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Abstract

Digestive strategies have been recognized to be a key factor for healthy growth in juvenile Galapagos giant tortoises (Geochelone nigra). The aim of present study was to investigate digestive coefficients with special regard to fiber fractions. Four captive bred Galapagos giant tortoises 4-5 years of age were fed a controlled diet for 32 days. The diet consisted of 77% hay, 15% tortoise pellets, and 8% apples on a dry matter basis. On a dry matter basis diet analysis showed: 95.7% organic matter, 11.3% crude protein, 20.5% crude fiber, 22.6% acid detergent fiber, 5.0% acid detergent lignin, and 17.6% cellulose. Based on total fecal collection during 7 days average dry matter digestibilities were calculated: 65% for dry matter, 67% for organic matter, 63% for crude protein, 55% for crude fiber, 49% for acid detergent fiber, 41% for acid detergent lignin, 54% for cellulose. An increase in crude fiber content resulted in a reduced digestibility in comparative evaluations of data for different tortoise species, and in a comparison of tortoises and mammalian hindgut fermenters. Compared to some mammalian hindgut-fermenting herbivore species (domestic horses, Asian elephants, Indian rhinoceroses) on a diet of hay and concentrates, the juvenile Galapagos giant tortoises showed a digestion of similar efficiency. If a reduction in dietary digestibility is warranted in juvenile Galapagos giant tortoises, it is concluded that dietary fiber levels should be increased and it is proposed that crude fiber levels of 30-40% on a dry matter basis should be achieved.

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Brief Report

Fiber Digestibility in Juvenile Galapagos tortoises (*Geochelone nigra*) and Implications for the Development of Captive Animals

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Digestive strategies have been recognized to be a key factor for healthy growth in juvenile Galapagos giant tortoises (*Geochelone nigra*). The aim of present study was to investigate digestive coefficients with special regard to fiber fractions. Four captive bred Galapagos giant tortoises 4–5 years of age were fed a controlled diet for 32 days. The diet consisted of 77% hay, 15% tortoise pellets, and 8% apples on a dry matter basis. On a dry matter basis diet analysis showed: 95.7% organic matter, 11.3% crude protein, 20.5% crude fiber, 22.6% acid detergent fiber, 5.0% acid detergent lignin, and 17.6% cellulose. Based on total fecal collection during 7 days average dry matter digestibilities were calculated: 65% for dry matter, 67% for organic matter, 63% for crude protein, 55% for crude fiber, 49% for acid detergent fiber, 41% for acid detergent lignin, 54% for cellulose. An increase in crude fiber content resulted in a reduced digestibility in comparative evaluations of data for different tortoise species, and in a comparison of tortoises

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Key words: crude fiber; acid detergent fiber; lignin; cellulose

INTRODUCTION

Although Galapagos giant tortoises (*Geochelone nigra*) are regularly on display throughout the world, their reproduction outside the Galapagos archipelago remains sporadic [Furrer et al., 2004]. Considering that the Galapagos giant tortoises are classified as threatened or endangered depending on the subspecies [Groombridge, 1993], successful breeding and raising in zoological institutions are of critical importance for the conservation of this species.

In a 4-year comparative study on the growth of juvenile Galapagos giant tortoises in their natural habitat on the Charles Darwin Research Station (CDRS) and under captive conditions a great discrepancy was observed: captive tortoises were approximately twice the size and weighed ten times more than tortoises at the CDRS of the same age. The diet was recognized as the key factor for this discrepancy, and an increase in fiber levels was proposed to reduce the rate of development that was considered to result in a shorter life expectation [Furrer et al., 2004]. Data on digestibility coefficients achieved by Galapagos giant tortoises has been published regarding minerals and organic matter [Liesegang et al., 2001; Hatt et al., 2002], but not with regard to fiber fractions. To increase the existing data pool as a basis for future evaluations of dietary manipulations, a study was undertaken to measure apparent digestibility of different fiber fractions in juvenile Galapagos giant tortoises.

MATERIALS AND METHODS

Four Galapagos tortoises, 4–5 years of age with an average body weight of 9.95 kg $\pm$3.09 were used in this study (Table 1). All animals had hatched at Zurich Zoo. During the trial, the tortoises were separated in individual indoor pens of 1.5 m^2 each. The ambient temperature and relative humidity were recorded daily during the trials.

