



Nutrient requirements of South American camelids: A factorial approach[☆]

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Abstract

Literature describing digestive physiology and defining specific nutrient requirements for llamas and alpacas was reviewed. Using data from studies defining maintenance energy and protein requirements, llamas and alpacas have lower energy and protein requirements compared to other ruminants; however, they have a greater protein requirement per unit of energy. This is consistent with observed differences in urea and glucose metabolism between camelids and other ruminants suggesting a reliance on protein catabolism to maintain blood glucose concentrations. Evidence suggests llamas and alpacas may have a greater requirement for Vitamin D, but no other evidence of significant differences in requirements between camelids and other ruminants. There are limited data defining other nutrient requirements or differences in requirements based on physiologic state for llamas and alpacas. In spite of limited data, a factorial approach to estimate nutritional requirements of llamas and alpacas was described. Defined maintenance energy and protein requirements were extrapolated to other physiologic states using beef cattle, sheep and goat data as templates. Models were developed to predict energy, protein, mineral and vitamin requirements for growth, pregnancy and lactation. Model development was based on determining beef cattle and sheep nutrient requirements on an amount per kg of body weight and assuming no inherent metabolic differences among species. An averaged value was calculated and used as a basis for defining requirements for llamas and alpacas. Amount per kg body weight requirements were converted to a recommended dietary nutrient density basis using an observed lower dry matter intake per unit body weight. Factorially derived models were in better agreement with North American feeding recommendations compared to predicted requirements using current North American-based requirement models. North American-based requirement equations over predicted energy and protein, resulting in required dietary nutrient densities in excess of practical feeding practices. The proposed factorial models need to be critically validated, but provides a starting point for discussion in advancing the study and application of llama and alpaca nutrient requirements. There are tremendous gaps in our knowledge of llama and alpaca requirements, requiring further basic research especially in the areas of neonatal and fetal growth and composition, lactational performance and mineral bioavailability.

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1. Introduction

Nutrition is the cornerstone of efficient and profitable agricultural production. Although llamas and alpacas, in countries other than their native South America, are not considered significant agricultural production species compared to other ruminants, good nutritional practices are key to sustaining a productive and successful industry. To date there is no National Research Council (NRC) or similar scientific body, report detailing nutrient requirements to provide guidance in feeding llamas and alpacas. Describing energy and protein requirements are the foundation of understanding a species' nutrient requirements. For llamas and alpacas, only three studies have addressed this issue. Alpaca protein requirements are based on a single study, a B.S. Thesis from Peru (Huasaquiche, 1974). Llama maintenance energy was described by two research groups, but results were very divergent (Engelhardt and Schneider, 1977; Carmean et al., 1992). Modification to energy and protein requirements to support different physiologic states have not been addressed.

A limited number of studies have attempted to define suggested nutrient requirements, but these were not based on controlled feeding trials. No study has directly compared llamas to alpacas relative to possible nutritional differences. Articles addressing some aspect of nutrition represented less than 10% of total citations on South American camelids covering the years 1967–2001 in a web-based bibliography (Anon., 2001). Most of the nutritional citations addressed digestive function, feed preference, comparative digestive efficiency and nutritional disease with only a couple specifically addressing nutrient requirements. Obviously, this lack of information prevents good science-based nutritional recommendations from being presented.

Most feeding recommendations for llamas and alpacas applied outside of South America have been observational. Diets fed to animal groups where no disease problems were observed, were considered adequate and dietary nutrient content determined to make feeding recommendations. A number of descriptive reviews have been published on llama and alpaca digestive anatomy and physiology and its impact on feeding practices (Engelhardt et al., 1984; Johnson, 1989, 1994; San Martin and Bryant, 1989; San Martin, 1991;

Fowler, 1992, 1998; Hospinal, 1997). As the South American camelid industry grows in North America, Europe and Australia, there is greater need for refined nutrient requirements, especially in support of efficient reproduction and fleece growth. An initial attempt was made to move our application of llama and alpaca nutrition to a new level, using a factorial approach to define nutrient requirements (Van Saun, 2003).

The objective of this paper is to describe methodologies used to determine a factorial-based approach to describing llama and alpaca nutrient requirements. Current status of llama and alpaca nutrient requirements will be reviewed and unique aspects of their digestive anatomy and physiology that impacts our understanding of nutrient assimilation and utilization will be applied. Using available data and extrapolating from other species, specific models characterizing energy, protein, mineral and vitamin requirements for maintenance, growth, pregnancy and lactation are described. Throughout this paper, the term "camelid" will be used to refer specifically to llama and alpacas.

2. Applied digestive anatomy and physiology

2.1. Anatomic differences

Ruminant herbivores are unique in their ability to derive nutrients from low quality forages. This ability has nothing to do with the animal's digestive enzymes, but totally dependent upon the symbiotic relationship between host animal and microbial populations residing in the anaerobic fermentation system. What separates ruminant from nonruminant herbivores is their ability to regurgitate swallowed feed material for remastication. This provides rumen microbes greater feed surface area allowing greater extent of degradation.

New and Old World camelids (suborder Tylopoda) are ruminant animals in that they have an expanded forestomach to facilitate microbial fermentation of ingested feedstuffs and they chew their cud. However, camelids are not considered "true ruminants" as a result of some distinct anatomic and physiologic digestive tract differences compared to ruminant species. Although both groups seemingly have evolved a similar system of nutrient assimilation, it was accomplished

through a process of parallel evolution (Timm and Smith, 1991).

Studies of fermentation characteristics show that the anaerobic fermentation process and end-product volatile fatty acids (VFA) production for camelids are similar to true ruminants (Vallenas and Stevens, 1971; Vallenas et al., 1973a,b). Microorganisms found in the camelid forestomach are the same ones found in other anaerobic fermentation systems (Navarre et al., 1999). This observation is also supported by an ability to transfaunate camelids with rumen contents from cattle, sheep or goats. Population dynamics of the different bacteria species found in the forestomach will be dependent upon the prevailing source of ingested material.

The most striking difference between camelid and ruminant digestive tracts is anatomic, camelids having only three distinct compartments associated with the foregut and stomach as compared to the four compartment ruminant organ (Vallenas et al., 1971). Ruminant terminology to label chambers of the camelid forestomach is not used. The large anaerobic fermentation chamber is divided into two distinct compartments labeled C-1 and C-2. The fermentation chamber is connected to the third forestomach component (C-3) by a small tubular canal. Compartment 3 is an elongated tubular organ that has fermentation activity in the proximal portion, with lower one-fifth having gastric secretions containing proteolytic digestive enzymes and hydrochloric acid. This would be similar to the digestive activity of our stomach. Proportional volumes of the forestomach from the three compartments are 83 (C-1), 6 (C-2) and 11 (C-3) percent (Vallenas et al., 1971; San Martin and Bryant, 1989).

Another unique feature of the camelid forestomach is the presence of small saccules in both C-1 and C-2 (Vallenas et al., 1971). These saccules are lined with a glandular (e.g., secretory function) epithelium as compared to the stratified squamous (e.g., protective and absorptive function) epithelium of the remaining area (Rübsamen and von Engelhardt, 1979). Two functions have been attributed to the saccule's glandular epithelium. A secretory function in which bicarbonate and phosphate ions are released aiding fermentation buffering capacity (Eckerlin and Stevens, 1973). Increased C-1 buffering capacity would maintain a more stable pH, complementing the buffering function of saliva and promoting greater microbial fermentation. Other inves-

tigators did not find significant secretory capacity, but suggested that these saccules aid in rapid absorption of fermentation end products (e.g., volatile fatty acids) and solutes (Rübsamen and von Engelhardt, 1979). Compared to other ruminants, llamas and alpacas had higher C-1 pH and greater volatile fatty acid absorption following feeding suggesting that both functions may be present in these saccules (Vallenas et al., 1973a,b; Lemosquet et al., 1996).

2.2. Foregut motility

Motility of the forestomach is a critical function with regard to continual fermentation activity. Forestomach motility ensures constant exposure of the ingested feedstuffs to microbial attachment and subsequent degradation. Similar to true ruminants, forestomach motility in camelids occurs in two distinct phases, A and B waves compared to α and β waves in true ruminants (Heller et al., 1984). Beyond this, forestomach motility is dramatically different. In camelids, C-2 contracts strongly followed by contraction of the distal aspect of C-1 (A phase). Phase B initiates when the cranial portion of C-1 contracts followed by contraction of C-2 and the caudal portion of C-1. This B phase may repeat itself three to six times during a cycle before a brief rest period and beginning of a new cycle.

Eructation may occur three to four times during each motility cycle. In comparison, camelids have greater forestomach activity compared to the single bi- or triphasic contraction per minute of true ruminants (Heller et al., 1984). This increased motility pattern found in camelids may also have some bearing on the observation that these animals are fairly resistant to forestomach gas accumulation or bloat as opposed to true ruminants. Increased motility patterns are also account for the more thoroughly mixed homogeneous nature of camelid forestomach contents compared to more stratified air, fibrous mat and liquid layers found in true ruminants.

