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Studies on feed digestibilities in captive Asian elephants (*Elephas maximus*)

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Summary

In order to test the suitability of the horse as a nutritional model for elephants, digestibility studies were performed with six captive Asian elephants on six different dietary regimes, using the double marker method with acid detergent lignin as an internal and chromium oxide as an external digestibility marker. Elephants resembled horses in the way dietary supplements and dietary crude fibre content influenced digestibility, in calcium absorption parameters and in faecal volatile fatty acid composition. However, the absolute digestibility coefficients achieved for all nutrients are distinctively lower in elephants. This is because of much faster ingesta passage rates reported for elephants. No answer is given to why elephants do not make use of their high digestive potential theoretically provided by their immense body weight. Differences in volatile fatty acid concentrations between these captive elephants and those reported from elephants from the wild are in accord with a reported high dependence of free-ranging elephants on browse forage.

Zusammenfassung

Untersuchungen zur Verdaulichkeit von Futtermitteln bei Asiatischen Elefanten (Elephas maximus)

Um zu überprüfen, ob das Pferd als ernährungsphysiolgisches Modelltier für Elefanten herangezogen werden kann, wurden Verdaulichkeitsstudien an sechs im Zoo gehaltenen Indischen Elefanten mit sechs verschiedenen Futterrationen durchgeführt. Dabei wurde die Doppelindikatormethode mit Lignin als internem und Chromoxid als externem Marker verwendet. Elefanten ähnelten Pferden hinsichtlich der Art und Weise, wie sich Ergänzungsfuttermittel und der Rohfasergehalt der Ration auf die Verdaulichkeit auswirkten, hinsichtlich der Kalziumabsorption, und hinsichtlich der Zusammensetzung der flüchtigen Fettsäuren im Kot. Die von Elefanten erzielten absoluten Verdaulichkeitswerte sind jedoch für alle Nährstoffe deutlich niedriger als bei Pferden, was auf die schnellere Passage der Ingesta durch den Verdauungstrakt der Elefanten zurückzuführen ist. Die Frage, warum Elefanten ihr großes Potential zu hohen Verdauungleistungen nicht ausnutzen, das ihnen theoretisch aufgrund ihrer immensen Körpermasse gegeben ist, ist noch nicht beantwortet. Unterschiede in den Konzentrationen von flüchtigen Fettsäuren im Kot zwischen diesen Zoo-Elefanten und Elefanten aus freier Wildbahn spiegeln den hohen Laubanteil in der Nahrung freilebender Tiere wieder.

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Introduction

Elephants are the largest mammalian herbivores (OWEN-SMITH, 1988). In mammals, energy requirements scale to metabolic body weight ($BW^{0.75}$), whereas the capacity of the gastrointestinal tract (GIT) of mammalian herbivores tends to scale directly to BW^1 (PARRA, 1978). The larger a herbivore the larger its GIT capacity relative to its energetic requirements. This led PARRA (1978) and DEMMENT and VAN SOEST (1985) to conclude that larger herbivores are able to subsist on a food of poorer quality. In accord with their predictions, VAN HOVEN (1982) found stomach contents in African elephants with a cell wall content of above 70% and a lignin content of above 20% of the dry matter (DM).

Because of a lack of knowledge on the digestive physiology of many wild animals, zoo animal nutrition has to use domestic species as 'model animals' when designing diets for captive specimens. For large hindgut fermenters like elephants and rhinoceroses, the horse has been propagated as the appropriate model (OFTEDAL et al., 1996). However, reports on comparatively fast passage rates (LOEHLEIN et al., 2003) and low digestion coefficients (c.f. Table 7) raised doubts about the validity of the equine model for elephants. We therefore intended to generate more data that allowed a more direct comparison between elephant and horse digestive processes.

Animals, materials and methods

Six Asian elephants at the Zoological Garden of Munich were used for this study (see Table 1). Their body weights were estimated according to HILE et al. (1997) and ranged from 888 to 4013 kg (Table 1). The animals were kept in a large indoor/outdoor enclosure and were not chained overnight. Six different rations were fed to these animals; two meadow hays and combinations with either of four additional feedstuffs (see Table 2). For each ration, a 5-day adaptation period was followed by a 10-day collection period. Acid detergent lignin (ADL) was used as an internal, and chromium oxide as an external marker. Acid detergent lignin has repeatedly been used as a digestibility marker in elephants (ULLREY et al., 1979; REICHARD et al., 1982; FUJIKARA et al., 1989). Chromium oxide had been validated as a marker in a preceding study (LOEHLEIN et al., 2003) that yielded excellent marker recoveries (97.1 ± 3.7%) and mean retention time data (see Table 1). Chromium oxide was applied individually in two daily doses of 250 mg per animal, in emptied loaves of bread that were swallowed whole on command by the elephants. Hay was always fed to the whole group; therefore, individual intake could not be measured and the double marker method had to be applied. The additional feedstuffs were fed individually, and were always consumed completely. The elephants were observed during the day to allocate dung piles to individuals. Dung piles were collected *in toto*. The outer layer of dung balls was removed to avoid contamination of the sample. The rest of the material was thoroughly mixed, and a subsample representing 10% of the whole sample was taken and frozen at −20 °C. In fresh faeces, the pH was measured (two to three times

Table 1. **Animals used in this study, estimated body weights according to HILE et al. (1997) and mean retention times of chromium oxide determined in LOEHLEIN et al. (2003)**

Animal no.	Age (years)	Sex	BW (kg)	MBW ($kg^{0.75}$)	MRT (h)
1	4	M	888	163	21.8
2	4	F	1067	187	21.4
3	8	F	2200	321	32.0
4	31	F	3217	427	–
5	27	F	3177	423	28.1
6	38	F	4013	504	32.1

