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Adaptation strategies of camels on a thornbush savannah pasture: comparison with other domestic animals

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Introduction

In many semi-arid areas of the world unequal distribution of rain leads to severe seasonal fluctuations in the forage available to the animals. During severe dry seasons the amount of forage is reduced. At the same time, the plant cell wall constituents, especially of grasses, increase while the proportion of easily digestible cellular contents is reduced[1]. Some herbivores, especially certain indigenous animals, are able to survive under harsh conditions and these animals are often indispensable to men living under such conditions because, in addition to producing high quality protein for human food, they are also used as draught and pack animals, and they supply leather and wool.

Herbivores use several strategies to adapt to severe dietary conditions[2]. These include selective feeding behaviour and/or an improved digestion of cellulose. A limiting factor for the cellulose digestion is the slow microbial fermentation. Cellulose digestibility increases with longer mean retention time of particles in the fermentation chamber. Compared to hindgut fermenters, foregut fermenters have longer mean retention times of particles in the forestomach and hence a higher cellulose digestibility[3]. A long retention time of feed particles can be achieved by a large volume of the fermentation chamber and/or by a selective retention of feed particles. Different species of herbivores possess a variable ability for feed selection[4] and cellulose digestion[1, 3] and therefore use various strategies to adapt to harsh grazing conditions.

Camelids and ruminants developed independently from each other a highly specialized forestomach fermentation system[5]. Comparative studies have shown similarities as well as differences between camelids and ruminants. Both have forestomachs divided into several compartments. However, the morphology[6] and histology[7, 8] are different between camelids and ruminants. The general pattern of fermentation in the forestomach of a camel and a zebu steer fed a similar diet is basically the same[9]. However, camelids have higher absorption rates of solutes and water from the forestomach than ruminants[5]. Both camels and ruminants do ruminate. On the other hand, the pattern of forestomach motility is different between camelids and ruminants[10, 11, 12]. The structure and function of the salivary glands as well as salivary composition and secretion rates are comparable between camels and ruminants[13].

The aim of this paper is to examine the apparent adaptation strategies of the camel on a thornbush savannah pasture. Comparisons with domestic ruminants, cattle, sheep and goats will be given.

Dietary preference and multispecies grazing systems

An important survival strategy of herbivores in a harsh environment is the ability to select the more nutritious parts of a plant. In a wide ranging morphological study and from the feeding habits in wild and domestic ruminants, Hofmann[14]

classified them into: a) grass and roughage eaters or grazers; b) intermediate feeders or adaptable mixed feeders, and c) concentrate selectors or browsers. The ability of grazers like cattle to select plants in a natural pasture is little developed. On the other hand, browsers like camels and goats, and to a less extent intermediate feeders (sheep), are able to seek out herbs, fruits and succulent leaves of a great variety of plants (figure 1). According to KAY et al.[15], ruminants that are predominantly grazers have a more voluminous reticulorumen and a longer retention of feed particles than the browsers and concentrate selectors. Grazing ruminants or roughage eaters therefore utilize fibrous diets more efficiently than concentrate selectors. On the other hand, concentrate selectors are able to choose the easily digestible plants from the vegetation in a harsh environment.

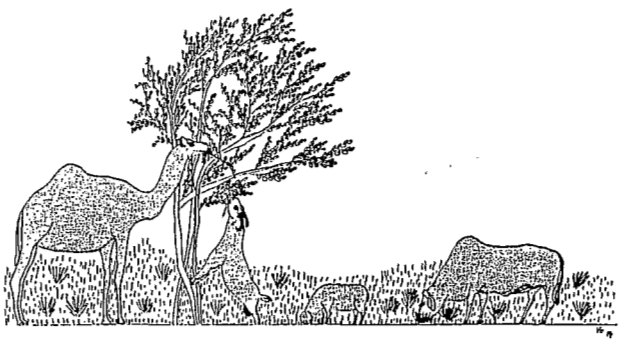

Figure 1. Sketch of dietary preference of camels, goat, sheep and cattle. From Engelhardt et al.[16].

