

The digestive performance of mammalian herbivores: why big may not be that much better

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ABSTRACT

1. A traditional approach to the nutritional ecology of herbivores is that larger animals can tolerate a diet of lesser quality due to a higher digestive efficiency bestowed on them by comparatively long ingesta retention times and lower relative energy requirements.

2. There are important physiological disadvantages that larger animals must compensate for, namely a lower gut surface : gut volume ratio, larger ingesta particle size and greater losses of faecal bacterial material due to more fermentation. Compensating adaptations could include an increased surface enlargement in larger animals, increased absorption rates per unit of gut surface, and increased gut motility to enhance mixing of ingesta.

3. A lower surface : volume ratio, particularly in sacciform forestomach structures, could be a reason for the fact that methane production is of significant scope mainly in large herbivores and not in small herbivores with comparably long retention times; in the latter, the substrate for methanogenesis – the volatile fatty acids – could be absorbed faster due to a more favourable gut surface : volume ratio.

4. Existing data suggest that in herbivores, an increase in fibre digestibility is not necessarily accompanied by an increase in overall apparent dry matter digestibility. This indicates a comparative decrease of the *apparent* digestibility of non-fibre material, either due to a lesser utilization of non-fibre substrate or an increased loss of endogenous/bacterial substance. Quantitative research on these mechanisms is warranted in order to evaluate whether an increase in body size represents a net increase of digestive efficiency or just a shift of digestive focus.

Keywords: allometry, body size, digestibility, digestive physiology, gut motility, herbivory, 'Jarman–Bell-principle'

INTRODUCTION: THE TRADITIONAL CONCEPT OF INCREASING DIETARY TOLERANCE WITH INCREASING BODY SIZE

Based on observations of African ungulates of varying body size, Jarman (1968, 1974) and Bell (1969, 1971) noted that specific metabolic rate decreases with increasing body weight (BW) but gut capacity remains a constant fraction of BW. Therefore, they concluded that larger animals should be able to tolerate a lower minimum dietary quality than smaller species. This concept was called the 'Jarman–Bell-Principle' by Geist (1974), and its applicability has not been challenged since: In mammals, the validity of the Kleiber scaling coefficient for basal metabolic rate of $BW^{0.75}$ is generally undisputed, even if individual species or taxonomic groups may deviate substantially from the value predicted by this coefficient

(McNab, 2002), and Parra (1978) supplied a quantitative verification of the concept by demonstrating that gut capacity, measured as gut contents, increases linearly with BW. This finding is supported by Demment (1982) for the ruminant forestomach and Demment & Van Soest (1985) for the entire gut, and by interspecific studies of larger scope in which not the gut contents, but the geometric volume of different compartments of the digestive tract was calculated from anatomical measurements (Chivers & Hladik, 1980; Snipes & Kriete, 1991; Snipes, 1997). Demment (1983) and Demment & Van Soest (1985) postulated that the main effect of increasing BW, and hence gut capacity, should be an increase in ingesta retention (mean retention time, MRT) and thus time available for digestion. In this context, Langer & Snipes (1991) demonstrated the correlation of larger gastrointestinal compartments with longer retention times, and Illius & Gordon (1992), collating data from Warner (1981) and Foose (1982), finally quantified the correlation of body size and retention time, demonstrating that MRT scales to $BW^{0.25}$ or $BW^{0.27}$ in both ruminants and hindgut fermenters. In a more recent data collection for hindgut fermenters, Cork, Hume & Faichney (1999) found that MRT scaled to $BW^{0.19}$. An important implication of this general concept is that larger ungulates can support their lower specific metabolic requirements either by accepting forage of lower quality, or by ingesting lesser amounts of regular-quality forage per day, or some combination of both (Owen-Smith, 1988; Van Soest, 1996). Therefore, larger animals should eat diets of lower nutritional quality than those selected by smaller herbivores, but the difference should be less marked than predicted simply on the basis of the body size–metabolic rate relationship.

