CHAPTER 55

The Nutrition of "Browsers"

MARCUS CLAUSS AND ELLEN S. DIERENFELD

Historically, "browsers"—whether leaf-eating primates, browsing ruminants, or browsing rhinoceroses—have often been considered difficult to maintain under conventional zoo feeding regimens. Although epidemiologic studies are generally lacking, several problems seem to have a high prevalence in browsing species. Browsing ruminants seem to be particularly susceptible to rumen acidosis in captivity and also to "ill thrift" and poor body condition in general.[11] In two large representative samples, the latter observation has led to explicitly recognized "syndromes": the "wasting syndrome complex" in moose *(Alces alces)*[9,69] and the "peracute mortality syndrome" or "serous fat atrophy syndrome" in giraffe *(Giraffa camelopardalis)*.[31,61] In tapirs (*Tapirus* spp.)[48] and langurs,[56] a soft fecal consistency is frequently observed, and browsing arboreal foregut fermenters, such as sloths or langurs, have a high prevalence of gastrointestinal (GI) upsets.[25,26]

The objective of this chapter is to outline common denominators of "browsers" that need to be considered when developing management plans for browsing species.

BROWSERS ARE HERBIVORES FIRST

Browsers are herbivorous animals that feed, in the wild, predominantly or exclusively on dicotyledonous plant material, including the leaves and twigs of trees and shrubs, herbs, and forbs, but also wild fruits. This definition applies to a variety of reptile, bird, and mammal species. Among the mammals, species from different taxonomic groups, such as marsupials, rodents and lagomorphs, primates, edentates, artiodactyla and perissodactyla, are typically referred to as "browsers." Within these groups, "browsers" are usually contrasted to other feeding types.

However, all browsers are not similar in feed choices, and these internal categories may have implications for appropriate feed types. In taxa where no "grazers" (species feeding predominantly or exclusively on monocot plant material) exist, such as the primates or the edentates, "browsers" are often termed *folivores* ("leaf eaters") as opposed to omnivorous species. The term "folivore" is not used in taxons in which both "browsers" and "grazers" exist, because some grazers also ingest preferentially the blades ("leaves") of grass.

Vertebrates cannot digest plant cell walls autoenzymatically. Therefore, herbivorous animals have to rely on the fermentation activity of symbiotic gut bacteria for the digestion of plant cell walls.[68] These bacteria are contained in one or two major fermentation sites within the GI tract: in a foregut, a hindgut, or both.

The basic challenge in herbivore nutrition is to maintain a healthy, stable gut microflora in the herbivorous animal. The most common problem in herbivore nutritional management is a relative lack of plant cell wall material (fiber) and a relative oversupply of easily digestible and fermentable substrates (mostly soluble carbohydrates, e.g., sugar and starch; in extreme cases, perhaps protein). Such an oversupply will lead to direct disturbances of the microflora in foregut fermenters (comparable to rumen acidosis in domestic ruminants). In hindgut fermenters, these substrates are primarily absorbed from the small intestine before reaching the hindgut fermentation site, where they will only cause disturbances (comparable to cecal acidosis in domestic horses, the major cause of laminitis) if given in particular oversupply. This dualism may be illustrated with two primate groups: in captivity, with an oversupply of easily fermentable carbohydrates in conventional diets, langurs (foregut fermenters) have a history of digestive upsets and malnutrition,[26] whereas lemurs (omnivores and some hindgut-fermenting herbivores) have a history of being obese.[68] Similarly, among the ungulates, foregut-fermenting browsers such as giraffe or moose have a history of poor body condition in captivity,[9,62] whereas hindgut fermenters, such as tapirs, rhinos, or elephants, are often overweight.[1,60,75]

In zoos, browsers have been traditionally recognized as animals with a difficult nutritional management.

