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Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate

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Summary

We performed intake and digestibility studies in four common (*Hippopotamus amphibius*) and four pygmy (*Hexaprotodon liberiensis*) hippos from two zoological institutions, using acid detergent lignin as an internal marker for the quantification of faecal output. In the case of one pygmy hippo, where total faecal collection was also possible, there was no distinct difference between the two methods of faecal output quantification. Two animals from each species were tested on a conventional zoo diet of hay and concentrates (diet HC) and on hay only (diet H). The other two animals received fresh grass at two different levels of intake (diets G1 and G2). Dry matter (DM) intake was higher on HC than on H or G diets, and averaged 37 ± 11 for common and 35 ± 14 g/kg$^{0.75}$ for pygmy hippos. There were no species differences in the average digestibility (aD) coefficients. Non-dietary faecal nitrogen averaged $65 \pm 4\%$ of total faecal nitrogen, aD of crude protein (CP) averaged $67 \pm 9\%$ and true protein digestibility $89 \pm 3\%$. Average digestibility of DM and crude fibre averaged $54 \pm 11\%$ and $45 \pm 17\%$, respectively. In comparison with ruminants, hippos generally achieve lower aD for DM, organic matter and fibre parameters, but equal or higher aD CP coefficients. This is most likely due to the absence of significant fermentative activity in the hindgut and the corresponding low metabolic faecal nitrogen losses. Digestible energy intake was higher on HC than on H or G diets and averaged 0.30 ± 0.11 MJ/kg$^{0.75}$ metabolic body mass. This value is extremely low for ungulates, supporting earlier suspicions that hippos have particularly low metabolic rates, and explains the proneness of this species to obesity in captivity when fed energy-dense pelleted feeds.

Introduction

Hippopotamidae (the common hippo *Hippopotamus amphibius* and the pygmy hippo *Hexaprotodon liberiensis*) are ungulates that are easy to keep and feed in captivity and pose few veterinary problems. Whereas the design of appropriate and attractive housing can be challenging, reproduction and health maintenance in these species generally require little effort (Eulenberger, 1995). The placement of surplus offspring is considered to be the most difficult issue in captive hippo management, and hormonal birth

control is a matter of routine and used in many institutions (Michele, 2003). Known digestive disorders mainly concern the ingestion of foreign bodies that obstruct the small intestine (Eulenberger, 1995).

Hippos are strict herbivores, with an elaborate, extremely capacious foregut fermentation system (Langer, 1988). Numerous studies have shown the common hippo to be an exclusive grazer (e.g. Field, 1970; Mackie, 1976; Scotcher et al., 1978). In contrast, there is only one study on the ecology of the pygmy hippo that suggested that pygmy hippos ingest mainly ferns, herbs and wild fruits, with grasses playing no role in its natural diet (Hentschel, 1990). Feeding recommendations for hippos in captivity include the use of grass hay for common hippos and lucerne hay for pygmy hippos, supplemented with a pelleted compound, at a roughage:pellets ratio of 2.3:1 for pygmy hippos and up to 3:1 for common hippos (Lintzenich and Ward, 1997). Both natural and recommended captive herbivorous diets differ from the diets these species actually receive in captivity, as e.g. recorded for Great Britain by Frost (1996): sources of easily fermentable carbohydrates such as commercial fruits, vegetables, cereals, bread and pelleted feeds are offered in addition to hay or fresh roughage. While there are no reports of negative effects of these easily fermentable carbohydrates on the digestive physiology of hippos – such as rumen acidosis in ruminants – the appropriateness of such diets is unclear and they may possibly contribute to obesity, a known nutritional problem in other large zoo animals such as elephants (Ange et al., 2001) and rhinoceroses (Atkinson et al., 2004). No comparative data exist on the body weights of free-ranging and captive hippos, and a body condition scoring system remains to be developed for these species. However, without giving data, Puschmann (1989) and Michele (2003) explicitly state that hippos are particularly prone to obesity.

Should the avoidance of obesity be an objective in captive hippo management, then guidelines for the appropriate level of energy supply and the kinds of possible supplementation of roughage-dominated diets are warranted. During a feeding experiment where we looked at base parameters of digestion (Clauss et al., 2004), we also assessed diets of captive hippos in these respects.

