



## The influence of natural diet composition, food intake level, and body size on ingesta passage in primates

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### ABSTRACT

An important component of digestive physiology involves ingesta mean retention time (MRT), which describes the time available for digestion. At least three different variables have been proposed to influence MRT in herbivorous mammals: body mass, diet type, and food intake (dry matter intake, DMI). To investigate which of these parameters influences MRT in primates, we collated data for 19 species from trials where both MRT and DMI were measured in captivity, and acquired data on the composition of the natural diet from the literature. We ran comparative tests using both raw species values and phylogenetically independent contrasts. MRT was not significantly associated with body mass, but there was a significant correlation between MRT and relative DMI (rDMI, g/kg<sup>0.75</sup>/d). MRT was also significantly correlated with diet type indices. Thus, both rDMI and diet type were better predictors of MRT than body mass. The rDMI–MRT relationship suggests that primate digestive differentiation occurs along a continuum between an “efficiency” (low intake, long MRT, high fiber digestibility) and an “intake” (high intake, short MRT, low fiber digestibility) strategy. Whereas simple-stomached (hindgut fermenting) species can be found along the whole continuum, foregut fermenters appear limited to the “efficiency” approach.

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### 1. Introduction

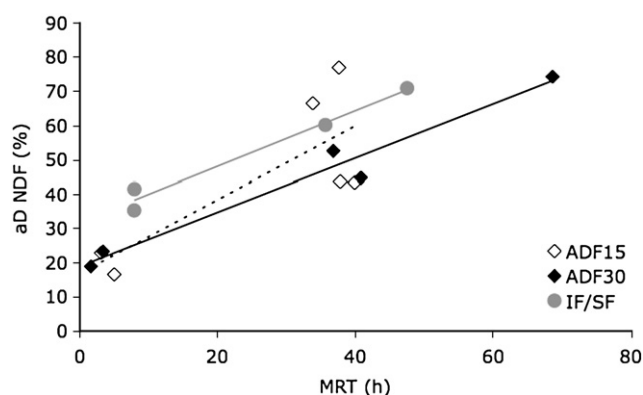
Digestion is a time-dependent process. This is especially true for herbivores, which have to rely on the fermentative activity of symbiotic gut microbes for the digestion of fibrous plant cell walls (Stevens and Hume, 1998). Positive correlations between ingesta mean retention time (MRT) and digestive efficiency have been shown in domesticated and wild herbivores (c.f. Fig. 3 in Udén et al., 1982; Clauss et al., 2007b), and are also evident from *in vitro* digestion assays in which primate feces were used as inoculum source (Campbell et al., 2002). The relevance of time available for microbial fermentation (“allo-enzymatic” digestion) can also be demonstrated in primates using *in vivo* data on particle MRT and the digestibility of cell wall from feeding experiments (Fig. 1). In contrast, the “auto-enzymatic” digestion (by enzymes produced by the herbivore itself) of proteins, lipids and soluble carbohydrates

usually occurs at high rates that make ingesta passage less critical in granivorous, insectivorous or carnivorous animals.

Here, we use existing data on primate ingesta retention to investigate a critical assumption that has become textbook knowledge (e.g. McNab, 2002; Karasov and Martínez del Río, 2007) in herbivore ecology: in herbivores, MRT is assumed to be a function of body mass (BM). This idea originated from theoretical work on a primate species (Demment, 1983). It is generally assumed that herbivore gut capacity scales to BM<sup>1</sup> (Parra, 1978; Demment and Van Soest, 1985; Clauss et al., 2005b), but that energy requirement – the determinant of food intake – scales to BM<sup>0.75</sup>. Based on these scaling relationships, the time required for the material to pass through the gut should scale to BM<sup>0.25</sup> (Calder, 1984; McNab, 2002). Illius and Gordon (1992) found that MRT scaled to BM<sup>0.25</sup> and BM<sup>0.26</sup> for ruminant and hindgut fermenting mammals, respectively, but the validity of these results has been questioned on the basis of a large collection of empirical data (Clauss et al., 2007a). Moreover, a series of recent publications have reported results that appear to contradict the prediction that larger animals have longer MRTs than smaller ones (reviewed in Clauss et al., 2007a). For primates, Milton (1984) found notable exceptions to the general rule of increasing ingesta passage (measured as transit time) with increasing BM. Similarly, Lambert (1998) demonstrated that body mass explained only a small proportion of the variation observed

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**Fig. 1.** Correlation of particle mean retention time (MRT, h) and the apparent digestibility (aD) of plant cell wall (measured as NDF) in different primate species fed experimental diets of different fiber contents (diets with 15 or 30% acid detergent fibre ADF from Edwards and Ullrey, 1999a; Edwards and Ullrey, 1999b; IF/SF diets from Campbell et al., 2004).

in the measure of transit time. Caton and Hume (1996) did not find a correlation between BM and MRT in small New World primates, and Nijboer et al. (2007) did not find a correlation between BM and MRT in foregut fermenting primates.