Partly, this reflects a basic problem in herbivore nutrition. As evolved omnivores, humans value easily digestible carbohydrates such as sugars and starches. We have a long history of cultivating grains and fruits for their respective starch and sugar content, and we intuitively want to include these items in the diets of animals we keep. Herbivores have also evolved to select for these items. In the natural environment, their sparse availability limits any potential danger of oversupply; in captivity, however, situations might exist in which the offer of these items is not limited. A restricted supply of such items, with a generous supply of high-fiber feeds, is therefore the fundamental approach to herbivore nutrition.

BROWSERS ARE DIFFERENT

Nevertheless, compared with other herbivores, browsers still appear to be particularly sensitive. Possibly, one should not prioritize the investigation of other nutritional factors besides a high-fiber diet at first. In free-ranging browsers, a high fiber content is the major determining characteristic of their natural diet (Table 55-1); free-ranging browser diets are not distinctively "lower in fiber" than those of grazing species. In terms of fiber and carbohydrate content, a pelleted feed for "browsers" should therefore be suitable for "grazers" as well.

For the digestive physiology of many species, the provision of nonpelleted high-fiber diet items, that is, *forage,* is crucial. In ruminants, for example, the provision of structured fiber is a prerogative for proper rumen function, and in most herbivores, forage material is the only guarantee for a "normal" fecal consistency. In addition, forage addresses the most basic ethologic requirements of animals that have evolved physiologic and psychologic adaptations for the handling of (complex) food items, and oral stereotypies have been observed in many species such as cattle,[64]

Table 55-1

Fiber Content of Natural Diet of Different Free-Ranging Herbivores*

Species	Crude Fiber (% Dry Matter)	NDF† (% Dry Matter)	Source (Reference)
Giraffe *(Giraffa camelopardalis)*	—	50-70	(61)
Okapi *(Okapia johnstoni)*	—	43-48	(59)
Moose *(Alces alces)*	20-45	50-70	(5)
White-tailed deer *(Odocoileus virginianus)*	—	35-50	(79)
Duikers (various spp.)			(24)
Forage		5-70	
Fruits		30-60	
Buffalo *(Syncerus caffer)*	30-40		(30)
Waterbuck *(Kobus ellipsiprymnus)*	30-40		(80)
Black rhino *(Diceros bicornis)*	20-60	40-70	(4)
White rhino *(Ceratotherium simum)*	36	75	(47)
African elephant *(Loxodonta africana)*	35-50	60-70	(53)
Three-toed sloth *(Bradypus tridactyla)*		40	(31)
Colobus monkeys (different species)			(49, 55)
Forages		30-70	
Fruits		50-70	
Ring-tailed lemur *(Lemur catta)*		30-50	(22)
Howler monkey *(Alouatta aloutta)*			(70)
Forages		20-80	
Fruits		20-70	
Gorilla *(Gorilla gorilla)*		40-80	(65)
Orangutan *(Pongo pygmaeus)*		40-60	(34)
Browsing kangaroo *(Macropus fuliginosus)*		60-80	(21)
Grazing kangaroo *(Macropus rufus)*		50-80	(21)

*Note that free-ranging browser diets (even fruits) do not have particularly lower fiber levels than those of other herbivores.
†Neutral detergent fiber, a measure of cell wall (fiber) content.

okapi and giraffe,[42] and horses[81] eating forage-deprived or low-fiber diets. Particularly with respect to the suitability of forage, browsers are different: in contrast to the situation with grazing herbivores, the staple provision with a forage that is readily accepted by browsers without causing GI problems may be challenging in certain species.[11]

This general discrepancy between grazers and browsers is reflected in the traditional recipes for pelleted feeds provided by commercial manufacturers. Although there is no indication that browsers are adapted to a higher fiber intake than grazers, experience has led to the development of particular "browser" pellets high in fiber. In contrast, "regular herbivore" or "grazer" products contain less fiber because these animals readily accept the staple fiber source offered to them in addition to the pellets: grass hay. Using the product ranges of both U.S. Mazuri (PMI Nutrition International, St. Louis, Mo) and U.K. Mazuri (SDS, Essex),* it may be demonstrated that the recipes for ungulates increase in fiber content according to the difficulty of providing the target species with readily acceptable forage material, with moose being recognized as a large browsing species particularly reluctant to accept hay (Table 55-2).

