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Herbivorous reptiles and body mass: Effects on food intake, digesta retention, digestibility and gut capacity, and a comparison with mammals

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ABSTRACT

Differences in the allometric scaling between gut capacity (with body mass, $BM^{1.00}$) and food intake (with $BM^{0.75}$) should theoretically result in a scaling of digesta retention time with $BM^{0.25}$ and therefore a higher digestive efficiency in larger herbivores. This concept is an important part of the so-called 'Jarman–Bell principle' (JBP) that explains niche differentiation along a body size gradient in terms of digestive physiology. Empirical data in herbivorous mammals, however, do not confirm the scaling of retention time, or of digestive efficiency, with body mass. Here, we test these concepts in herbivorous reptiles, adding data of an experiment that measured food intake, digesta retention, digestibility and gut capacity in 23 tortoises (*Testudo graeca*, *T. hermanni* , *Geochelone nigra*, *G. sulcata*, *Dipsochelys dussumieri*) across a large BM range (0.5–180 kg) to a literature data collection. While dry matter gut fill scaled to $BM^{1.07}$ and dry matter intake to $BM^{0.76}$, digesta mean retention time (MRT) scaled to $BM^{0.17}$; the scaling exponent was not significantly different from zero for species >1 kg. Food intake level was a major determinant of MRT across reptiles and mammals. In contrast to dietary fibre level, BM was not a significant contributor to dry matter digestibility in a General Linear Model. Digestibility coefficients in reptiles depended on diet nutrient composition in a similar way as described in mammals. Although food intake is generally lower and digesta retention longer in reptiles than in mammals, digestive functions scale in a similar way in both clades, indicating universal principles in herbivore digestive physiology. The reasons why the theoretically derived JBP has little empirical support remain to be investigated. Until then, the JBP should not be evoked to explain niche differentiation along a body size axis in terms of digestive physiology.

1. Introduction

Body size is often considered the most important characteristic of an organism (Peters 1983; Calder 1996). Small or large body size may have effects that convey comparative advantages and hence favour evolution of certain body sizes (Hone and Benton 2005). Studying the correlation of body size with physiological functions allows us to not only extrapolate measurements to species of known body size that have not been investigated yet, but also to compare species across the body size range (Karasov and Martínez del Rio 2007). Relationships between a physiological measure and body size (mostly measured as body mass, BM) are often not linear (isometric) but follow 'another pattern', or, in other words, an 'allometric' pattern (Peters 1983).

Allometric considerations play an important role in theoretical concepts about niche differentiation in mammalian herbivores (reviewed in Clauss et al. 2007a). In brief, the so-called Jarman–Bell principle (JBP) (Bell 1971; Geist 1974; Jarman 1974) explains the observation that herbivores of larger size ingest food of lower nutritional quality with the increasing gut capacity per unit energy requirement or unit food intake in larger organisms. As gut capacity scales to $BM^{1.00}$, but energy requirements and food intake to $BM^{0.75}$, larger animals have theoretically more gut capacity available per unit food intake, which translates into longer digesta retention times that should scale to $BM^{0.25}$ (Parra 1978; Demment and Van Soest 1985; Illius and Gordon 1992). According to this concept, larger animals should achieve higher digestibilities (on similar foods) due to their longer digesta retention times. However, although this concept has found widespread acceptance, empirical evidence does not indicate a systematic scaling of digesta retention, nor an increase in digestibilities with body mass (Smith 1995; Pérez-Barberìa et al. 2004; Clauss et al. 2007a; Pérez-Barberìa et al. 2008; Clauss et al. 2009; Steuer 2010).

The theoretical approach of the JBP is not related to a particular level of metabolism. Therefore, the same considerations should apply to other groups of vertebrate herbivores — for example reptiles (Parmenter 1981). The microbial digestion of plant cell wall in reptiles

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has many similarities to that in herbivorous mammals (Troyer 1991; Bjorndal 1997). In herbivorous reptiles, limited evidence suggests that gut capacity scales to BM in a similar, linear fashion as it does in mammals (Troyer 1984a; Bjorndal 1997; Franz et al. 2009). Energy requirements – estimated as basal metabolic rates or field metabolic rates – scale roughly to metabolic body mass (~$BM^{0.75}$) as they do for mammals (Bennett and Dawson 1976; Nagy et al. 1999). Therefore, it is reasonable to assume that food intake scales in a similar fashion. Intake has so far only been analysed across a larger body size range within species, with conflicting results: Meienberger et al. (1993) found that dry matter intake (DMI) scaled to $BM^{0.71}$ in desert tortoises (*Xerobates agassizii*), and the results from Hamilton and Coe (1982) in Aldabra tortoises (*Dipsochelys dussumieri*) translate into a scaling of DMI with $BM^{0.77}$–$BM^{0.81}$, whereas Baer et al. (1997) found a linear scaling of DMI with BM in growing green iguanas (*Iguana iguana*). There is also no uniformity in the results reported for relationships between BM and digesta retention or digestibility. Several authors showed that within species, digesta retention was hardly correlated to BM or other measures of body size (Parmenter 1981; Bjorndal 1987; 1989; Brand et al. 1990; Meienberger et al. 1993; Hatt et al. 2002), whereas only two studies demonstrated an increase of digesta retention with BM in reptiles (Hamilton and Coe 1982; Troyer 1984b). Instead, some authors suggested that the level of food intake determined digesta retention (Bjorndal 1987; 1989; Zimmerman and Tracy 1989; Brand et al. 1990; van Marken Lichtenbelt 1992; Meienberger et al. 1993); the same conclusion has been reached for mammals, both within and between species (Clauss et al. 2007a,b; 2008). Except for one study in green turtles (*Chelonia mydas*) (Bjorndal 1980), no effect of BM on digestibility was found in herbivorous reptiles (Hamilton and Coe 1982; Troyer 1984b). Although in part contradictory, these findings suggest that herbivorous reptiles might show a similar pattern as herbivorous mammals: a scaling of gut capacity and food intake as predicted by the JBP, without the theoretically corresponding scaling of digesta retention and digestive efficiency.

We performed intake, passage and digestion studies with herbivorous tortoises of five species across a BM range from 0.5 to 180 kg, and added these data to a data collection on digestive parameters in herbivorous reptiles from the literature. In doing so, we tested whether allometric relationships between body mass and food intake, digesta retention and gut capacity in herbivorous reptiles resemble those of herbivorous mammals, and whether body mass itself has a relevant influence on digestive functions in herbivorous reptiles. Additionally, we compared the basic influence of fibre and protein composition of the diet on digestive efficiency between herbivorous reptiles and mammals to test for basic principles in vertebrate herbivory.

