

REVIEW ARTICLE

Allometry and Ecology of Feeding Behavior and Digestive Capacity in Herbivores: A Review

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The purpose of this review is to give some perspective of the factors that influence feeding behaviors and the ability of herbivores to adapt to diets. The most important of these are digestibility, ability to select feed, and achievement of a nutritionally adequate intake. Plant morphology, observed feeding behavior, body size, and gut architecture and size impinge upon these factors. Feeding behavior and dietary specializations are associated with adaptations of gut and mouth parts as well as body size. Parallel and overlapping behaviors occur among herbivores and particularly between ruminants and nonruminants. The conventional classifications of grazers, browsers, and selective feeders are blurred by these evolutionary developments. © 1996 Wiley-Liss, Inc.

Key words: herbivores, feeding behavior, digestion

INTRODUCTION

The feeding of animals in zoos has the challenge of diversity in feeding behavior and nutritional requirements. Unlike domesticated animal species, there are few guides as to standards for requirements or for nutritive value of feedstuffs. Nutritive value is a particular problem for herbivores because of the variation in composition of plants and the variable abilities of different herbivorous species to extract energy from cellulosic carbohydrates.

Evolution of herbivores has followed that of plants and plant interactions with the animals. Many plants have utilized animal vectors for seed dispersal, while maintaining some quality as feed either as forage, seeds or fruit. However, plants also have evolved protection mechanisms against animals that lower availability of nutrients. Animal evolution has responded with various alternative strategies. One is to select against the unavailable fractions; another is to consume large volumes and tolerate low extraction. The most complex adaptation is that of microbial fermenta-

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tion in the gut to make better use of valuable cellulose, hemicellulose, and pectin for which animals lack the enzymes for digestion. Evolution of gut morphology has led to two major adaptations, pregastric and postgastric fermentations [Janis, 1976; Langer, 1987]. There are important subdivisions within these groups. The capacity for fermentive digestion tends to be limited by body size. However, evolutionary modifications of the gut have altered the limits of size, particularly in ruminants. For this reason allometric relationships are examined.

ALLOMETRY

Allometry involves the relationship between organism size and biological function and is too large a topic for full coverage here. A selective review in relation to feeding and digestion is given. For further reading, see the book by Peters [1986].

Body size influences the ability of herbivorous animals to feed and digest. As will be shown in the following discussions, increased body size promotes gastrointestinal retention and digestive capacity, while smaller size promotes selective feeding behavior for more immature plant parts. These two factors, retention and selection, are compensatory relative to the achievement of a sufficient nutrient intake and lead to specializations in diverse species.

Allometric relationships between body parts and body mass tend to be isometric (power one) when the body part parameter is a weight measurement and the part (head, gastrointestinal tract, etc.) is three-dimensional [Peters, 1986]. Surface relationships (viz. heat loss, energy requirements) are two-dimensional and tend to relate to body mass in an exponential relationship at two-thirds to three-quarter power. Linear measurements (length of limbs, etc.) may relate at the one-third power [Peters, 1986]. Functions like the amount of food per bite or ingesta per rumination chew relate isometrically to body weight of adult ruminant species [Van Soest, 1994].

The size of the intestinal tract in mammals, from mice to elephants, is isometric (power one) with body weight. All species fall into this relationship without separation between ruminants and nonruminants [Parra, 1978; Demment and Van Soest, 1985; Van Soest, 1994]. On the other hand, energy requirements are generally related to the three-quarter power of body weight. Thus, gut capacity increases in proportion to body weight, while energy requirements lag at the three-quarter power of body weight. This leads to an expected greater retention time in larger animals. The greater retention time is associated with an ability to utilize the slower digesting substrates like mature plant fiber and crystalline celluloses (see section on digestibility) but is not an important advantage for the faster digesting proteins and carbohydrates (see section on dietary fiber).

The expected limitation of body size upon retention and digestion must not be taken as a fixed limitation because evolution has stretched the limits relative to certain adaptations. Selective retention in combination with pregastric fermentation has allowed ruminants to achieve retentive capacity at a relatively smaller size as compared with nonruminants [Foose, 1982]. However, the size limitation appears to exert its limits in ruminants and nonruminants with different calibrations [Van Soest et al., 1982].

Other adaptations may be the water content of the gut, stretching of the gut [Brosh et al., 1988], adjustment in feed intake [Foose, 1982] and lowering of the

metabolic rate in small animals, hibernation, etc. [McNab, 1980] (see also the section on selective feeding and small ruminants).

The problem of size impinges not only upon interspecific ranges but also upon intraspecific disparities between immature and mature individuals of the same species. Infant animals are generally unable to cope with adult diets and reflect the lack of gastrointestinal development and also disparate small size. This has been most commonly observed in ruminants, such as calves, lambs, kids, and fawns, where rumen development is lacking. However, here the disparity between infant and adult capacity is greater than what would be expected from the size differences alone [Hooper and Welch, 1983; Welch, 1982].

DIETARY FIBER

All higher animals lack enzymes to digest structural carbohydrates of plants, and herbivores that utilize these carbohydrates have evolved symbiosis with gut microorganisms that have enzymes to digest the respective carbohydrates. The current definition of dietary fiber evolved out of the developments regarding fiber and human health since about 1970 [Southgate, 1969, 1976a]. Dietary fiber is defined as the polysaccharides and lignin that are not degradable by mammalian enzymes. The defined entity includes the insoluble fiber (neutral-detergent fiber [NDF]) and also gums including pectin, beta glucans, and other relatively soluble polysaccharides not physically fibrous but nevertheless resistant to mammalian enzymes. This latter fraction is termed (somewhat self-contradictorily) in the human literature as "soluble fiber" and is an important category in nonruminant nutrition [Southgate, 1976b].

The distinction between soluble and insoluble fibrous fractions is physiologically significant in that the soluble fraction has high water-holding capacity (gelling capacity) and delays gastric emptying and absorption of sugar and vitamins in the upper digestive tract of nonruminants and humans [Anderson, 1985]. These soluble carbohydrates are rapidly fermentable in the cecum, or colon, as well as in the rumen. In ruminants, the distinction between soluble and insoluble fiber has not been emphasized, since the distinction between available polysaccharides like starch as opposed to pectin, unavailable to mammalian enzymes but relatively soluble, becomes moot, as all are fermentable in the rumen. The soluble fiber-related carbohydrates do not yield lactic acid as can starch and sugar [Strobel and Russell, 1986], and high pectin feeds (viz. citrus pulp, beet pulp) may be effective in regulating rumen acidosis associated with high grain feeding [McBurney et al., 1983].

Lignification

The vascular tissues of most higher plants tend to lignify with maturity. This is most pronounced in cultivated forages but is unimportant in vegetables. Lignification leads to rendering of a portion of the structural carbohydrate indigestible. The relation of lignin content to indegradability is exponential to the two-thirds power and follows the law of surface limitation [Conrad et al., 1984; Weiss et al., 1992]. The most lignified plant materials are perennial woods of very low digestibility. This is an important factor in the selective feeding of browsers upon less lignified vegetative parts and cambial layers.

The non-cell wall fractions of plants, exclusive of the soluble fiber components,

are highly available to all animals without any fermentation [Fonnesbeck, 1968; Van Soest, 1967, 1994]. For example, the panda which specializes upon bamboo is able to utilize the non-cell wall fraction, mostly proteins and available carbohydrates, of bamboo (about 15% of dry matter) even though fiber fermentation is virtually non-existent [Dierenfeld et al., 1982]. Mean digestibility for pandas in the natural habitat in China is about 17% of dry matter [Schaller et al., 1985].

NUTRITIVE DIFFERENTIATION IN FORAGES

The indigestible parts of forages and browses alike consist of a lignified matrix that is an unavailable sink to plant metabolism. This unavailable fraction, exclusively a part of plant cell walls, tends to accumulate in the plant with maturity and is composed of lignin and part of the cellulose and hemicellulose.

