

MAMMALIAN STRATEGIES FOR UTILIZING HIGH FIBRE DIETS

I.D. HUME*

SUMMARY

A number of different strategies have evolved among mammals for utilizing fibrous diets. The Ruminantia are best equipped for fibre digestion, but on very high fibre diets their nutrient intake is severely limited by a slow rate of passage of food residues out of the reticulo-rumen. Foregut fermenters such as the macropod marsupials and hindgut fermenters do not suffer from this limitation on very high fibre diets, but fibre digestion is less complete. The relative advantages and disadvantages of these alternative strategies are discussed in relation to feeds of different fibre concentrations.

INTRODUCTION

The Fifth International Symposium on Ruminant Physiology held in France in 1979 contained a section on comparative digestive physiology of herbivores. This was a new development, and reflects the recent increase in interest in comparative studies of digestive physiology in several centres around the world, including the University of New England. Many of these studies have been concerned with alternative strategies found among mammals in their utilization of poor quality, high fibre roughage diets.

Ruminants

There is no doubt that among the various groups of mammals the Ruminantia are best equipped for fibre digestion. This is basically because of a physiological mechanism at the reticulo-omasal orifice which has been shown to selectively retain within the reticulorumen the larger food particles (Stevens *et al.* 1960). This mechanism has only been demonstrated in the domestic ruminants, but similar anatomy suggests its presence in at least some of the other bovids (i.e. sheep, cattle, goat, gazelle) and probably the cervids (deer), giraffids (giraffe, okapi) and antilocaprids (oronghorn antelope). The camelids (camel, llama) have an apparently analogous constriction between the second and third compartments of the stomach (Vallenas *et al.* 1971), but it is not known whether an analogous function exists. No similar structure or function is known in any other foregut fermenter, passage from the fermentative to the acidic part of the stomach being little if at all impeded.

* Department of Biochemistry and Nutrition, University of New England, Armidale, N.S.W. 2351

The mechanism whereby the larger feed particles are selectively retained in the, reticulorumen has several important consequences for ruminants. First; there is efficient separation of the fermentative from the acid-secreting region of the stomach. This has allowed development of the most obvious special feature of the ruminants, rumination, whereby forestomach digesta are regurgitated, rechewed and reswallowed in a frequent, regular pattern.. This pattern may be repeated some 500 times a day, occupying a total of more than 8 hours, and involving more than 25,000 chews (Gordon 1968). Rumination occurs in all the Ruminantia and the Camelidae. While it is claimed that some other herbivores ruminate (Hendricks 1965), this is incorrect.

The second consequence of importance is that retention times of coarse feed particles in the reticulorumen can be quite long, with mean residence times exceeding 60 hours. This, in combination with the mechanical breakdown achieved by rumination, results in the efficient digestion of fibre which is characteristic of the ruminants. However, a further consequence of this mechanism at the reticulo-omasal orifice is that on the most highly fibrous feeds retention is so long that undigested material accumulates in the rumen and food intake and therefore nutrient supply is reduced,. The relationship between food intake by ruminants and increasing content of cell-wall constituents, one measure of fibre, is shown in Fig. 1.

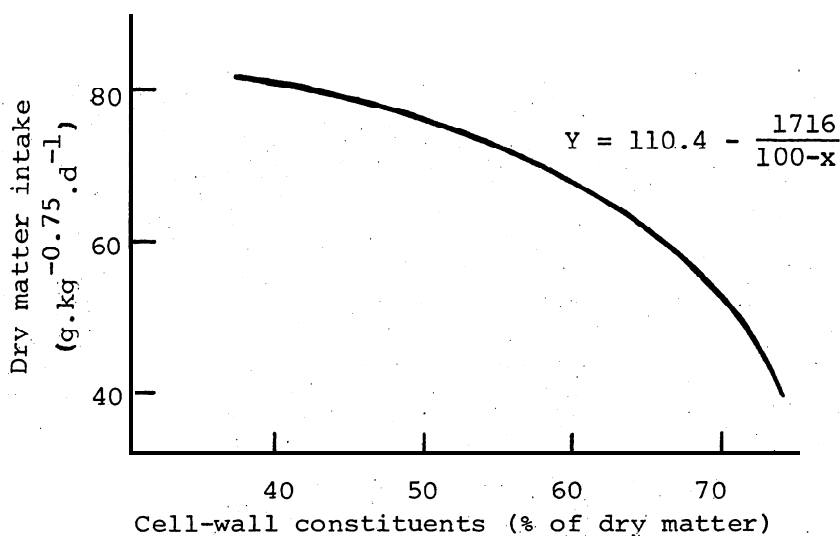


FIGURE 1 Relationship between dry matter intake by ruminants and fibre content of forages measured as cell-wall constituents. From: Van Soest (1965).

