

Grazers and Browsers: How Digestive Morphology Affects Diet Selection

Lisa A. Shipley

Abstract

Grasses (monocots), forbs and browse (dicots) differ in structure and chemistry. Grasses have a thicker cell wall containing potentially digestible structural carbohydrates, fewer secondary plant chemicals, and have a relatively low and homogenous growth relative to browses. Mammalian herbivores can be classified along a continuum according to which plant type they prefer. Diet choices correspond with morphological specialization within the gastro-intestinal tract, including the mouth and teeth, which may confer increased efficiency for extracting nutrients from grasses and browses. These differences are confounded with body size, and thus the full extent of the effects of morphology on digesting and harvesting foods is unclear. However, understanding the feeding niche of herbivores may help understand competitive interactions among herbivores and proper range management.

Introduction

An animal's anatomy and physiology clearly affect its food choices. Characteristics of food, in turn, are one of the primary forces that shape animal behavior, physiology and anatomy. The most basic difference among food choices is between meat and plants as food. Because these food resources differ in so many ways, carnivores and herbivores face completely different obstacles in satisfying their nutritional requirements (Table 1). Carnivores must spend much time and energy searching for and capturing their rare prey that have mastered hiding, fleeing, and fighting. In contrast, herbivores spend less time and energy finding and capturing bites of vegetation because plants are stationary and relatively abundant in the environment.

However, some key differences between plant and animal cells reduces the attractiveness of plants as food.

Plant cells have a cell wall that acts as a fibrous "skeleton" for plants, whereas animal cells have only a cell membrane. The cell wall is made up of fibers consisting of structural carbohydrates (e.g., cellulose) and other compounds (e.g., lignin) that are not degradable by mammalian enzymes (Gibson 1978). Herbivores must rely on symbiotic microbes that can ferment these structural carbohydrates into energy-rich byproducts, primarily volatile fatty acids (VFAs) (Hungate 1966, Stevens 1988). Herbivores then use the VFAs as their primary energy source. Therefore, cell fibers make plants difficult and energetically costly to chew and digest. Plants typically are lower in protein (Bodmer 1990) and may contain toxic allelochemicals that further reduce their nutritional quality (Robbins et al. 1995). Because plant species, individual plants, and plant parts vary in allelochemicals and amount of cell wall composition, plants are low and variable in nutritional quality, whereas meat is high and uniform in nutritional quality. Because herbivores eat a low-quality diet, they must eat a greater quantity to meet energy requirements than do carnivores (Demment and Van Soest 1985). For example, herbivores search for and crop up to 10,000 bites of plants per day (Senft et al. 1987), whereas a carnivore may consume less than 1 to a few prey items per day. Harvesting thus becomes time-consuming for herbivores.

Differences Between Grasses and Browses

The variability in the morphology and chemistry of plants has led to numerous adaptations in anatomy and behavior within the herbivore community. Some fundamental differences exist between herbaceous forages consumed by herbivores, particularly between grasses (monocots) and browses (herbaceous and woody dicots such as forbs, shrub leaves and stems; Hofmann and Stewart 1972, Jarman 1974). These differences are seen in cell structure, plant chemistry, plant architecture, and plant dispersion (Table 2). First, grasses tend to have a thicker cell wall than browses, and their cell walls consist mainly of slowly-digestible plant fibers such as cellulose (Demment and Van Soest 1985). In contrast, forbs, leaves, and some woody stems have a thinner cell wall and more cell contents that contain completely digestible and rapidly fermentable compounds such as sugars, proteins, and lipids (Bodmer 1990, Gordon and Illius 1994, Owen-Smith 1997). Within the cell wall, however, browses usually contain more indigestible fibers such as

Lisa Shipley is Professor of Wildlife Ecology, Department of Natural Resource Sciences, Washington State University, Pullman, WA, 99164-6410.

Presented in "Grazing Behavior of Livestock and Wildlife." 1999. Idaho Forest, Wildlife & Range Exp. Sta. Bull. #70, Univ. of Idaho, Moscow, ID. Editors: K.L. Launchbaugh, K.D. Sanders, J.C. Mosley.

Table 1. A relative comparison of foraging between herbivores and carnivores.

