The digestive morphophysiology of wild, free-living, giraffes

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ABSTRACT

We have measured rumen-complex (rumen, reticulum, omasum, abomasum) and intestine (small and large combined) mass in 32 wild giraffes of both sexes with body masses ranging from 289 to 1441 kg, and parotid gland mass, tongue length and mass, masseter and mandible mass in 9 other giraffes ranging in body mass from 181 to 1396 kg. We have estimated metabolic and energy production rates, feed intake and home range size. Interspecific analysis of mature ruminants show that components of the digestive system increase linearly (Mb^1) or positively allometric ($Mb^{>1}$) with body mass while variables associated with feed intake scale with metabolic rate ($Mb^{.75}$). Conversely, in giraffes ontogenetic increases in rumen-complex mass were negatively allometric ($Mb^{<1}$), and increases in intestine mass, parotid gland mass, masseter mass, and mandible mass were isometric (Mb^1). The relative masseter muscle mass (0.14% of Mb) and the relative parotid mass (0.03% of Mb) are smaller than in other ruminants. Increases in tongue length scale with head length$^{0.72}$ and $Mb^{.32}$ and tongue mass with $Mb^{.69}$. Absolute mass of the gastrointestinal tract increased throughout growth but its relative mass declined from 20% to 15% of Mb. Rumen-complex fermentation provides ca 43% of daily energy needs, large intestine fermentation 24% and 33% by digestion of soluble carbohydrates, proteins, and lipids. Dry matter intake (kg) was 2.4% of body mass in juveniles and 1.6% in adults. Energy requirements increased from 35 Mj/day to 190 Mj/day. Browse production rate sustains a core home range of 2.2–11.8 km^2.

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1. Introduction

While much is known about the diets of wild giraffes (e.g. Hall-Martin and Basson, 1975; Pellew, 1984A) and their feeding ecology (Leuthold and Leuthold, 1972; Pellew, 1983A,B; du Toit, 1990A,B,C; Young and Isbell, 1991; Woolnough and du Toit, 2001; Cameron and du Toit, 2007), how and where the browse they eat is processed to provide the energy and nutrients they need is relatively unknown. The anatomy of their mouths and adnexal structures has been described in detail by Owen (1838), Joly and Lavocat (1846), and Perez et al. (2012), as has the relevance of the shape of their maxilla (Solounias and Moelleken, 1993). Systematic analysis of the structure and development of their brachydont, selenodont teeth and their dental formula has been described by Singer and Boné (1960) and Hall-Martin (1976), but no analysis of their role in the acquisition of browse has been done. Anecdotally Hamilton (1978) suggested that the bilobed lower canine functioned to strip browse, and as the ridge–basin structure of molars in southern African browsers is highly conserved we assume that their function follows the typical pattern as described by Archer and Sanson (2002): the selenodont ridges act to shear browse and the basins crush it. There

have been sporadic measurements of salivary gland mass (Robbins et al., 1995; Hofmann et al., 2008) but no systematic analysis of their ontogeny. Masseter muscle mass has been reported in a single captive giraffe by Clauss et al. (2008) and by us in wild giraffes in the context of the anatomy of their head and skull and not digestion (Mitchell et al., 2013B). Similarly, we have reported mandible mass, and tongue length and mass (Mitchell et al., 2013B).

There has also not been a systematic analysis of the ontogeny of their gastrointestinal tract. Studies on ruminants in general have concluded that the size of the gastrointestinal tract should increase linearly with increases in body mass (Demment, 1982; Demment and van Soest, 1985; Ginnett and Demment, 1997). Ginnett and Demment (1997) qualitatively confirmed this conclusion in giraffes by studying the eating habits of males and females. Males eat more in a shorter time than females and as males are larger than females they must also have a larger rumen. Clauss et al. (2003A) suggested that the most important function of the rumen is to delay the passage of ingesta and prolong digestion time. Delayed passage implies a slowly emptying rumen which inhibits intake, so its absolute and relative mass should increase linearly with body mass to compensate for both intake limitation and for the greater absolute energy needs that large size demands. In a seminal but controversial study Hofmann (1989) classified giraffe as concentrate selectors or obligatory browsers and, therefore, the structure of their gastrointestinal tract should be different to that of grazers. Browsers have relatively small rumens (Giesecke and van Gylswyk, 1975),