Table 2. **Nutrient composition of feedstuffs used for feeding trials**

Food	DM (%)	GE (MJ/kg DM)	CA (% DM)	CP (% DM)	EE (% DM)	CF (% DM)	NFE (% DM)	NDF (% DM)	ADF (% DM)	ADL (% DM)	HC (% DM)	C (% DM)	Ca (g/kg DM)	P (g/kg DM)
Hay 1	86.3	18.1	5.4	8.4	1.4	36.0	49.0	73.7	43.6	6.8	30.1	36.8	5.3	0.9
Hay 2	86.1	17.6	9.8	6.3	0.8	35.0	51.8	69.4	42.7	7.3	26.7	35.4	3.5	1.1
Pelleted feed	87.5	17.0	10.7	17.5	1.4	8.5	61.9	43.6	21.7	2.8	22.0	18.9	14.4	7.0
Oats	86.4	18.6	2.7	10.2	2.5	9.6	75.0	38.1	12.9	2.7	25.2	10.2	1.2	2.3
Red clover	21.1	17.3	14.1	18.6	1.9	20.6	44.8	45.1	29.6	6.6	15.6	23.0	13.7	2.9
Beets	13.0	15.8	10.1	11.4	0.4	8.3	69.7	16.3	10.5	5.2	5.8	5.3	1.9	1.3

GE, gross energy; CA, crude ash; CP, crude protein; EE, ether extracts; CF, crude fibre; NFE, nitrogen-free extracts; NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; HC, hemicellulose; C, cellulose; Ca, calcium; P, phosphorus per day per animal). A subsample of fresh faeces preserved in orthophosphoric acid was used for the determination of faecal volatile fatty acid (VFA) content.

After thawing, the faeces of the whole collection period were pooled for each animal and thoroughly mixed. Samples of feedstuffs and faeces were analysed for DM, crude protein (CP), crude ash (CA), crude fibre (CF) and ether extract (EE) according to NAUMANN and BASSLER (1988) and for neutral detergent fibre (NDF), acid detergent fibre (ADF) and ADL according to VAN SOEST (1967). Nitrogen-free extracts (NFE) were calculated as 100-CP–CA–CF–EE, hemicelluloses (HC) as NDF–ADF and cellulose (C) as ADF–ADL. Gross energy (GE) was determined by bomb calorimetry using an IKA®-Calorimeter C 4000 adiabatic (Janke & Kunkel, Staufen, Germany). Chromium oxide was determined according to PETRY and RAPP (1970). After wet ashing, calcium (Ca) was determined by flame photometry (Eppendorf® Elex 6361, Eppendorf, Hamburg, Germany) and phosphorus (P) by measuring the increase in coloration of the ashed sample with ammonium molybdic acid and ammonium vanadic acid (1 : 1) by spectralphotometry. Faecal pH was measured with an electric pH-meter. The total VFA concentration was determined by gas chromatography (Pye Unicam® Series 204, glass column length 1.8 m, 3 mm Ø, column 130 °C, detector and injection block 165 °C, filling 'chromosorb WAW 60/100' , carrier gas N_2, flow rate 30 ml/min, sample 2 μl) (Unicam, Offenbach, Germany).

The apparent digestibilities (aD) of nutrients (N) for hay-only rations were calculated as:

$$aD_N(\%) = 100 - \frac{\%Mi_{Feed}}{\%Mi_{Faeces}} \times \frac{\%N_{Faeces}}{\%N_{Feed}} \times 100$$

with ADL as internal marker (Mi). For combined rations (hay + feed2), the amount of total faecal excretion was calculated using the intake (I) and the external marker chromium oxide (Me):

$$\text{Faeces (kg DM/day)} = \frac{I_{Me}(\text{g/day})}{Me_{Faeces}(\text{g/kg DM})}$$

The amount of excreted faeces and their internal marker content were used to calculate the intake of internal marker:

$$I_{Mi}(\text{kg/day}) = \frac{\text{Faeces (kg DM/day)} \times Mi_{Faeces}(\%)}{100}$$

This allowed to calculate the amount of internal marker ingested from hay only as:

$$Mi_{Hay}(\text{kg}) = I_{Mi}(\text{kg/day}) - \frac{\text{Feed2 (kg DM)} \times Mi_{Feed2}(\%)}{100}$$

and then the amount of hay ingested as:

$$I_{Hay}(\text{kg DM/day}) = \frac{100 \times Mi_{Hay}(\text{kg})}{Mi_{Hay}(\%)}$$

Thus, total feed intake could be calculated as:

$$I_{Total\ feed}(\text{kg DM/day}) = I_{Hay}(\text{kg DM/day}) + I_{Feed2}(\text{kg DM/day})$$

and the concentration of external marker in the total ration as:

$$Me_{Total\ feed}(\%) = \frac{I_{Me}(\text{kg/day})}{I_{Total\ feed}(\text{kg DM/day})} \times 100$$

The apparent digestibilities (aD) of nutrients (N) for mixed rations were then calculated as:

$$aD_N(\%) = 100 - \frac{\%Me_{Total\ feed}}{\%Me_{Faeces}} \times \frac{\%N_{Faeces}}{\%N_{Feed}} \times 100$$

To compare two mean values, Student's *t*-test was used, and for the comparison of dependent data the paired *t*-test. Correlations were studied by simple regression analysis.

