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**De Cuyper, A, Meloro, C, Abraham, AJ, Müller, DWH, Codron, D, Janssens, GPJ and Clauss, M**

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### Article

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**De Cuyper, A, Meloro, C, Abraham, AJ, Müller, DWH, Codron, D, Janssens, GPJ and Clauss, M (2020) The uneven weight distribution between predators and prey: Comparing gut fill between terrestrial herbivores and carnivores. Comparative Biochemistry and Physiology Part A: Molecular**

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1 **The uneven weight distribution between predators and prey: comparing gut fill between**  
2 **terrestrial herbivores and carnivores**

3

4 Annelies De Cuyper<sup>1</sup>, Carlo Meloro<sup>2</sup>, Andrew Abraham<sup>3</sup>, Dennis W. H. Müller<sup>4</sup>, Daryl  
5 Codron<sup>5</sup>, Geert P.J. Janssens<sup>1</sup>, Marcus Clauss<sup>6</sup>

6

7 *<sup>1</sup>Department of Nutrition, Genetics and Ethology, Faculty of Veterinary Medicine, Ghent*  
8 *University, Merelbeke, Belgium*

9 *<sup>2</sup> uni Carlo*

10 *<sup>3</sup> uni Andrew*

11 *<sup>4</sup> Dennis in Berlin or Zurich?*

12 *<sup>5</sup> Daryl uni*

13 *<sup>6</sup>Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich,*  
14 *Zurich, Switzerland*

15

16

17 **Abstract**

18 The general observation that carnivores ingest highly digestible diets and have simple short  
19 guts and small abdominal cavities intuitively results in the assumption that carnivores or  
20 predators carry less digesta in their gut compared to herbivores. Due to logistic constraints,  
21 this assumption has not been tested quantitatively so far. In this contribution, we estimated  
22 the dry matter gut contents (DMC) for 25 Carnivora species (including two herbivorous ones,  
23 the pandas) using the physical ‘Occupancy Principle’, based on a literature data collection on  
24 dry matter intake (DMI), apparent dry matter digestibility (aD DM) and retention time (RT),  
25 and compared the results to an existing collection for herbivores. Scaling exponents with  
26 body mass (BM) for both carnivores and herbivores were in the same range with  $DMI \sim$   
27  $BM^{0.75}$ ;  $aD\ DM \sim BM^0$ ;  $RT \sim BM^{0.11}$  and  $DMC \sim BM^{0.88}$ . The trophic level (carnivore vs  
28 herbivore) significantly affected all digestive physiology parameters except for RT.  
29 Numerically, the carnivore DMI level reached 77%, the RT 32% and DMC only 29% of the  
30 corresponding herbivore values, whereas the herbivore aD DM only reached 82% of that of  
31 carnivores. Thus, we quantitatively show that carnivores carry less inert mass or gut content  
32 compared to herbivores, which putatively benefits predators in predator-prey interactions and  
33 might have contributed to the evolution towards a passive limb support apparatus in  
34 herbivores. As expected, the two panda species appeared as outliers in the dataset with low  
35 aD DM and RT for a herbivore but extremely high DMI values, resulting in DMC in the  
36 lower part of the herbivore range. Whereas the difference in DMI and DMC scaling in  
37 herbivores might allow larger herbivores to compensate for lower diet quality by ingesting  
38 more, this difference may allow larger carnivores not to go for less digestible prey parts, but  
39 mainly to increase meal intervals, i.e. not having to hunt on a daily basis.

40

41 **Keywords**

42 Carnivore – Herbivore – Body Size – Gut Fill/Content – Predator – Prey – Retention time

43

44

## 45 **Introduction**

46 The natural diets of carnivores are more digestible than those of herbivores. A variety of  
47 observations have been explained with this fact, including that carnivores putatively have  
48 shorter digestive tracts of lower capacity and lesser complexity (Chivers and Hladik 1980;  
49 Stevens and Hume 1998; Langer and Clauss 2018; McGrosky et al. 2019a; McGrosky et al.  
50 2019b), and therefore also have abdominal cavities of lesser capacity than herbivores (Clauss  
51 et al. 2017). One important consequence should be that in predator-prey interactions, prey  
52 species have more inert mass to move in proportion to their muscle mass.

53 The difference in body composition, with respect to the contribution of gastrointestinal  
54 contents to overall body mass has, to our knowledge, rarely been investigated quantitatively.  
55 In relation to species differences with respect to the pharmacokinetic distribution of drugs,  
56 Davis et al. (1975) compared the body composition of domestic goats (*Capra aegagrus*  
57 *hircus*) and dogs (*Canis lupus familiaris*), whose total gut contents represented 13.9 % and  
58 0.7 % of their body mass, respectively; when compared on the basis of gut-contents-free  
59 body mass, few differences between the species remained. In particular, muscle and bone  
60 mass, which were less in goats when total body mass was used as the basis for comparison,  
61 did no longer differ.

62 However, to our knowledge, data on gut contents in carnivores is scarce. In terrestrial  
63 vertebrate herbivores, ample information about the contribution of gut contents to overall  
64 body mass exist, measured in animals taken from the wild, by dissection (reviewed in Clauss  
65 et al. 2007; Clauss et al. 2013). By contrast, similar data is not available for carnivores, most  
66 likely for two reasons. (i) Killing free-ranging carnivores for study purposes is socially less  
67 accepted than killing herbivores. (ii) Herbivores more or less feed continuously, and therefore  
68 have a constant gut fill; even if fluctuations between seasons or even between hours of the  
69 day have been reported (Owen-Smith 1994; Barboza et al. 2006; Weckerly 2010), gut

70 contents are always present in relevant and measurable amounts. In carnivores, however, gut  
71 contents may differ dramatically with time since the last meal. Because some carnivores may  
72 have to feed repeatedly throughout the day, but some may have a period of fasting after a  
73 gorging day (De Cuyper et al. 2019), measuring the gut contents of carnivores killed in the  
74 wild may not appear as a promising research strategy.