The two major plant families, Graminae and Fabaceae (legumes), form the bulk of cereals, forages, and browses offering food to herbivores. These plant sources contrast greatly in their morphology, offering the opportunity of alternative feeding behaviors. Grasses contain the greater part of lignified tissue in the midrib portions of leaves [Deinum, 1976], while stems can be more digestible if the pith is a storage site for plant reserve carbohydrates. Only the cortex of the stems of grasses is lignified [Van Soest, 1994]. Because of this, grasses may be more difficult than legumes to selectively feed upon. In contrast, the leaves of legumes and other forbs are unligified, with leaves occurring at the end of lignified stems, allowing animals to selectively pick. Legume leaves do not decline in digestibility with age; only lignifying stems do. Grass leaves, on the other hand, decline in digestibility as well as the stems [Mowat et al., 1965].

Both grass and legumes have a varied digestibility of parts within a standing plant. This variation is larger in warm season forages and narrower in herbaceous cool season forages [Deinum and Dirven, 1975, 1976], particularly temperate grasses. Tropical and warm season forages are less digestible than cool season forages [Deinum et al., 1968; Van Soest et al., 1978]. This is due to the promotion of lignification by higher temperatures and the higher contents of cell wall in forage species adapted to warm climates [Reid et al., 1988; Wilson, 1981]. Tropical grasses generally offer a greater range in dietary selection, because the morphology and differentiation of nutritional parts (e.g., leaves vs. stems) is much more pronounced in warm season forages. Temperate grazers, particularly cattle, are less adapted to selective feeding because of their evolutionary adaptation to more uniform temperate pastures [Van Soest, 1994]. For the same reasons, many tropical herbivores tend to be more selective feeders [Hofmann, 1988]. Most temperate grazers are larger animals, while most small ruminants originated from warmer climates. Sheep and mountain goats are exceptions. Many tropical ruminants, large or small, are probably more selective feeders than temperate grazers.

Legumes and grasses contrast in relation to their consumptive intake and digestibility. Under similar growth conditions, legumes have low NDF but high lignification of cell wall, while grasses have high NDF and low lignification of cell wall. This promotes equal digestibility in grasses at higher NDF content than legumes but also lower intake at equivalent digestibility [Van Soest, 1965; Osbourn et al., 1974].

SEQUENCES OF DIGESTION IN HERBIVORES

Fibrous carbohydrates must be digested symbiotically by gut microorganisms in all higher animals, which have not evolved to produce cellulases, hemicellulases, or pectinases. These carbohydrases are produced by various microorganisms in the guts of herbivores; thus, fermentation chambers to harbor microbes are important evolutionary adaptations in the digestive sequence. Characteristic organisms normal to the rumen are also found in many nonruminant herbivores, occurring in the cecum and colon [Hobson, 1988]. These organisms consist of anaerobic bacteria, protozoa, and fungi [Theodorou et al., 1994] that are adapted to the utilization of available carbohydrates (largely fibrous) upon which they grow. They collectively secrete a wide spectrum of carbohydrases for digestion of pectins, hemicellulose, and cellulose but not lignin, which is phenolic. Some microbial species live on by-products of fermentation. The main net products of mixed gut fermentation are volatile fatty acids (VFA), principally acetic, propionic, and butyric acids, CO₂, methane, and possibly hydrogen, and the cellular growth of the microorganisms containing potential protein (amino acids), vitamins, and some lipids.

The VFA are permeable to the gut wall and are utilized as an energy source by all higher animals [Stevens, 1988; McNeil et al., 1978]. However, utilization of the microbial bodies requires gastric digestion, so that pregastric fermenters (e.g., ruminants) will utilize this source of amino acids and vitamins efficiently, whereas postgastric fermenters (colonic and cecal) will tend to lose this microbial resource in the feces. Some postgastric fermenters have adapted to the eating of feces (coprophagy or cecotrophy) to utilize gut microbial nutrient resources.

The ability of microbial organisms to grow in the gut is related to their generation time, which must be less than the retention time of the gut or else they will not survive and be washed out. Thus, slow fermenting species, adapted to slow digesting substrates like crystalline cellulose, may not occur in animal species with fast gut transit. Examples of these microbes include some cellulolytic bacteria, methanogens, protozoa, and fungi.

The health and well-being of gut microbes is dependent upon the dietary quality of the fibrous carbohydrates. These are supplied by good forage and by-product feeds.

Digestive sequences and associated gut morphology show considerable variation [Stevens, 1988]. The simplest digestive sequence is that exemplified by man, dog, and carnivores in which a cecum as a separate compartment is essentially lacking (Fig. 1). Many herbivorous animals, including man, have sacculated colons. Sacculatation probably helps slow the passage of fibrous solids and leads to more efficient extraction of fermentable energy and likely represents an herbivorous evolutionary ancestry [Stevens, 1988]. Nonruminants like the pig, horse, and elephant, also possess a sizeable cecum (though relatively smaller than the colon), which is the main site of fermentation [Stevens, 1988]. The ostrich has a dominant colonic fermentation and a secondary one in the cecum [Swart et al., 1993a,b].

The main site of fermentation in many rodents lies in the cecum, which is dominant over the colon (Fig. 2). Many of these animals practice coprophagy, which is a device to capture microbial protein and vitamins. Within this group there are even more specialized species, such as rabbits and lemmings, where the cecum selectively admits only fine matter, coarse fiber being excluded and excreted in day feces [Bjorn-

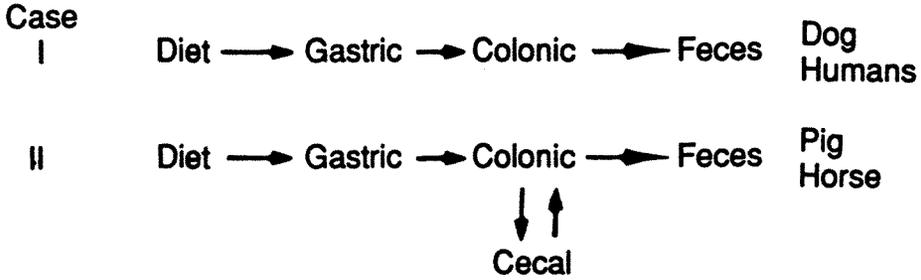


Fig. 1. Sequence of digestion in nonruminants. The simplest case with little or no cecal digestion occurs in most carnivores, dog, and man. The main site of fermentation is in the colon of large herbivores [Stevens, 1988].

hag, 1972; Uden et al., 1982]. Night feces are reingested, allowing utilization of microbial protein and vitamins derived from the most fermentable substrates. Because the coarse fiber is rejected, fiber utilization is very low in these animals. These animals probably exploit vegetative tissues containing pectin and other rapidly fermentable unglignified carbohydrates. Coprophagy can be viewed as an adaptation of small herbivores to overcome the limiting effect of rapid rate of passage, due to high energy demand relative to the size of their gastrointestinal tracts. This strategy allows these small herbivores to consume fiber with reduced penalty of energy intake restriction, although many potentially digestible cellulosic carbohydrates may be lost in the feces.

There are also animals that possess pregastric fermentation without rumination (Fig. 3). These comprise a wide spectrum of mammals, including some kangaroos [Hume, 1982], hamsters [Ehle and Warner, 1978], voles [Keys and Van Soest, 1970], colobine [Stevens, 1988] and langur monkeys, [Bauchop and Martucci, 1968], and hippopotamus, [Moir, 1968]. At least one bird, the hoatzin, possesses pregastric fermentation [Grajal et al., 1989]. Probably, other species remain to be discovered and described. Pregastric fermentation was discovered in the hamster when it was noted that these animals were not responsive to amino acid deficient diets [Banta et al., 1975]. Subsequent examination revealed cellulolytic digestion in the distal sac of the stomach [Ehle and Warner, 1978]. It is speculated that some of the large herbivorous dinosaurs may have had a pregastric fermentation chamber in the crop [Farlow, 1987]. Cannonball sized stones plus a heavy musculature allowed the gizzard-like organ to do the equivalent of rumination, while the animal was allowed greater freedom to feed, in contrast to modern ruminants [Bakker, 1986].