Characteristics	Herbivores	Carnivores
Food source	<ul style="list-style-type: none"> Plants Stationary Abundant 	<ul style="list-style-type: none"> Animals Mobile (hide, fight, or flee) Rare
Capturing food source	<ul style="list-style-type: none"> Little energy & time spent in search, pursuit, & capture High success of capture 10,000 bites per day High dry matter intake 	<ul style="list-style-type: none"> Much energy & time spent in search, pursuit, & capture Low success of capture 1 > prey/day to > 10 Low dry matter intake
Quality of food source	<ul style="list-style-type: none"> Low protein Low digestible energy High fiber in cell wall Quality varies among plants and plant parts 	<ul style="list-style-type: none"> High protein High digestible energy No cell wall/fiber Quality uniform among prey
Digesting food source	<ul style="list-style-type: none"> Much chewing required Complex digestive tract Energy derived from microbial fermentation of plant fiber and cell contents in foregut and/or hindgut Protein derived from digesting rumen microbes Slow passage through system 	<ul style="list-style-type: none"> Little chewing required Simple digestive tract Energy and protein derived from breakdown of proteins, fats, and carbohydrates in stomach and intestines Plant fiber not digested Rapid passage through system

Table 2. A relative comparison of chemical and structural differences between grasses (monocots) and browses (herbaceous and woody dicots).

Characteristic	Grasses	Browses
Cell wall	<ul style="list-style-type: none"> Thick Greater proportion is cellulose/hemicellulose 	<ul style="list-style-type: none"> Thin Greater proportion is lignin
Plant defense compounds	<ul style="list-style-type: none"> Silica 	<ul style="list-style-type: none"> Phenolics – tannins Terpenes Alkaloids & other toxins
Plant architecture	<ul style="list-style-type: none"> Fine-scaled heterogeneity in nutritional quality within a plant New growth added at base Low growth form 3-dimensional volume 	<ul style="list-style-type: none"> Coarse-scaled heterogeneity in nutritional quality within a plant New growth added at tips Low to high growth form Complex, diffuse, branching architecture
Dispersion	<ul style="list-style-type: none"> Uniform 	<ul style="list-style-type: none"> Dispersed/discrete

lignin. The amount of cell wall and lignin (and thus the nutritional value) changes more drastically among seasons and with age in grasses than in browses (Van Soest 1996). The thicker, more fibrous cell wall also makes grass more difficult and energy-expensive to fracture (bite and chew) than the more fragile leaves of browses (Choong et al. 1992, Robbins 1993, Wright and Illius 1995). However, woody stems of dicots contain more lignin than almost any forage and are classified as “browse” (Van Soest 1996).

Second, the types of plant secondary chemicals that influence forage quality differs among grasses and browses. Grasses tend to have a higher silica concentration that can increase tooth wear (McNaughton and Georgiadis 1986) and reduces the ability of herbivores to digest fiber (Robbins 1993). In contrast, browses tend to have more phenolics, including tannins that reduce protein digestibility, terpenes that can reduce dry matter digestibility, and toxins such as alkaloids (Robbins 1993, Robbins et al. 1995).

Third, grasses and browses differ in architectural arrangement which creates unique challenges for herbivores when harvesting bites. Grasses consist of leaves, stem, sheath, and fruit that differ in quality and form over only a very fine-scale that cannot be differentiated easily by large mammalian herbivores while foraging (Jarman 1974). Grasses thus provide a relatively homogeneous food source for larger herbivores (Jarman 1974). In contrast, browses tend to contain a more heterogeneous assembly of plant parts of various nutritional quality, including nutritious buds, mature leaves, and woody stems (Jarman 1974). The low growth form of grasses, in which new tillers are added at the base of the plant, creates a rather continuous 3-dimensional layer of vegetation with a relatively constant density (Jarman 1974). Moreover, grasses typically grow in continuous dispersion (i.e., the next nearest plant is likely a grass). In contrast, new plant tissue is added at the tips of browses, creating a branching geometry that is diffuse and irregular (Jarman 1974, deReffye and Houllier 1997). Many browse species also have spines, prickles, curved thorns or short, stubby branches that slow cropping and form an impenetrable mat (Cooper and Owen-Smith 1986, Belovsky et al. 1991). Finally, browses tend to be more discrete in dispersion, where their nearest neighbor is less likely to be a browse.

