereli*, *Hapalemur griseus griseus*, *Varecia variegata*, and *Eulemur fulvus*): does fiber type affect digestive efficiency? *Am. J. Primatol.* 64, 323-335.
- Clauss, M., Schwarm, A., Ortmann, S., Alber, D., Flach, E.J., Kühne, R., Hummel, J., Streich, W.J., Hofer, H., 2004. Intake, ingesta retention, particle size distribution and digestibility in the *hippopotamidae*. *Comp. Biochem. Physiol. A* 139, 449-459.
- Clauss, M., Froeschle, T., Castell, J., Hummel, J., Hatt, J.M., Ortmann, S., Streich, W.J., 2005a. Fluid and particle retention times in the black rhinoceros (*Diceros bicornis*), a large hindgut-fermenting browser. *Acta Theriol.* 50, 367-376.
- Clauss, M., Polster, C., Kienzle, E., Wiesner, H., Baumgartner, K., von Houwald, F., Ortmann, S., Streich, W.J., Dierenfeld, E.S., 2005b. Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*). *J. Anim. Physiol. Anim. Nutr.* 89, 229-237.
- Clauss, M., Castell, J.C., Kienzle, E., Dierenfeld, E.S., Flach, E.J., Behlert, O., Ortmann, S., Streich, W.J., Hummel, J., Hatt, J.M., 2006. Digestion coefficients achieved by the black rhinoceros (*Diceros bicornis*), a large browsing hindgut fermenter. *J. Anim. Physiol. Anim. Nutr.* 90, 325-334.
- Clauss, M., Besselmann, D., Schwarm, A., Ortmann, S., Hatt, J.M., 2007a. Demonstrating coprophagy with passage markers? The example of the plains viscacha (*Lagostomus maximus*). *Comp. Biochem. Physiol. A* 147, 453-459.
- Clauss, M., Schwarm, A., Ortmann, S., Streich, W.J., Hummel, J., 2007b. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comp. Biochem. Physiol. A* 148, 249-265.
- Clauss, M., Lang-Deuerling, S., Müller, D.W.H., Kienzle, E., Steuer, P., Hummel, J., 2010. Retention of fluid and particles in captive tapirs (*Tapirus* spp.). *Comp. Biochem. Physiol. A* 157, 95-101.
- Colucci, P.E., Chase, L.E., Van Soest, P.J., 1982. Feed intake, apparent diet digestibility, and rate of particulate passage in dairy cattle. *J. Dairy Sci.* 65, 1445-1456.
- Comizzoli, P., Peiniau, J., Dutertre, C., Planquette, P., Aumaitre, A., 1997. Digestive utilization of concentrated and fibrous diets by two peccary species (*Tayassu peccari*, *Tayassu tajacu*) raised in French Guyana. *Anim. Feed Sci. Technol.* 64, 215-226.
- Conklin, N.L., Dierenfeld, E.S., 1994. Digestibility and passage of standard zoo diet fed to greater Asian mouse deer (*Tragulus naphu*). *Malayan Nature Journal* 48, 41-51.
- Conklin-Brittain, N.L., Dierenfeld, E.S., 1996. Small ruminants: digestive capacity differences among four species weighing less than 20 kg. *Zoo Biol.* 15, 481-490.
- Dellow, D.W., 1982. Studies on the nutrition of macropodine marsupials. III. The flow of digesta through the stomach and intestine of macropodines and sheep. *Aust. J. Zool.* 30, 399-406.
- Dellow, D.W., Hume, I.D., 1982. Studies on the nutrition of macropodine marsupials. I. Intake and digestion of lucerne hay and fresh grass. *Aust. J. Zool.* 30, 391-398.
- Edwards, M.S., Ullrey, D.E., 1999. Effect of dietary fiber concentration on apparent digestibility and digesta passage in non-human primates. II. Hindgut- and foregut-fermenting folivores. *Zoo Biol.* 18, 537-549.