Grazing ruminants are animals that have evolved a filter system to enhance retention of slow digesting cellulosic carbohydrates, and passage is promoted by rumination of ingesta to a particular size that will pass (Fig. 4). This strategy allows a more efficient extraction of available energy in forages somewhat at the expense of feed intake. Selector ruminants tend to have smaller rumens and larger hindguts than do grazers. There is thus compensation between gut capacity for fermentation between the rumen and the hindgut across species [Hofmann, 1988, 1989]. Most non-ruminant herbivores have hindgut capacities that compare to ruminants of similar body size [Van Soest, 1994].

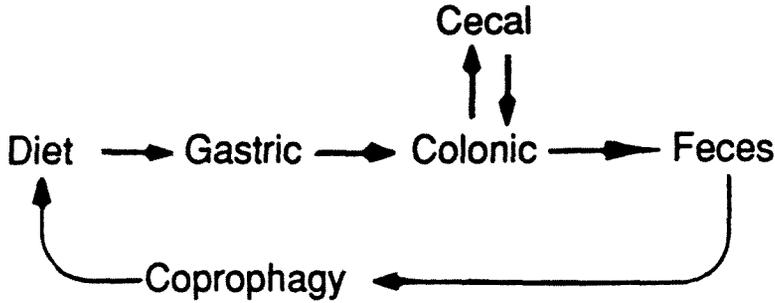
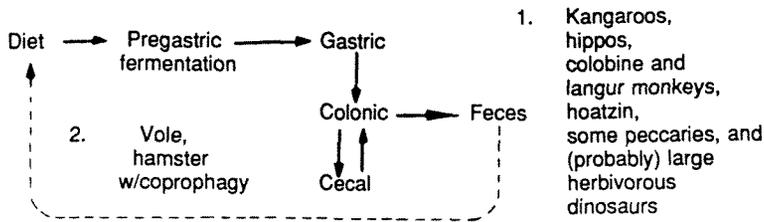


Fig. 2. Sequence of digestion in rodents, most of which practice coprophagy. Cecal fermentation is dominant over a secondary colonic one. Some rodents (hamster and vole) have pregastric digestion.



- 1. Kangaroos, hippos, colobine and langur monkeys, hoatzin, some peccaries, and (probably) large herbivorous dinosaurs

Fig. 3. Sequence of digestion in nonruminants with pregastric digestion. Two modifications are shown: one without coprophagy and one with. For discussion of digestive physiology in herbivorous dinosaurs, see Bakker [1986] and Farlow [1987].

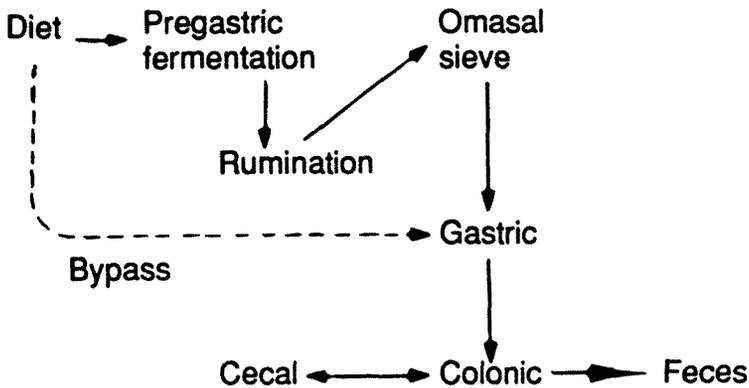


Fig. 4. Sequence of digestion in ruminants. The sieving system of the omasum is much more developed in grazing species, which makes them more sensitive to the particle size of fiber. The capacity of the colon and cecum in grazers is comparatively small relative to other nonruminants. For discussion of newer views on ruminant bypass, see Hofmann [1989].

Thus, the classification of ruminants and nonruminants is an oversimplification. Ruminant-like capacities (e.g., pregastric fermentation) exist in combination with grazing and selector types of feeding and in true ruminant and nonruminant groups. Small African ruminants may be competitive with primates [Van Soest, 1994].

CLASSIFICATION OF FEEDING BEHAVIOR OF HERBIVORES

Hofmann [1973, 1989] has classified mammalian herbivorous animals into three major classes based on dietary selectivity, including concentrate selectors, intermediate feeders, and bulk and roughage eaters. Langer [1988] has classified these animals according to a herbivory rating from 1 to 6, which is parallel to that of Hofmann. Yet another system is that of Bodmer [1990], which is based on the proportion of grass in the diet as a criterion for classification, suggesting a continuum between grazing and browsing. The problem with all of these classifications is the assumption that grazers are less selective than browsers. All are unidirectional systems describing niches going from most to least, whether grazing or selecting. However, there can be very selective grazers [Hofmann, 1989] as well as less selective browsers, such as elephants.

Concentrate selectors are unable to tolerate large amounts of fiber in their diet and are thus limited to selective feeding on low fiber portions of plants. Examples are primates and very small ruminants. Humans, if considered as herbivores, would fall into this group, although they may also be claimed as omnivores. An intermediate group includes animals adapted to rapid digestive passage and limited use of the plant cell wall components in order to ingest sufficient amounts of the readily available plant parts. They may be adapted to either browsing or grazing. Thirdly, there are those animals adapted to the use of the potentially digestible cell wall components. They are the grazing ruminants and some large nonruminant herbivores.

The system of Langer [1988] presumes that grasses are more fibrous and less utilizable than nongrass forage. On the average this is true, but not universal. For example, in browsing, fiber intake may depend upon how much wood is eaten. Most woods contain more fiber and lignin than any grass.

The complexity of feeding behavior has led to a two-dimensional classification in which both ruminant and nonruminant herbivores may be compared (Fig. 5) and allows the demonstration of intermediate species like the goat that have considerable versatility in feeding behavior. The goat, a well-described species, is a comparatively selective feeder and is inferior to cattle and sheep as a digester of fiber [Huston et al., 1986], despite the claims in the literature that the goat can digest almost anything [Devendra, 1978].

Body size is likely negatively related to selective feeding if for no other reason than clumsiness in feeding upon small items of food. All small herbivores are selectors, being constrained in digestive capacity (mean retention) by their size. However, there are a few large selectors, as, for example, the eland that has a small rumen and poor ability to utilize the fiber [Arman and Hopcraft, 1975]. Some large ruminants such as the giraffe are browsers but are likely less selective than the small ruminants. The giraffe has a greater digestive capacity than the smaller selectors, and for its size should be more tolerant to lower quality browse. In contrast, the oribi (16 kg antelope) appears to be a highly selective grazer [Hofmann, 1989]. Research in North America by Kautz and Van Dyne [1978] reported the order of selectivity: deer > pronghorn > cattle = sheep > bison.

The intermediate feeders are adapted to either browsing or grazing and can eat a wide variety of plants. This group shifts feeding behavior according to the availability of forage and season and is more versatile than concentrate selectors or obligate grazers. Grasses are usually eaten only when immature, and, as forage matures,

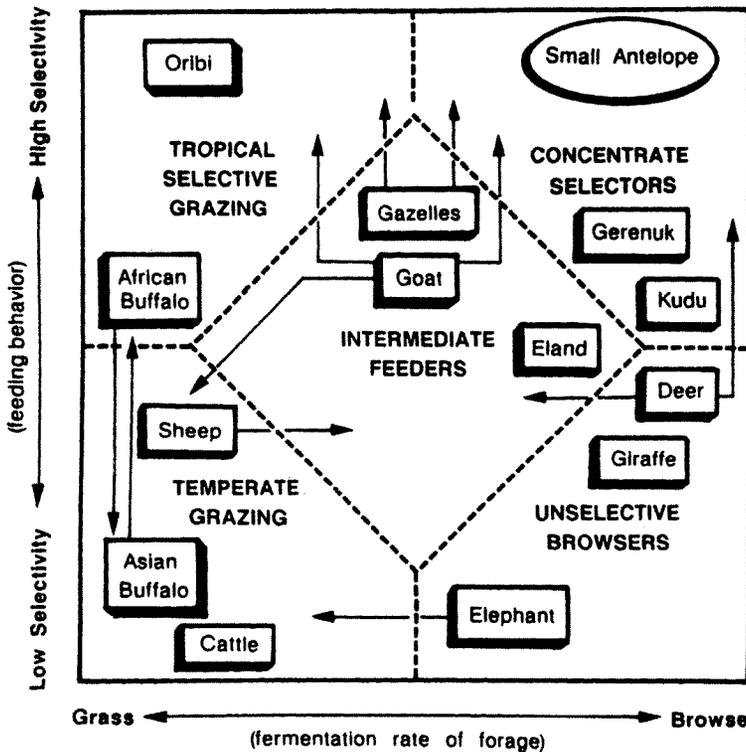


Fig. 5. An ordination of herbivore species based on diet. The axes are the degree of feeding selectivity and the amount of grass vs. browse in the diet. The arrows indicate mobility of a species with respect to these axes [Van Soest, 1988].