In contrast to this “body mass” hypothesis, other researchers have argued that MRT is more fundamentally linked to the composition of the natural diet and to food intake level. On theoretical grounds, it is assumed that the evolved ingesta retention mechanisms should reflect the diet of an organism (Sibly, 1981). In ruminants and rhinoceroses, it has been suggested that due to systematic differences in the fermentation pattern between grasses and browse, dietary niche should be an important predictor of ingesta retention (Clauss and Lechner-Doll, 2001; Clauss et al., 2005a; Clauss et al., 2006; Hummel et al., 2006b). In a similar manner, the composition of the natural diet of primates should predict MRT, with a decreasing retention time as the proportion of leaves decreases. Milton (1984) and Lambert (1998) interpreted the noted deviations of transit time measurements from a body size-rule as indications of physiological adaptations to the diet of particularly herbivorous primate species. Additionally, observations within different mammal species have shown that MRT is highly dependent on the food intake (Fryxell et al., 1994; Reid and Brooks, 1994; Clauss et al., 2004); therefore, the intake level of a species might be a better predictor of its MRT than its body mass (Clauss et al., 2007a).

In primates, “herbivory” is more difficult to define than in ruminants or perissodactyls because the trophic niche of primates varies from pure folivory to varying proportions of folivory, frugivory, and insectivory. To some degree, primate trophic niche shows a correlation with body size, with very small species tending towards insectivory, and pure folivory being predominant in the larger species (Clutton-Brock and Harvey, 1983; Sailer et al., 1985). However, outliers – especially very small folivorous species – make generalizations difficult (Yeager, 1989). Insects can be digested adequately by auto-enzymatic processes, and it is assumed that these processes play a larger role in the digestion of fruit as compared to leaves. In parallel with observations in Serengeti ungulates (Bell, 1971; Jarman, 1974), the division of smaller primate species feeding on “higher quality” diets (auto-enzymatic digestion) and larger primate species feeding on “lower quality” diets (allo-enzymatic digestion by gut microbes) has been termed the “Jarman–Bell-principle” (Gaulin, 1979). On the one hand, the “Jarman–Bell-principle” can be interpreted as a simple function of availability – at the foraging scale of larger animals with their higher absolute energy requirements, “high-quality” food is usually not consistently available, forcing such animals to feed on lower quality food. On the other hand, an often-quoted, intrinsic

assumption in the “Jarman–Bell-principle” is that larger species have a “digestive advantage” due to the increasing difference between gut capacity and metabolic requirements (Parra, 1978; Demment and Van Soest, 1985). Ultimately, increasing body size is considered a key adaptation to digestive challenges posed by certain trophic niches (low quality food of high abundance). However, more complete digestion at larger body sizes can be difficult to demonstrate (Pérez-Barbería et al., 2004; Clauss and Hummel, 2005), and a recent evaluation of mammalian herbivore passage data did not support the concept of increasing ingesta retention with increasing body size above a threshold of 0.5–1 kg body mass (Clauss et al., 2007a). In primates, the concept that physiological adaptations to the natural diet could ‘bend’ presumed body size-rules was outlined by Lambert (2002), who showed that some cercopithecine species had, for their size, unexpectedly long ingesta passage times.

To investigate variation in MRT, we collated data on MRT and dry matter intake (DMI) in primates from the published literature. We tested predictions involving the following specific associations: (1) Based on the “body mass” hypothesis for ingesta passage rates, we tested whether body mass is positively correlated with MRT. (2) Based on theoretical arguments for a tighter functional link between diet and digestive function, we predicted a negative correlation between DMI and MRT and (3) a positive correlation between the proportion of foliage in the natural diet and MRT. More generally, we expect that DMI and proportion of foliage are better predictors of MRT than is body mass. We investigated these predictions using non-phylogenetic comparative tests of species data and after controlling for primate phylogeny.

## 2. Methods

Ingesta retention in primates has been assessed by using “transit times” (Milton, 1984; Lambert, 1998). Transit time is defined as the time between marker feeding and the first appearance of the marker in the feces. However, as the first marker appearance rarely coincides with the peak, mean or total marker excretion, it is usually not considered the best parameter for the characterization of a species’ digestive physiology, and mean retention time is preferred (Warner, 1981); actually, there may even be no significant correlation between transit times and MRTs measured in the same individuals (e.g. Clauss et al., 2005a). Therefore, we focused on particle MRT data; henceforward, “MRT” denotes particle MRT in the total digestive tract. Only sources that provided BM, DMI and MRT together were used, thus excluding publications which gave MRT measurements but did not measure food intake in their animals, such as the work of Caton and co-workers (Caton et al., 1996; Caton and Hume, 1996; Caton, 1999; Caton et al., 1999; Caton et al., 2000). To obtain an adequate sample size for the comparative test, both chromium-mordanted fiber particles and plastic particles were accepted as passage markers; the diets used in the experiments also varied between investigations (see Appendix A). For each species, one average value for BM, MRT and DMI was calculated using all available data from the cited publications. For most species, only one set of measurements for one DMI level was available. The data and their sources are summarized in the Appendix A. The 19 species were identified as simple-stomached ( $n=13$ ) or foregut fermenters ( $n=6$ ) based on Chivers and Hladik (1980). Due to the low  $n$ , however, these categories were not analyzed individually. The characterization of the natural diet of the species followed the principle of Sailer et al. (1985) with given proportions for structural plant parts ( $s$ , %leaves), reproductive plant parts ( $r$ , %flowers and fruits), and animal matter ( $a$ , %insects and vertebrates). From these proportions, we calculated a dietary quality index ( $dq$ ) as  $s+2r+3.5a$  (Sailer et al., 1985; see Appendix A for data).

