Available online at www.sciencedirect.com

ScienceDirect

Theriogenology 70 (2008) 508–514

Theriogenology

www.theriojournal.com

# Effect of nutrition on reproduction in llamas and alpacas

R.J. Van Saun *

*Department of Veterinary & Biomedical Sciences, Pennsylvania State University, 115 Henning Building, University Park, PA 16802-3500, USA*

**Abstract**

The role of nutrition, especially the role of energy and protein status, on reproductive performance of production animals has been well documented. Comparatively, there is a true paucity of literature regarding nutritional mediation of reproductive performance in llamas and alpacas. Following seasonal patterns of feed availability in South America, adverse effects of nutritional deprivation on reproductive performance are well recognized, suggesting similar nutrition–reproduction interrelationships. Camelids, with their unique metabolism, may have some peculiar interrelationships between reproduction and protein and phosphorus nutrition. This presentation will review basic issues of energy and protein nutrition relative to reproductive performance in llamas and alpacas, based primarily on hypotheses and extrapolation from other species. Opportunities for research on this topic will be discussed, including preliminary data from current research.


*Keywords:* Energy balance; Nutrition; Reproduction; Llamas; Alpacas

## 1. Introduction

South American camelids (SAC), primarily the llama (*Lama glama*) and alpaca (*Lama pacos*), are being presented with greater frequency to veterinarians for infertility evaluations. Like most other species, infertility is a frustrating and important problem for both producer and veterinarian. The reproductive tract of SAC was seemingly designed by a committee, having anatomic and physiologic characteristics in common with multiple species [1]. Like most other domestic species, causes of infertility may be divided into four broad, non-exclusive categories: (1) anatomic abnormalities, (2) physiologic conditions, (3) infectious agents, and (4) management factors. Clinical research data defining precise causes of infertility in SAC are limited [2], though they seemingly have a higher prevalence of congenital anatomic defects and uterine infections of varying severity [2–7].

Nutrition is one of the most important and controllable management factors influencing reproduction [8]. Various interactions between nutrition and reproduction have been the subject of numerous reviews in the beef [9,10] and dairy cattle literature [11–14]. Volumes of research studies have shown the critical nature of energy [15–18] and protein [19–21] status, either prior to or following parturition, on reproductive performance. Beyond energy, protein, and their interaction, dietary status of many minerals and vitamins also influences reproductive performance [22–24]. Nutrition not only has a direct effect on reproductive performance, but it can also increase metabolic and infectious disease susceptibility, due to aberrant physiologic and immunologic alterations near the time of parturition [25]. Consequently, nutrition adversely affects reproductive performance indirectly through its

* Tel.: +1 814 865 6995; fax: +1 814 863 6140.
*E-mail address:* rjv10@psu.edu.

0093-691X/$ – see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.theriogenology.2008.04.025

mediation of periparturient disease prevalence [12,26–29].

Relative to other species, there is a paucity of published information documenting nutritional mechanisms on reproductive performance in llamas and alpacas. However, most authors addressing reproductive problems in llamas and alpacas suggest or hypothesize a critical role for nutrition, consistent with associations in other species [2–4,7,30]. This presentation will review known mechanisms (using dairy cattle as a model and extrapolate concepts to those appropriate for SAC) as well as hypothesized mechanisms of nutritional influences on reproductive performance in llamas and alpacas. Potential opportunities for further research and current studies in progress will be highlighted.

## 2. Nutrition and the fertility cycle

Reproductive performance is the culmination of many complex and integrated anatomic, developmental, physiologic, and behavioral processes (Fig. 1). When one truly envisions what must occur for successful, let alone efficient reproduction, one often wonders how it is achieved. The concept of homeorrhesis [31] suggests reproduction has lower priority compared to other physiologic states of maintenance, lactation, and growth when available nutritional resources are limiting. Consequently, there is apparently a strong underpinning between nutritive status and reproductive performance. Nutritional deficiencies or excesses may impede anatomical development (puberty, embryonic or fetal growth), hormone production (cyclicity, pregnancy maintenance), alter immune response (disease conditions, fetal and neonatal viability), or directly affect reproductive function (folliculogenesis, ovulation, CL function).