Results

The general health of the animals during the study period did not seem to be compromised except for animal no. 6 which had problems with tooth eruption and a subsequent peridontitis. While this did not influence its general composure, its faeces consisted of conspicuously larger particles than those of the other elephants. All animals seemed to lose weight on the rations with hay 2, as judged by the decreasing prominence of flanks and facial features. Animal no. 3 did not consistently accept the chromium oxide marker, and therefore was omitted from the last four diets.

The food intake for the different diets is recorded in Table 3. The growing bull (animal no. 1) had a significantly higher intake than the other elephants (Table 4; $p < 0.001$). The faecal DM output per unit BW of this animal was also significantly higher than that of all other animals ($p < 0.001$). The average faecal DM content varied between 20 and 21% and did not differ between feeding periods or animals. The individual digestibility coefficients for different nutrients are listed in Table 5. There was a significant difference in the average digestibility of CF, NFE, ADF and C between hay 1 and hay 2, and between all rations that included hay 1 and all with hay 2. The addition of the pelleted feed significantly increased the digestibilities of DM, OM, CP, NFE, GE, ADF and C, and decreased the absorption of Ca; similarly, the addition of oats significantly increased the digestibilities of DM, OM, CP, NFE and GE. Animal no. 6 did not differ significantly in any digestibility coefficient from the other animals; neither did animal no. 1. There was no correlation between Ca absorption and dietary Ca intake; however, Ca absorption on diets including pelleted feeds was significantly lower than on other diets. The average faecal pH was 6.36 (±0.50) for all animals and all diets (c.f. Table 6). There were no significant differences between individuals or feeding regimes. The concentration and the proportions of the VFAs are listed in Table 6. There was a significantly lower faecal VFA concentration on the hay-only diets compared with the diets that were supplemented. The proportions of the individual VFAs did not differ between the treatments.

The influence of dietary CF content on DM digestibility (aD DM) was calculated by regression analyis, using our and all other available data from the literature (c.f. Table 7), to be aD DM = 81.9 – 1.18 CF ($n = 31$; $r^2 = 0.35$) in elephants.

Table 3. **Dry matter intake (kg/d) of individual elephants of different feedstuffs for the different feeding periods**

	Trial 1	Trial 2		Trial 3		Trial 4	Trial 5		Trial 6	
Animal	Hay 1	Hay 1	Pelleted Feed	Hay 1	Red Clover	Hay 2	Hay 2	Oats	Hay 2	Beets
1	18.90	18.62	1.75	18.16	2.11	19.90	20.27	2.59	20.76	1.30
2	15.12	16.40	1.75	15.05	2.11	18.17	17.67	2.59	17.88	1.04
3	24.91	27.52	2.62	–	–	–	–	–	–	–
4	41.70	41.41	3.50	36.32	4.05	42.48	43.25	5.19	41.23	3.25
5	38.65	38.38	3.50	40.80	4.18	37.28	39.12	5.19	36.20	3.25
6	52.96	47.67	3.50	55.42	4.22	51.48	52.34	5.19	48.87	3.25

Table 4. **Dry matter (DM) and gross energy (GE) intake of individual elephants during the different feeding periods. DM intake expressed as percentage of body weight and as g/kg BW$^{0.75}$ (metabolic body weight)**

	Hay 1			Hay 1 + pelleted feed			Hay 1 + red clover			Hay 2			Hay 2 + oats			Hay 2 + beets		
	DM intake		GE intake (MJ)	DM intake		GE intake (MJ)	DM intake		GE intake (MJ)	DM intake		GE intake (MJ)	DM intake		GE intake (MJ)	DM intake		GE intake (MJ)
Animal	% BW	g/kg MBW		% BW	g/kg MBW		% BW	g/kg MBW		% BW	g/kg MBW		% BW	g/kg MBW		% BW	g/kg MBW	
1	2.13	116.2	341.5	2.29	125.2	366.2	2.28	124.6	364.6	2.24	122.3	350.4	2.57	140.5	405.1	2.48	135.6	386.2
2	1.42	81.0	273.2	1.70	97.2	326.1	1.61	91.9	308.4	1.70	97.3	320.0	1.90	108.5	359.3	1.77	101.3	331.3
3	1.13	77.5	450.1	1.37	93.8	541.9	–	–	–	–	–	–	–	–	–	–	–	–
4	1.30	97.6	753.5	1.40	105.1	807.8	1.25	94.5	726.3	1.32	99.4	748.1	1.51	113.4	858.2	1.38	104.1	777.5
5	1.22	91.3	698.4	1.32	99.0	753.1	1.42	106.3	809.5	1.17	88.1	656.5	1.39	104.7	785.4	1.24	93.2	689.0
6	1.32	105.0	957.0	1.28	101.5	920.9	1.49	118.3	1074.4	1.28	102.1	906.6	1.43	114.1	1018.2	1.30	103.4	912.1

Table 5. **Apparent digestibility coefficients of individual elephants for the different feeding periods for dry matter (DM), organic matter (OM), gross energy (GE), crude protein (CP), crude fibre (CF), nitrogen-free extracts (NFE), acid detergent fibre (ADF), cellulose (C), calcium (Ca) and phosphorus (P)**

