Nutrition Of The Enigmatic Browser: Comparative Bioenergetics, Digestion And Feeding Of Northern Versus Tropical Ungulates

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ABSTRACT

Wild ungulates use time, habitat, and food in complex ways in relation to social, security, comfort, and bioenergetic needs to optimization fitness from decisions during day-to-day living. Species in highly seasonal environments experience changes in nutritional requirements in association with adaptations to quality and quantity of available food. Evolutionary implications are closely tied to seasonal bioenergetic cycles and become extremely important in understanding survival strategies and nutritional food habits. Concomitantly, food habits are linked to digestive morphology and processing which can become very specialized for the browser. Captive feeding programs must integrate the browser nutritional needs, seasonal bioenergetic cycles, and specific adaptations that relate to a specific body size.

Keywords: captive feeding; food habits; ruminant; seasonal environments

INTRODUCTION

Wild ungulates inhabit regions from the arctic tundra to the tropical rainforest and are confronted with a variety of environmental cues both daily and seasonally. The ability of a species to survive is undoubtedly related to its ability to adapt and evolve to seasonal modulations in climate, habitat, and food resources. Ultimately, survival is closely tied to the animal's decision-making ability and making day-to-day tradeoffs in order to balance energy and nutrient balances.

The ruminants appeared in the Eocene period and radiated in great variety and with success that was largely attributed to their perfection of digestion. The ruminant digestive system with its characteristic four-chambered stomach was designed to extract nutrients from many fibrous foods and plant materials [Foose, 1982]. Diets of browse, forbs and grasses are retained in the rumen until adequate nutrients are extracted from fibrous material and particle-size reduction has occurred. Based on the degree of specialization in forage selection and digestive anatomy, ruminants have been classified into three groups: a) browsers and concentrate selectors, b) grazers (grass or roughage feeders) and c) mixed or intermediate feeders [Hofmann, 1973; Hofmann, 1985].

Browsers

Browsers differ from other ruminant groups both in foraging and adaptation of the digestive tract. Typically, as a group, they consume plant species (browse) and parts (twigs and foliage) high in readily fermentable cell solubles and avoid fibrous fractions of plant material that would impede digesta flow. Extensive ruminoreticular papillation has developed which facilitates absorption of volatile fatty acids produced from rapidly fermented substrates. Rumens of selective feeders are small and lack well-developed barriers that would delay passage of digesta. Members of this group have developed relatively large salivary glands in relation to body weight; high flow rates of saliva increase the buffering capacity of the rumen during rapid fermentation and accelerate passage of sugars through the ruminoreticulum for absorption in the small intestine [Hofmann, 1973; Kay et al., 1980].

Typically, browsers are small and include the diminutive dik-diks (*Madoqua* spp.) and suni (*Nesotragus moshatus*) and the small forest-dwelling duikers (*Cephalopus* spp.) that largely consume fruits, forbs, and dicotyledonous foliage [Hofmann, 1973]. Browsers rely on high quality foods with rapidly fermentable substrates that will supply adequate energy to compensate for the metabolic constraints of a small size. Consequently, concentrate selectors do not have the ability to expand diets to include fibrous forage [Foose, 1982]. Intake is constrained largely by the ability of the animal to find high quality foods, maximize forage consumption, and maintain high rates of passage.

Browsers also include the black-tailed deer (*Odocoileus hemionus, columbianus*), white-tailed deer (*O. virgininus*), roe deer (*Capreolus capreolus*), kudu (*Tragelaphus* spp.), gerenuk (*Litocranius walleri*) and the larger giraffe (*Giraffa* spp.) and moose (*Alces alces*) [Hofmann, 1973; Hofmann, 1985; Hofmann, 1989]. These species select mainly tree and shrub foliage. However, species in northern latitudes eat woody twigs during winter. Nevertheless, these large browsers have a small ruminoreticulum and are faced with a similar need for high quality forages that maintain rapid passage rates.

Bioenergetics

Bioenergetics is the process of energy exchange with the environment and distribution with the animal body. To maintain body homeostasis, browsers like other ungulates require energy for basal metabolism, thermoregulation, movement and productive functions. When a surplus is available then it is diverted to growth, gain, or reproduction.

In temperate, arctic, and arid environments, plant growth is pulsed seasonally. Browsers must acquire sufficient nutrients to meet daily costs of existence during the short late spring, summer and early autumn period of green plant production. For adult browsers, this implies the need for a sufficient surplus of energy for the function of breeding and to replenish fat stores.