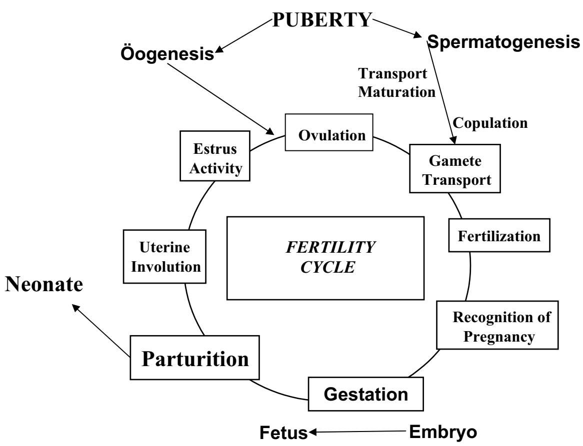


Fig. 1. Diagram of the overall fertility cycle, initiated with puberty and gaining the ability to reproduce through the sequences of physiologic processes that produce viable offspring and reinitiate reproductive cyclicity.

Camelids are equally fertile compared to other domestic species, with 90% of females typically conceiving within three mating attempts [32]. However, reproductive performance, as defined by pregnancy or birth rates, can range widely from <50% to 90%, depending upon many factors, including nutrition [32]. Common reproductive problems and their estimated prevalence in female camelids have been categorically summarized as repeat breeding (75.6%), early pregnancy loss (18.3%), anatomic defects (4.9%), and behavioral concerns (2.4%) [32,33]. Uterine infections are the most commonly diagnosed problem and probably contribute to observed repeat breeding and early pregnancy losses [7,33,34]. Early embryonic death is also common in camelids, with a prevalence from 50% (through 30 d) to 58.7% (through 45 d), though more recent prevalence data were lower (35% through 45 d) [7,35,36]. Fetal losses (>100 d gestation) have been estimated to occur in 2–15% of all pregnancies [33], although there are reports of losses as high as 25% [37]. Although camelids can be highly fertile, the observed wide range in disease rates and higher inherent prevalence of uterine infections and embryonic death suggest a strong nutritional component to the pathogenesis of reproductive disease. The potential role of various nutritional entities as a component in reproductive disease in camelids will be further explored. Extrapolation from documented nutritional relationships in dairy cattle will be the template for forming hypothetical mechanisms in camelids, setting the stage for further study and providing starting guidelines for preventive programs.

## 3. Energy and role of body condition

Energy status has been the most intensively studied nutritional entity relative to reproductive performance. Both extremes of energy status, recognized as thin or obese body condition, adversely affect the fertility cycle, from puberty to postpartum cyclicity.

### 3.1. Energy status scenarios

An extensive pastoral feeding system based on native forages is the traditional South American management approach [38–40]. No supplements and rarely conserved hay are fed, due to associated costs, availability, or traditional practices [39]. Available

Andean grassland ecosystems, i.e., altiplano, pajonales, and bofedale, are traditionally used for pasture. The Andean high plains (puna) are located at elevations exceeding 4000 m (>13,000 feet) and are characterized by cool temperatures, intense solar radiation, and seasonally intermittent rainfall [38–40]. Annual rainfall in this region ranges from 10 to 100 cm (3.9 and 39.4 in.), 80% of which comes between December and April, establishing a defined wet and dry seasonal pattern [38–40].

Seasonal growth and forage quality, and consequently animal energy status, are determined by this precipitation pattern. Plant growth is rapid and of high-quality during the wet season, but this period is only 3–4 mo in duration. In contrast, growing conditions for a majority of the year are associated with minimal precipitation and sparse plant growth. Forage availability is extremely limited during the dry season; the forage is very mature and of low-quality [39,40]. Their capacity for selective feeding and ability to utilize lower-quality forages more efficiently allow llamas and alpacas to survive and flourish under such seemingly harsh conditions. Body weight and condition score changes mimic seasonal forage growth patterns.