- Felicetti, L.A., Shipley, L.A., Witmer, G.W., Robbins, C.T., 2000. Digestibility, nitrogen excretion, and mean retention time by North American porcupines (*Erethizon dorsatum*) consuming natural forages. *Physiol. Biochem. Zool.* 73, 772-780.
- Flores-Miyamoto, K., Clauss, M., Ortmann, S., Sainsbury, A.W., 2005. The nutrition of captive lowland anoa (*Bubalus depressicornis*): a study on ingesta passage, intake, digestibility, and a diet survey. *Zoo Biol.* 24, 125-134.
- Foose, T.J., 1982. *Trophic strategies of ruminant versus nonruminant ungulates*. University of Chicago, Chicago.

- Foot, J.Z., Romberg, B., 1965. The utilization of roughage by sheep and the red kangaroo (*Macropus rufus*). Austr. J. Agric. Res. 16, 429-435.
- Forbes, D.K., Tribe, D.E., 1970. The utilization of roughages by sheep and kangaroos. Aust. J. Zool. 18, 247-256.
- Franz, R., Kreuzer, M., Hummel, J., Hatt, J.-M., Clauss, M., 2011. Intake, selection, digesta retention, digestion and gut fill of two coprophageous species, rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*), on a hay-only diet. J. Anim. Physiol. Anim. Nutr. 95, 564-570.
- Freudenberger, D.O., Hume, I.D., 1992. Ingestive and digestive responses to dietary fibre and nitrogen by two macropodid marsupials (*Macropus robustus erubescens* and *M. r. robustus*) and a ruminant (*Capra hircus*). Aust. J. Zool. 40, 181-194.
- Gross, J.E., Alkon, P.U., Demment, M.W., 1996. Nutritional ecology of dimorphic herbivores: digestion and passage rates in Nubian ibex. Oecologia 107, 170-178.
- Hackenberger, M.K., 1987. Diet digestibilities and ingesta transit times of captive Asian and African elephants. MSc Thesis. University of Guelph, Guelph.
- Hammond, K.A., Wunder, B.A., 1991. The role of diet quality and energy need in the nutritional ecology of a small herbivore (*Microtus ochrogaster*). Physiol. Zool. 64, 541-567.
- Holand, O., 1994. Seasonal dynamics of digestion in relation to diet quality and intake in European roe deer (*Capreolus capreolus*). Oecologia 98, 274-279.
- Holleman, D.F., White, R.G., 1989. Determination of digesta fill and passage rate from non absorbed particulate phase markers using the single dosing method. Can. J. Zool. 67, 488-494.
- Hume, I.D., Morgan, K.R., Kenagy, G.J., 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. Physiol. Zool. 66, 396-411.
- Hummel, J., Clauss, M., Zimmermann, W., Johanson, K., Norgaard, C., Pfeffer, E., 2005. Fluid and particle retention in captive okapi (*Okapia johnstoni*). Comp. Biochem. Physiol. A 140, 436-444.
- Hummel, J., Pfeffer, E., Norgaard, C., Johanson, K., Clauss, M., Nogge, G., 2006. Energetic nutrition of the okapi in captivity: intake and digestion trials. Zoo Biol. 25, 303-316.
- Jiang, Z., Hudson, R.J., 1996. Digestive responses of wapiti to seasonal forages. Acta Theriol. 41, 415-425.
- Karasov, W.H., Petrossian, E., Rosenberg, L., Diamond, J.M., 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminant mammals? J. Comp. Physiol. B 156, 599-609.
- Kennedy, P.M., McSweeney, C.S., Welch, J.G., 1992. Influence of dietary particle size on intake, digestion, and passage rate of digesta in goats and sheep fed wheat (*Triticum aestivum*) hay. Small Rum. Res. 9, 125-138.
- Luginbuhl, J.M., Pond, K.R., Burns, J.C., 1990. Physical limits to ruminal escape: experiences with the blue duiker, in: O.T. Oftedal, P.S. Barboza (Eds.), Digestive strategies of animals, a symposium. National Zoological Park, Smithsonian Institution, Washington DC, 10-11.
