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The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups

Marcus Clauss, W. Jürgen Streich, Angela Schwarm, Sylvia Ortmann and Jürgen Hummel

M. Clauss (mclauss@vetclinics.unizh.ch), Div. of Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, Univ. of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland.-W. J. Streich, A. Schwarm and S. Ortmann, Leibniz-Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Str. 17, DE-10315 Berlin, Germany. – J. Hummel, Inst. of Animal Science, Animal Nutrition Group, Endenicher Allee 15, DE-53115 Bonn, Germany and Zoological Garden of Cologne, Riehler Str. 180, DE-50735 Köln, Germany.

Digestion, especially of plant material, is a time-dependent process. In herbivores, an increase in food intake is usually correlated to an acceleration of ingesta passage through the gut, and could hence depress digestive efficiency. Therefore, the nature of the relationship between food intake and ingesta passage (i.e. whether the increase in ingesta passage due to the increase in food intake is mild or drastic) should determine the flexibility of the feeding strategy of herbivore and omnivore species. Using two megaherbivore groups, the elephants and the hippopotamuses, as examples from opposing ends of the range of potential adaptations to this problem, we demonstrate that the species-specific relationship of food intake and ingesta passage can precisely predict feeding ecology and activity budgets. In hippos, the distinct acceleration in ingesta passage due to increased intake limits the additional energy gained from eating more forage, and explains the comparatively low food intake and short feeding times generally observed in these animals. In elephants, increased food intake only leads to a very moderate increase of ingesta passage, thus theoretically allowing to optimize energy gain by eating more, which is in accord with the high food intake and long feeding times observed in these animals. We suggest that the characterization of the intake-passage relationship in herbi- and omnivorous species is of much higher ecological relevance than the determination of a supposedly species-specific "passage time/mean retention time".

> *"I can eat fifty eggs."*
> *Paul Newman in* Cool Hand Luke *(1967)*

Digestion is a time-dependent process. Vertebrate herbivores cannot digest plant fibers enzymatically but have to rely on the help of symbiotic gut bacteria that ferment these fibers (Stevens and Hume 1998). In order to ensure the efficacy of this process, herbivores have evolved ingesta retention mechanisms, which facilitate the delay necessary for adequate bacterial fermentation (Langer and Snipes 1991). This delay is of particular relevance for herbivores, because the digestion rate of fibrous plant material in the gut is of similar scope as the passage rate of the material from the gut (Mertens 1993), in contrast to the low-fiber diets of omnivores and carnivores, where digestion rate usually exceeds gut passage rate by magnitude.

Accordingly, the mean retention time (MRT, h) of ingesta is usually understood as a species-specific parameter that is determined by the species-specific body mass, and that characterizes the digestive efficiency of a herbivore (Demment and Van Soest 1985, Illius and Gordon 1992, Robbins 1993). There is a general consensus that an increase in body size is accompanied by an increase in gut volume and hence capacity for ingesta retention, which is considered the reason why larger herbivores can use forage of comparatively high fiber content, i.e. of "low quality" (Parra 1978, Demment and Van Soest 1985, Illius and Gordon 1992).

However, in contrast to adult body mass, which varies only little, individual investigations on MRT showed a tremendous range of MRT variation within a species. For example, an MRT range of 8–80 h was measured in beavers (*Castor canadensis*) (Fryxell et al.

1994) or of 32–107 h in pygmy hippopotamus (*Hexaprotodon liberiensis*) (Clauss et al. 2004). Such enormous ranges make the use of one “species-specific value” seem dubious, and warrant explanation by other physiological measurements beyond body mass. Many authors have noted a negative correlation between food intake and MRT, not only in herbivorous species (Halse 1984, Wetherbee and Gruber 1990, Lechner-Doll et al. 1991, Fryxell et al. 1994, Reid and Brooks 1994, McClelland et al. 1999, Pearson et al. 2001, Clauss et al. 2004, Clauss et al. 2005). Actually, the belief that relative dry matter intake (DMI, g $kg^{-0.75}$ metabolic body mass day^{-1}) is negatively correlated with MRT in the gastrointestinal tract is an integral part of digestion theory (Silby and Calow 1986).