With respect to this general concept, Clauss *et al.* (2003) outlined some limitations due to the fact that digestive efficiency cannot be optimized endlessly as, at some point, complete fibre fermentation (and increasing energetic losses due to methane production) must be expected. In this review, we collated data on ingesta retention in the ruminant forestomach measured by comparable methods and did not find, in contrast to Illius & Gordon (1992), an allometric relationship between BW and MRT. In this review, we want to present some additional considerations that have not received particular attention in the discussion on the influence of body size on herbivore digestive efficiency.

ALLOMETRIC SCALING OF GUT SURFACE AREA

A starting point for a consideration that has a major influence on estimates of digestive efficiency stems from a simplistic cubic model that relies on the assumption that gut capacity increases linearly with body size (Fig. 1a–c). In such a cubic model, body surface increases at body volume^{0.67}. For the sake of this review, we will assume that this exponent reflects the exponent used to calculate metabolic body size from BW (usually: 0.75). For a detailed discussion on the origin of the exact value of this exponent, see the study by McNab (2002; chapter 3) and the most recent biological literature (e.g. Savage *et al.*, 2004). If it is assumed that gut volume represents a constant fraction of total body volume (Fig. 1a), two extreme models represent the range of options by which this fraction can be kept constant when body size is increased.

On the one hand, this can be achieved by simply putting gut volumes of the initial shape in sequence (Fig. 1b). This would keep the gut surface : gut volume ratio constant, and gut surface (and gut length) would increase linearly with body size.

On the other hand, this can be achieved by arranging the initial gut volumes next to each other, resulting in a shorter gut of larger diameter with a lesser gut surface : gut volume ratio (Fig. 1c). In this case, gut surface would increase at body volume^{0.67} or, given the assumption stated above, linearly to *metabolic body size*.

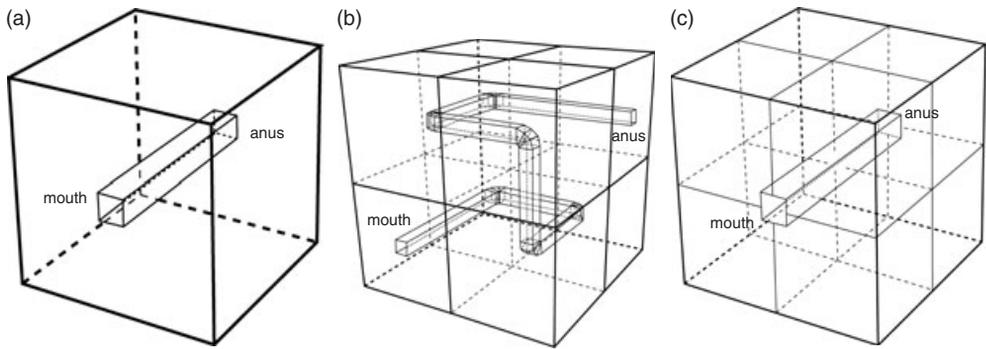


Fig. 1. (a) Idealized model of an animal. (b) Model from (a) increased in size while keeping the gut surface : gut volume ratio constant. (c) Model from (a) increased in size with identical effects on the surface : volume ratio for the whole body and for the gut.

In reality, a combination of both possibilities seems probable; however, common sense alone predicts that some increase in diameter has to occur, with corresponding losses in the gut surface : gut volume ratio.

Numerous studies have measured gut surface areas in individual species. In studies that investigated or collated data on a multitude of species, it was found repeatedly that the surface area of the small intestine or other gut compartments scales to $BW^{0.75}$ (Chivers & Hladik, 1980; Martin *et al.*, 1985; MacLarnon Chivers & Martin, 1986; Snipes & Kriete, 1991; Woodall & Skinner, 1993; Snipes, 1997; in contrast, Pappenheimer, 1998, collated data from different sources, including selected values from Chivers & Hladik, 1980, and found that the surface of the small intestine scaled to $BW^{0.6}$). For the digestive efficiency, this has the important implication that the ratio of gut surface : gut volume decreases with BW; in other words, larger animals have less absorptive gut surface at their disposal per unit gut volume. One would expect various morphophysiological counter-measures that balance this digestive disadvantage.