Hume and Warner (1980) consider that maximal efficiency of fibre digestion by this strategy' would be adaptively important only if the quantity of food was limiting, and that food poorly digested. This suggests that the special features of ruminant digestion evolved in regions where both quality and quantity of forage were either irregularly or seasonally limiting, such as in hot deserts, cold deserts (tundra) or deciduous forests. Relatively few modern ruminants live in the sort of environment for which their special: ruminant adaptations evolved, due either to migration or to a change of climate. These adaptations are of no great disadvantage except at very high fibre concentrations in the food (Janis 1976); the ruminant is still a very

efficient foregut fermenter with all its advantages. It seems likely that the camelids, with their similar digestive physiology, evolved in a similar way, though all the modern wild representatives remain in arid environments similar to those postulated for the origin of their special adaptive features.

Hindgut fermenters

Compared with ruminants, fibre digestion is less efficient in all the hindgut fermenters studied. However, among the hindgut fermenters there are significant differences in efficiency of fibre digestion. There is much less information available on fibre digestion in the caecum and colon than in the reticulorumen, but it appears that, among the hindgut fermenters, at least two alternative strategies have evolved. Hume and Warner (1980) refer to these as 'colon fermentation' and 'caecum fermentation'.

Colon fermentation

In colon fermenters the primary expansion of the hindgut is in the proximal colon; expansion of the caecum is also usual, but a few exceptions exist, such as the wombat and the giant panda, which rely entirely on a colonic fermentation to utilize fibre. The caecum, if developed, appears to function simply as an extension of the proximal colon as the site of fermentation, with the contents of the two organs mixing together with little, if any, separation of fluid and particles. In the horse, particulate digesta pass through the digestive tract a little more slowly than fluid (Argenzio *et al.* 1974), but this appears to be a simple mechanical function of the haustrations of the hindgut, without any special mechanism for separation as found in caecum fermenters or in the ruminant forestomach. The overall faster rate of passage of digesta through the horse is the main reason for the lower efficiency of fibre digestion in this and other colon fermenters.

All large (over about 50 kg) hindgut fermenters appear to be colon fermenters. This is probably due in part to the increased ability of a larger animal to tolerate a poorer quality diet because it needs less energy and less protein per unit of body weight, in part because digesta can be retained in the gut of larger animals for longer periods, allowing more-extensive fermentation (Parra 1978). Thus among hindgut fermenters the horse and other colon fermenters are generally more efficient fibre digesters than the smaller caecum fermenters (Table 1).

TABLE 1 Crude fibre digestion in two types of hindgut fermenters, large 'colon fermenters' and a small 'caecum fermenter'

Species	Bodyweight kg	Diet	Crude fibre digestibility %
Colon fermenters:			
Horse	430	lucerne hay	34.7
		lucerne hay and grain	38.6
Pony	159	lucerne hay	38.1
		lucerne hay and grain	40.9
Caecum fermenter:			
Rabbit	2.8	lucerne hay	16.2
		lucerne hay and grain	18.1

From: Slade and Hintz (1969)

The other important advantage of the colon fermentation strategy, at least in the Equidae (horses, zebra), is the ability to increase greatly their dry matter intake as the fibre content of the food. increases at the expense of efficiency of digestion (Janis 1976), so that they occupy a niche at the extreme end of the range of food fibre content, though it is uncertain what proportion of their energy comes from fibre as distinct from cell contents. Thus zebra have been shown to Select plant species and plant parts of higher fibre content than ruminants (wildebeest) grazing the same low quality herbage, despite the presumed lower digestibility of the more fibrous material (Bell 1969, Owaga 1975).