Beyond the forestomach system, camelid small intestinal digestion and absorptive processes seem to be identical to ruminant and nonruminant animals. The hindgut also has some fermentation capacity, but to a much lesser extent compared to the forestomach. The primary purpose of the hindgut is water absorption along with some absorption of VFAs, vitamins

and minerals. Very little data are available detailing the role of hindgut function in camelids.

2.3. Rate of passage and digestive efficiency

Similar to ruminants, llamas were shown to have differential selectivity in retaining water and particles within C-1/C-2, based on size (Heller et al., 1986). Water passed through C-1/C-2 more quickly than particles and larger particles (2.5–4 cm) were retained slightly longer than smaller particles (0.2–1 cm). Comparative studies between camelids and true ruminants show that consumed feed material passes more slowly through C-1 than the rumen (Florez, 1973; Clemens and Stevens, 1980; San Martin, 1987). This slower rate of passage results in feed materials being retained within the fermentation chamber for a prolonged period of time. As a direct consequence of longer retention time, camelids have greater degradation of ingested feed material compared to true ruminants, especially for the cell wall fraction (Florez, 1973; Hintz et al., 1973; San Martin et al., 1986; San Martin, 1987, 1991; Cordesse et al., 1992; Genin et al., 1994; Genin and Tichit, 1997; Hospinal, 1997; Fraser and Baker, 1998; Lopez et al., 1998). The camelid digestive advantage over ruminants is most obvious when comparing the digestion of poor quality, low protein forages (San Martin and Bryant, 1989; Warmington et al., 1989; San Martin, 1991; Genin and Tichit, 1997; Lopez et al., 1998). This digestive advantage is minimized when feeding higher-quality forages.

Studies looking at the liquid passage rate suggest a more rapid movement of liquid through the forestomach of camelids than true ruminants (Clemens and Stevens, 1980; San Martin, 1987, 1991). This observation may explain the greater buffering capacity of camelids resulting from more microbial VFA end-products being washed out of the fermentation system (Vallenas and Stevens, 1971; Vallenas et al., 1973b). A more rapid liquid passage rate would result in greater microbial yield as a consequence of more cells being in a state of active growth (Van Soest, 1994, pp. 274–277). The combination of greater degree of degradability coupled with increased microbial yield provides camelids with a distinct advantage in dealing with lower quality feeds compared to other ruminants.

3. Unique metabolic differences of camelids

3.1. Urea metabolism

Dietary nitrogen is composed of various nonprotein (NPN) and α -amino nitrogen (amino acids and true protein) sources. Fermentation bacteria are capable of utilizing many sources of nitrogen to support microbial protein production, whereas the host animal has an absolute requirement for amino acids to support physiologic function. The host animal synthesizes urea in the liver from nitrogenous waste generated by animal and bacteria. Animals generate waste nitrogen (ammonia) from protein breakdown during cell turnover as well as use of amino acids for energy or glucose production. Generation of nitrogen, usually in the form of ammonia, from the fermentation system results from a complex interaction between availability of dietary nitrogen and fermentable energy and rates of protein degradation and passage. When available dietary nitrogen sources exceeds microbial capacity to incorporate into bacterial protein, this excess nitrogen will pass into the portal venous system and be delivered to the liver for detoxification into urea.

In addition to eliminating urea via the kidney, ruminant animals can recycle urea through saliva back into the fermentation system (Van Soest, 1994, pp. 299–301). This evolutionary adaptation in ruminant animals provides the rumen microbial population with needed nitrogen even when dietary protein is limited. In return, the microbial population provides the ruminant animal with high quality microbial protein, thus giving the rumen animal a distinct advantage over nonruminant herbivores in meeting the challenges of utilizing low quality forages.

Serum urea nitrogen (SUN) concentration measures the amount of urea present and often is used as a clinical measure of kidney function. Serum urea concentration can also be used to assess dietary protein status in ruminants (Hammond, 1997; Melendez et al., 2003; Nousiainen et al., 2004). A number of clinical pathology laboratories have determined and published reference ranges for a variety of clinical chemistry parameters, including SUN (Lassen et al., 1986; Fowler and Zinkl, 1989; Kaneko, 1989, pp. 886–891; Simons et al., 1993). Reported SUN reference range appears similar for cattle and sheep compared to llamas and alpacas. Reference ranges reported for cattle and sheep usually

represent a normal expected SUN concentration range relative to kidney function. From a nutritional perspective, a working range for SUN concentration would be 7.1–14.3 mmol/l, with values <7.1 and >14.3 mmol suggesting low or excessive protein, respectively. Most dairy cattle will maintain a SUN concentration between 8.6 and 12.9 mmol/l (Hammond, 1997; Melendez et al., 2003; Nousiainen et al., 2004). Llama and alpaca reference ranges reflect summary data of samples collected from healthy animals, suggesting no indication of kidney disease. None of these studies had any data as to the level of dietary protein supplementation. However, in comparing llama and alpaca to ruminant SUN data, it would seem camelids have higher SUN concentrations with a mean value >18.6 mmol/l (Lassen et al., 1986; Fowler and Zinkl, 1989; Kaneko, 1989, pp. 886–891; Simons et al., 1993).

Higher SUN concentrations in camelids suggests they are being overfed protein relative to requirements, metabolize urea differently from other ruminants, have an inherently high metabolic rate of protein turnover or some combination of these factors. Data from Hinderer and von Engelhardt, 1975 suggest llamas have a lower rate of urea turnover and kidney urea excretion rate compared to other ruminants. These differences allow the llama to recycle more urea to the forestomach for use by bacteria to produce microbial protein. In addition to recycling more urea to bacteria, llamas have been shown to have greater urease activity, the enzyme needed to metabolize urea, compared to other ruminants (Hinderer and von Engelhardt, 1975). Greater urea recycling and utilization coupled with the slower rate of passage in C-1/C-2 are critical physiologic adaptations of camelids allowing them to survive in their native environment under harsh conditions consuming low-quality forages for a significant portion of the year.

3.2. Glucose metabolism

Glucose metabolism in camelids is an enigma. Ruminant animals maintain low blood glucose concentration (2.5–4.2 mmol/l) compared to nonruminant animals (4.2–6.4 mmol/l, horse; 4.7–8.3 mmol/l, pig) (Kaneko, 1989, pp. 886–891). Preweaned milk-fed calves are not functional ruminants and will maintain a higher blood glucose concentration similar to nonruminant animals. As the rumen becomes functional, blood glucose will decline to adult concen-

trations. In contrast to ruminants, llamas and alpacas maintain higher blood glucose concentrations (mean: 7.0 mmol/l, range: 4.6–8.9 mmol/l) more similar to that of nonruminant animals. Although there is some variation among laboratory ranges, all show higher concentrations for camelids compared to ruminants (Lassen et al., 1986; Fowler and Zinkl, 1989; Kaneko, 1989, pp. 886–891). Llamas and alpacas also display an extreme hyperglycemic response (blood glucose concentrations >11.1–16.6 mmol/l) in response to even minimal stress situations (Fowler and Zinkl, 1989; Cebra et al., 2001a,b). Elevated blood glucose can be somewhat explained by recent studies showing a sluggish insulin response and moderate insulin resistance, somewhat similar to a diabetes condition, in llamas and alpacas (Cebra et al., 2001a,b).

How can llamas and alpacas maintain these high blood glucose concentrations and display such hyperglycemia in a dietary situation that seemingly is limited in available glucose or glucose precursors? In ruminant animals, glucose is primarily derived by hepatic gluconeogenesis using propionate from ruminal fermentation of sugars and starches. Given the low amounts of sugars and starch in the typical camelid diet, production of glucose from propionate would be considered minimal. Amino acids can also be a substrate for gluconeogenesis. Perhaps camelids utilize amino acids in support of blood glucose content, which would possibly explain the observed higher SUN concentrations.

Supportive evidence for this hypothesis comes from data generated in a feed restriction study of hepatic lipidosis (Tornquist et al., 2001). In this study, feed restriction resulted in a significant decline in SUN concentration over time, consistent with observed responses in ruminants. When individual llama responses were evaluated, a differential response in SUN was noticed relative to lactation status. Nonlactating and late lactation (>10 weeks) llamas showed a gradual decline in SUN concentration in association with feed restriction. In contrast, lactating llamas showed marked increases in SUN with a decline occurring following refeeding (Tornquist et al., 2001). Lactose content of llama milk is greater (65 versus 50 g/kg) compared to ruminant animals (Morin et al., 1995), requiring more glucose as a substrate for lactose synthesis. One could speculate that the increase in SUN was a result of body protein mobilization in support of milk production, given that the nursing crias did not lose weight during the trial.

Insulin resistance can also result in higher blood glucose concentrations, but an alternative energy source would be needed. Camelids may preferentially metabolize short chain volatile fatty acids (acetate and butyrate), which would be readily available from foregut fermentation of forage-based diets. More realistically, a combination of these factors might account for the observed higher blood glucose concentration in camelids. Clearly, further research into glucose and protein metabolism in camelids is warranted.