In contrast to the South American situation, North American llamas and alpacas can potentially receive high- or low-quality forages throughout the year, with availability only constrained by sporadic regional drought conditions. Consequently, energy balance problems range the full spectrum from potential malnutrition to obesity, with a trend toward a greater incidence of obesity [41].

### 3.2. Negative energy balance effects

Adverse effects of negative energy balance (NEB) on various components of reproduction have been well characterized in dairy cattle. Cows with severe NEB in early lactation, evidenced by excessive body condition score losses (>1 score), had longer intervals to first estrus and ovulation, lower conception risk, and lower blood progesterone concentrations [11,12,15–17]. A follicular memory hypothesis has been proposed to explain how nutritional insults during the peripartum period may adversely affect the hormonal milieu controlling maturation and ovulation of the growing follicle, ultimately resulting in impaired oocyte viability (conception failure, embryonic loss) and CL function (reduced progesterone secretion) [42]. Proposed mediators between nutritive status and reproductive regulation include insulin, IGF-1, leptin, ghrelin, and myostatin [12,14]. Energy or generalized nutritional deprivation during early development will delay puberty. Postpartum NEB has also alters immune cell function, thus increasing infectious uterine disease susceptibility and secondarily impeding reproductive performance [13,28].

Although camelids are not considered seasonal breeders [32], breeding management practices in South America are directed toward a seasonal breeding pattern to match forage availability in an effort to maximize reproductive efficiency. Llamas and alpacas will gain substantial body weight and condition and will give birth during the wet season, coincident with availability of high-quality forages. During the dry season, animals lose considerable weight and body condition, reflecting varying degrees of NEB [38,39]. Survivability and productivity will depend upon body reserves from the previous wet season. As a consequence of this ‘‘feast and famine’’ seasonal cycle, reproductive rates are low (40–60%), suckling crias have high mortality rates (30%), and growing animals have low body weight gains [38,39]. Time to puberty is also reflected by forage availability and time of birth relative to the wet season [30]. As with other species, puberty is attainable when body weight reaches 60–65% of mature weight.

Observations of impaired reproductive efficiency in concert with NEB-associated body condition loss in llamas and alpacas are consistent with those documented in other species. Presumably similar mechanisms are in place, although physiologic differences in glucose metabolism and postpartum breeding practices are unique to camelids compared to dairy cattle. Similar to horses, llamas and alpacas are rebred within 30 d after parturition, in an effort to produce a cria yearly. However, conception risk is lower (21.4%) when postpartum breeding occurs at 10 d compared to 20 or 30 d (77.5–84.6%) [30]. Adverse effects of a contaminated uterine environment on sperm or embryo may reduce fertility. Llamas and alpacas do not experience the severe lactational energy drain similar to dairy cattle, but may be sufficient to compromise uterine immunologic defense mechanisms and exacerbate infectious conditions. Given the high prevalence of uterine disease in camelids, further investigation into nutritional mediation of immune response in the postpartum period is warranted.

According to the follicular memory hypothesis [42], NEB immediately postpartum adversely affects growing follicles destined to potentially mature and ovulate 40–60 d postpartum. This timing is not aligned with breeding practices of llamas and alpacas, thus calling into question the role of NEB on postpartum fertility. Of greater concern with early postpartum breeding practices is nutritional status during late pregnancy.

Nutritional support of the gravid uterus has a high priority [31], resulting in maternal tissues being harvested as a nutrient source to support fetal development in the face of dietary insufficiency [43,44]. Prolonged NEB during late pregnancy could adversely affect growing follicles destined to be ovulated postpartum. A collaborative project among the author and other investigators is currently underway in Peru that is evaluating nutritional and metabolic status of alpacas from late pregnancy through lactation, to assess impacts on reproductive and lactational performance. Similar to other species, NEB is an important nutritional mediator of reproductive performance in llamas and alpacas, although exact mechanisms remain to be elucidated.

