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

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Abstract

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

Keywords

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

Introduction

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

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

However, to our knowledge, data on gut contents in carnivores is scarce. In terrestrial vertebrate herbivores, ample information about the contribution of gut contents to overall body mass exist, measured in animals taken from the wild, by dissection (reviewed in Clauss et al. 2007; Clauss et al. 2013). By contrast, similar data is not available for carnivores, most likely for two reasons. (i) Killing free-ranging carnivores for study purposes is socially less accepted than killing herbivores. (ii) Herbivores more or less feed continuously, and therefore have a constant gut fill; even if fluctuations between seasons or even between hours of the day have been reported (Owen-Smith 1994; Barboza et al. 2006; Weckerly 2010), gut contents are always present in relevant and measurable amounts. In carnivores, however, gut contents may differ dramatically with time since the last meal. Because some carnivores may have to feed repeatedly throughout the day, but some may have a period of fasting after a gorging day (De Cuyper et al. 2019), measuring the gut contents of carnivores killed in the wild may not appear as a promising research strategy.

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

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

Methods

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

If intake and digestibility were not provided but only MRT or TT, publications were nevertheless considered if the nutrient composition of the diet used was either given, or could be assumed using its description in the publication and standard nutrient composition feed tables (Supplement 1). For carnivores, diet digestibility can be estimated by standard equations from diet nutrient composition (NRC 2006), with no relevant differences between mammalian carnivore species (Clauss et al. 2010). Using the same approach, the metabolisable energy (ME) content of the diet was estimated as the basis for the intake estimation. The maintenance requirement (MER) of a specimen for which intake was not measured directly (only for dogs, bears, raccoon and cats in this dataset) was calculated based on the equation from NRC (2006), which yields an estimate in MER. The intake was then estimated as the amount of diet (with the estimated ME content) needed to meet that requirement. The equations used for estimation are given in Table 1. The data collection, including references and indications which estimation steps were made, is given as Table 2. The full set of data (i.e. not the species averages but each data point) is available as a supplement (Supplement 2).

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

To account for any phylogenetic influence on these allometries, we performed analyses in Generalized Least Squares (GLS) and Phylogenetic Generalized Least Squares (PGLS), using a mammalian supertree (Fritz et al. 2009), pruned to include the relevant taxa in our dataset. The tree was then correlated with our dataset in PGLS, and strength of the phylogenetic signal (λ) estimated by maximum likelihood (this was not possible in the scaling model for carnivore retention times, where λ was therefore manually set to 1; in our experience, this occurs, albeit rarely, in software package used). All analyses were carried out in R v 3.3.2 (R_Core_Team 2015), with the package ‘nlme’ (Pinheiro et al. 2011) for GLS and the package ‘caper’ (Orme et al. 2013) for PGLS analyses. The significance level was set to 0.05.

Results

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

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

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

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

Discussion

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

All investigated factors were different between the trophic levels in both GLS and PGLS (Table 4), suggesting convergent patterns across the herbivores from different clades (including the Carnivora). The only exception were retention times measures, which only differed between the trophic groups in GLS but not in PGLS (Table 4), most likely due to the general uniformity of this measure within clades, with the herbivorous Carnivora – the pandas – having retention times as short as those of carnivorous Carnivora. However, even though a significant difference was detected for these measurements of digestive physiology, there was always overlap in the 95% confidence intervals of the intercept of the models between herbivores and carnivores (Table 3), and the differences between the trophic groups were less pronounced than expected. Given the difference in wet gut contents between dog and goat cited in the Introduction (Davis et al. 1975), we would have expected that gut fill in carnivores is rather of a magnitude of 0.5-1 % of that of herbivores rather than the 20-30 % found in the present study.

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

Possibly more importantly, however, is a constraint in the dataset that relates directly to the focus of our study: We must assume that the body mass data for herbivores includes an (unknown) proportion of wet gut contents. If one would express herbivore body mass on an estimated gut contents-free basis, subtracting roughly 10% of raw body mass data, the herbivore regression lines in Fig. 2A-D would all shift horizontally to the left, and differences to carnivores would be increased. As for the less than expected RT difference between herbivores and carnivores, it should be noted that this may be due to the common observation that carnivores can retain their faeces and time defecations behaviourally to a greater extent than most herbivores, which defecate more regularly. This difference is also evident in the significant effect of relative food intake on retention time in the herbivores and its absence in carnivores (Fig. 2E), again suggesting that carnivores can afford to uncouple defecation from other digestive processes to a higher degree. One interesting observation on carnivore retention times is that carnivore groups with shorter retention times (<10 h) were typically from the mustelid family (e.g. *Neovison vison; Mustela putorius; Martes melampus; Arctitis binturong; Lontra Canadensis; Pteronura brasiliensis*), the procyonid family (*Potos flavus*) and ursid family (*Ailurus fulgens; Ailuropoda melanoleuca; Ursus arctos; Ursus americanus*) – all groups whose digestive tract does not comprise a caecum (McGrosky et al. 2016).