2. Materials and methods

We performed measurements in 23 individual tortoises of the species *Testudo graeca* ($n=4$), *T. hermanni* ($n=6$), *Geochelone nigra* ($n=2$), *G. sulcata* ($n=8$), and *D. dussumieri* ($n=3$) (Table 1). Animals were kept individually for 30 days at 27–30 °C for intake measurements after an adaptation period of one week. The diet consisted of grass hay (whole or chopped in varying degrees) and lettuce (*Lactuca sativa*) in varying proportions. We decided for such a feeding regime, which allowed smaller animals to select higher proportions of lettuce, because pilot observations had indicated that smaller individuals would not ingest hay-only diets, and because we did not want to force-feed animals (as would have been necessary for a consistent diet for all individuals). Water was available ad libitum at all times. Faeces were collected from the enclosure floor, which consisted of plastic in the case of smaller tortoises, plastic, wood panels or concrete in the case of mid-sized tortoises, and the natural floor of the Masoala Exhibit at the Zurich Zoo (Bauert et al. 2007) in the case of the three largest individuals. While loss of faecal material or contamination of faeces was not judged substantial in individuals from 5 kg upwards, smear losses of faeces (from animals moving over their own faeces) in the smallest tortoises was judged problematic. Food offered and left over was quantified, and faeces were collected completely on a daily basis. If several defecations occurred in one day, they were sampled individually. Representative subsamples were used to determine dry matter (DM), ash, crude protein, neutral detergent fibre (NDF) and acid detergent fibre (ADF) concentrations using standard methods (AOAC 1997). Daily DM intake (DMI) was quantified for the whole trial period. Additionally, we used the DMI and the faecal excretion

Table 1
Tortoises used in this study, body mass (BM), dry matter intake (DMI), diet nutrient composition and digestibility, mean retention time (MRT) and calculated dry matter gut fill.

Species	ID	BM	DMI		Ingested diet composition				Apparent digestibility					MRT		Gut fill
			[1])	[2])	Ash	CP	NDF	ADF	DM	OM	CP	NDF	ADF	part.	sol.	
		kg	g d^{-1}		%DM				%					h		%BM
T. graeca	1	0.52	4.6	5.0	7.3	15.0	37.8	24.5	83	–	–	–	–	89	–	1.52
T. graeca	2	0.69	3.4	3.6	5.1	11.2	29.6	15.9	85	86	82	69	–	190	–	1.76
T. graeca	3	0.90	4.2	3.9	6.1	17.0	38.5	19.2	94	94	95	89	88	137	–	0.90
T. graeca	4	0.86	5.9	5.5	7.5	12.8	42.4	28.1	94	95	94	93	92	238	–	2.24
T. hermanni	5	0.91	5.7	5.2	7.1	13.9	42.5	29.2	94	94	93	92	90	90	–	0.78
T. hermann	6	0.96	4.2	4.2	6.0	14.5	34.1	20.9	87	88	87	78	72	143	–	1.10
T. hermann	7	1.01	4.5	4.3	6.1	13.4	39.6	22.1	82	–	80	74	–	150	–	1.33
T. hermann	8	1.44	3.9	3.7	5.6	13.8	43.7	22.2	95	–	95	94	89	133	–	0.48
T. hermann	9	1.64	4.8	4.8	7.0	15.3	33.8	24.3	90	91	91	83	78	96	–	0.46
T. hermann	10	1.72	7.0	6.7	7.6	14.5	44.9	30.2	74	76	76	64	58	147	–	1.35
G. nigra	11	5.30	19.2	18.3	6.0	13.2	47.8	37.8	66	68	71	57	59	197	139	1.82
G. nigra	12	5.70	35.8	35.5	7.6	13.2	51.2	34.4	63	65	65	55	49	131	65	2.18
G. sulcata	13	7.24	35.4	43.2	7.5	12.4	56.3	35.0	51	53	65	44	33	262	152	3.83
G. sulcata	14	10.47	42.7	38.0	6.5	10.9	60.0	40.2	72	74	67	70	70	209	153	2.00
G. sulcata	15	12.23	33.3	32.3	7.9	13.5	55.1	40.7	64	66	72	61	55	368	260	2.63
G. sulcata	16	21.5	20.3	13.5	12.6	13.1	53.7	–	74	80	78	77	48	–	–	–
G. sulcata	17	26.0	32.1	20.9	10.0	9.5	54.7	30.2	79	81	75	79	72	556	340	1.45
G. sulcata	18	47	103.0	100.8	13.1	10.5	57.8	27.8	62	62	54	62	40	241	99	1.42
G. sulcata	19	48	90.1	90.1	13.4	10.8	56.4	23.8	65	66	53	66	43	266	104	1.28
G. sulcata	20	50	–	–	–	–	–	–	–	–	–	–	–	554	340	–
D. dussumieri	21	104	216.1	175.6	5.8	12.2	63.6	29.7	53	61	75	45	23	210	149	1.28
D. dussumieri	22	140	494.0	342.5	5.5	11.4	66.2	32.1	51	59	71	49	39	203	125	2.13
D. dussumieri	23	180	375.0	283.2	1.3	13.6	64.0	30.0	52	58	69	46	29	202	141	1.24

CP crude protein, NDF neutral detergent fibre, ADF acid detergent fibre, DM dry matter, OM organic matter, part. particles, sol. solutes.
[1]) DMI used for digestibility calculation (see Materials and methods), [2]) DMI during the complete trial period.

data of those days that were separated by the resulting particle mean retention time (MRT, see below) for each individual for the calculation of digestibility. Apparent digestibility (aD) of dry matter, nutrients and energy were calculated as aD = (intake − excretion)/intake × 100, where intake and excretion are expressed as absolute mean values (grams per day).

MRT was determined by feeding a particle (chromium-mordanted fibre, <2 mm) and a solute (cobalt-EDTA) marker prepared according to Udén et al. (1980). The solute marker was only given to animals >2 kg. Marker analysis followed the procedure outlined by Behrend et al. (2004) and Hummel et al. (2005); in doing so, wet ashing with sulphuric acid was followed by atom absorption spectroscopy. The MRT of the total gastrointestinal tract was calculated according to Thielemanns et al. (1978) as $MRT = \sum(t_i \times dt \times c_i) / \sum(dt \times c_i)$; with t_i = time after marker application (h), dt = time interval represented by marker concentration (calculated as $(((t_{i+1} - t_i) + (t_i - t_{i-1}))/2)$, and c_i = faecal marker concentration at time i (mg/kg DM). The marker was assumed to have been excreted completely once the faecal Co and Cr concentrations were similar as pre-dose levels. The selectivity factor was calculated as $MRT_{particles}/MRT_{solutes}$. We followed Barboza (1995a) in calculating the indigestible gut content (V_N) and the total gut content (V) in dry matter according to Holleman and White (1989) as $V_N = F$ MRT; with F = faeces output (kg DM/h) and MRT = the average (2 mm) particle passage time through the entire digestive tract (h), and $V = (V_N - (V_N/(1 - (aD\ DM/100)))/\ln(1 - (aD\ DM/100))$; assuming an exponential absorption of ingested food with time spent in the digestive tract.

Comparative data were compiled from the literature (Bjorndal 1980; Karasov et al. 1986; Nagy and Medica 1986; Bjorndal 1987; 1989; Davenport et al. 1992; van Marken Lichtenbelt 1992; Bjorndal and Bolten 1993; Meienberger et al. 1993; Barboza, 1995a,b; Baer et al. 1997; Hailey 1997; Liesegang et al. 2001; Hatt et al. 2002; Hatt et al. 2005; Bouchard and Bjorndal 2006). Publications that did not allow linking body mass data to other measurements were not included.

Data were analysed by correlation analysis (after ln-transformation of parameters without normal distribution), by General Linear Models (GLM; assessing normal distribution of studentized residuals), and using regression analysis indicating 95% confidence intervals (95% CI) according to $y = a\ BM^b$ (after ln-transformation) or $y = ax + b$ (without transformation). Analyses were performed with PSAW 18.0 (SPSS Inc., Chicago, IL, USA). When dealing with large data collections, we also calculated species means; when applying analyses to our own experimental data, we used all individual data because, due to our limited species variety, sample size would otherwise have been reduced drastically. In cases where data on MRT and transit time (TT, time of first marker appearance) from the literature were combined, we speak of 'passage times'.