We carried out comparative studies of the dietary preferences of indigenous camels, cattle, sheep and goats on a semi-arid thornbush savannah in Northern Kenya. Cattle and sheep were found to prefer vegetation at ground level (approximately 70% of their total feeding time). Their diet mostly consisted of grasses, herbs and small shrubs. This type of vegetation undergoes more severe seasonal fluctuations in quantity and quality than deep rooted large bushes and trees which are not used by cattle and sheep. On the other hand, goats can browse up to 2 meters above the ground with approximately 60% of their total feeding time being spent at a height between 0.7 and 1.2 m. above the ground level. Camels are capable of reaching plants up to a height of 3 meters[17, 18]. That means that during the dry season when leaves of big trees may be the only green vegetation available, camels and to some extent goats benefit greatly compared to cattle and sheep. Therefore, cattle and sheep which mainly feed at ground level are more confronted with large differences between seasons in respect to quantity and quality of forage.

When the number of plant species selected by the animals are taken into consideration, camels, goats as well as sheep consume 30-60 different plant species whereas cattle feed on only 30 different plant species[17]. In 90% of the total feeding time during the dry season, camels, goats and sheep each consumed 22-27 plant species compared to only 8 taken by cattle. That indicates that if some plants may not be present during the dry season, camels, goats and sheep can still select other plants. However, this may not be the case with cattle because cattle consume a limited number of plants.

The plants selected by the animals were divided into 3 groups; low, medium and high quality according to their dry matter disappearance rates (DMDR) from nylon bag studies[17, 20]. The proportion of poor quality plants in the diet of the animals during the dry and green season is given in figure 2. The proportion of poor quality plants in the diet of camels was lowest and did not vary from season to season. Cattle consumed a high proportion of poor quality plants during the green season (40% of the total feeding time). During the dry season cattle spent 80% of feeding time on poor quality plants. Sheep spent about 20% and 45% of their total feeding time on poor quality plants during the green and dry season, respectively. During the green season goats spent 5% of their feeding time on poor quality plants but this increased to 20% during the dry season. The highest proportion of time spent feeding on poor quality plants especially during the dry season was obtained from cattle followed by sheep. This can be expected because cattle and sheep consumed a high proportion of monocotyledons and the DMDR of monocotyledons was found to be 50-60% lower during the dry season compared to the green season[20]. On the other hand the DMDR of dicotyledons was only 8% lower during the dry season compared to the green season. Since monocotyledons are of low digestibility during dry season, obviously camels are able to avoid the changes in feed quality because monocotyledons account for less than 1% of their total feeding time[17].

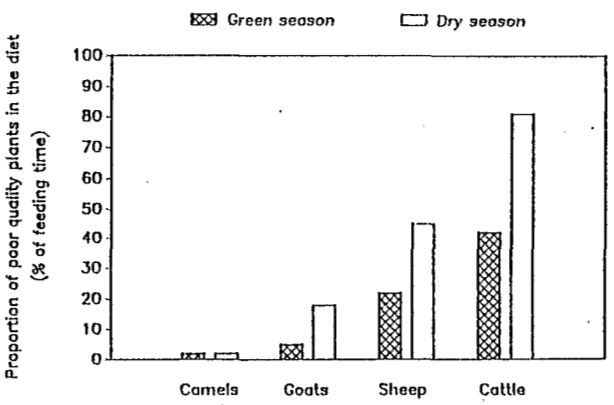

Figure 2. Time spent feeding on poor quality plant species during the dry and green seasons expressed as percentage of total feeding time. Data from Lechner-Doll et al.[19].