4. Dry matter intake (DMI)

Although the observed slowed rate of passage in C-1/C-2 has digestive advantages, it comes with a potentially negative consequence, reduced feed intake capacity. Beef cattle, sheep and goats at maintenance have a predicted DMI between 1.5 and 2.0% of body weight (NRC, 1981a, 1985, 1996). There is much individual variation as well as feed ingredient-based issues that control feed intake. For ruminants, amount of dietary fiber measured as neutral detergent fiber (NDF) directly impacts intake capacity. As NDF content of feeds goes up, intake capacity is reduced (Mertens, 1987). Observations of feeding behavior in North America would suggest that camelids at maintenance have a DMI between 1.0 and 1.5% of body weight, although higher intakes are feasible (Fowler, 1998; Johnson, 1989, 1994). On average, this is about a 30% decline in intake capacity compared to other ruminants.

Measuring DMI for an animal is a difficult procedure if it is not housed individually. Obtaining DMI for pastured animals is a real challenge. A number of studies have measured camelid DMI under varying feeding and housing conditions in comparison to sheep (San Martin, 1987, 1991; San Martin et al., 1986; Reiner et al., 1987; San Martin and Bryant, 1989; Cordesse et al., 1992; Lemosquet et al., 1996). There is not complete agreement among study findings and some studies show similar intake levels (% body weight basis) as previously described, while others show slightly higher intake levels. Most studies confirmed that camelids had lower intake levels compared to sheep, but others showed no difference (Fraser and Baker, 1998) or even higher intake by camelids (Warmington et al., 1989). Differences in DMI results across studies may reflect wide differences in the forage quality used. Both

NDF (Lopez et al., 1998) and protein (San Martin and Bryant, 1989; San Martin, 1991) content influence intake capacity, somewhat differentially for camelids and ruminants.

San Martin and Bryant (1989) summarized intake data from a large number of studies for alpacas and llamas compared to sheep in penned and pasture situations. Average intake for llamas and alpacas was 2.0 and 1.8% of body weight, respectively. These are higher values than typically expected, but still were lower than what was observed for sheep fed the same diets. Alpacas ate on average 20% less than sheep across studies, whereas llamas ate more than 30% less than sheep. When intake for llamas and alpacas were adjusted for metabolic body weight, there were no differences between llamas and alpacas but, intake was 26% lower for improved and 36% lower for unimproved pastures compared to sheep (San Martin, 1987).

5. Estimated nutrient requirements

A requirement for an essential nutrient is based on maintenance of normal body functions over time and is adjusted accordingly to accommodate other physiologic states (growth, pregnancy, lactation and work). In spite of the aforementioned anatomic and physiologic differences, no available data suggest inherent metabolic differences between camelids and ruminants in essential nutrient requirements to support various physiologic functions. For the most part in the United States, camelid feeding recommendations have been extrapolated from those of sheep (NRC, 1985), goats (NRC, 1981a) and beef cattle (NRC, 1996).

5.1. Water

Water is the most essential nutrient; however, it is also the most neglected nutrient. Water plays important roles in body temperature regulation and provides an aqueous medium for all metabolic reactions. Young animals are approximately 85–90% water whereas adults are between 60 and 70% depending upon fat content (Rübsamen and von Engelhardt, 1975). Llama milk is 87% water, therefore, water consumption is critical to lactating animals (Morin et al., 1995). An animal's ability to consume feed dry matter is dependent upon water availability, however, llamas were shown to have

less reduction in dry matter intake compared to goats when water was restricted (Rübsamen and von Engelhardt, 1975). Fresh, clean, high quality water should be available free choice at all times.

Total water requirement is determined by body weight, physiologic state, level of activity, production level, dietary composition and environmental conditions. The water requirement has been related to energy intake (1 ml/kcal of metabolizable energy intake) or metabolic body weight (122 ml/kg BW^{.75}) (Fowler, 1998). A more general rule of thumb for water intake is two to three times dry matter intake or 3% (adult maintenance) to 8% (growth, lactation level) of body weight daily. Water intake should be increased in hot weather and humid conditions to approximately 10–15% of body weight daily.

5.2. Energy

From an animal performance perspective, energy is quantitatively the most important nutrient as it supports all physiologic states. In two different studies, the maintenance metabolizable energy (ME) requirement for llamas was determined to be 61.2 (Schneider et al., 1974; Engelhardt and Schneider, 1977) and 84.5 kcal/kg BW^{.75} (Carmean et al., 1992). The notable difference in ME estimates may be explained by differences in methodologies used to measure energy balance and diets between studies. Fasting energy expenditure in llamas was determined to be 52 kcal (Schneider et al., 1974) and 59 kcal (Carmean et al., 1992) per kg BW^{.75}, which is lower compared to other ruminants. These fasting metabolism values are in good agreement, suggesting dietary differences or extrapolation method to determine zero energy gain were different between studies. Carmean et al. (1992) attempted to adjust their zero energy extrapolation method and determined maintenance ME to be 74 kcal/kg BW^{.75}, still significantly higher than the previous study.

The higher value is generally used and believed to better reflect North American feeding conditions. Also this value is similar but, somewhat lower than maintenance ME values determined for sheep (99.9 kcal/kg BW^{.75}) (NRC, 1985), goats (101.4 kcal/kg BW^{.75}) (NRC, 1981a) and cattle (133 kcal/kg BW^{.75}) (NRC, 1996). However, until more studies measuring camelid energy metabolism are completed, neither study should be ignored. Typical

of other scientific reports summarizing animal nutrient requirements, results from multiple studies are averaged to determine a suggested model. Given problems with obesity in the North American camelid population and season nutrient deprivation in South America, an averaged value of 72.85 kcal ME/kg BW^{.75} might be a reasonable alternative until more data are available. The ensuing discussion on a factorial approach to determining nutrient requirements for camelids will use this averaged maintenance energy value as a foundation for other energy and protein requirements. This approach will be defined as Model 1. A comparison will be made using the higher maintenance energy equation of Carmean et al. (1992), termed Model 2.

Given most management systems for llamas and alpacas are pasture-based, maintenance energy requirement needs to be adjusted for activity level. Activity level accounts for muscular energy expended as the animal roams its environment in search for food. In confinement feeding systems where animals are housed comfortably and provided feed, activity expenditures are minimal and maintenance ME needs not to be adjusted. The approach used for goats to adjust maintenance energy requirements seems a reasonable starting point. Goat maintenance energy is increased by 25, 50 or 75% for broadly defined categories based on descriptions of pasture quality (intensive management or tropical range, semiarid rangeland, arid rangeland, respectively) and topography (flat, slightly hilly, mountainous, respectively) (NRC, 1981a). The same adjustments to maintenance energy are suggested for camelids (Table 1). These adjustments to maintenance energy are also consistent with the system used to adjust energy requirement for work status in horses (NRC, 1989) and would be applicable for work status for pack llamas.

Amount of ME required to support growth will depend upon rate of gain (g/day) and composition of gain (fat and protein percent). Growth data are lacking for alpacas and limited for llamas and composition of gain data are lacking for both. Growth curves were developed for llamas and alpacas, based on the llama data from Smith et al. (1992). Using mean body weights for each time interval, average daily gain (g/day) and cumulative body weight models were developed based on birth weight. The llama model was proportionally scaled for body weight to predict an average growth curve for alpacas (Fig. 1). From these models, average

Table 1

Metabolizable energy (ME) and crude protein (CP) prediction models for llamas and alpacas in various productive functions. Total daily energy (kcal/day) or crude protein (g/day) requirement for a given animal will be the sum of the appropriate physiologic states

Physiologic state	Prediction Model	Comment/description
Maintenance	ME (kcal/day) = 72.85 kcal/kg BW ^{0.75} (Model 1); ME (kcal/day) = 84.5 kcal/kg BW ^{0.75} (Model 2); CP (g/day) = 3.5 g CP/kg BW ^{0.75}	Needed to support all basic body functions without any environmental stresses
Activity/work level ^a		
Low	1.25 × Maintenance	Light work or grazing on moderate to good pasture quality
Moderate	1.50 × Maintenance	Moderate work or grazing semiarid rangeland pasture, hilly conditions
High	1.75 × Maintenance	Heavy work or grazing sparse grassland, mountainous conditions
Growth	ME (kcal/day) = 7.25 kcal/g of gain; CP (g/day) = 0.284 g CP/g of gain	Based on goat data and does not account for changes in composition of gain. This amount is added to maintenance for energy and protein
Pregnancy	ME (kcal/day) = 66.0 kcal/kg BW ^{0.75} ; CP (g/day) = 1.62 g/kg BW ^{0.75}	Alternative model for only last 3 months of gestation. Add to maintenance energy and protein
1–8 months	ME (kcal/day) = 72.85 kcal/kg BW ^{0.75} ; CP (g/day) = 3.5 g CP/kg BW ^{0.75}	Maintenance energy and crude protein only, no significant pregnancy requirement
8th to 9th month	ME (kcal/day) = 65.34 × Birth wt. (kg) – 33.50; CP (g/day) = 0.94 g CP/kg BW ^{0.75} (95% CI = 0.62–1.26)	Add pregnancy energy and protein to maintenance energy and protein values
9th to 10th month	ME (kcal/day) = 131.68 × Birth wt. (kg) – 39.74; CP (g/day) = 1.94 g CP/kg BW ^{0.75} (95% CI = 1.30–2.58)	
10th to 11th month	ME (kcal/day) = 203.51 × Birth wt. (kg) + 86.12; CP (g/day) = 3.23 g CP/kg BW ^{0.75} (95% CI = 2.37–4.09)	
Lactation	ME (kcal/day) = 946.2 kcal/kg milk (95% CI = 697.2–1195.2 kcal/kg); CP (g/day) = 60.6 g CP/kg of milk (95% CI = 46.6–74.6 g CP/kg)	Multiply this value by estimated daily milk production (kg) for total lactation energy or protein and add to maintenance. This model assumes no change in milk composition over time
Fleece ^b	ME (kcal/day) = 30 kcal/kg fleece; CP (g/day) = 4.283 g/kg fleece	Multiply by estimated yearly fleece weight and add to maintenance energy and protein

^a Based on descriptions from NRC (1981a).

