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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*)

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ABSTRACT

The digestion of plant material in mammalian herbivores basically depends on the chemical and structural composition of the diet, the mean particle size to which the forage is processed, and the ingesta retention time. These different factors can be influenced by the animal, and they can presumably compensate for each other. The pygmy hippopotamus, a non-ruminating foregut fermenter, has longer mean retention times than ruminants; however hippos do not achieve higher (fibre) digestibilities on comparable diets, which could be due to ineffective mastication. We performed feeding trials with six pygmy hippos (*Hexaprotodon liberiensis*) and six banteng cattle (*Bos javanicus*) on a grass diet. As predicted, both species achieved similar dry matter, organic matter, crude protein and gross energy digestibilities. However, neutral and acid detergent fibre digestibility was lower in pygmy hippos. Apparently, in these species, fibre digestibility was more influenced by particle size, which was larger in pygmy hippos compared to banteng, than by retention time. In spite of their higher relative food intake, the banteng in this study did not have greater relative gut fills than the hippos. Ruminants traditionally appear intake-limited when compared to equids, because feed particles above a certain size cannot leave the rumen. But when compared to nonruminating foregut fermenters, rumination seems to free foregut fermenters from an intrinsic food intake limitation. The higher energy intakes and metabolic rates in wild cattle compared to hippos could have life-history consequences, such as a higher relative reproductive rate.

1. Introduction

Herbivores rely on symbiotic microorganisms for the digestion of plant material. These microorganisms are located in voluminous anatomical structures where the fermentative digestion takes place; hence, these structures are mostly referred to as fermentation chambers (Stevens and Hume, 1998). Gut bacteria are considered to be very old organisms in an evolutionary sense, and they do not differ fundamentally in their biology and ecology between host species and thus in the ability to digest similar plant material (Van Soest, 1994). Therefore, the extent and rate of the fermentation process for a given forage type will basically depend on three factors: the chemical composition of the diet, the ingesta particle size, and the ingesta retention time.

Forage digestibility is considered to be inversely related to the amount of cell wall and lignification (Karasov and Martínez del Rio, 2007; in vitro e.g. Hummel et al., 2006; in vivo e.g. Barboza, 1993), because lignin is indigestible, and because the digestible portions of cell wall are fermented at a slower rate than other nutrients. The advantage of small over large ingesta particles is the larger relative surface area exposed to microbial attack resulting in higher (fibre) digestion rates for small particles (Bjorndal et al., 1990, cf. Clauss and Hummel, 2005; in vitro e.g. Gerson et al., 1988, in vivo e.g. Bowman and Firkins, 1993). Furthermore, if ingesta retention time, and thus the time for microbial fermentation, is short, digestive efficiency decreases (Clauss et al., 2007b; in vitro e.g. Hummel et al., 2006, in vivo e.g. Udén et al., 1982).

Animals have evolved different adaptations to optimize digestive efficiency, i.e. altering diet composition, particle size and retention time. The chemical composition of the ingested diet can be influenced by diet selection, i.e. selecting food items with a lower fibre and lignin content (Illius and Gordon, 1993; Sprent and McArthur, 2002). Food particle size is primarily reduced by mastication — during ingestion and, in ruminants, during rumination (Wilson et al., 1989). The degree of comminution, and thus chewing efficiency, is a multifactorial function of tooth morphology, efficiency of masticatory movement,

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diet properties, the time spent chewing and the number of chews per quantity of food (Pérez-Barbería and Gordon, 1998a). In this regard, ruminants are particularly interesting: they possess molars with enamel ridges that form a complex tridimensial structure of characteristic crescent-shaped cusps (Pérez-Barbería and Gordon, 1998b), and they submit the ingesta to repeated mastication, achieving equal or finer ingesta particles than other "similar-sized" herbivores (Van Soest, 1994). The period of ingesta retention finally is a physiological characteristic of a species and will vary, both within and between species, with food intake level (Clauss et al., 2007a; Clauss et al., 2008) and with the volume of the gastrointestinal tract (Langer and Snipes, 1991; Karasov and McWilliams, 2005).

It is reasonable to assume that these different factors (diet composition, particle size and retention time) can compensate for each other. For example, Karasov et al. (1986) explained that herbivorous reptiles (lizards) achieve almost the same digestibilities on the same diet as nonruminant mammals (woodrat, mouse). The lack of a masticatory apparatus was presumably outbalanced by lower food intakes and longer ingesta retention times in reptiles. Among mammals, Clauss et al. (2005) outlined that, compared to horses, Indian rhinoceros (*Rhinoceros unicornis*) have longer, and elephants have similar ingesta retention times; yet, this does not result in higher digestibility coefficients in the rhino, and elephants nevertheless achieve even lower digestibilities. The authors speculated that this was due to a reduced ingesta particle size reduction in these two herbivore groups as compared to horses. However, studies in which all the relevant variables were measured simultaneously are rare.

We investigated the digestive efficiency in two different foregut fermenters, the non-ruminating pygmy hippopotamus (*Hexaprotodon liberiensis*) and the ruminating banteng cattle (*Bos javanicus*). Hippos have longer mean retention times than ruminants (common and pygmy hippo: Foose, 1982; Clauss et al., 2004; pygmy hippo: Schwarm et al., 2008); however they do not achieve higher (fibre) digestibilities on comparable diets (common hippo: Arman and Field 1973; Abaturov et al., 1995; common and pygmy hippo: Foose, 1982; Schwarm et al., 2006), which could be due to ineffective mastication (Arman and Field 1973; Clauss et al., 2004). So far, the knowledge on digestion coefficients in hippos is based on low sample sizes, without direct comparisons to ruminants. Thus, to facilitate an interspecific comparison we investigated six pygmy hippo and six banteng on a constant diet by measuring intake, nutrient composition of the offered and ingested food, particle size, nutrient digestibility and retention time.