3. Results

3.1. Own results

The results of our own experiments are summarized in Table 1. DMI (g d^{-1}) scaled to 4.8 (95%CI 3.6–6.5) $BM^{0.75\ (95\%CI\ 0.64–0.87)}$ ($n = 22$, $r^2 = 0.90$, $p < 0.001$) for intake measured during the whole trial period, and to 4.8 (95%CI 3.7–6.3) $BM^{0.80\ (95\%CI\ 0.70–0.90)}$ ($n = 22$, $r^2 = 0.93$, $p < 0.001$) for intake during those days used for digestibility calculation.

BM was positively correlated to the NDF ($n = 22$, $R = 0.93$, $p < 0.001$) and ADF ($n = 21$, $R = 0.45$, $p = 0.040$) of the ingested diet. BM, the relative DMI (rDMI, $g^{-1}\ kg^{-0.75}\ d^{-1}$) and diet NDF content were all negatively correlated to digestibility estimates (e.g. for aD DM $n = 22$, $R = -0.83$, $p < 0.001$; $R = -0.48$, $p < 0.025$; and $R = -0.83$, $p < 0.001$, respectively; or for aD NDF $n = 21$, $R = -0.69$, $p = 0.001$; $R = -0.58$, $p = 0.006$; and $R = -0.66$, $p = 0.001$, respectively). rDMI was not correlated to diet NDF content ($n = 22$, $R = 0.26$, $p = 0.236$). In a GLM with aD DM as the dependent variable and BM, rDMI and diet NDF content as covariates ($n = 22$, $r^2 = 0.78$, $F = 20.850$, $p < 0.001$), only NDF ($F = 15.595$, $p = 0.001$) and rDMI ($F = 5.862$, $p = 0.026$) were significant but not BM ($F = 1.111$, $p = 0.297$). The regression equation for the relationship of aD of organic matter (OM) and NDF was aD OM = 125.7 (95%CI 106.2–145.2) − 1.02 (95%CI −1.40 to −0.64) NDF ($n = 19$, $r^2 = 0.65$, $p < 0.001$).

The marker excretion curves showed single marker excretion peaks (Fig. 1a,c,d) in 16 animals and double marker peaks (Fig. 1b) in 6 cases. In one animal, the marker excretion pattern and faecal marker concentration indicated that the majority of the marker had not been excreted within the experimental period. Because this animal (*G. sulcata* 16) also had the lowest rDMI (1.35 $g^{-1}\ kg^{-0.75}\ d^{-1}$) of all animals, this interpretation was considered plausible, and MRTs were not calculated for this animal. A gradual marker increase prior to the peak (Fig. 1c) was observed in six cases; a gradual particle marker decrease after the peak (Fig. 1d) was only observed in two cases of *T. graeca*.

$MRT_{particles}$ (h) scaled to 145 (95%CI 113–186) $BM^{0.16\ (95\%CI\ 0.06–0.25)}$ ($n = 22$, $r^2 = 0.37$, $p = 0.003$). If only animals >2 kg were considered, there was no significant scaling for $MRT_{particles}$ ($BM^{0.04\ (95\%CI\ -0.20\ to\ 0.28)}$, $n = 12$, $r^2 = 0.01$, $p = 0.726$) and $MRT_{solutes}$ ($BM^{-0.03\ (95\%CI\ -0.71\ to\ 0.66)}$, $n = 12$, $r^2 = 0.00$, $p = 0.935$). rDMI was not correlated to $MRT_{particles}$ ($n = 21$, $R = -0.24$, $p = 0.298$), but diet NDF was ($n = 21$, $R = 0.46$, $p = 0.037$). In a GLM with $MRT_{particles}$ as the dependent variable and BM, rDMI and diet NDF content as covariates ($n = 21$, $r^2 = 0.47$, $F = 5.082$, $p = 0.011$), only NDF ($F = 12.215$, $p = 0.003$) and rDMI ($F = 6.402$, $p = 0.022$) were significant but not BM ($F = 2.917$, $p = 0.106$).

Gut content (kg DM) scaled to 0.013 (95%CI 0.009–0.017) $BM^{1.07\ (95\%CI\ 0.95–1.19)}$ ($n = 21$, $r^2 = 0.95$, $p < 0.001$).

3.2. Complete data collection

We compared both, available individual data for DMI and calculated species means, to the collection of species means for herbivorous mammals from Clauss et al. (2007a). Because of an overrepresentation of small individuals with low food intake in the total dataset, the scaling exponent of all individuals was higher than $BM^{0.75}$ (Fig. 2a). In contrast, species means scaled to metabolic body mass (Fig. 2b). The 95%CI for the factor a did not overlap between mammals and reptiles; this factor was ten times lower in reptiles than in mammals.

In the literature, both MRT and transit times (TT) are recorded for reptiles. Given the predominance of abrupt, single-peak excretion patterns in our own data (Fig. 1a), one could assume that TT should be representative for MRT in reptiles (Bjorndal 1997); alternatively, one could assume that TT are usually shorter than MRT. If all individual MRT and TT data are combined, there is no scaling of passage time with BM in reptiles (Fig. 3a). Using species averages (if both TT and MRT were given for a species, only MRT data were used), MRT scaled to $BM^{0.17}$ (Fig. 3b). If the BM range was confined to species >1 kg (similar to the considerations in Clauss et al. 2007a), the scaling exponent was similar $BM^{0.17\ (95\%CI\ -0.05\ to\ 0.38)}$ but not significantly different from zero ($n = 11$, $r^2 = 0.26$, $p = 0.112$). When compared for similar BM, reptile passage times were on average five times longer than mammal MRTs.

Using all individual MRT and TT data in a GLM with BM and rDMI as covariates ($n = 70$, $r^2 = 0.35$, $F = 18.377$, $p < 0.001$), only rDMI ($F = 36.496$, $p < 0.001$) was significant but not BM ($F = 0.239$, $p = 0.627$). If only MRT was used as the dependent variable in the GLM ($n = 30$, $r^2 = 0.08$, $F = 1.177$, $p = 0.324$), neither rDMI nor BM significant. Using the species' average MRT and TT data in a GLM with BM and rDMI as covariates ($n = 17$, $r^2 = 0.10$, $F = 0.762$, $p = 0.485$), neither rDMI nor BM was significant. If only species-average MRT data were used as the dependent variable in the GLM ($n = 10$, $r^2 = 0.10$, $F = 0.379$, $p = 0.698$), again neither rDMI nor BM was significant.