### *3.3. Excessive body condition effects*

In contrast to the South American situation, obesity associated with excessive energy intake is of greater concern in North American camelid management systems [45]. Obese females may be more prone to dystocia, which could decrease neonate viability and reduce the efficiency of colostrum absorption. Furthermore, obese pregnant or lactating females are more susceptible to hepatic lipidosis [46].

Although NEB is most frequently associated with aberrant hormonal profiles and follicle or CL dysfunction, clinical observations suggest it reduces blood progesterone concentrations, perhaps due to increased hepatic clearance, in over-conditioned camelids (Tibary A., personal communication). Lower progesterone concentrations might contribute to early embryonic loss and repeat breeding infertility in females with high body condition. This intriguing relationship is currently being investigated by the group at Washington State University.

## 4. Protein nutrition and uterine disease—a critical flaw?

Camelid protein nutrition is somewhat of an enigma. First, perceptions suggest they have a low protein requirement; however, careful evaluation of energy and protein requirements shows a higher requirement on a caloric basis [47]. Another unresolved issue with camelids is the normally higher concentration of blood urea nitrogen (BUN) in their blood compared to other ruminants [48,49]. In ruminants, BUN concentration reflects protein level of the diet. Low protein diets result in low BUN, whereas high BUN is associated with high protein diets or excessive protein breakdown. Higher BUN concentrations in camelids suggest 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 [47]. Results from a llama urea metabolism study suggested llamas have a lower rate of urea turnover, and kidney urea excretion rate compared to other ruminants [50]. It has been hypothesized that camelids metabolize amino acids to support their blood glucose status, thus accounting for higher BUN concentrations, and suggesting a higher than perceived protein requirement [47].

In dairy cattle reproduction, elevated BUN concentrations has been negatively associated with reduced conception rates and increased early embryonic death [11,19,20]. Current theories suggest a negative effect of ammonia directly on embryonic development [51] or an alteration of uterine environment by the cleavage of urea [52]. These observations may help to explain the higher prevalence of early embryonic death and repeat breeding in camelids. Higher BUN concentration can also exacerbate NEB, as energy is required to generate urea in excreting excess nitrogen [13]. Other data would also suggest a greater prevalence of uterine infections associated with higher BUN concentrations (Van Saun R., unpublished data). This effect may result from the altered NEB status on immune response, or a direct effect of urea promoting bacterial growth conditions in the uterine lumen. Given these potential issues, camelids may be inherently more susceptible to uterine infections as a result of their physiologic adaptations for higher BUN concentrations. Feeding higher protein diets will also increase BUN concentrations and may further contribute to the problem. Clearly more information is needed on protein requirements of camelids and potential effects on uterine environment.

## 5. Minerals and vitamins

Reproductive consequences of mineral and vitamin nutritive status are primarily mediated secondarily through increased susceptibility to periparturient metabolic or infectious diseases. Parturition is a stressful event; recent information in dairy cattle suggests a dramatic decline in immune function around the time of calving [25]. One would expect this to occur in other species, including camelids. Selected trace minerals, namely copper, selenium, and zinc, as well as fat-soluble vitamins A and E, are key nutrients supporting immune function of the dam and neonate. Deficiencies in these minerals and vitamins may also play a role in reproductive losses due to pregnancy wastage and perinatal mortality.

### 5.1. Phosphorus

Historically, phosphorus deficiency has been linked to reproductive inefficiency, primarily anestrus [53]. This implication had led to routine excessive dietary phosphorus supplementation in the dairy industry, which has ultimately led to environmental pollution concerns. Recent research has not shown improved reproductive performance with phosphorus supplementation in diets of high-producing dairy cattle [54]. Clinical observations in llamas and alpacas suggest a role of low phosphorus in the ability to ovulate (Tibary A., personal communication).