^b Derived from data in NRC (1981a).

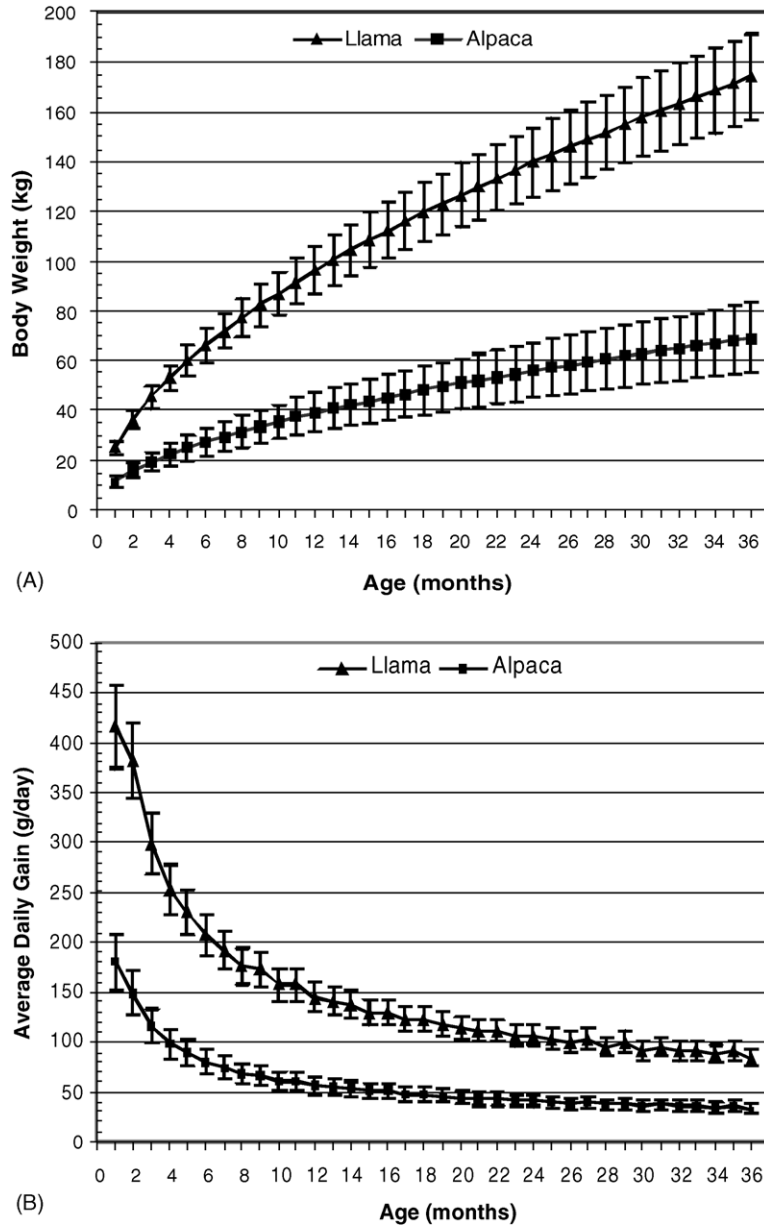


Fig. 1. Predicted cumulative body weight (A) and average daily gain (B) for llamas (birth weight 12.5 kg) and alpacas (birth weight 6 kg) from 1 to 36 months. Growth data based on llama growth characteristics (Smith et al., 1992) and scaled to alpaca body weight. Error bars show a 15% variation of mean growth data. From Van Saun (2003) with permission.

daily gain ranged from 80 to 400 and 30 to 180 g/day for llamas and alpacas, respectively.

Until more definitive data on rate of gain and compositional changes are obtained, energy requirement to support growth in camelids can be estimated

using the NRC goat model, 7.25 kcal ME/g gain (NRC, 1981a), since goats have a similar range for growth rate (50–250 g/day). This estimated value for gain is similar to that suggested by Fowler (1998), 8.92 kcal DE/g equivalent to 7.31 kcal ME/g. These models will over-

estimate energy for gain in younger, rapidly growing animals compared to older animals. Younger animals will deposit more protein early, then more fat as they age. Energy required for gain must be added to maintenance for total growing animal energy requirement. Using this model, total requirement (maintenance + growth) ranges from 3.7 to 1.19 (llama) and 2.9 to 1.14 (alpaca) times maintenance from 2 to 36 months of age, respectively. These values are in reasonable agreement with similar relationships for sheep (NRC, 1985) and goats (NRC, 1981a).

Pregnancy ME requirement is a function of energy needs to support fetal, placental, uterine and mammary gland growth. Llamas were found to gain between 10 and 15% of their live weight at conception over the gestation period, with majority of weight gain (>60%) occurring during the last 2 months (Smith et al., 1992). This fetal growth pattern is similar to other species and suggests changing requirements as the pregnant camelid progresses through the last 3 month of gestation.

Fowler (1998) suggested adding 93 kcal DE/kg BW^{0.75} (76.26 kcal ME/kg BW^{0.75}) to maintenance to account for pregnancy energy requirements during the last 3 months of gestation. This is an increase of 104 or 90% above maintenance depending upon which energy model was used. A model using metabolic BW to predict maintenance and pregnancy requirement was extrapolated from a sheep equation by proportionally decreasing the coefficient multiplier to account for the lower maintenance energy need of camelids compared to sheep (NRC, 1985). The resulting equation would be either 138.8 or 160.9 kcal/kg BW^{0.75} depending upon whether the maintenance energy coefficient was 72.85 (Model 1) or 84.5 (Model 2), respectively. Each model predicts a 90% increase in maintenance energy to account for pregnancy. The second model using the higher maintenance energy requirement is identical to the recommendation made by Fowler (1998). These models do not account for the exponential fetal growth curve, nor do they allow for variation in cria birth weight to modify pregnancy requirements. If these models are targeted to meet an overall average late pregnancy requirement, then camelids in the last month of gestation will be underfed, potentially leading to negative energy balance and metabolic derangements. If the models are targeted to meet maximal pregnancy requirements, then animals in their eight or ninth month

of gestation will be overfed, potentially leading to obesity and parturition problems.

A second method used sheep data describing conceptus net energy deposition on differing days of gestation (100, 120 and 140 days) by the number of fetuses (single, twins and triplets) (NRC, 1985). Total fetal mass for single, twin and triplet pregnancies were 5, 9 and 11.5 kg, respectively, a similar range in birth weight for camelids. To generate a camelid model, sheep pregnancy net energy data were converted to ME values, scaled to account for maintenance energy differences and regressed onto birth weight (Table 1). Day of gestation for each model were scaled to month of gestation for camelids resulting in models predicting pregnancy ME for 8–10 months of gestation (Fig. 2). Using these models, estimated pregnancy requirement at 8–10 months of gestation averaged 1.27, 1.55 and 1.92 times maintenance, respectively. These values are consistent with observations for other species.

Using a body weight range of 50–160 kg and assuming a cria birth weight of 10% of maternal BW, these pregnancy models were compared. The metabolic BW equation, based on the averaged maintenance energy, averaged 241% (range: 193–323%) and 65% (range: 44–101%) greater than pregnancy energy predicted for 8 and 9 month of gestation, respectively. This model averaged 1.4% (range: –11 to 12%) below pregnancy ME predicted by the 10th month of gestation model. Similarly, the model proposed by Fowler (1998) averaged 294, 91 and 14% greater than values predicted at 8, 9 and 10 months of gestation, respectively. These comparisons show the metabolic BW models are targeted to meet gestation requirements for the last month and are overfeeding in earlier gestation. Month of gestation regression models seemingly better fit the known biology of fetal growth. However, there is a need to develop a better database of information for camelids on which to establish an improved prediction model. A model for both alpacas and llamas may not be appropriate, but this seems to be a reasonable starting point for development.