75       One way to estimate gut contents in live animals without killing and dissecting them is to  
76 use, based on physical principles, information on food intake, digestibility, and digesta  
77 retention from feeding experiments (Blaxter et al. 1956). This method was refined by  
78 Holleman and White (1989), based on the ‘Stewart-Hamilton Principle’ or ‘Occupancy  
79 Principle’ (Steele 1971; Shipley and Clark 1972). They provided equations for the calculation  
80 (additionally explained and discussed in detail by Müller et al. 2013). This approach was  
81 validated in sheep (Munn et al. 2015), and was used in a large number of intra-specific and  
82 inter-specific studies of herbivores (e.g., Baker and Hobbs 1987; Gross et al. 1996; Franz et  
83 al. 2011; Fritz et al. 2012; Munn et al. 2012; Müller et al. 2013). Even though the principle is  
84 applicable to any organism, it has not been used so far to estimate the gut contents of  
85 carnivores.

86       Therefore, the aim of the present study was to collate data on food intake, digestibility  
87 and digesta retention in mammalian terrestrial carnivores, to compare these measures, as well  
88 as the derived estimated gut fill, to an existing collection on herbivores (Müller et al. 2013).  
89 Given the general understanding of herbivory and carnivory, our prediction was that  
90 carnivore data would display a generally lower food intake, higher digestibility, shorter  
91 digesta retention, and lower gut fill than herbivores.

92

93 **Methods**

94 For herbivores, the data collection on food intake, digestibility and digesta retention and the  
95 derived gut fill from Müller et al. (2013) was used. For carnivores, a similar data collection  
96 was collated. Because many studies with carnivores report data in a less consistent manner  
97 than studies in herbivores, and with data on body mass, food intake, digestibility and digesta  
98 retention often not given in the same publication, the following estimations were made. Body  
99 mass was taken from the publication itself if given. When not given, body mass was taken  
100 from the data collection of Wilman et al. (2014), or, for dog breeds, from a related  
101 publication of the same research group that performed the digestion study. Digesta retention  
102 was generally reported as the transit time (TT; time till first marker appearance) or the mean  
103 retention time (MRT; calculated by various methods). If both measures were provided, MRT  
104 was used. Marker excretion patterns in carnivorous species often consist of a single major  
105 peak rather than the more gradually increasing and decreasing marker excretion pattern in  
106 herbivores (Fig. 1), and therefore, using TT and MRT interchangeably was considered  
107 permissible.

108 If intake and digestibility were not provided but only MRT or TT, publications were  
109 nevertheless considered if the nutrient composition of the diet used was either given, or could  
110 be assumed using its description in the publication and standard nutrient composition feed  
111 tables (Supplement 1). For carnivores, diet digestibility can be estimated by standard  
112 equations from diet nutrient composition (NRC 2006), with no relevant differences between  
113 mammalian carnivore species (Clauss et al. 2010). Using the same approach, the  
114 metabolisable energy (ME) content of the diet was estimated as the basis for the intake  
115 estimation. The maintenance requirement (MER) of a specimen for which intake was not  
116 measured directly (only for dogs, bears, raccoon and cats in this dataset) was calculated based  
117 on the equation from NRC (2006), which yields an estimate in MER. The intake was then  
118 estimated as the amount of diet (with the estimated ME content) needed to meet that

119 requirement. The equations used for estimation are given in Table 1. The data collection,  
120 including references and indications which estimation steps were made, is given as Table 2.  
121 The full set of data (i.e. not the species averages but each data point) is available as a  
122 supplement (Supplement 2).

123 Data were analysed to establish scaling relationships for dry matter intake (DMI),  
124 retention time (RT, a mix of TT and MRT in the case of carnivores), apparent digestibility of  
125 dry matter (aD DM) and the dry matter gut contents (DMC) with body mass as  $y = a BM^b$ ,  
126 with 95% confidence intervals for parameter estimates, using log-transformed data and linear  
127 regression analysis. The relationship of RT with relative DMI (per unit metabolic body  
128 weight,  $\text{kg}^{0.75}$ ) was analyzed in the same manner, due to the overarching effect of food intake  
129 on digesta retention (Levey and Martínez del Río 1999). These analyses were all performed  
130 for herbivores and carnivores separately, and for both groups combined. An additional set of  
131 analyses assessed, in the combined dataset, the effect of trophic level (carnivore/herbivore).  
132 These models were first run with the interaction term. Because this was always non-  
133 significant, they were repeated without, and only those results are reported here. The two  
134 panda species were ascribed to the herbivore trophic niche, but displayed separately in graphs  
135 due to their phylogenetic membership in the Carnivora.

136 To account for any phylogenetic influence on these allometries, we performed analyses  
137 in Generalized Least Squares (GLS) and Phylogenetic Generalized Least Squares (PGLS),  
138 using a mammalian supertree (Fritz et al. 2009), pruned to include the relevant taxa in our  
139 dataset. The tree was then correlated with our dataset in PGLS, and strength of the  
140 phylogenetic signal ( $\lambda$ ) estimated by maximum likelihood (this was not possible in the scaling  
141 model for carnivore retention times, where  $\lambda$  was therefore manually set to 1; in our  
142 experience, this occurs, albeit rarely, in software package used). All analyses were carried out  
143 in R v 3.3.2 (R\_Core\_Team 2015), with the package ‘nlme’ (Pinheiro et al. 2011) for GLS

144 and the package ‘caper’ (Orme et al. 2013) for PGLS analyses. The significance level was set  
145 to 0.05.