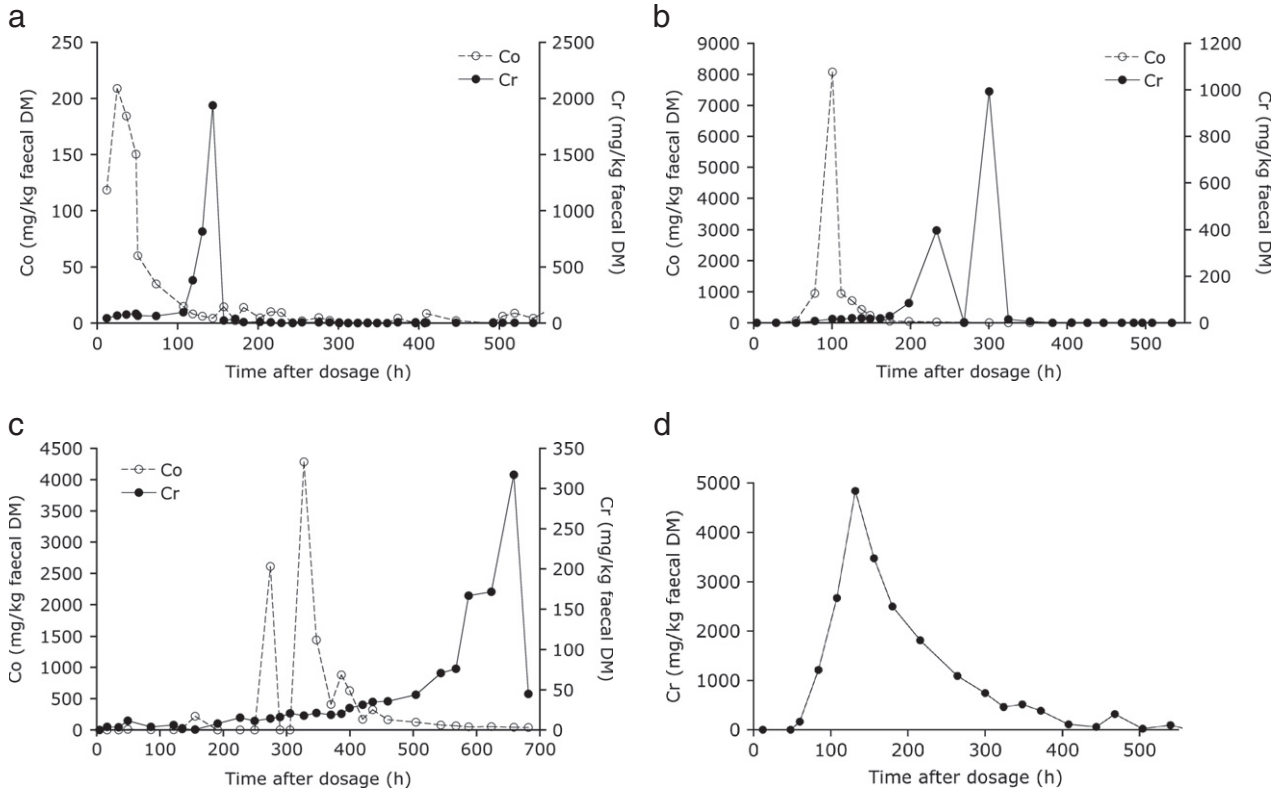

Fig. 1. Marker excretion patterns in herbivorous tortoises: a) single marker peaks (*Geochelone nigra* 12) as seen in 16 animals of this study; b) double particle marker peak (*Geochelone sulcata* 19) as seen in six animals of this study; c) a very gradual increase in particle marker excretion prior to the major excretion peak (*Geochelone sulcata* 20) as seen in varying degrees in six animals of this study (see also Fig. 1a); d) a gradual decrease after the marker peak (*T. graeca* 2) as seen in 2 animals of this study.

A comparison of the relationship between rDMI and passage parameters between mammals (species averages) and reptiles (individual data for MRT and TT) indicated a common pattern of increasing passage time with decreasing intake (Fig. 4). At similar intake levels reptiles still had about 1.6 times longer passage times; the difference was, however, not significant due to overlapping confidence intervals (Fig. 4).

Comparing the calculated DM gut content of the tortoises of this study with similar data for mammals shows that in both groups, gut content scales linearly with BM (Fig. 5).

A combination of literature and own data on the relationship showed no significant decrease of DM digestibility with dietary NDF content (Fig. 6a; $n=45$, $R=-0.26$, $p=0.086$). When using data on dietary ADF content and the digestibility of organic matter, the negative correlation was significant ($n=38$, $R=-0.43$, $p=0.007$). In a GLM with organic matter digestibility as the dependent variable and BM, rDMI and dietary ADF as covariates ($n=38$, $r^2=0.21$, $F=2.950$, $p=0.046$), only ADF ($F=5.402$, $p=0.026$) was significant but not BM ($F=0.217$, $p=0.644$) or rDMI ($F=0.693$, $p=0.411$). BM was not correlated to the digestibility of NDF in the overall dataset ($n=48$, $R=-0.029$, $p=0.847$; Fig. 6b). The regression equation for the relationship of aD of organic matter (OM) and NDF was aD OM = 87.7 (95%CI 65.6–109.8) − 0.47 (95%CI −0.94–0.00) NDF ($n=35$, $r^2=0.11$, $p=0.051$).

Relating data on dietary crude protein content to the content of the digestible crude protein content (Fig. 7) allows estimation of the true digestibility and endogenous/metabolic losses (Robbins 1993). Estimated true protein digestibility was 81% for the whole dataset, with metabolic protein losses estimated at 2.49 g/100 g DMI.

4. Discussion

This study confirms that herbivorous reptiles have a lower food intake and longer digesta retention times than herbivorous mammals, whereas gut capacity is comparable. Additionally, Fritz et al. (in press) showed that reptiles have larger digesta particles than mammals. These findings corroborate the assumption that a higher metabolic level (as in mammals) is linked to a higher food intake (Karasov et al. 1986). Because of the similarity in anatomy (an 'amniote *bauplan*'), gut capacity remains more or less constant and hence higher food intake leads to shorter digesta retention, which could compromise digestibility (Meienberger et al. 1993; Clauss et al. 2007b). Therefore, adaptations for particle size reduction become crucial for the evolution of a higher level of metabolism, because a reduction in particle size can compensate for shorter digesta retention (Bjorndal et al. 1990; Clauss et al. 2009; Schwarm et al. 2009).

A fascinating result of the comparisons between herbivorous mammals and reptiles is that although differences in the levels of various physiological measures are found, the scaling of these measures with BM is similar between both groups (Figs. 2–5; cf. Fig. 1 in Fritz et al. in press), suggesting fundamental scaling principles for terrestrial vertebrate herbivores.

4.1. Limitations of this study

One limitation of this study could have been the smear losses of faecal material in the smallest individuals mentioned in the Materials and methods section. Although this will not have influenced intake and passage measurements, these putative smear losses could have