Lactational energy requirements are a function of milk composition and total yield in addition to maintenance requirements. Llama milk composition was determined in 83 animals on eight farms in four states (Morin et al., 1995). Reported mean milk composition was 131 g/kg total solids, 65 g/kg lactose, 34 g/kg protein and 27 g/kg fat. Compared to other ruminants,

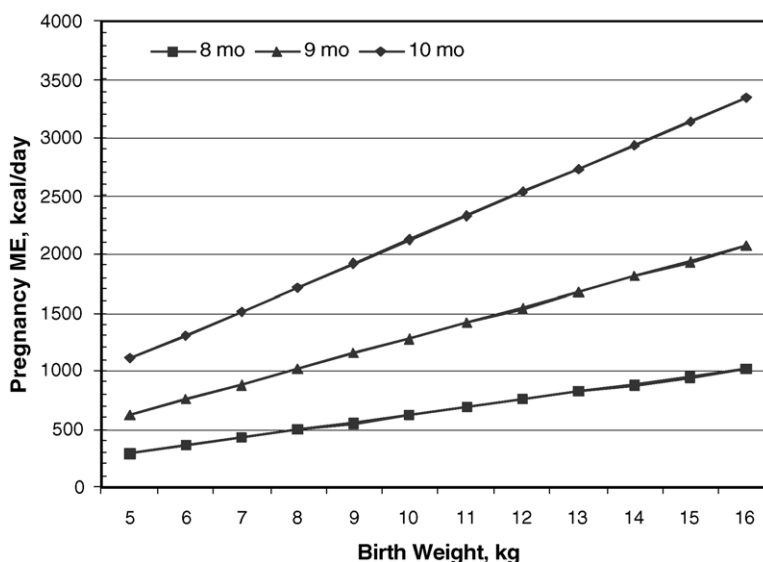


Fig. 2. Predicted metabolizable energy (ME) requirement to support pregnancy during the last 3 months of gestation by expected birth weight. Models for predicting ME requirement are based on sheep data (see Table 1 for equations).

llama milk is higher in lactose and slightly lower in fat. Lactose content was slightly lower in first lactation llamas and milk protein content varied by farm, suggesting dietary influences. Based on these composition data, llama milk contains 700.2 kcal NE/kg. Using a 74% efficiency of converting ME to milk energy (NRC, 1985) results in 946.2 (697.2–1195.2, 95% confidence interval) kcal ME/kg of milk produced. This value is between estimates of llama milk energy of 1257 kcal ME/kg and 822 kcal ME/kg suggested by Fowler (1998) and Johnson (1994), respectively. These differences most likely reflect differences in milk composition based on available data. Milk production during lactation has not been well quantified or modeled for camelids. Suggested production amounts range between 0.75 and 2.5 kg/day, equivalent to 710 and 2082 kcal ME needed per day to support lactation.

A final productive function requiring additional energy and protein above maintenance is growth of fiber or fleece. Energy deficiency or restriction has been shown to slow wool growth and reduce fiber diameter in sheep (NRC, 1985). In severe cases of energy deficiency, wool growth will cease, creating a weak spot or “break” in the staple of wool (NRC, 1985). Somewhat similar effects of nutrition on fleece characteristics were found in alpacas. Male alpacas fed either a low energy, low protein sub-maintenance diet had

lower clean fleece weight, fiber length and length to diameter ratio compared to alpacas fed a high energy, high protein diet (Russel and Redden, 1997). Fiber diameter was slightly higher in alpacas fed the better diet, but the difference was not significant. In contrast to nutritional influences on wool growth characteristics in sheep, alpaca fiber has differential growth in length and diameter where fiber length is augmented better than fiber diameter. Recommendations for energy and protein requirements to support mohair production by Angora goats have been generated (NRC, 1981a). These recommendations can be used as general guidelines in accounting for fleece production in llamas and alpacas (Table 1).

Using the factorial requirement system, two different animals were described and energy requirements determined (Table 2). A comparison was made in determining energy requirements using the suggested averaged maintenance energy and gestation month equations (Model 1) or the higher maintenance energy model and Fowler (1998) pregnancy requirement (Model 2). This first example of an adult, pregnant alpaca shows a 43.4% increase in requirement for Model 2 compared to Model 1. This increase is primarily the result of the greater pregnancy requirement. A second example describes energy requirements a growing llama. Predicted energy requirement for Model 2

Table 2

Example calculations of metabolizable energy (ME) and crude protein (CP) requirements for llamas and alpacas using a proposed factorial system (see equations in Table 1)

Physiologic state	Animal description			
	ME required (Mcal/day)		CP required (g/day)	
	Model 1 ^a	Model 2 ^b	Model 1 ^a	Model 2 ^b
Adult 60 kg alpaca female, 9 month pregnant (6 kg birth weight), not lactating, 2.5 kg fleece, good quality pasture system				
Maintenance	1.57	1.82	75.5	68.9
Activity adjustor	0.39	0.46	0	0
Fleece	0.075	0.075	11.5	11.5
Growth	0	0	0	0
Pregnancy	0.75	1.64	41.8	62.0
Lactation	0	0	0	0
Total	2.79	4.0	128.8	142.4
Growing 20-month-old, 110 kg llama, 95 g/day gain, 2 kg fleece, not pregnant, non-lactating, confined feeding system				
Maintenance	2.47	2.87	118.9	108.5
Activity adjustor	0	0	0	0
Fleece	0.06	0.06	9	9
Growth	0.69	0.69	27	27
Pregnancy	0	0	0	0
Lactation	0	0	0	0
Total	3.22	3.62	154.9	144.5

^a Based on maintenance energy equation of 72.85 kcal ME/kg BW^{0.75} and factorially derived models.

^b Based on maintenance energy equation of 84.5 kcal ME/kg BW^{0.75} and single equation pregnancy model of 76.26 kcal/kg BW^{0.75}. Protein requirements were calculated as 31 g CP/Mcal ME for maintenance and pregnancy.

is only 12% greater than Model 1. This difference here is primarily due to maintenance.

The comparison between predicted energy requirements for these two models does not suggest either one being correct. Further comparison was made by calculating needed dietary energy density (ME and Total Digestible Nutrients (TDN) basis) over a range of DMI (1.0–2.5% of BW). In the alpaca example, energy density of the diet exceeds practicality for intake levels less than 1.75% of BW (Table 3). For these diets, the calculated energy concentration exceeds a concentrate only diet. A dietary energy concentration more typical of a forage with some grain is seen with intakes >1.75% of BW. Intakes much more than 2% of BW would not be expected in a late pregnant animal. In comparison, dietary energy density using predicted energy needs from Model 2 results in excessive energy density through 2.25% of BW intake. This would suggest predicted energy requirement using the typical North American standards is excessive. A similar comparison for the llama example shows similar expected dietary nutrient densities within a realistic range of intakes.

Overall these comparisons would suggest Model 1 was a better predictor of camelid energy requirements compared to the currently used system in North America. More studies are needed to better define pregnancy requirements.

5.3. Protein

Current methods to estimate protein requirements for sheep and cattle are based on a factorial approach. Models are developed to estimate protein needed for maintenance, growth, pregnancy, lactation and wool production and summed to determine total protein requirement. However, protein requirements are much more complicated than digestible or crude protein (CP) for a ruminant animal. In ruminant animals, protein requirements are defined relative to microbial and animal needs. Dietary protein can be fractionated according to its solubility and degradability within the fermentation vat. Microbial populations can utilize highly soluble and degradable dietary protein and nonprotein nitrogen whereas; daily amino acid requirements for

Table 3
Comparison of dietary nutrient density calculated for a range of dry matter intakes based on predicted energy and protein requirements

Dietary nutrient density (DM basis)	Level of dry matter intake, % of body weight						
	1.0	1.25	1.5	1.75	2.0	2.25	2.5
Adult 60 kg alpaca female, 9 month pregnant (6 kg birth weight), not lactating, 2.5 kg fleece, good quality pasture system							
Model 1 ^a							
ME (Mcal/kg)	4.65	3.72	3.10	2.66	2.33	2.07	1.86
TDN (g/100 g)	128.9	103.1	85.9	73.6	64.4	57.3	51.6
CP (g/100 g)	21.5	17.2	14.3	12.3	10.7	9.5	8.6
Model 2 ^b							
ME (Mcal/kg)	6.67	5.33	4.44	3.81	3.33	2.96	2.67
TDN (g/100 g)	184.8	147.8	123.2	105.6	92.4	82.1	73.9
CP (g/100 g)	23.7	19.0	15.8	13.6	11.9	10.5	9.5
Growing 20-month-old, 110 kg Llama, 95 g/day gain, 2 kg fleece, not pregnant, non-lactating, confined feeding system							
Model 1 ^a							
ME (Mcal/kg)	2.93	2.34	1.95	1.67	1.46	1.30	1.17
TDN (g/100 g)	81.1	64.9	54.1	46.4	40.6	36.1	32.5
CP (g/100 g)	14.1	11.3	9.4	8.0	7.0	6.3	5.6
Model 2 ^b							
ME (Mcal/kg)	3.29	2.63	2.19	1.88	1.65	1.46	1.32
TDN (g/100 g)	91.2	73.0	60.8	52.1	45.6	40.5	36.5
CP (g/100 g)	13.1	10.5	8.8	7.5	6.6	5.8	5.3

^a Model 1 has maintenance energy system based on 72.85 kcal/kg BW^{.75} and factorially derived models.