Materials and methods

The trials were performed with four common hippos and four pygmy hippos at Whipsnade Wild Animal Park (WWAP), Bedfordshire, UK, and the Zoological Garden of Berlin (ZGB), Germany, between October 2002 and October 2003. Body mass (BM) of pygmy hippos was measured during the trial period, but BM of the common hippos could only be estimated. Details of the animals are listed in Table 1.

Each individual trial lasted 7 days. During this time, the animals were kept individually. Food items offered, consumed and left behind were weighed. During the day (approximately 08:00–17:00 hours), the animals were kept on land with no access to a water pool. They were either given the opportunity to drink during these periods when they were doused, or had small drinking troughs available. During the night (approximately 17:00–08:00 hours), all animals had free access to a water pool.

Each animal was tested on two different food rations. The animals at WWAP were first supplied with their regular diet (diet HC) which consisted of grass hay (common hippos) or lucerne hay (pygmy hippos) and a mixture of fruits, vegetables and concentrates (Rhino Supplement, Special Diets Services, Essex, UK and Whipsnade Grazer Ration, Clark & Butcher, Cambs, UK). During the second trial, they were limited to the respective roughage-only diets (diet H). The animals at ZGB received only rations of fresh grass at two different levels of intake (diets G1 and G2). For each new ration, an adaptation period of at least 8 days was allowed to pass before a trial started. Animals 1, 5 and 6 were tested on diet HC in a pilot study (Schwarm et al., 2003); these results are included here. Animal 6 was tested a second time on diet HC in parallel to animal 2.

Each individual defecation was collected during the day, thoroughly mixed, and a representative subsample taken and frozen at −17 °C. Subsamples

Table 1. Details of the animals and diets used in this study

Species	Animal no.	Sex	Age (years)	Body mass (kg)	Diet used	Zoo
H. amph.	1	m	38	2300*	HC, H	WWAP
H. amph.	2	f	25	1900*	HC, H	WWAP
H. amph.	3	f	28	2500*	G1, G2	ZGB
H. amph.	4	m	8	2000*	G1, G2	ZGB
H. liber.	5	f	27	254	HC, H	WWAP
H. liber.	6	f	5	243	2 × HC, H	WWAP
H. liber.	7	f	20	235	G1, G2	ZGB
H. liber.	8	m	18	220	G1, G2	ZGB

H. amph., common hippo; *H. liber.*, Pygmy hippo; HC, hay and concentrates; H, hay only diet; G1, fresh grass, level 1; G2, fresh grass, level 2
*Estimated

were later pooled per animal and experimental period. We did not attempt to sample faeces voided into the water pool at night; however, faeces voided at night on land were collected on the following morning and added to the faeces of that day. Representative samples of all food items offered and left over were taken and stored frozen as well; in the case of fresh grass, a representative subsample was taken from each daily batch of grass, and these subsamples were later pooled across a trial period for analysis.

The laboratory analyses and calculations followed the same protocol as outlined for Indian rhinoceroses in Clauss et al. (2005). Analyses included dry matter (DM), crude protein (CP), crude ash (CA), crude fibre (CF) and ether extract (EE), neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL), gross energy (GE), and non-dietary faecal nitrogen (NDFN) determined according to Mason and Fredericksen (1979). Note NDFN is determined by analysing the N content of the NDF residue in faecal samples; this measure, and the assumed true protein digestibility calculated with it, are therefore, by definition, different from measurements of true dietary protein absorption in livestock which is quantified using ileally fistulated animals. Faecal output was calculated using ADL as an internal marker. During trial G1, animal 8 never defecated in its water pool but always on land, thus enabling us to collect a complete batch of faeces and compare digestion coefficients calculated from the complete defecation material and from the internal marker.

Hypothetical endogenous faecal losses (EFL) of CP and EE were calculated using two approaches: (1) plotting data on intake vs. excretion of the nutrient per kg BM or kg metabolic body mass (MBM) and (2) by plotting nutrient content of the diet against its digestible nutrient content. In the latter case, the slope of the regression line corresponds to the 'true' digestibility of the nutrient, and the intercept represents the endogenous losses per 100 g DM intake (DMI) (Robbins, 1993).