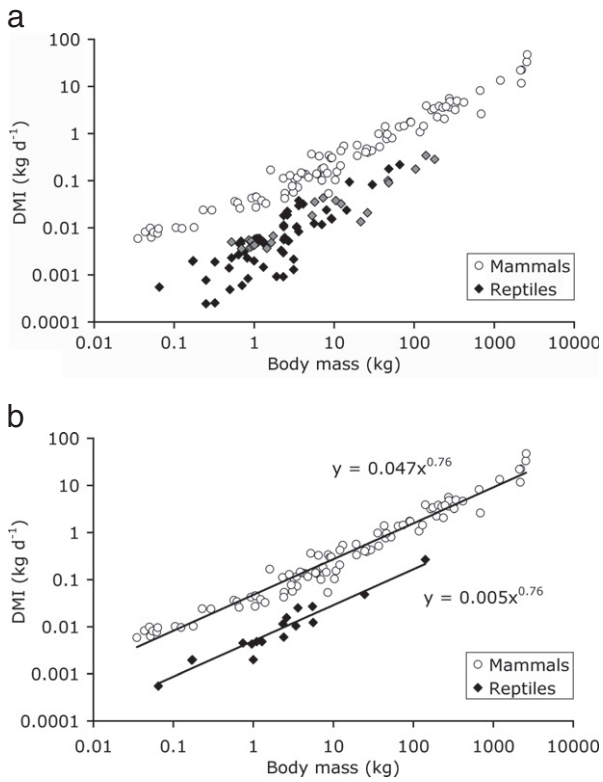

Fig. 2. Relationship between body mass (BM, kg) and dry matter intake (DMI, kg d^{-1}) in herbivorous reptiles and mammals. a) All available data for reptiles from the literature and this study on an individual basis; own measurements in grey. b) Calculated species means. Regression equations for reptiles in a) is 0.003 (95%CI 0.003–0.004) $BM^{0.87\ (95\%CI\ 0.76–0.97)}$ ($n=85$, $r^2=0.76$, $p<0.001$) and in b) 0.005 (95%CI 0.004–0.006) $BM^{0.76\ (95\%CI\ 0.64–0.88)}$ ($n=17$, $r^2=0.92$, $p<0.001$). Species means for mammals from Clauss et al. (2007a) with the regression equation 0.047 (95%CI 0.042–0.053) $BM^{0.76\ (95\%CI\ 0.73–0.79)}$ ($n=93$, $r^2=0.96$, $p<0.001$). Reptile data from this study and literature sources (see Materials and methods).

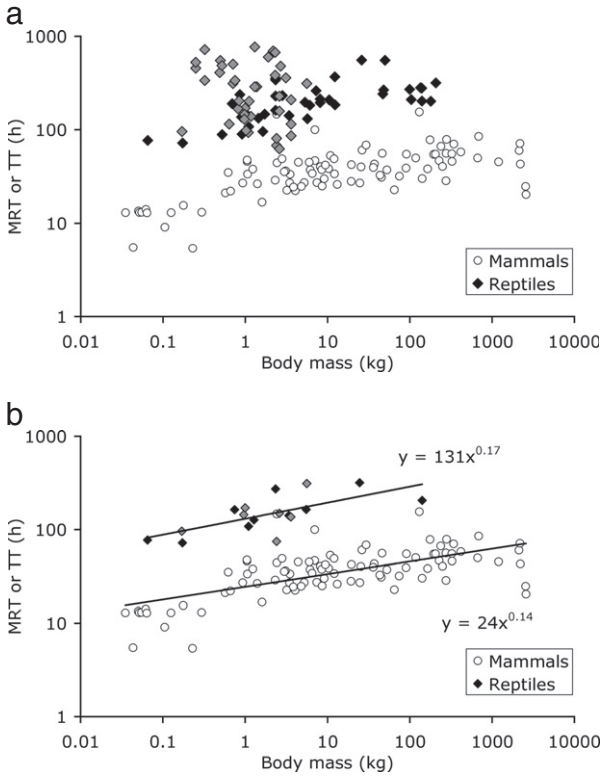

Fig. 3. Relationship between body mass (BM, kg) and mean retention time (MRT, black symbols) and transit time (TT, grey symbols) in herbivorous reptiles and MRT in mammals. a) All available individual data for reptiles; b) species means for reptiles (when both MRT and TT were given for a species, only MRT data were used) with the regression equation 131 (95%CI 108–158) $BM^{0.17\ (95\%CI\ 0.07–0.27)}$ ($n=17$, $r^2=0.47$, $p=0.002$). Species means for mammals from Clauss et al. (2007a) with the regression equation 24 (95%CI 22–28) $BM^{0.14\ (95\%CI\ 0.10–0.17)}$ ($n=93$, $r^2=0.42$, $p<0.001$). Reptile data from this study (MRT) and literature sources for MRT and TT (see Materials and methods).

led to particularly high calculated digestibilities in the smallest individuals (Table 1) and thus led to a steeper NDF–aD DM-relationship in the data from this study as compared to literature data (Fig. 6a). However, digestibility coefficients of similar (high) magnitudes had also been observed in larger tortoises where smear losses should not be a problem (Liesegang et al. 2001).

A period of 30 days for the intake and digestion studies was adequate in all but one case for passage marker recovery. However, a longer time period would be desirable for the determination of intake, faecal excretion and hence digestibility.

A major difficulty in this study was the variation of nutrient composition in the ingested diet. Because recording voluntary food intake and corresponding passage measurements was our defined aim, and thus force-feeding of animals (with a uniform diet) was not an option, diet selection on the part of the animals could not be prevented. Actually, hay offered to larger tortoises would physically not have been acceptable for the smallest individuals. The increase of dietary NDF with BM reflects the opportunity for selective feeding in smaller individuals already noted by Bjorndal and Bolten (1992). Therefore, the effects of body size on digestibility need to be assessed with the difference in the ingested diet in mind (i.e. including nutrient levels in a General Linear Model). The observation that smaller tortoises fed more selectively in this study, and that larger tortoises accepted a higher proportion of hay in their diet, is in accord with similar observations made during the formulation of the Jarman–Bell principle (JBP; Bell 1971; Geist 1974; Jarman 1974). It should be noted that it is not this part of the JBP that is under debate here, but the explanation of this pattern by metabolic and digestive allometries.

4.2. Passage marker excretion in reptiles

Rick and Bowman (1961) already noted that digesta passage in tortoises was very long, exceeding 14 days in an experiment of seed

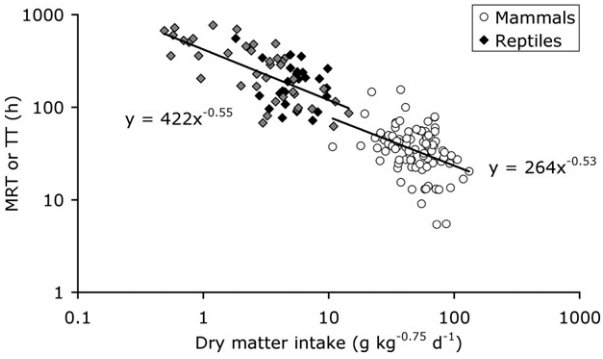

Fig. 4. Relationship between relative dry matter intake (rDMI, g $kg^{-0.75}$ d^{-1}) and particle mean retention time (MRT, black symbols) or transit time (TT, grey symbols) in individual herbivorous reptiles compared to species mean MRT for mammals. The regression equation for reptiles is 422 (95%CI 338–527) $rDMI^{-0.55\ (95\%CI\ -0.70\ to\ -0.39)}$ ($n=70$, $r^2=0.44$, $p<0.001$). Mammal data from Clauss et al. (2007a) with the regression equation 264 (95%CI 94–739) $rDMI^{-0.53\ (95\%CI\ -0.79\ to\ -0.26)}$ ($n=93$, $r^2=0.15$, $p<0.001$). Reptile data from this study (MRT) and literature sources for MRT and TT (see Materials and methods).