animals move to browses. Northern and Arctic species such as moose similarly need to adapt to summer and winter conditions and forage availabilities. Moose are classified as concentrate selectors, yet vary their diet seasonally because of the problem of available forage in winter. In Alaska considerable wood may be taken from willow species, but even in this case moose are very selective, consuming cambial layers, buds, etc. [Nygren and Hofmann, 1990; Hofmann and Nygren, 1992]. Other animal species adapted to tundra conditions include the yak in the Tibetan plateau that selectively feed on sparsely distributed grasses, sedges, and forbs. These very large animals are able to cope on coarse forage as well as selectively feed [Cincotta et al., 1991]. Other species of similar behavior are the camelids in the Altiplano of South America [Van Soest, 1994].

Some of the smaller African intermediate feeders and grazers may selectively feed on the nutritively differentiated tropical grasses between wet and dry seasons such that there is some inexactitude about the definition of a grazer and its supposedly poorer ability to select. The problem of selective feeding is related to the range in nutritive classes available in a habitat.

The small rumens in selector ruminants indicates that rumen size may not be a limitation in these animals and that selective feeding for faster digestion and more digestible food is the principal means by which these animals obtain their energy

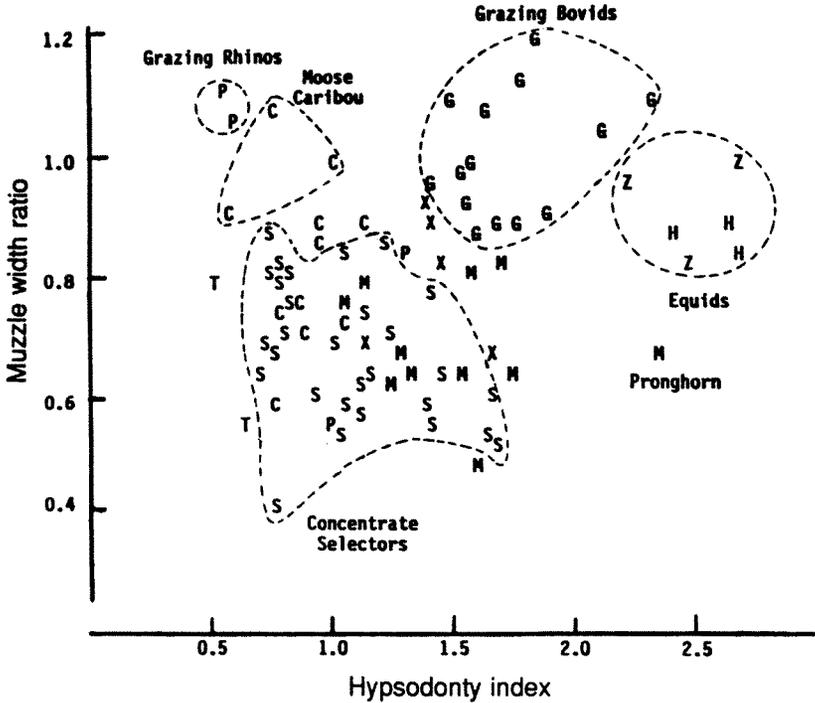


Fig. 6. Plot of muzzle width index vs. hypsodonty index of herbivores classed according to feeding habit. Based on Janis and Ehrhardt [1988] in Van Soest [1994]. Equids (H, Z), grazing bovids including antelope (G), selective grazers (X), mixed and intermediate feeders (M), caprids (C), ruminant concentrate selectors (S), rhinos (P), and tapirs (T). Classification system includes Hofmann's (1973) system. See also Janis and Fortelius (1988).

requirements. In line with this observation are their adaptations relative to mouth parts and dentition [Janis and Erhardt, 1988; Janis and Fortelius, 1988]. Narrow muzzles and prehensile lips are features of selective feeding, while wide muzzles and high-crowned molars (a feature of chewing and rumination) are present in both ruminant and nonruminant grazers (Fig. 6). There is divergence in both muzzle width and hypsodonty (crown height) index. For example, arctic ruminants and rhinoceroses have low hypsodonty but wide muzzle width, which must have some significance in their feeding behaviors.

Subclasses of the bulk and roughage eaters include (in decreasing order of their need for water) fresh grass eaters, roughage eaters, and dry region grazers [Hofmann, 1973; Janis and Erhardt, 1988]. Temperate cattle are listed under fresh grass eaters, mainly because of their need for water. Actually, they are among the most unselective. The adaptation to dry conditions involves a variety of factors which include the ability for renal concentration, colonic absorption of water, and use of the rumen as a water reservoir [Brosh et al., 1988]. The use of the rumen as a reservoir for water slows passage and increases digestion.

COMPARATIVE DIGESTION STUDIES

A number of digestion and passage studies has been conducted to obtain comparative abilities of herbivores to utilize fiber [Foose, 1982; Uden and Van Soest,

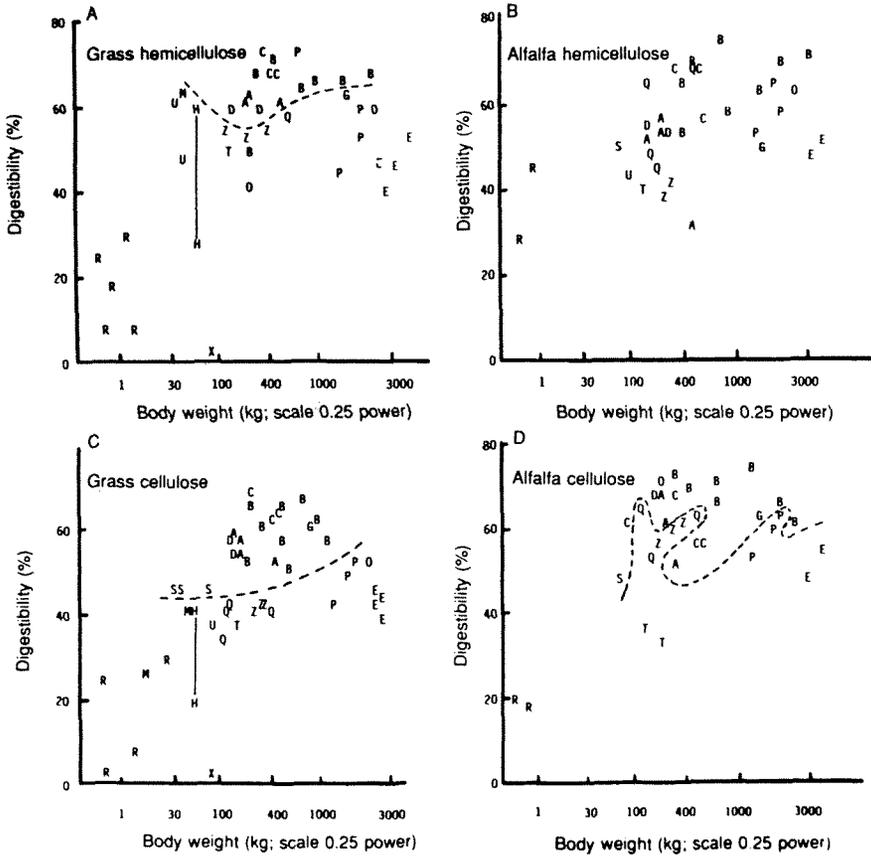


Fig. 7. The relation between digestion of hemicellulose and cellulose of alfalfa- and grass-based diets and body weight for diverse species of ruminants and nonruminants [Van Soest, 1994]. Data of Dierenfeld et al. [1982], Ehle et al. [1982], Foose [1982], Keys et al. [1969], Keys and Van Soest [1970], Milton and Demment [1988], Uden and Van Soest [1982a], and Van Soest et al. [1978]. Identification of species: antelope, A; grazing bovids, B; camelids, C; deer, D; elephants, E; giraffe, G; humans, H (shown in the figure by the vertical lines); baboons, M; hippo, O; rhino, P; horses, Q; rodents and lagomorphs, R; sheep and goats, S; tapirs, T; pigs, U; panda, X; zebras, Z.