Classification of Herbivores by Diet Choices

Ecologists have long-observed that many herbivores, even those from different taxonomic groups, tend to focus on either the grass or browse component of habitats. These observations have led to various classification schemes for mammalian herbivores, primarily ruminants (e.g., feeding niches: Bell 1970, 1971, Jarman 1974; herbivory rating: Langer 1988; browser-frugivore continuum: Bodmer 1990; selectivity axes: Van Soest 1996). However, the classification system of Hofmann and Stewart (1972) based on diet choices and related to specialized morphology of ruminants (and expanded by others to include non-ruminant herbivores) has been embraced by most herbivore ecologists, if only for its heuristic value (Robbins et al. 1995), as a key to understanding diet selection and community dynamics of

herbivores. Hofmann and Stewart (1972) classified as: 1) Bulk and Roughage Feeders or Grazers that select diets containing < 25% browse; 2) Concentrate Selectors or Browsers that select diets containing at least 75% fruits, dicot foliage, and tree and shrub stems and foliage; or 3) Intermediate or Mixed Feeders that select both grasses and browses. Using this scheme to classify 65 ruminants on 4 continents, Hofmann (1989) found that 25% were grazers, 40% were browser/fruit-eaters, and 35% were mixed feeders. Many have argued that tree and shrub foliage and stems should not be considered “concentrates”, because they are heavily defended by plant secondary compounds (Robbins et al. 1995) and lignin, and thus fruit selectors (true concentrates) and browsers should form separate categories (Bodmer 1990). Others suggest that these categories only reflect trends in body mass, because smaller herbivores tend to select concentrates whereas larger ones tend to choose roughage or grass (Gordon and Illius 1994, Robbins et al. 1995). For example, in tropical areas frugivores average 24 kg, browsers 394 kg, intermediate feeders 695 kg, and Grazers 670 Kg (Bodmer 1990).

Differences in digestion between grazers and browsers

Differences between browsers and grazers extend beyond diet selection—they include specialization within the digestive tract that may allow grazing and browsing herbivores to better extract nutrients from their preferred forage class (Table 3). Grazers and browsers have measurable differences in the morphology of the foregut (rumen-reticulum-omasum), the hindgut, salivary glands, liver, mouth, teeth, and body mass that may influence their ability to digest and harvest grasses and browses. All herbivores have one or more enlarged portions of the gut used to house the microbes that ferment plant fiber (Langer 1988). All ruminants have a pouch (rumen/reticulum) that lies before the true (acid-pepsin) stomach (abomasum) in which the bulk of fermentation occurs. Plant fiber floats on the rumen liquid and is regurgitated and rechewed until particles are small enough to escape through the opening between the reticulum and omasum (Langer 1988, Van Soest 1994). The length of time food resides in this chamber depends on its size and the size of the opening. The longer plant fiber is retained in the rumen, the more complete the digestion of cellulose and other structural carbohydrates (Demment and Van Soest 1985). Nonruminant herbivores rely on enlarged portions of the lower intestinal tract or hind-gut where additional microbial fermentation occurs, including the cecum and parts of the large intestine (Langer 1988).

Hofmann (1989) characterized the anatomy of the foregut and hindgut of ruminants in detail and suggested

Table 3. A relative comparison of digestive anatomy between grazers and browsers based on Hofmann (1989), Hoeck (1975), and Robbins et al. (1995).

Characteristic	Grazers	Browsers
Foregut	<ul style="list-style-type: none"> • Large • Subdivided • Smaller opening between reticulum & omasum • Sparser, more uneven papillae 	<ul style="list-style-type: none"> • Small • Simple • Larger opening between reticulum & omasum • Denser, more even papillae
True stomach (abomasum)	<ul style="list-style-type: none"> • Smaller 	<ul style="list-style-type: none"> • Larger
Hindgut	<ul style="list-style-type: none"> • Smaller cecum and intestines 	<ul style="list-style-type: none"> • Larger cecum and intestines
Salivary glands	<ul style="list-style-type: none"> • Smaller parotid salivary glands 	<ul style="list-style-type: none"> • Larger parotid salivary glands
Liver	<ul style="list-style-type: none"> • Smaller 	<ul style="list-style-type: none"> • Larger
Mouth	<ul style="list-style-type: none"> • Wider muzzle and incisor row • Lower incisors of similar size • Incisors project forward • Smaller mouth opening and stiffer lips 	<ul style="list-style-type: none"> • Narrower muzzle and incisor row • Central incisors broader than outside ones • Incisors more upright • Wider mouth opening with longer tongue
Teeth	<ul style="list-style-type: none"> • Higher crowns in some species 	<ul style="list-style-type: none"> • Lower crowns in some species