Diet	Animal no.	DM	OM	GE	CP	CF	NFE	ADF	C	Ca	P
Hay 1	1	30.7	33.6	31.1	53.2	28.0	36.3	26.0	30.8	66.3	52.8
	2	25.7	29.7	27.1	49.2	24.1	32.6	23.0	27.2	72.4	−2.7
	3	38.6	40.5	38.1	54.3	36.4	42.9	35.1	41.6	51.8	26.2
	4	34.7	36.6	34.5	46.5	35.0	38.6	33.5	39.7	54.9	21.8
	5	33.9	35.8	32.9	49.9	33.3	37.8	33.0	39.0	49.3	9.2
	6	35.2	37.0	33.4	50.1	34.0	39.0	33.5	39.7	59.9	5.7
Hay 1	1	33.1	36.1	34.4	54.8	28.3	39.3	26.4	31.2	60.5	41.1
+ pelleted feed	2	29.2	32.3	30.3	53.1	24.4	35.2	22.9	27.1	57.6	52.8
	3	41.5	43.3	40.6	58.3	39.1	45.0	36.9	43.7	42.3	31.0
	4	37.6	39.3	37.4	53.2	36.6	40.4	35.6	42.0	15.7	16.8
	5	37.4	39.1	36.2	53.5	34.2	41.9	35.2	41.6	20.9	29.6
	6	37.6	39.4	35.9	54.0	34.0	42.1	34.3	40.6	39.5	22.8
Hay 1	1	30.5	33.9	31.2	55.7	27.6	36.7	26.7	31.7	65.1	68.2
+ red clover	2	26.1	29.2	25.8	49.5	24.2	30.1	23.8	28.4	59.2	44.2
	4	35.9	37.5	33.9	46.7	35.0	39.8	33.9	40.4	48.5	−17.2
	5	34.1	35.2	32.2	47.8	32.9	36.4	30.1	35.9	58.7	4.9
	6	35.7	36.9	34.2	53.8	33.8	37.6	31.6	37.5	59.1	12.1
Hay 2	1	34.5	37.0	33.7	56.6	24.9	44.1	23.6	28.4	69.3	14.2
	2	30.0	31.6	29.3	51.6	17.8	39.4	18.2	22.0	54.9	−5.9
	4	39.6	40.2	36.9	51.4	29.2	47.9	28.6	34.5	69.1	10.1
	5	30.7	31.6	28.5	52.0	19.1	39.0	21.5	25.9	45.1	15.2
	6	33.7	34.9	30.1	48.0	21.7	43.9	24.6	29.7	67.0	5.5
Hay 2 + oats	1	37.1	39.5	36.5	58.3	25.9	46.4	26.1	31.5	54.1	4.7
	2	33.7	36.1	33.3	54.4	22.2	42.9	15.0	18.1	48.0	15.2
	4	41.5	42.4	39.1	53.3	31.6	48.7	25.1	30.3	51.2	−4.4
	5	35.3	36.5	33.0	54.2	21.4	45.0	18.3	22.1	51.6	−0.4
	6	35.3	36.3	32.3	48.9	21.5	45.7	21.9	26.4	39.7	30.6
Hay 2 + beets	1	34.9	36.9	33.3	57.8	25.4	42.8	20.4	24.7	63.2	48.9
	2	30.5	32.0	28.7	51.5	18.0	39.6	13.8	16.7	56.5	8.6
	4	40.3	40.5	37.3	51.1	30.8	46.2	23.2	28.2	43.8	11.2
	5	31.4	31.8	30.1	53.2	18.4	38.6	12.9	15.7	49.6	−11.9
	6	34.2	34.3	31.0	47.8	21.8	41.6	16.3	19.8	67.1	8.8

Discussion

Comparison with other elephant data

Intake and digestibility data

The results of this study are generally in accord with corresponding literature data (Table 7). High intakes in that data set were achieved by growing animals (Monfort and Monfort, 1979; Spala et al., 1990), which compares well with the intake observed in elephant no. 1 from this study. The highest intake record, however, stems from Bhashkaran Nair and Ananthasubramaniam (1979) who fed their elephants on palm leaves only; the exceptionally high digestibility coefficients of that study raised doubts about its compatibility with the other studies. The high digestibility coefficients from Spala et al. (1990) can probably be explained by the method employed; the authors used acid insoluble ash as an internal marker; this method is prone to deviations because of soil ingestion and contamination of faeces (Kotb and Luckey, 1972) . The high protein

Table 6. **Content of volatile fatty acids (VFA) and pH in faeces or colon contents of elephants. Acetic acid (C2), propionic acid (C3), butyric acid (C4)**

Reference	Diet	*n*	C2 (%)	C2 (mmol/L)	C3 (%)	C3 (mmol/L)	C4 (%)	C4 (mmol/L)	VFA total (mmol/L)	C2 : C3	pH
This study	Hay 1	6	76	38.4	18	9.2	6	2.8	50.4	4.2	6.38
This study	Hay 1 + pelleted feed	6	76	50.2	19	12.3	5	3.6	66.1	4.1	6.38
This study	Hay 1 + clover	6	77	49.9	19	12.1	5	3.1	65.1	4.1	6.32
This study	Hay 2	6	77	39.0	18	9.1	5	2.3	50.4	4.3	6.40
This study	Hay 2 + oats	6	76	50.0	18	12.2	5	3.5	65.6	4.1	6.33
This study	Hay 2 + beets	6	76	48.1	19	11.9	5	3.1	63.1	4.1	6.38
Clemens and Maloiy (1982)	Free-ranging (Africa)	3	74	47.6	13	8.6	8	5.1	61.3	6.3	7.01
Van Hoven et al. (1981)	Free-ranging (Africa)	11	75	57.9	9	7.3	9	7.2	72.3	8.0	
Van Hoven et al. (1981)	Free-ranging (Africa)	19	70	64.7	11	10.2	11	10.1	85.0	6.3	
Van Hoven et al. (1981)	Free-ranging (Africa)	15	75	69.5	11	10.5	9	8.5	88.4	6.6	
Van Hoven et al. (1981)	Free-ranging (Africa)	4	75	44.2	11	6.3	9	5.1	55.6	7.0	
Van Hoven et al. (1981)	Free-ranging (Africa)	4									6.78