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

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

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

Such a difference between gorge and fasting days would reduce differences in gut fill of large carnivores to herbivores on gorge days, where wolves (*Canis lupus*), for example, may consume up to 22% of their own body mass (Stahler et al. 2006). On the other hand, this would even increase the difference in gut fill between large carnivores and herbivores on the carnivore’s fasting day preceding their next hunt, giving them a physical advantage over their large prey. A constant food intake, on which the calculations of the present study are based, is more representative for another group of carnivores such as wild cats (*Felis silvestris*) with frequent meals throughout the day (Bradshaw 2006); arguably, the large discrepancy between the body size of these species and their small prey makes the physical advantage of an empty gastrointestinal tract less necessary.

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

The final conclusion of this contribution is that terrestrial carnivorous mammals indeed carry quantitatively less content in their gut than do herbivorous mammals. As suggested before, in the light of predator-prey interactions, this implies that the predator has less inert mass to move in proportion to muscle mass. Although predators have higher muscle fibre power than their prey, the lower amount of inert gut contents will also contribute their greater capacities for acceleration and deceleration (Wilson et al. 2018). The inert digesta mass may also have been one (of many) contributing selective pressures for the evolution of cost-efficient locomotion with unguligradism and energy-storing tendon systems in larger herbivores (McHorse et al. 2019).

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

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

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

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

Species	N° of studies	BM (kg)	N° of BM estimated	N° of nutrient composition estimated[a]	DM intake (kg)	N° of DM intake estimated	aD DM (%)	N° of aD DM estimated	RT (h)	DMC (kg)	References
Acinonyx jubatus	1	32.17	0/1	1/1	0.77	0/1	94.05	1/1	25.34	0.430	Leemans et al. (2015)
Ailuropoda melanoleuca	2	102.24	0/2	0/2	3.89	0/2	47.13	0/2	8.25	1.028	Mainka et al. (1989)
Ailurus fulgens	1	5.13	0/1	1/1	0.56	0/1	33.70	0/1	3.96	0.082	Wei et al. (1999)
Arctictis binturong	1	18.90	0/1	1/1	0.13	0/1	73.88	1/1	6.50	0.023	Lambert et al. (2014)
Canis familiaris	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)
Caracal caracal	1	8.25	0/1	0/1	0.13	0/1	72.19	0/1	24.00	0.082	Edwards et al. (2001)
Chrysocyon brachyurus	1	25.80	0/1	0/1	0.55	0/1	65.70	0/1	14.15	0.217	Sanford and Angel (2006)
Felis catus	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)

Leopardus pardalis	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)
Leopardus wiedii	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)
Lontra canadensis	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)
Martes melampus	1	1.60	0/1	1/1	0.03	0/1	82.42	1/1	5.52	0.004	Tsuji et al. (2015)
Mustela putorius	1	1.36	0/1	0/1	0.06	0/1	88.05	1/1	3.03	0.004	Bleavins and Aulerich (1981)
Neovison vison	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)
Panthera onca	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)
Potos flavus	1	4.25	0/1	1/1	0.08	0/1	73.74	1/1	2.50	0.005	Lambert et al. (2014)
Prionailurus bengalensis	1	5.88	0/1	0/1	0.09	0/1	70.15	0/1	35.00	0.087	Edwards et al. (2001)
Procyon lotor	1	5.52	1/1	1/1	0.16	1/1	69.18	1/1	11.00	0.047	Clemens and Stevens (1980)
Pseudalopex culpaeus	1	5.24	0/1	0/1	0.21	0/1	57.80	0/1	19.67	0.111	Silva et al. (2005)
Pteronura brasiliensis	1	15.33	0/1	1/1	0.70	0/1	87.84	1/1	3.13	0.052	Carter et al. (1999)
Tremarctos ornatus	1	140.00	1/1	1/1	2.24	0/1	60.50	0/1	16.00	1.042	Goldman et al. (2001)
Ursus americanus	1	46.95	0/1	0/1	0.66	0/1	69.35	0/1	9.90	0.160	Pritchard and Robbins (1990)
Ursus arctos	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)
Ursus maritimus	1	350.00	0/1	0/1	1.90	0/1	82.24	0/1	20.28	0.890	Best (1985)
Ursus thibetanus	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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[a] 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