It should be noted that the fiber levels reported in Table 55-2 are still in the lower range of the fiber levels reported in diets of free-ranging animals (see Table 55-1). Interestingly, this discrepancy is even greater if the primate diets of commercial manufacturers (Table 55-3) are compared to the diets of free-ranging primates (see Table 55-1).

This chapter contrasts selected peculiarities of browsing and grazing herbivores, which are adaptations to certain characteristics of their natural diets, and links this with health problems in captivity and problems in diet design for captive animals. In the absence of systematic research on the nutritional managements of browsers, including normal gut microbiology, the suggestions for feeding browsers must, by necessity, remain speculative.

DIFFERENCES BETWEEN GRAZERS AND BROWSERS

A fascinating multitude of anatomic and physiologic differences has been postulated (and sometimes demonstrated) between browsing and grazing herbivores and their respective diets.[18] Internal and external differences in muzzle width, tooth form, salivary gland size and saliva composition, and GI tract morphology have been suggested as underlying features of importance in differential nutrition of browsing herbivores.

*The use of product information from commercial suppliers has solely didactic purposes and does not imply a particular recommendation or warning.

Table 55-2

Declared Crude Fiber Content of Select Herbivore Feeds from Catalogs of Two Commercial Suppliers*

Diet Name	Crude Fiber (% Dry Matter)	NDF† (% Dry Matter)
Herbivore 16-ADF[1]	16.7	32.2
Herbivore 25-ADF[1]	25.6	43.4
Browser breeder[1]	27.8	43.6
Browser maintenance[1]	31.1	48.1
Moose maintenance[1]	35.6	54.8
Grazer[2]	11.2	
Browser breeder[2]	18.6	
Browser maintenance[2]	21.4	
Moose[2]	24.0	

*Note that fiber levels do not reflect differences in "fiber requirements" between target species, but that fiber content increases with the recognized target species' reluctance to accept grass or alfalfa (lucerne) hay forage.
†Neutral detergent fiber, a measure of cell wall (fiber) content.
[1]Mazuri (PMI, St Louis, Mo USA).
[2]Mazuri (SDS, Essex, UK).

Table 55-3

Declared Crude Fiber Content of Select Primate Feeds

Diet Name	Crude Fiber (% Dry Matter)	NDF* (% Dry Matter)
Leaf-Eater Primate diet[1]	15.6	27.4
Primate High Fiber Sticks[1]	16.1	32.9
Primate Browse Biscuit[1]	17.8	29.4
Leaf Eater Primate[2]	13.8	
High-fiber primate diet[3]	10.0	
Leaf Eater Red Apple[4]	14.4	20.8

*Neutral detergent fiber.
[1]Mazuri (PMI, St Louis, Mo USA).
[2]Mazuri (SDS, Essex, UK).
[3]HMS (Bluffton, Ind USA).
[4]Marion Zoological (Plymouth, Minn USA).

Not all these differences are of direct relevance for zoo animal feeding. The following differences, however, most likely are important for the nutritional management of browsers:

Chemical Composition of Forages

Browse is regularly reported to contain more protein than grasses.[18] On the one hand, this is most likely due to analytic difficulties: protein content is usually assessed by analyzing nitrogen and multiplying by the factor of 6.25. However, browse may contain significant amounts of nonproteinaceous nitrogen in secondary plant compounds, and it has been suggested, at least for tropical browse, that the true conversion factor for the calculation should be as low as 4.4.[54] Lignin also contains nitrogen in a chemically unavailable form.[77] Therefore, bound nitrogen may erroneously contribute to higher protein values reported for many browses unless available versus bound protein fractions are analyzed separately. On the other hand, high reported protein contents should not automatically lead to the assumption that browsers have higher protein requirements.

