Digestive tract pathology of captive giraffe. A unifying hypothesis


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DIGESTIVE TRACT PATHOLOGY OF CAPTIVE GIRAFFE (Giraffa camelopardalis) 
AN UNIFYING HYPOTHESIS

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Abstract
Captive giraffe (Giraffa camelopardalis) are affected by four major pathological conditions linked to their nutrition: (1) the so-called "peracute mortality syndrome" with complete absence and serous atrophy of body fat stores, (2) phytobezoars, i.e. fibrous conglomerates of plant material, in the omasum and abomasum, (3) rumen acidosis or (4) partial loss of the dorsal ruminal papillation. We hypothesise that all four conditions can be explained by the fact that the giraffe, like other browsing ruminants, is not adapted to the physical structure of grass or lucerne hay, and ingests this material in comparatively lesser amounts than grazing ruminants would.

Zusammenfassung

Résumé
En captivité, giraffes souffrent, en général, de quatre malaises alimentaires: (1) le "syndrome de mortalité peracut" avec l’atrophie totale ou l’absence complet de toute matière grasse, (2) des phytobezoares, i.e. E. Conglomerats fibreux du matériel plantier dans l’omasum ou l’abomasum, (3) de l’acidose ruminale et (4) la perte des papilles du rumen dorsal. Nous présentons l’hypothèse que ces quatre malaises sont le conséquence du fait que les giraffes, comme d’autres ruminants folivores, ne sont pas adaptées à la structure physique du foin d’herbe ou de lucerne et consomment ces matériaux en moindres quantités que les ruminants adaptés à l’herbe.

Key words: Giraffa camelopardalis, peracute mortality syndrome, phytobezoar, rumen acidosis, physical structure of forage, browser/grazer-dichotomy

Introduction
The giraffe (Giraffa camelopardalis) is regarded as a typical browser or "concentrate selector" (32). Browsing ruminants are especially difficult to feed in captivity (33). At the same time, the giraffe is the largest living ruminant species, with males surpassing the one-ton threshold set by Owen-Smith (50) for the status of a "megaherbivore". If we assume that the feeding regime for browsing
ruminants in zoos is generally inadequate, the large absolute amounts ingested by the giraffe should lead to an obvious gap between “requirements” and dietary provision.

**Nutritional pathology in captive giraffe**

There are several reports of deficiencies of both vitamin E (4, 7, 28, 31, 57) and calcium (6, 25, 29, 36, 43, 61) in captive giraffe; however, these deficiencies occur in numerous other zoo animals, not only in browsing ruminants. In this review, we want to focus on four particular disease syndromes typical for captive giraffe, and probably other browsers as well:

1. The “peracute mortality syndrome”
   For general reviews of this syndrome, see (22) and (38). Typically giraffe die suddenly, often directly after a stressful episode. At necropsy a distinct cause of death is absent, but there is serous atrophy of all body fat stores. Total absence of body fat has been reported in captive giraffe in an alarming number of cases, and from as early as 1854 (1, 7, 8, 9, 16, 17, 21, 22, 23, 29, 37, 38, 40, 45, 48, 57, 58). While it has been speculated that cold stress might play a crucial role in triggering the syndrome (11), the absence or atrophy of fat stores most probably indicates a fundamental dietary deficiency.

2. Phytobezoars
   Phytobezoars are “ball-shaped” conglomerates of plant material that form spontaneously in the gastrointestinal tract and can lead to mucosal irritation and blockage of the passage of ingesta. They have been reported repeatedly in giraffe (1, 5, 23, 24, 26, 27, 39, 47) and in at least one other browsing ruminant in captivity, the mule deer (*Odocoileus hemionus*, 55), while there are no reports in captive wild grazing ruminants. The phytobezoars are located mainly in the abomasum, and often associated with a high fibre or grass intake, and several authors recommend mowing the grass of a giraffe enclosure regularly in order to prevent grass ingestion by the animals.