It may be concluded that camels and to some extent goats are able to select plants whose quality does not change greatly between seasons. On the other hand, cattle and to a certain extent also sheep fed on plants of lower quality during the dry season because they spent longer feeding on monocotyledons. An important adaptation strategy by camels is the ability to select dicotyledons of high

digestibility. In addition the digestibility of the plants selected by camels does not change greatly from season to season. The fact that camels can feed selectively at a height which other domestic animals do not reach enables them to have an advantage over the other indigenous animals studied.

The time spent feeding on various plants was different between various animal species in terms of number of plant species, type of plants and height above the ground. Thus, feeding behaviour of indigenous animals in our study area was complementary rather than competitive. Therefore, in a thornbush savannah pasture like our study area, instead of having only one animal species, a multiple species grazing system may help to reduce the grazing pressure and its consequency, the overgrazing of the biotipe.

Adaptation of animals to utilize poor quality forage

Efficiency of digestion of poor quality cellulose-rich forage can be enhanced if the retention time of digesta in the forestomach is prolonged[3]. Retention time of feed particles in the forestomach may be a critical limiting factor for the ability of the animal to adapt to harsh pasture conditions. Retention time is prolonged by increasing the forestomach volume, the selective retention of feed particles in the forestomach or by a reduction of feed intake.

Mean retention time (MRT) of particles

In ruminants and camelids fed on roughage diets, particles are retained in the forestomach considerably longer than fluid[1, 21, 22, 23]. In our experiments with free ranging animals in northern Kenya, small particles were retained 1.7-3.1 times longer than fluid[23]. The longest MRT of particles were measured in cattle (28 ± 5 h. in the green and 36 ± 9 h. in the dry season). Camels had longer MRT of small particles in the forestomach (25 ± 2 h.) than goats (21 ± 7 h.) and sheep (20 ± 8 h .) in the green season. No significant difference between sheep and camels was found in the dry season (29 ± 8 h. and 29 ± 4 h., respectively). There are several reasons for the increase of MRT of particles.

Changes in forestomach volume and feed intake

All animals increased the forestomach volume in the dry season compared to the green season. Mean forestomach volumes of camels were 9 ± 1% of body weight (BW) during the green season but increased to 11 ± 2% during the dry season. The other animal species had larger rumen volumes than camels 11 ± 3% and 16 ± 5% of BW during the green and dry seasons, respectively. The relative increase of the forestomach volume and MRT of small feed particles in the dry season are given in table 1.

Table 1

RELATIVE INCREASE OF THE FORESTOMACH VOLUME AND MRT OF SMAL FEED PARTICLES IN THE DRY SEASON (AS A PERCENTAGE OF THE GREEN SEASON VALUE)

ANIMAL SPECIES	FORESTOMACH VOLUME	SMALL PARTICLES RETENTION
Camels	35.2%	17,9%
Cattle	56.8%	27.3%
Sheep	74.8%	46.1%
Goats	40.7%	22.0%

It is known for conventional breeds of cattle and sheep that forestomach retention time of digesta is negatively correlated with feed intake[25, 26, 27]. In these experiments reduced feed intake led to an increase of retention time of particles and a reduction of the rumen volume. Although fibre digestion is improved when feed intake is reduced the lower intake of total dry matter cannot be compensated. Therefore, such a short term effect can not be considered to be an adaptation process to low quality forage. In the present study, increase in the MRT of particles and forestomach volume were measured during the dry season. In all the animal species the relative increase in the size of the fermentation chambers was greater than the relative increase in the mean retention time of particles (table 1). Therefore, the long retention time of particles may be explained by the large forestomach volume and not a reduced feed intake. Thus our indigenous animals adapted to the poor feeding conditions by increasing the volume of the fermentation chamber and this enabled them to retain particles for a longer time.