how grazers and browsers should differ in rate and extent of digestion. Although differences in morphometrics are well-documented, the predicted effects of morphology on digestive physiology remain untested or unclear. Grazers tend to have larger, more muscular, subdivided rumen/reticulum, and a smaller opening between the reticulum and omasum than browsers. This adaptation may serve to retard the passage of digesta to lower tract, giving more time for fermentation of plant fiber (cellulose). Because a greater proportion of grass cell is cellulose, this adaptation would presumably allow grazers to digest the cell wall more thoroughly and obtain more energy per unit of food. However, if food moves more slowly through the digestive tract, food intake may also decline. In contrast, most browses contain less cell wall and fibers within their cell wall are more lignified and indigestible, so the smaller rumen of browsing animals should allow indigestible food particles to flow more rapidly through the tract. This rapid flow should promote a higher food intake. Browsers tend to have extensive dense papillae in all parts of the rumen, enlarging the surface area by 22 times, which may allow efficient absorption of VFAs from the rapidly-fermenting cell contents of the browse plants. In contrast, grazers have fewer, uneven papillae that limits the absorptive capacity of the rumen. Browsers have a proportionately large abomasum, or true stomach, a larger hindgut (cecum and colon), and the ventricular groove in the rumen/reticulum may allow some cell contents to escape inefficient rumen fermentation in favor of direct digestion in the abomasum and lower digestive tract.

Besides differences in the structure of the gastrointestinal tract, grazers and browsers also differ in the relative size of the parotid salivary glands (which lie below the ear along the jaw line) and composition of saliva. Parotid salivary gland weight increases linearly with body mass in both grazers and browsers, but averages 4 times larger in browsers than in grazers (Robbins et al. 1995). Although Hofmann (1989) suggested that larger parotid salivary glands yield greater flow of liquids to the digestive tract and buffer fermentation, Robbins et al. (1995) did not find differences in the resting rate of saliva production between grazers and browsers. Cattle and sheep saliva is thin and watery compared to mule deer saliva which is viscous and gelatinous. These observations suggest that the larger parotid salivary glands of browsers produce tannin-binding salivary proteins that may prevent tannins in browses from greatly reducing protein digestibility (Austin et al. 1989, Robbins et al. 1995). Hofmann (1989) also noticed that browsers have up to 100% more liver tissue for their body size than grazers. Because allelochemicals present in browses may be detoxified in the liver (Foley et al. 1995; Pfister, this volume), a large liver might be an additional adaptation to the chemicals in browses that do not commonly occur in grasses.

Differences in harvesting skills between grazers and browsers

Besides differences in digestive morphology, grazers and browsers seem to possess different adaptations for harvesting grasses and browses (Table 3). To meet their metabolic needs on high fiber diets, herbivores must spend up to 10 hours a day foraging (Bunnell and Gillingham 1985). Adaptations that increase harvesting efficiency reduce foraging time and free up time for other activities that influence fitness, such as reproducing, thermoregulation, and avoiding predators. The rate at which an animal harvests food depends on how rapidly bites of food can be cropped (severed from the plant) and chewed, and the size of bite the animal takes (Spalinger and Hobbs 1992). Harvesting rate can increase up to 10 times simply by taking larger bites (Shipley and Spalinger 1992). Chewing, cropping, and harvesting differ depending on class of forage (grass or browse).

First, differences between browsers and grazers exist in the structure of molars, which would be expected to influence chewing rates and longevity of teeth. Herbivores in general tend to have a high level of hypsodonty – meaning that teeth have high crowns that allow for longer wear (Vaughan 1986). This adaptation is especially valuable for grazers that consume more fibrous and silica-laden grasses. Differences in molar structure in two species of hyraxes (small, nonruminant, African herbi-

vores), seems to correspond with their preferred diets (Hoeck 1975, 1989). Molars and premolars of rock hyraxes (*Procapra johnsoni*), which feed preferentially on grasses, are hypsodont, having high crowns and short roots. In contrast, yellow-spotted hyraxes (*Heterohyrax bruceii*), a browsing species, have brachydont tooth structure with shorter crowns and longer roots. However, similar patterns in tooth structure are not found in ruminants.

Second, measurable differences in mouth structure among herbivores may influence cropping rates and bite size. Grazers tend to have wide muzzles, with lower incisors of similar size that project forward in a spatulate fashion (Janis and Ehrhardt 1988). The greater incisor width of grazers should serve to maximize bite size (and thus harvest rate) of herbivores when feeding on a continuous distribution of grasses (Illius and Gordon 1987, Janis and Ehrhart 1988). However, wider muzzles reduce the grazer's ability to select the smaller, more nutritious portion of grasses (Janis and Ehrhardt 1988). The rate of cropping grass depends on its toughness, a function of the age and diameter of grass (Wright and Illius 1995).