146

## 147 **Results**

148 We collated data for 25 species of Carnivora, including the two herbivorous panda species  
149 (Table 2). The allometric regression analyses mostly had a significant phylogenetic signal,  
150 and while the scaling exponent did not change in magnitude between GLS and PGLS for the  
151 dry matter intake or the digestibility, it decreased in magnitude from GLS to PGLS for  
152 retention time and gut contents (Table 3). The scaling exponents (‘slopes’) hardly differed  
153 between carnivores and herbivores, leading to parallel patterns (Fig. 2A-D), and were roughly  
154  $BM^{0.75}$  for intake,  $BM^{0.11}$  for retention time,  $BM^0$  (no scaling) for digestibility, and  $BM^{0.88}$  for  
155 dry matter gut contents. The scaling factors (‘intercepts’) for herbivores and carnivores  
156 overlapped for food intake (with a numerical difference of carnivores consuming 77% of the  
157 intake level of herbivores), retention time (with carnivores having 32% of the retention time  
158 of herbivores), digestibility (with herbivores achieving only 82% of that of carnivores), and  
159 also for gut contents in PGLS (with carnivores having 29% of the gut contents of herbivores)  
160 (Table 3).

161 The pandas appeared as particular outliers in the dataset. Their food intake level was  
162 higher than that of any other animals for their respective body size (Fig. 2A), and the  
163 digestibility values they achieved were not only the lowest of all Carnivora, but among the  
164 lowest ones in the herbivores (Fig. 2C).

165 In carnivores, there was no significant relationship between retention time and the  
166 relative food intake, whereas that relationship was significantly negative in the herbivores,  
167 and it was also significant for the combined dataset (but only in PGLS; Table 3; Fig. 2E).



168 In the combined dataset, when adding trophic level as a cofactor, it was significant in the  
169 case of food intake, digestibility and gut content in both GLS and PGLS (Table 4), most  
170 likely because trophic level and phylogeny did not reflect the same patterns in these cases  
171 (with pandas resembling other herbivores more than other Carnivora). For models including  
172 retention time, however, trophic level was only significant in GLS but not in PGLS (Table 4),  
173 most likely because retention time is conservative within taxa, as for example the pandas  
174 resemble other Carnivora.

175

## 176 **Discussion**

177 We provide quantitative evidence for the common sense assumption that carnivores carry  
178 less contents in their digestive tracts than herbivores. By means of a distinct example: a 1.6  
179 kg Japanese marten (*Martes melampus*) has on average a dry matter gut fill of 0.26% of body  
180 mass, compared to a 1.2 kg rufous hare-wallaby (*Lagorchestes hirsutus*) that has on average  
181 a dry matter gut fill of 3.18% of BM. This carnivore-herbivore gut fill discrepancy appears  
182 logical given the morphological and physiological adaptations associated with carnivory -  
183 shorter and simpler gastrointestinal tracts (Chivers and Hladik 1980; Langer and Clauss 2018;  
184 McGrosky et al. 2019a) and smaller abdominal cavities (Clauss et al. 2017), typically  
185 explained by the assumption of higher diet digestibility and a lesser need for prolonged  
186 retention times (Sibly 1981; Hume 1989).

187 All investigated factors were different between the trophic levels in both GLS and PGLS  
188 (Table 4), suggesting convergent patterns across the herbivores from different clades  
189 (including the Carnivora). The only exception were retention times measures, which only  
190 differed between the trophic groups in GLS but not in PGLS (Table 4), most likely due to the  
191 general uniformity of this measure within clades, with the herbivorous Carnivora – the pandas  
192 – having retention times as short as those of carnivorous Carnivora. However, even though a

193 significant difference was detected for these measurements of digestive physiology, there was  
194 always overlap in the 95% confidence intervals of the intercept of the models between  
195 herbivores and carnivores (Table 3), and the differences between the trophic groups were less  
196 pronounced than expected. Given the difference in wet gut contents between dog and goat  
197 cited in the Introduction (Davis et al. 1975), we would have expected that gut fill in  
198 carnivores is rather of a magnitude of 0.5-1 % of that of herbivores rather than the 20-30 %  
199 found in the present study.

200 This might be due to several constraints of our dataset. Our data originated from  
201 controlled feeding experiments, and are not uniform with respect to the kind of diets used.  
202 The herbivore dataset, for example, contains complete pelleted diets, mixtures of roughages  
203 and concentrates, and pure roughage diets; in herbivores, additions of concentrates may  
204 decrease intake compared to a more natural diet. Similarly, for the carnivore collection,  
205 commercial petfoods or whole prey diets are included. It is therefore difficult to judge to what  
206 degree the dataset reflects a putative difference that would arise if only natural diets were  
207 used.

208 Possibly more importantly, however, is a constraint in the dataset that relates directly to  
209 the focus of our study: We must assume that the body mass data for herbivores includes an  
210 (unknown) proportion of wet gut contents. If one would express herbivore body mass on an  
211 estimated gut contents-free basis, subtracting roughly 10% of raw body mass data, the  
212 herbivore regression lines in Fig. 2A-D would all shift horizontally to the left, and differences  
213 to carnivores would be increased. As for the less than expected RT difference between  
214 herbivores and carnivores, it should be noted that this may be due to the common observation  
215 that carnivores can retain their faeces and time defecations behaviourally to a greater extent  
216 than most herbivores, which defecate more regularly. This difference is also evident in the  
217 significant effect of relative food intake on retention time in the herbivores and its absence in

218 carnivores (Fig. 2E), again suggesting that carnivores can afford to uncouple defecation from  
219 other digestive processes to a higher degree. One interesting observation on carnivore  
220 retention times is that carnivore groups with shorter retention times (<10 h) were typically  
221 from the mustelid family (e.g. *Neovison vison*; *Mustela putorius*; *Martes melampus*; *Arctitis*  
222 *binturong*; *Lontra Canadensis*; *Pteronura brasiliensis*), the procyonid family (*Potos flavus*)  
223 and ursid family (*Ailurus fulgens*; *Ailuropoda melanoleuca*; *Ursus arctos*; *Ursus americanus*)  
224 – all groups whose digestive tract does not comprise a caecum (McGrosky et al. 2016).