All animals received the same diet, which consisted of 77% hay, 15% pellets, and 8% apples on a dry matter (DM) basis. Pellets were commercial tortoise pellets (Dorswal, Roswal Products, Zurich, Switzerland). The food was chopped to 5 mm to reduce the possibility of selective uptake. The nutrient composition of the complete ration is given in Table 2. Food was divided into portions that were offered at 08:00, 10:00, and 13:00. The individual tortoises were offered daily amounts of food on a fresh matter (FM) basis: 45 g, 22 g, 30 g, and 29 g, respectively. The amount of food

Table 1. Captive Galapagos tortoises (*Geochelone nigra*)

Tortoise No.	Age (years)	Sex	Body mass (kg)
1	5	Male	14.3
2	5	Female	7.0
3	4	Female	9.2
4	4	Female	9.3

Table 2. Analysis of a mixed diet fed to captive juvenile Galapagos tortoises (*Geochelone nigra*)[a]

Chemical compound		
Dry matter	% FM	51.0
Organic matter	% DM	95.7
Crude protein	% DM	11.3
Crude fiber	% DM	20.5
Acid detergent fiber	% DM	22.6
Acid detergent lignin	% DM	5.0
Cellulose	% DM	17.6

[a]Values are expressed on a fresh matter (FM) or dry matter (DM) basis.

was determined based on a previous investigation, so that no refusals would occur (Gisler, personal observation).

The experimental period lasted 32 days. This time included 25 days of adaptation to the diet to reach a steady state in the gastrointestinal tract followed by 7 days of fecal collection. The length of the adaptation period was based on the experience made during a previous study with these animals [Liesegang et al., 2001]. Total intake measurement and total fecal collection was carried out.

Samples of diets and pellets were analyzed for contents of DM, crude protein (CP), crude fiber (CF), and organic matter (OM) using standard procedures for proximate analysis. Furthermore, acid detergent lignin (ADL) and acid detergent fiber (ADF) were analyzed according to the systems of Van Soest [1994]. Cellulose was calculated by subtracting ADL from ADF.

For the estimation of the apparent digestibility (aD) of nutrients this standard equation was used:

$$aDN = 100 \times (IN - EN)/IN$$

where IN represents the amount of nutrient ingested (g DM) and EN is the amount of excreted fecal nutrient (g DM).

Results are presented throughout as means $\pm$ standard deviation (SD) and n is the number of individuals or samples. Regression coefficients were calculated with the software package SPSS 11.5 for Windows (SPSS Schweiz AG, Zurich, Switzerland).

RESULTS

Ambient temperature during the trial was $23.2 \pm 1.0^{\circ}C$ and relative humidity $88.5 \pm 9.7\%$. All animals were active and appeared healthy throughout the study. Data of intake and apparent digestibility coefficients are summarized in Table 3.

Table 3. Analysis of apparent digestibilities (%) of captive juvenile Galapagos tortoises (*Geochelone nigra*) fed a diet consisting of 77% hay, 15% tortoise pellets (Dorswal, Roswal Products, Zurich, Switzerland), and 8% apples on a dry matter (DM) basis

	Tortoise No.					
	1	2	3	4	Average	SD
Dry matter intake						
% body weight	0.167	0.167	0.173	0.166	0.168	0.003
g/kg MBW	3.25	2.72	3.01	2.89	2.97	0.22
Apparent digestibility						
Dry matter	59	73	80	49	65	14
Organic matter	61	75	81	53	67	13
Crude protein	54	72	78	48	63	14
Crude fiber	50	65	73	31	55	19
Acid detergent fiber	44	61	71	19	49	23
Acid detergent lignin	33	62	75	−8	41	37
Cellulose	50	63	71	31	54	18

Fecal output of individuals was very variable. On an average daily basis, Tortoise 1 had an output of 10.2 g DM (number of defecations, $n = 6$), Tortoise 2 produced 3.3 g DM ($n = 4$), Tortoise 3 produced 3.4 g DM ($n = 5$), and Tortoise 4 produced 8.2 g DM ($n = 5$). On days where two fecal samples were collected from individual animals, samples were pooled in proportional amounts.