Table 7. **Comparative digestibility data for African and Asian elephants from the literature; calculated averages per dietary regime**

Source	Diet type	*n*	BW (kg)	DM Intake (% BW)	Diet comp. (% DM)			Apparent digestibilities (%)										
					CF	ADF	C	DM	OM	CP	EE	CF	NFE	NDF	ADF	HC	C	GE
African elephant																		
Monfort and Monfort (1979)	Free range	2	504	1.81				42.2										42.2
Meissner et al. (1990)	Free range	3	4500	1.38		49.6	33.6		35.6					19.9	12.6	47.6	18.8	
Foose (1982)	Grass hay	3	2873	1.19		42.2	33.9		45.2	87.5				43.4	41.8	45.8	44.5	
Hackenberger (1987)	Grass hay	15	2660	1.70				39.2		45.5	25.0	27.8	47.4	38.9	36.7	43.9	41.2	49.9
Roehrs et al. (1989)	Grass hay	2	1320	1.47		50.7		37.1		37.6	−13.4			31.7	30.1			37.9
Foose (1982)	Alfalfa hay	3	2873	1.25		32.7	23.7		61.7	95.2				51.1	45.5	70.6	51.3	
Hackenb and Atkinson (1982)	Zoo diet	3	2367	1.58	27.1			32.9		46.0	29.7	44.6	49.8					51.8
Rees (1982)	Zoo diet	2						22.4										
Spala et al. (1990)	Zoo diet	2	622	1.73	17.9			65.8		71.1	35.6	32.9	78.9					64.6
Kozaki et al. (1991)	Zoo diet	3	4900	1.27		40.8			37.3	57.3					5.4			
Tomat et al. (1999)	Zoo diet	7						45.9	49.2					23.8	9.2	45.6		44.3
Asian elephant																		
Bhashkaran Nair and Ananthasubramaniam (1979)	Palm leaves	4	1555	4.43	24.0			72.8		81.2	69.2	47.1	85.0					
Reichard et al. (1982)	Oat Hay	2				37.4		35.0		24.0	22.5			20.0	10.5			42.5
Benedict (1936)	Grass hay	1	3550	1.29	36.4			43.8	44.6	48.3	1.3	37.7	50.6					40.0
Foose (1982)	Grass hay	2	2665	1.20		41.9	32.2		46.4	86.5				44.9	39.3	53.5	45.7	
Hackenb and Atkinson (1982)	Grass hay	3	2813	1.03	34.1			53.3		56.5	36.7	47.6	59.9					54.9
Reichard et al. (1982)	Grass hay	2				43.4		39.0		47.5	21.0			33.0	21.5			35.5
Hackenberger (1987)	Grass hay	37	2502	1.30				43.1		54.1	29.9	31.7	52.5	42.6	41.2	46.0	44.3	58.0
This study	Grass hay 1	6	2427	1.42	36	43.6	36.8	33.1	35.5	50.5	−37.3	31.8	37.9		30.4		36.3	32.9
This study	Grass hay 2	5	2472	1.54	35	42.7	35.4	33.7	35.1	51.9	−46.7	22.5	42.8		23.3		28.1	31.7
Foose (1982)	Alfalfa hay	1	3402	1.12		41.9	30.6		58.9	95.5				46.1	45.2	49.3	55.6	
Fujikara et al. (1989)	Zoo diet	1		1.20		29.9		33.3							3.2			
This study	Zoo diets	6	2459	1.64	33.4	41.0	34.2	34.9	36.6	52.9	−23.4	27.9	40.2		25.3		30.2	33.7
Both species																		
Ullrey et al. (1979)	Grass hay					44.0				43.0				31.0	20.0			35.0

digestibilities analysed by Foose (1982) cannot be explained. Other studies that used lignin as an internal marker (Ullrey et al., 1979; Reichard et al., 1982; Fujikara et al., 1989; Kozaki et al., 1991) found consistently lower digestibility coefficients than studies that used total faecal collection. However, our own study is comparable with those that used total faecal collection. Hackenberger (1987) found that Asian elephants achieve higher digestibility coefficients and longer mean ingesta retention times than African elephants. The author suggested a difference in evolutionary adaptation to the difference in browse content between the species. The only other data set that compared both elephant species, albeit with a much lower number of animals (Foose, 1982), found a similar intake of grass hay between the species and a slightly higher organic matter digestibility in Asian elephants, and a drastically higher intake of alfalfa hay and higher digestibility coefficients in African elephants. As alfalfa hay is generally accepted to be more similar to browse than grass hay, these results support the view suggested by Hackenberger (1987). Data on free-ranging elephants demonstrates that although both species depend mainly on browse, Asian elephants include a higher proportion of grass in their natural diet (Cerling et al., 1999).

Faecal VFA composition

A comparison of the VFA concentrations found in our captive Asian elephants, especially on the hay-only diets, with values of free-ranging African elephants (c.f. Table 6), suggests that elephants are adapted to diets with higher fermentation potential than the grass hays of this study. The difference in VFA proportions indicates that free-ranging elephants do not use seeds or other 'concentrate'-like diet items in higher proportions, but achieve their higher VFA concentrations by more fibre fermentation activity. Accordingly, free-ranging elephants seem to have a more variate faecal microflora than captive specimens (Smith et al., 1982). This discrepancy could be indicative of a basic difference in the diets and corresponds to the finding by Cerling et al. (1999) that elephants are mainly browsers: browse can be fermented much faster than grass (Short et al., 1974); therefore, the proportion of VFA produced from a browse-based diet, within the short period of time ingesta is retained in the GIT of elephants, should be higher than from a grass- or hay-based diet. On grass, the maximum VFA production could only be reached by longer ingesta retention times.