^b Model 2 has maintenance energy system based on 84.5 kcal/kg BW^{.75} and single equation pregnancy model of 76.26 kcal/kg BW^{.75}. Protein requirements were calculated as 31 g CP/Mcal ME for maintenance and pregnancy.

the animal are derived from digestion of microbes and undegradable dietary protein.

Unfortunately, there are no data for camelids relative to these protein fraction requirements. Using the limited available data to estimate camelid maintenance protein requirement, specific models to predict protein requirements for other physiologic states were developed to establish a starting point in refining camelid protein requirements (Table 1). Clearly there is a tremendous need for more information on protein metabolism and dietary needs in camelids.

Maintenance protein requirement accounts for endogenous nitrogen losses in feces, urine and scurf. Using a nitrogen balance study, Huasaquiche (1974) estimated maintenance protein requirement to be 2.38 g digestible protein/kg BW^{.75}, equivalent to 3.5 g CP/kg BW^{.75} for alpacas. There are no data specific for llamas and the requirement will be assumed to be equivalent. This value is lower than estimates for goats (2.82 g digestible protein/kg BW^{.75} or 4.15 g CP/kg BW^{.75}), sheep (4.74 g CP/kg BW^{.75}) and dairy cattle (4.09 g CP/kg BW^{.75}) (NRC, 1981a, pp. 4–5).

Another suggested requirement is 31 g CP per 1 Mcal digestible energy (Fowler, 1998). This is consistent with recommended calorie to protein ratios for goats, as well as other species. A calorie to protein ratio of 1 Mcal digestible energy to 22 g digestible or 32 g CP was used to predict goat protein requirements (NRC, 1981a). Using a ratio of 31 g CP/Mcal of digestible energy, maintenance CP requirements would be 78 or 91% of the value predicted by 3.5 g CP/kg BW^{.75}, for maintenance energy Models 1 and 2, respectively. For example, an adult 70 kg camelid at maintenance would require 66.7 or 77.3 g/day CP using the calorie to protein ratio for Models 1 and 2, respectively, compared to 84.7 g/day predicted using the metabolic BW model.

At first glance this perceived lower maintenance protein requirement for camelids compared to other ruminants is not consistent with the proposed hypothesis of higher protein metabolism to support gluconeogenesis as previously described. However, if one calculates the protein to calorie ratio using the data of Huasaquiche (1974) and Engelhardt and Schneider (1977), the ratio is much higher, 32 g digestible

or 47 g crude protein per 1 Mcal digestible energy. These ratios are equivalent to 39 g digestible and 57 g crude protein per Mcal ME. This is a much higher ratio recommended for other species, and if correct, would support the hypothesis that camelids utilize amino acids to a greater extent to support metabolic functions. Response of a debilitated llama treated with parenteral nutrition solution containing a much lower calorie to protein ratio than used in other species also supports this hypothesis (Van Saun et al., 2000). Using the averaged maintenance energy equation and suggested protein requirement from Huasaquiche (1974), results in CP to ME ratio of 48 g/Mcal. This is an intermediate value between recommendations for ruminants and calculated ratio from previous camelid data and will be used as a guide in developing additional protein requirement models. Clearly, more research is needed to better define amino acid and glucose metabolism and their interrelationship as it impacts protein nutrition of camelids.

Protein to support tissue gain will be dependent upon composition and rate of gain, similar to that described for energy. As observed in other species, composition of gain varies with age, sex, genetics and other factors. Younger animals have greater protein accretion and efficiency of gain compared to growing animals nearing maturity. Without data on rates or composition of gain, a more generic model used for goats would be reasonable. In growing kids, 0.284 g of CP is required for every gram of gain (NRC, 1981a). Total growth requirement (maintenance plus growth) results in an average protein to calorie ratio of 45 g CP/Mcal ME, which is reasonably close to the desired ratio. Additional data characterizing composition of gain over the growing period is necessary to make further refinements to this model.

Protein requirement to support pregnancy includes the necessary amino acids needed to support fetal, placental, uterine and mammary development. With the typical fetal growth curve, significant protein needs to support pregnancy most likely occur during the last 3 month of gestation. Although, data are needed to confirm this supposition. Hospinal (1997) suggested a 68% increase in maintenance CP requirement to support pregnancy (2.38 g CP/kg BW^{.75}), equivalent to 5.88 g CP/kg BW^{.75} for maintenance and pregnancy. This is consistent with suggested increase in pregnancy protein requirements for goats from 4.15

to 6.97 g CP/kg BW^{.75} (NRC, 1981a). Using 5.88 g CP/kg BW^{.75} and 138.8 kcal ME/kg BW^{.75} as the pregnancy protein and energy requirement, a calorie to protein ratio 42.4 g CP per 1 Mcal ME was calculated. This is less than desired for camelids and may be of concern given the important role amino acids play in fetal growth and metabolism (Bell, 1995). Neither model predicting camelid pregnancy energy or protein requirements account for changes in fetal growth.

Protein requirements to support pregnancy in horses, beef and dairy cattle, or sheep recognize the exponential fetal growth curve and make appropriate modifications to requirements. Using the proposed energy models to predict pregnancy ME requirements for the last 3 months of gestation, estimated CP requirement was calculated using a defined ratio of 48 g CP per 1 Mcal ME to support pregnancy. Using the proposed energy models (Table 1), ME requirement was predicted for the 8th, 9th and 10th month of gestation for a range of maternal BW from 60 to 160 kg. Within body weight, cria birth weight was varied from 8, 10 and 12% of maternal BW. Predicted gram of CP requirement was then divided by metabolic body size to determine a coefficient. Coefficients were averaged over body weight and birth weight simulations. The final models are presented in Table 1. For these models, the overall averaged coefficient is 5.54 g CP compared to 5.88 g CP/kg BW^{.75}, which is reasonable agreement between models. Predicted CP requirement by month of gestation were 76, 92 and 114% of the single requirement value based on metabolic body weight for the 8th, 9th and 10th months, respectively.

Protein requirement to support lactation is related to level of milk production and true protein content of milk. Milk composition data for camelids is limited. One study using 83 llamas is the best available information on milk composition (Morin et al., 1995). In this study, average milk protein composition was 34(±4) g/kg. Milk protein content was found to vary significantly by farm, suggesting a nutritional influence. Methodology problems were also of concern as the dye-binding assay were 18% less than total nitrogen assay method. A greater percent of total milk nitrogen was found to be in NPN form in llama (19.3) compared to other ruminants (5–7). Although one would want to exclude NPN from determining milk protein requirement, given the paucity of data and methodology limitations, the 34 g/kg was used as a basis to determine

a initial lactational CP requirement. This value should overestimate the true requirement and provide a bit of a safety factor. To convert actual milk protein into a dietary CP requirement, one must account for dietary protein source digestibility and utilization efficiency. Based on sheep data (NRC, 1985), total tract protein digestibility of 85% and biologic value of 66% were assumed, resulting in a lactational dietary CP requirement of 60.6 (46.6–74.6, 95% CI) g CP/kg milk.

Factorially derived protein requirements and associated dietary protein density were compared (Tables 2 and 3). For the pregnant alpaca example, total required CP was 11% greater for Model 2 compared to Model 1 equations. Model 2 used the suggested 31 g CP/Mcal digestible energy for maintenance and pregnancy using the Carmean et al. (1992) and Fowler (1998) equations. Although total CP is greater for Model 2, the calculated protein to energy ratio is lower (35.6 versus 44.4) compared to Model 1. Calculated dietary protein density is of interest as it is quite high for expected lower intakes. However, for the typical expected intake range, the calculated dietary protein density for Model 1 is consistent with North American recommendations. For the llama example, both models are in reasonable agreement, differing only slightly by maintenance protein requirements. The calculated dietary protein concentrations are well within typical recommendations for this age animal.

5.4. Minerals

Minerals are inorganic elements classified into two groups, macrominerals (g/day) or microminerals (mg/day or $\mu\text{g/day}$), based on daily amounts required. Although there are no data defining mineral requirements, there also is no data suggesting that camelids are distinctly different than other ruminants with regard to any specific mineral. Assuming no inherent differences among species, mineral requirements for beef cattle, sheep and goats were used to generate camelid requirements. Mineral requirement equations for goats were limited and only used to qualitatively adjust extrapolated beef cattle and sheep requirements as necessary. Beef cattle (NRC, 1996, pp. 54–74) and sheep (NRC, 1985, pp. 11–22) maintenance macromineral requirements were determined across a wide range of BW by either defined prediction models or calculated by defined dietary concentration times expected dry mat-

ter intake obtained by nutrient requirement tables. Once the daily mineral requirement was determined, amount of mineral required per kg BW was calculated. These values were then averaged across body weights within species and compared. Surprisingly, mineral requirements per kg BW were very similar between beef cattle and sheep, supporting the contention of no differences across species.