Pearson's correlation coefficient and linear regression analysis were used to evaluate potential associations. The statistical tests were performed using SPSS 9.0 (SPSS, Chicago, IL, USA). The significance level was set to $\alpha = 0.05$.

Results

The animals appeared to be healthy throughout the study. Judged by external appearance, no animal lost weight during the study period.

Dry matter intake and composition of the diets offered are listed in Table 2. Dry matter intake averaged 37 ± 11 g/kg$^{0.75}$ MBM for common and 35 ± 14 g/kg$^{0.75}$ MBM for pygmy hippos and was higher on HC than on H or G diets. Fibre levels were generally lower in the HC compared with H and G diets.

Table 2. Dry matter intake (DMI) and nutrient composition of hippo diets used in this study

| Animal No. | Species | Diet | DMI | | | % DM | | | | | | | GE (MJ/kg DM) |
			kg	% BM	g/kg$^{0.75}$MBM	CA	CP	EE	CF	NDF	ADF	ADL	
1	*H. amph.*	HC	13.8	0.6	41	6.9	10.8	2.9	24.3	46.1	23.2	2.0	17.3
1	*H. amph.*	H	12.7	0.6	38	4.9	6.0	0.6	29.9	59.0	32.4	2.9	16.7
2	*H. amph.*	HC	16.8	0.9	58	6.7	8.3	1.3	25.2	54.5	29.6	3.0	17.0
2	*H. amph.*	H	13.0	0.7	45	4.5	6.2	0.6	30.3	63.4	35.7	3.3	16.7
3	*H. amph.*	G1	9.8	0.4	28	7.9	10.4	2.2	30.5	59.6	33.0	2.9	16.6
3	*H. amph.*	G2	10.9	0.4	31	6.8	8.8	2.2	29.9	60.3	32.5	3.3	16.6
4	*H. amph.*	G1	9.2	0.5	31	5.8	8.3	2.2	30.7	66.7	38.1	4.4	16.6
4	*H. amph.*	G2	6.6	0.3	22	7.2	12.4	2.2	30.7	61.5	32.1	3.6	16.6
5	*H. liber.*	HC	3.0	1.2	47	8.3	12.3	2.7	29.4	45.4	28.9	5.1	17.3
5	*H. liber.*	H	2.4	1.0	38	5.8	16.1	0.7	34.8	47.5	37.3	8.5	16.4
6	*H. liber.*	HC a	2.7	1.1	43	8.5	12.6	2.9	27.9	44.4	27.5	4.8	17.3
6	*H. liber.*	HC b	3.4	1.4	55	6.6	11.4	1.4	33.6	50.7	35.4	7.3	17.1
6	*H. liber.*	H	2.8	1.2	46	5.9	12.3	0.7	42.2	61.3	47.2	8.9	16.5
7	*H. liber.*	G1	1.3	0.6	21	9.1	11.0	2.2	30.0	58.4	31.1	2.9	16.6
7	*H. liber.*	G2	1.1	0.5	18	6.8	8.8	2.2	29.9	60.3	32.5	3.3	16.6
8	*H. liber.*	G1	1.4	0.7	25	5.8	8.3	2.2	30.7	66.7	38.1	4.0	16.6
8	*H. liber.*	G2	1.3	0.6	22	6.6	15.5	2.2	30.9	58.4	30.3	4.3	16.6

H. amph., common hippo; *H. liber.*, Pygmy hippo; BM, body mass; MBM, metabolic BM; CA, crude ash; CP, crude protein; EE, crude fat; CF, crude fibre; NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; GE, gross energy

The excreted total daily amount of faecal DM, as measured by total faecal collection (TFC) in animal 8 on diet G1, was 0.68 kg compared with 0.61 kg as calculated using ADL as an internal marker. The digestibility coefficients using TFC and ADL, respectively, were 51% and 56% for DM, 57% and 61% for OM, 53% and 57% for CP, and 57% and 62% for CF.