Body size is related to both food requirements and digestive capacity in ruminants. Browsers like other ungulates must extract adequate nutrients from ingested food to meet metabolic requirements. Larger browsers are expected to require greater absolute amounts than small herbivore species because body size scales isometrically to digestive capacity [Van Soest, 1982]. However, energy needs scale to body weight (kg)$^{0.75}$ [Kleiber, 1975]. This confers on small selective feeders a penalty of high relative maintenance costs concomitant with limited digesta storage features [Demment and Van Soest, 1985].

A fundamental problem confronting ruminants is the acquisition of sufficient nutrients within the constraints of their changing environments. Energy metabolism for ruminant species in pulsed environments shows marked seasonal fluctuations. This is especially true for browsers that inhabit the colder northern latitudes [White et al., 1987]. Seasonal changes are further heightened by variation in forage intake, demands of body growth, pregnancy, lactation, weapon/ornament production (i.e. velvet antlers), and thermoregulation.

For smaller species, such as white-tailed deer and roe deer, this implies specific habitat selection (thermal cover), effective insulation, and possible food selection to optimize energy intake in order to mitigate the energy drain of colder winter temperatures and remain in their thermoneutral range. But, food quality and quantity in pulsed environments is also seasonal so little opportunity is available for large changes in decision-making in food selection for energy density sources during winter. In captive situations, diet can be modified seasonally to make energy adjustments during periods of cold that fall below thermoneutral limits.

In a browser like moose, the larger body size conserves heat and reduces energy requirements during winter when quantity and quality of available forage are insufficient to meet maintenance requirements [Renecker and Schwartz, 1998]. Hot weather can be oppressively uncomfortable to moose that show heat stress at about –0.4°C in winter and 14°C in summer [Renecker and Hudson, 1992]. This can lead to higher energy expenditures and a suppression of activity. In winter, this is apparent when animals have maximum thermal insulation and are physiologically adapted to the environment [Renecker and Hudson, 1989]. In summer, large browsers can attempt to offset these extra demands by taking advantage of long appendages, shade and cooling effect of wind and especially water to dissipate heat [Renecker and Hudson, 1992].

In northern ruminant species, such as moose, metabolic rate and intake appear to uncouple in early spring [Renecker, 1987]. This is perhaps an adaptive characteristic to the brief pulse of green forage during summer months. Moose anticipate green-up and therefore body metabolism begins to increase in advance of a rise in intake and forage quality. This may allow northern native browsers to develop maximum metabolic efficiency in order to make immediate use of high quality forage when leaf flush occurs in mid spring. Concomitant with this early spring rise in metabolism and energy need is the potential for greater weight loss (this innate response can also be coupled with higher thermoregulatory costs for heat stress, production costs of gestation or antler production, or reduced energy intake and disparity if green-up is delayed). The consequence in management of captive populations is again a seasonal increase in energy supply of the diet to mitigate major changes in body weight and animal condition.

Digestion and Feeding

Feeding habits of ruminants are expected to vary with body size. Larger ruminants would be influenced by the ability to maintain intake on highly fibrous diets. However, the grazing strategy influences foraging time and allows them less time to be selective. Browsers allocate more time for searching for highly digestible food. Browsers must use energy dense and rapidly degradable substrates in order to meet the high metabolic demands of their smaller body. In adapting to its niche, the small browser has traded off the ability to digest fibrous forage in exchange for rapid passage rate of highly lignified foods through the digestive tract. To counter the high energy requirements, these browser herbivores consume forages high in readily fermentable cell solubles. For small browsers, absolute quantities are much lower, thus in wild populations these animals have more time to search for small patches of high quality food.

Larger browsers, such as moose, have adapted to utilize highly lignified food like woody browse. They appear to have more rapid turnover times for browse in comparison to grass forages which may be an adaptation to maximize returns through optimal retention [Renecker and Hudson, 1990]. Also, as quality of food deteriorates (either as a result of summer drought or senesce) rate of intake must increase in an attempt to support requirements. However, browsers will encounter some level of diet quality where intake no longer compensates for fibrosity. This level undoubtedly will vary with body size of the ungulate. Greater fiber content in the diet can also increase retention times that will develop greater demands for rumination requirements [Renecker and Hudson, 1985; Renecker and Hudson, 1993]. Grazers, such as bison (*Bison bison*), and mixed feeders, such as wapiti (*Cervus elapus nelsoni*), tolerate levels of fibrosness in their rumens that maximize absorption [Renecker and Hudson, 1990]. Browsers do not appear to develop the distinct stratified layers of digesta in the rumen as is found in grazers (cattle) and mixed feeders (wapiti).