This type of hindgut fermentation seems to be the most primitive. It is also found as a secondary fermentation in the hindgut of ruminants, macropods, and probably other foregut fermenters.

Caecum fermentation

The best known caecum fermenter is the rabbit. In this strategy the enlarged caecum is used in a different way, not as a simple extension of the proximal colon, but as a fermentation chamber specifically for the solutes and small digesta particles, rather than the coarse, high fibre, high lignin particles. These latter, the less digestible components of the diet, pass rapidly through the hindgut, while the potentially more digestible components are retained for fermentation (Björnhag 1972; Pickard and Stevens 1972). This is a means of utilizing fibrous diets without the encumbrance of an over-large gut, and is more important for small animals than for large because of the effect of body size on nutrient requirements. It is therefore no surprise that all animals known to have adopted this strategy are relatively small, the largest being perhaps the koala (about 10 kg), although the capybara and other large rodents' (up to 50 kg) may also be of this type.

A few animals have adopted caecum fermentation in its simple form. For example, the koala retains, presumably in the extremely long caecum; the fluid part of the digesta with overall retention times of 8-9 days, compared with 5-6 days for particles (Cork *et al.* 1977). However, many other caecum fermenters combine selective retention of fluid and small particles with coprophagy (eating of faeces) in some form. This allows easier assimilation of microbially synthesised vitamins and also makes microbial protein available for digestion by the host animal.

Thus, among hindgut fermenters, colon fermentation allows retention of a large mass of digesta, with retention of particles for a longer time than fluid digesta, so that fibre digestion is maximal, although generally less than in ruminants because of shorter overall retention times. The smaller caecum fermenters, however, avoid the coarse fibrous portion of the food by passing it through the gut more rapidly, and concentrate instead on the more digestible solutes and fine particles. Consequently fibre digestion is often poor (Table 1).

Macropods

We have recently completed a comprehensive study of digestive function and digesta flow through the gut of kangaroos and wallabies (i.e. members of the subfamily Macropodinae within the marsupial family Macropodidae). The macropodines are foregut fermenters as are ruminants, but their stomach differs from the ruminant stomach in that it is essentially tubular, rather than saccular, and in many respects resembles in structure the proximal colon (Fig. 2). There is no obvious anatomical constriction or physiological mechanism to selectively retain coarse feed particles as in the ruminant. The differential flow of particles and fluid is the result of the tubular flow of digesta along the stomach, assisted by contractions of the haustra of the gastric wall: this results in the caudal extrusion of liquid through the particulate digesta (Dellow 1979).

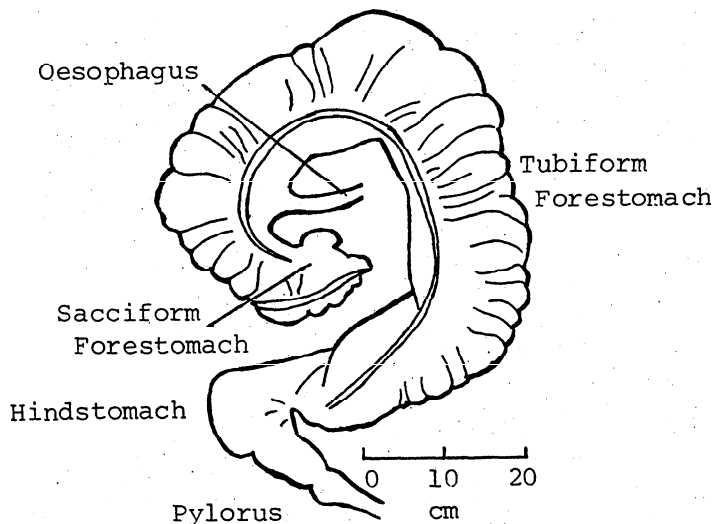


FIGURE 2 The stomach of the eastern grey kangaroo (Macropus giganteus)

The anatomical arrangement of the macropodine stomach (Fig. 2) results in several important differences in digestion from ruminants.