1982a]. These studies utilized standard sources of fiber. Other studies by Prins et al. [1983] compared diverse diets containing fiber of varying quality. Variation in fiber quality was accounted for by making the comparisons on the basis of degradable fiber only. Values for efficiency of fiber utilization were presented as the proportion of available potentially digestible fiber actually digested by the respective species.

The thesis of Foose [1982] presents comparative digestion data on 36 species of ruminants and nonruminants of widely differing feeding strategies, conducted at Franklin Park (Boston), Oklahoma City, Philadelphia, Burnet Park (Syracuse), and Metro Toronto zoos. Two standard diets were offered: low quality grass (timothy) and alfalfa hays. The timothy diets offered the more stringent test for digestive capacity for cellulose. Results of this study are included in Figure 7.

Other digestion passage trials on domestic species were conducted at Cornell by

Foose [1982] and Uden [1978]. Human data were studied from the Cornell dietary fiber study with 24 men [Heller et al., 1980] using standard wheat bran. Similar nonhuman primate studies are reported by Milton and Demment [1988]. Results of these studies are included in Figure 7.

A summary of the comparative digestion data for various species of ruminants and nonruminants of various sizes is shown in Figure 7A–D. The forages were offered as sole feed under restricted feeding to limit selective feeding. The data are shown for digestibilities of cellulose and hemicellulose in low quality timothy and higher quality alfalfa. These carbohydrate fractions show a range in digestion rates that are related to carbohydrate structure. Linear molecules like cellulose may be more crystalline when mature, thus slower digesting, and present a harsher test for digestive capacity. Hemicelluloses and pectin, on the other hand, are branched molecules, making it more difficult for them to crystallize [Van Soest, 1994]. Legume fiber (alfalfa) tends to be of higher nutritional quality than of grasses.

The digestive capacities of ruminants, including antelope, grazing bovids, camelids, deer, giraffe, sheep, and goats, to digest grass cellulose is somewhat greater than nonruminants, but in both cases smaller species are at a disadvantage. Values for man are somewhat less than the figure for pigs or baboons but more than that for rodents. Some large animals (hippo, rhino) may approach the capacity of ruminants, but elephants, equids, and tapirs are less efficient. Very small animals (rodents and lagomorphs) have very low digestibilities. The giant panda, while not small, is lowest of all [Dierenfeld et al., 1982].

Faster fermentive digestion of the more branched hemicelluloses as compared with linear (and more crystalline) cellulose is expected [Van Soest, 1994]. For example, nonruminants typically digest hemicellulose better than cellulose [Keys et al., 1969]. Moreover, rates of digestion of structural carbohydrates are almost always faster in legumes as compared to mature grasses. Only in the case of grass cellulose is the association of digestibility and body size significant, although reduced digestibilities of cellulose and hemicellulose appear in small nonruminants. The difference between ruminants and nonruminants becomes increasingly difficult to distinguish as one proceeds from grass cellulose to grass hemicellulose to alfalfa cellulose and to alfalfa hemicellulose as shown in Figure 7A–D.

The body weight above which no effect of body weight upon digestibility can be discerned is about 90 kg for alfalfa cellulose. It appears that any constraint of body size becomes nonlimiting in the case of quality forage carbohydrates. This is about the size range suggested by Demment and Van Soest [1985] as the critical size relative to sexual dimorphism and the need for females to select a higher quality diet.

Digestive capacity in larger animals is constrained only in the case of low quality grass, although there is some advantage of grazing ruminants over grazing nonruminants, as shown in Figure 7. The principal advantage of ruminant digestive anatomy is that it allows greater digestion of cellulose at a smaller animal size, and this ability is somewhat at the expense of food intake [Foose, 1982].

Comparative digestion trials such as those presented in Figure 7 represent attempts to feed identical diets in several species. For grazing species such as cattle and sheep, the problems of disparity of the diet offered relative to the dietary preference is not large, although significant. However, as the disparity in feeding behavior widens, choice of a common diet for comparison becomes more problematic. Feeding of a diet closer to the adaptive preference for species A will disadvantage species B.

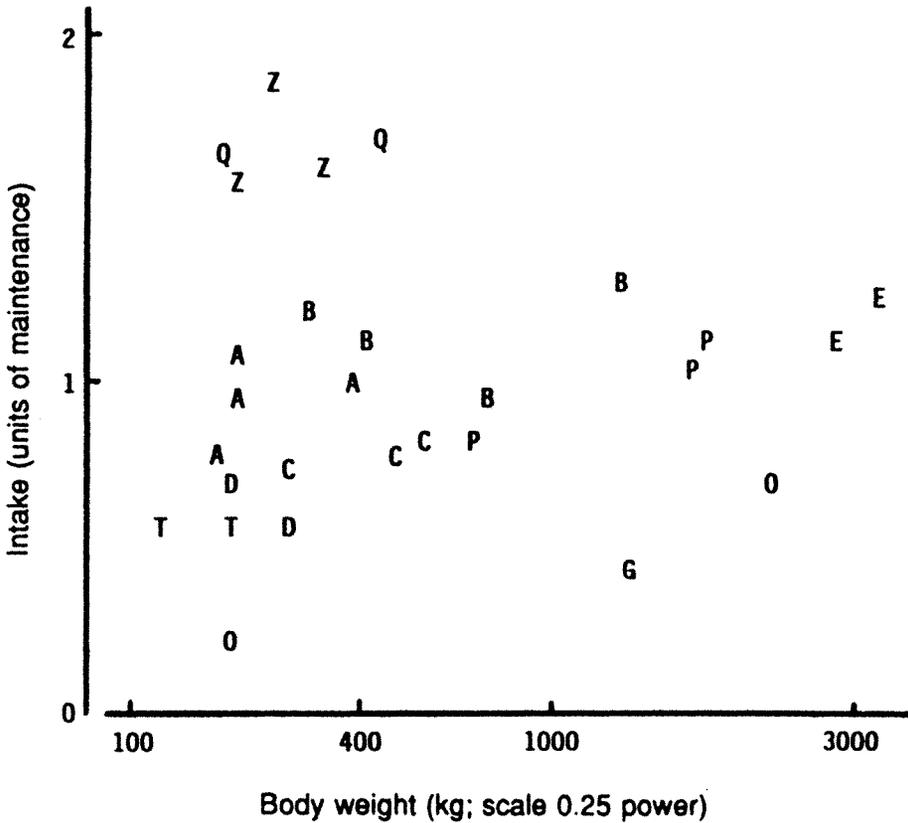


Fig. 8. Comparative intakes of poor grass hay (intake of digestible dry matter divided by the estimate for maintenance) relative to body weight. Note the high intake by equids (Q, Z). Some of the selector ruminants cannot achieve maintenance on this diet [Data of Foose, 1982]. Antelope, A; camelids, C; deer, D; giraffe, G. Data also is shown for some nonruminants: hippopotamus, O; tapirs, T. Other species shown are bovids (B), rhinos (P), and elephants (E).

A particular problem is that it may be difficult or impossible to force certain selector species to consume the standard diet of comparison [Tessema, 1972; Sands, 1982].