A classic case of an assumed high protein requirement in a browser is that of giraffe. It was suspected that low-protein diets play an important role in the serous fat atrophy syndrome (peracute mortality syndrome) observed in captive giraffes,[32] and high protein levels of 18% dry matter (DM) were consistently recommended for this species. However, it was later reported that the problem also occurs in animals with "adequate" protein provision.[45] A comparative evaluation of experimentally determined protein requirements in ruminants does not reveal relevant differences between the different feeding types.[11] The fact that browsers do have higher fecal and urinary nitrogen losses when kept on browse does not reflect higher true endogenous losses, but rather is caused by the secondary plant compounds in the browse fed. If the same animals are kept on a diet without secondary compounds, the nitrogen balance is "back to normal."[66] As a logical consequence of such considerations, the recommended protein levels for giraffe, for example, have recently been reduced to 12% DM.[34] Particularly high protein levels for browsers appear unnecessary.

Browsing ruminants have traditionally been termed "concentrate selectors."[40] This may have led to a widespread conception that browsers particularly prefer (and require) easily digestible carbohydrates such as starch and sugars, and that such animals may receive higher proportions of concentrate feeds. However, comparative evaluations of ruminant necropsies have revealed a higher prevalence of GI disorders, particularly acidosis, in browsers compared with grazers. Evidently, the so-called concentrate selectors often suffer from a condition triggered by too much "concentrate feeds."[11] Therefore, for didactic reasons alone, the term "concentrate selector" should be avoided. Actually, there is no indication that browse has a higher sugar or starch content than grass; however, browse contains higher proportions of soluble fibers, such as pectins.[66] Pectin sources have been recognized in domestic ruminant nutrition as high-energy "concentrates" that may favorably replace starch-containing grain products because of a significantly less acidotic potential compared to grains.[78] Therefore, pectin sources may be considered excellent energy-supplying diet items, both for browsers and grazers alike.[41,46]

The fiber component of browse is generally more lignified than that of grasses.[77] *Lignin* is a basically indigestible material, and thus more highly lignified fiber is less digestible. Broad surveys of various forages have shown lignification indices (% lignin/% neutral detergent fiber [NDF]) approaching 20% to 30% of total fiber in browses, compared with perhaps half that proportion in grasses. To date, no observations indicate that a deliberate inclusion of lignin, rather than a general increase in overall fiber levels, is of particular health relevance for browsing animals. However, it is most certainly associated with decreased forage digestibility in a variety of herbivore species.

Browse plants, in particular the leaves of woody plants, often contain secondary plant compounds that may act as digestibility reducers or toxins that may serve as feeding deterrents. As adaptations, browsing animals may produce salivary proteins that reduce the effect of such substances (e.g., the tannin-binding proteins), and are likely to have evolved a variety of metabolic detoxification mechanisms.[6] Because of the enormous variety of secondary plant compounds, general rules are difficult to distill from the literature. Some positive effects of some of these compounds have been reported (e.g., as antioxidants or anthelmintic substances, or by "protecting" dietary protein from ruminal degradation and thus enhancing intestinal digestion). In roe deer *(Capreolus capreolus)* fawns, an increased food conversion and a tendency for higher circulating antioxidant levels have been reported on a pelleted diet with added tannin.[12] In black rhinoceros *(Diceros bicornis)* feces, the antioxidant capacity was higher on tannin-containing diets.[17] However, the experimental evidence is still extremely limited. More studies are needed before any recommendations about the deliberate inclusion of such substances may be made.

Fermentation Characteristics

In the few published in vitro studies, browse material *reached its maximum of fermentation sooner* than grass material, most likely because of a higher content of slowly fermenting cellulose fiber in grass and more rapidly fermenting pectin and indigestible lignin fiber in browse.[43] This has important implications for GI physiology. In theory, it would not make sense for a browser to retain ingesta as long as a grazer does; compared with grass, browse does not yield relevant amounts of energy after a certain digestion time. Indeed, there have been numerous indications that browsing ruminants and browsing rhinos have shorter ingesta retention times than their grazing counterparts,[16,19] but for a comprehensive comparative evaluation, the existing database is still too small.