3. Rumen acidosis
   Marholt (46) documented that more than 80 % of all browsing zoo ruminants investigated showed pathological evidence of (chronic) rumen acidosis; unfortunately, no giraffes were included in his study. Krische and Elze (42) demonstrated that certain rations fed to giraffe could trigger acidosis, but did not investigate living or deceased animals. Therefore, while it is very likely that the findings of Marholt (46) can be transferred to giraffe as well, Clauss (9) remains the only report of changes of the ruminal mucosa in a deceased giraffe indicative of chronic acidosis. However, in the pathology archives of the IZW Berlin, the case of a giraffe in poor body condition is recorded that underwent periods of trembling over a year before it died after such an episode. At necropsy, there were copious amounts of rumen contents, which had a pH of 5.0. The histological examination of the ruminal mucosa yielded changes consistent with rumen acidosis.

4. Partial loss of the dorsal ruminal papillation
   Hofmann and Matern (35) reported changes in rumen appearance in two zoo giraffe that differed drastically from Hofmann’s (32) findings in free-ranging wild specimens: while in giraffe from the wild the rumen papillation is evenly distributed over the whole organ surface, the dorsal papillation in these two zoo giraffe had atrophied and partially disappeared, resulting in a rumen that resembled those of grazing ruminants. The authors contributed their finding to a diet too high in dietary fibre. Fox (23) made a similar observation in a zoo giraffe he dissected. However, not knowing that animals from the wild look quite different, he simply stated that the giraffe has a rumen “like a cow”.

We propose that these four different syndromes can be explained by one mechanism, namely that the giraffe, like other browsing ruminants, is not adapted to the physical structure of grass hay.
The interaction between natural forage and ruminant feeding type

Traditionally, zoo ruminant nutrition has focused on the chemical composition of the natural forages of grazers and browsers, i.e. the content of protein, crude fibre, soluble carbohydrates etc. While the difference in nutrients between different forages has been extensively described (e.g. 54), the difference in physical structure has received much less attention. However, it has been hypothesised that it is rather the physical structure of forage than its chemical composition that the different ruminant feeding types have adapted to (fig. 1, 14). Grass, grass hay and lucerne hay are typically broken down into longish, fibre-like particles (59) that form a "fibrous raft" in the rumen, which is responsible for the "stratification" of rumen contents typically found in grazers (32). This fibrous raft floats on the liquid layer of rumen contents. It is only when the large particles have been reduced in size (mainly by rumination) so that they are no longer trapped in the fibrous raft, and have become more dense in the process, that they can sink through the liquid layer to the bottom of the rumen, from where they are expelled into the next forestomach chamber with the next rumen contraction (44). This mechanism takes time, which explains why particles are retained much longer in a grazer's rumen than fluids (10), and ensures that only small particles leave the rumen of a grazer. Grazers have evolved anatomical adaptations to the tendency of grass to form a fibrous raft and stratified rumen contents: as there is a distinct gas layer above the fibrous raft, the dorsal part of the rumen mucosa is not papillated (32), as no fermentation takes place in the gas layer. The rumen itself is equipped with thick pillars and strong muscle layers (32) that facilitate a proper handling of the comparatively tough fibrous raft. In this respect, the dorsal attachment of the rumen to the abdominal wall (32) might act as a lever point against which the rumen muscles can pull. On the other hand, browse is typically broken down into polygonal particles (56, 60) that cannot form a fibrous raft. Therefore, the rumen contents of a free-ranging browser are not stratified (12, 32). The lack of stratification allows for a faster passage of particles from the rumen (10), and allows comparatively larger particles to escape (15). As browsers do not have to deal with a fibrous raft in nature, there was no need to evolve strong muscle layers, thick rumen pillars or a dorsal attachment of the rumen (32). As there is no distinct gas layer, the rumen of a browser is evenly papillated (32).