Phosphorus metabolism in ruminants and especially camelids is unique. Blood phosphorus is recycled to the rumen through saliva. This physiologic mechanism is thought to provide needed phosphorus to rumen microbes, as phosphorus is a critically limiting mineral for grazing animals. In camelids, seasonal changes in blood phosphorus concentrations are associated with vitamin D status; concentrations were lowest during the winter months [55]. A clinical hypophosphatemic rickets condition occurs in growing crias during the winter months, due to vitamin D deficiency [56].

Metabolism of calcium and phosphorus are intertwined with vitamin D. There is a dynamic balance among dietary ingestion and absorption of calcium and phosphorus from the intestines, resorption or deposition in the bone, recycling of phosphorus via the saliva, and elimination of calcium and phosphorus via the urine, feces and milk. Vitamin D is of central importance in calcium and phosphorus metabolism, with a direct effect on the rate of intestinal absorption, bone deposition, and urinary loss. Of particular importance is the role of vitamin D in stimulating intestinal absorption and decreasing urinary losses of calcium and phosphorus. Without sufficient vitamin D activity, intestinal absorption efficiency of dietary phosphorus is greatly diminished. Reduced intestinal absorption of phosphorus resulting from vitamin D inadequacy would potentially result in greater losses of endogenous phosphorus from salivary recycling. This situation, coupled with low dietary intake of phosphorus, could potentially lead to a hypophosphatemic condition. Further research on the potential role of phosphorus in camelid nutrition is in progress.

### 5.2. Trace minerals

Trace minerals, copper, selenium, and zinc, have been implicated in reproductive function primarily as mediators of the immune response, but also play important roles in conceptus viability, growth, development, and survival [57]. The developing conceptus is completely dependent upon the dam for provision of essential nutrients, including minerals. Most minerals are efficiently transferred across the placenta and stored in the fetal liver at concentrations exceeding maternal concentrations [58,59]. A similar relationship has been observed in camelid fetuses (Van Saun R., unpublished data). These fetal liver reserves are utilized by the neonate in support of metabolic and immunologic functions, as a milk-based diet is typically low in most trace minerals.

In cattle, moderate to severely deficiencies of most trace minerals are associated with early embryonic and fetal developmental abnormalities and possibly death [57]. A similar relationship would be expected in camelids. Selenium deficiency has been implicated in the ability to ovulate in llamas and alpacas (Tibary A., personal communication). Selenium also plays a role in iodine metabolism, through its role in a deiodinase enzyme that converts thyroxin to the biologically active triiodothyronine. Therefore, selenium deficiency could induce hypothyroidism, with adverse effects on many aspects of reproductive performance. These observations emphasize the critical role of mineral supplementation during late pregnancy to ensure good reproductive performance. More research on the role of trace minerals in reproductive performance and improvement of diagnostic capabilities is needed.

### 5.3. Vitamins

Similar to the trace minerals, fat-soluble vitamins A and E are important mediators of the immune response and may play a role in reproductive performance indirectly through this modality. In contrast to the situation with microminerals, fat-soluble vitamins like vitamins A and E do not appreciably cross the placenta, resulting in no gestational liver reserve [60,61]. The neonate's primary source of vitamins A and E comes via colostrum ingestion supplied from an adequately supplemented dam [61]. There are mechanisms for placental transport of fat-soluble vitamins [61], most likely to ensure sufficient amounts to meet fetal metabolic needs. Deficiencies of vitamins A and E may have a role in early embryonic death, although this has not been documented [7]. Vitamin nutrition is clearly another area requiring further research relative to possible roles in reproduction.