The effect of body size

In interspecific comparisons, elephants have surprisingly fast ingesta passage rates for their body size (Loehlein et al., 2003). In intraspecific comparisons in free-ranging elephants, it has been observed that the larger males tolerate more fibrous material in their diets (Stokke and du Toit, 2000), and it has been shown that mean retention times (MRT) correlate positively and significantly with body size in captive elephants (Hackenberger, 1987), a trend that is obvious within our elephant group as well (c.f. Table 1). As MRT correlates significantly with fibre digestibility (Hackenberger, 1987), larger elephants therefore achieve higher fibre digestibility coefficients. This trend could be observed in our elephants as well, but not as consistently. Presently, no answer is given to why elephants apparently do not make use of the digestive potential theoretically provided by their body size (Parra, 1978; Demment and Van Soest, 1985).

Comparison with the horse

Digestibility data

When compared with digestibility data from horses (Fig. 1), it is obvious that the absolute digestibility coefficients achieved by elephants are distinctively lower. These low

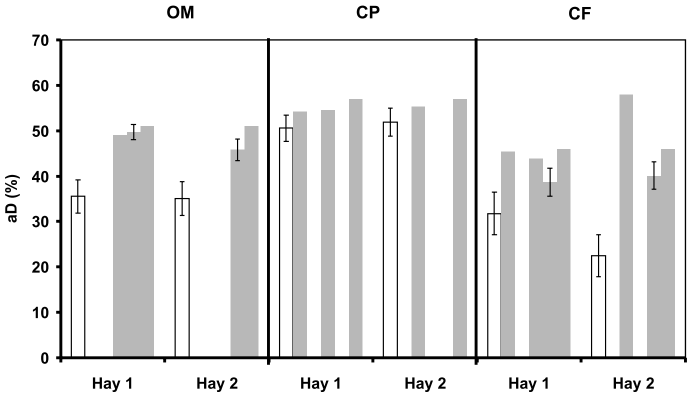

Fig. 1. Comparison of apparent digestibility coefficients for organic matter (OM), crude protein (CP) and crude fibre (CF) in □ Asian elephants and ■ horses. Data (average, SD) from six captive Asian elephants (this study) and from six horses (Fonnesbeck et al., 1967; no SD given), four horses (Darlington and Hershberger 1968; no SD given), eight horses (Vander Noot and Gilberath 1970; no SD given), DLG-Futterwerttabellen Pferd (1995; no *n* or SD given). Horse data was chosen to match elephant data in dietary nutrient composition.

digestibility coefficients can be explained by the significantly faster passage rates of elephants (Loehlein et al., 2003). In horses, an increase in the concentrate component of the diet results in slower passage rates (Coenen et al., 1990); however, Hackenberger (1987) observed the opposite effect in (African) elephants. The influence of dietary CF content on DM digestibility (aD DM) for elephants (aD DM = 81.9 – 1.18 CF) resembles the influence of dietary CF on organic matter digestibility determined by Fehrle (1999; aD OM = 88.6 – 1.07 CF). Interestingly, in spite of the peridontitis and the consecutive less thorough mastication in elephant no. 6, the digestibility results were not significantly affected, whereas similar disturbances in horses lead to reduced digestibilities (Meyer and Coenen, 2002). This suggests that the thoroughness of mastication has a lesser influence on digestibility in the elephant. In contrast, Reichard et al. (1982) found that the onset of tooth eruption problems in an Asian elephant led to a decrease of digestibility coefficients for DM, CP, EE, NDF, ADF and starch digestibility.

Calcium metabolism

In horses, Ca absorption averages 60% independent from the dietary concentration (Meyer and Coenen, 2002). This value is in excellent accord with the Ca absorption coefficients of captive Asian elephants. In our data set, no dependence of Ca absorption from dietary concentrations could be detected. Horses generally absorb a greater proportion of dietary calcium and therefore excrete less calcium in their faeces than ruminants on comparable diets (Schryver et al., 1970, 1974). Digestion studies in a small number of zoo herbivores confirmed this (Hintz et al., 1976). Other members of the perossidactyla obviously share this characteristic with equids, and elephants as well (Schryver et al., 1983). Excess Ca is excreted in the urine in horses (Meyer and Coenen, 2002), and Rüedi (1995) found the according high urinary Ca concentrations in captive elephants. In horses, Ca absorption is decreased significantly by the addition of pelleted feeds (Stadermann et al., 1992; Meyer et al., 1993); accordingly, Ca absorption on the hay/pelleted feed diet was significantly lower in the elephants than on all other diets.

VFA and pH patterns

The VFA concentrations and proportions in faeces of the elephants studied are within the ranges reported for horses (Argenzio et al., 1974; Günther, 1984; Krull, 1984; Drochner and Meyer, 1991). An increase after concentrate supplementation, as has been observed in horses (Günther, 1984), was also observed in the elephants. This increase in total VFA concentration was not accompanied by a change in VFA proportions in our elephants. Schwabenbauer et al. (1982) found no influence of different dietary supplements on the VFA proportions in the equine caecum, whereas Zeyner et al. (1992) demonstrated an increase of the propionic acid proportion with increased concentrate supplementation. In the case of our elephants, the proportion of concentrates was probably too low to trigger the expected effects. In contrast to observations by Günther (1984), the faecal pH did not decrease in our elephants with increasing VFA concentration. As elephant faeces contain a higher proportion of undigested protein which acts a a buffer, variations in faecal pH are unlikely in elephants.

