NUTRIENT METABOLISM OF NON RUMINANTS IN RANGELAND SYSTEMS

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Contents

Summary

Non ruminant herbivores include a wide range species including hippopotamus, hamster, horses, zebras, donkeys, kangaroo, sloth and certain primates in which a

sacculated stomach serves as primary site of microbial activity. Most of non-ruminant herbivores rely on the hindgut as primary site of fermentation. Nutrient metabolism of horses is a review on equid nutrition on pasture. Comparison of horse and ruminant nutrition is made. Digestibility of feedstuffs and passage rate are compared in horses and ruminants. Digestion and absorption of feedstuffs are reviewed, as well as nutrients and nutrient metabolism. Feeding different classes of horses exclusively on pasture is discussed as well as behavior of horses on pasture. Comparisons between equine and ruminant digestive systems are made.

1. Introduction

Herbivores are animals (vertebrates or invertebrates) that can subsist on a diet consisting primarily of fibrous plant material. Non ruminant herbivores include a wide range species including hippopotamus, hamster, horses, zebras, donkeys, kangaroo, sloth and certain primates in which a sacculated stomach serves as primary site of microbial activity. The majority of non-ruminant herbivores rely on the hindgut as primary site of fermentation.

The horse, the principal focus of this chapter, evolved grazing and browsing as a hindgut fermenting herbivore. Horses are classified as bulk and roughage eaters and they feed predominantly on leaves, buds, plant stems and high amounts of grass. Starch rich components of plants play only a minor role in wild equids. The ability to digest different feedstuffs brought the disadvantage of the horse having a less efficient for the use of plant fibers. In comparing horses to ruminants the digestion of grasses, if high in crude fiber, is less efficient than ruminants in the absorption of protein, sugar, starch or fat. These disadvantages are compensated with continuous selective grazing

habits and a higher intake and faster rate of passage in horses compared to ruminants. Horses also are able to utilize nutrients from young grasses directly, through releasing the nutrients by mastication with their potent molar teeth and absorption of nutrients by the small intestine. When horses are housed and fed rations that contain high levels of concentrates they can be classified in an intermediate feeding class.

Domestication of horses probably occurred around 4000 to 3000 BC by nomads in south Russia and at that time nutrition of horses did not change much from the natural environment. Horses were subjected to fluctuating food supply with season variation. During 2000 BC, horses started to be used more intensively in a more systematic way in Egypt as a load animal, pulling chariots, and being ridden. During that time large numbers of horses were maintained at kingdoms in the Orient. For example, King Solomon (965-926 BC) had around 12000 riding and 4000 driving horses.

Intensive use of horses brought a need for better feed use and feeding techniques. Increased energy consumption due to increased demands of work, limited time to use the horse due to the long feed ingestion times, and when large number of horses were maintained, it was logistically difficult to maintain horses on forage only. Wheat, barley and hay were used at that time. With the development of agriculture in Europe in 1000, an intense use of the horse was possible in war and agriculture itself. Horses that were not used intensively were still maintained on pasture however.

For practical feeding of horses now a days it is clear that the horses' digestive system has some elasticity and different feedstuffs can be used to feed horses. Basic concepts of nutrition physiology have been the same for the last 6000 years in the horse as well as the function of the digestive system and the rhythm of the feed intake. Scientific papers on digestive physiology, protein and energy metabolism were only published in the 19th century.

2. Feeding Habits Comparing Equids to Ruminants

Equids can be classified as generalist herbivores that co-exist with bovids in guilds of grazing herbivores in tropical ecosystems like in Africa. During the evolution during the Holocene equids shared the same grazing areas with bison species and wild cattle in temperate ecosystems. The co-existence of bovids and equids has been subject of scientific debates. Some scientists argue that their different digestive systems could lead species to adopt different foraging systems. The ruminant digestive system allows for extraction of more digestible dry matter than equids from medium quality forage (defined by their fiber content). The equid digestive system, in contrast, allows for extraction of forages higher in fiber, since the digestive system has a higher passage rate.