## 6. Summary

Nutrition has been substantially studied relative to its role in controlling reproductive performance of production animals. The role of energy balance and body condition on all aspects of the reproductive cycle has been well characterized, though underlying mechanisms remain to be elucidated. Although studies are not in complete agreement, protein effects on reproduction have also been defined. Beyond clinical impressions and anecdotal observations, there is a true void of controlled studies addressing nutrition-reproductive relationships in camelids. Apparently, camelids respond in a similar fashion to other species, based on reproductive performance in South America, where pastorally raised camelids experience large swings in energy status. Unique metabolic and reproductive differences compared to other ruminants were described for camelids that may explain their greater prevalence of reproductive failure due to embryonic loss and uterine infections. Potential concerns relative to the historic issue of phosphorus status and reproduction were highlighted. Research addressing a number of these issues is currently underway, but clearly there are many areas of nutritive status of llamas and alpacas that need to be explored relative to their impact on reproductive efficiency.

## References


[1] Sumar JB, Adams GP. Reproductive anatomy and physiology of the female llama. In: Youngquist RS, editor. Current therapy in large animal theriogenology. WB Saunders; 1997. p. 792–8.

[2] Peter AT, Smith CL. Infertility in the female llama. In: Youngquist RS, editor. Current therapy in large animal theriogenology. WB Saunders; 1997. p. 827–31.

[3] Tibary A, Anouassi A. Theriogenology in camelidae. United Arab Emirates: Abu Dhabi Printing and Publishing Co.; 1997.

[4] Johnson LW. Llama reproduction, vol. 5. Vet Clinics NA: Food Animal Practice; 1989. p. 159–182.

[5] Fowler ME. Medicine and surgery of South American camelids, 2nd ed., Ames, IA: Iowa State University Press; 1998.

[6] Greene GM. Examination of the female reproductive tract. In: Youngquist RS, editor. Current therapy in large animal theriogenology. WB Saunders; 1997. p. 799–807.

[7] Tibary A. Breeding soundness evaluation and subfertility in female llamas and alpacas. In: Youngquist R, Threlfall W, editors. Current therapy in large animal theriogenology. 2nd ed., St. Louis, MO: Saunders/Elsevier; 2007. p. 878–83.

[8] Senger PL. Review: fertility factors in high producing dairy cows-which ones are really important? Prof Anim Scientist 2001;17:129–38.

[9] Short RE, Adams DC. Nutritional and hormonal interrelationships in beef cattle reproduction. Can J Anim Sci 1988;68:29–39.

[10] Dunn TG, Kaltenbach CC. Nutrition and the postpartum interval of the ewe, sow and cow. J Anim Sci 1980;51(Suppl. 2):29–39.

[11] Butler WR. Nutritional interactions with reproductive performance in dairy cattle. Anim Reprod Sci 2000;60–61:449–57.

[12] Ferguson JD. Nutrition and reproduction in dairy cows, 21. Vet Clinics NA: Food Anim Pract; 2005. p. 325–347.

[13] Roche JF. The effect of nutritional management of the dairy cow on reproductive efficiency. Anim Reprod Sci 2006;96:282–96.

[14] Chagas LM, Bass JJ, Blache D, Burke CR, Kay JK, Lindsay DR, et al. Invited review: new perspectives on the roles of nutrition and metabolic priorities in the subfertility of high-producing dairy cows. J Dairy Sci 2007;90:4022–32.

[15] Beam SW, Butler WR. Energy balance, metabolic hormones, and early postpartum follicular development in dairy cows fed prilled lipid. J Dairy Sci 1998;81:121–31.

[16] Butler WR, Smith RD. Interrelationships between energy balance and postpartum reproductive function in dairy cattle. J Dairy Sci 1989;72:767–83.

[17] de Vries MJ, Veerkamp RF. Energy balance of dairy cattle in relation to milk production variable and fertility. J Dairy Sci 2000;83:62–9.

[18] Pushpakumara PGA, Gardner NH, Reynolds CK, Beever DE, Wathes DC. Relationships between transition period diet, metabolic parameters and fertility in lactating dairy cattle. Theriogenology 2003;60:1165–85.