In contrast, browsers tend to have a narrower muzzle (Janis and Ehrhardt 1988) and a relatively larger mouth opening that permits sideways stripping of leaves. Some larger browsers, such as giraffes and black rhinos, have a longer tongue and prehensile lips (Hofmann 1989). The lower incisors are inserted in a more upright position with a cupped appearance, and the central incisors are broader than the lateral ones (Janis and Ehrhardt 1988). The smaller width of incisors and other adaptations allow for easier selection of specific plant parts that have less cell wall (Owen-Smith 1982). Structural defenses found on browses, such as thorns, slow harvesting by interfering with cropping (e.g., catching lips on thorns) and by separating leaves and reducing bite size available (Cooper and Owen-Smith 1986, Belovsky et al. 1991).

Finally, differences in the dispersion of grasses and browses may require different methods of searching and scales of food selection. Herbivores select food in a hierarchical fashion, making different decisions at different spatial scales ranging from the plant part or bite to the landscape and region (Jarman 1974, Senft et al. 1987). Because many grasses have a more continuous dispersion (Jarman 1974), they tend to be rather homogeneous except at very fine and large scales. Therefore, grazers are expected to choose diets based on the characteristics of the patch, pasture, or landscape, rather than individual plant or plant part. For example, grazers may select patches that provide the tallest, youngest, or most

nutritious grasses (Lanvatin and Hanley 1993). In contrast, nutritional quality and bite size of browse varies greatly among plant parts, and thus browsers must choose bites carefully, selecting leaves over stem, or selecting the shrub with the larger leaves or thickest twigs (Shiple et al. 1998). Browsers, therefore, may make decisions on how to maximize nutrient intake more frequently than do grazers. Clearly experience and learning influence harvesting efficiency within limits set by herbivore morphology (Provenza, this volume).

The influence of body size on grazing and browsing

Although Hofmann's (1989) predictions about digestion between grazers and browsers seems logical from differences observed in their anatomy, few have been tested quantitatively. Recent studies indicate that the characteristics of the food and the animal's body size, rather than anatomical adaptations for grazing and browsing, have greater significance for the nutritional ecology of the herbivore. For example, by developing a mechanistic model of the herbivore's digestive system, and by analyzing data contained in the literature for African ruminants, Gordon and Illius (1994, 1996) found that the mass of the digestive tract contents, rates of microbial fermentation, and the time food spent in the digestive tract were strongly related to body mass, but not on their classification as grazers or browsers. Likewise, Robbins et al. (1995) found that the liquid passage rates, extent of fiber digestion and the flow of saliva and rumen fluids did not differ between grazers and browsers, but were related strongly to body size.

Body size may obscure the effects of gut anatomy on digestion of grasses and browses. Larger animals, which tend to be grazers, have a proportionately larger gastrointestinal tract than do small animals, which tend to be browsers (Case 1979, Van Soest 1994). The larger rumen/reticulum of large animals promotes longer retention of food and thus greater nutrient extraction via microbial fermentation (Demment and Van Soest 1985). Small animals, which have less body mass to fuel, require less energy to survive, and thus need to obtain less food per day (Peters 1986). However, small animals require more energy per unit weight to fuel a higher mass-specific metabolism, and thus must obtain a high rate of energy return per gram of food ingested (Peters 1986). Therefore, large herbivores are better suited to extract energy from high-fiber grasses and small animals from the cell contents of browses (Demment and Van Soest 1985). Therefore, the influence of subtle morphological differences on digestion between grazers and browsers within a size class may be hard to detect.