- Luginbuhl, J.M., Pond, K.R., Burns, J.C., 1994. Whole-tract digesta kinetics and comparison of techniques for the estimation of fecal output in steers fed coastal bermudagrass hay at four levels of intake. J. Anim. Sci. 72, 201-211.
- Mathers, J.C., Baber, R.P., Archibald, R.F., 1989. Intake, digestion and gastro-intestinal mean retention time in Asiatic buffaloes and Ayrshire cattle given two contrasting diets and housed at 20° and 33°C. J. Agric. Sci. 113, 211-222.
- McIntosh, D.L., 1966. The digestibility of two roughages and the rates of passage of their residues by the red kangaroo and the merino sheep. CSIRO Wildl. Res. 11, 125-135.
- Moore-Colyer, M.J.S., Morrow, H.J., Longland, A.C., 2003. Mathematical modelling of digesta passage rate, mean retention time and in vivo apparent digestibility of two different lengths of hay and big-bale grass silage in ponies. Br. J. Nutr. 90, 109-118.
- Munn, A.J., Dawson, T.J., 2006. Forage fibre digestion, rates of feed passage and gut fill in juvenile and adult red kangaroos (*Macropus rufus*): why body size matters. J. Exp. Biol. 209, 1535-1547.
- Nijboer, J., Clauss, M., Van de Put, K., Van der Kuilen, J., Wouterse, H., Beynen, A.C., 2007. Influence of two different diets on fluid and particle retention time in Javan langur (*Trachypithecus auratus auratus*). Zool. Garten NF 77, 36-46.
- Norconk, M.A., Oftedal, O.T., Power, M.L., Jakubasz, M., Savage, A., 2002. Digesta passage and fiber digestibility in captive white-faced sakis (*Pithecia pithecia*). Am. J. Primatol. 58, 23-34.
- Pagan, J.D., Harris, P., Brewster-Barnes, T., Duren, S.E., Jackson, S.G., 1998. Exercise affects digestibility and rate of passage of all-forage and mixed diets in thoroughbred horses. J. Nutr. 128, 2704S-2707S.
- Pearson, R.A., Merritt, J.B., 1991. Intake, digestion and gastrointestinal transit time in resting donkeys and ponies and exercised donkeys given ad libitum hay and straw diets. Equine Vet. J. 23, 339-343.
- Pearson, R.A., Archibald, R.F., Muirhead, R.H., 2001. The effect of forage quality and level of feeding on digestibility and gastrointestinal transit time of oat straw and alfalfa given to ponies and donkeys. Br. J. Nutr. 85, 599-606.
- Pearson, R.A., Archibald, R.F., Muirhead, R.H., 2006. A comparison of the effect of forage type and level of feeding on the digestibility and gastrointestinal mean retention time of dry forages given to cattle, sheep, ponies and donkeys. Br. J. Nutr. 95, 88-98.
- Pei, Y.X., Wang, D.H., Hume, I.D., 2001a. Selective digesta retention and coprophagy in Brandt's vole (*Microtus brandti*). J. Comp. Physiol. B 171, 457-464.

- Pei, Y.X., Wang, D.H., Hume, I.D., 2001b. Effects of dietary fibre on digesta passage, nutrient digestibility, and gastrointestinal tract morphology in the granivorous Mongolian gerbil (*Meriones unguiculatus*). *Physiol. Biochem. Zool.* 74, 742-749.
- Remis, M.J., Dierenfeld, E.S., 2004. Digesta passage, digestibility and behavior in captive gorillas under two dietary regimes. *Int. J. Primatol.* 25, 825-845.
- Sakaguchi, E., Itoh, H., Uchida, S., Horigome, T., 1987. Comparison of fibre digestion and digesta retention time between rabbits, guinea-pigs, rats and hamsters. *Br. J. Nutr.* 58, 149-158.