It is difficult to obtain precise estimates of daily food intake and digestion of free ranging animals. Feeding trials done in single species using staled animals show that horses can ingest more dry forage per kg of body weight per day, and extract more nutrients than cattle on different kinds of forages. Cattle have a lower intake, may feed more selectively and use a wider range of plant species. Extraction of medium quality forages appears to be higher in horses than cattle. Some other views argue that cattle digests better all components in grasses, with the exception of protein and nitrogen–free extract, which is similar between the two species. Horses, being non-ruminant herbivores, with a large cecum, do not efficiently digest nutrients from feedstuffs that are high in crude fiber. Apparently the horse's lower digestive capacity, led them to develop behavioral strategies such as 14-16 hours per day of grazing. Donkeys can graze for 14-17 hours a day. Cattle spend only 6-10 hours grazing and 6-8 hours ruminating. Horses, with their main post gastric site of fermentation are able to absorb available carbohydrates and protein without potential loss of substrates associated with the microbial processes. However, there is less opportunity for the absorption of microbial digestion end products than ruminants. Feeding trials comparing ruminant and equine species in their ability to digest forage diets showed that digestibility of feed components is higher in ruminant species on hay diets than in horses and similar on legume and mature grasses. Digestibility of cell contents in ruminants is close to 100% and some studies show that horses have similar cell wall content digestibility. In free ranging horses and cattle grazing in wetlands, horses were shown to extract about 50% more organic matter than ruminants, because more hours are spent grazing daily.

Equids in free ranging situations also actively select higher quality diets than cattle. A faster rate of passage of digesta through the digestive tract of the horse is thought to be associated with decreased digestibility of feed components compared with ruminants. Comparison of feed intake in free ranging cattle and horses in more recent studies shows that horses spend more time eating than cattle (63%) so that even on medium quality forages the horses acquire more digestible nutrients daily. Equids achieve higher nutrient extraction rates than bovids on all forages at pasture or in stalls. Nutrient extraction from horses in temperate ecosystems in the winter is lower when snow is present, horses spend less time grazing. More studies are necessary in tropical ecosystems, where grasslands have low basal cover in the winter and may be less favorable for equids. The energy cost for the high intake strategy in horses on pasture has also not been evaluated and could influence energy requirements.

Comparison of intakes of different forages by ruminants has been shown to have an expected correlation with chemical parameters that have been used to predict forage intake in ruminants (NDF, ADF, CP). In equids, however considerable variation has been shown. Dry matter intake in free ranging horses has a relation to crude protein and nitrogen free extract; however annual variation is not completely explained by those factors. It has been suggested that the natural photoperiod within an endogenous seasonal rhythm of appetite may regulate intake, but currently not enough evidence exists. An evolutionary adaptation to seasonally changing environmental conditions is a vital part of the general survival strategy of every species. Endogenous annual rhythms are an evolutionary response towards regularly changing environments, mainly in temperate climates. A seasonal energy adjustment of Przewalsky horses was observed in a group of horses maintained in free ranging situation in a temperate climate with low winter temperatures (-40 ^{o}C) and high summer temperatures (40 ^{o}C). Horses showed physiologic adaptation to winter starvation. Metabolic rate was reduced by means of absence of advanced gestation or peak lactation, and by reduced physical activity. A reduced body mass (lower weight) and probable reduced organ weight and a higher tolerance to a lower body temperature also help to reduce metabolism. The winter adaptation however was found to be different form pure starvation. Seasonal changes in behavioral and behavioral parameters appeared to be under endogenous control because they occurred before seasonal changes.

3. Extracting Nutrients from Plant Tissue

The rate at which an individual animal extracts nutrients depends on the daily intake, the digestibility, and the metabolic losses of the nutrients. In most digestion studies apparent digestibility is measured. Apparent digestibility is the true digestibility minus metabolic fecal losses, which are mucous and epithelial cells from the gut wall. Equids have a higher rate of fecal loss than ruminants, and the apparent intake is the most significant measure for comparison between equids and other herbivores. Extensive work has been done on food intake and digestibility in and results have shown that there are two main classes of determinants involved: animal factors and forage factors.

In horses feed factors include chemical composition of feeds and its energy content. Amongst these are the fracture properties of the plants as well as the feed particle size that will influence how digestive enzymes in the small intestine and microbial population will interact with ingesta. Treatment of processed feeds will also influence nutrient extraction. Orosensory sensations are defined as palatability and are also considered to be a plant factor. These sensations include smell, texture, and taste. Coarseness and brittleness can negatively affect intake.

Animal factors include intake capacity and appetite. The horse's physiological condition has a direct effect on intake, where early lactation mares have the highest intake. Intake increases of 65% above gestation have been reported in lactating mares. Lowest intake occurs usually in idle horses, but individual variation exists. Previous experience on available forage will also have an influence on intake, where horses tend to consume forage that they are accustomed to, although trying from new forages. Herd social order is also an important factor determining intake. Age and residency time in the herd are main factors that determine social rank in wild equids and Icelanding horses. Hierarchy should be observed within grazing herds so that obesity and malnutrition can be avoided. On the other side, isolation of subordinated horses is not indicated because their eating seems to be stimulated by the visual contact with their companion horses. Dental condition is another animal factor that will directly influence intake. If dentition problems are present, intake will be lower. Quidding, feed refusal, slow chewing and food pocketing are signs of dental problems. Diseases will affect feed intake and usually the initial sign of a disease is innapetence.