225 Another limitation of our study is that due to our method of calculating dry matter gut  
226 fill, putative additional differences arising from differences in the moisture content of the  
227 digesta remain ignored. If we assumed that in herbivores, there is often more moisture in the  
228 fermentation chambers (e.g. due to frequent occurrence of digesta washing (Müller et al.  
229 2011)), the difference demonstrated here is a conservative view at the gut fill difference  
230 between herbivores and carnivores. The contribution of digestive fluids to total GIT wet  
231 weight is most likely substantial. For example, in a study comparing domestic pigs on a low  
232 or a high fibre diet, Jensen and Jørgensen (1994) documented that wet total GIT contents  
233 were 3.6 and 10.7 % of body mass (with the high-fibre diet evidently approaching the  
234 mammalian herbivore average (Müller et al. 2013)); when expressed as dry matter gut fill,  
235 these values reduced to 0.7 and 1.2% of body mass. Most notably, the overall difference in  
236 digesta dry matter concentration was very large, at 23.4% in the low fibre diet and 14.3% in  
237 the high fibre diet (Jensen and Jørgensen 1994). We are not aware of comprehensive  
238 comparative studies on the dry matter content of the gastrointestinal contents across  
239 mammals. Compiled data from the literature (Table 5) suggests that on the one hand, larger  
240 herbivores have more fluid digesta than smaller herbivores, as already suggested by Müller et  
241 al. (2013). On the other hand, the only carnivore data – for domestic dogs – supports the

242 notion that the digesta dry matter concentration might differ between larger carnivores and  
243 herbivores.

244 Traditional approaches to herbivore ecology emphasize the discrepancy in the scaling of  
245 intake (in the present study: at  $BM^{0.76}$  in GLS) and that of gut capacity (in the present study  
246 measured as DMC: at  $BM^{0.93}$  in GLS, with linear scaling not included in the 95% confidence  
247 interval). This has traditionally been interpreted as causing longer retention times in larger  
248 herbivores, where more gut capacity is available per unit intake, due to the presumed  
249 discrepancy in scaling. Larger animals do not achieve a higher digestibility due to increased  
250 retention times (this study; Steuer et al. 2013; Steuer et al. 2014), but likely use the additional  
251 gut capacity to increase intake to compensate for the lower digestibility of their lower-quality  
252 diet (reviewed in Clauss et al. 2013; Müller et al. 2013). As in the very similar dataset of  
253 Müller et al. (2013), the scaling of retention time ( $BM^d$ ) corresponded to the scaling of gut  
254 capacity ( $BM^a$ ), intake ( $BM^b$ ) and digestibility ( $BM^c$ ) at  $d = a - b + c$  in both GLS and PGLS.

255 In carnivores, the same relationship held in GLS but not in PGLS, because the scaling of  
256 retention time could not be assessed with  $\lambda$  determined by maximum likelihood in this case  
257 (Table 3). In carnivores, the discrepancy between the scaling of intake (at  $BM^{0.77}$  in GLS)  
258 and capacity (at  $BM^{0.98}$  in GLS) is typically not interpreted as facilitating the intake of lower  
259 quality diets in larger species, but in a reduced kill frequency, where species above a certain  
260 body size threshold theoretically can eat only every second day if hunting their average prey  
261 (De Cuyper et al. 2019).

262 Such a difference between gorge and fasting days would reduce differences in gut fill of  
263 large carnivores to herbivores on gorge days, where wolves (*Canis lupus*), for example, may  
264 consume up to 22% of their own body mass (Stahler et al. 2006). On the other hand, this  
265 would even increase the difference in gut fill between large carnivores and herbivores on the  
266 carnivore's fasting day preceding their next hunt, giving them a physical advantage over their

267 large prey. A constant food intake, on which the calculations of the present study are based, is  
268 more representative for another group of carnivores such as wild cats (*Felis silvestris*) with  
269 frequent meals throughout the day (Bradshaw 2006); arguably, the large discrepancy between  
270 the body size of these species and their small prey makes the physical advantage of an empty  
271 gastrointestinal tract less necessary.

272 The panda species (greater panda *Ailuropoda melanoleuca*; red panda *Ailurus fulgens*),  
273 two herbivorous Carnivora feeding mainly on bamboo, appear as outliers in the data  
274 collection, which is not unexpected. In spite of their strictly herbivorous diets, pandas show a  
275 variety of features typically not associated with herbivory, including simple digestive tracts  
276 and a microbiome not geared towards fibre fermentation (reviewed in Sponheimer et al.  
277 2019). Greater pandas feeding on bamboo only show a dry matter digestibility of less than  
278 20%, and compensate with a high dry matter intake (up to 6% BM), with a total gut clearance  
279 in less than 12 hours (Dierenfeld et al. 1982). As such they do not fit the typical carnivore  
280 profile of high digestibility, low food intake, short retention time and low gut contents but  
281 rather an ‘in between group’ between carnivores and herbivores, with very short retention  
282 times, very low digestibilities, high food intakes and intermediate gut loads. How pandas can  
283 maintain their dietary niche remains speculative. It has been suggested that this is linked to  
284 the very high abrasiveness of bamboo on composite teeth of typical herbivores (Martin et al.  
285 2019) but especially the low digestibility of bamboo in fermentation systems (Xi et al. 2007),  
286 which make typical herbivores less competitive on bamboo than on other plant diets  
287 (Sponheimer et al. 2019). This scenario matches the observation that over evolutionary time,  
288 the diet niche of pandas has narrowed from a more varied to their current bamboo-only diet  
289 (Han et al. 2019).