- Sakaguchi, E., Hume, I.D., 1990. Digesta retention and fibre digestion in brushtail possums, ringtail possums and rabbits. *Comp. Biochem. Physiol. A* 96, 351-354.
- Sakaguchi, E., Kaizu, K., Nakamichi, M., 1992a. Fibre digestion and digesta retention from different physical forms of the feed in the rabbit. *Comp. Biochem. Physiol. A* 102, 559-563.
- Sakaguchi, E., Nabata, A., 1992. Comparison of fibre digestion and digesta retention time between nutrias and guinea-pigs. *Comp. Biochem. Physiol. A* 103, 601-604.
- Sakaguchi, E., Nippashi, K., Endoh, G., 1992b. Digesta retention and fibre digestion in maras (*Dolichotis patagonium*) and guinea-pigs. *Comp. Biochem. Physiol. A* 101, 867-870.
- Sakaguchi, E., Ohmura, S., 1992. Fibre digestion and digesta retention time in guinea-pigs, degus and leaf-eared mice. *Comp. Biochem. Physiol. A* 103, 787-791.
- Schaefer, A.L., Young, B.A., Chimwano, A.M., 1978. Ration digestion and retention times of digesta in domestic cattle (*Bos taurus*), American bison (*Bison bison*), and Tibetan yak (*Bos grunniens*). *Can. J. Zool.* 56, 2355-2358.
- Schaub, D., 2005. Der Einfluss von Futterrationen mit unterschiedlichen physikalischen Eigenschaften auf Futteraufnahme, Verhalten und weitere verdauungsphysiologische Parameter bei Giraffen (*Giraffa camelopardalis*). Diss. thesis, University of Zurich. Abteilung für Zoo-, Heim- und Wildtiere, Vetsuisse Fakultät.
- Schwarm, A., Ortmann, S., Wolf, C., Streich, W.J., Clauss, M., 2008. Excretion patterns of fluids and particle passage markers of different size in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*): two functionally different foregut fermenters. *Comp. Biochem. Physiol. A* 150, 32-39.
- Schwarm, A., Ortmann, S., Wolf, C., Streich, W.J., Clauss, M., 2009a. Passage marker excretion in red kangaroo (*Macropus rufus*), collared peccary (*Pecari tajacu*) and colobine monkeys (*Colobus angolensis*, *C. polykomos*, *Trachypithecus johnii*). *J. Exp. Zool.* A 311, 647-661.
- Schwarm, A., Ortmann, S., Wolf, C., Streich, W.J., Clauss, M., 2009b. More efficient mastication allows increasing intake without compromising digestibility or necessitating a larger gut: comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*). *Comp. Biochem. Physiol. A* 152, 504-512.
- Steuer, P., Clauss, M., Südekum, K.-H., Hatt, J.-M., Silinski, S., Klomburg, S., Zimmermann, W., Hummel, J., 2010. Comparative investigations on digestion in grazing (*Ceratotherium simum*) and browsing (*Diceros bicornis*) rhinoceroses. *Comp. Biochem. Physiol. A* 156, 380-388.
- Udén, P., Rounsaville, T.R., Wiggans, G.R., Van Soest, P.J., 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (*Phleum pratense*) hay. *Br. J. Nutr.* 48, 329-339.
- Udén, P., Van Soest, P.J., 1982. Comparative digestion of timothy fiber by ruminants, equines and rabbits. *Br. J. Nutr.* 47, 267-272.
- Whetsell, M.S., Prigge, E.C., Nestor, E.L., 2004. Influence of mass of ruminal contents on voluntary intake and digesta passage in steers fed a forage and a concentrate diet. *J. Anim. Sci.* 82, 1806-1817.
- Woodall, P.F., 1989. The effects of increased dietary cellulose on the anatomy, physiology and behaviour of captive water voles (*Arvicola terrestris*). *Comp. Biochem. Physiol. A* 94, 615-621.