POTENTIAL ADAPTATIONS TO COUNTER A DECREASE IN ABSORPTIVE SURFACE WITH INCREASING BODY WEIGHT

Increasing the surface enlargement factor (SEF)?

Absorptive villi or papillae are considered to enlarge the surface available for absorption. With respect to intestinal villi, however, Pappenheimer (1998) summarizes arguments that support the concept that basal intestinal area and total intestinal area (i.e. including surface enlargement by villi) are functionally similar, because absorption is limited to an (admittedly unknown) proportion of the luminal tip of the villi. Snipes (1997) demonstrated that the correlations of basal and total gut area with BW were of nearly identical slope. In contrast, Van Wieren (1996), using data on the maximal SEF in the rumen of wild ruminants determined by Hofmann (1973), found a positive correlation of the ruminal SEF with BW. The system of taeniae and haustra present in the intestines of many mammalian herbivores might represent another morphological adaptation for an increased internal surface (Langer & Takács, 2004).

Increasing the absorption rate per unit absorptive surface?

Using data on rats, dogs and humans, Pappenheimer (1998) demonstrated that paracellular glucose absorption per unit gut surface increases with BW. Karasov & Diamond (1988)

collated data on glucose and proline absorption in 42 vertebrate species covering a BW range from 3 to 5 kg and expressed the results as the quotient of total glucose uptake/total proline uptake. This quotient was independent of BW in the data collection; however, this does not rule out the possibility that absorption rate increases proportionally per unit absorptive surface in animals of increasing BW. To our knowledge, comparative studies on other absorption mechanisms, especially among herbivorous animals, over a wider range of body sizes, do not exist. The conceptual problem of such comparisons lies in the choice of the substance investigated: from the data on mammals from Karasov & Diamond (1988) it seems that the absorption of glucose and proline scales to BW at different exponents, and differences between herbivores, omnivores and carnivores do occur. In strict herbivores, glucose absorption might not be an adequate measure of an overall absorptive capacity, as e.g. in some ruminants, intestinal sodium-glucose cotransporters occur less frequently than in ruminants of another feeding type (Rowell *et al.*, 1997).

Increasing gut content stir by increasing gut motility?

The forestomach volume of ruminants increases linearly with BW (Demment, 1982; see above). In contrast, the forestomach content of folivorous, foregut-fermenting primates increases with $BW^{0.78}$, and the hindgut contents of folivorous, hindgut-fermenting primates increases with $BW^{1.20}$ [Chivers & Hladik, 1980; note that the authors did not correlate their data with actual BWs but with body length³ (cm³)/1000 as a surrogate measure]. These authors interpret this difference as an indication of problems arising from a small surface : volume-quotient; this quotient decreases more distinctly in sacciform (forestomach) structures than in tubiform (hindgut) structures. The comparatively lesser increase in fermentation contents in forestomach fermenting primates therefore suggests a comparative absorptive inefficiency of larger sacciform stomachs. Ruminants have not only evolved ruminal papillae for surface enlargement, but their forestomach physiology is also characterized by frequent ruminal contractions (Dziuk, Fashingbauer & Idstrow, 1963; Dziuk, 1965; Dziuk & McCauley, 1965) that ensure a constant mixing of the ingesta. This has also been demonstrated in camelids (Vallenas & Stevens, 1971). To our knowledge, neither the general occurrence nor a potential frequency of forestomach motility in folivorous primates or sloths has been measured. A potential difference between foregut-fermenting ungulates and arboreal folivores (colobine primates, sloths) with respect to forestomach motility could mean that the latter group depend, to a larger extent, on the slow process of diffusion along osmotic gradients alone for the absorption of fermentation products from the forestomach, whereas a higher rate of ingesta mixing in the former will greatly accelerate the absorptive process. Such a difference could contribute to the fact that, while sloth and foregut-fermenting primates are characterized by particularly low metabolic rates (McNab, 1978; Ross, 1992), ungulate foregut fermenters are able to maintain metabolic rates close to the interspecific average (McNab, 2002).

