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Review Article

Gastrointestinal Nitrogen Metabolism of Equids and Impact on Protein Requirement

Nathalie L. Trottier [a,*], Rebecca C. Bott [b], Adrienne Woodward [a], Elizabeth A. Greene [c], Carey A. Williams [d], Michael L. Westendorf [d], Ann M. Swinker [e], Sara L. Mastellar [b], Krishona Martinson [f]

[a] Department of Animal Science, Michigan State University, East Lansing, MI
[b] Department of Animal Science, South Dakota State University, Brookings, SD
[c] School of Animal Comparative and Biomedical Sciences, University of Arizona, Tucson, AZ
[d] Department of Animal Sciences, Rutgers, the State University of New Jersey, New Brunswick, NJ
[e] Department of Animal Science, Pennsylvania State University, University Park, PA
[f] Department of Animal Science, University of Minnesota, St. Paul, MN

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ABSTRACT

Equids evolved grazing forage of low-protein and high-fiber content. However, present day horse feeding management typically consists of higher protein and less fiber, often exceeding protein requirements. The impact of feeding excessive proteins to equids on nitrogen (N) excretion and contamination of ground water is of particular concern and relevance in areas close to water ways. A review was prepared as part of an initiative by the USDA Multi-State project NE-1041 committee on “Environmental Impacts of Equine Operations” to build programs aimed at mitigating N excretion from equine feeding operations. This review presents information on dietary protein utilization in equids and identifies knowledge gaps for potential key future research areas to build upon. The review addresses the gastrointestinal (GIT) anatomy of equids with an emphasis of evolutionary dietary and anatomic adaptations. Challenges in assessment of protein quality of feeds are emphasized in particular in regard to the significance of prececal and postcecal protein digestibility and the contribution from hindgut N and amino acid (AA) metabolism and absorption. The need for greater understanding of GIT protein digestion processes, anatomic site of N and AA absorption, and systemic access to protein and AA digestibility estimates of equine feeds to refine current CP and generate AA requirement estimates is discussed.

1. Introduction

It is common in the horse industry to feed proteins in excess of requirement [1]. The potential impact of feeding excessive proteins to equids on nitrogen (N) excretion and contamination of ground water is of particular concern and relevance in areas close to water ways [1]. Designing and implementing plans to mitigate the impact of equine feeding practices on the environment (reviewed in [1]) entails accurate predictions of dietary N utilization and excretion. In livestock, successful predictions of N utilization and excretion are primarily based on knowledge of feed protein quality and understanding of the digestive processes. Equids are fed a wide diversity of forages, cereal grains, and oil seeds that vary in protein quality, but there is poor systematic availability of such information. In addition, processes of protein digestion and amino acid (AA)

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* Corresponding author at: Nathalie L. Trottier, 2209 Anthony Hall, East Lansing, Michigan 48824.
E-mail address: trottier@msu.edu (N.L. Trottier).

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absorption are less well documented in equids compared to other livestock. The shortage of information has precluded building models of N and AA utilization that are needed for the factorial estimation of N and AA requirement for equids. This review was prepared as part of an initiative by the USDA Multi-State project NE-1041 committee on “Environmental Impacts of Equine Operations” to build programs aimed at mitigating N excretion from equine feeding operations. Our goal was to assemble information on dietary protein utilization in equids and identify knowledge gaps for potential key future research areas to build upon. The review begins by describing the gastrointestinal (GIT) anatomy of equids, highlighting evidence of their evolutionary dietary and anatomic adaptation to high-fiber, low-protein plant material. Challenges in assessment of protein quality of feeds are emphasized in particular in regard to the significance of prececal and postcecal protein digestibility and the contribution from hindgut N and AA metabolism and absorption. The need for greater understanding of GIT protein digestion processes, anatomic site of N and AA absorption, and systemic access to protein and AA digestibility estimates of equine feeds to refine current CP and generate AA requirement estimates is discussed.