The calculated apparent digestibility coefficients are listed in Table 3. In general, there were no species differences in the mean values. Non-dietary faecal nitrogen averaged $65 \pm 4\%$ of total faecal nitrogen when both species are considered together. Apparent digestibility of CP averaged $67 \pm 9\%$ and true protein digestibility averaged $89 \pm 3\%$; both parameters showed a significant positive association (common hippo: $r = 0.97$, $p < 0.001$; pygmy hippo: $r = 0.93$, $p < 0.001$; both species: $r = 0.95$, $p < 0.001$). Apparent digestibility of DM, CF and NDF averaged $54 \pm 11\%$, $45 \pm 17\%$ and $45 \pm 19\%$, respectively; pygmy hippos achieved high NDF digestibilities on diets G (68%). There was no significant correlation between dietary CF content and DM, OM or GE digestibility in either species.

The linear relationships between (1) intake and excretion of a nutrient ($g/kg^{0.75}$ MBM for CP; g/kg BM for EE) and (2) nutrient and digestible nutrient content ($g/100$ g DM) for CP and EE are described in Table 4. Using relationship (1), there was a significant linear relationship only for CP in pygmy hippos. In contrast, there was a significant linear relationship for CP and EE in relationship (2) in both species.

Digestible energy intake (DEI) was higher in HC than H or G diets (Table 3), and averaged 0.30 ± 0.11 $MJ/kg^{0.75}$ MBM.

Discussion

Digestion trials with hippos are challenging because of their semi-aquatic lifestyle, and one has to decide whether the animals should be allowed access to a water pool. Arman and Field (1973) observed that digestion was problematic for a hippo in Africa without access to a water pool. Foose (1982) also housed hippos on 'dry dockage' during his digestion trials and obtained rather long retention times, and we therefore decided to perform trials with overnight access to a water pool (Schwarm et al., 2003). Yet, the results suggest that in temperate zone zoos where hippos might experience less heat stress than under the conditions of the study of Arman and Field (1973), access to a water pool did not significantly influence digestion (cf. Table 5). Based on the results of animal 8 where digestibilities were calculated from both total faecal weights and lignin as an internal marker, it appears that the results gained in this study using lignin are representative.

Compared with results from other studies, the hippos in this study showed slightly lower digestion coefficients (Table 5). In general, hippos show DM and fibre digestibilities that are lower than those reported

Table 3. Apparent digestibility coefficients (in %) of hippos measured in this study; for abbreviations of nutrients see Table 2

No.	Species	Diet	DM	OM	CP	EE	CF	NDF	ADF	GE	TPD	NDFN	DEI
1	*H. amph.*	HC	64	64	80	89	38	44	38	65	94	69	0.47
1	*H. amph.*	H	44	44	52	30	31	32	28	45	83	64	0.28
2	*H. amph.*	HC	54	53	62	65	40	42	37	55	88	69	0.54
2	*H. amph.*	H	50	50	53	35	37	44	40	49	85	68	0.37
3	*H. amph.*	G1	63	64	75	65	58	60	55	64	92	70	0.14
3	*H. amph.*	G2	61	63	71	79	58	58	52	62	89	64	0.32
4	*H. amph.*	G1	43	45	65	71	35	41	36	41	87	62	0.21
4	*H. amph.*	G2	61	61	81	79	52	54	44	59	93	65	0.22
5	*H. liber.*	HC	53	54	66	81	34	33	32	55	87	62	0.44
5	*H. liber.*	H	45	47	73	−18	31	25	28	44	90	63	0.25
6	*H. liber.*	HC a	48	49	65	84	25	25	24	n.a.	87	63	n.a.
6	*H. liber.*	HC b	35	35	62	64	17	10	11	35	87	66	0.33
6	*H. liber.*	H	44	46	64	−19	38	36	38	42	87	63	0.23
7	*H. liber.*	G1	77	80	79	77	80	78	75	78	94	73	0.28
7	*H. liber.*	G2	65	68	61	74	69	67	61	75	88	69	0.31
8	*H. liber.*	G1	56	61	57	74	62	63	61	55	84	61	0.13
8	*H. liber.*	G2	59	64	74	71	66	63	57	62	90	62	0.26

H. amph., common hippo; *H. liber.*, Pygmy hippo; TPD, true protein digestibility (%); NDFN, non-dietary faecal nitrogen (in % of total faecal nitrogen); DEI, digestible energy intake (in $MJ/kg^{0.75}$ metabolic body mass)

Table 4. Linear regression of (1) nutrient intake vs. nutrient excretion and (2) nutrient vs. digestible nutrient content, for each hippo species and data from both species combined. Regression equation was $y = a \times x + b$. For nutrient abbreviations, see Table 2