METHANE PRODUCTION AND BODY SIZE

Based on calculations derived from *in vitro* studies and domestic ruminants, the growth of gastrointestinal methanogenic bacteria has been postulated to be a limiting factor in large herbivore digestive physiology (Prins & Kreulen, 1991), and the comparatively fast passage rates in the largest extant terrestrial mammal, the elephant, have been interpreted in part as a counter-measure against the danger of disproportional methanogene growth (Clauss *et al.*, 2003). However, some smaller mammalian and reptilian herbivores achieve particle retention times that even surpass the 4-day threshold that Van Soest (1994) postulates for the dispro-

portionate growth of methanogene bacteria [e.g. koalas: 99 hours for particles and 213 hours for solutes (Cork & Warner, 1983); giant tortoises: 287 hours for particles and 222 hours for solutes (Hatt *et al.*, 2002)]. In these species, methanogenes do occur (Hackstein & Van Alen, 1996). A possible explanation could be that the higher surface : volume ratio in these species allows a better absorption of fermentation products that therefore are not available as substrate for slow-growing methanogenes.

There are few studies that related the effect of BW to the production of methane. Galbraith *et al.* (1998) showed that in white-tailed deer *Odocoileus virginianus*, wapiti *Cervus elaphus* and bison *Bison bison*, weighing on average 35, 151 and 196 kg, respectively, on a lucerne diet, methane production as a function of dry matter intake (DMI) increased from 15.0 L/kg DMI in the small deer to 23.5 L/kg DMI in wapiti and 30.1 L/kg DMI in bison. Corresponding energy losses (in percentage of gross energy intake) were 3.3%, 5.2% and 6.6%, respectively. Aguilera & Prieto (1991) determined losses due to methane production relative to gross energy intake in goats (no BW given) on lucerne to average 4.5%, and Belyea, Marin & Sedgwick (1985) determined these losses in 240-kg cattle on lucerne to be 9.9%. In cattle of 265–313 kg BW on a lucerne diet, daily methane production rates of 28.1–33.3 L/kg DMI were measured (Hironaka *et al.*, 1996). These data indicate that in ruminants, methane production per unit energy or DMI scales – maybe linearly – with BW. The more voluminous forestomachs of larger ruminants, with their potentially longer retention times and their lesser surface : volume ratios, might therefore be particularly favourable for methane production.

Although herbivorous hindgut fermenters generally harbour methanogenic bacteria (Miller & Wolin, 1986; Hackstein & van Alen, 1996; Hackstein, Langer & Rosenberg, 1996), methane production is not considered to be of the same daily scope in these species as it is in ruminants (Crutzen, Aselmann & Seiler, 1986). Yet, experimental data on large hindgut fermenters is largely missing. Kempton, Murray & Leng (1976) found that methane production in kangaroos may be negligible, and von Engelhardt *et al.* (1978) demonstrated a lesser methane production in tammar wallabies *Macropus eugenii* and hyraxes *Procavia habessinica* as compared to ruminants. Crutzen *et al.* (1986) calculated methane productions for various wild mammalian herbivores, using a theoretical approach that is not, to date, confirmed by empirical data. In those calculations, methane production in hippos was calculated as for other hindgut fermenters instead of as for other foregut fermenters. Jensen (1996) cited these data without indicating that it is derived from theoretical calculations only. A potentially low methane production in the hindgut of rodents, pigs and ruminants is explained by Prins & Lankhorst (1977), Jensen (1996) and Immig (1996), respectively, by speculating that in the hindgut, other hydrogen sink mechanisms than methane production are involved in removing hydrogen from the fermentation chambers. Empirical data from Prins & Lankhorst (1977) for rodents and from Fievez *et al.* (2001) for ostriches indicate that reductive acetogenesis (the formation of acetate and water from H₂ and CO₂) does occur in the hindgut. Yet, this process does not rule out methanogenesis completely, as, e.g. Fievez *et al.* (2001) determined methane in the lower colon of ostriches as well. Amongst other factors, the absence of protozoa in the hindgut of ruminants is considered a cause for lower methane production in the hindgut (Jensen, 1996; Immig, 1996). However, in the large intestine of equids, rhinoceroses and elephants, protozoa have been documented extensively (e.g. Hsiung, 1930; Hoare, 1937; Thurston & Noirot-Tiomotheè, 1973; Eloff & Van Hoven, 1980; Frape *et al.*, 1982; Van Hoven *et al.*, 1998). In culled elephants, methane comprised 44–69% of the total fermentation gas volume in the caecum and colon (Van Hoven, Prins & Lankhorst 1981). Whereas Crutzen *et al.* (1986) calculated a daily methane production for a 1750-kg elephant as 110 L, Benedict (1936) determined, by respiration chamber, a daily methane production of 655 L for an