Any potential correlation between DMI and MRT, therefore, sets the stage for a tradeoff scenario each herbivore species will have to face: ingesting a low amount of forage, resulting in a long MRT and efficient digestion, or ingesting a high amount of forage, resulting in a short MRT and inefficient digestion. A gentle slope of the DMI–MRT regression line would, in theory, be generally advantageous for herbivores, because then, a significant increase in food intake would only entail a mild shortening of MRT and hence only a mild loss of digestive efficiency.

We used data on DMI, MRT and digestive efficiency from two extreme megaherbivore cases, captive hippopotamuses (Clauss et al. 2004) and elephants (Hackenberger 1987), to specify the range of different adaptive solutions to the problem how to optimize food intake and net energy gain, and to discuss the potential ecological and behavioral consequences.

Material and methods

For the model calculations outlined in Fig. 1, data on dry matter intake, apparent dry matter digestibility, and particle mean retention time from feeding trials with captive hippopotamuses (Clauss et al. 2004) and elephants (Hackenberger 1987) were used. The data represent two species per group – the common (*Hippopotamus amphibius*) and the pygmy hippo, and the Asian (*Elephas maximus*) and the African elephant (*Loxodonta africana*), with repeated measurements on eight individual hippos and 50 individual elephants. In the case of the hippos, chromium-mordanted fibre (< 2 mm) had been used as a particle marker. For the elephants, rubber rings had been used, after a pilot study had revealed no difference in the retention of these rings and chromium-mordanted fibres. Data on faecal marker excretion had been used to calculate MRT according to Thielemans et al. (1978) in the case of the hippos; for the elephants, the data on faecal marker excretion given in the appendix of Hackenberger (1987) was used to calculate MRT by the same method in order to guarantee comparability.

The relationship between apparent digestibility of dry matter (aD DM) and MRT was characterized for each herbivore group by an exponential function usually applied to forage fermentation data (Blümmel and Ørskov 1993). In theory, a simple linear regression could have been applied to the data to describe the relationship of MRT and aD DM; using such a regression did not change the resulting pattern in Fig. 1c that represents the main result of our model. However, as linear equations could be extrapolated to digestibility coefficients above 100%, we decided to use a biologically meaningful, non-linear regression that represents the fact that digestibility cannot be optimized endlessly, and that has been used to describe the dependence of (in vitro) forage fermentation on time (Ørskov and McDonald 1979, McDonald 1981, Blümmel and Ørskov 1993).

Results

Hippopotamuses and elephants significantly differ in their MRT-response to increased food intake, as characterized by the equation:

$$\mathrm{MRT} = \mathrm{a} + \mathrm{b}\ \mathrm{DMI}\ \text{(Fig. 1a)} \qquad (1)$$

with an astounding steep decline in MRT in hippos and a very moderate effect in elephants. Considering aD DM as a function of MRT, as characterized by the equation:

$$\mathrm{aD\ DM} = \mathrm{c} + \mathrm{d}\ (1 - \mathrm{e}^{(\mathrm{fMRT})})\ \text{(Fig. 1b)}, \qquad (2)$$

with increasing digestibility as time available for digestion increases, a theoretical daily digestible dry matter intake (DDMI, g $kg^{-0.75}$ day^{-1}) range can be calculated for both elephants and hippos by using the parameters from Eq. 1 and 2 in the following equation

$$\text{(III)}\ \mathrm{DDMI} = \mathrm{DMI} \times \mathrm{aD\ DM}/100\ \text{(Fig. 1c)}.$$

Using this equation with the respective parameters, it is also possible to extrapolate the hypothetical DDMI for each herbivore group for the combined range of intakes (interrupted lines in Fig. 1c indicating the range of extrapolation).