Thus, the digestive physiology of the elephant resembles that of the horse in the way dietary CF concentrations influence DM digestibility, in the way the presence of pelleted feeds influences calcium absorption, and in the way concentrate feeds lead to an increase in faecal volatile fatty acids. However, the digestive physiology of elephants differs from that of horses because of distinctively lower absolute digestibility coefficients that are related to faster passage rates.

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References

Argenzio, R. A.; Southworth, M.; Stevens, C. E., 1974: Sites of organic acid production and absorption in equine gastrointestinal tract. Am. J. Physiol. *226*, 1043.

Benedict, F. G., 1936: The Physiology of the Elephant. Carnegie Institution of Washington, Publication No. 474, Washington DC.

Bhashkaran Nair, V.; Ananthasubramaniam, C. R., 1979: Studies on the nutritional requirements of the elephant (*Elephas maximus*): I. Evaluation of the nutritive value of palm leaf (*Caryota urens*). Indian Vet. J. *56*, 667.

Cerling, T. E.; Harris, J. M.; Leakey, M. G. 1999: Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia *120*, 364.

Clemens, E. T.; Maloiy, G. M. O., 1982: The digestive physiology of three East African herbivores: The elephant, rhinoceros and hippopotamus. J. Zool. (Lond.) *198*, 141.

Coenen, M.; Meyer, H.; Stadermann, B., 1990: Füllung des Magen/Darmtraktes bei Pferden in Abhängigkeit von Futterart, Fütterungszeit und Bewegung. Adv. Anim. Physiol. Anim. Nutr. *21*, 7.

Darlington, J. M.; Hershberger, T. V., 1968: Effect of forage maturity on digestibility, intake and nutritive value of alfalfa, timothy and orchardgrass by equine. J. Anim. Sci. *27*, 1527.

Demment, M. W.; Van Soest, P. J., 1985: A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. *125*, 641.

DLG, 1995: Futterwerttabellen für Pferde. 3. Auflage, DLG-Verlag, Frankfurt/M.

Drochner, W.; Meyer, H., 1991: Verdauung organischer Substanzen im Dickdarm verschiedener Haustierarten. Adv. Anim. Physiol. Anim. Nutr. *22*, 18.

Fehrle, S., 1999: Untersuchungen zur Verdaulichkeit von Mischfutter beim Pferd in Abhängigkeit von der Rauhfutteraufnahme. Dissertation, München.

Fonnesbeck, P. V.; Lydmann, R. K.; der Noot, G. W.; Symons, L. D., 1967: Digestibility of the proximate nutritients of forage by horses. J. Anim. Sci. *26*, 1039.

Foose, T. J., 1982: Trophic strategies of ruminant versus nonruminant ungulates. PhD Dissertation, University of Chicago Chicago, IL.

Fujikara, T.; Oura, R.; Sekine, J., 1989: Comparative morphological studies on digestion physiology of herbivores: I. Digestibilitiy and particle distribution of digesta and feces of domestic and feral animals. J. Fac. Agric. Tottori Univ. *25*, 87.

Günther, C., 1984: Untersuchungen über die Verdaulichkeit und Verträglichkeit von Hafer, Quetschhafer, Gerste und Mais beim Pferd. Dissertation, Hannover.

Hackenderger, M. K.; Atkinson, J. L., 1982: Digestibility studies with captive Asian and African elephants. In: Proceedings of the Annual Conference of the American Association of Zoological Parks and Aquariums, pp. 129–137.

Hackenberger, M. K., 1987: Diet Digestibilities and Ingesta Transit Times of Captive Asian and African Elephants. MS Thesis, University of Guelph, Canada.

Hile, M. E.; Hinz, H. F.; Erb, H. N., 1997: Predicting body weight from body measurements in Asian elephants. J. Zoo Wildlife Med. *28*, 424.

Hintz, H. F.; Sedgewick, C. J.; Schryver, H. F., 1976: Some observations on digestion of a pelleted diet by ruminants and nonruminants. Int. Zoo Yb. *16*, 54.

Kotb, A. R.; Luckey, T. D., 1972: Markers in nutrition. Nutr. Abstr. Rev. *42*, 813.

Kozaki, M. R.; Oura, R.; Sekine, J., 1991: Studies on digestion physiology of herbivorous feral animals: II. The comparison of intake of total digestible nutrients among diverse sizes of ruminant and monogastric animals. J. Faculty Agri., Tottori University *27*, 61.

Krull, H.-D., 1984: Untersuchungen über Aufnahme und Verdaulichkeit von Grünfutter beim Pferd. Dissertation, Stuttgart-Hohenheim/Hannover.

Loehlein, W.; Kienzlf, E.; Wiesner, H.; Clauss, M., 2003: Investigations on the use of chromium oxide as an inert, external marker in captive Asian elephants (*Elephants maximus*): passage and recovery rates. In: Fidgett, A.; Clauss, M.; Ganslosser, U.; Hatt, J.-M.; Nijboer, J. (eds), Zoo Animal Nutrition Vol. *II*, Filander Verlag, Fürth (in press).

Meissner, H. H.; Spreeth E. B.; De Villiers, P. A.; Pieterson, E. W.; Hugo, T. A.; Terblanche, B. F., 1990: Quality of food and voluntary intake by elephants as measured by lignin index. S. Afr. J. Wildl. Res. *20*, 104.

Meyer, H.; Coenen, M., 2002: Pferdefütterung. 4. Aufl. Paul Parey Verlag, Berlin.