Body size may also obscure any effects of mouth and tooth morphology on harvesting rate of grazers and browsers. Small animals naturally have smaller mouths that may help them to crop small bites of browse more efficiently, and limit the size of bite they can take on grass swards (Illius and Gordon 1987, Shipley et al. 1994). No definitive study has compared harvesting rates of browsing and grazing animals of the same size feeding on similar diets of grass and browse. Most evidence for the relationship between mouth structure and efficient harvesting is anecdotal and theoretical. For example, Shipley et al. (1994) found no noticeable patterns in maximum harvesting rate and chewing efficiency among 13 species of grazing, browsing, and intermediate herbivores feeding on alfalfa. However, the grazers tended to crop bites of alfalfa more efficiently than many of the intermediate and browsing species. Clarifying the independent roles of body size and morphological specialization on digestion, harvesting, and diet selection is difficult because relatively few browser-grazer "pairs" or "groups" of similar size exist that would allow a rigorous test of differences in harvesting and digestion among herbivores. In addition, virtually all studies comparing anatomy and physiology of browsers and grazers focus on ruminants, and thus fail to consider similar adaptations by other types of herbivores, such as hindgut-fermenters (e.g., rodents, rabbits, horses) and non-ruminant foregut-fermenters (e.g., kangaroos, sloths).

Ecological and Management Implications of Grazing and Browsing

To better manage range livestock and habitats of free-ranging herbivores, ecologists and range managers often wish to estimate their forage intake rate. Morphological characteristics of grasses makes it easier to estimate the intake rate of grazers than that of browsers. Intake rate of grasses is predictable from estimates of pasture biomass, because bite size is directly related to grass biomass (Short 1985). Bite size on grasses is a function of incisor width (or diameter of tongue sweep) and grass height and density (Illius and Gordon 1987). Bite size, and thus intake rate, is reduced on shorter swards, and with successive grazing (Ungar et al. 1991, Ungar and Noy-Meir 1988). In contrast, intake rate cannot be predicted from the biomass of browse, because bite size is usually independent of browse biomass (Spalinger et al. 1988). The complex geometry and discontinuous arrangement of nutritious plant parts makes bite size difficult to estimate (Shiple et al. 1994).

Preference for grass or browse, regardless of body size and anatomy, seems to be an important feature of resource partitioning among herbivores (McNaughton and Georgiadis 1986). For example, the seasonal varia-

tion in patterns of habitat and forage use within ruminant and nonruminant herbivores in African savannas allow an astonishing array of wild herbivores to coexist (Jarman 1974). Sequential use of vegetation throughout the seasons and adaptations for different types of vegetation by one group of herbivore species can actually improve forage conditions for other groups of herbivores in an ecological relationship called "facilitation" (Bell 1970, 1971). Large grazers that require a large volume of food, but can efficiently digest fibrous food, may remove standing dead or mature grasses, promoting access to, and growth of, small forbs that may be used by small concentrate selectors (Bell 1970, 1971). However, when resources are scarce, particularly during the dry season or winter, more dietary overlap occurs among herbivores and interspecific competition is increased (Jenkins and Wright 1987). Within hyrax communities, for example, differences in diet between the grazing rock hyrax and the browsing yellow-spotted hyrax may reduce competition for food and allow these two species to coexist, frequently occupying the same rock outcrops, sharing burrows and raising their young in communal nurseries (Hoeck 1975, 1989). However, during droughts, rock hyraxes switch to browses. If poor forage conditions continue, yellow-spotted hyraxes may eventually disappear from the habitat (Hoeck 1975, 1989). Therefore, close coexistence of grazers and browsers and complex herbivore communities may only be possible when forage is relatively abundant.

Preference for browses or grasses may also play a role in effective range management. Often foraging by wild herbivores, which tend to be browsers or intermediate feeders in temperate ecosystems (e.g., deer, pronghorn, jackrabbits), has only a minimal influence on production of domestic livestock, which tend to be grazers (e.g., cattle, sheep, horses). However, foraging by intermediate or mixed feeders, such as elk, can occasionally reduce production of cattle (Hobbs et al. 1996a, b). Ranchers in Africa have taken advantage of the natural partitioning between browsing and grazing herbivores of different sizes in range management and meat production through game ranching. Game ranching is the husbandry of native animals in their natural habitat for the production of meat and other products (Bolen and Robinson 1999). Because some wild herbivores are grazers and others are browsers, nearly all forms of vegetation within a pasture are consumed (Western 1975, Taylor and Walker 1978). Likewise, a mix of domestic species (e.g., cattle, sheep, and goats) consisting of grazing and browsers to reflect the forage available is most productive and protects the plant resource in the same way as mixes of native ungulates (MacNab 1991).

The harvesting and digestion constraints of herbi-

vores must also be considered when selecting animals for prescription grazing applications. The careful application of domestic livestock is currently being explored to accomplish agronomic, silvicultural, and ecological goals. For example, livestock grazing can be used to improve growth of trees in pine plantations (Doescher et al. 1987), for weed control on rangelands (Olson and Lacey 1994), and to improve wildlife habitat (Severson, 1990). In each of these prescriptions, understanding the herbivore's dietary constraints and opportunities can improve the manager's ability to alter the plant community and reach an ecological goal.