We predicted that pygmy hippos would display similar nutrient digestibilities as banteng on the same diet. Longer ingesta retention times in hippos would outbalance their less effective ingesta mastication. These longer ingesta retention times could be a consequence of instrinsic characteristics as a lower food intake, or a greater gut volume, or both. Based on previous reports on hippo food ingestion (reviewed in Clauss et al., 2007b) and gut fill (reviewed in Clauss et al., 2003), we predicted that pygmy hippos would display both, a lower food intake and a greater gut fill than the ruminant.

2. Material and methods

The trials were performed with six pygmy hippos and six banteng at the Zoological Gardens of Berlin (ZGB) and Halle (ZGH) in summer 2005 and 2006. Body mass (BM) of the pygmy hippos was measured at the beginning and the end of each trial period, whereas BM of the banteng were estimated by the keepers by visual judgement (height and width) and age and sex as reference. Details of the animals are summarized in Table 1.

Table 1
Details of the pygmy hippos (*Hexaprotodon liberiensis*) and banteng (*Bos javanicus*) studied at the Zoological Gardens of Berlin (ZGB) and Halle (ZGH).

Species	Animal	Born	Sex	BM (kg)	Facility	Year of trial
Pygmy hippo	1	1985	Male	248±4	ZGB	2005
	2	1983	Female	225±3	ZGB	2005
	3	1997	Female	238±2	ZGB	2006
	4	1998	Female	203±3	ZGH	2006
	5	1976	Female	202±4	ZGH	2006
	6	2000	Male	196	ZGH	2006
Banteng	7	2002	Male	550 [a]	ZGB	2005
	8	2004	Female	220 [a]	ZGB	2005
	9	2004	Male	200 [a]	ZGB	2005
	10	1996	Female	700 [a]	ZGB	2006
	11	2001	Female	600 [a]	ZGB	2006
	12	1997	Female	650 [a]	ZGB	2006

In pygmy hippos body mass was measured four times (before and after each trial) and given values are means (±SD).
BM = body mass.
[a] Estimated.

The animals were fed fresh grass only, the staple diet at both zoos during summer. Grass (C3-species) was harvested from mixed swards of the surrounding countryside. Since the grass diet was usually supplemented with fruits and vegetables in hippos and with sugar beet pulp in banteng, an adaptation period of 14 days was allowed to pass before the trial started. It was planned to study each animal in two trials on different intake levels (with a second adaptation period of 5 days in between) — *ad libitum* (high intake, HI), and, subsequently, at approximately 75% of the individual *ad libitum* intake (low intake, LI). Each trial lasted 7 days. Due to a shortage of grass (the weather being too hot for sufficient regrowth or too wet for the mechanical harvest, respectively), one pygmy hippo (animal 6) and three banteng (animals 10–12) could only be assessed at one intake level (HI). For the same reason, some animals had to be fed grass hay (soaked in water) at one day during one trial (animal 2, HI: at day one after marker feeding; animal 4, LI: day six; animal 7, LI: day one; animal 8, LI: day two; animal 9, HI: day two).

All animals were fed separately. Due to the husbandry techniques at the respective zoos, not all animals could be kept separately at all times, and feeding regimens differed. Three pygmy hippos (animals 1–3) received food once daily, approximately at 17:00 h and had access to the food until the next morning. The other pygmy hippos (animals 4–6) as well as three banteng (animals 7–9) received food twice daily, at approximately 08:30 h and 17:00 h. These animals had access to the food until the next meal was offered. Three banteng (animals 10–12) were kept together between the feeding times; in these animals, the individual access to food was limited from 08:30 h to 11:00 h and from 15:30 h to 18:00 h. Food items offered and leftovers were quantified on a daily basis by weighing, and representative samples (for each individual) of food offered and leftovers were stored frozen (−20 °C). During the day (approximately 08:00 h–18:00 h), the pygmy hippos were kept on land with no access to a water pool. During the night (approximately 18:00 h–08:00 h), the pygmy hippos had free access to a water pool, with the exception of animal 1 on the high intake level. Drinking water was always accessible for ad libitum consumption by all animals.

Two of three banteng that were kept together received a coloring agent in their ration (animal 10: titanium dioxide 40 g/d; animal 11: brilliant blue food colour, Sensient Food Colors, Geesthacht, Germany, 2 g/d; both fed twice daily; the blue color was mixed in approx. 200 g sugar beet pulp for better acceptance), so that faeces could be ascribed to the individual animals. Defaecations were collected completely in regular intervals, cleaned from sand (when contaminated), weighed, thoroughly mixed, and an aliquot (200–400 g) was taken and stored frozen. Faeces voided by hippos into the water pool at night were not sampled.

For nutrient analyses food and faecal samples were dried at 40 °C and 60 °C, respectively. Dry matter (DM) content of food and faecal subsamples was determined by drying at 103 °C to constant weight. Samples were ground with a 'Nossener mill' (Gebrüder Jehmlich,