From this model we conclude that hippos are limited to a maximum DDMI (= maximum energy gain) by feeding on 45–50 g $kg^{-0.75}$ DMI daily; any additional DMI would reduce MRT and hence aD DM to such an extent that overall DDMI would be reduced. In contrast, elephants continue to gain in DDMI with increasing DMI way beyond a theoretical daily DMI of 150 g $kg^{-0.75}$ – in other words, for elephants, maximum DDMI is limited by the maximum DMI they can achieve.

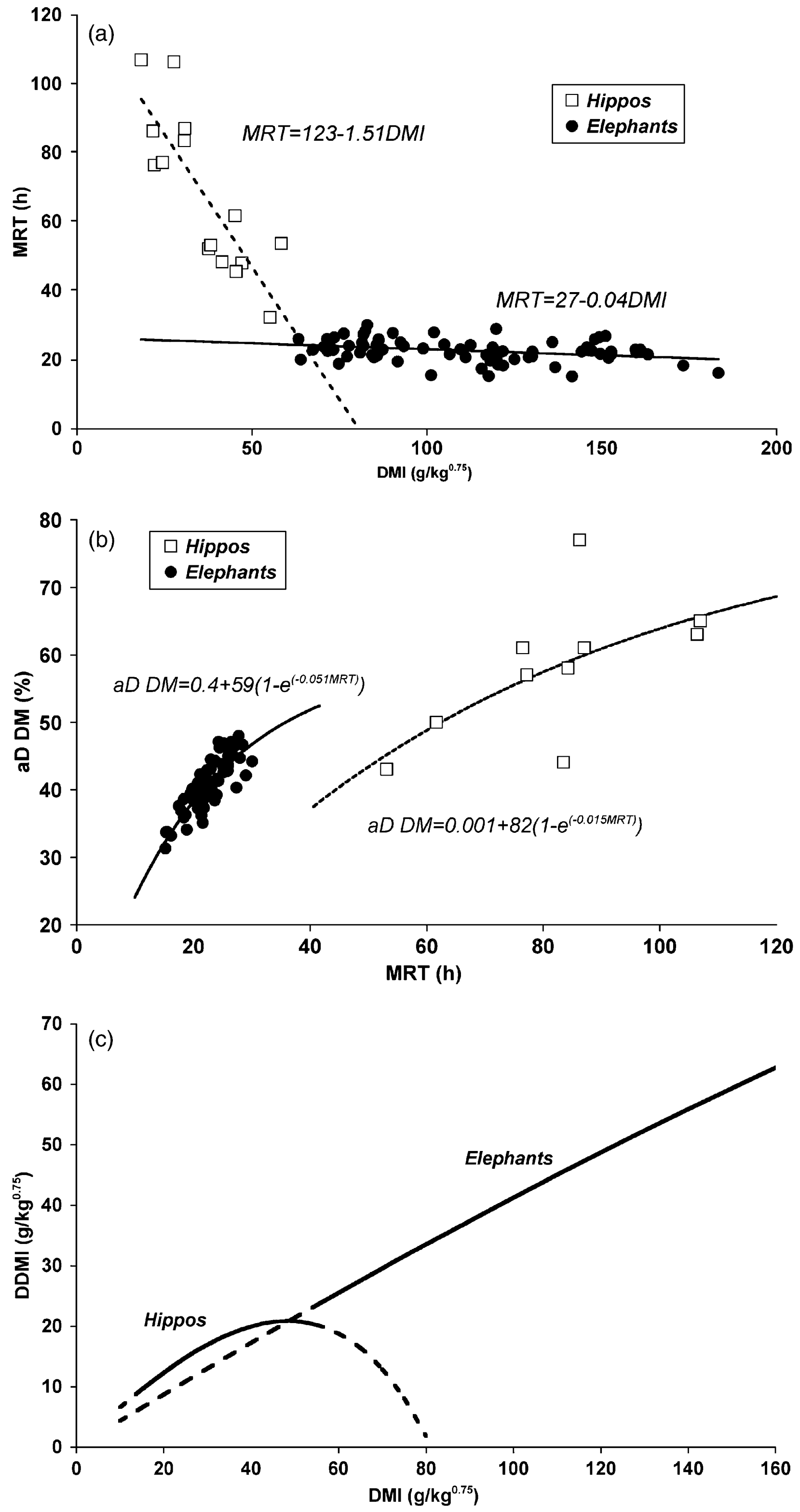

Fig. 1. Modeling the relationships of (a) relative daily dry matter intake (DMI, g kg$^{-0.75}$) and particle mean retention time (MRT, h), (b) MRT and apparent dry matter digestibility (aD DM,%) for grass (hay) diets, and (c) the derived relationship of DMI and daily digestible dry matter intake (DDMI, g kg$^{-0.75}$) in hippopotamuses and elephants. The interrupted lines in 1c indicate the extrapolated range.

It is also suggested that the hippo digestive strategy is advantageous at low food intakes (Fig. 1c).

Discussion

From common hippos on roughage diets we know that DMI ranges from 22–45 g $kg^{-0.75}day^{-1}$ which nicely matches the predicted limitation (Field 1970, Arman and Field 1973, Clauss et al. 2004); in contrast, the reported or estimated food intake of elephants is between 98–157 g $kg^{-0.75}day^{-1}$ for free-ranging (Monfort and Monfort 1979, Meissner et al. 1990, Ruggiero 1992) and 63–183 g $kg^{-0.75}day^{-1}$ for captive elephants on forage-only diets (Hackenberger 1987, Roehrs et al. 1989, Clauss et al. 2003). Free-ranging elephants spend 75% of the day foraging (Hendrichs 1971, Wyatt and Eltringham 1974, Vancuylenberg 1977), in contrast to hippos which are known to spend only 30% of the day foraging (Verheyen 1954, Owen-Smith 1988). Thus, by extrapolation, the nature of the DMI–MRT relationship can predict