The averaged value for beef cattle and sheep was averaged across species, and adjusted as necessary based on published goat mineral requirements (NRC, 1981a), to determine a mineral requirement (mg or $\mu\text{g/kg BW}$) for camelids (Table 4). Again, this assumes no inherent differences in mineral digestion, absorption and utilization across species. Expected range in daily mineral intake was calculated for a 60 and 160 kg BW camelid. The extrapolated requirement was converted to a suggested dietary nutrient density (g/100 g dry matter) by assuming a DMI range between 1.25 and 1.5% of body weight. If mineral requirements differed by physiologic state, a similar mathematical process was completed, but using BW and corresponding DMI for growing, lactating or late pregnant animals. Different models were then defined accordingly. A similar process, using expected dietary concentration and DMI over a range of BW for beef cattle and sheep, was used to determine micromineral required per kg BW and extrapolated into suggested daily micromineral amount and dietary content required by camelids (Table 5).

There was sufficient information to use a factorial approach in calculating calcium (Ca) and phosphorus (P) requirements. For beef cattle and sheep, factorial models were developed to predict net Ca and P requirements for maintenance, growth, lactation and pregnancy. Total dietary amounts to support a given physiologic state were determined using defined bioavailability values for Ca and P by species and physiologic state. Total requirement was used to calculate mg, Ca or P required per kg BW (maintenance), milk (lactation) or fetus (pregnancy). Again, maintenance Ca and P requirements were not significantly different between species when adjusted for bioavailability (30 versus 29 mg/kg BW). Lactational requirements were based on published llama milk composition (Morin et al., 1995) and an assumed bioavailability of 0.55 Ca and 0.7 P, based on beef cattle and sheep data. Fetal requirements were based on beef cattle composition data suggesting 13.7 g Ca and 7.6 g P per kg of fetus.

Table 4

Suggested minimal llama and alpaca macromineral requirements for differing physiologic states, based on beef cattle, sheep and goat data

Mineral	Averaged requirement ^a	Extrapolated requirement			MTL ^e
		Daily intake ^b (g/day)	Diet ^c	Group ^d	
Calcium	30 mg/kg BW	1.8–4.8	0.2–0.24	M	2.0
	145 mg/kg BW		0.53–0.73	G (1–12 mo)	
	60 mg/kg BW	0.30–0.48	G (12–36 mo)		
	0.40 g/kg Fetus	2.4–6.4	0.45–0.56	P	
	3.0 g/kg Milk	2.3–7.5	0.45–0.62	L	
Phosphorus	26 mg/kg BW	1.6–4.2	0.17–0.21	M	1.0
	75 mg/kg BW		0.27–0.38	G (1–12 mo)	
	42 mg/kg BW	0.21–0.28	G (12–36 mo)		
	0.15 g/kg Fetus	0.9–2.4	0.28–0.33	P	
	1.7 g/kg Milk	1.3–4.25	0.32–0.45	L	
Magnesium ^f	19.4 mg/kg BW	1.2–3.1	0.13–0.16	M, G	0.4
	27.3 mg/kg BW	1.6–4.4	0.18–0.22	P, L	
Potassium	92.6 mg/kg BW	5.6–14.8	0.6–0.7	M, G, P	3.0
	121 mg/kg BW	7.3–19.4	0.8–0.96	L	
Sodium	10.5 mg/kg BW	0.6–1.7	0.07–0.08	M, G, P	2.0
	17.5 mg/kg BW	1.1–2.8	0.12–0.14	L	
Sulfur	28.5 mg/kg BW	1.7–4.6	0.19–0.23	M, G, P, L	0.4

^a Extrapolated from nutrient requirements for beef cattle (NRC, 1996), sheep (NRC, 1985) and goats (NRC, 1981a).

^b Estimated daily requirement based on a range of adult body weights from 60 to 160 kg. Calcium and phosphorus pregnancy and lactation intake requirements based on a range of 6–16 kg fetal weight and 0.75–2.5 kg milk production, respectively. Values are in addition to maintenance for total requirement.

^c Dietary concentration (g/100 g) on dry matter (DM) basis for total requirement. Nutrient density calculations based on an assumed range of DM intake between 1.25 and 1.5% of body weight (maintenance and pregnancy) and 2.0 and 2.75% of body weight (lactation).

^d Physiologic states of maintenance (M), growth (G), lactation (L) and pregnancy (P) for which the requirement is defined.

^e Maximum tolerable level (g/100 g), defined as largest dietary concentration of a given mineral that could be fed for short periods (3 month) without problems. Based on data from NRC (1980).

^f May need to be increased (0.25–0.35%) if forages containing high amounts of potassium (>1.5%) are being fed.

Fetal mass was assumed to range from 6 to 16 kg and the required amount is averaged over the last 70 days of gestation. Predicted fetal requirements shown in Table 4 are added to maintenance to determine total pregnancy requirements. The dietary nutrient content range shown is for the total pregnancy plus maintenance requirement. The lactation requirement is used in the same manner.

Developing models to predict Ca and P requirements to support growth was more difficult. There are tremendous differences between beef cattle and sheep in body size and growth rate. Using tabular data within species, BW, average daily gain (g/day) and predicted Ca and P (g/day) requirement were obtained. Required Ca and P (mg/kg BW) over a range of BW and daily gains were calculated. This value varied greatly, from over 200 to less than 30 mg/kg BW. Apparently, a single

prediction model would not be very useful. To reduce inherent variation, gain was calculated as a percent of BW and ranked within species, including llamas and alpacas. In reviewing the calculated values, a decision was made to split the data into two groups: >0.19% BW gain and <0.2% BW gain. There was a marked difference in Ca and P requirements between these defined groups. Based on the developed camelid growth models, this division separated camelids in terms of growth models at 12 months of age. Models to predict total Ca and P requirements to support maintenance and growth are divided into 1–12 and 13–36 months prediction models (Table 4). With more growth composition data, these models can be further refined. The recommended dietary mineral content shown in Tables 4 and 5 are slightly different from previous recommendations (Van Saun, 2003). In the previous attempt to character-

Table 5

Suggested minimal llama and alpaca micromineral requirements for differing physiologic states, based on data derived from beef cattle, sheep and goats

Nutrient	Averaged requirement ^a	Extrapolated requirement			MTL ^e
		Daily intake ^b (mg/day)	Diet ^c	Group ^d	
Cobalt	1.76 µg/kg BW	0.11–0.28	0.12–0.14	M, G, P, L	10
Copper	0.15 mg/kg BW	9–24	9–12	M, G, P, L	30
Iodine	9.5 µg/kg BW	0.57–1.5	0.6–0.76	M, G	50
	16 µg/kg BW	0.96–2.6	1.1–1.3	P, L	
Iron	0.7 mg/kg BW	42–1120	47–56	M	500
	0.9 mg/kg BW	54–144	60–72	G, P, L	
Manganese	0.36 mg/kg BW	21.6–57.6	24–29	M, G	1000
	0.8 mg/kg BW	48–128	53–64	P, L	
Selenium	5.3 µg/kg BW	0.3–0.85	0.35–0.42	M, G	5
	6.0 µg/kg BW	0.36–0.96	0.4–0.48	P, L	
Zinc	0.53 mg/kg BW	31.8–84.8	35–45	M, G	500
	0.67 mg/kg BW	40.2–107	45–54	P, L	

^a Extrapolated from nutrient requirements for beef cattle (NRC, 1996), sheep (NRC, 1985) and goats (NRC, 1981a).

^b Estimated daily requirement based on a range of adult body weights from 60 to 160 kg.

^c Dietary concentration (mg/kg) on dry matter (DM) basis. Nutrient density calculations based on an assumed range of DM intake between 1.25 and 1.5% of body weight.

^d Physiologic states of maintenance (M), growth (G), lactation (L) and pregnancy (P) for which the requirement is defined.

^e Maximum tolerable level (mg/kg), defined as largest dietary concentration of a given mineral that could be fed for short periods (3 month) without problems. Based on data from NRC, 1980.

ize camelid mineral requirements, suggested dietary macromineral densities for beef cattle and sheep were used as a basis to correct for differences in DMI compared to camelids. The current methodology systematically accounts for mineral required per kg BW and should provide a more accurate method of describing the requirement.

These extrapolated nutrient recommendations can be used as a starting point for minimum suggested nutrient requirements and concentrations in formulating diets. These values need to be tested and validated. Herdt (1995) evaluated selenium (Se) status of llamas and showed pregnant and lactating llamas had improved blood Se status when fed >1 mg Se per day. However, llamas receiving lower Se intake were able to maintain reasonably normal blood Se concentrations. This value is consistent with the minimal value predicted (0.96 mg/day) with the Se model for pregnant and lactating camelids. Further refinement of these prediction models can be made with mineral bioavailability determinations specifically for the llama and alpaca. Given the inherent differences in fermentation

efficiency and rate of passage between camelids and ruminants, one might expect some differences in mineral availability.

5.5. Vitamins

Vitamins are organic compounds that function as co-factors in nearly all metabolic processes and cannot be endogenously synthesized sufficiently to meet daily requirements. Vitamins are generally classified by their solubility in either lipid or water. Vitamin requirements are also not well understood for camelids. As with other ruminants, it is hypothesized that all necessary B-vitamins (water-soluble) are synthesized by bacteria in the forestomach, and therefore, are not required in the diet. However, under certain stress conditions or fermentation disorders, B-vitamin supplementation may be beneficial.