The nutritional dilemma of captive giraffe: to choose between concentrates and hay

What happens if a browser, with its particular anatomical structures, faces a feeding regime in which only very little of its natural forage (i.e. browse) is offered, and where it has to choose between concentrates/produce and ad libitum hay instead? The different options and their hypothetical consequences are illustrated in fig. 2. Depending on the feeding habit of the animal, and the detailed characteristics of the concentrate feeds and the hay quality, it can choose anything between a high proportion of concentrates and a high proportion of hay fibre. Should the animal refuse to ingest the hay in larger proportions, because it is not anatomically equipped to handle it, its rumen contents will be unstratified, but the disproportionately high intake of concentrates will lead to a (chronic) rumen acidosis. Should the animal on the other hand ingest hay in larger proportions, it will have a certain amount of longish, fibre-like particles in its still relatively unstratified rumen ingesta. As larger particles can escape from a browser's rumen as stated above, these longish particles can pass on into the following forestomach chambers, where they can conglomerate to form phytobezoars. On the other hand, as a slight stratification might develop due to a high proportion of hay fibre, a small gas layer might develop above the would-be fibrous raft, resulting in a loss of the dorsal ruminal papillation. In any case, as the rumen of the giraffe is not anatomically equipped to handle even the beginning of a fibrous raft as efficiently as it would handle unstratified ruminal contents, it cannot pass the ingesta contents with hay particles as fast — the rumen is "blocked" — and thus the animal has to reduce its overall food intake; satiety signals derived from receptors responsive to forestomach fill might reinforce this tendency. A generally low food intake, of course, will not allow the animal to build fat stores, and therefore might make it more susceptible to particularly stressful episodes. It should be noted that a suboptimal, varying food intake has also been reported for chronic acidosis in cattle (53).
Experimental evidence

Several investigators have measured the food intake in free-ranging and captive giraffe (2, 13, 18, 20, 30, 41, 49, 51, 52). In an experiment by Foose (20), different zoo herbivores, amongst which were ruminants of the grazer and the intermediate feeding type and giraffes, were fed ad libitum grass hay or lucerne hay only. The results of the intake measurements are displayed in fig. 3. Obviously, food intake increases with increasing animal body weight. On the ad libitum grass hay feeding regime, it seems that grazers ingested on average slightly more than intermediate feeders, a difference that seems to disappear for the ad libitum lucerne hay feeding regime. This might suggest that lucerne hay, which is broken down into fibre-like particles of a somewhat lesser length than grass hay (59), is more suitable for intermediate feeders. The giraffes, however, have very low intake values for either ad libitum hay-only diet.

In another experiment (13), it was noted that a group of captive giraffe fed ad libitum lucerne hay and an ad libitum maintenance pelleted diet had low food intakes compared to data from other zoo giraffes or from free-ranging animals. Although the low sample size did not allow statistically significant statements, it seemed that the animals increased their intake when offered additional amounts of browse or of linseed extraction chips. This was interpreted as an indication that both forage of a favourable physical structure and a more palatable concentrate feed could have beneficial effects on overall food intake.

Conclusion

The reality of digestive processes in giraffe will be more complex than presented in our simplified scheme. Depending on numerous factors, hay or grass intake need not invariably lead to bezoar formation, and chronic acidosis need not necessarily lead to a general reduction in food intake. However, the hypothesis presented provides a reasonable concept that explains observations reported in this and in other species (14). More detailed nutritional studies, and especially thorough pathological investigations of deceased animals combined with recorded feeding histories, will finally determine the value of this hypothesis. Our theory emphasises the importance of an appropriate physical structure of the fibre source offered to the animals. A year-round supply of browse would obviously be the desired feeding regime, but this will pose enormous logistic problems for many facilities. Other fibre sources than grass and lucerne hay could be tested, e.g. certain silage’s; in two other browsing species, the moose and the roe deer, good experiences have been made with the use of chopped hay (3, 19). Clearly, further intake studies, using different fibre sources, are warranted in giraffe.

References


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Fig. 1. Schematic correlation between the physical structure of forages and the anatomical adaptations of ruminant feeding types to the consequences of these physical properties. (From 14, rumen images adapted from 32,34.)
Fig. 2. Schematic display of the different dietary options open to captive giraffe fed a diet based on concentrates and hay, and their hypothetical consequences.
Fig. 3. Food intake (expressed as kg organic matter) of different ruminant species on an *ad libitum* grass hay-only and an *ad libitum* lucerne hay-only diet. (Data from 20).