Conclusion

Understanding the basis for diet selection by mammalian herbivores is clearly complex. The digestive system of most herbivores allows them to extract nutrients from a wide variety of vegetation. However, animals that are most efficient at obtaining required nutrients are those that will be most likely to survive, reproduce, and produce products such as meat and milk. Predicting diets selected by herbivores leads to better habitat and range management, and allows better understanding of interactions among wild and domestic herbivores. Therefore the relationship between "form" (morphology) and "function" (nutrient extraction and diet selection) in herbivores is a research priority for the next century.

Literature Cited

- Austin, P.J., L.A. Suhar, C.T. Robbins, and A.E. Hagerman. 1989. Tannin binding proteins in saliva in deer and their absence in saliva of sheep and cattle. *J. Chem. Ecol.* 15:1335-1347.
- Bell, R.H.V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. p. 111-123. *In*: A. Watson (ed.). *Animal Populations in Relation to Their Food Resources*, Tenth Symposium of the Brit. Ecol. Soc. Blackwell Scientific Publications, Oxford.
- Bell, R.H.V. 1971. A grazing system in the Serengeti. *Sci. Am.* 224:86-93.
- Belovsky, G.E., O.J. Schmitz, J.B. Slade, and T.J. Dawson. 1991. Effects of spines and thorns on Australian arid zone herbivores of different body mass. *Oecologia* 88:521-528.
- Bodmer, R.E. 1990. Ungulate frugivores and the browser-grazer continuum. *Oikos* 57:319-325.

- Bolen, E.G. and W.L. Robinson. 1999. *Wildlife Ecology and Management*. 4th ed. Prentice Hall, Upper Saddle River, N.J.
- Bunnell, F. and M.P. Gillingham. 1985. Foraging behavior: Dynamics of dining out. p. 53-79 *In*: R.G. White and R.J. Hudson (eds.). *Bioenergetics of Wild Herbivores*. CRC Press, Boca Raton, Fla.
- Case, T.J. 1979. Optimal body size and an animal's diet. *Acta Biotheor.* 28:54-69.
- Choong, M.F., P.W. Lucas, J.S.Y. Ong, B. Pereira, H.T.W. Tan, and I.M. Turner. Leaf fracture toughness and sclerophylly: Their correlations and ecological implications. *New Phytol.* 121:597-610.
- Cooper, S.M. and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446-455.
- Demment, M.W., and P.J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641-672.
- deReffye, P. and F. Houllier. 1997. Modelling plant growth and architecture: Some recent advances and applications to agronomy and forestry. *Current Science* 73:984-992.
- Doescher, B.S., S.D. Tesch, and M. Algado-Castro. 1987. Livestock grazing: A silvicultural tool for plantation establishment. *J. Forestry* 85:29-37.
- Foley, W.J., S. McLean, and S.J. Cork. 1995. Consequences of biotransformation of plant secondary metabolites on acid-base metabolism in mammals: A final common pathway. *J. Chem. Ecol.* 21:721-743.
- Gibson, T. 1968. Microbial digestion of aromatic compounds. *Science* 161:1093-1100.
- Gordon, I.J., and A.W. Illius. 1994. The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia* 98:167-175.
- Gordon, I.J., and A.W. Illius. 1996. The nutritional ecology of African ruminants: A reinterpretation. *J. Anim. Ecol.* 65:18-28.
- Hobbs, N.T., D.L. Baker, G.D. Bear, and D.C. Bowden. 1996a. Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. *Ecol. Appl.* 61:200-217.
- Hobbs, N.T., D.L. Baker, G.D. Bear, and D.C. Bowden. 1996b. Ungulate grazing in sagebrush grassland: Effects of resource competition on secondary production. *Ecol. Appl.* 61:218-227.
- Hoeck, H. N. 1975. Differential feeding behaviour of the sympatric hyrax *Procavia johnstoni* and *Heterohyrax brucei*. *Oecologia* 22:15-47.
- Hoeck, H.N. 1989. Demography and competition in hyrax: A17 year study. *Oecologia* 79:353-360.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysical adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia* 78:443-457.
- Hofmann, R.R., and D.R.M. Stewart. 1972. Grazer or browser: A classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* 36:226-240.
- Hungate, R.E. 1966. *The Rumen and its Microbes*. Academic Press, N.Y.
- Illius, A.W., and I.J. Gordon. 1987. The allometry of food intake in grazing ruminants. *J. Anim. Ecol.* 56:989-999.
- Janis, C. M., and D. Ehrhardt. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* 92:267-284.
- Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behav.* 48:215-267.
- Jenkins, K. J., and R. G. Wright. 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. *Can. J. Zool.* 65:1397-1401.
- Langer, P. 1988. *The Mammalian Herbivore Stomach. Comparative Anatomy, Function and Evolution*. G.Fischer, Stuttgart, New York.
- Langvatn, R., and T.A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency. *Oecologia* 95:164-170.
- MacNab, J. 1991. Does game cropping serve conservation? A re-examination of African data. *Can. J. Zool.* 69:2283-2290.