Allometric regression (i.e., linear regression between the logarithmic values) was performed between body mass (independent variable) and both absolute DMI (aDMI, in kg) and MRT. Linear regression analysis was

**Table 1**  
Tests of phylogenetic signal<sup>a</sup>

	MSE data	Mean MSE permutation	p-value (signal)
Log body mass	0.113	0.408	<0.001
Log aDMI	0.12	0.305	<0.001
Log rDMI	0.00805	0.119	0.056
MRT	167	339	0.017
dq	1748	3301	0.006
%leaves	1054	1904	0.022
%fruit	845	1330	0.043
Log %animal	0.382	0.577	0.071

<sup>a</sup> Tests were run using data and branch length transformations that best meet the assumptions of independent contrasts, and thus correspond to the other analyses. The *P*-value indicates whether the mean square error (MSE) for the data set is significantly lower than the mean MSE on permuted data sets, as such a result would indicate significant phylogenetic signal.

performed between relative DMI (rDMI in g/kg<sup>0.75</sup>/d; independent variable) and MRT. Additionally, correlations between parameters characterizing the natural diet and physiological parameters were investigated. Two species, *E. fulvus* and *V. variegata*, were regarded as outliers in terms of their extremely short MRTs (e.g. in Fig. 3, the vertical distance in MRT-direction of these two species from the robust regression line MRT=49.5–0.243 DMI for raw data is beyond the three-fold interquartile range from the median of all vertical distances; robust regression calculated with the raw data using NCSS 2004, NCSS, Kaysville, UT, USA); analyses were performed with and without these two species. Finally, a multiple regression analysis was performed, testing the effect of body mass, relative DMI, and %leaves on MRT. We calculated variance inflation factors (VIF) in the multiple regression analyses to assess whether correlations among the predictor variables might produce unstable results, with VIF>10 indicating the presence of collinearity (Petraitis et al., 1996). In all tests, however, the VIF never exceeded 2.0.

Analyses were performed for the original species data and then repeated using phylogenetically independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991; Nunn and Barton, 2001). Contrasts represent evolutionary change since two species last shared a common ancestor and therefore provide a means to control for the non-independence of species data. Contrasts were based on a recent phylogenetic hypothesis for primate evolutionary relationships (Bininda-Emonds et al., 2007) and calculated using the PDAP module (Midford et al., 2005) of Mesquite (Maddison and Maddison, 2006). We tested the assumptions of independent contrasts (Garland et al., 1992) and found that the branch lengths as estimated were adequate. In some cases, however, log<sub>10</sub> transformation of the data was necessary for meeting the assumptions (for body mass, aDMI, rDMI and animal matter in the diet, after adding 1 to variables that included values of zero). For allometric relationships involving MRT, we log<sub>10</sub>-transformed this variable, but otherwise use untransformed data. All regressions were conducted through the origin, as required when analyzing independent contrasts (Garland et al., 1992). The PDAP module uses positivized values of the independent variable; in some cases, we therefore investigated whether contrasts in the dependent variable were consistently positive or negative using a sign test (Midford et al., 2005).

In addition, we tested the assumption that more closely related species have more similar trait values, i.e. phylogenetic signal (Blomberg et al., 2003). For this, we used the program Phylogenetic Signal (Blomberg et al., 2003). We tested whether a trait showed significant phylogenetic signal using a randomization test based on 1000 permuted data sets, which tests whether the data show more signal (less variance) than expected under a null hypothesis of no correspondence between the data and the phylogeny (Blomberg et al., 2003). In general, we found support for the hypothesis that traits are correlated with phylogeny (Table 1).

The hypotheses predicted directional associations between measures of MRT and BM (increasing MRT with increasing BM), DMI (decreasing MRT with increasing DMI), and diet type indices (increasing %leaves with increasing BM and MRT and decreasing DMI; increasing %fruits, %animals or dq with decreasing BM and MRT and increasing DMI). When testing these specific predictions, we therefore used directed tests rather than two-tailed tests, as these enable detection of patterns that are opposite to predictions while retaining much of the statistical power of one-tailed tests. Directed tests allocate a disproportionate probability under the null hypothesis to the tail of the distribution in the predicted direction ( $\gamma$ ), while retaining a smaller probability in the other tail to detect unexpected deviations in the opposite direction ( $\delta < \gamma$ ). Directed tests are subject to the constraint that  $\delta + \gamma = \alpha$ . We followed the guidelines in Rice and Gaines (1994) by setting  $\gamma/\alpha$  to 0.8, giving values of  $\gamma=0.04$  and  $\delta=0.01$ .