DISCUSSION

The aim of the present study was to measure apparent digestibility of different fiber fractions in juvenile Galapagos giant tortoises and to discuss them in the view of using an increased fiber content in the diet for a healthy development.

In general, the diet used in this study may be described as a high fiber diet (crude fiber 20.5% DM) compared to other published giant tortoise zoo diets. In the study by Liesegang et al. [2001] involving two groups of captive juvenile Galapagos giant tortoises, dietary crude fiber contents varied between 6.4–15.3% (DM) (Table 4). It is also higher than the 15.3% (DM) crude fiber content of the diet fed to captive Aldabra giant tortoises (*Geochelone gigantea*) reported by Edwards [1991]. In contrast, the natural diets analyzed by Hamilton and Coe [1982] for Aldabra giant tortoises contained between 61.0–65.9% (DM) holocellulose (Cellulose and hemicellulose). In general, apparent digestibility coefficients for juvenile giant tortoises are particularly high on foods of low to very low fiber content [Liesegang et al., 2001; Liesegang, unpublished]. If the data from this study is compared to those trials, a decrease in digestibility with increasing fiber content is obvious, even if the linear correlation of crude fiber content and apparent digestibility of organic matter is not significant ($r^2 = 0.20$). The available data on desert tortoises [Meienberger et al., 1993; Barboza, 1995] indicate a negative correlation between dietary cell wall (NDF) content and dry matter digestibility ($r^2 = 0.64$); the available data on red- and yellow footed tortoise [Björndal, 1989] indicate a negative correlation between dietary lignocellulose (ADF) and organic matter digestibility ($r^2 = 0.98$).

Table 4. Apparent digestibilities (%) on a dry matter (DM) basis of fiber fractions in different tortoise species

Source	Species	Species	Food/Diet	Diet composition			Apparent digestibilities[a]			
				NDF %	ADF %	CF %	DM	OM	NDF	CF
Meienberger et al., 1993	Desert tortoise	*Xerobates agassizii*	*Erodium cicutarium*	25.7	—	—	63	—	37	—
Meienberger et al., 1993	Desert tortoise	*Xerobates agassizii*	*Schismus barbatus*	72.4	—	—	50	—	59	—
Barboza, 1995	Desert tortoise	*Xerobates agassizii*	Grass	64.6	—	—	63	—	67	—
Barboza, 1995	Desert tortoise	*Xerobates agassizii*	Herbage	29.1	—	—	69	—	54	—
Barboza, 1995	Desert tortoise	*Xerobates agassizii*	Low fiber pellet	18.1	—	—	76	—	57	—
Barboza, 1995	Desert tortoise	*Xerobates agassizii*	High fiber pellet	48.4	—	—	53	—	30	—
Bjorndal, 1989	Red-footed tortoise	*Geochelone carbonaria*	Guava fruit	55.8	44.6	—	—	36	7	—
Bjorndal, 1989	Red-footed tortoise	*Geochelone carbonaria*	Mango fruit	27.4	18.1	—	—	69	40	—
Bjorndal, 1989	Red-footed tortoise	*Geochelone carbonaria*	Lantana foliage	48.9	37.2	—	—	38	37	—
Bjorndal, 1989	Yellow-footed tortoise	*Geochelone denticulata*	Guava fruit	55.8	44.6	—	—	36	7	—
Bjorndal, 1989	Yellow-footed tortoise	*Geochelone denticulata*	Mango fruit	27.4	18.1	—	—	71	42	—
Bjorndal, 1989	Yellow-footed tortoise	*Geochelone denticulata*	Lantana foliage	48.9	37.2	—	—	41	41	—
This study	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	22.6	20.5	65	67	—	55
Liesegang et al., 2001	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	—	14.9	—	91	—	93
Liesegang et al., 2001	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	—	15.3	—	93	—	82
Liesegang et al., 2001	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	—	6.4	—	96	—	75
Liesegang unpubl	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	—	12.1	—	74	—	95
Liesegang unpubl.	Galapagos giant tortoise	*Geochelone nigra*	Zoo mix	—	—	17.3	—	95	—	82

[a]NDF = Neutral detergent fiber; ADF = Acid detergent fiber; CF = Cude fiber; OM = Organic matter.