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a relationship confirmed by a meta-analysis of published data (Clauss et al., 2003B), and relatively big intestines (Hofmann, 1989). However, no quantitative data exists to support either one or the other of these possibilities, or to describe changes in the mass of the major components of the gastrointestinal tract in wild giraffes during growth.

With some exceptions (Weckerly, 2010; Luna et al., 2012) many of the data used to describe the gastrointestinal morphophysiology of ruminants have been derived from interspecific studies of mature animals with different body masses. In the study reported here measurements of gastrointestinal dimensions in 32 wild giraffes of body mass ranging from 289 to 1441 kg were used to generate intraspecific, ontogenic, allometric equations to describe changes in their gastrointestinal morphology during growth and to provide a basis for an analysis of their digestive physiology. In 9 other giraffes of body mass ranging from 181 to 1396 kg the growth patterns of the parotid glands, masseter muscles, mandible and tongue have been analyzed. Our data have allowed us to estimate giraffe energy requirements, feed intake and the home range size needed to support their metabolism. The hypothesis on which the study was based is that giraffe digestive morphophysiology will be uniquely adapted and different to that of grazing ruminants as predicted by Hofmann (1989).

2. Method

2.1. Body mass (Mb, kg)

In total, body mass was measured in 30 female giraffes (Mb range 147 to 1029 kg) and 30 male giraffes (Mb range = 181 to 1441 kg) that had been culled as part of the Bubye Conservancy management program in Zimbabwe. Of these, 32 constituted the study group for analysis of gastrointestinal morphology and 9 for analysis of the masticatory apparatus. At the time of cull giraffes were browsing/standing quietly. 22 (13 + 9) of the giraffe were culled at the start of the wet season (November) and 19 at the end of the wet season (April). Giraffe were culled opportunistically between 0600 and 1700 h. The content of their gastrointestinal tract was natural browse existing at the time of cull. Two methods were used to determine body mass to take into account loss of tissue during dissection and variation with season. First, before any dissection took place length (L) and girth (G) in meters were measured and body mass (kg) was calculated from regression equations developed for giraffes by Hall-Martin (1977). These equations are:

$$\text{Males} : 26.117 * L * G^2 + 33.945$$
$$\text{Females} : 25.400 * L * G^2 + 66.109$$

where L (meters) is the total length measured from the tip of the nose to the tip of the tail and G (meters) is the girth of the thorax measured immediately caudal to the front legs. Secondly, the giraffes were weighed piecemeal as described previously (e.g. Mitchell et al., 2009). The body mass used in our analyses was the mean of the mass calculated from the relevant gender specific equation and the mass obtained by piecemeal weighing. In males the relationship between piecemeal and calculated Mb is Calculated Mb = $0.86 * \text{PiecemealMb} \wedge 1.03$ ($\text{CI}_{\text{exp}} = .97$–1.09; $R^2 = .9754$), and in females CMb = $1.39 * \text{PMb} \wedge .96$ ($\text{CI}_{\text{exp}} = .90$–1.02; $R^2 = .9792$). Before piecemeal weighing both parotid salivary glands, both masseter muscles, and the tongue were removed by dissection. The mandibles were cleaned by boiling. All components were weighed to an accuracy of 2 g using an electronic scale, and in the case of tongue length, it was measured to an accuracy of 1 cm.