For the design of zoo animal rations, this could mean that browsers should not be able to digest any given forage as efficiently as a grazer (due to shorter retention times, i.e., less time available for digestion). Therefore, if a browser accepted a grass hay diet, for example, it might have to ingest more of it to achieve a similar uptake of digestible energy as a grazer of comparable size. In ruminants, shorter retention times within the rumen will also translate into less degradation of substances susceptible to bacterial fermentation; for example, polyunsaturated fatty acids are hydrogenated to a lesser degree, and one would expect less bacterial transformation of proteins and less degradation of vitamin A or vitamin E.[7]

However, these characteristics are unlikely to be of practical relevance; one could save on vitamins, or on "protected proteins," in browser diets. As long as quantitative information on these effects is lacking, however, it is advisable to keep vitamin levels as high as in domestic (grazing) ruminants. The impact of rumen-protected proteins has not been examined in zoo ungulates and probably has more applications, particularly economic, for livestock species.

Physical Characteristics

The physical differences between grass and browse are suspected to be responsible for the widespread reluctance among browser species to ingest grass hay, and in some cases perhaps even alfalfa hay, in similar amounts as grazers.[11]

Many grasses defend themselves against herbivores by abrasive silica. Browse is generally less abrasive and contains less acid-insoluble ash. As adaptations, grazers of all taxons have a hypsodont dentition (high-crowned teeth) that may be worn down throughout their lifetime, whereas browsers mostly have low-crowned teeth.[18] For free-ranging browsers such as moose, it has been postulated that the animals should select against an abrasive diet,[36] and for roe deer, it was shown that the diet selected contained less silica than the available forage.[76] For captive browsers, even if only partly fed on grass hay, this should mean that after years in captivity, they should display more severe tooth wear than grazers. In this respect, unnatural tooth wear has been identified as an important problem in a captive browser, the giraffe.[20,28]

Differences in fracture properties between forages—with browse being more brittle (requiring crushing dentition) and fractionating into more polygonal particles, and grass being more flexible (requiring cutting dentition) and fractionating into longer, fiberlike particles—have thus far only been sparsely documented.[18] Nevertheless, these differences have most likely driven the evolution of tooth shape and also gut anatomy. It may be expected that the respective dentitions of browsers and grazers are adapted to finely comminute their respective natural diets. In comparative assays, this should mean that browsers do not chew grass hay/ conventional zoo diets into as fine particles as grazers do (documented in ruminants[10] and macropods[50]), and that the feces of free-ranging browsers should contain finer particles than those of captive specimens. The latter hypothesis has been confirmed for tapirs,[48] even though the captive animals ingested a high proportion of finely ground "concentrates." Differences in fracture properties, with an increased tendency of grass material to form a "fiber mat" in the rumen (a prerequisite of efficient particle retention in domestic ruminants), have been linked to the reluctance of browsers, whose rumen lacks the strong musculature of grazers, to ingest grass material in large proportions.[13]

Certain Forages Are Inappropriate for Browsers

In conclusion, browsers should have evolved to avoid grass because of the abrasiveness of this diet, both grass and (to a certain extent) alfalfa because of problems in food communition from an unsuitable dentition, and problems in ruminal food processing because of unsuitable rumen morphology. Reluctance to ingest grass or even alfalfa hay has been documented in numerous ruminant browsers,[11] in macropod browsers,[50] in the browsing suid babirusa *(Babyrousa babyrussa)*[51] and is also reflected in the well-known reluctance of many tapirs to ingest such forages. In contrast, Marcus Clauss has seen black rhinoceroses readily ingest grass hay and thrive on grass hay–based diets for long periods, but with excessive tooth wear. Intuitively, grass and alfalfa are rarely offered to those browsers termed "folivores" (sloths or primates), except the largest apes (gorillas).