the feeding pattern of free-ranging herbivores and contribute to our causal understanding of their feeding ecology. Additionally, considering the calculated higher DDMI in the lower DMI range for hippos, this relationship could help explain the competitive advantages of the respective digestive systems in herbivore niche separation (in the case of hippos, the combination of a foregut fermentation system (Langer 1988) with low metabolic energy requirements (Schwarm et al. 2006)).

Several assumptions can be based on the pattern described by this model. Generally, a low slope in the DMI–MRT relationship will allow animals to increase their DDMI for a given forage, while a steep slope will impose a limit on optimal DMI by reducing DDMI at higher intakes. In order to ensure dietary flexibility, therefore, a low DMI–MRT slope can be considered a significant adaptive characteristic that one would expect in many animal species. Actually, the adaptation that an increase in DMI does not automatically lead to a concomitant decrease of MRT has been demonstrated for a variety of vertebrate species of different feeding types (Toloza et al. 1991, Bozinovic and Nespolo 1997, McWilliams and Karasov 1998a, 1998b, Peltier et al. 2003, Trumble et al. 2003). Steep slopes of the DMI–MRT relationship may only be feasible in herbivores that have access to a uniform food source of consistent availability and quality (like the grass consumed by common hippos, Verweij et al. 2006), or in omnivores that also feed on easy-to-digest, non-fibrous food. In omnivores, one could even hypothesize that the steeper the DMI–MRT-relationship is, the higher is the species' dependence on non-fibrous foods. Low slopes, in contrast, should be beneficial for herbivores that have to compensate for variations in quality of their fibrous food supply by increasing DMI.