### 3. Results

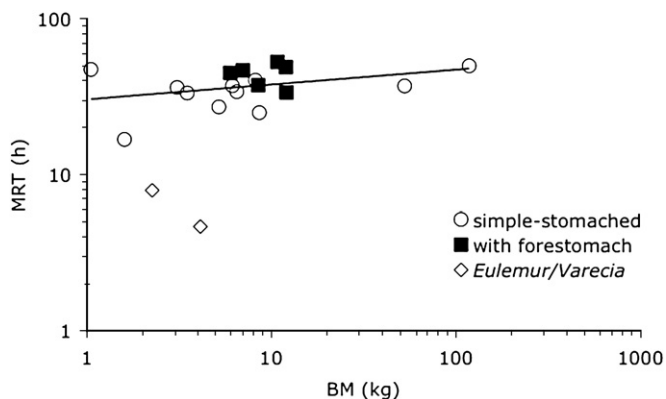
In the data set, there was a significant allometric relationship between BM and absolute DMI (in g/d) for both the raw data ( $p<0.001$ ) and the independent contrasts ( $p=0.005$ ). The 95% confidence interval for the allometric exponent included 0.75 in both analyses.

#### 3.1. Prediction 1. Correlation between body mass and ingesta retention

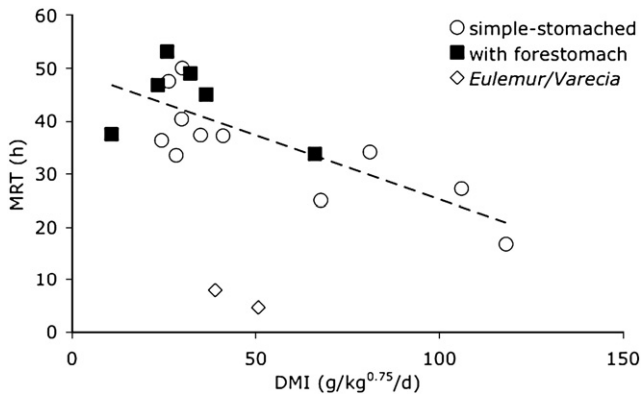
For the complete data set, conventional analysis revealed a non-significant trend for MRT to increase with BM ( $p=0.073$ ), and this trend disappeared when using independent contrasts ( $p=0.469$ ). Only when the two outlier species were excluded was there a significant correlation for independent contrasts ( $p=0.033$ ). In this case, however, only 8 of 16 contrasts showed the predicted positive effect (i.e., positive increase in MRT with positive increase in BM), producing a non-significant result in a sign test ( $p=1.0$ ) and indicating that the association between these traits is not general across primates (Fig. 2).

#### 3.2. Prediction 2. Correlation between intake level and ingesta retention

As predicted, we found a significant negative correlation between rDMI and MRT in the conventional analysis ( $p=0.016$  for all data,  $p<0.001$  without outliers) and for independent contrasts ( $p=0.036$  for all data,  $p=0.045$  without outliers) (Fig. 3).



**Fig. 2.** Correlation in data from primate species, displayed separately as simple-stomached species, species with a forestomach, and the two species (*E. fulvus*, *V. variegata*) treated as outliers between body mass (BM, kg) and mean retention time (MRT, h) (regression line  $MRT=30.4 \text{ BM}^{0.10}$ ,  $r^2=0.13$ ,  $p=0.093$  for raw data without outliers).



**Fig. 3.** Correlation in data from primate species, displayed separately as simple-stomached species, species with a forestomach, and the two species (*E. fulvus*, *V. variegata*) treated as outliers between relative dry matter intake (rDMI, g/kg<sup>0.75</sup>/d) and mean retention time (MRT, h) (regression line  $MRT = 49.5 - 0.243 \text{ DMI}$ ,  $r^2 = 0.62$ ,  $p < 0.001$  for raw data without outliers).

### 3.3. Prediction 3. Correlation between diet type indices and ingesta retention

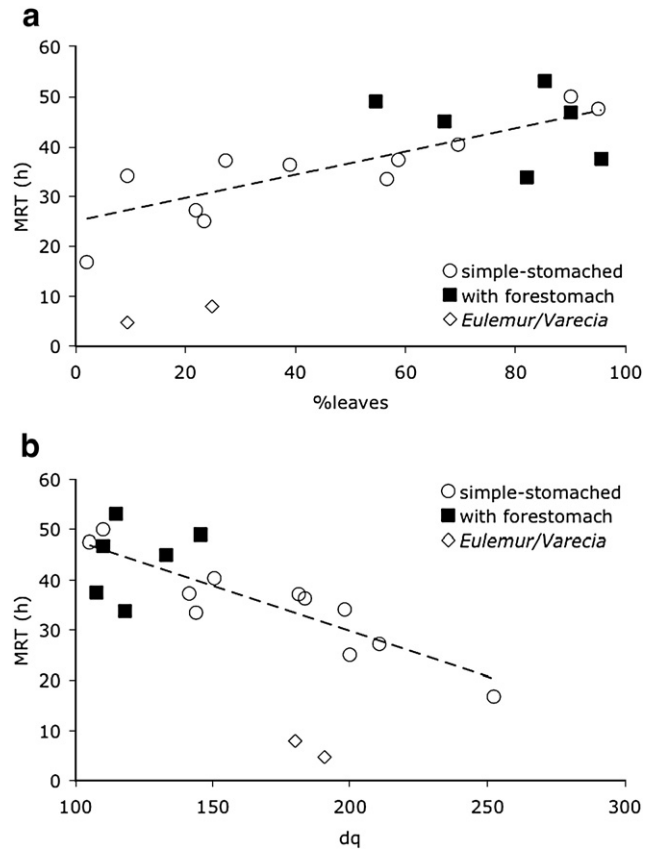
As predicted, we also found a significant correlations between all diet type indices and MRT (Table 2); in particular, %leaves was positively correlated with MRT (Fig. 4a), whereas the dietary quality index dq was negatively correlated with MRT (Fig. 4b).