If browsers are fed on such inappropriate forages, the following two consequences are to be expected:

1. Low acceptance of the forage, resulting in an unintended, high proportion of "concentrate" feeds, which may result in acidosis (particularly in foregut fermenters). This has been reported in ruminants[11] or suspected in colobines,[73] with associated laminitis, liver abscesses, oral stereotypies, or poor body condition; or resulting in obesity (particularly in hindgut fermenters); and generally in poor fecal consistency.
2. If the forage is accepted, increased tooth wear (in the case of grass) and a less effective particle reduction, resulting in an increased risk of phytobezoar formation, as reported in giraffe or mule deer.[11] In this context, even certain browse species may be inappropriate for animals adapted to different browse items (e.g., acacia-induced phytobezoars in langurs, but note that phytobezoars must also frequently occur in free-ranging langurs[57]).[3,29]

To our knowledge, the long-term consequences of these effects have not been assessed; however, in individual browsing species, short life spans in captivity have been noted, including the well-documented mortality peak in captive moose at 6 to 8 years of age[9] and the high mortality in captive langurs[26] and sloths.[25,63]

PRACTICAL FEEDING

Pellet Design

Historically, the development of the aspen sawdust–based, pelleted ration for moose at the Kenai Moose Research Center in Alaska[67] is the hallmark of a major breakthrough in the nutrition of captive browsers (NDF = 57% DM). The success of this ration was probably not a result of the woody component itself, but simply because the sawdust ingredient ensured a high fiber content of the final product.[14] Ironically, the primary incentive for the use of the sawdust ingredient seemingly was not an increase of the overall fiber level; rather, it was argued that lignified forage has different fracture properties than grass. However, sawdust is a poor source of lignin (but rather a good source of cellulose), and in a milled and pelleted compound feed, the original fracture properties of the ingredient materials are of no relevance.

In subsequent steps the recipe of the pellet was refined[69]; the most important refinement probably was the inclusion of beet pulp as a pectin-rich energy source and a corresponding decrease in or exclusion of grain (including corn) products. The use of beet pulp as a pectin source instead of grains in the nutrition of herbivores has been advocated increasingly over the past decades[78] and has been tested successfully with moose, giraffe, and okapi.[44,46,69]

Basically, a safe pellet for any herbivore, including browsers, should be based on a forage meal, whether sawdust, alfalfa meal, grass meal, sunflower or soy hulls, cellulose powder, or mixture of these, to ensure a high fiber content; should use unmolassed beet pulp as an energy source; and should not include significant amounts of grains or corn. Linseed products might be useful to increase the omega-3 fatty acid content,[8,72] especially if soy products are included to increase protein levels, and sodium bicarbonate may also be used as a buffer further to prevent acidosis.[2] A practice to use (and market) such a pellet for browsers only, but not for grazers, cannot be based on physiologic considerations. However, because animals will need higher amounts of such high-fiber, low-energy feeds, grazers might, for financial reasons, receive restricted amounts of more energy-dense feeds of lower fiber content, under the assumption that they will readily consume the staple hay item.

Table 55-4 provides two examples of recipes for pelleted diets.

Forage Choice

The major challenge in the nutrition of browsers is to find a forage material that is both suitable and readily accepted by the animals and logistically easy to acquire. For most browsing species, alfalfa hay is used as a surrogate, although chemically it may not be the best nutrient substitute. The chemical composition of alfalfa hay differs among the continents, with mostly early-bloom alfalfa used in the United States, and differs from browse material as well (Table 55-5).