290 The final conclusion of this contribution is that terrestrial carnivorous mammals indeed  
291 carry quantitatively less content in their gut than do herbivorous mammals. As suggested

292 before, in the light of predator-prey interactions, this implies that the predator has less inert  
293 mass to move in proportion to muscle mass. Although predators have higher muscle fibre  
294 power than their prey, the lower amount of inert gut contents will also contribute their greater  
295 capacities for acceleration and deceleration (Wilson et al. 2018). The inert digesta mass may  
296 also have been one (of many) contributing selective pressures for the evolution of cost-  
297 efficient locomotion with unguligradism and energy-storing tendon systems in larger  
298 herbivores (McHorse et al. 2019).

299

### 300 **Acknowledgements**

301 We thank Barbara Schneider and Jacqueline Wick for support in literature acquisition.

302

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445 **Table 1** Estimation equations for metabolisable energy (ME) in diets, dry matter digestibility  
 446 (aD DM) of diets and maintenance energy requirements (MER) of carnivores

Parameter	Estimating equation(s)	Reference
Metabolisable energy (ME) <sup>a</sup>	1. $GE \text{ (kcal)} = (5.7 \times g \text{ CP}) + (9.4 \times g \text{ EE}) + [4.1 \times (g \text{ NfE} + g \text{ CF})]$ <sup>b</sup> 2. Percentage aE = $91.2 - (1.43 \times \text{percentage CF on DM base})$ <sup>c</sup> 3. $DE \text{ (kcal)} = (GE \times (\text{percentage aE}/100))$ <sup>d</sup> 4. $ME \text{ (kcal)} = DE - (1.04 \times g \text{ CP})$	NRC (2006)
Dry matter digestibility (aD DM) <sup>e</sup>	Percentage aE = $91.2 - (1.43 \times \text{percentage CF on DM base})$ <i>Or</i> Percentage aE = $96.6 - (0.95 \times \text{percentage TDF on DM base})$ <sup>f</sup>	NRC (2006)
Maintenance energy requirement (MER)	Laboratory kennel dogs or active pet dogs <i>130 kcal/kg BW</i> <sup>0.75g</sup> Young adult laboratory dogs or active pet dogs <sup>h</sup> <i>140 kcal/kg BW</i> <sup>0.75</sup> Lean domestic cats <i>100 kcal/kg BW</i> <sup>0.67</sup>	NRC (2006)

447 *a* ME equation for processed food; *b* GE = gross energy, CP = crude protein, EE = ether extract or crude fat, NfE = nitrogen  
 448 free extract, CF = crude fibre; *c* aE = energy digestibility, DM = dry matter; *d* DE = digestible energy; *e* Percentage energy  
 449 digestibility was used as an approximation for dry matter digestibility; *f* This equation was used when total dietary fibre  
 450 (TDF) values were given but no CF values were present, the latter was preferred over estimating the CF content; *g* BW =  
 451 bodyweight; *h* This equation was used when 'young adult' was explicitly mentioned

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454 **Table 2** The average body mass, dry matter (DM) intake, dry matter digestibility (aD DM), retention time (RT) and dry matter gut content  
 455 (DMC) per carnivore species including indications of estimated parameters

Species	N° of studies	BM (kg)	N° of BM estimated	N° of nutrient composition estimated <sup>a</sup>	DM intake (kg)	N° of DM intake estimated	aD DM (%)	N° of aD DM estimated	RT (h)	DMC (kg)	References
<i>Acinonyx jubatus</i>	1	32.17	0/1	1/1	0.77	0/1	94.05	1/1	25.34	0.430	Leemans et al. (2015)
<i>Ailuropoda melanoleuca</i>	2	102.24	0/2	0/2	3.89	0/2	47.13	0/2	8.25	1.028	Mainka et al. (1989)
<i>Ailurus fulgens</i>	1	5.13	0/1	1/1	0.56	0/1	33.70	0/1	3.96	0.082	Wei et al. (1999)
<i>Arctictis binturong</i>	1	18.90	0/1	1/1	0.13	0/1	73.88	1/1	6.50	0.023	Lambert et al. (2014)
<i>Canis familiaris</i>	12	17.28	3/12	5/12	0.32	7/12	85.67	7/12	27.28	0.208	Clemens and Stevens (1980); Burrows et al. (1982); Fahey et al. (1990a); Fahey et al. (1990b); Fahey et al. (1992); Lefebvre et al. (2001); Rolfe et al. (2002); Hernot et al. (2005); Childs-Sanford and Angel (2006); Boillat et al. (2010a); Boillat et al. (2010b); De Cuyper et al. (2018)
<i>Caracal caracal</i>	1	8.25	0/1	0/1	0.13	0/1	72.19	0/1	24.00	0.082	Edwards et al. (2001)
<i>Chrysocyon brachyurus</i>	1	25.80	0/1	0/1	0.55	0/1	65.70	0/1	14.15	0.217	Sanford and Angel (2006)
<i>Felis catus</i>	2	3.93	0/2	1/2	0.06	1/2	73.03	1/2	23.78	0.040	Peachey et al. (2000); Loureiro et al. (2017)