[19] Butler WR. Review: effect of protein nutrition on ovarian and uterine physiology in dairy cattle. J Dairy Sci 1998;81:2533–9.

[20] Ferguson JD, Chalupa W. Impact of protein nutrition on reproduction in dairy cows. J Dairy Sci 1989;72:746–66.

[21] Tamminga S. The effect of the supply of rumen degradable protein and metabolisable protein on negative energy balance and fertility in dairy cows. Anim Reprod Sci 2006;96:227–39.

[22] Hurley WL, Doane RM. Recent developments in the roles of vitamins and minerals in reproduction. J Dairy Sci 1989;72: 784–804.

[23] Smith OB, Akinbamijo OO. Micronutrients and reproduction in farm animals. Anim Reprod Sci 2000;60–61:549–60.

[24] Wilde D. Influence of macro and micro minerals in the periparturient period on fertility in dairy cattle. Anim Reprod Sci 2006;96:240–9.

[25] Goff JP, Horst RL. Physiological changes at parturition and their relationship to metabolic disorders. J Dairy Sci 1997;80:1260–8.

[26] Barker AR, Schrick FN, Lewis MJ, Dowlen HH, Oliver SP. Influence of clinical mastitis during early lactation on reproductive performance of Jersey cows. J Dairy Sci 1998;81:1285–90.

[27] Walsh RB, Walton JS, Kelton DF, LeBlanc SJ, Leslie KE, Duffield TF. The effect of subclinical ketosis in early lactation on reproductive performance of postpartum dairy cows. J Dairy Sci 2007;90:2788–96.

[28] Hammon DS, Evjen IM, Dhiman TR, Goff JP, Walters JL. Neutrophil function and energy status in Holstein cows with uterine health disorders. Vet Immunol Immunopathol 2006;113: 21–9.

[29] Kimura K, Goff JP, Kehrli ME. Decreased neutrophil function as a cause of retained placenta in dairy cattle. J Dairy Sci 2002;85: 544–50.

[30] Bravo PW. The reproductive process of South American Camelids. Salt Lake City, UT: Seagull Printing; 2002.

[31] Bauman DE, Currie WB. Partitioning of nutrients during pregnancy and lactation: a review of mechanisms involving homeostasis and homeorhesis. J Dairy Sci 1980;63:1514.

[32] Vaughan JL, Tibary A. Reproduction in female South American camelids: a review and clinical observations. Small Rumin Res 2006;61:259–81.