First, overall retention times of both fluid and particulate digesta are shorter than in the ruminant. Consequently fibre digestion is generally less efficient (Table 2), although one exception to this has been found in the euro, Macropus robustus (Hume 1974). Second, macropods do not ruminate, perhaps as a consequence of the lack of a well-defined sphincter separating the fermentative and acidic regions of the stomach. They do regurgitate, but the act is much more irregular and infrequent than in rumination, and involves much less chewing; Barker et al. (1963) recommend that this process be termed 'merycism'. Instead of ruminating, macropodines chew their food more finely initially, and consequently eat more slowly than do ruminants..

TABLE 2 Fibre digestion in two types of foregut fermenters, the ruminant and the macropod

Species	Diet	Fibre fraction	Fibre digestibility %	Reference
Ruminant				
Sheep	clover hay	ADF*	60	Hume and Purser (1975)
Cattle	lucerne hay	cellulose	62	Hinders and Owen (1968)
Goat	hay	cellulose	72	Porter and Singleton (1971)
Deer	hay	cellulose	52-66	Maloiy <u>et al.</u> (1968)
Reindeer	lichen	crude fibre	75	Jacobsen and Skjenneberg (1975)
Macropod				
Eastern grey kangaroo	lucerne hay	ADF	32	Hume (unpublished)
Red kangaroo	lucerne hay	ADF	36	Hume (1974)
Euro	lucerne hay	ADF	46	Hume (1974)

* Acid-detergent fibre (Van Soest 1963)

Finally, as in the horse, the kangaroo appears to be able to maintain its intake on highly fibrous diets better than can ruminants, thereby maintaining its digestible nutrient supply at a higher level than would otherwise be possible, at the expense of high unit digestive efficiency.

This conclusion is based on limited data. The often reported finding that mature kangaroos eat no more of high fibre diets than do sheep does not destroy the argument. This is because the maintenance energy requirement of macropodines is at least 20% below that of sheep. (Hume 1974). Only if the total energy requirement of the macropodine was greater than that of the ruminant would a higher digestible energy intake, be expected. Only one experiment has been reported which compares intake of a high fibre diet between mature ruminants and growing kangaroos, when the total energy requirement of the kangaroos may be expected to be substantially higher than maintenance. I n t h e

study of Foot and Romberg (1965) (Table 3) young red kangaroos, *Macropus rufus*, consumed less of the high quality chopped lucerne hay diet than did mature Corridale wethers. However, on the poor quality chopped oaten straw diet, although dry matter intake by both herbivores declined, intake by the young red kangaroos was 40% greater than by the sheep. Thus it appears that at least the red kangaroo is able to better maintain its intake of a high fibre diet than is the sheep. Similar studies with other macropodid species would be necessary to fully test this idea.

TABLE 3 Intake and digestion by three young red kangaroos and three mature sheep

	Red kangaroo	Sheep	Red kangaroo as % of sheep
Body weight (kg)	11.4	38.8	
Dry matter intake ($\text{g.kg}^{-0.75} \cdot \text{d}^{-1}$)			
Lucerne hay	58.1	71.7	81
Oaten straw	40.4	28.9	140
Apparently digestible dry matter intake ($\text{g.kg}^{-0.75} \cdot \text{d}^{-1}$)			
Lucerne hay	31.4	45.1	70
Oaten straw	14.5	11.4	127

From Foot and Romberg (1965)

CONCLUSIONS

Herbivores, both foregut and hindgut fermenters, appear to have evolved a number of different strategies for utilizing high fibre diets. Among the foregut fermenters the ruminant system is the best equipped to maximise fibre digestion, but suffers from the disadvantage that on very high fibre diets dry matter intake is severely limited by slow passage out of the rumen of coarse feed particles. The macropodines, which have a stomach more like the proximal colon than the rumen in gross morphology, do not suffer from this intake limitation to the same degree but are generally less efficient in their digestion of fibre.

Among the hindgut fermenters the colon fermentation system is generally superior to the caecum fermentation system in fibre digestion. but it can only be adopted by herbivores of large body size. (Smaller hindgut fermenters) because of their higher nutrient requirements per unit of body weight, instead have adopted the strategy whereby fluid and fine particles are selectively retained for fermentation in the caecum, while the coarse, less digestible particles are excreted.

This is a new way of looking at the relative advantages and disadvantages of alternative herbivore digestive systems, and may help us to better understand the potentials and limitations of our domestic livestock as we strive to maximise production from poorer quality roughages and by-product feedstuffs.

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