elephant of approximately 3670 kg, and Ritzman & Benedict (1938) report a daily methane production of 148 L for a 675-kg horse. As already emphasized by Cumming & Cumming (2003), experimental studies on the methane production of large herbivores are warranted.

BODY SIZE AND INGESTA PARTICLE SIZE

The few comparative studies on ingesta particle size (measured as faecal particle size; Udén & Van Soest, 1982a; Okamoto, 1997; Clauss, Lechner-Doll & Streich, 2002) indicate that ingesta particle size generally increases with body size (cf. Figs 2 and 3). Although ruminants comminute their food into remarkably small particles and have smaller faecal particles than equids (Udén & Van Soest, 1982a; Grenet, Martin-Rosset & Chenost, 1984), the trend of larger particle sizes in larger animals is obvious in this group as well. For humans, Julien *et al.* (1996) demonstrated an effect of body size on several parameters determining chewing efficiency. Based on observed correlations between BW and different parameters that affect chewing efficiency (Fortelius, 1985; Druzinsky, 1993; Shipley *et al.*, 1994), Pérez-Barberia & Gordon (1998) concluded that ingesta particle size should scale positively, allometrically to BW.

The particle size that the ingesta is comminuted into has an important effect on microbial fibre digestion: a limited amount of studies have demonstrated that the efficiency of both *in vitro* and *in vivo* fermentation is correlated to particle size (Dehority & Johnson, 1961; Robles *et al.*, 1977, 1980; Bjorndal Bolten & Moore, 1990; Udén, 1992; Bowman & Firkins, 1993). Larger plant particles need to be retained in a fermentation chamber for longer periods of time to yield the same amount of energy as an corresponding sample of small particles. Therefore, large particles impose a serious intake limitation, and most herbivorous mammals

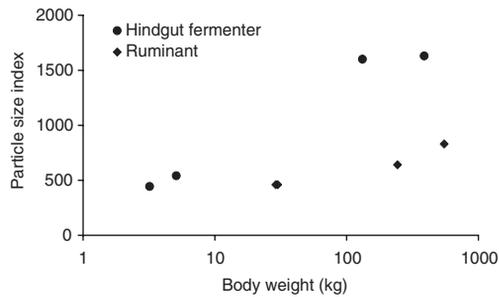


Fig. 2. Comparative faecal particle size in hindgut fermenters (rabbits, horses) and ruminants (sheep, cattle). Data from Udén & Van Soest (1982a).

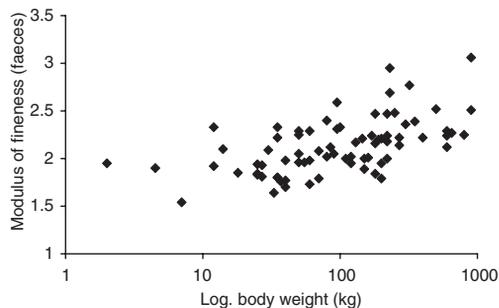


Fig. 3. Comparative faecal particle size in ruminant species (after Clauss *et al.*, 2002).