Selective retention of small particles

The selective retention of small particles relative to the retention time of fluid (selectivity factor) in the forestomach of our indigenous animals has been recently published[24]. There was no difference in the selectivity factor between seasons. However, camels and cattle had higher selectivity factors than sheep and goats. The higher selectivity factor of particles in camels and cattle may be explained by the more effective retention of small particles within the mass of large particles in the forestomach by a phenomenon called «Filter bed or Matting effect»[23, 28, 29]. Hence differences in the selectivity of particles over fluid may be one of the reasons for a longer MRT of particles in these species. The selective retention of plastic particles of different sizes (1 and 10 mm. long) and densities (0.91, 1.03, 1.22 and 1.44 g. ml^{-1}) was studied in the reticulorumen of sheep fed a hay diet. Plastic particles with a length of 10 mm. were retained 23 h. longer than 1 mm. long particles of the same density. The mean retention time was mostly influenced by particle density and less by particle size[30]. It can thus be concluded that the breakdown rate of large particles is higher than the outflow rate of small particles. Passage of digesta is mainly limited

by the density increase of the feed particles; for feed particles with a higher density the probability of outflow increases considerably. The preferential passage of small dense particles achieves a long retention time of the lighter, larger undigested particles and thus a better cellulose digestion in the forestomach.

The resulting improvement of the digestibility due to a longer retention time of particles in the forestomach was estimated by the nylon bag technique[20, 24]. The digestibility in the forestomach of the slowly digestible, poor quality plants increased by about 12% in sheep compared to 7% in cattle, 6% in goats and 5% in camels due to the respective increase of particle retention. This increase of the digestibility of poor quality forage as a result of increasing MRT of particles is more meaningfull for cattle and sheep because they consume a higher proportion of poor quality forage than goats and camels[19]. Obviously under the present experimental conditions cattle and sheep adapted to the poor forage conditions by increasing the mean retention time of particles. They were thereby able to improve the digestion of poor quality forage. In our earlier experiments carried out in Khartoum, camels retained small particles (2 mm.) in compartments 1 and 2 for about 41 hours when fed a very poor quality feed[21, 23]. Such a long retention time of particles in the forestomach of the camel is a prerequisite for an effective digestion of a fibrous diet. This shows that camels are also capable of increasing mean retention time of particles if forced to live on poor quality forage. In the present study in the thorn bush savannah, camels obviously could select a diet of high quality in sufficient quantities and it was not essential for them to increase mean retention time of particles in order to improve the digestibility of poor forage.

Summary and conclusions

Similarities as well as differences in the digestive physiology exist between camels and ruminants. In the present study adaptation of camels and ruminants grazing the same pasture were compared. Table 2 summarizes adaptation strategies of camels, cattle, sheep and goats to harsh grazing conditions during the dry season in Isiolo District Northern Kenya.

In the thornbush savannah, camels seem to adapt to poor feeding conditions by selecting a diet of high quality throughout all the seasons. This can be attributed to the fact that camels prefer mainly dicotyledon plants of a high digestibility irrespective of the season. In addition camels feed at a higher level from the ground than any other domestic animal species. Therefore, camels are able to avoid competition for the available forage.

An increase in MRT of particles was found to increase the dry matter disappearence rate of poor quality forage. Compared to other animals under thornbush savannah conditions, camels had the smallest increase in MRT of particles. That means, in the present study camels did not improve the digestibility of poor quality forage considerably.

Table 2

A SUMMARY OF ADAPTATION STRATEGIES OF CAMELS AND INDIGENOUS RUMINANTS TO HARSH GRAZING CONDITIONS DURING THE DRY SEASON IN ISIOLO DISTRICT NORTHERN

STRATEGY	CAMEL	CATTLE	SHEEP	GOAT
Selection of high quality feed	+++	—	+	+++
Retention of feed particles	+	+++	+++	++
Increase in digestibility of poor quality forage due to a longer mean retention time	+	+++	+++	++

+++ High or more developed.
++ Medium.
+ Slight or less developed.
— Poor.

On the other hand, it is known that camels are capable of increasing the retention time of particles if they are forced to feed exclusively on poor quality forage. However, in the present study camels were not forced to live on poor quality forage because they were able to select a diet of good quality throughout all the seasons.