[33] Tibary A, Anouassi A, Memon AM. Approach to infertility diagnosis in camelids: retrospective study in alpacas, llamas and camels. J Camel Pract Res 2001;8:167–79.
[34] Powers BE, Johnson LW, Linton LB, Garry F, Smith J. Endometrial biopsy technique and uterine pathologic findings in llamas. J Am Vet Med Assoc 1990;197:1157–62.
[35] Fernandez-Baca S, Hansel W, Novoa C. Embryonic mortality in the alpaca. Biol Reprod 1970;3:243–51.
[36] Diaz D. La influencia del estado reproductive en la mortalidad embrionaria de alpacas. Fac Agron Zoot, Thesis. Cusco, Peru: Univ Nac San Antonio Abad; 1999.
[37] Knight TW, Ridland M, Scott I, Death AF, Wyeth TK. Foetal mortality at different stages of gestation in alpacas (*Lama pacos*) and the associated changes in progesterone concentrations. Anim Reprod Sci 1995;40:89–97.
[38] Sumar J. Demographics and herd management practices in South America. In: Youngquist R, Threlfall W, editors. Current therapy in large animal theriogenology. 2nd ed., St. Louis, MO: Saunders/Elsevier; 2007. p. 845–51.
[39] San Martin FA, Bryant FC. Nutrition of domesticated South American llamas and alpacas. Small Rumin Res 1989;2:191–216.
[40] Reiner RJ, Bryant FC. Botanical composition and nutritional quality of alpaca diets in two Andean rangeland communities. J Range Manag 1986;39:424–7.
[41] Van Saun RJ. Nutritional diseases of South American camelids. Small Rumin Res 2006;61:153–64.
[42] Britt JH. Impacts of early postpartum metabolism on follicular development and fertility. In: Proc 24th Ann Conv Am Assoc Bovine Practitioners; 1991.p. 39–43.
[43] McNeill DM, Slepetis R, Ehrhardt RA, Smith DM, Bell AW. Protein requirements of sheep in late pregnancy: partitioning of nitrogen between gravid uterus and maternal tissues. J Anim Sci 1997;75:809–16.
[44] Bell AW. Regulation of organic nutrient metabolism during transition from late pregnancy to early lactation. J Anim Sci 1995;73:2804–19.
[45] Johnson LW. Llama nutrition, 10. Vet Clinics NA: Food Animal Practice; 1994. p. 187–201.
[46] Tornquist SJ, Cebra CK, Van Saun RJ, Smith BB. Metabolic changes and induction of hepatic lipidosis during feed restriction in llamas. Am J Vet Res 2001;62:1081–7.
[47] Van Saun RJ. Nutrient requirements of South American camelids: a factorial approach. Small Rumin Res 2006;61:165–86.
[48] Lassen ED, Pearson EG, Long P, Schmotzer WB, Kaneps AJ, Riebold TW. Clinical biochemical values of llamas: reference values. Am J Vet Res 1986;47:2278–80.
[49] Simons JA, Waldron DL, Hennessy DP. Clinical biochemical reference ranges for female alpacas (*Lama pacos*). Comp Biochem Physiol 1993;105B:603–8.
[50] Hinderer S, von Engelhardt W. Urea metabolism in the llama. Comp Biochem Physiol 1975;52A:619–22.
[51] Sinclair KD, Kuran M, Gebbie FE, Webb R, McEvoy TG. Nitrogen metabolism and fertility in cattle. II. Development of oocytes recovered from heifers offered diets differing in their rate of nitrogen release in the rumen. J Anim Sci 2000;78:2670–80.
[52] Elrod CC, Butler WR. Reduction of fertility and alteration of uterine pH in heifers fed excess ruminally degradable protein. J Anim Sci 1993;71:694–701.
[53] Theiler A, Green HH, DuToit PJ. Studies in mineral metabolism. III. Breeding of cattle on phosphorus deficient pasture. J Agric Sci (Camb) 1928;18:369–71.
[54] Wu Z, Satter LD, Soja R. Milk production, reproductive performance, and fecal excretion of phosphorus by dairy cows fed three amounts of phosphorus. J Dairy Sci 2000;83:1028–41.
[55] Smith BB, Van Saun RJ. Seasonal changes in serum calcium, phosphorus and vitamin D concentrations in llamas and alpacas. Am J Vet Res 2001;62:1187–93.
[56] Van Saun RJ, Smith BB, Watrous BJ. Evaluation of vitamin D status in llamas and alpacas with hypophosphatemic rickets. J Am Vet Med Assoc 1996;209:1128–33.
[57] Hostetler CE, Kincaid RL, Mirando MA. The role of essential trace minerals in embryonic and fetal development in livestock. Vet J 2003;166:125–39.
[58] Abdelrahman MM, Kincaid RL. Deposition of copper, manganese, zinc, and selenium in bovine fetal tissue at different stages of gestation. J Dairy Sci 1993;76:3588–93.
[59] House WA, Bell AW. Mineral accretion in the fetus and adnexa during late gestation in Holstein cows. J Dairy Sci 1993;76:2999–3010.
[60] Van Saun RJ, Herdt TH, Stowe HD. Maternal and fetal vitamin E concentrations and selenium-vitamin E interrelationships in dairy cattle. J Nutr 1989;119:1156–64.
[61] Herdt TH, Stowe HD. Fat-soluble vitamin nutrition for dairy cattle, 7. Vet Clinics NA: Food Anim Pract; 1991. p. 391–415.