<i>Leopardus pardalis</i>	1	11.90	1/1	1/1	0.19	0/1	87.91	1/1	34.00	0.148	Vásquez-Vargas and Brenes-Soto (2015)
<i>Leopardus wiedii</i>	1	3.25	1/1	1/1	0.11	0/1	87.91	1/1	34.00	0.086	Vásquez-Vargas and Brenes-Soto (2015)
<i>Lontra canadensis</i>	3	8.32	2/3	1/3	0.25	1/3	90.00	3/3	4.89	0.027	Davis et al. (1992); Ormseth and Ben-David (2000); White et al. (2007)
<i>Martes melampus</i>	1	1.60	0/1	1/1	0.03	0/1	82.42	1/1	5.52	0.004	Tsuji et al. (2015)
<i>Mustela putorius</i>	1	1.36	0/1	0/1	0.06	0/1	88.05	1/1	3.03	0.004	Bleavins and Aulerich (1981)
<i>Neovison vison</i>	2	1.08	0/2	0/2	0.02	0/2	70.25	0/2	2.32	0.001	Sibbald et al. (1962); Bleavins and Aulerich (1981)
<i>Panthera onca</i>	1	100.00	1/1	1/1	0.49	0/1	87.91	1/1	43.00	0.496	Vásquez-Vargas and Brenes-Soto (2015)
<i>Potos flavus</i>	1	4.25	0/1	1/1	0.08	0/1	73.74	1/1	2.50	0.005	Lambert et al. (2014)
<i>Prionailurus bengalensis</i>	1	5.88	0/1	0/1	0.09	0/1	70.15	0/1	35.00	0.087	Edwards et al. (2001)
<i>Procyon lotor</i>	1	5.52	1/1	1/1	0.16	1/1	69.18	1/1	11.00	0.047	Clemens and Stevens (1980)
<i>Pseudalopex culpaeus</i>	1	5.24	0/1	0/1	0.21	0/1	57.80	0/1	19.67	0.111	Silva et al. (2005)
<i>Pteronura brasiliensis</i>	1	15.33	0/1	1/1	0.70	0/1	87.84	1/1	3.13	0.052	Carter et al. (1999)
<i>Tremarctos ornatus</i>	1	140.00	1/1	1/1	2.24	0/1	60.50	0/1	16.00	1.042	Goldman et al. (2001)
<i>Ursus americanus</i>	1	46.95	0/1	0/1	0.66	0/1	69.35	0/1	9.90	0.160	Pritchard and Robbins (1990)
<i>Ursus arctos</i>	2	135.21	1/2	1/2	1.14	0/2	74.91	1/2	10.08	0.291	Pritchard and Robbins (1990); Elfström et al. (2013)
<i>Ursus maritimus</i>	1	350.00	0/1	0/1	1.90	0/1	82.24	0/1	20.28	0.890	Best (1985)
<i>Ursus thibetanus</i>	1	65.00	0/1	1/1	0.98	1/1	71.56	1/1	18.12	0.473	Koike et al. (2010)

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<sup>a</sup> If nutrient composition is estimated and DM intake and aD DM are not, it means that the DM% was estimated to calculate DM intake from fresh matter intake; N° = number, DM = dry matter, aD DM = dry matter digestibility, RT = retention time, DMC = dry matter gut contents

459 **Table 3** Scaling relationships according to  $y = a x^b$  in mammalian terrestrial carnivore (n=23) and herbivore (n=82) species, for the body mass  
460 scaling of dry matter intake (DMI, in kg/d), digesta retention (RT, in h), apparent dry matter digestibility (aD DM, in %) and dry matter gut  
461 contents (DMC, in kg dry matter), and the scaling relationship of RT with the relative DMI (per unit metabolic body weight,  $\text{kg}^{0.75}$ ). Analyses  
462 performed in Generalized Least Squares (GLS) and Phylogenetically Generalized Least Squares (PGLS).

Model	Stat	$\lambda$	Carnivores		$\lambda$	Herbivores		$\lambda$	Carnivores & Herbivores	
			<i>a</i>	<i>b</i>		<i>a</i>	<i>b</i>		<i>a</i>	<i>b</i>
DMI ~ BM	GLS	-	0.034 (0.023;0.050)	0.75 (0.63;0.88)	-	0.047 (0.041;0.053)	0.77 (0.73;0.80)	-	0.043 (0.038;0.043)	0.76 (0.73;0.80)
	PGLS	0.10	0.034 (0.022;0.051)	0.75 (0.62;0.88)	0.86***	0.044 (0.026;0.074)	0.76 (0.72;0.81)	0.83***	0.041 (0.023;0.074)	0.76 (0.71;0.81)
RT ~ BM	GLS	-	6.7 (3.3;13.5)	0.23 (0.00;0.46)	-	21.3 (17.9;25.4)	0.15 (0.11;0.20)	-	17.2 (14.0;21.1)	0.16 (0.10;0.21)
	PGLS	0.89***	8.1 (3.5;18.9)	0.14 (-0.04;0.31)	0.99**	25.6 (9.7;68.0)	0.11 (0.04;0.17)	0.96***	25.8 (10.1;65.5)	0.11 (0.05;0.17)
aD DM ~ BM	GLS	-	77 (69;86)	-0.00 (-0.04;0.03)	-	65 (61;68)	-0.02 (-0.04;-0.01)	-	68 (64;71)	-0.02 (-0.04;-0.01)
	PGLS	0.04**	77 (68;86)	-0.00 (-0.04;0.04)	0.62***	63 (52;76)	-0.03 (-0.05;-0.01)	0.62***	65 (53;78)	-0.03 (-0.05;-0.01)
DMC ~ BM	GLS	-	0.006 (0.003;0.012)	0.98 (0.73;1.23)	-	0.028 (0.024;0.032)	0.93 (0.89;0.96)	-	0.020 (0.016;0.025)	0.93 (0.87;0.99)
	PGLS	(1)	0.009 (0.003;0.032)	0.77 (0.56;0.98)	0.71***	0.031 (0.018;0.054)	0.89 (0.83;0.94)	0.94***	0.030 (0.011;0.084)	0.88 (0.80;0.95)
RT ~ rDMI	GLS	-	26.4 (1.3;532.3)	-0.22 (-1.06;0.63)	-	488.3 (122.8;1942.6)	-0.71 (-1.06;-0.36)	-	73.1 (17.9;299.8)	-0.28 (-0.64;0.09)
	PGLS	0.91*	15.8 (2.4;104.7)	-0.09 (-0.58;0.41)	0.96*	181.8 (43.8;754.4)	-0.45 (-0.74;-0.15)	0.97***	86.6 (23.7;317.2)	-0.25 (-0.49;-0.02)