References

1. VAN SOEST, P. J. (1982): Nutritional ecology of the ruminant. O & B Books Inc., Corvallis, Oregon.

2. LANGER, P. (1988): The mammalian herbivore stomach. Comparative anatomy, function and evolution. Gustav Fischer, Stuttgart, New York.

3. VAN SOEST, P. J.; JERACI, J.; FOOSE, K.; WRICK, K., and EHLE, F. (1983): Comparative fermentation of fibre in man and other animals. In: *Fibre in Human an Animal Nutrition* (eds.: G. Wallace and L. Bells), Wellington, New Zealand, Royal Society of New Zealand, Bull. 20, 75-80.

4. HOFMANN, R. R. (1973): *The ruminant stomach.* East Africa literature Bureau, Nairobi.

5. RÜBSAMEN, K.; ENGELHARDT, W. V. (1978): Bicarbonate secretion and solute absorption in forestomach of the llama. *Am. J. Physiol. 235,* E1 - E6.

6. VALLENAS, A.; CUMMINGS, J. F., and MUNNELL, J. F. (1971): A gross study of the compartmentalized stomach of two New-World camelids, the llamma and guanaco. *J. Morphol., 134,* 399-424.

7. CUMMINGS, J. F.; MUNNEL, J. F., and VALLENAS, A. (1972): The mucigenous glandular mucosa in the complex stomach of two New-World camelids, the llamma and guanaco. *J. Morphol., 134,* 399-424.

8. LUCIANO, L.; VOSS-WERMBTER, G.; BEHNKE, M.; ENGELHARDT, W, V., and REALE, E. (1979): Die Structur der Magenschleimhaut beim Lama (Lama guanacoe and Lama lamae) I. Vormägen. *Gegenbaurs Morphol. Jahrb.* 125, 519-549.

9. MALOIY, G. M. O. (1972): Comparative studies on digestion and fermentation rate in the forestomach of the one humped camel and the zebu steer. *Res. Vet. Sci.,.* 13, 476-481.

10. HELLER, R.; GREGORY, P. C., and ENGELHARDT, W. V. (1984): Pattern of motility and flow of digesta in the forestomach of llama (Lama guanacoe f. glama). *J. Comp. Physiol.,* 154B, 529-533.

11. GREGORY, P. C.; HELLER, R., and ENGELHARDT, W. V. (1985): Control of stomach motility in the llama (Lama guanacoe f. glama). *Quart. J. Exp. Physiol.,* 70, 51-61.

12. HELLER, R.; LECHNER, M., and ENGELHARDT, W. V. (1986): Forestomach motility in the camel (camelus dromedarius). *Comp. Biochem. Physiol.,* 84A, 285-288.

13. HOPPE, P.; KAY, R. N. B.; MALOIY, G. M. O. (1975): Salivary secretion in the camel. *J. Physiol.,* 244, 32P - 33P.

14. HOFMANN, R. R. (1988): Morphophysiological evolutionary adaptations of the ruminant digestive system. In: *Aspects of Digestive Physiology in Ruminants* (eds.: A. Dobson and M. J. Dobson). Comstock Publishing Associates, pp. 1-20.

15. KAY, R. N. B.; ENGELHARDT, W. V., and WHITE, R. G. (1980): The digestive physiology of wild ruminants. In: *Digestive Physiology and Metabolism in Ruminants* (eds.: Y. Ruckebusch and P. Thivend), MTP Press, Lancaster, pp. 743-761.

16. ENGELHARDT, W. V.; LECHNER-DOLL, M.; HELLER, R.; H. J. SCHWARTZ; RUTAGWENDA, T., and SCHULTKA, W. (1988): Physiology of the forestomach in camelids with particular reference to adaptation to extreme dietary conditions. A comparative approach. *Animal Res. Developm.* 28, 56-70.