Browsers like the moose consume lignified forage that rapidly fracture during mastication and rumination into cuboidal particle types. Particles of grasses tend to be long and curved and have delayed passage in browsers and require additional particle size reduction in comparison to browse. The close association found between the liquid and solid phases in the rumen of browsers permits rapid flushing of digesta through the reticulo-omasal orifice by volumes of liquids. Thus the browser can eat browse species, flush cell solubles through the rumen into the intestine for rapid absorption, lightly digest the remainder of the forage, pass the larger particles rapidly, and then get onto the next meal. As a result, daily feeding patterns are composed of multiple bouts whereby the rumen is more constantly being “topped-up” in comparison to grazing strategy which requires large amounts of forage only 2-3 times per day.

Application to Captive Feeding

Knowledge of the seasonal energy and nutrient cycle of browsers is extremely critical in the development of feeding programs. In species where seasonality is apparent, feeding programs must adjust dietary energy, protein and mineral levels to reflect the animal adaptation to native environment. In northern species, this implies lower energy and protein levels during winter. A failure to adjust diets can lead to founder or laminitis or ulcerations or secondary infections of genitalia as a result of excessive energy or protein, respectively.

Seasonality of environments and production aspects of browsers must also be combined in feeding programs. Undoubtedly, there will be the demand for species to breed, reproduce, grow, and lactate. For males, breeding success is highly connected to body and weapon size. In northern cervids, antler growth begins near the spring solstice of March 21. Energy and protein requirements of males begin to increase just prior to the new growth of antlers and place constraints on the animal’s daily energy budget. Studies in wapiti have shown that nutritional modulation can improve antler production by an average of 8-10% in bulls 2-9 years of age [Renecker et al., 2001]. Through modulation of the feeding program in synchrony to these innate cycles, larger antler ornaments can be produced in addition to an assurance that sufficient condition is attained for successful, autumn breeding and tissue stores to assist the species to coast through the winter metabolic low period. Similar nutritional strategies must be applied to female browsers and account for proper nutrient balances for each trimester of gestation, lactation/flushing and autumn breeding.

Mineral needs are important for all browsers and will vary between genera, however, it is unfortunate that little knowledge is known about animal mineral requirements and body use in many ruminant species. Nevertheless, consideration should be given to monitoring blood and liver levels of minerals and adjustment of seasonal levels offered in the diets. For example, many deer species such as wapiti require extra amounts of copper in comparison to cattle (probably because of poor absorption or storage capabilities). Artificial diets should contain extra copper, however, research has also shown that unless the inclusion of these minerals also follows the seasonal cycle amounts can accumulate over time and can potentially reach toxic limits. Therefore feeding programs should consider the cyclic nature of nutrient needs in highly seasonal browsers.

Because browsers have adapted to this special food resource the type and level of fiber in the diet is essential in captive diets. The type of fiber must be highly lignified in order to mimic browse and therefore pass through the gut relatively fast and maintain good function. Aspen sawdust and sunflower hulls have often been used as a woody substitute in pelleted rations. Fiber types associated with energy sources are also critical in order to maintain good gut function and avoidance of rapid starch release i.e. oats versus corn, barley or wheat. Choice of energy source for browsers and other native ungulates is exceptionally critical during the seasonal metabolic lows of winter or perhaps dry season and it is at this time that the choice of energy commodities with poor fiber characteristics should be avoided.

CONCLUSIONS

1. Nutrition of browsers in seasonal environments requires diet adjustments to follow the natural adaptive cycle whereas species that live in less pulsed environments will require more constant nutrient levels. However, natural dietary choices of wild species should be monitored and evaluated seasonally in order to develop a true knowledge of how the browser alters forage selection in order to modify nutrient intake. This then can be applied to diet formulation.
2. Browsers appear to be digestively successful through consumption of lignified food that has abundant cell solubles, can be lightly digested and passes rapidly.
3. Captive diets for browsers must contain adequate fiber that mimics browse and the be closely tied to natural seasonal cycles.

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