Compared to some mammalian hindgut-fermenting herbivore species (domestic horses, Asian elephants, Indian rhinoceroses) on a diet of hay and concentrates, the juvenile Galapagos giant tortoises of this study show a digestion of similar efficiency (Fig. 1). The average dry matter digestibility coefficients for these four species show a highly significant correlation with the dietary crude fiber content, underlining the fundamental principle of decreasing overall digestibility with increasing fiber content in vertebrate herbivores. It has been observed earlier [reviewed by Farlow, 1987] that herbivorous reptiles, in general, are able to attain digestibility coefficients comparable to those seen in mammals; Karasov et al. [1986] suggested that this was possibly due to their comparatively slower ingesta passage rates caused by their lower metabolic rates. The principal difference between mammals and reptiles, in this respect, probably does not lie in the relative digestibility coefficients but in the absolute amounts of digested nutrients per unit time.

These results all underline that the fiber content of the diet has a reducing effect on digestibility coefficients. Given the suspicion that many captive Galapagos giant tortoises receive a diet that is too digestible, resulting in accelerated growth with the negative consequences on life expectation, an increase in dietary fiber levels is an appropriate prophylactic measure to counteract this tendency. Ideally, fiber contents in captivity should be adjusted according to values measured in the food of free-ranging specimens. As long as such data is lacking and based on comparison with other hindgut-fermenting herbivore species (Fig. 1), crude fiber levels in the diet of Galapagos giant tortoises of 30–40% DM seem reasonable. Studies to corroborate this hypothesis are encouraged.

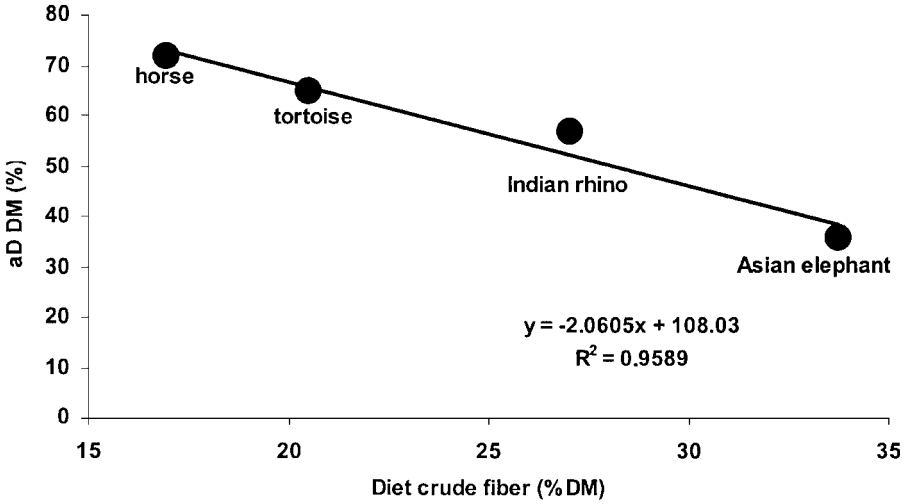

Fig. 1. Comparison of dietary crude fiber contents and apparent digestibility (aD) coefficients for dry matter (DM) for average values for hindgut-fermenting mammals on a diet of grass hay and concentrates and the juvenile Galapagos giant tortoises (*Geochelone nigra*) of this study. Data from Kienzle et al. [2002] (horse), Clauss et al. [2003] (elephant), and Clauss et al. [2004] (Indian rhinoceros).

CONCLUSIONS

Compared to some mammalian hindgut-fermenting herbivore species (domestic horses, Asian elephants, Indian rhinoceroses) on a diet of hay and concentrates, the juvenile Galapagos giant tortoises show a digestion of similar efficiency. An increase in crude fiber content results in a reduced digestibility in comparative evaluations of data for different tortoise species, and in a comparison of tortoises and mammalian hindgut fermenters. If a reduction in dietary digestibility is warranted in juvenile Galapagos giant tortoises, dietary fiber levels should be increased and crude fiber levels of 30–40% DM seem reasonable, but need to be tested.

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