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SHORT COMMUNICATION

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Testing predictions on body mass and gut contents: dissection of an African elephant *Loxodonta africana* Blumenbach 1797

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Abstract The values reported in the literature for the total gastrointestinal tract (GIT) content mass of elephants are lower than expected from interspecific mammalian regression. This finding agrees with theoretical considerations that elephants should have less capacious GITs than other herbivorous mammals, resulting in short ingesta retention times. However, the data on elephants was so far derived from either diseased zoo specimens or free-ranging animals subjected to an unknown hunting stress. In this study, we weighed the wet contents of the GIT segments of a captive African elephant that was euthanased because of a positive serological tuberculosis test, but that was clinically healthy, did not show a reduced appetite, and ingested food up to the time of euthanasia. The animal weighed 3,140 kg and its total gut contents were 542 kg or 17% of body mass. This is in close accord with the published mammalian herbivore regression equation of Parra (Comparison of foregut and hindgut fermentation in herbivores. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington DC, pp205–230, 1978) and contradicts the notion that elephants have comparatively less capacious gastrointestinal tracts. Data on the individual gut segments, however, do support earlier suspicions that elephants have a comparatively less capacious caecum and a disproportionally capacious colon.

Keywords *Loxodonta africana* · Gastrointestinal tract · Gut fill · Body mass · Digestive anatomy · Digestive physiology

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Introduction

Ever since the milestone publication of Parra (1978) it has been accepted that the mass of the wet GIT contents of herbivores scales linearly with body mass (BM). The relevance of this fact lies in its contrast to energy requirements that scale to $BM^{0.75}$, thus granting larger herbivores more GIT capacity relative to their energy needs (Parra 1978; Demment and Van Soest 1985).

In the dataset of Parra (1978), who used data from Hungate et al. (1959) on the contents of the "*fermentation chamber*" (i.e., caecum and proximal colon), the largest extant herbivore, the elephant (here, *Loxodonta africana* Blumenbach 1797), seems to have a fermentation chamber capacity slightly below the interspecific regression line. This finding is interesting insofar as the elephant also displays surprisingly short ingesta retentions times for its BM (Loehlein et al. 2003), which could be explained, amongst other factors, by a comparatively short GIT (Shoshani et al. 1982; Clauss et al. 2003) and a decreased GIT capacity. Clauss et al. (2003) explained that existing data, though scarce, particularly indicated the possibility that elephants have a comparatively small caecum. However, correlated data on BM and the contents of the *individual segments* of the GIT of elephants is, to our knowledge, missing, with the exception of the stomach (Buss 1961; Laws and Parker 1968).

To date, the only information on the BM of individual elephants and their *total* GIT contents are from two diseased zoo animals (Benedict 1936; citing Gilchrist 1851; Noback 1932) and three culled free-ranging individuals (Robertson-Bullock 1962). When the BMs and GIT contents of these animals are compared to the predictions based on the equations established by Parra (1978) for hindgut fermenters in particular and herbivores in general:

- GITcontent (kg) in hindgut fermenters $= 0.1020\ BM^{1.0799}$
- GITcontent (kg) in herbivores in general $= 0.0936\ BM^{1.0768}$

it is evident that the GIT contents of these five animals are distinctively less than what would have been expected (Table 1).

On the one hand, these findings could be interpreted as supportive of the argument that the particularly short ingesta retention times measured in elephants are indicative of a disproportionally small GIT capacity. Based on the two diseased zoo individuals, Benedict (1936) already concluded that the intestinal contents of an elephant represented *"a far smaller proportion of the total body weight"* than in other herbivores. Such an interpretation would be of particular relevance for the extrapolation of GIT capacities to extinct animals even bigger than the elephants.

On the other hand, these data should be regarded with scepticism. Diseased captive animals could be suspected to have died after a period of ill thrift and reduced food intake. Animals culled in the wild might have been submitted to the stress of the hunt, leading to excessive emptying of the GIT by defecation, with an unknown period of time between the last feeding and death. Buss (1961) documented that the time between the last feeding and the culling of elephants has a distinctive influence on the fill of the stomach and a similar effect can be assumed for the total GIT as well. Ideally, therefore, data on GIT contents should be collected in animals that died in good health and without any possible restriction of food intake prior to being sampled. Evidently, such opportunities are rare.

The euthanasia of an African elephant that was tested positive for tuberculosis, did not show any clinical signs of disease, and that in particular had no reduced appetite, allowed the measurement of these parameters in one captive individual. At the same time, it allowed to test whether an animal that had continued to ingest food right up to the point of being euthanased had capacities of the individual sections of its gastrointestinal tract that were lower than expected on the basis of interspecific comparisons.