Intake rates are more difficult to predict because they are affected by animal and forage⁄feed factors. The final determinant of food intake is the animals' nutrient requirements. Cattle will eat more as the digestibility of feed declines up to a certain threshold, if digestibility is below a threshold intake declines. Plant factors are the principal determinants of digestibility and intake in coarser forages that are consumed by free ranging ruminants. Horses do not have a threshold for forage intake and increase intake despite lower digestibility.

4. Factors that Affect Digestibility of Forages in Equids

Digestibility can be measured as DDM in some studies or digestibility of organic matter (DOM) in others. Both measures are related (DDM=1.04 DOM- 0.88). Forage factors, mainly fibrousness will strongly affect dry matter digestibility.

4.1. Animal Factors

Comparison studies between wild and domestic equids showed that different equid species digest forages and legumes to a similar extent. Gut morphology is similar across species and although processes of mastication and digestion differ among animals of different sizes, species and size do not affect digestibility in equids. Studies comparing donkeys and horses have shown higher apparent digestibility of dietary energy and fiber in donkeys. In a study comparing digestibility in geldings and steers, no differences were found between protein and nitrogen free extract digestibility. Dry matter digestibility was higher for steers compared to horses eating timothy, bromegrass and orchardgrass, but not for alfalfa. Steers also digested ether extract, cellulose and crude fiber more efficiently than geldings. As crude fiber content increases, the digestibility of several nutrients decreases. In bovines, forages with higher fiber content are digested more slowly and retained for longer than good quality forages. In equids passage time will only slightly increase or not at all as fibrousness increases in forage. The general strategy adopted by horses is to ingest relatively more forages than ruminants, especially high fiber foods. Digesta passes relatively quickly trough the cecum and colon in equids without having the retention in the rumen, and therefore equids can ingest large amounts of cell rich forage. With that horses extract 50% more organic matter than cattle per day. In free ranging situations donkeys and ponies select higher quality diets than cattle. The lower digestibility in horses related to the lower retention times can also be related to a reduced opportunity to absorb the end products of microbial digestion compared with ruminants.

4.2. Forage Factors

Crude fiber content has been shown to be the most important factor of digestibility over a wide range of feeds. Equids exclusively on pasture have a diet composed exclusively by grasses and forbs. When analyzing forage only the most adequate predictor of digestibility is crude protein, although crude fiber also has significance. Digestibility has also been negatively correlated to cell wall fraction. The digestibility of forages in ruminants can be predicted by an equation where NDF and lignin ration have additive effects.

4.2.1. Passage Rate

It is thought that particle size has an effect on passage rate in equids. Smaller particles have a higher rate of passage compared to larger particles. When fed on high quality legumes, high rates of passage and digestion may allow for horses to have a higher intake. Horses have preferences of alfalfa over grass hays. Comparison of cattle and horses has shown that particle retention time is twice as long in cattle compared to horses (79 hours vs 29 hs). The high passage rate of food in equids allows them to achieve high intake rates. The intake values in horses do not seem to be affected by forage factors. In bovines, however, intake in highly affected by animal and forage factors. The most productive bovines will consume more (i.e. lactating cows) and neutral detergent fiber (NDF) is a good predictor for intake. The high intake rates for equids compensate for their lower coefficients of digestibility and allow equids to extract more nutrients than bovids across the range of quality encountered in natural forages. The difference in nutrient extraction rates between equids and bovids is greater on coarse than on high quality forages. It is clear that the rumen is more efficient than the gastro intestinal tract of equids, however the equid tract maintains a higher daily rate of nutrient extraction.

The different digestive system of hind-gut fermenters may impose different patterns of behavior (i.e. feeding, anti-predator, social) on equids. This may also explain why grazing bovids are more abundant than equids in all natural ecosystems. The amounts of food in natural grasslands may be inadequate for free-ranging equids for them to be able to consume the large quantities they need. The ruminant digestive system may allow them to use plants that are not attractive to equids. Diets of donkeys are usually high in fiber and low in nitrogen with a metabolizability rarely above 0.4 for the most part of the year (Pearson and Dijkmann, 1994). Comparison of passage rate, digestibility of horses, donkeys and ponies is shown in Table 1.

5. Digestive System Digestion and Absorption

In ruminants ingested feed is subjected to microbial fermentation in the rumen and reticulum before it passes through the abomasum for further digestion and absorption. In equids the feed is partially digested in the stomach and small intestine before it is subjected to microbial fermentation in the hindgut.