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 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 contents (DMC, in kg dry matter), and the scaling relationship of RT with the relative DMI (per unit metabolic body weight, kg$^{0.75}$). Analyses performed in Generalized Least Squares (GLS) and Phylogenetically Generalized Least Squares (PGLS).

			Carnivores			Herbivores			Carnivores & Herbivores	
Model	Stat	λ	*a*	*b*	λ	*a*	*b*	λ	*a*	*b*
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)

* λ significantly different from 0, ** λ significantly different from 1, *** λ significantly different from 0 and 1;
(1) λ set to 1 because the maximum likelihood method did not work in this case

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 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 retention (RT, in h), apparent dry matter digestibility (aD DM, in %) and dry matter gut contents (DMC, in kg dry matter), and the scaling relationship of RT with the relative DMI (per unit metabolic body weight, $kg^{0.75}$). Analyses performed in Generalized Least Squares (GLS) and Phylogenetically Generalized Least Squares (PGLS).

			Carnivores & Herbivores			
Model	Stat	λ	*a*	*b*	*c*	p (*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

* λ significantly different from 0, ** λ significantly different from 1, *** λ significantly different from 0 and 1;

Table 5 Literature data on the dry matter concentration of the total gastrointestinal contents wet mass in various species (mean ±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 ±1.2	Elsden et al. (1946)
Guinea pig	12	16.3	Cizek (1954)
Rabbit	5	17.8 ±4.6	Elsden et al. (1946)
Rabbit	16	17.8	Cizek (1954)
Dog	10	21.5	Cizek (1954)
Pig	4	19.4 ±1.5	Elsden et al. (1946)
Goat	1	19.0	Cizek (1954)
Goat	14	16.9 ±1.9	data from Hatt et al. (2019)
Sheep	4	12.2 ±3.9	Elsden et al. (1946)
Sheep	21	14.1 ±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 ±0.9	Elsden et al. (1946)

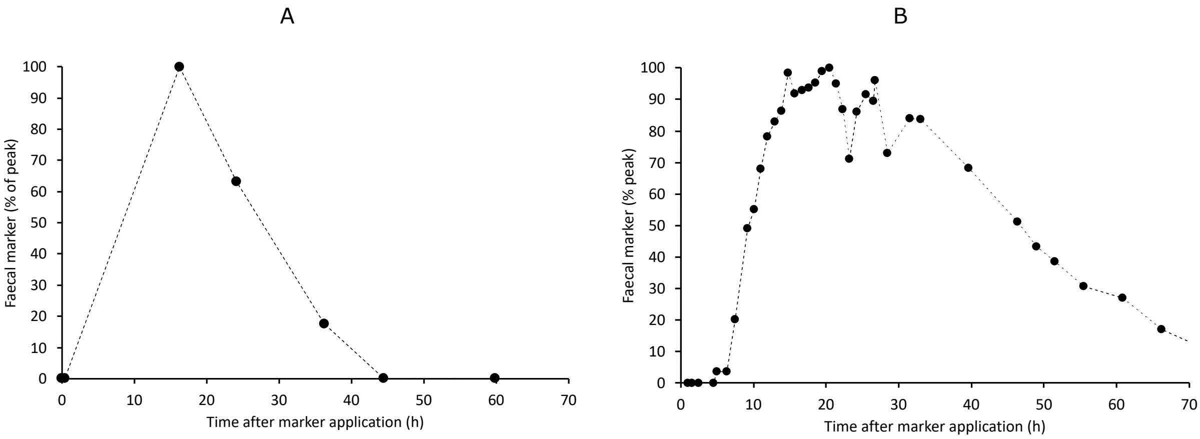

Figure 1 Examples of small particle marker excretion curves in (A) a carnivore, the domestic dog (*Canis lupus familiaris*) from the study of De Cuyper et al. (2018; titanium oxide), and (B) a herbivore, the proboscis monkey (*Nasalis larvatus*), from Matsuda et al. (2015; chromium-mordanted fibre).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