	H. amph			H. liber.			Both species		
	a	b	R^2	a	b	R^2	a	b	R^2
(1)									
g/kg^0.75 MBM									
CP	0.25	0.23	0.32	0.34***	−0.06	0.85***	0.33***	−0.01	0.75***
g/kg BM									
EE	0	0.03*	0	−0.02	0.06*	0.06	0.07	0.03**	0.06
(2)									
g/100 g DM									
CP	1.11***	−3.64***	0.99***	0.87***	−2.38	0.93***	0.86***	−1.81*	0.93***
EE	0.97***	−0.43*	0.97***	1.15***	−0.88***	0.99***	1.05***	−0.64***	0.97***

H. amph., common hippo; H. liber., Pygmy hippo.
*p < 0.05, **p < 0.01, ***p < 0.001.

Table 5. Digestion studies in hippopotamidae

Species	n	BM kg	Experimental conditions	DMI g/kg^0.75 MBM	CP	CF	NDF	ADF	DM	OM	CP	CF	NDF	ADF	TPD* (%)	Source
					Dietary nutrient content (% DM)				Apparent digestibility (%)							
H. amph.	1	225	No pool, TFC, grass	134	10.5	26.8	–	–	35	–	58	35	–	–	–	Arman and Field (1973)
H. amph.	1	1200	With pool, Cr, grass	39	10.2	–	–	42.4	68	–	88	–	–	62	–	Arman and Field (1973)
H. amph.	3	2268	No pool, TFC, grass hay	47	5.2	–	72.9	–	–	55	–	–	52	49	89	Foose (1982)
H. amph.	4	2211	No pool, TFC, lucerne hay	69	19.4	–	41.5	–	–	74	–	–	60	59	98	Foose (1982)
H. amph.	1	n.n.	ADL, natural forage	–	9.6	30.2	–	–	45	–	67	57	–	–	–	Abaturov et al. (1995)
H. amph.	2	2100	With pool, ADL, grass hay/conc.	50	9.6	24.8	50.3	26.4	59	59	71	39	43	38	91	This study
H. amph.	2	2100	With pool, ADL, grass hay	42	6.1	30.1	61.2	34.1	47	47	53	34	38	34	84	This study
H. amph.	2 × 2	2250	With pool, ADL, grass	28	10.0	30.5	62.0	33.9	57	58	73	51	53	47	90	This study
H. liber.	2	181	No pool, TFC, grass hay	21	6.8	–	59.5	–	–	39	–	–	32	23	86	Foose (1982)
H. liber	3	219	No pool, TFC, lucerne hay	49	19.0	–	37.0	–	–	69	–	–	54	54	97	Foose (1982)
H. liber	2 + 1	249	With pool, ADL, lucerne hay/conc.	48	12.1	30.3	46.8	30.6	45	35	64	25	23	22	87	This study
H. liber	2	249	With pool, ADL, lucerne hay	42	14.2	38.5	54.4	42.3	45	47	69	35	24	26	89	This study
H. liber	2 × 2	228	With pool, ADL, grass	22	10.9	30.4	61.0	33.0	64	68	68	69	68	64	89	This study

H. amph., common hippo; H. liber., Pygmy hippo; BM, body mass; TFC, total faecal collection; ADL, lignin used as internal marker; Cr, chromium oxide used as external marker; DMI, dry matter intake; MBM, metabolic body mass; DM, dry matter; CP, crude protein; CF, crude fibre; NDF, neutral detergent fibre; ADF, acid detergent fibre; OM, organic matter.
*True protein digestibility (TPD) calculated according to Mason and Frederiksen (1979) in this study using the protein content of the faecal NDF residue; in Foose (1982), the faecal ADF residue was used for the calculation.

in ruminants, with the exception of pygmy hippos on grass diets (Arman and Field, 1973; Foose, 1982; Abaturov et al., 1995, cf. Table 6). These low digestibilities are unexpected in view of the comparatively long ingesta retention times measured in hippos and might be due to the large average ingesta particle size observed in these species (Clauss et al., 2004). It is also remarkable that DM digestibility was not clearly affected by dietary fibre content in either hippo species. Additionally, fibre digestibilities depended on

diet and were drastically higher in common hippos feeding on grass (G) than grass hay (H), although the fibre of fresh grass was more lignified. However, this is most likely due to an increase in retention times caused by a lower DMI on the grass diet. Hippos seem to belong to a set of species where the effect of DMI on digestibility is directly transmitted via the variation in retention time (Clauss et al., 2004) and this can easily overrule effects of nutrient composition. Thus, the addition of concentrates (diet HC) did not