An important question resulting from these considerations is by what means the digestive system achieves a low DMI–MRT slope. The only possible explanation is the widespread existence of a "spare capacity" (Toloza et al. 1991) or "volume buffer" in the gastrointestinal tract. The costly maintenance of significant spare capacity of a physiological system is in contrast to the common assumption that the capacity of any such system closely matches the load on that system (McWilliams and Karasov 1998). A possible mechanism for the adaptation of such a spare capacity to capacity need is the often-documented ability of birds or small mammal species to adjust gut length and gut tissue weight to a variety of dietary intake and diet composition levels (Dykstra and Karasov 1992, Cork et al. 1999, Pei et al. 2001a, 2001b). To our knowledge, according mechanisms have not been demonstrated in larger herbivores yet but could nevertheless be expected to operate as well. However, as a spare capacity has also been demonstrated in species in which the experimental setup did not allow time for a tissue response (Karasov and Cork 1996, McWilliams and Karasov 1998), other mechanisms such as a suppression of gut motility and simply spare gut volume have been suggested.

A logical consequence of the use of any kind of spare capacity is an increase in gut volume, and thus in most cases also in total volume of the abdominal cavity. The distension of the abdominal wall due to an increased gut volume has, to our knowledge, never been quantified in any animal species. Nevertheless, it is common knowledge in horse owners that on roughage-dominated diets, horses show the typical "hay belly" after feeding. With respect to a similar phenomenon in elephants, McKay (McKay 1973) reported to have "frequently observed elephants [. . .] to look quite slender as they begin feeding; but after as few as five to six hours of intensive feeding, these same individuals have extremely bulging bellies. It would appear reasonable that if the rate at which an elephant can ingest food greatly exceeds the rate at which the intestines and caecum can process it, there would be a distinct advantage to the possession of a very elastic stomach." In ruminants, an increase in forestomach volume with increasing food intake has been demonstrated in numerous studies (Grovum and Williams 1977, Mudgal et al. 1982, Shaver et al. 1986, Lindberg 1988, Lechner-Doll et al. 1990, Barboza et al. 2004), presumably by simple distension of the organ. A macroanatomical solution to the question of spare capacity in many herbivores might be found in the work of Langer (Langer 1988, Langer and Takács 2004). The anatomical structures of taeniae and haustrae, which are a characteristic of gut segments of many larger animals, serve not only as means to retain digesta, but also allow a significant distension of the according gut section (Langer and Takács 2004). The presence of these structures might explain the flexibility that characterises many animal species with respect to their DMI–MRT relationship. Animals with a highly consistent forage resource may not have had to evolve such adaptations.

We consider it a coincidence that the two animal groups used in this contribution represent foregut (hippos) and hindgut fermenters (elephants), respectively. We do not claim that the difference in the DMI–MRT relationship identified between hippos and elephants is by necessity representative of a hypothetical, fundametal difference between foregut and hindgut fermenters in general; differences in this relationship might occur as well within each of these groups. For example, it has been speculated that the foregut-fermenting macropods might be more able to compensate a decline in dietary quality by an increase in DMI than the foregut-fermenting ruminants (Hume 1999). A similar hypothesis lies at the core of the so-called "Bell/Janis/Foose model" for the ecophysiological niche separation between ruminants and equids, which both compete for the same forage resource (Bell 1971, Janis 1976, Foose 1982). This model predicts that ruminants are more efficient in the use of medium-quality forage due to the generally higher digestibility coefficients they achieve, but that equids are at an advantage on lower-quality diets because they can more easily compensate for the decrease in dietary quality by increasing intake and hence absolute digestible nutrient gain. The Bell/Janis/Foose model can be divided into a static and a dynamic argument. The static argument is that on a comparable diet, the ruminant digestive strategy is characterised by a higher digestive efficiency and a lower intake, and the equid strategy by a lower digestive efficiency but a higher intake; this postulated difference has been confirmed experimentally (Duncan et al. 1990, Menard et al. 2002). The dynamic argument is that ruminants cannot compensate a decrease in forage quality by increasing food intake as well as equids; this argument silently assumes that in ruminants, a "spare capacity limit" is reached sooner, and that the increased intake in equids does not disproportionately reduce digestive efficiency in itself. Our approach of treating the DMI–MRT relationship as a physiological meaningful parameter that describes a species or a group of species complements the Bell/Janis/Foose model; in fact, available DMI–MRT data for cattle, sheep, horses and donkeys seems to reflect the difference between these species implicit in the Bell/Janis/Foose model, with lower DMI–MRT slopes in the equids (Fig. 2).