Fat-soluble vitamins, namely Vitamins A, D and E, are the most important for camelids and should be supplemented in the diet. Vitamins A and E will be adequately ingested if llamas and alpacas are grazing fresh

Table 6

Suggested minimal llama and alpaca Vitamins A, D and E requirements for differing physiologic states, based on data derived from beef cattle and sheep

Nutrient	Averaged requirement ^a (IU/kg BW)	Extrapolated requirement		
		Intake ^b (IU/day)	Diet content ^c (IU/kg)	Group ^d
Vitamin A	45	2700–7200	3000–3600	M, G
	70	4200–11200	4700–5600	P
	88	5280–14080	3500–5900	L
Vitamin D	6 ^e	360–960	400–480	M, G, P, L
	30 ^f	1800–4800	2000–2400	M, G, P, L
Vitamin E	0.28	16.8–44.8	18.7–22.4	M
	1.1	66–176	73.3–88	G, P, L

^a Extrapolated from nutrient requirements for beef cattle (NRC, 1996) and sheep (NRC, 1985).

^b Estimated daily requirement based on a range of adult body weights from 60 to 160 kg.

^c Dietary concentration on dry matter (DM) basis. Nutrient density calculations based on an assumed range of DM intake between 1.25 and 1.5% of body weight.

^d Physiologic states of maintenance (M), growth (G), lactation (L) and pregnancy (P) for which the requirement is defined.

^e These values may maintain minimal serum Vitamin D concentrations and may not prevent Vitamin D rickets.

^f Adjusted Vitamin D requirement, based on preliminary data suggesting a higher Vitamin D requirement of 25–30 IU/kg BW. Extrapolated requirements reflect this higher requirement for camelids.

pasture as a result of the high content of carotenoid and tocopherols in green plants. However, when fed stored, sun-cured hay, Vitamins A and E may be insufficient (Herd, 1995; Dart et al., 1996; Smith et al., 1998). In contrast, Vitamin D is very low in pasture but, is higher in sun-cured forages although possibly not high enough to meet needs without supplementation (Smith and Wright, 1981, 1984). Vitamin D deficiency has been implicated in a hypophosphatemic rickets syndrome of young growing crias (Hill et al., 1994; Van Saun et al., 1996; Judson and Feakes, 1999).

A similar mathematical extrapolation process was completed to generate suggested fat-soluble vitamin requirements for camelids (Table 6). Similar to predicted mineral requirements, dietary vitamin concentrations are slightly higher for camelids to account for lower dry matter intake. Vitamin A requirement models were established for maintenance and growth, pregnancy and lactation, based on data from both beef cattle and sheep suggesting increasing requirement for differing physiologic states. One IU of Vitamin A activity is defined as 0.300 µg all *trans*-retinol.

One unique feature of llamas and alpacas seems to present with Vitamin D. A requirement based on beef cattle and sheep data was calculated. Preliminary research on oral Vitamin D supplementation has shown that minimal serum Vitamin D concentrations can be maintained by suggested requirements based on other

species, but dietary supplementation at higher levels may be necessary to minimize potential problems with Vitamin D-responsive rickets (Smith and Van Saun, 1996; Van Saun, unpublished data). Based on these preliminary data, a second model was developed. One IU of Vitamin D activity was defined as 0.025 µg cholecalciferol.

Vitamin E requirements for cattle and sheep are not well defined. The interaction with dietary Se is an important modifier of Vitamin E requirement. Vitamin E requirements for beef cattle were defined between 15 and 60 IU/kg dry matter. For sheep, Vitamin E requirements were defined between 15 and 20 IU/kg dry matter. One IU of Vitamin A is defined as 1 mg D,L- α -tocopheryl acetate. Two models for Vitamin E requirements were developed, based on the 15 and 60 IU/kg dry matter. These were converted to IU/kg BW and extrapolated to camelid intake and dietary concentration needs. The lower model might be used for animals on pasture, whereas the second model might be applied for hay feeding systems to ensure adequate intake.

5.6. Fiber

Fiber is not a specifically required nutrient relative to the llama or alpaca. Without the forestomach fermentation system, the animal is incapable of extracting any nutrients from dietary fiber. However, fiber is an

essential nutrient substrate for forestomach microbial populations. Dietary fiber is classically defined as any carbohydrate compound that cannot be broken down by animal digestive enzymes (Van Soest, 1994, pp. 140–155). However, all carbohydrates, excluding sugars and starches, are considered dietary fiber by this definition. Difficulties arise in being able to analyze total dietary fiber on a practical basis. Traditionally, crude fiber has been used to quantify the fiber portion of the diet. However, crude fiber is inadequate in truly characterizing the total cell wall portion of a feed (Van Soest, 1994, pp. 140–155). A better methodology to quantify total cell wall content and less fermentable fiber is neutral (NDF) and acid detergent (ADF) fiber methods (Goering and Van Soest, 1970).

Current recommendations would suggest a minimum of 25% crude fiber in the diet (Johnson, 1989, 1994). Fiber consumption limits DMI intake in ruminants, the same would be expected of camelids. Mertens (1987) has suggested an optimum NDF intake of 1.2% BW to support productive functions and meet ruminal fiber needs. Minimum NDF requirement is dependent upon effectiveness of fiber (degree of lignification) and particle size. A higher value might be expected for camelids given their greater efficiency to ferment dietary fiber. A suggested minimum dietary fiber content for camelid diets would be 21–25% ADF and 30–35% NDF, until more information is available.

6. Modifiers of nutrient requirements

Similar to recommendations made by the NRC for nutrient requirements of various animal species, extrapolated requirements for camelids discussed, thus far have assumed an isothermic environment. This means the environmental temperature is within a range in which the animal does not need to expend additional energy to either generate more heat to keep warm (cold stress) or reduce heat production to keep cool (heat stress). Upper and lower environmental temperatures where an animal does not need to expend additional energy to regulate body temperature is called the thermoneutral zone (NRC, 1981b). Ruminant animals generally have a lower thermoneutral zone compared to humans as a result of the heat generated by forestomach fermentation activity. This gives ruminant animals an advantage in surviving in cold environ-

ments, which is a great advantage to llamas and alpacas in their native environment. Alpacas exposed to cold temperatures over time will require additional dietary energy to maintain body temperature. This is even more important in crias as they have greater surface area to body mass and lose more heat to the environment. Camelids are very sensitive to heat stress and reduce DMI, thus requiring some adjustment to nutrient content to meet daily requirements (Johnson, 1994; Fowler, 1998). Heat stress was attributed to an outbreak of hepatic lipidosis in a group of lactating llamas (Van Saun et al., 2000).

Besides environmental temperature, humidity and wind speed can impact animal energy requirements (NRC, 1981b). Animal insulation factors such as skin thickness, length of fleece and coat condition (dry, wet, muddy, etc.), can lead to either increased to decreased conduction and convection heat losses to the environment (NRC, 1981b). Environmental temperature, wind speed and animal insulation factors are all additive. Models predicting cattle energy requirements in varying environmental conditions show upwards to a 75% increase in maintenance when an animal is exposed to cold, windy conditions and their hair coat is wet or muddy (NRC, 1981b, 1996). This has implications for crias in winter months and emphasizes how important it is to keep them dry and out of prevailing winds. There are no data to develop environmental factors as modifiers of camelid requirements, but they need to be considered in practical feeding situations.

7. Conclusions

Tremendous gaps exist in our knowledge of llama and alpaca nutrient requirements. Since the comprehensive review of llama and alpaca nutrition by San Martin and Bryant (1989), very little specific requirement studies have been completed. Limited studies have characterized protein and energy requirements. Within available energy data, there is not good agreement between studies. No studies were identified characterizing differences in nutrient requirements based on physiologic state. In spite of the paucity of information, a factorial approach to quantify nutritional requirements of llamas and alpacas has been described. Published summaries of beef cattle, sheep and goat nutrient requirements were used as a template to

develop camelid requirement models. Model development was based on determining nutrient requirement on a BW basis and converted to a nutrient density basis using the observed lower DMI per unit BW for camelids. Consequently, most recommended nutrient densities were greater than those recommended for beef cattle and sheep. Metabolic differences between camelids and ruminant animals in regard to urea and glucose metabolism were described and incorporated into requirement models by increasing protein to calorie ratio above what is defined for other ruminants.

Underlying all prediction models was the assumption of no inherent metabolic differences between nutrient requirement among species. In reviewing beef cattle and sheep data, there were surprisingly minimal differences in nutrient requirements when expressed on a amount per BW basis. It was then assumed the same relationship held for camelids. There were no data to contradict this assumption, with the exception of Vitamin D, based on some preliminary data. However, there also are no scientific data to support this assumption. Observational data and current feeding recommendations, as described by desired nutrient densities, are in agreement with predicted requirements, suggesting some validity to the models. This modeling process moves the application of camelid nutrition forward, but also defines tremendous needs in nutritional research. Clearly, these prediction models need to be critically tested and further refined. Much more research is needed to define fetal and neonatal growth patterns and composition, lactational production dynamics and mineral bioavailability.

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