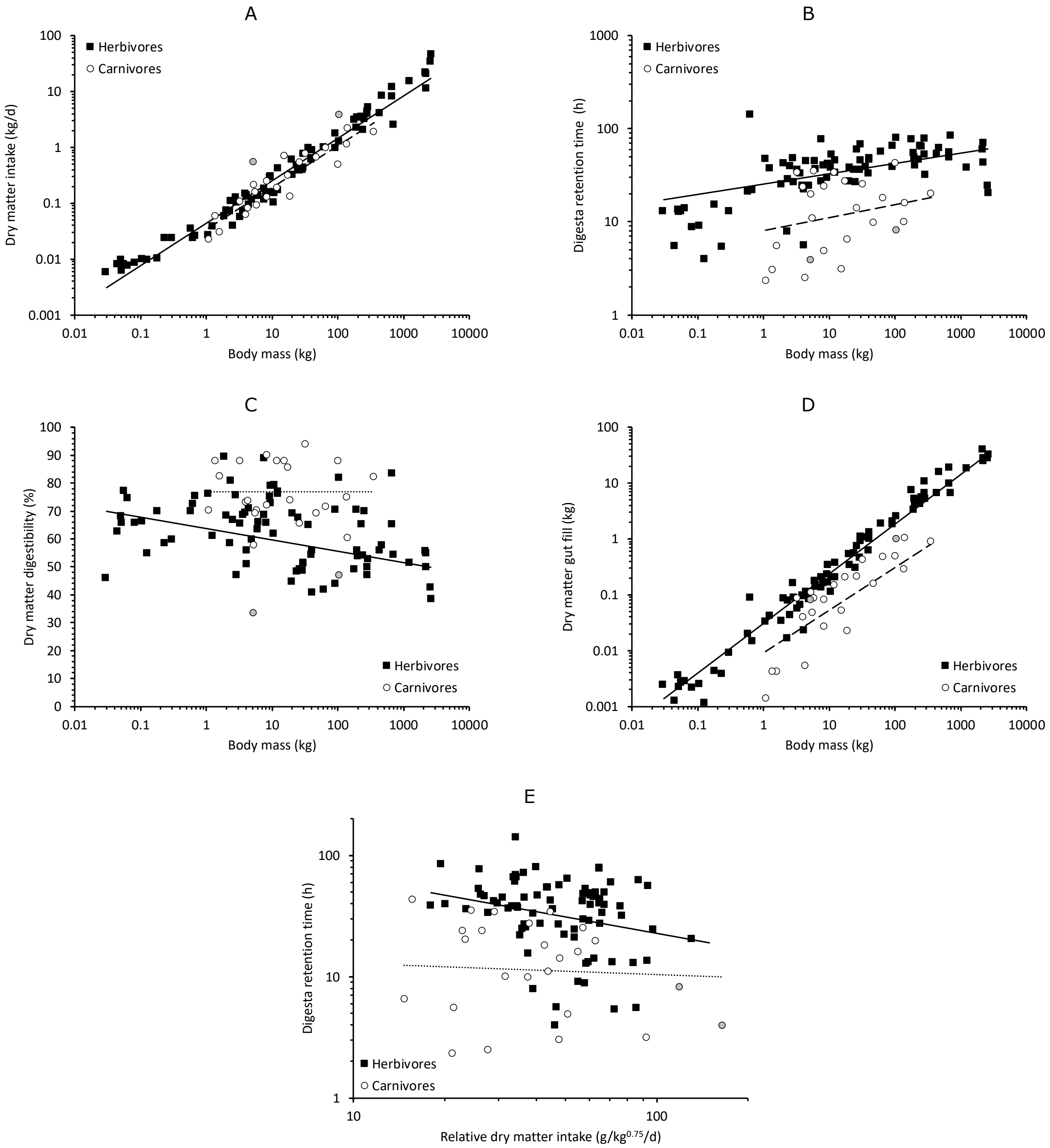

Figure 2 Scaling relationships in herbivores and carnivores between (A) body mass and dry matter intake, (B) body mass and the retention time of the digesta, (C) body mass and the apparent digestibility of dry matter, (D) body mass and the estimated dry matter contents of the total gastrointestinal tract,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

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