2. Evolutionary Adaptation to High Dietary Fiber and Low Protein

2.1. Evidence of Relatively Low Dietary Protein Requirement of Equids Among Herbivorous Mammals

Unlike many herbivorous animals, which eat the reproductive products of plants including fruits, seeds, and berries, the equidae subsist on the structural parts of the plant. These include the stems and leaves, which contain significant amounts of structural polysaccharides, including cellulose, hemicelluloses, and lignin [2]. Foraging ungulates comprising the artiodactyl and perissodactyl orders have adopted a unique strategy in the herbivore community. They select different plant taxa in the same habitat [3] and show differential preference for certain parts of the plant or certain growth stages within a given plant taxon [4]. Modern equids’ low species diversity among the modern perissodactyls (equidae, tapir, and rhinoceros), compared to that of the modern artiodactyls, highlight their relatively unselective behavior with respect to the plant taxon [5]. Thus, equids have uniquely and successfully evolved with dentition and hindgut fermentation that have allowed them to use a diet higher in fiber and lower in protein compared to other grazing herbivores.

Just as their modern equidae family counterparts, including zebras, wild asses, onagers, and Przewaldski’s horses, feral horses have often lived in areas with sparse, low-quality vegetation that does not support many species of resident artiodactyls [6]. It has been suggested that the perissodactyls adopted a high cellulose containing diet in the late Paleocene, since early members had fairly flat, grinding molars with more recent members developing a cecal site of fermentation [7]. The equidae have likely achieved ecological separation from the other perissodactyl groups by adopting a high-fiber dietary consumption strategy early in their evolution. The changes in equids relative food intake, and hence the fiber content of the diet, can be estimated from the change in the postcanine teeth surface area [7]. Throughout their evolution, equids have increased the complexity of the enamel pattern on the occlusal surfaces and molarized the premolars [7]. The far greater molarization of the premolars compared to other contemporaneous perissodactyls indicates their greater feed intake and thus higher fiber containing diets.

When compared to other grazing animals, equids have a greater feed intake per unit body weight and shorter passage time [8,9]. Such a digestive strategy has been suggested as being essential for the use of high-fiber herbage and survival on a diet which similar body sized ruminants cannot maintain themselves. Demment and Soest [10] reported that among herbivores, body size is critical in predicting the fiber-to-protein ratio that is needed in the diet, with larger animals requiring less protein and tolerating a larger proportion of cellulose.

2.2. Gastrointestinal Functional Anatomy of Equids Favor High-Fiber, Low-Protein Feeds

Given these dietary strategies, equids are equipped with a highly specialized GIT system and have adopted cecal, rather than ruminal digestion. Consequently, the equine stomach is simple and of small capacity (8–16 L) relative to the entire GIT tract, due in part to the adaptation of equids as bulk-feeding grazers [9,11]. The cranial half is lined with non–glandular-stratified squamous epithelium, and the caudal half is, for the most part, lined with proper gastric and pyloric glandular mucosa [9]. The proportion of proper gastric mucosa to the entire stomach mucosa in horses is significantly less than that of humans, dogs, and pigs [12]. The notion that less than half of the equid’s stomach is composed of proper gastric mucosa supports the earlier suggestion of an evolutionary strategy favoring dietary selection for higher fiber and lower protein content herbage. Passage of gastric chyme through the pyloric sphincter into the proximal duodenum and of digesta through the small intestine is relatively rapid in equids [13]. Briefly, the duodenum segment is approximately 3 m in length and is attached to the dorsal body by a short mesentery, which prevents torsion colic [13]. The duodenum passes over the base of the cecum in the paralumbar fossa region where the mesentery lengthen, marking the beginning of the jejunum [13]. The jejunum is approximately 20 m in length and lies dorsally to the cecum and large colon [13]. The ileum is 45 cm in length, and the transition from the distal jejunum and ileum is characterized by thickening of the intestinal wall, narrowing of the intestinal lumen, and the beginning of the antimesenteric mesentery [13].

In contrast to the small intestine, passage of digesta through the large intestine is slow because of the extensive digestive and fermentation processes taking place [14]. The large intestine of equids is complex and voluminous. The cecum is relatively large and haustrated, and the colon is voluminous, haustrated, and segmented [9]. Among herbivorous mammals, the greatest capacity and complexity of the colon is seen in the Perissodactyla (Equus, Diceros, and Tapyra) and the Proboscidea (Asian and African elephants) [9]. The anatomic complexity and