– with the notable exception of ruminants – selectively expel large particles at a faster rate from their gut (cf. Clauss, 2004). Small particles usually have a greater relative surface area exposed to microbial attack (Pond, Ellis & Akin, 1984) and thus lead to a greater rate of digestion (Bjorndal & Bolten, 1992). The ingesta particle size is a probably even more important determinant of enzymatic digestion. Numerous studies on domestic animals have demonstrated that the particle size of substances that are subject to mainly enzymatic digestion has a distinct effect on the digestive efficiency (e.g. Meyer *et al.*, 1993; Livesey *et al.*, 1995; Wondra *et al.*, 1995). With respect to plant forages, it could be expected that cell content digestibility is increased by decreasing particle size, as more cells are likely to be damaged and hence made vulnerable to enzymatic attack.

Bjorndal & Bolten (1992) found that small freshwater turtles digested identical food as well as drastically larger, adult specimens in spite of much higher mass-specific intake rates. They attributed this to the advantages of small bite size in the juvenile turtles and the corresponding higher degree of surface area vulnerable to microbial or digestive attack. Clauss *et al.* (2005) collated data that indicate that, on comparable diets, Indian rhinoceroses *Rhinoceros unicornis* achieve similar digestion coefficients as horses, in spite of distinctively longer ingesta retention time; in contrast, elephants achieve lesser digestion coefficients in spite of similar ingesta retention time. Again, the authors speculated that this might in part be due to the lesser degree of food communitation in the larger species. Thus, any digestive advantage gained by longer retention time may at least in part be offset by the disadvantage of larger ingesta particles that need longer retention time for thorough fermentation. However, the existing data on ingesta particle size in herbivores are too limited to draw any quantitative conclusions.

CHANGES OF DIGESTIVE EFFICIENCY WITH BODY SIZE: A SHIFT OF PRIORITIES

There is a limited amount of evidence in the scientific literature indicating that with increasing BW, digestive priorities might shift between forage ingredient fractions. For the sake of this short review, we focus on hindgut fermenters only, and collate data from various sources. As coprophagy was demonstrated to be of no systematic influence on apparent dry matter and fibre digestibility coefficients in rabbits (Udén & Van Soest, 1982b), values for rodents determined without prevention of coprophagy were included. Note that in most feeding trials, the *apparent* digestibility of a nutrient is measured, as it is difficult to differentiate between those fractions in the faeces that actually are the undigested remains of the diet, and those that stem from endogenous (secretion/metabolic/microbial) losses of the animal. Hence, values for the apparent digestibility of dry or organic matter may be influenced by unknown proportions of endogenous losses, while values for the apparent digestibility of fibre are a good approximation of the true digestibility, because fibre substances are not endogenously excreted by animals in significant proportions. Data collection on achieved apparent digestibility coefficients for either a grass hay or a lucerne diet seem to indicate a common trend (Figs 4 and 5). The obvious limitation of these data compilations is that differences in food intake and in selectivity could not be accounted for, but will influence the results. Savadogo, Zemmeling & Nianogo (2000) provide examples of how different degrees of selectivity, depending on trial set-up, can influence the achieved digestibility coefficients. Justice & Smith (1992) and Smith (1995) demonstrated an increasing selectivity with decreasing BW in feeding trials with woodrats *Neotoma* spp.. One conceptual problem with an empirical testing of differences in digestive efficiency between animals of considerable body size differences is that, in order to avoid selective food intake, a common food source would have to be fed as

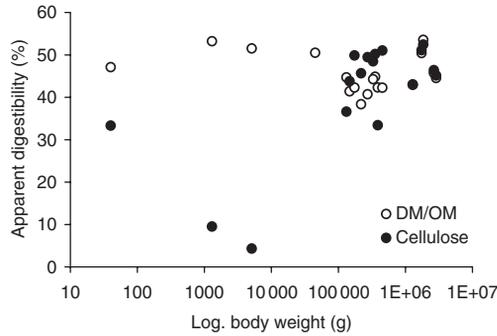


Fig. 4. Apparent digestibility coefficients for dry or organic matter (DM/OM) and cellulose (C) in different herbivorous hindgut fermenters on a grass hay diet. Data from Baldizan, Dixon & Parra (1984; capybara, DM digestibility only), Foose (1982; OM and C digestibility for different zoo equids, tapirs, rhinoceroses and elephants), Keys & Van Soest (1970; DM and C digestibility for meadow voles), Udén & Van Soest (1982b; DM and C digestibility for rabbits and horses; rabbits did not receive a hay-only diet but a diet consisting of hay : supplement 60:40). Note that the achieved apparent DM/OM digestibilities remain on a relatively constant level while the apparent cellulose digestibility tends to increase.