In particular, an exclusive consumption of alfalfa leaves only could, in combination with a low-fiber pelleted compound, result in a diet of comparatively high

Table 55-4

Example Recipes for Pelleted Diets Fed to Browsers*

Ingredient	% Original Weight
Example 1	
Sawdust	22.5
Beet pulp	20.0
Canola meal	20.0
Alfalfa meal	10.0
Sucrose	5.5
Soybean meal	5.0
Dried orange peel	5.0
Mineral/vitamin supplements	12.0
NDF† (% dry matter)	42.7
Example 2	
Beet pulp	22.5
Soy extraction meal	22.5
Alfalfa meal	22.5
Sunflower hulls	12.5
Wheat	8.0
Molasses	2.5
Cellulose powder	2.5
Linseed	2.0
Sodium bicarbonate	1.0
Mineral/vitamin supplements	4.0
NDF† (% dry matter)	40.7

From Berndt C, Klarenbeek A, Clauss M, et al: *Proc Eur Assoc Zoo Wildl Vet* 5:371-372, 2004; and Schochat E, Robbins CT, Parish SM, et al: *Zoo Biol* 16:479-494, 1997.
*Suitable for grazers as well.
†The calculated/analyzed neutral detergent fiber *(NDF)* value is given as well for comparison with Tables 55-1 and 55-2.

protein and low fiber levels. Excessively high protein contents could, for example, lead to the formation of copper-sulfide bonds in the rumen, thus reducing copper availability.[23,74] For example, a low copper status has been observed in duikers, small ruminants that selectively ingest the leaves, but not the stems, of the alfalfa hay offered.[33]

In Europe, alfalfa is much less common in dairy or beef rations and thus much more difficult to acquire for many zoos, as reflected in the ranges for alfalfa (lucerne) hay from Europe with high fiber and low protein levels (see Table 55-5). Direct contracts with local farmers might be a good alternative in such situations. However, the provision of browse material itself in large quantities should be the ultimate goal of any zoo interested in browser husbandry, even though this goal implies logistical and nutritional challenges.

From a logistical point of view, browse is labor intensive to harvest, difficult to store, only seasonally available in the temperate zone, and often not available in large amounts. With regard to availability, zoos with browser breeding programs should either initiate cooperation with the local forestry agencies, with the result of a constant supply, or establish a browse plantation of their own.[39] Browse may be harvested on a daily or weekly basis and may be dried (even commercially available), frozen, or ensiled.[36] The acceptance of the different conservation methods may vary among species.

From a nutritional point of view, the use of browse infers a high degree of uncertainty, especially in regard to potentially toxic secondary plant compounds, which may vary seasonally or geographically, even within the same plant species. Therefore, the reasonable admonition is that the feeding of browse should be based on scientific recommendations.[58] In practice, such a demand is difficult to fulfill because of the variety and variation in secondary compound contents, even within the same plant species. Additionally, experiences with cases of plant poisoning and the uneventful feeding of browse may be used; recently, such observations have become more easily accessible by the establishment of browse databases (e.g., www.foragerssource.org). In any case, it is advisable to offer a variety of (reportedly harmless) browse species because this will increase overall intake and allow the animal to select among different items (all of high fiber content), and the ingestion of smaller amounts of different secondary compounds is usually considered less dangerous than the ingestion of a larger amount of any one particular toxin.

Ration Composition

Following widespread (but not always heeded) recommendations, rations of browsers, as with other herbivores, should not contain rapidly fermentable carbohydrates, such as the sugars and starch contained in commercial fruits and grain products, including bread and grain-based pellets.[58] Instead, rations should be composed of a high-fiber pellet and adequate roughage, such as grass and alfalfa hays (in ungulates) or green leafy vegetables with stem fractions (in primates).