Table 6. Comparison of apparent digestibility coefficients achieved by hippopotamidae in this study and domestic ruminants on comparable diets (DLG, 1997)

		CP % DM	CF	Apparent digestibility (%)		
				OM	CP	CF
Ruminants	Grass hay	8	32	59	49	59
Hippos (*H. amph.*)	Grass hay	6	30	47	53	34
Ruminants	Lucerne hay	15	41	50	60	38
Hippos (*H. liber.*)	Lucerne hay	14	39	47	69	35
Ruminants	Grass	11–12	29–31	63–67	60–61	65–69
H. amph.	Grass	10	30	58 (45–64)	73 (65–81)	51 (35–58)
H. liber.	Grass	11	30	68 (61–80)	68 (57–79)	69 (62–80)

Dietary content of crude protein (CP) and crude fibre (CF) in % dry matter; apparent digestibilities of organic matter (OM), CP and CF in %

H. amph., common hippo, *H. liber.*, pygmy hippo

markedly increase fibre digestibility, although such an effect is regularly observed in ruminants and hind-gut fermenters such as horses (e.g. Van Soest et al., 1983). Any positive effect of readily available energy from concentrates on the forestomach microbes was probably levelled by shorter ingesta retention because of an increase in DMI. In this respect, it would be interesting to investigate the effect of different fractions of concentrates at an otherwise constant level of DMI in hippos.

In contrast to the low overall digestibility, the apparent protein digestibility in hippos is similar or even higher than in ruminants (Arman and Field, 1973, Table 6), which might be attributable to the anatomy of the hippos' digestive tract. Hippos possess no caecum (Stevens and Hume, 1995) and only little microbial activity has been measured in the short colon (Clemens and Maloiy, 1982), thus leading to particularly low losses of bacterial protein via the faeces. Mason and Frederiksen (1979) reported that 80–90% of the faecal protein in sheep was of non-dietary, i.e. mainly bacterial origin, in contrast to hippos (this study) which reached NDFN values of approximately 65%, measured with the same method. Thus, although the true protein digestibility is similar across herbivore species (Foose, 1982), apparent digestibilities for protein in hippos are particularly high. Whether the digestive strategy of hippos provides an ecological advantage in this respect remains to be demonstrated.

Two different approaches were used to calculate EFL (Table 4). From absolute intake/excretion data on a per unit BM or MBM basis we calculated EFLs for CP of 0–230 mg/kg$^{0.75}$ MBM, which appears low compared with 169–625 mg CP/kg$^{0.75}$ MBM in horses, 376 mg CP/kg$^{0.75}$ MBM in Indian rhinoceroses (Clauss et al., 2005) or 578 mg CP/kg$^{0.75}$ MBM in elephants (from Clauss et al., 2003). Calculated EFLs for EE were 30–60 mg/kg BM in hippos compared with 50–100 mg EE/kg BM in horses, 67 mg EE/kg BM in Indian rhinos or 85 mg EE/kg BM in elephants. Although the correlation coefficients in this study were low, this calculation approach supports the concept of low endogenous metabolic losses in hippos. In contrast, using DMI as the base for EFL calculation (approach 2), very high correlations can be observed, and EFL are 2.4–3.6 g CP/100 g DM and 0.4–0.9 g EE/100 g DM; these values are within the range observed in horses, elephants and rhinos (cf. Clauss et al., 2006), which supports a concept of forage digestion being a generally uniform process among different herbivorous species. The slope of the regression line for CP, representing the true protein digestibility, was 0.86 for both species combined and thus closely resembled the true protein digestibility coefficient of 89% calculated with NDFN determined after Mason and Frederiksen (1979). A conclusive comparison of EFL between species remains one of the major challenges in comparative nutrition.