Selector types did not eat enough of the timothy forage in the Foose study to achieve maintenance (Fig. 8). Only equids were able to consume low quality timothy hay at reportable levels of feed intake. Higher intakes tend to promote faster passage rates and lower digestibilities in equids [Van Soest, 1994]. Thus, digestibilities in Figure 7A–D may be overestimated in cases where maintenance intake was not achieved. Retention is highly associated with digestibility [Van Soest, 1994]; hence, mere digestion coefficients apart from other data may overvalue the capacity of smaller animals and selectors.

OTHER DIGESTION STUDIES

Prins et al. [1983] compared ruminants eating diverse diets by making a correction for indigestible matter, the assumption being that the proportion of available fermented plant cell wall utilized by an animal species is a basis of comparison.

Indigestible matter was measured as the residue remaining after 14 days *in vitro* rumen fermentation of the various feedstuffs. Results of this study were obtained from several European zoos and are shown in Table 1.

This kind of comparison has the advantage of demonstrating the utilization of neutral-detergent fiber (plant cell wall) under practical zoo feeding conditions and avoids the problem of offering unsustainable diets for some selector animals. It, however, ignores the problem of selection and variable rates of fermentation of the available substrates.

The data do disclose important differences in efficiency of cellulose digestion within the classified groups. For example, tedal sheep and European mouflon are less efficient than other grazers and intermediate feeders. Similarly, red deer are less efficient than other cervids, while the kudu and pudu are less efficient than the giraffes.

A variety of digestion studies not included in Figure 7 exist in the literature, which are difficult to compare because of dietary diversity and lack of compositional data. These are summarized in Table 2. Comparison of different feeding studies for a given animal species discloses wide variability in digestibility, depending on fiber sources. An example is the pig. Immature pigs utilize alfalfa less well than adults [Kass et al., 1980].

Asian elephants, though slightly smaller than African elephants, tend to have higher digestion of hemicellulose and cellulose and longer retention times than do African elephants. The digestion coefficients are low by ruminant standards, and both species tend toward higher intakes and faster passage than many other large herbivores. Equids tend to have a similar feeding and digestive behavior [Foose, 1982].

VERY SMALL RUMINANTS

While sheep and goats are the smallest domesticated ruminants, a variety of smaller wild species exist down to 1–3 kg body weight, occurring principally in the tropics. Most of these species are forest dwellers and feed upon fruits and leaves. Their feeding ecology is poorly understood, leading to problems in managing them in zoos and in attempts to domesticate them. Maintaining them on coarse forages in the manner of larger ruminants has led to mortality, as, for example, the blue duikers that were imported to Pennsylvania State University for the naive purpose of evaluating forages more cheaply [Cowan, 1982].

However, high digestibilities and retention times in very small ruminants are reported [Conklin and Dierenfeld, 1994; Conklin-Brittain et al., *in press*]. Cases in point are recent digestion and passage studies on small ruminants shown in Table 3; duikers are African bovid antelope, while pudu and brocket are South American forest deer. Notice in all cases that digestibilities of hemicellulose are consistently higher than cellulose, as in many nonruminants. Fecal metabolic losses, an indication of the magnitude of microbial fermentation, varies upward with body weight. Such observations must be understood in the context of possible adaptations that reduce potential limitations of size.

Asian mouse deer were offered a concentrate pellet, produce, and no coarse forage [Conklin and Dierenfeld, 1994]; other species were offered grass (64% NDF, pudu, and brocket) or mixed grass-legume hay (53% NDF, duikers) in addition to pellets and produce. Only small amounts of the hays (3–22% of that offered) were

TABLE 1. Digestibilities of ruminants in zoos [from Prins et al., 1983]

Species	Zoo	R/C ^a	NDR Dig. ^b	ANDR Dig. ^c
Temperate species, Grazers and mixed				
American bison	C	.6	63.5	85.6 ± 2.4 (3)
American bison	C	1.7	60.6	90.4
American bison	A	3.5	59.7	92.0 ± 4.1 (3)
American bison	B	1.7	62.9	86.3 ± 2.9 (5)
European bison	B	3.0	63.0	86.0 ± .9 (6)
European bison	A	2.2	52.2	82.7 ± 6.1 (5)
European bison	A	2.7	56.4	86.6 ± 5.3 (3)
European bison	A	1.5	46.0	77.4 ± .9 (2)
Dwarf goat	B	.7	53.6	75.4
Tedal sheep	A	4.1	44.6	69.2
European mouflon	A	6.4	45.7	69.0
Mean				81.9 ± 8.0
Mixed feeders, tropical				
Springbok	B	.9	52.0	73.4 ± 9.4 (2)
Springbok	A	2.3	37.9	62.7
Mixed Temperate				
Fallow deer	B	1.1	59.1	81.6
Fallow deer	C	.6	59.0	80.3
Fallow deer	C	.6	53.4	83.1
Wapiti	B	2.5	57.9	79.2 ± 1.5 (6)
Pere David's	A	1.0	53.0	74.5
Red deer	C	.3	41.3	56.1
Mean				75.8 + 10.0
Arctic ruminants				
Reindeer	A	4.4	68.3	88.4
Reindeer	B	1.8	53.7	83.7
Moose	A	0.4	41.8	78.3
Moose	B	1.9	48.7	86.5 ± 3.4 (2)
Mean				84.2 + 4.4
African concentrate selectors (except as noted)				
Giraffe	A	1.9	49.4	83.4 ± 2.2 (6)
Giraffe	B	1.3	34.8	66.7 ± 8.5 (6)
Giraffe	C	0.5	59.0	80.3
Giraffe	C	0.8	61.7	87.9
Pudu (S. America)	B	2.4	33.4	54.8 ± 13.5 (2)
Greater Kudu	B	1.7	14.7	34.6 + .4 (2)
African Grazers, except as noted				
African buffalo	A	5.3	57.6	88.6 ± 2.2 (3)
Watusi	B	9.3	62.2	85.7 ± .2 (2)
Watusi	C	11.2	65.5	87.9
Banteng (Asiatic)	B	6.3	62.2	84.3 ± .9 (4)
Blesbok	C	0.3	61.6	84.0
Roan antelope	B	1.6	57.7	80.2 ± 8.3 (4)
Oryx	B	3.8	48.8	80.6
Gayal (Asiatic)	A	2.9	50.8	81.4 ± 3.5 (4)
Gayal (Asiatic)	C	0.8	50.5	78.6 ± 2.4 (3)
Waterbuck	A	2.6	38.0	70.8 ± .7 (2)
Waterbuck	B	1.1	58.5	81.1 ± 2.6 (4)
Hartebeest	A	4.1	38.6	63.1
Mean				82.1 ± 4.9

^aRoughage to concentrate ratio.

^bObserved cell wall digestibility in vivo.

^cANDR: available neutral-detergent residue (cell wall) obtained by dividing animal digestible cell wall with the result of long time in vitro digestion with rumen microorganisms.