5.1. The Mouth

The entrance of the digestive system forms the mouth, which is limited by strong very mobile lips. Horses get feed mainly with their lips and tongue. While grazing the incisor teeth are used intensively. Compared to cattle, horses can graze closely to the ground. Due to the high mobility of the horses' lips, feedstuffs can be selected reducing the chance for the ingestion of foreign objects. The long tactile hair on the muzzle may be important in the process of grazing, mainly in the process of grazing short sward heights. The horse's tongue moves the ingested material to the cheek teeth for grinding. The lips also work as a funnel for the suction of water. The tongue is the main prehension organ in cattle, but not in sheep. The ingestion of rate of hay is faster in cattle and sheep than in ponies and horses. Horses consequently need longer periods of grazing compared to ruminants. During chewing the feed is reduced to small particles (2 mm diameter and 1-4 mm in length). This reduction in particle size is necessary for the passage through the gastrointestinal tract. During mastication the feed is squeezed and nutritious material is released (protein and sugars) and is digested in the small intestine. For mastication intact dentition is necessary and dental problems reduce the horse's ability to chew. The high crown depth and high muzzle width index in horses has been suggested to lead to a greater efficiency in chewing of feeds compared to ruminants. Problems with the incisor teeth can lead to abnormal feed intake. Irregular wear of molar teeth, alteration in the mandibular joint and chewing muscles lead to hooks and make chewing difficult. Teeth abnormalities, losses or steps leads to slower feed intake and can increase the risk for impactions.

The role of taste in equines has been investigated by different authors. It has been suggested that sensory processes control voluntary intake by horses. Horses can associate differences in flavor (garlic and mint flavors) and texture in relation to nutrient density. However limited studies have analyzed the impact of texture on the processes of intake in horses. Palatability can be measured as the characteristics of a feed which invoke sensory response in the animal. Palatability together with previous experience of a feed are the first and most direct regulators of food intake and chewing behavior in horses. In foals, the transmission of food preferences from the mother occurs and social facilitation also plays a role in voluntary intake.

5.2. Saliva

During chewing saliva is formed mainly by the parotid salivary glands and mixed with the feed. Large horses produce about 40-60 ml of saliva per minute, whereas small horses 20-60 ml/min. Saliva assists with swallowing. In horses, food must be present in the mouth for saliva to flow. The stimulus for saliva flow is the presence of feed in the mouth and its moisture content. Roughage intake leads to higher saliva production (3-5 kg/kg) than concentrate intake (1-1.5 kg/kg). Saliva does not contain digestive enzymes but is rich in minerals and bicarbonate. Bicarbonate buffers digesta in the upper region of the stomach, allowing for neutralization of acids produced locally. Saliva also allows for fermentation to occur in the stomach.

5.3. Teeth

The surface morphology, shape of crown of tooth, and contact of occlusal surfaces are important factors in the physical reduction of feeds. Mastication and the addition of saliva start the processes of digestion. Effective mastication of food is essential for the efficient utilization of nutrients. The dental architecture of the horse differs from that of the ruminant. Horses have upper and lower incisor teeth implanted in the premaxilla and mandible. Dental formulas are different between equines and ruminants. The equine mandible is one third narrower that the maxillary jaw causing discrepancy in the occlusal contact of molars. This leads to the formation of sharp apexes on the buccal side of the upper molars and the lingual side of the lower molars. Sharp edges may cause discomfort during eating and possibly to a reduction in grinding efficiency, loss of feed from the mouth during mastication, and may lead to laceration and ulceration of the soft tissues in the mouth (gums, tongue and cheeks). Corrective dentistry has become a routine procedure in horse management. The primary function of the teeth is mastication and communition of the feed. Chewing is more frequent for the ingestion of forages versus grain. Studies have shown that corrective dental treatment decreased chewing time and increased intake. Also, reduction of enamel points results in increased digestibility of all nutrients in forage fed horses. Particle size of fecal material is smaller in ruminants compared to horses because of the ruminating process.

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Biographical Sketch

Dr Tanja M. Hess is a Brazilian that grew up in a bilingual German Brazilian family and school. She graduated in veterinary medicine in 1990 and worked as an equine practitioner in the areas of equine reproduction, nutrition and exercise physiology. She pursued her masters at the Federal Rural University of Rio de Janeiro in Veterinary clinics in 1997 and her PhD in Equine Nutrition and Exercise physiology at the Virginia Polytechnic Institute and State University in 2005. During her PhD studies she worked with electrolyte supplementation of endurance horses and energy metabolism of endurance horses. She also helped with studies on equine pasture nutrition and on equine pasture associated laminitis. She worked as clinical instructor at the Large Animal Hospital of the Federal Rural University of Rio de Janeiro for eight years. She joined Colorado State University in January of 2008 as an Assistant Professor in the Equine Sciences Department. Her current research area is on the effects of omega 3 fatty acids on equine insulin sensitivity, inflammation and joint health. She also consults on equine nutrition through her outreach part of her job.