463 \*  $\lambda$  significantly different from 0, \*\*  $\lambda$  significantly different from 1, \*\*\*  $\lambda$  significantly different from 0 and 1;

464 (1)  $\lambda$  set to 1 because the maximum likelihood method did not work in this case

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466 **Table 4** Results of analyses for an effect of trophic level (tl) on scaling relationships according to  $\log(y) = a + b \log(x) + c$  (tl) in mammalian  
467 terrestrial carnivore (n=23, tl=1) and herbivore (n=82, tl=2) species, for the body mass scaling of dry matter intake (DMI, in kg/d), digesta  
468 retention (RT, in h), apparent dry matter digestibility (aD DM, in %) and dry matter gut contents (DMC, in kg dry matter), and the scaling  
469 relationship of RT with the relative DMI (per unit metabolic body weight,  $\text{kg}^{0.75}$ ). Analyses performed in Generalized Least Squares (GLS) and  
470 Phylogenetically Generalized Least Squares (PGLS).

Model	Stat	Carnivores & Herbivores				p (c)
		$\lambda$	a	b	c	
DMI ~ BM	GLS	-	-1.634 (-1.780;-1.469)	0.76 (0.73;0.80)	0.151 (0.063;0.240)	0.001
	PGLS	0.81***	-2.081 (-2.503;-2.087)	0.76 (0.71;0.80)	0.365 (0.179;0.550)	<0.001
RT ~ BM	GLS	-	0.497 (0.244;0.751)	0.16 (0.11;0.21)	0.412 (0.277;0.548)	<0.001
	PGLS	0.96***	1.409 (0.718;2.100)	0.11 (0.05;0.17)	0.001 (-0.291;0.292)	0.995
aD DM ~ BM	GLS	-	2.013 (1.945;2.081)	-0.02 (-0.04;-0.01)	-0.102 (-0.138;-0.066)	<0.001
	PGLS	0.54***	2.098 (1.953;2.243)	-0.03 (-0.04;-0.01)	-0.152 (-0.219;-0.085)	<0.001
DMC ~ BM	GLS	-	-2.803 (-3.032;-2.575)	0.93 (0.89;0.98)	0.621 (0.499;0.743)	<0.001
	PGLS	0.89***	-2.499 (-3.171;-1.828)	0.87 (0.81;0.94)	0.504 (0.215;0.794)	0.001
RT ~ rDMI	GLS	-	1.505 (0.964;2.046)	-0.59 (-0.92;-0.26)	0.493 (0.333;0.653)	<0.001
	PGLS	0.97***	1.719 (0.977;2.461)	-0.29 (-0.54;-0.04)	0.142 (-0.174;0.459)	0.379

\*  $\lambda$  significantly different from 0, \*\*  $\lambda$  significantly different from 1, \*\*\*  $\lambda$  significantly different from 0 and 1;