**Table 2**

Correlations between mean retention time (MRT, h), body mass (BM, kg) and dry matter intake (DMI, g/kg<sup>0.75</sup>/d) and dietary type indices (% of leaves, fruits and animals in the natural diet, and the corresponding dietary quality index dq [see Methods for calculation]), including and excluding the two outlier species *E. fulvus* and *V. variegata* (outlier status ascribed due to particularly low mean retention times)

Correlation	Data set	Raw data		independent contrasts	
		Pearson's <i>r</i>	<i>p</i>	Pearson's <i>r</i>	<i>p</i>
MRT					
%leaves	All data	0.754	<0.001	0.607	0.004
	Without outliers	0.751	<0.001	0.457	0.041
%fruits	All data	-0.734	<0.001	-0.509	0.016
	Without outliers	-0.617	0.005	-0.261	0.194
%animals	All data	-0.425	0.070	-0.428	0.042
	Without outliers	-0.798	0.001	-0.549	0.014
dq	All data	-0.708	<0.001	-0.621	0.003
	Without outliers	-0.814	<0.001	-0.560	0.013
BM					
%leaves	All data	0.248	0.191	0.220	0.228
	Without outliers	0.174	0.316	0.355	0.101
%fruits	All data	-0.180	0.288	-0.042	0.539
	Without outliers	-0.070	0.493	-0.172	0.318
%animals	All data	-0.307	0.202	-0.370	0.074
	Without outliers	-0.356	0.161	-0.370	0.089
dq	All data	-0.291	0.142	-0.351	0.088
	Without outliers	-0.249	0.209	-0.454	0.042
DMI					
%leaves	All data	-0.692	<0.001	-0.582	0.006
	Without outliers	-0.756	<0.001	-0.571	0.011
%fruits	All data	0.530	0.013	0.526	0.013
	Without outliers	0.621	0.005	0.514	0.022
%animals	All data	0.772	<0.001	0.106	0.416
	Without outliers	0.785	<0.001	0.113	0.416
dq	All data	0.778	<0.001	0.551	0.009
	Without outliers	0.804	<0.001	0.531	0.018

For each test, the *p*-value adjusted for directed tests (Rice and Gaines, 1994) is provided (based on the predictions stated for each test).



**Fig. 4.** Correlations in data from primate species, displayed separately as simple-stomached species, species with a forestomach, and the two species (*E. fulvus*, *V. variegata*) treated as outliers between the mean retention time (MRT, h) and (a) the proportion of leaves in the natural diet (regression line  $MRT = 25.0 + 0.233 \text{ \%leaves}$ ,  $r^2 = 0.56$  for raw data without outliers) and (b) the dietary quality index dq [see Methods for calculation] (regression line  $MRT = 66.0 - 0.181 \text{ dq}$ ,  $r^2 = 0.66$  for raw data without outliers).

### 3.4. Multiple regression analysis

We also investigated the links among predictor variables (diet type indices, BM, and DMI). We found no significant correlations between body mass and diet type indices; diet type indices were significantly associated with relative DMI (g/kg<sup>0.75</sup>/d) (Table 2). We included body mass, relative DMI, and %leaves in a multiple regression model to assess their independent effects on MRT. The multiple regression analysis revealed that only the %leaves had a significant effect (Table 3).

## 4. Discussion

The results of this study show that in the primate species for which comparative data are available, either the level of food intake or a supposed morpho-physiological adaptation to the natural feeding

**Table 3**

Results of multiple regression analyses to test whether body mass (BM), relative dry matter intake (DMI, g/kg<sup>0.75</sup>/d) or the percentage of leaves in the natural diet (%leaves) account for explains particle mean retention time (MRT), according to the equation  $MRT = a \ln(BM) + b \text{ rDMI} + c \text{ \%leaves} + \text{const}$

Raw data			Independent contrasts		
$R^2 = 0.625$ ; $p = 0.002$			$R^2 = 0.400$ ; $p = 0.037$		
Term estimate	Standardized beta	<i>p</i>	Term estimate	Standardized beta	<i>p</i>
a: 3.029	0.243	0.157	a: 1.61	0.024	0.527
b: 0.020	0.042	0.849	b: -6.13	-0.135	0.373
c: 0.306	0.723	0.005	c: 0.206	0.507	0.036