17. LECHNER-DOLL, M.; RUTAGWENDA, T.; SCHWARTZ, H. J., and ENGELHARDT, W. V. (1988): Fressverhalten und Anpassung von Haustierarten in der Dornbuschsavanne Nordkenias. In: *Tropische Weiden und Futterresourcen* (ed.: Alkämper) Giessener Beiträge zur Entwicklungsforschung, pp. 249-253.

18. SCHWARTZ, H. J. (1988): Verbesserte Nutzung natürlicher Weiden in den Trockenzonen Afrikas durch Besatz mit gemischten Herden. In: *Beispiele deutscher Agrarforschung in den Tropen und Subtropen* (ed.: J. H. Weniger), I. C. T., Berlin, pp. 33-44.

19. LECHNER-DOLL, M.; RUTAGWENDA, T.; SCHWARTZ, H. J., and ENGELHARDT, W. V. (1989): Seasonale Veränderungen der Verweilzeit von Futterpartikeln im Vormagen von afrikanischen Hauswiederkäuern und Kamelen. *J. Anim. Physiol. A. Anim. Nutr.* (in press).

20. RUTAGWENDA, T. (1989): Adaptation of sheep and goats to seasonal changes of forage on a semi-arid thornbush savannah pasture in northern Kenya. *Diss., Tierärztl. Hochsch.* Hannover.

21. HELLER, R.; LECHNER, M.; WEYRETER, H., and ENGELHARDT, W. V. (1986): Forestomach Fluid Volume and Retention time of Fluid and Particles in the Gastrointestinal Tract of the Camel, *J. Vet. Med. A.,* 33, 396-399.

22. LECHNER-DOLL, M. (1986): Selektive Retention von Futterpartikeln verschiedener Größe im Magen - Darmkanal von Kamelen im Vergleich mit Rindern und Schafen im Sudan. *Diss., Tierärztl. Hochsch.* Hannover.

23. LECHNER-DOLL, M. and ENGELHARDT, W. V. (1989): Particle size and passage from the forestomach in camels (Camelus dromedarius) compared to cattle and sheep fed a similar diet. *J. Anim. Physiol. A. Anim. Nutr.,* 61, 120-128.

24. LECHNER-DOLL, M.; RUTAGWENDA, T.; SCHWARTZ, H. J.; SCHULTKA, W., and ENGELHARDT, W. V. (1989): Seasonal changes of ingesta mean retention time and forestomach volume in indigenous grazing camels, cattle, sheep and goats on a thornbush savannah pasture (in press).

25. MUDGAL, V. D.; DIXON, R. M.; KENNEDY, P. M., and MILLIGAN, L. P. (1982): Effect of two intake levels on retention times of liquid, particle and microbial markers in the rumen of sheep. *J. Anim. Sci.* 54, 1051-1055.

26. POPPI, D. P.; MINSON, D. J., and TERNOUTH, J. H. (1981): Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Aust. J. Agric. Res.,* 32, 99-108.

27. VARGA, G. A., and PRIGGE, E. C. (1982): Influence of forage species and level of intake on ruminal turnover rates. *J. Anim. Sci.* 55, 1498-1504.

28. SNIFFEN, C. J.; HOPPER, A. P.; WELCH, J. G.; RANDY, H. A., and THOMAAS, E. V. (1986): Effect of hay particle size on chewing behavior and rumen mat consistency in steers. *J. Dairy Sci.* 69 (Supplement 1), 135.

29. FAICHNEY, G. J. (1986): The kinetics of particulate matter in the rumen. In: *Digestion and metabolism in ruminants* (ed.: L. P. Milligan, W. L. Grovum and A. Dobson), Reston Book, Prentice Hall, Englewood Cliffs, New Jersey, pp. 173-195.

30. KASKE, M. and ENGELHARDT, W. V. (1989): *The effect of size and density on mean retention time of particles in the gastrointestinal tract of sheep* (in press).