a homogenate (i.e. a pelleted food), but this would in turn diminish any differences that would have occurred due to different particle size reductions. Nevertheless, Wolter, Nouwakpo & Durix (1980) found that when horses and rabbits were fed the same complete pelleted diet, apparent dry matter digestibility did not differ significantly between the species (63% in the horses and 62% in the rabbits, respectively), whereas cellulose digestibility was much higher in the horses than in the rabbits (51% vs. 26%).

These data collections seem to indicate that, while fibre digestibility increases with body size, the apparent dry or organic matter digestibility achieved seems to be relatively constant for a given forage. The same effect can be demonstrated in the data obtained by Slade & Hintz (1969) in a comparative feeding trial with guinea pigs, horses and rabbits (Fig. 6): on an alfalfa-only diet, the same discrepancy between an increase in fibre digestibility and a relatively constant apparent dry matter digestibility over a large body size range can be observed. On a diet of alfalfa and grains (which was not fed to the guinea pigs), fibre digestibility hardly changes, whereas overall apparent dry matter digestibility increases, indicating that an increased provision of material susceptible to enzymatic digestion will lead to higher apparent dry matter digestibilities in all species.

In a similar way, in the turtle trials mentioned above (Bjorndal & Bolten, 1990), the overall apparent dry matter digestibility did not differ significantly between the larger adult and the smaller juvenile animals (28% vs. 32%, respectively), whereas the cell wall digestibility did (16% vs. 11%).

The observed discrepancy between an increase in fibre digestibility and no simultaneous corresponding increase in apparent dry matter digestibility could be due to one of the two following reasons, or a combination of both:

1. The fact that fibre digestibility increases with body size while overall apparent dry matter or organic matter digestibility does not (or not to the same extent) led Cheeke (1987; p. 88) to suspect that the smaller animals must use the non-fibre components particularly efficiently. A less efficient digestion of non-fibre components (i.e. enzymatic digestion) could be a consequence expected due to a lesser gut surface : gut volume ratio and larger ingesta particle size in larger animals. Should this view be correct, then one would expect higher amounts of nutrients – which are normally digested enzymatically – to enter the

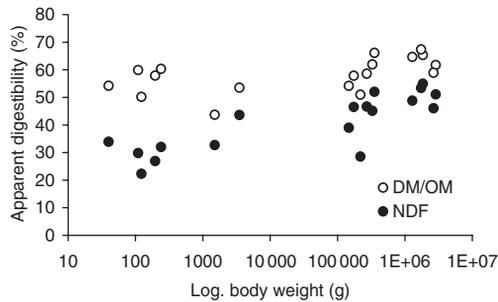


Fig. 5. Apparent digestibility coefficients for dry or organic matter (DM/OM) and neutral detergent fibre (NDF) in different herbivorous hindgut fermenters on a lucerne hay diet. Data from Keys & Van Soest (1970; DM and NDF digestibility for meadow voles), Foose (1982; OM and NDF digestibilities for different zoo equids, tapirs, rhinoceroses and elephants), Paul-Murphy *et al.* (1981; DM and NDF digestibilities for rabbits and rock hyraxes), Loeb, Schwab & Demment (1991; OM and NDF digestibilities for pocket gopher), Smith (1995; OM and NDF digestibilities for different *Neotoma* species). Note that the achieved apparent OM digestibilities remain on a relatively constant level while the apparent NDF digestibility tends to increase with body size.