niche explain the observed variation in particle mean retention time. By comparison, body mass was generally non-significant. Further studies that record both DMI and MRT in more primate species are needed to corroborate and extend these findings, particularly in large-bodied species, such as the orangutan (*Pongo pygmaeus*) or smaller, specialized herbivores, such as bamboo lemurs (*Hapalemur* spp.). This study supports the concept that with respect to digestive physiology, adaptations to the diets animals consume in the wild may be more important than effects contributed to body mass alone (Clauss et al., 2003; Clauss et al., 2006; Hummel et al., 2006b; Clauss et al., 2007a). This interpretation is reinforced by the fact that in the data set used, body mass did not correlate with diet type indices (Table 2). The most important conclusion of this finding is that hypothetical digestive advantages, theoretically derived from the “Jarman–Bell-principle”, should be used cautiously when explaining the evolution of larger body sizes in primates. Our result is in accord with the findings of Lambert (1998) who also found that the correlation between body mass and a different parameter to measure ingesta passage (transit time) was weak, and who showed, with the example of forest guenons, that also small herbivorous primates can have adaptations to a diet that requires long ingesta retention (Lambert, 2002). It should be noted that these results do not, per se, refute the theory that hypothetical differences in digestive physiology related to body mass differences are important *within* a species, and could therefore be a basis for sexual segregation, as suggested for primates (Demment, 1983), ruminants (Barboza and Bowyer, 2000) and elephants (Stokke and du Toit, 2000).

Using a variety of data from different individual trials means accepting several sources of variation in the results. The problem of using data from different trial setups, diets of differing similarity to the diets actually consumed by the species in the wild, and different passage markers, have been addressed repeatedly (Warner, 1981; Clauss et al., 2007a). In particular, the data points in this data collection rarely represent averages of measurements in a species on a variety of food intake levels, but mostly just one measurement. The use of different passage markers (e.g., different types of plastic particles and mordanted fibres from different batches) will imply that neither size nor specific gravity of the markers was uniform; additionally, the variety in diets used (ranging from complete feeds as used for laboratory animals to zoo diets that may not or may – with varying success – attempt to mimic the natural diet of the species) might be considered problematic. Ideally, comparative studies such as this one should be based on data gained in one set of trials, performed with markers prepared from one batch, using diets that correspond to one clear concept, such as identical diets for all species investigated, or diets modified according to the natural diets of the species. Studies of such large scope are, due to their logistic complexity, rare (but see Foote, 1982 for ungulates). Therefore, variation in the data due to the factors mentioned has to be accepted, if the data gained by studies on individual species are to be used in comparative evaluations.

Several of our analyses suggest that some of these limitations did not impact our conclusions. Among vertebrates, food or energy intake usually scales to  $BM^{0.75}$  (reviewed in Clauss et al., 2007a). The exponent obtained in the regression analysis of absolute DMI on mass in this study did not exclude 0.75 in the 95% confidence interval. Therefore, the allometry usually observed in food intake is also present in the data generated by the cited feeding experiments; this makes the finding of no significant correlation between MRT and BM in the same data set more robust. As further support for the validity of our measures, we found significant phylogenetic signal in the variables (Table 1). Had experimental and individual variation been so great that species estimates would have been unreliable, these measures of signal would have been more difficult to detect statistically.

The inter-specific correlation between rDMI and MRT (Fig. 3) suggests that primate digestive strategy differentiation occurs along a continuum between an “efficiency approach” (low throughput but high digestive efficiency, probably facilitated by long MRT in animals

consuming predominantly leaves) and an “intake approach” (high throughput with less digestive efficiency, probably due to short MRT in animals consuming more fruits and animal matter) (Milton, 1998). In theory, both approaches should be possible on any type of diet, as suggested by the well-known dichotomy of ruminants (efficiency) and equids (intake) (Janis, 1976) or that between hippopotamuses (efficiency) and elephants (intake) (Clauss et al., 2007b). Among herbivores, the most extreme example of the “intake approach” is the giant panda (*Ailuropoda melanoleuca*), which combines a high intake of plant material with a short retention, focusing on the use of auto-enzymatically digestible components of plant cell contents without using the energy potentially available in plant cell walls by allo-enzymatic digestion (Dierenfeld et al., 1982); a similar strategy seems to have been adopted by the frugivorous *E. fulvus* and *V. variegata* in the present data set, although these species also had lower-than-expected food intake levels (Fig. 3).

The results of the correlations of dietary niche indicators with ingesta retention measurements (Fig. 4) suggest a specific scenario for the adaptation to herbivorous diets. For this scenario, an understanding of the nutrient composition of “fruits” is required. Fruits are usually more patchily distributed in space and time than leaves, and primates specializing on fruits have larger home ranges than primates specializing on leaves (Milton, 1981). Although often considered “higher quality” food than leaves, fruits consumed by many free-ranging primates contain fiber levels similar to, or even exceeding, the tree foliage consumed by the same species, while containing lower levels of protein and plant secondary compounds (Oftedal, 1991; data for langurs reviewed in Nijboer and Clauss, 2006). Nevertheless, the sugar contents of fruits may often surpass that of leaves (Danish et al., 2006). In other words, a diet of fruits, although it may represent similar levels of allo-enzymatically digestible energy substrate, may represent higher levels of auto-enzymatically digestible energy substrate.