Meyer, H.; Stadermann, B.; Radicke, S.; Kienzle, E.; Nyari, A., 1993: Untersuchungen zum Einflu ß der Futterart auf Füllung und Zusammensetzung des Verdauungskanals sowie postprandiale Blut- und Harnparameter. Pferdeheilkd *9*, 15.

Monfort, A.; Monfort, N., 1979: Rendement d'assimilation et bilan énérgétique chez les éléphanteaux d'Afrique (*Loxodonta africana* Blumenbach). Mammalia *43*, 543.

Naumann; C.; Bassler, R. (eds), 1988: Die chemische Untersuchung von Futtermitteln. Band III. Verlag Naumann-Neudamm, Methodenbuch.

Oftedal, O. T.; Baer, D.J.; Allen, M. E., 1996: The feeding and nutrition of herbivores. In: Kleimann, D. G.; Allen, M. E.; Thompson, K. V.; Lumpkin, S. (eds), Wild Mammals in Captivity: Principles and Techniques. University of Chicago Press, Chicago, pp. 129–138.

Owen-Smith, R. N., 1988: Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, Cambridge, UK.

Parra, R., 1978: Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery, G. G. (ed.), The Ecology of Arboreal Folivores. Smithsonian Inst Press, Washington DC, pp. 205–230.

Petry, H.; Rapp, W., 1970: Zur Problematik der Chromoxidbestimmung in Verdauungsversuchen. Z. Tierphys. Tierern. Futtermittelkunde *27*, 181.

Rees, P. A., 1982: Gross assimilation efficiency and food passage time in the African elephant. Afr. J. Ecol. *20*, 193.

Reichard, T. A.; Ullrey, D. E.; Robinson, P. T., 1982: Nutritional implications of dental problems in elephants. In: Proceedings of the Second Annual Dr Scholl Nutrition Conference on the Nutrition of Captive Wild Animals, Chicago, pp. 63–67.

Roehrs, J. M.; Brockway, C. R.; Ross, D. V.; Reichard, T. A.; Ullrey, D. E., 1989: Digestibility of timothy hay by African elephants. Zoo Biol. *8*, 331.

Rüedi, D., 1995: Elefanten. In: Gölthenboth, R.; Klös, H.-G. (eds): Krankheiten der Zoo- und Wildtiere, Blackwell Wissenschaftsverlag, Berlin, pp. 156–189.

Schryver, H. F.; Craig, P. H.; Hintz, H. F., 1970: Calcium metabolism in ponies fed varying levels of calcium. J. Nutr. *100*, 955.

Schryver, H. F.; Hintz, H. F.; Lowe, J. E., 1974: Calcium and phosphorus in the nutrition of the horse. Cornell. Vet. *64*, 493.

Schryver, H. F.; Foose, T. J.; Williams, J.; Hintz, H. F., 1983: Calcium excretion in feces of ungulates. Comp. Biochem. Physiol. *74A*, 375.

Schwabenbauer, K.; Meyer, H.; Lindemann, G., 1982: Gehalt an flüchtigen Fettsäuren und Ammoniak im Caecuminhalt des Pferdes in Abhängigkeit von Futterart, Futterreihenfolge und Fütterungszeitpunkt. Adv. Anim. Physiol. Anim. Nutr. *13*, 24.

Short, H. L.; Blair, R. M.; Segelquist, C. A., 1974: Fiber composition and forage digestibility by small ruminants. J. Wildl. Manage. *38*, 197.

Smith, T. P.; Jollie, K. G.; Mohr, J. L., 1982: Gut protozoans of zoo elephants. Abstract, J. Protozool. *29*, 482.

Spala, P.; Vahala, J.; Hradecky, P., 1990: Lameness in young African elephants (*Loxodonta africana*) caused by inadequate nutrition. Zool. Garten N. F. *60*, 244.

Stadermann, B.; Nehring, T.; Meyer, H., 1992: Calcium- und Magnesiumabsorption bei Rauhfutter oder Mischfutter. In: Pferdeheilkd, 1. Europ. Conf. on the Nutrition of the Horse, TiHo Hannover, pp. 77–80.

Stokke, S.; du Toit, J., 2000: Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. Ecography *23*, 70.

Tomat, L.; Schumann, B.; Atkinson, J. L.; Valdes, E. V., 1999: Digestibility studies with captive African elephants (Loxodonta africana). In: Abstract Book of the First European Zoo Nutrition Meeting, Rotterdam, Netherlands, p. 76.

Ullrey, D. E.; Robinson, P. T.; Whetter, P. A., 1979: Comparative Digestibility Studies with Zoo Herbivores. In: Am. Assoc. Zoo Vet. Ann. Proc., Denver, pp. 120–121a.

Van der Noot, G. W.; Gilberath, E. B., 1970: Comparative digestibility of components of forages by geldings and steers. J. Anim. Sci. *31*, 351.

Van Hoven, W.; Prins, R. A.; Lankhorst, A., 1981: Fermentive digestion in the African elephant. S. Afr. J. Wildl. Res. *11*, 78.

Van Hoven, W., 1982: African elephant and hippopotamus: the results of nutritional research. In: Proceedings of the Second Annual Dr. Scholl Nutrition Conference on the Nutrition of Captive Wild Animals, Chicago, pp. 47–61.

Van Soest, P. J., 1967: Development of a comprehensive system of feed analysis and its application to forages. J. Anim. Sci. *26*, 119.

Zeyner, A.; Geissler, C.; Kaske, H.; Fuchs, R., 1992: Untersuchungen zur Beurteilung der Futterration mittels Kotwasseranalysen (Wasser, pH, org. Säuren). In: Pferdeheilkd, 1. Europ. Conf. on the Nutrition of the Horse. TiHo Hannover, pp. 88–91.

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