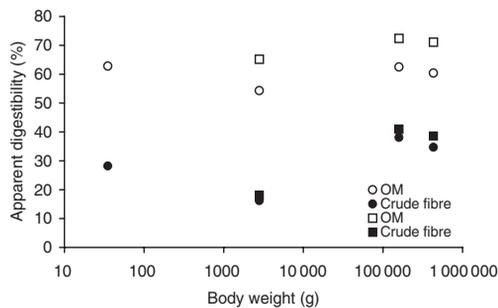


Fig. 6. Apparent digestibility coefficients for organic matter (OM, circles) and crude fibre (CF, squares) in guinea pigs, rabbits, ponies and horses on a lucerne diet (filled symbols) and a diet of lucerne and grains (open symbols, not fed to the guinea pigs). Data from Slade & Hintz (1969). Note that the achieved apparent OM digestibilities remain on a relatively constant level while the CF digestibility increases with body size. The additional provision of a material that is readily enzymatically digestible increases the overall apparent OM digestibility.

hindgut of larger herbivores, where they would be subjected to (energetically less valuable) fermentation.

2. On the other hand, the observed discrepancy could be the result of an increasing loss of bacterial material that occurs in more efficient fibre fermentation in hindgut fermenters. An indication for the relevance of this explanation stems from a comparison with ruminants. In three species of domestic ruminants, in contrast to the data on hindgut fermenters presented above, dry matter digestibility was closely correlated to fibre digestibility (Fig. 7). In ruminants, the majority of bacteria that are produced as a consequence of fibre fermentation (i.e. the ruminal bacteria pool) are submitted to enzymatic digestion, and only a smaller fraction of fibre-fermenting bacteria in the hindgut are lost via the faeces. Should this view be correct, then one would expect higher amounts of 'endogenous' bacterial material in the faeces of larger herbivores.

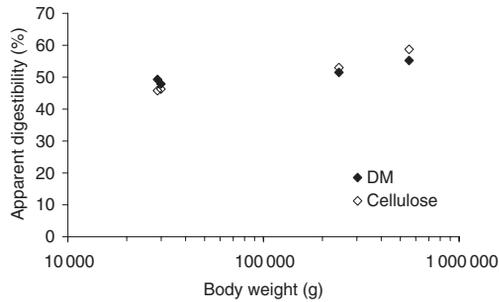


Fig. 7. Apparent digestibility coefficients for dry matter (DM) and cellulose in goats, sheep and two size classes of cattle on a grass hay diet. Data from Udén & Van Soest (1982b). Note that both digestibility coefficients are closely correlated.

CONCLUSION

Bjørndal & Bolten (1992) conclude that herbivory does not require a large body size, but that herbivory allows animals to attain a large body size, which has many selective advantages, amongst which is a low relative metabolic rate. Herbivory may allow larger body sizes because the potential losses in enzymatic digestibility of cell contents, which accompany a body size increase due to lesser gut surface : gut volume ratios and larger ingesta particle sizes, can be levelled by long ingesta retention time and corresponding fibre fermentation. However, increased bacterial fibre fermentation is connected with faecal losses of those bacteria, and therefore might not result in corresponding increases in overall apparent dry matter digestibility. Animals of larger body size tend to feed less selectively and hence consume a diet of 'lesser quality', i.e. higher fibre content (Owen-Smith, 1988). They are enabled to make use of this ubiquitous dietary niche, not because of a 'more efficient digestion', but because of a shift of digestive priorities.

More comparative research on aspects of digestive efficiency in dependence of the gut surface : gut volume ratio or the ingesta particle size, and on metabolic faecal losses, is needed for a quantitative understanding of these digestive shifts or trade-offs.

ACKNOWLEDGEMENTS

We thank Peter Langer for valuable advice on the first draft of this manuscript and Eberhard Rensch for graphics design. This is contribution No. 2 of the DFG research unit 'Biology of the Sauropod Dinosaurs'.

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Submitted 29 September 2003; returned for revision 12 January 2004; revision accepted 16 March 2004
Editor: RM