Allo-enzymatic digestion is costly in at least two respects: for dietary substrates that can also be used auto-enzymatically, the energetic loss due to allo-enzymatic digestion will lead to a less efficient use of such substrates in foregut fermenters (Stevens and Hume, 1998). Additionally, the protagonists of allo-enzymatic digestion, the gut microbes, need to be harbored in particularly voluminous anatomical gut structures (Stevens and Hume, 1998), resulting in an overall increase in gut tissue in herbivores as compared to faunivores (Chivers and Hladik, 1980). As additional gut tissue is costly to maintain and thus uses energy that cannot be channeled into other directions (Aiello and Wheeler, 1995), herbivores should, in theory, keep the proportion of allo-enzymatic digestion (and thus retention times) as low as possible in their particular dietary niche. Maintaining a voluminous gut and a large population of microbes on a diet that (although high in allo-enzymatically digestible components) could also sustain a more auto-enzymatically oriented and thus more economic competitor organism, should lead to a competitive disadvantage. Therefore, retention time decreases with increasing proportion of fruits: a more thorough fermentative digestion of fruits would be possible, but less economical than the alternative. That a focus on auto-enzymatic digestion of fruits, in the “intake approach”, might result in lower costs for digestive tract maintenance, could help to explain (as one factor among many) the finding of Clutton-Brock and Harvey (1980) that folivorous primates have lower brain sizes than frugivores, or of Chapman et al. (1990) that primates consuming a diet of fruits and insects have larger litter sizes as compared to those consuming fruits and/or leaves.

A visual inspection of Fig. 3 suggests that the simple-stomached digestive system is spread over the whole efficiency–intake–continuum, whereas the foregut fermenting system is rather constrained to the efficiency end of the continuum. This difference is explained by the different kinetics of microbial (allo-enzymatical) fermentation of those substrates that could also be digested auto-enzymatically (simple sugars, starches) and those that cannot (plant fiber). Sugars and starches ferment at a much faster rate than fiber (Hummel et al.,

2006a,b). Thus, it is inevitable that foregut fermenters will lose a substantial part of the auto-enzymatically digestible substrate anyhow, so it appears reasonable that efficient fiber utilisation is the only option open to them.

It has been speculated repeatedly for ruminants (Hofmann, 1989) and colobines (Cork, 1994; Chivers, 1995) that a part of the auto-enzymatically digestible food entering the forestomach could be directly channeled into the glandular part of the stomach in order to circumvent energetic losses due to allo-enzymatical digestion. Such a mechanism has not been demonstrated experimentally to date; in ruminants (roe deer *Capreolus capreolus*), a comparison of experimental data rather suggests that such a mechanism is not operative (Behrend et al., 2004). In feeding trials with orally ingested markers, one would expect fluid passage markers, representing the soluble fraction, to pass through the forestomach at a faster rate than particle markers. The data from feeding studies in foregut fermenting primates with the simultaneous application of a fluid and a particle marker does not indicate such differential passage (Nijboer et al., 2007).

Hindgut fermenters (i.e., simple-stomached animals) can have both a high or a low throughput strategy, as they will always use the auto-enzymatically digestible substrate optimally before it can reach the fermentation site, from which the fibrous substrate can be either expelled rather quickly or where it can be retained longer for efficient allo-enzymatical digestion. This fundamental difference between hindgut and foregut fermenters can lead to the hypothesis that within mammalian herbivores, foregut fermenters – with the exception of the ruminants, a case of their own – have lower food intakes and lower metabolic rates than other digestive types (as indicated in Clauss et al., 2007a); this hypothesis remains to be tested.

A certain proportion of leaves in the natural diet may be important even for primates with shorter retention times. In bats – animals known

for particularly short ingesta retention times (e.g. Stalinski, 1994) – it has been suggested repeatedly that leaves can be an important source not of energy, but of protein (Courts, 1998) and calcium (Nelson et al., 2005), which both generally occur in higher concentrations in leaves than fruits, and which may both be critical for successful reproduction. Therefore, although leaves are generally considered “low quality” forage due to their high content of allo-enzymatically digestible components, it should not be forgotten that they also contain relevant proportions of auto-enzymatically digestible substrates, too, and that using them as part of an “intake” approach can serve to supplement the diet with important nutrients otherwise lacking.

In conclusion, we found that the dietary niche rather than body mass per se is the best predictor of ingesta retention time in primates. These findings are linked to the digestive strategy, where strategy refers to a continuum between an “efficiency approach” of low intake and high fiber digestibility and an “intake approach” of high intake and low fiber digestibility. A more precise definition of this continuum, and the determination of threshold points at which a switch in approach is observed, remain challenging topics in comparative herbivore physiology. Drastic deviations from the general intake–retention pattern must be balanced by other physiological or ecological mechanisms. Both species displaying particularly short MRTs for their moderate DMI (Fig. 3b), *V. variegata* and *E. fulvus*, can be hypothesized to have particularly low metabolic rates – the only evident solution to a situation of moderate intake yet low digestive efficiency, in which the short retention is not balanced by a particularly high-quality diet. Indeed, both species deviate substantially from the metabolic rate expected based on body mass, having distinctively lower values (Snodgrass et al., 2007). These deviations from the general pattern serve, if anything, to remind us that there are always more solutions to a problem than one simple pattern.