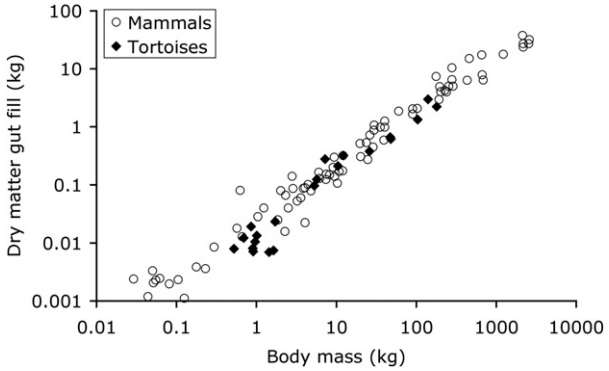

Fig. 5. Relationship between body mass (BM, kg) and dry matter gut content (kg) calculated from intake, digesta retention and digestibility data (Holleman and White 1989). Data for tortoises from this study with a regression equation of 0.013 (95%CI 0.009–0.017) $BM^{1.07\ (95\%CI\ 0.95–1.19)}$ ($n=21$, $r^2=0.95$, $p<0.001$). Mammal data are species averages from DWH Müller, D Codron, A Schwarm, J Hummel, M Clauss, (pers. obs.) with the regression equation 0.024 (95%CI 0.022–0.029) $BM^{0.94\ (95\%CI\ 0.90–0.97)}$ ($n=80$, $r^2=0.97$, $p<0.001$).

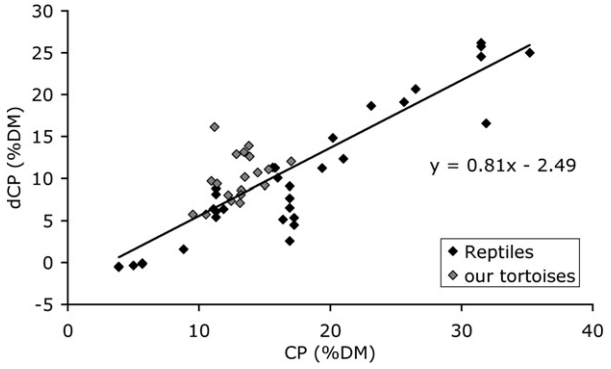

Fig. 7. Relationship between dietary crude protein content (CP, %dry matter) and digestible crude protein content (dCP, %DM) in herbivorous reptiles (tortoises from this study in grey) from this study and the literature. The linear regression equation is 0.81 (95%CI 0.69–0.93) CP − 2.49 (95%CI −4.51 to −0.48). Data from this study and literature (see Materials and methods).

passage in two *Geochelone nigra* specimens (5 and 11 kg). Besides the generally much longer retention time, the excretion of passage markers also differs in its pattern between reptiles and mammals. In many hindgut-fermenting mammals, such as horses, tapirs, rhinoceroses or elephants, the excretion pattern of the marker is usually that of a peak with a steep increase and a gradual decline (Udén et al. 1982; Loehlein et al. 2003; Clauss et al. 2010; Steuer et al. 2010), indicative of a mixing compartment (Martinez del Rio 1994; Jumars 2000). However, such a pattern is only rarely found in reptiles (Fig. 1d; cf. Zimmerman and Tracy 1989; Barboza 1995a) and a steep-peaked pattern with an abrupt decline is the more common finding (Fig. 1a; cf. Karasov et al. 1986; Hatt et al. 2002). Such a pattern indicates a low degree of digesta mixing and passage of digesta as a plug in a plug-flow reactor, and matches the generally tubiform shape of the reptilian digestive tract (with the exception of colonic compartimentalisation in iguanids) (Bjorndal 1997). The pattern of an even more gradual increase in passage marker before the peak than the subsequent decrease observed in this and other studies (Fig. 2c; cf. Barboza 1995a; Hatt et al. 2002) could be a consequence of using particle markers that are smaller than the average digesta (note the higher particle size of ingesta in reptiles as described by Fritz et al., in press), and that are therefore partly washed out of their plug in the gastrointestinal tract by the fluid fraction. Although the absolute duration of digesta passage is much higher in reptiles than in mammalian herbivores, $MRT_{particles}$ is longer than $MRT_{solutes}$ by a factor of only 1.4–2.6 in this study, 1.9–2.1 in the study of Barboza (1995a), and 0.8–1.5 in the study of Hatt et al. (2002), and thus in a similar range as that observed in mammals (Clauss et al. 2010; Steuer et al. 2010). This indicates that relative to food intake and digesta passage, reptiles secrete similar amounts of fluids into their digestive tract, and thus submit digesta to a similar degree of 'washing' as mammalian herbivores.

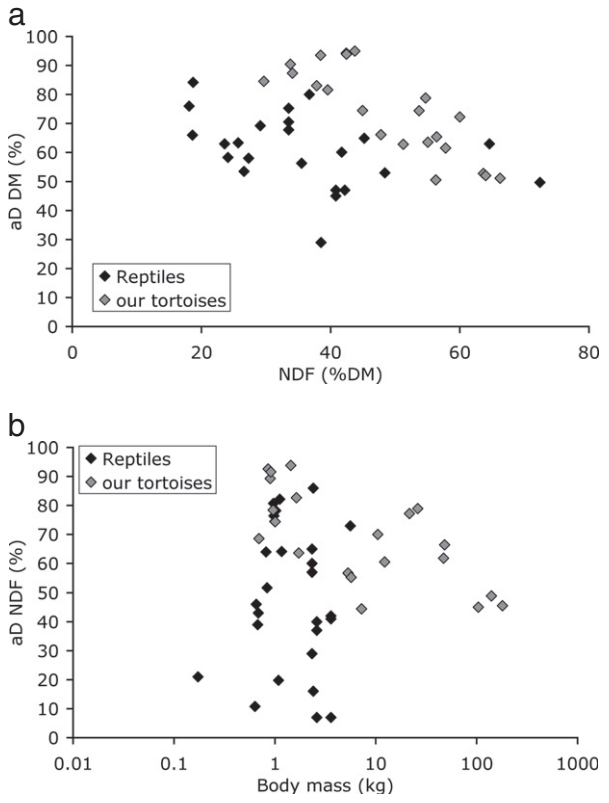

Fig. 6. Relationship between a) dietary neutral detergent fibre (NDF, %dry matter) and the apparent digestibility (aD, %) of dry matter (DM) and b) body mass (BM) and the aD NDF in herbivorous reptiles. Data from this study in grey.

4.3. Digestion in reptiles

Bjorndal (1997) summarized physiological data that indicate that herbivorous reptiles achieve similar digestibilities as mammalian herbivores. The results of our study support this conclusion. Digestibility is usually a negative function of dietary fibre content (Karasov and Martínez del Rio 2007), as demonstrated within iguanas by van Marken Lichtenbelt (1992). The general similarity of this relationship in reptiles with those found in herbivorous mammals is striking (Table 2) and supports previous suggestions that fibre level might influence digestibility in a similar way in both clades (Hatt et al. 2005). Similarly, metabolic protein losses and true protein digestibility, as estimated by regression analysis, are similar between reptiles

Table 2
Relationship between the apparent digestibility (aD) of organic matter (OM) in herbivorous reptiles and mammals.

Animal group	Equation	Source
Iguana iguana	aD OM = 96 − 1.15 NDF	van Marken Lichtenbelt (1992)
Tortoises	aD OM = 126 − 1.02 NDF	This study
Herbivorous reptiles	aD OM = 88 − 0.47 NDF	Data collection in this study
Browsing rhinoceroses	aD OM = 101 − 0.98 NDF	Clauss et al. (2006)
Grazing rhinoceroses	aD OM = 81 − 0.42 NDF	Clauss et al. (2006)

NDF in % dry matter.

Table 3
Relationship between the crude protein content (CP, in % dry matter) of the diet and its apparently digestible CP (dCP, in % dry matter) in herbivorous reptiles and mammals. Note that the slope of the equation represents the true protein digestibility, and the intercept the endogenous/metabolic protein losses.