Methods

A female African elephant, aged 21 years, kept at Safari de Peaugres, was tested for tuberculosis by MultiAntigen Print ImmunoAssay MAPIA test. After a positive test result, the animal was kept separated from the rest of the herd until arrangements for euthanasia and necropsy had been made. The animal did not show any clinical signs of the disease and displayed a normal food intake. In order to ensure a physiological gut fill at death, the animal was offered grass hay ad libitum until being euthanased. Its regular diet consisted of grass hay, horse pellets, fruits, and vegetables. After euthanasia, the animal was loaded on a truck whose weight had been determined at a truck weighing station and the weight of the truck and its cargo was measured again at the same station. The BM of the elephant was calculated by subtraction. The error due to the consumption of petrol by the truck was considered negligible.

Necropsy was performed in an abattoir. The stomach and intestines were removed intact from the abdominal cavity after the dissection of both the legs and the opening of the abdominal and thoracic cavities on one side. The carcass was then lifted by a winch allowing traction on the GIT and cutting of the mesenteria. Subsequently, all adhering mesenteria were removed from the GIT, which was spread out on the floor in order to identify the individual segments.

The GIT was separated by ligations into the stomach, small intestine, caecum, colon, and rectum according to Clemens and Maloiy (1982). The individual segments were placed in a plastic container and weighed on a scale (Barres de pesée, modele PM 700, Marechalle pesage constructeurs, Chauny, France) to the nearest kilogram.

Table 1 Reported measurements of body mass (kg) and GIT contents mass (kg) of elephants from the literaturecompared to predicted GIT contents based on the equations from Parra (1978)

Source	Animal	Death due to	Body mass	Predicted GIT contents		GIT contents measured
				Hindgut fermenters	Herbivores	
Robertson-Bullock (1962)	Free-ranging	Culling	4,380	873	781	409
Robertson-Bullock (1962)	Free-ranging	Culling	5,149	1,040	929	538
Robertson-Bullock (1962)	Free-ranging	Culling	6,004	1,227	1,096	625
Gilchrist (1851)	Captive	Disease	1,975	369	331	241
Noback (1932)	Captive	Disease	4,713	945	845	338

Table 2 Organ and wet content weights of an African elephant (kg) of a total body weight of 3,140 kg as compared to literature data (no body mass given)

Organ	Organ mass	Contents mass			Contents (% body mass)	Contents (% of total contents)
	This study	This study	Van Hoven et al. (1981)	Clemens and Maloiy (1982)	This study	This Study
Stomach	32	122	51	58	3.9	22.6
Small intestine	50	7	38	28	0.2	1.3
Caecum	15	57	86	75	1.8	10.5
Colon	74	323	289	204	10.3	59.6
Distal fermentaion chamber	89	380	375	279	12.1	70.1
Rectum	12	33	23	50	1.0	6.0
Total	182	542	487	415	17.3	100.0

In order to facilitate the weighing of the colon, this section had to be separated into two parts. Afterwards, the individual GIT sections were opened, cleared of all ingesta, washed, and weighed again. The weight of the ingesta was calculated by subtraction.

Results

The BM of the elephant was 3,140 kg. A moderate amount of body fat was present in the abdominal cavity. The animal was considered to be in a good condition but not obese. All GIT sections appeared to be well filled. The weights of the different GIT sections and their contents are recorded in Table 2. The total GIT contents amounted to 542 kg or 17.3% of BM.

Discussion

Conclusions based on one individual animal must always remain speculative. Usable results from zoo animals are only to be expected in very rare circumstances as in this case where no clinical problems and no loss of appetite were observed. The BM of the animal investigated is at the upper end of the range given for female African elephants of this age by Laws and Parker (1968). However, the animal had only moderate amount of adipose tissue and was not considered to be overweight. Therefore, the high BM might be an indication of accelerated body development under captive conditions.

Compared to stomach fills of free-ranging elephants reported by Laws et al. (1975) (in % BM) with a maximum of 4% BM, the elephant of this study had a stomach fill close to this maximum (3.9%). Buss (1961) reported stomach fills even up to 5.9% BM. Yet, in general, the data on the GIT organs and contents of these elephants are higher than other data reported in the literature (cf. Tables 1 and 2). This difference will most likely be due to the variation in the time elapsed since the last feeding. The fact that our elephant had been feeding just prior to euthanasia explains the close to maximum GIT fill.