- McNaughton, S.J. and N.J. Georgiadis. 1986. Ecology of African grazing and browsing mammals. *Ann. Rev. Ecol. Syst.* 17:39-65.
- Olson, B.E., and J.R. Lacey. 1994. Sheep: A method for controlling rangeland weeds. *Sheep and Goat Res. J.* 10:105-112.
- Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. p. 359-404. *In:* B.J. Huntley and B.H. Walker (eds.) *The Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany
- Owen-Smith, N. 1997. Distinctive features of the nutritional ecology of browsing versus grazing ruminants. p. 176-191 *In:* Proc. of the 1st International Symposium on Physiology and Ethology of Wild and Zoo Animals. Berlin, Germany.
- Peters, R.H. 1986. The ecological implication of body size. Cambridge Univ. Press, Cambridge, England
- Robbins, C.T. 1993. *Wildlife Feeding and Nutrition*. Academic Press, Inc. San Diego, Cal.
- Robbins, C.T., D.E. Spalinger, and W. Van Hoven. 1995. Adaptation of ruminants to browse and grass diets: Are anatomical-based browser-grazer interpretations valid? *Oecologia* 103:208-213.
- Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37: 789-799.
- Severson, K.E. (ed). 1990. *Can Livestock Be Used As a Tool to Enhance Wildlife Habitat?* US Forest Sev. Rocky Mtn. Forest and Range Exp. Sta. Gen. Tech. Rep. RM-194
- Shiple, L.A., J.E. Gross, D.E., Spalinger, N.T., Hobbs, and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. *Am. Nat.* 143:1055-1082.
- Shiple, L.A., S. Blomquist, and K. Danell. 1998. Diet choices by free-ranging moose in relation to plant distribution, chemistry and morphology in northern Sweden. *Can. J. Zool.* 76:1-12.
- Shiple, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches: Influence of plant and animal morphology on intake rate. *Can. J. Zool.* 70:1743-1752.
- Short, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *J. Appl. Ecol.* 22:435-447.
- Spalinger, D.E., T.A. Hanley, and C.T. Robbins. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecol.* 69:1166-1175.
- Spalinger, D.E. and N.T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: New models of functional response. *Am. Nat.* 140:325-348.
- Stevens, C.E. 1988. *Comparative Physiology of the Vertebrate Digestive System*. Cambridge Univ. Press, N.Y.
- Taylor, R.D. and B.H. Walker. 1978. Comparisons of vegetation use and herbivore biomass on a Rhodesian game and cattle ranch. *J. Appl. Ecol.* 15:565-581.
- Ungar, E.D. and I. Noy-Meir. 1988. Herbage intake in relation to availability and sward structure: Grazing processes and optimal foraging. *J. Appl. Ecol.* 25:1045-1062.
- Ungar, E.D., A. Genizi, and M.W. Demment. 1991. Bite dimensions and herbage intake by cattle grazing short hand-constructed swards. *Agron. J.* 83:973-978.
- Van Soest, P.J. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: A review. *Zoo Biol.* 15:455-479.
- Van Soest, P.J. 1994. *Nutritional Ecology of the Ruminant*. 2nd ed. Comstock, Cornell Univ. Press, Ithaca, NY.
- Vaughan, T. A. 1986. *Mammalogy*. 3rd ed. Saunders College Publ. Philadelphia, Penn.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *E. Afr. Wildl. J.* 13:265-286.
- Wright, W., and A. W. Illius. 1995. A comparative study of the fracture properties of five grasses. *Funct. Ecol.* 9: 269-278.