Animal group	Equation	Source
Herbivorous reptiles	dCP = 0.81 CP − 2.5	Data collection in this study
Horses	dCP = 0.86 CP − 2.8	Collection in Clauss et al. (2006)
Black rhinoceros	dCP = 0.88 CP − 3.7	Clauss et al. (2006)
Indian rhinoceros	dCP = 0.71 CP − 1.5	Clauss et al. (2005)
Hippopotamuses	dCP = 0.86 CP − 1.8	Schwarm et al. (2006)

and mammals (Table 3). This similarity suggests a homology in the fundamental mechanisms of digestion, even if different characteristics of digestive physiology (retention time, temperature constancy, fermentation rate) apply in the different clades.

4.4. Body mass

The findings of this study corroborate findings in herbivorous mammals, in which a discrepancy in the scaling of gut capacity, food intake, and digesta retention was documented (Clauss et al. 2007a). In reptiles, as in mammals, the scaling exponent for the relationship of digesta retention and body mass is lower than expected on theoretical terms by the Jarman–Bell principle, and may become even smaller when only a body mass range >1 kg is analysed. The reasons for this absence of scaling remain to be investigated. The level of food intake is a major determinant of digesta retention both within and between species, which emphasizes that variation in the metabolic level between species may be more important for digesta retention than their body mass. Additionally, differences between species in their particular digestive niches – such as the degree of herbivory or the botanical group of plants they specialize on – are important modulators of digestive adaptations, as shown for browsing and grazing ruminants (Pérez-Barberìa et al. 2004), or for tortoises varying in their intestinal morphology according to their feeding style (Hailey 1997). These results therefore emphasize that even though the theoretical background of the Jarman–Bell principle is appealing, it should not be evoked to explain niche differentiation along a body mass axis in terms of digestive physiology.

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References

AOAC, 1997. Official Methods of Analysis. Association of Official Analytical Chemists, Arlington, VA, USA.
Baer, D.J., Oftedal, O.T., Rumpler, W.V., Ullrey, D.E., 1997. Dietary fiber influences nutrient utilization, growth and dry matter intake of green iguanas (*Iguana iguana*). J. Nutr. 127, 1501–1507.
Barboza, P.S., 1995a. Digesta passage and functional anatomy of the digestive tract in the desert tortoise (*Xerobates agassizii*). J. Comp. Physiol. B 165, 193–202.
Barboza, P.S., 1995b. Nutrient balances and maintenance requirements for nitrogen and energy in desert tortoises consuming forages. Comp. Biochem. Physiol. A 112, 537–545.
Bauert, M., Furrer, S.C., Zingg, R., Steinmetz, H.W., 2007. Three years of experience running the Masoala Rainforest ecosystem at Zurich Zoo, Switzerland. Int. Zoo Yb. 41, 203–216.
Bell, R.H.V., 1971. A grazing ecosystem in the Serengeti. Sci. Am. 225, 86–93.
Bennett, A.F., Dawson, W.R., 1976. Metabolism. In: Gans, C., Dawson, W.R. (Eds.), Biology of the Reptilia. : (Physiology A), vol. 5. Academic Press, New York, pp. 127–223.
Bjorndal, K.A., 1980. Nutrition and grazing behavior of the green turtle (*Chelonia mydas*). Mar. Biol. 56, 147–154.
Bjorndal, K.A., 1987. Digestive efficiency in a temperate herbivorous reptile, *Gopherus polyphemus*. Copeia 714–720.
Bjorndal, K.A., 1989. Flexibility of digestive responses in two generalist herbivores, the tortoises *Geochelone carbonaria* and *Geochelone denticulata*. Oecologia 78, 317–321.
Bjorndal, K.A., Bolten, A.B., Moore, J.E., 1990. Digestive fermentation in herbivores: effect of food particle size. Physiol. Zool. 63, 710–721.
Bjorndal, K.A., Bolten, A.B., 1992. Body size and digestive efficiency in a herbivorous freshwater turtle: advantages of small bite size. Physiol. Zool. 65, 1028–1039.
Bjorndal, K.A., Bolten, A.B., 1993. Digestive efficiencies in herbivorous and omnivorous freshwater turtles on plant diets: do herbivores have a nutritional advantage? Physiol. Zool. 66, 384–395.
Bjorndal, K.A., 1997. Fermentation in reptiles and amphibians. In: Mackie, R.I., White, B. A. (Eds.), Gastrointestinal Microbiology. : Gastrointestinal Ecosystems and Fermentations, vol. 1. ITP, New York, pp. 199–230.
Bouchard, S.S., Bjorndal, K.A., 2006. Ontogenetic diet shifts and digestive constraints in the omnivorous freshwater turtle *Trachemys scripta*. Physiol. Biochem. Zool. 79, 150–158.
Brand, S.J., Lanyon, J.M., Limpus, C.J., 1990. Digesta composition and retention times in wild immature green turtles (*Chelonia mydas*): a preliminary investigation. Mar Freshw Res 50, 145–147.
Calder, W.A., 1996. Size, Function and Life History. Havard University Press, Cambridge, MA.
Clauss, M., Polster, C., Kienzle, E., Wiesner, H., Baumgartner, K., von Houwald, F., Ortmann, S., Streich, W.J., Dierenfeld, E.S., 2005. Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*). J. Anim. Physiol. Anim. Nutr. 89, 229–237.
Clauss, M., Castell, J.C., Kienzle, E., Dierenfeld, E.S., Flach, E.J., Behlert, O., Ortmann, S., Streich, W.J., Hummel, J., Hatt, J.M., 2006. Digestion coefficients achieved by the black rhinoceros (*Diceros bicornis*), a large browsing hindgut fermenter. J. Anim. Physiol. Anim. Nutr. 90, 325–334.
Clauss, M., Schwarm, A., Ortmann, S., Streich, W.J., Hummel, J., 2007a. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. Comp. Biochem. Physiol. A 148, 249–265.
Clauss, M., Streich, W.J., Schwarm, A., Ortmann, S., Hummel, J., 2007b. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. Oikos 116, 209–216.
Clauss, M., Streich, W.J., Nunn, C.L., Ortmann, S., Hohmann, G., Schwarm, A., Hummel, J., 2008. The influence of natural diet composition, food intake level, and body size on ingesta passage in primates. Comp. Biochem. Physiol. A 150, 274–281.
Clauss, M., Nunn, C., Fritz, J., Hummel, J., 2009. Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores. Comp. Biochem. Physiol. A 154, 376–382.
Clauss, M., Lang-Deuerling, S., Müller, D.W.H., Kienzle, E., Steuer, P., Hummel, J., 2010. Retention of fluid and particles in captive tapirs (*Tapirus* spp.). Comp. Biochem. Physiol. A 157, 95–101.
Davenport, J., Wong, T.M., East, J., 1992. Feeding and digestion in the omnivorous estuarine turtle *Batagur baska*. Herpetol. J. 2, 133–139.
Demment, M.W., Van Soest, P.J., 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. Am. Nat. 125, 641–672.
Franz, R., Hummel, J., Kienzle, E., Kölle, P., Gunga, H.C., Clauss, M., 2009. Allometry of visceral organs in living amniotes and its implications for sauropod dinosaurs. Proc. R. Soc. B 276, 1731–1736.
Fritz, J., Hummel, J., Kienzle, E., Streich, W.J., Clauss, M., 2010. To chew or not to chew: faecal particle size in herbivorous reptiles and mammals. J Exp Zool A (in press). doi:10.1002/jez.629.
Geist, V., 1974. On the relationship of social evolution and ecology in ungulates. Am. Zool. 14, 205–220.
Hailey, A., 1997. Digestive efficiency and gut morphology of omnivorous and herbivorous African tortoises. Can. J. Zool. 75, 787–794.
Hamilton, J., Coe, M., 1982. Feeding, digestion and assimilation of a population of giant tortoises (*Geochelone gigantea*) on Aldabra atoll. J. Arid Environ. 5, 127–144.
Hatt, J.M., Gisler, R., Mayes, R., Lechner-Doll, M., Clauss, M., Liesegang, A., Wanner, M., 2002. The use of dosed and herbage n-alkanes as markers for the determination of intake, digestibility, mean retention time and diet selection in Galapagos tortoises. Herpetol. J. 12, 45–54.
Hatt, J.M., Clauss, M., Gisler, R., Liesegang, A., Wanner, M., 2005. Fiber digestibility in juvenile captive Galapagos tortoises (*Geochelone nigra*). Zoo Biol. 24, 185–191.
Holleman, D.F., White, R.G., 1989. Determination of digesta fill and passage rate from non absorbed particulate phase markers using the single dosing method. Can. J. Zool. 67, 488–494.
Hone, D.W.E., Benton, M.J., 2005. The evolution of large size: how does Cope's rule work? Trends Ecol. Evol. 20, 4–6.
Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434.
Jarman, P.J., 1974. The social organization of antelope in relation to their ecology. Behaviour 48, 215–266.
Jumars, P.A., 2000. Animal guts as nonideal chemical reactors: partial mixing and axial variation in absorption kinetics. Am. Nat. 155, 544–555.
Karasov, W.H., Petrossian, E., Rosenberg, L., Diamond, J.M., 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminants mammals? J. Comp. Physiol. B 156, 599–609.
Karasov, W.H., Martínez del Rio, C., 2007. Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. Princeton University Press, Princeton, New Jersey, USA.
Liesegang, A., Hatt, J.M., Nijboer, J., Forrer, R., Wanner, M., Isenbügel, E., 2001. Influence of different dietary calcium levels on the digestibility of Ca, Mg, and P in captive-born juvenile Galapagos giant tortoises (*Geochelone nigra*). Zoo Biol. 20, 367–374.
Loehlein, W., Kienzle, E., Wiesner, H., Clauss, M., 2003. Investigations on the use of chromium oxide as an inert, external marker in captive Asian elephants (*Elephas*