If the data on total GIT content weight are compared to the data from Parra (1978), it becomes evident that the elephant cannot be regarded as an outlier among mammals but follows the general pattern in an interspecific context (Fig. 1). However, based on the

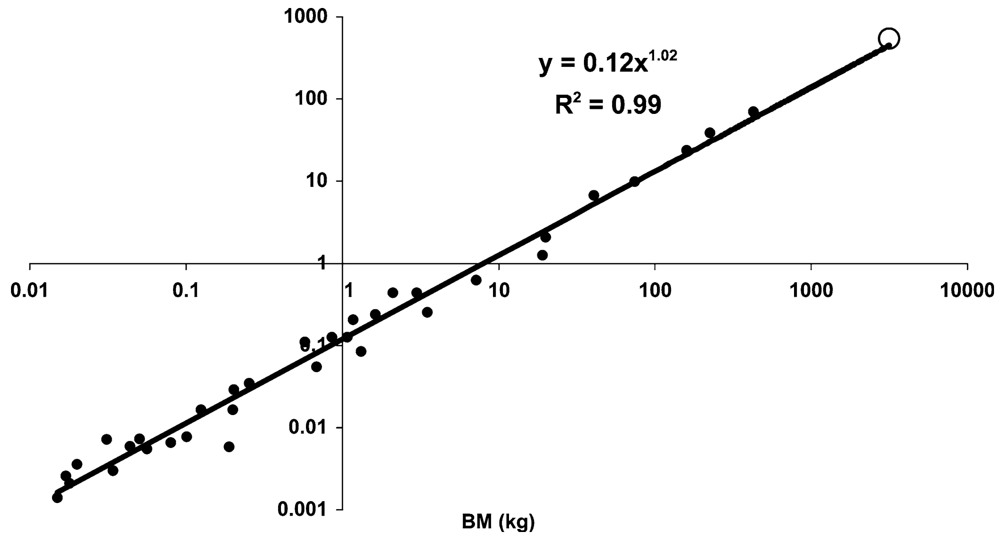

Fig. 1 Data on body mass and total gastrointestinal tract contents (kg) from Parra (1978). Data from this study given as *open symbol*

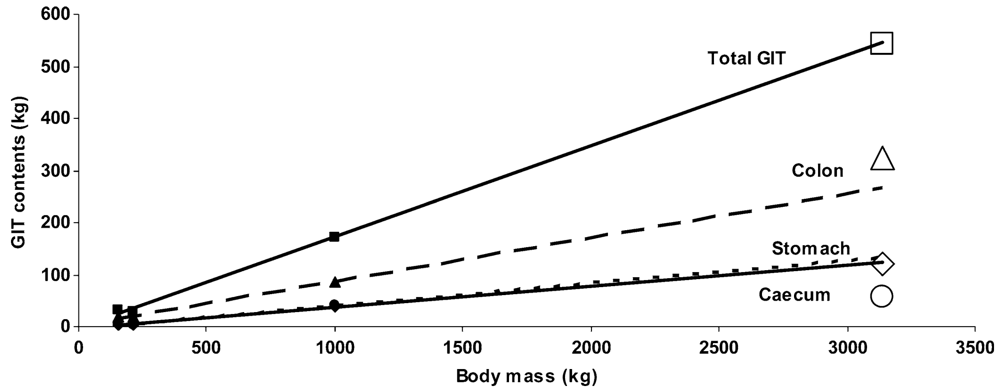

Fig. 2 Correlation of body mass and contents of the total gastrointestinal tract (GIT), colon, caecum (*circles*) and stomach (*diamond*) in ponies and black rhinoceros from the literature (*closed symbols*) and the elephant investigated in this study (*open symbols*) (modified from Clauss et al. 2003). Extrapolations (*regression lines*) based on horse and rhinoceros data only

equation derived by Parra (1978) for the total GIT contents of hindgut fermenters, the expected total GIT content for our elephant would have been 609 kg. In contrast, the equation derived by the same author for herbivores in general (regardless of whether they are foregut or hindgut fermenters) predicted total GIT contents of 546 kg, which is nearly identical to the value measured in our elephant. These calculations indicate that the equation for hindgut fermenters, based mostly on small species, might overestimate the total GIT contents if applied to larger species and that the general herbivore equation is probably more adequate.

Clauss et al. (2003) demonstrated the difficulty in evaluating elephant GIT contents data without a corresponding BM. Using the same data sources as in that publication for a comparison between ponies, the black rhinoceros (*Diceros bicornis* Linné 1758) and our elephant (Fig. 2), it is evident that the elephant GIT contents are in good accord with extrapolations based on these other two species; this is particularly evident for the total GIT contents. The hypothesis offered in Clauss et al. (2003) that elephants have a distinctively decreased GIT capacity, therefore, appears unlikely. Figure 2 also shows a good accord of the stomach content of the elephant investigated with the value expected from extrapolation from horse and rhinoceros. In contrast, the contents of the caecum are lower than would be expected from extrapolation. Clauss et al. (2003) already indicated the likelihood of a disproportionally small caecum in elephants. Reducing the dead-end space of the caecum and increasing, in compensation, the capacity of the in-line colon, could be a morphological correlate of the fast ingesta passage observed in elephants.

In conclusion, the necropsy of this captive individual suggests that the *capacity* of the GIT of elephants does not deviate from the interspecific average. In combination with the particularly short *length* of the GIT of elephants (Shoshani et al. 1982; Clauss et al. 2003), this finding gives rise to the question as to what factors determine the remarkable uniformity of the BM–GIT capacity relationship among mammals (and possibly other species).

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