TABLE 2. Some reported digestibilities of fiber components in various species*

Species	Body weight (kg)	Diet	Digestibility		Reference
			Hemicellulose	Cellulose	
Rat	0.2	Microcrystalline cellulose	—	9	Hsu and Penner, 1989
Guinea pig		Vegetables	50–95	38–63	Nyman et al., 1990
		Alfalfa	—	49	Fahey et al., 1979
Rabbit	3	Cellulose	—	84	Fahey et al., 1979
		Timothy	11–13	7–9	Uden and Van Soest, 1982a
		Alfalfa	47	21	Uden and Van Soest, 1982a
Turkey	4–6	Cellulose	—	3	Duke et al., 1984
Howler Monkey	5.2–8.4	Fruit	16–21	20–33	Milton et al., 1980
		Leaves	57–69	66–69	Milton et al., 1980
Dog	10	Cellulose ^a	—	5–10	Burrows et al., 1982
		Brewer's grains	30–60	7–25	Visek and Robertson, 1973
Beaver	14–22	Poplar	—	30	Hoover and Clarke, 1972
Kangaroos					
Euro	23–31	Alfalfa	38	46 ^b	Hume, 1974
		Oat straw	27	21 ^b	Hume, 1974
		Wheat straw	40	39 ^b	Hume, 1974
Red	27–33	Alfalfa	33	36 ^b	Hume, 1974
		Oat straw	17	17 ^b	Hume, 1974
		Wheat straw	43	33 ^b	Hume, 1974
Ostrich	5–10	Mixed feed	69	42	Swart et al., 1993a
		Mixed feed	63	38	Swart et al., 1993a
		Mixed feed	66	35	Swart et al., 1993a
Capybara	41	Tropical grasses	—	52–61	Parra, 1978
Red deer	43–53	Alfalfa	—	64	Maloij and Kay, 1971
		Ryegrass	—	52–64	Maloij and Kay, 1971
Pig	44	Alfalfa	18–28	28–33	Kuan et al., 1983
		Alfalfa	23	7	Kass et al., 1980
Obese (fat)	83–100	Alfalfa	34–65	14–64	Varel et al., 1988
Lean (thin)	92–110	Alfalfa	44–84	30–78	Varel et al., 1988
		Cellulose ^a	88	48	Varel et al., 1988
	120	Rutabaga	—	93 ^c	Robertson et al., 1987
		Wheat bran	—	43 ^c	Robertson et al., 1987
Onager	—	Pellet diet	47	59	Hintz et al., 1976
Ponies	115–147	Alfalfa	60	51	Hintz et al., 1973
		Timothy	45	35	Hintz et al., 1973
Przewalski horse	—	Pellet diet	42	46	Hintz et al., 1976
Zebra	250	Pellet diet	39	50	Hintz et al., 1976
Horse	450	Alfalfa	55–72	45–66	Hintz et al., 1971
		Alfalfa	33	45	Fonnesbeck, 1968
		Grasses	42–53	42–49	Fonnesbeck, 1968
Asian elephants	2,623 ± 506	Grass hay	46	44	Hackenberger, 1987
African elephants	2,805 ± 813	Grass hay	41	40	Hackenberger, 1987

*This table reports values for species not reported in Fig. 6.

^aSolka flocc.

^bDigestibility of acid detergent fiber. Control sheep had digestibilities for hemicellulose in alfalfa of 43%, oat straw of 23%, wheat straw of 43%, and for ADF of 44%, 21%, and 39%, respectively.

^cHemicellulose and cellulose.

TABLE 3. Body weights, intake, retention time, and digestibility for some small ruminants [from Van Soest et al., 1995]

Species	Body weight (kg)	DM intake (g)	Mean retention time (hr)	Digestibility				
				Dry matter	NDF	C ^a	HC ^b	M ^c
Asian mouse deer	2.8	129	49	76	42	45	58	9.6
Pudu	9.1	299	30	75	59	62	67	9.9
Maxwell's duiker	9.4	305	42	74	49	53	55	10.8
Bay duiker	12.1	303	—	67	39	40	49	10.8
Brocket	20.2	431	—	73	54	50	67	11.3

^aCellulose.^bHemicellulose.^cNon-NDF matter in feces as a percent of dietary intake.

eaten by these small ruminants (Table 4), although the amounts of hay eaten represented larger proportions of the diet actually consumed (14–40%). These species clearly selected away from NDF and for the cell contents which include sugar, protein, pectin, and starch that have fast digestion rates. By selecting for the more rapidly degrading fractions, these animals were able to retain the digesta for a longer retention time and thus achieve good digestion of the cell wall fractions that they did eat. Because of the very high degree of selection of the hays, the analyzed composition of the hays has likely little relationship to the composition actually consumed.

EFFECTIVE FIBER

The problem of effective fiber is peculiar to ruminants that are required to ruminate coarse fiber entering the rumen down to a particle size that will pass the omasum. The limiting size is on the order of 2–4 mm for cattle and less than 1 mm for goats and sheep. The size limitation is probably related to body size in other ruminants, less well studied.

Particle sizes in the feces of horses and ponies are larger than those of ruminants (Table 5). Particle sizes in the rumen and feces of cattle are larger than in sheep and goats. Rumen contents of forage-fed small ruminants also tend to be less stratified than those of cattle, and do not possess a floating mat [J.G. Welch, University of Vermont, personal communication]. In the nonruminant, fine fiber tends to pass more slowly and can cause constipation. Thus, effective particle size of fiber has a role in nonruminants in promoting passage and gut motility [Heller et al., 1980; Stevens, 1988].

The rumination and chewing capacity of goats [Hooper and Welch, 1983] and of sheep and cattle [Welch, 1982; Bae, 1978] indicates that rumination capacity (gram coarse NDF ruminated per minute) is isometric (power one with body weight) with body size of adults [Van Soest, 1994]. Immature animals have an inferior ability to ruminate relative to adult animals [Van Soest, 1994].

Thus, it appears that goats and sheep are smaller machines relative to chewing capacity, processing less ingested coarse fiber for unit of body size, but at the same time chewing it to a smaller particle size. Because the rumination capacity (grams NDF/min) and digestive capacity are isometric (power one with body weight), while their energy requirements are related to body weight to the three-quarter power, small

TABLE 4. Hay consumption by four species of very small ruminants in zoo studies [Conklin-Brittain et al., in press; Van Soest et al., 1995]

Species	Hay refusal (%)	Hay in diet eaten (%)	Total diet NDF	
			Offered (%)	Eaten (%)
Pudu	96	23	56	36
Maxwell's duiker	81	14	42	31
Bay duiker	78	40	42	36
Brocket	97	19	56	34

TABLE 5. Comparison of fiber mean particle size (microns) of gastrointestinal contents for various animal species [Uden and Van Soest, 1982b]*

	Reticulo rumen	Omasum	Abomasum	Cecum	Feces
Large heifers	2,290				890
Small heifers	1,670				640
Goats	1,470	530	570	520 ^a	460
Sheep	1,290	550	530	490 ^a	460
Ponies					1,600
Horses					1,630
Rabbits				450	520

*Timothy hay was the sole feed except for rabbits, which were fed 60% hay and 40% concentrate. The hay was fed in long form to the horses, chopped to 5 cm for the heifers, goats, sheep, and ponies, and ground to 2 mm for the rabbits.

^aCecum-proximal colon.

ruminants are at a disadvantage relative to larger species. The available data suggest that the limiting particle size is smaller for goats than sheep and that NDF in concentrate sources provides effective fiber for goats and sheep.

PROBLEMS WITH PELLETED FORAGE AND FIBROUS BY-PRODUCT FEEDS

The practical aspects for the nutritionist compounding diets in zoos is that many herbivorous animals are likely intolerant of forage as a sole diet. This is particularly a problem with pelleted forage and high fiber by-products, because these feeds limit selection, leading to consumption of lignified fiber and forcing these animals to ruminate low quality plant parts not normally eaten. The limiting particle size for very small ruminants (i.e., dik dik or mouse deer) is likely even smaller than that for sheep and goats [Van Soest et al., 1995].

High fiber by-products, including feeds such as brewer's and distiller's grains, have the common characteristic of high NDF. They are often fed as protein supplements in prepared feeds. Because these feeds are of a small particle size, selective feeding is precluded. Recall, however, the finer fiber from prepared feeds is effective in the rumens of sheep and goats [Van Soest et al., 1994] and as such it competes with the forage source in contributing net fiber. This likely indicates a limitation to feeding pelleted forage to small ruminants in zoos.

Because of the finer particle size of prepared feeds, fiber quality becomes a

more stringent requirement, since selection is abolished and the poorer quality fiber must be consumed. Because the limiting particle size for rumination is smaller than that of the by-product feed, the small ruminant (as seen in goats) is at a disadvantage in utilizing these feeds, and intake suffers [Van Soest et al., 1994].