An important conceptual question, rarely addressed so far, is whether, in situations of forage scarcity, digestive efficiency can be increased by decreasing DMI and thus increasing MRT. In other words, why should e. g. the equids of the Bell/Janis/Foose model choose the high intake-low digestibility solution rather than a low intake-high digestibility solution? After all, the argument of a limited "spare capacity" that would

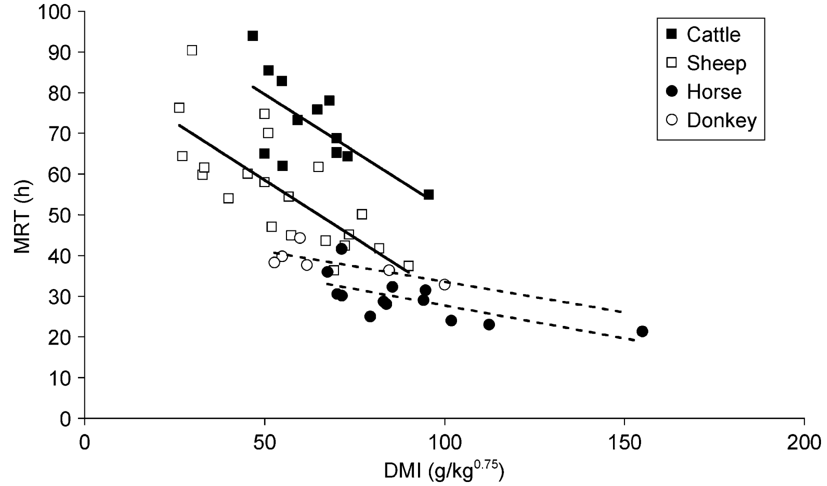

Fig. 2. Relationship between daily dry matter intake (DMI, g kg$^{-0.75}$) and particle mean retention time (MRT, h) in cattle (Schaefer et al. 1978, Udén et al. 1982, Udén and Van Soest 1982, McCollum and Galyean 1985, Ramanzin et al. 1991, Bartocci et al. 1997, Burns et al. 1997), sheep (Foot and Romberg 1965, Forbes and Tribe 1970, Udén et al. 1982, Udén and Van Soest 1982, Cherney et al. 1990, Cherney et al. 1991, Kennedy et al. 1992, Bartocci et al. 1997), horses (Wolter et al. 1976, Orton et al. 1985a, 1985b, Pagan et al. 1998, Pearson et al. 2001), and donkeys (Izraely et al. 1989, Pearson et al. 2001). Note that the difference in slope between the ruminants and the equids is in accord with the implication of the Bell/Janis/Foose model on ruminant-equid competition that ruminants are more intake-limited, whereas horses will not incur as significant losses in digestive efficiency with increased intake.

explain the absence of a high intake-strategy in ruminants does not apply to a low intake-situation in equids. In the absence of empirical data, the answer might be in postulated higher metabolic losses of the equid digestive system, that render a low intake-strategy unfeasible. Even in domestic ruminants, it has been demonstrated that a food intake at sub-maintenance level, although coupled with the expected additional increase in MRT, led to lower, not higher apparent digestive efficiency (Atti et al. 2002, Doreau et al. 2004) – an observation that is in accord with the assumption that at the lower end of intake, metabolic losses outweigh nutritive gains and hence lead to a depression of apparent digestibility coefficients. Determining metabolic losses in a comparative approach remains one of the important challenges in herbivore ecophysiology.

We suggest that further studies on the correlation of DMI and MRT, analysis of potential uncoupling mechanisms, and the determinants of metabolic losses, will allow a more precise understanding of physiology, resource use and activity patterns in many herbivorous and omnivorous species.

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