2.2. Rumen-complex and intestine mass (kg)

We measured total forestomach mass (rumen, reticulum, omasum and abomasum including their contents = rumen-complex) and total intestine mass (small and large intestines combined including their

contents = intestine). No attempt was made to separate mesenteries and/or adnexal adipose tissue or to weigh contents separately from organ tissue. Measurements of total gastrointestinal mass (kg; rumen-complex + intestines) were obtained from 30 giraffes (15 males Mb range 455–1441 kg), and 15 females (Mb range 414–1029 kg). Rumen-complex mass was recorded in 12 males (Mb = 455–1282 kg) and in 9 females (Mb = 399–992 kg). Combined intestinal mass was recorded in 13 males (Mb = 289–1282 kg) and in 8 females (Mb = 414–992 kg). Both measurements were recorded in 12 males (Mb = 455–1282 kg) and in 8 females (Mb = 414–992 kg). For the comparison with grazing ruminants we used the mass of the rumen–reticulum contents from 41 wild ruminants obtained from six species by Giesecke and van Gylswyk (1975), Demment (1982) and Maloiy et al. (1982). The six species analyzed were those classified as grazers by Hofmann (1989).

2.3. Intestine length (meters)

We did not measure intestine lengths but in the historical literature intestine length has been reported in 14 giraffes (7 female and 7 male), of age 2 months to 21 years and 3 months (Table 1B). More recently Perez et al. (2009) measured intestinal lengths in a two-year-old male weighing 754 kg and a 17 year-old female weighing 800 kg (Table 1B). These data were used to develop allometric equations to describe the growth of intestinal length with age. One other measured length is known in a giraffe of known body mass (545 kg) and it was reported to be 280 ft or 85 m (Goetz and Budtz-Olsen, 1955). This length:body mass relationship is not consistent with other data and was probably an error of reporting, so it has not been included in the analysis. The correct length was most probably 180 ft = 54 m. Intestine length of giraffes was also compared with the lengths found in 47 animals from 8 species of wild African grazing ruminants of body mass 29–240 kg and 50 animals from 8 species of wild African browsing/intermediate feeder ruminants of body mass 8.5–411 kg (Table 1C; Woodall and Skinner, 1993).

2.4. Energy balance

Three measures of energy consumption in a mammal are basal metabolic rate (BMR), resting metabolic rate (RMR) and field metabolic rate (FMR). The best measure of the minimum daily energy consumption is FMR. The main determinant of FMR in a ruminant is body mass as described by Nagy (2005); kj/day and it was estimated for the giraffes in this study by an allometric equation derived from data for FMR in ruminants (Nagy, 1994, 2005; Calder, 1996; McNab, 2002) and compared with estimates obtained empirically by Pellew in giraffes (Pellew, 1984A). Energy is produced by a combination of fermentation of the cell wall of browse eaten and fermentation and digestion of browse cell contents. The main product of fermentation is volatile fatty acids (VFAs). The main sites of fermentation are the rumen and large intestine. Fermentation in the abomasum and small intestine of giraffes is negligible accounting for 5.5% and 3.4% respectively of total VFA produced (Clemens and Maloiy, 1983). The energy content of VFA varies according to the ratio of the acetic: propionic: butyric acid mixture present but is remarkably constant varying by less than 5% across ruminants. Its average value in 20 species of ruminant was found to be 1125 ± 50 kj/mol VFA (Gordon and Illius, 1994). In eight browsers it was 1109 ± 49 kj/mol, in eight grazers 1151 ± 47, and in four intermediate feeders 1110 ± 51. The average value in six giraffes was 1095 kj/mol (Maloiy et al., 1982). The rate at which VFAs are produced in giraffes is 4.06 mol/kg dry matter/day (Maloiy et al., 1982). The concentration of dry matter (DM) in the rumen-complex (including the abomasum), and hindgut (caecum, proximal and distal colon) in giraffes has been measured by Clemens and Maloiy (1983) to be on average 13.5 ± 0.5% and 18.5 ± 2.0% of mass respectively. The amount of energy (kj/day) produced by fermentation in the rumen-complex and hind gut of the giraffes in this study was calculated from the fermentation data of Maloiy et al. (1982) and Clemens and Maloiy (1983) and from the masses of the rumen-complex and intestine