Hofmann [1989] points out that selective ruminants have comparatively larger lower digestive tracts relative to the rumen, emphasizing perhaps a reduced role for the rumen, which, despite the very high rates of production, appears to supply only 45–60% of the metabolizable energy for small ruminants in the form of VFA (shown in Fig. 9). The high rates reported in the smallest ruminants [Hoppe, 1977] are possible only on highly selected concentrate diets. Selectors do not seem to show any consistent trend, although their VFA yields are well below those for maintenance energy. This holds even for the small selectors like the suni and dik dik that have very high fermentation rates. Another possibility is that some of these species have low metabolic rates [McNab, 1980]. This leads to the probability suggested by Hofmann [1989] that there is important bypass or escape of high quality feed to the lower digestive tract in small selector ruminants. Hofmann [1989] compares these to other small nonruminant selectors.

TOTAL DIGESTIBLE NUTRIENT (TDN) VALUES FOR HERBIVORES IN ZOOS AND THEIR REQUIREMENTS

Most digestion balance data derive from cattle and sheep and were conducted at restricted intake to insure identical compositional intakes between the two species [Van Soest et al., 1978]. Thus, even these data have limited value in regard to practical intakes for production purposes in goats, sheep, and deer, which have lower digestibilities of fiber consistent with their metabolic size and expected shorter rumen retention times [Huston et al., 1986]. This relates to the problem of how one extrapolates domestic information to zoo animals of disparate size and feeding behavior.

A further problem in calculating the correct TDN value for zoo herbivores involves the question whether one estimates based on the whole forage offered or on those portions actually ingested. As selection increases, net utilization of forage offered declines, while digestion and utilization of that consumed increase (Table 6). The degree of this disparity varies with the range in relative value of the respective plant parts and the level of refusal allowed. Tessema [1972] found that while heifers would completely consume tropical grass, sheep could not be forced to consume the coarser stems. Olubajo et al. [1974] reported 50–60% refusal of tropical grasses offered to dwarf African sheep in Nigeria. Refusal was highly correlated with NDF content. Sands [1982] reported similar refusals in Napier grass fed to goats in Kenya. These observations probably apply to small selective herbivores, both ruminant and nonruminant.

In order to use TDN and net energy values for selector animals, it is necessary to comprehend the problem of selectivity. When goats were fed ad libitum with excess forage, the diet consumed had a higher nutritive value than that offered, the rejected parts being of correspondingly lower value [Van Soest et al., 1994]. As more feed is offered, net feed intake also increases because of the opportunity of selecting a better diet. There are thus two separate problems in adapting TDN values for practical feeding of small ruminants. First, the conversion to species-specific digest-

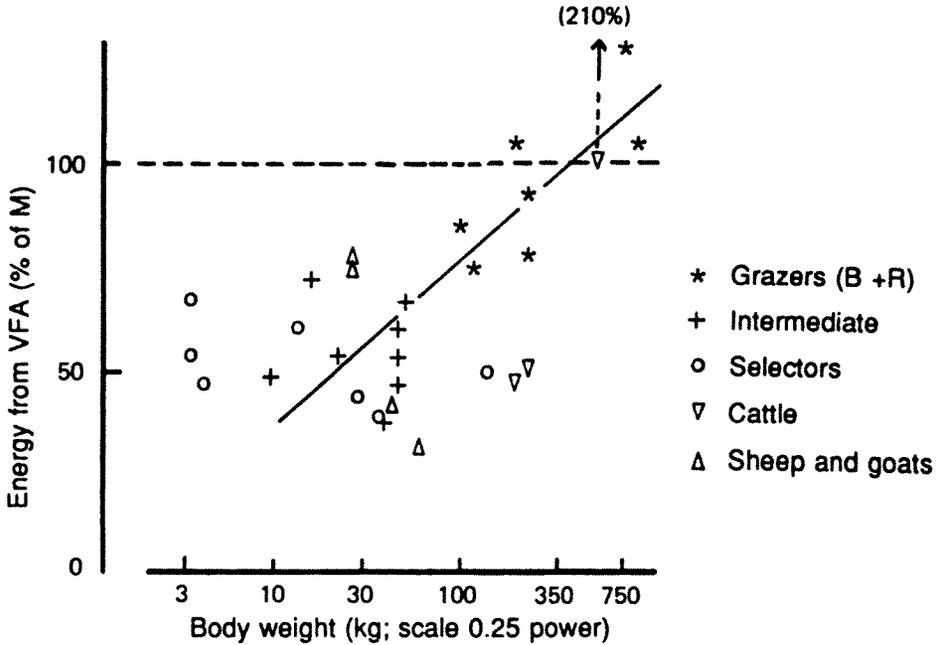


Fig. 9. Relationship between the percentage of dietary energy from VFA and body weight calculated as the percentage of calories from VFA that contribute to maintenance [Van Soest, 1994]. Summarized from Hungate et al. [1959, 1961], Allo et al. [1973], Giesecke and Van Gylswyck [1975], Hoppe [1977], and Parra [1978]. The regression line is for grazers (bulk and roughage eaters) and intermediate feeders ($r = +0.86$). Ranges in values for dairy cattle [Hungate et al., 1961] are indicated by arrows.

TABLE 6. Estimates of practical refusals for optimal lactational performance in goats [Van Soest et al., 1994]

Forage	Predicted digestibility ^a (%)	Refusal (%)	Digestibility of ingested forage (%)	Utilization ^b (%)
Alfalfa	65	15	69	59
	58	25	66	50
	50	35	60	39
Grass	70	20	75	60
	60	35	69	45
	50	50	60	30

^aFrom composition of the offered forage.

^bDigested matter actually ingested as percent of amount offered.

ibility, accounting for animal retention and metabolic losses (physiological), and, second, accounting for practical refusals at practical intakes (behavioral).

Because forages are generally analyzed as offered, the analytical values of composition do not represent what is eaten. Thus, at effective levels of feeding, the selective consumption of feed will need to be taken into account. The value of feed

offered underestimates the value of that actually eaten, while the overall utilization taking into account the refusal is a lower value (Table 6). The consequence is that the conversion of TDN relative to domestic ruminants (cattle and sheep) will be severely discounted if the feeding value is expressed in units of utilized (selected) energy per unit of feed offered.

The amount of information comparing other nondomestic species is much more limited, often relying only on a single or, at most, a few diets. In sorting through these types of data, it is important to examine digestion trial procedures, especially in the case of tropical and warm season forages that have nutritively disparate parts which offer animals adapted to specialization the opportunity to select.

CONCLUSIONS

1. Feeding behaviors of herbivores are diverse and involve interactions among types of plants, selectivity, and tolerance to plant diversity. The physical mechanisms that allow diversity in feeding behavior are dentition, mouth proportions, and gut morphology involved in the sequence of digestion. The largest contrast in gut morphology is between the large colonic fermentors and the pregastric fermentors, including ruminants. Both nonruminant herbivores and ruminants are diversified into parallel feeding types, including such adaptations as cecal fermentation dominant over colonic fermentation (as in rodents) and extreme selective behavior in small ruminants. In contrast, equids, elephants, and pandas are extreme bulk and roughage eaters and tend to consume volumes with lower extraction.

2. There is a probable coarse fiber requirement for normal gastrointestinal function in all grazing species, whether ruminant or nonruminant. There appears to be a critical size limit to unselective grazing behavior at about 90 kg which is the result of competition between required intake and gastrointestinal capacity. There is also a body size association between digestive capacity for cellulose in grasses for all grazing herbivores. This association is not found when faster-digesting carbohydrates are fed.

3. Ruminants smaller than 30 kg can have longer retention times than would be expected. These animals are extreme selectors, consume low cell wall diets, and appear intolerant to lignified fiber. Although small ruminants achieve rapid rates of fermentation by selective feeding, the net contribution of VFA to net digestible energy is lower than in larger ruminants.

4. There is a tendency to match the nutrition of wild species to related domestic species that have known requirements and nutritional values for feeds. However, this is not a safe extrapolation, since the feeding behavior of wild species in their native habitats is understudied and may significantly deviate from their matched domestic counterparts. A further problem, particularly with tropical herbivores kept in temperate zoos, is finding nutritionally similar substitutes for their native feeds, even when they are known.

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