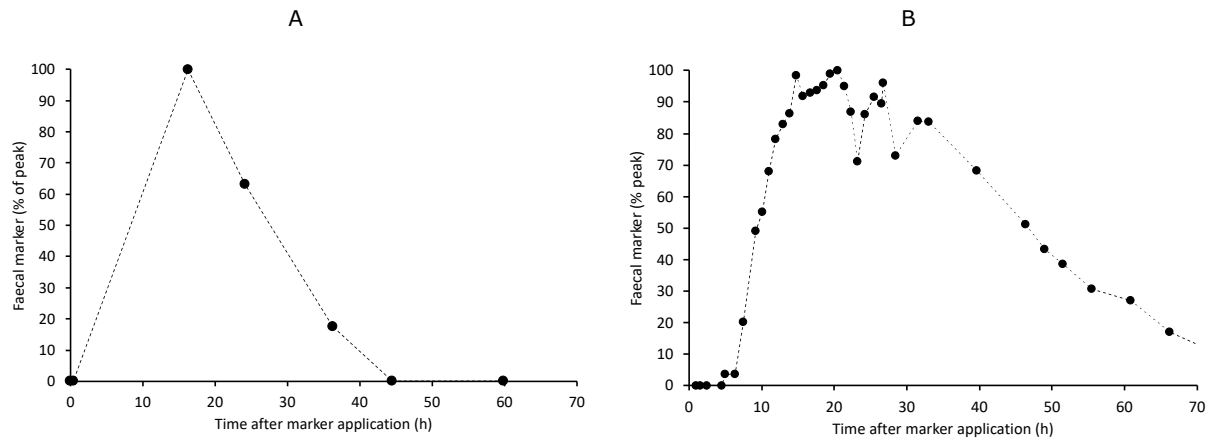
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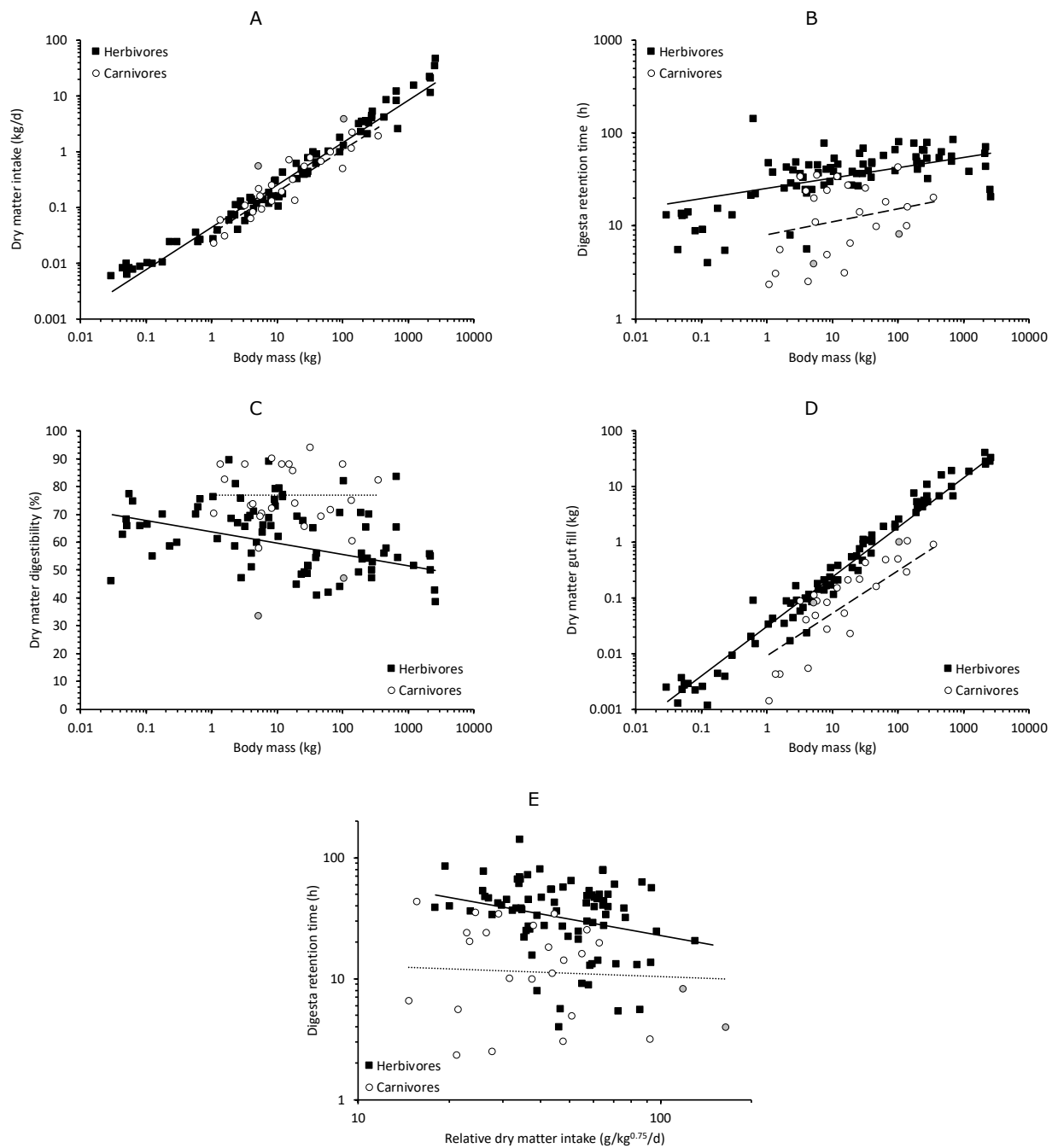
474 **Table 5** Literature data on the dry matter concentration of the total gastrointestinal contents wet mass in various species (mean  $\pm$ SD)

Species	n	Dry matter % wet mass	Source
Mouse	12	16.1	Cizek (1954)
Hamster	12	19.0	Cizek (1954)
Rat	24	20.2	Cizek (1954)
Rat	3	21.4 $\pm$ 1.2	Elsden et al. (1946)
Guinea pig	12	16.3	Cizek (1954)
Rabbit	5	17.8 $\pm$ 4.6	Elsden et al. (1946)
Rabbit	16	17.8	Cizek (1954)
Dog	10	21.5	Cizek (1954)
Pig	4	19.4 $\pm$ 1.5	Elsden et al. (1946)
Goat	1	19.0	Cizek (1954)
Goat	14	16.9 $\pm$ 1.9	data from Hatt et al. (2019)
Sheep	4	12.2 $\pm$ 3.9	Elsden et al. (1946)
Sheep	21	14.1 $\pm$ 1.2	data from Clauss et al. (2016)
Red deer	1	13.5	Elsden et al. (1946)
Cattle	2	12.9/16.1	Elsden et al. (1946)
Horse	3	10.6 $\pm$ 0.9	Elsden et al. (1946)





476 **Figure 1** Examples of small particle marker excretion curves in (A) a carnivore, the domestic  
 477 dog (*Canis lupus familiaris*) from the study of De Cuyper et al. (2018; titanium oxide), and  
 478 (B) a herbivore, the proboscis monkey (*Nasalis larvatus*), from Matsuda et al. (2015;  
 479 chromium-mordanted fibre). Note the difference in defecation frequency and the  
 480 corresponding shape of the marker excretion pattern.



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482 **Figure 2** Scaling relationships in herbivores and carnivores between (A) body mass and dry  
 483 matter intake, (B) body mass and the retention time of the digesta, (C) body mass and the  
 484 apparent digestibility of dry matter, (D) body mass and the estimated dry matter contents of  
 485 the total gastrointestinal tract, (E) the relative dry matter intake and the digesta retention time.  
 486 Solid regression lines – herbivores (all significant). Interrupted lines – significant carnivore  
 487 regression lines, dotted lines – non-significant carnivore regression lines. All regression lines

488 represent PGLS results (see Table 3 for statistics). The grey dots indicate the two panda  
489 species (*Ailurus fulgens*, *Ailuropoda melanoleuca*) that are herbivorous yet phylogenetically  
490 linked to the other carnivores.