The most impressive result of this study is the low DEI measured in all feeding trials in our hippos, suggesting relatively low energy requirements. This conclusion should be corroborated by respiration chamber, or long-term feeding trials. As no measurements of the basal metabolic rate (BMR) of hippos exist, BMR has to be calculated according to the allometric Kleiber equation with BMR = 0.29 MJ/(kg$^{0.75}$ day). To estimate the maintenance requirement in captivity (average daily metabolic rate), BMR is usually multiplied by a factor of 1.5 or 2 (Robbins, 1993; Kirkwood, 1996), resulting in maintenance requirements of metabolizable energy (ME) of between 0.44 and 0.59 MJ ME/(kg$^{0.75}$ day). To meet these requirements hippos have to consume at least 0.49–0.66 MJ DE/(kg$^{0.75}$ day), assuming ME to be approximately 90% of DE for herbivorous non-ruminants (Robbins, 1993). This range has been shown to adequately describe DEI in elephants

(Roehrs et al., 1989; Clauss et al., 2003) and Indian rhinoceroses (Clauss et al., 2005), and matches the maintenance requirement of domestic horses (Meyer and Coenen, 2002).

Yet, hippos showed drastically lower DEIs even on *ad libitum* forage diets (Table 3). Deviations from the calculated interspecies BMR have been reported frequently (McNab, 2002), but not in such large mammals. Our results support the opinion of Field (1968) and Eltringham (1999) that hippos have particularly low metabolic requirements. These findings are supported by the observation of relatively low core body temperatures in a common hippo of approximately 35–36 °C (Wright, 1987) and in pygmy hippos of 35.8–35.9 °C (immobilized adult specimens, Franz et al., 1978), which is below the temperature commonly found in domestic animals, and the observation of Puschmann (1989) and Michele (2003) that captive hippos are particularly prone to obesity, which in turn will exacerbate joint and foot problems. Michele (2003) cites a personal communication by Valdes that maintenance requirements of hippos should be calculated as 587 kJ/(kg$^{0.75}$ day), approximating two times the Kleiber value of 293 kJ/(kg$^{0.75}$ day). On the basis of our results, it would be difficult to persuade a hippo to ingest so much energy unless it is provided with a high proportion of concentrates in the diet. In contrast, Wright (1987) reports a metabolic heat production of a 860 kg common hippo to be 53.2 MJ/day, which translates into a maintenance requirement of 0.34 MJ ME/(kg$^{0.75}$ day). For comparison, domestic ruminants are reported to have ME maintenance requirements of 0.40–0.53 MJ/(kg$^{0.75}$ day) (GfE – Gesellschaft für Ernährungsphysiologie, 1995, 1996, 2001; Pfeffer, 2001). Assuming a conversion efficiency from DE to ME of 80–90%, the value reported by Wright (1987) would result in a maintenance requirement for hippos of 0.37–0.42 MJ DE/(kg$^{0.75}$ day). As most animals ingested energy below this range in this study (Table 3), even this estimate – obviously derived from a growing subadult – could be too high for adult captive hippos. Given these findings, it would be interesting to perform BMR measurements in a respiration chamber with pygmy hippos.

These observations are particularly interesting from an ecological point of view. Among mammals, gestation period increases with increasing BM and decreasing BMR (McNab, 2002). Given these assumptions, one would expect exceptionally long gestation periods in common hippos, being both very large and having a low metabolic rate. In contrast, gestation periods in common hippos are surprisingly short for an animal of this size, although the birth weight of the young does not deviate from the interspecific regression line with BM (Owen-Smith, 1988; Eltringham, 1999). Assuming a lactation period and inter-birth interval similar to other animals of their size, one would expect higher rates of population growth in hippos than in other very large herbivores (Owen-Smith, 1988). An appealing hypothesis is that their lower metabolic rate could allow hippos to invest more energy into growth or reproduction (cf. Steyermark, 2002), allowing them to rapidly occupy newly available geographical niches (Eltringham, 1999).

On the basis of our results, we hypothesize that the feeding of roughage-only diets to hippos should be sufficient from an energetic point of view, although this should possibly be confirmed in long-term studies with regular weighing. The well-known need for mineral/vitamin supplementation of roughage diets does not justify the use of mineralized *and* energy-dense pelleted feeds. Instead, this form of supplementation would be best provided by pure mineral/vitamin supplements.

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