## Appendix A

Data collection of body mass (BM), relative dry matter intake (rDMI) and particle mean retention time (MRT) in herbivorous primates. The dietary quality (dq) index (Sailer et al., 1985) is calculated by the equation  $dq = 1s + 2r + 3.5a$  ( $s$  = % of structural plant parts in diet;  $r$  = % of reproductive plant parts in diet;  $a$  = % of animal matter in diet). Due to discrepancies between the data given in Sailer et al. (1985) and the sources these authors reference for their data collection (in particular, they do not give  $r$  data, but subtracting the sum of their  $s$  and  $a$  values from 100 mostly does not result in the  $r$  value of their sources), we collated the information ourselves from the literature. The data represent a mixture of methods (% of observed foraging time, completely simulated diets, and stomach content analyses). In cases where, due to the procedure of averaging foraging observations, the total sum of  $r$ ,  $s$  and  $a$  did not add up to 100, the values were expressed as % of their total sum.

Species	BM (kg)	rDMI (g/kg <sup>0.75</sup> /d)	MRT (h)	Diet	Marker	MRT Sources	Natural diet				Diet sources
							s	r	a	dq	
Simple-stomached											
<i>Hapalemur griseus</i>	1.050	26	47.5	Lab diet	Cr-f	10	95.0	5.0	0.0	105.0	Tan (1999)
<i>Cercopithecus talapoin</i>	1.600	118	16.8	Zoo diet	Plastic particles	9	2.0	61.8	36.2	252.3	Gautier-Hion et al. (1980)
<i>Eulemur fulvus</i>	2.259	39	7.9	Lab diet	Cr-f	10	24.8	72.0	3.2	180.0	Tan (1999)
<i>Propithecus tattersalli</i>	3.087	24	36.3	Zoo diet	Cr-f	6	39.0	46.0	15.0	183.5	Meyers and Wright (1993)
<i>Propithecus verreauxi</i>	3.502	28	33.5	Zoo diet, lab diet	Cr-f	6,10	56.5	43.7	0.0	143.8	Simmen et al. (2003)
<i>Varecia variegata</i>	4.114	51	4.7	Extruded, lab diet	Cr-f	4,10	9.4	90.6	0.0	190.6	Tan (1999)
<i>Cercopithecus ascanius</i>	5.200	106	27.2	Zoo diet	Plastic particles	9	21.9	56.5	21.7	210.6	Chapman et al. (2002)
<i>Alouatta villosa</i> (= <i>pigra</i> )	6.150	35	37.3	Extruded	Cr-f	5	58.6	41.4	0.0	141.4	Pavelka and Knopff (2004)
<i>Cercopithecus neglectus</i>	6.500	81	34.1	Zoo diet	Plastic particles	9	9.4	85.7	4.9	198.0	Gautier-Hion et al. (1980)
<i>Alouatta seniculus</i>	8.180	30	40.4	Extruded	Cr-f	5	69.5	40.5	0.0	150.5	Ofedal (1991)
<i>Cercopithecus mitis</i>	8.600	68	25.0	Zoo diet	Plastic particles	9	23.4	61.1	15.5	199.9	Chapman et al. (2002)
<i>Pan troglodytes</i>	52.700	41	37.2	Zoo diet	Cr-f, plastic particles	1,9	27.3	67.0	5.7	181.3	Goodall (1996)
<i>Gorilla gorilla</i>	118.000	30	50.0	Zoo diet	Plastic particles	7	90.0	10.0	0.0	110.0	Gautier-Hion et al. (1980)
Foregut fermenter											
<i>Trachypithecus auratus</i>	6.000	36	45.0	Zoo diet	Cr-f	11	67.0	33.0	0.0	133.0	Kool (1993)
<i>Semnopithecus cristatus</i>	7.000	23	46.8	Pelleted	Cr-f	2	90.0	10.0	0.0	110.0	Brotoisworo and Dirgayusa (1991)
<i>Rhinopithecus bieti</i>	8.500	11	37.5	Browse lichens grass	Plastic particles	8	95.6	2.4	2.0	107.6	Xiang et al. (2007)
<i>Colobus guereza</i>	10.800	26	53.1	Extruded	Cr-f	5	85.3	14.7	0.0	114.7	Oates (1977)
<i>Nasalis larvatus</i>	12.000	32	49.0	Zoo diet	Plastic particles	3	54.5	45.5	0.0	145.5	Yeager (1989)
<i>Pygathrix nemaeus</i>	12.100	66	33.8	Extruded	Cr-f	5	82.0	18	0.0	118.0	Hara (2003)

Sources of MRT data: 1 (Milton and Demment, 1988), 2 (MRT and DMI relative to metabolic body weight from Sakaguchi et al., 1991; absolute BM assumed according to Silva and Downing, 1995), 3 (Dierenfeld et al., 1992), 4 (Edwards and Ullrey, 1999a), 5 (Edwards and Ullrey, 1999b), 6 (Campbell et al., 1999), 7 (Remis, 2000; DMI calculated using DM data on the diet items used from other sources), 8 (Kirkpatrick et al., 2001), 9 (Lambert, 2002), 10 (Campbell et al., 2004), 11 (Nijboer et al., 2007).

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