maximus): passage and recovery rates. In: Fidgett, A., Clauss, M., Ganslosser, U., Hatt, J.M., Nijboer, J. (Eds.), Zoo Animal Nutrition. : Filander, 2. Fuerth, Germany, pp. 223–232.
Martinez del Rio, e.a., 1994. Modelling gut function: an introduction. In: Chivers, Langer (Ed.), The Digestive System of Mammals: Food, Form and Function. Cambridge Univ. Press, Cambridge, pp. 25–53.
Meienberger, C., Wallis, I.R., Nagy, K.A., 1993. Food intake rate and body mass influence transit time and digestibility in the desert tortoise (*Xerobates agassizii*). Physiol. Zool. 66, 847–862.
Nagy, K.A., Medica, P.A., 1986. Physiological ecology of desert tortoises in Southern Nevada. Herpetologica 42, 73–92.
Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. Annu Revs Nutr 19, 247–277.
Parmenter, R.R., 1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. Comp. Biochem. Physiol. A 70, 235–238.
Parra, R., 1978. Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery, G.G. (Ed.), The Ecology of Arboreal Folivores. Smithsonian Institution Press, Washington DC, pp. 205–229.
Pérez-Barberìa, F.J., Elston, D.A., Gordon, I.J., Illius, A.W., 2004. The evolution of phylogenetic differences in the efficiency of digestion in ruminants. Proc. R. Soc. B 271, 1081–1090.
Pérez-Barberìa, F.J., Pérez-Fernàndez, E., Robertson, E., Alvarez-Enríquez, B., 2008. Does the Jarman–Bell principle at intra-specific level explain sexual segregation in polygonous ungulates? Sex differences in forage digestibility in Soay sheep. Oecologia 157, 21–30.
Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.
Rick, C.M., Bowman, R.I., 1961. Galapagos tomatoes and tortoises. Evolution 15, 407–417.
Robbins, C.T., 1993. Wildlife Feeding and Nutrition. Academic Press, San Diego.
Schwarm, A., Ortmann, S., Hofer, H., Streich, W.J., Flach, E.J., Kühne, R., Hummel, J., Castell, J.C., Clauss, M., 2006. Digestion studies in captive *hippopotamidae*: a group of large ungulates with an unusually low metabolic rate. J. Anim. Physiol. Anim. Nutr. 90, 300–308.
Schwarm, A., Ortmann, S., Wolf, C., Streich, W.J., Clauss, M., 2009. More efficient mastication allows increasing intake without compromising digestibility or necessitating a larger gut: comparative feeding trials in banteng (*Bos javanicus*) and pygmy hippopotamus (*Hexaprotodon liberiensis*). Comp. Biochem. Physiol. A 152, 504–512.
Smith, F.A., 1995. Scaling of digestive efficiency with body mass in *Neotoma*. Funct. Ecol. 9, 299–305.
Steuer, P., 2010. Limitation of Body Mass of Herbivores—Allometry of Food Quality and of Digestive Aspects. University of Bonn, Bonn, Germany.
Steuer, P., Clauss, M., Südekum, K.-H., Hatt, J.-M., Silinski, S., Klomburg, S., Zimmermann, W., Hummel, J., 2010. Comparative investigations on digestion in grazing (*Ceratotherium simum*) and browsing (*Diceros bicornis*) rhinoceroses. Comp. Biochem. Physiol. A 156, 380–388.
Thielemanns, M.-F., Francois, E., Bodart, C., Thewis, A., 1978. Mesure du transit gastrointestinal chez le porc à l´aide des radiolanthanides. Comparaison avec le mouton. Ann. Biol. Anim. Biochim. Biophys. 18, 237–247.
Troyer, K., 1984a. Structure and function of the digestive tract of a herbivorous lizard *Iguana iguana*. Physiol. Zool. 57, 1–8.
Troyer, K., 1984b. Diet selection and digestion in *Iguana iguana*: the importance of age and nutrient requirements. Oecologia 61, 201–207.
Troyer, K., 1991. Role of microbial cellulose degradation in reptile nutrition. In: Haigler, C., Weimer, P. (Eds.), Biosynthesis and Biodegradation of Cellulose. Marcel Dekker, New York, pp. 311–325.
Udén, P., Colucci, P.E., Van Soest, P.J., 1980. Investigation of chromium, cerium and cobalt as markers in digesta rates of passage studies. J. Sci. Food Agric. 31, 625–632.
Udén, P., Rounsaville, T.R., Wiggans, G.R., Van Soest, P.J., 1982. The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (*Phleum pratense*) hay. Br. J. Nutr. 48, 329–339.
van Marken Lichtenbelt, W.D., 1992. Digestion in an ectothermic herbivore, the green iguana (*Iguana iguana*): effect of food composition and body temperature. Physiol. Zool. 65, 649–673.
Zimmerman, L.C., Tracy, C.R., 1989. Interactions between the environment and ectothermy and herbivory in reptiles. Physiol. Zool. 62, 374–409.