The major problem in ration design for browsers and other herbivores is that the amount of forage offered, whether browse, alfalfa hay, or grass hay, is

Table 55-5

Composition of Selected Nutrients in Alfalfa Hay *(Medicago sativa)**

Feedstuff	% NDF	% Crude Fiber	% Crude Protein	% Ca	% Mg
Alfalfa Early bloom (USA)[1]	43	25	22	1.6	0.4
Alfalfa Midbloom (USA)[1]	47	28	19	1.4	0.4
Alfalfa Late bloom (USA)[1]	52	32	14	1.3	0.3
Alfalfa leaves only[1]	34	18	23	2.6	0.4
Lucerne hay (UK)[2]	46		18	1.5	0.3
Lucerne hay (Europe)[4]	36-69	23-43	12-19	0.9-3.8	0.1-0.2
Temperate browses					
Browse leaves[3]	27-66		13-23	0.3-3.0	0.1-0.3
Browse leaves[4]	43-54	13-26	14-18	1.4-2.1	
Browse twigs[3]	63-82		3-7	0.5-2.6	0.1-0.2
Browse twigs[4]	67-75	19-42	3-7	1.0-1.5	

*Harvested in the United States (USA) and United Kingdom (UK), and comparison with alfalfa leaves that may be selectively consumed by browsing herbivores compared to some temperate and native browses. All values on a dry matter (DM) basis. *NDF,* Neutral detergent fiber; *Ca,* calcium; *Mg,* magnesium.
[1]US-Canadian Tables of Feed Composition, NRC.
[2]UK Zoo Feed Ingredient Database; Fidgett A: Unpublished Data.
[3]Zootrition 2.5 database, St Louis, Mo USA.
[4]Data from references 4 and 5.

much more difficult to estimate than the amount of pellets or produce given. As target amounts of different food items, those given in the Nutrition Advisory Group (NAG) fact sheets for ungulates[52] and leaf-eating primates[27] may be used, and the amount of forage indicated in these guidelines may be replaced in part by browse. However, to control whether these target intake values are actually reached in a specific animal or animal group, sporadic weighing of foods offered and left over, possibly with a DM determination of a representative subsample, is necessary. Furthermore, restricted feeding of some preferred, but less nutritionally balanced, items may be an important aspect of nutritional management to encourage fiber consumption.

Browse material is difficult to quantify because it is generally offered as branches, the majority of which is not edible for most species. A weighing of a total branch offered therefore provides little information about the amount of edible browse offered. This problem is evidently easy to solve in the case of silages, or plucked leaves. In the case of whole branches, a rough estimation of the edible leaf and twig mass may be made using the diameter of the branch at the point of cutting and species-specific allometric equations.[15]

An important question for many zoos involves the quantity of browse to include in browser diets. To date, no scientific answer exists, and anecdotal experiences are insufficient to distill a rule of thumb. In captive giraffes it has been documented that the overall DM intake increased in one particular group with the addition of up to 3 kg of fresh, edible browse (i.e., not including large branches) compared with a diet without or with only 1 kg of browse. In contrast, the addition of 6 kg of the same browse material did not increase the overall intake any further.[37] However, the browse was always consumed completely, and total DM intake is only one parameter of interest; in particular, long-term effects of such a feeding regimen are difficult to document.

The use of safe browse species should be decided on the basis of data on the intake of the different diet items offered to the animals. In browsers, if the intake of the offered conventional forages is lower than recommended, the proportion of browse in the overall diet should be increased.

CONCLUSION

Moderately digestible, high-fiber and moderate-protein diets best duplicate—from a chemical point of view—the foodstuffs consumed by most browsers in nature, whether highly frugivorous, folivorous, or woody plant–part consumers. Many of the pellets currently fed to captive species are low in fiber and high in starch and protein, which may lead to health problems such as acidosis and mineral/electrolyte imbalances. Native chemistry should provide clues for more suitable captive diet formulations. Low-fiber foods containing sugars or starch, such as most domesticated fruits and grains, should not be used (except perhaps for training purposes).

Enrichment should be provided by variety of high-fiber forages, not by offering sugary or starchy items. The inclusion of tanniniferous foods in artificial diets should not be regarded as exclusively negative, and effects of tannins on animal response should be evaluated further. Incorporation of palatable, readily accepted sources of dietary fiber, to maintain digestive tract function and psychologic well-being, should be considered the highest priority in feeding all browsers. Facilities aiming for long-term browser husbandry should incorporate contingency plans for the provision of such forage materials into their overall management approach.

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