

Developmental programming of the neonatal period in ruminant livestock: a review

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Review

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Abstract

Early life, or the neonatal period, is perhaps the most challenging time for ruminant livestock, as they adapt to the extra-uterine environment, undergo important physiological maturation, and navigate harsh ambient conditions. Maternal influences during gestation, especially energy and protein nutrition in late pregnancy, can alter many processes that affect the neonatal period. These processes include fetal growth and development, gestation length, difficulty of parturition, and maternal behavior, which interact to affect offspring vigor at birth. Moreover, colostrum and early milk production and composition are affected by gestational nutrition, and these along with the previous factors affect the neonate's ability to obtain transfer of passive immunity, thermoregulate, perform basal metabolism, and ultimately survive to weaning. Often, the long-term effects of maternal nutrition during gestation on offspring are attributed solely to the prenatal environment, but it is critical to also consider influences of early life on later productivity and health. More research is needed to integrate these neonatal outcomes with prenatal and postnatal mechanisms as well as later ruminant livestock performance. Better understanding of the maternal environment's effects on the neonatal period provides opportunity for improved management of ruminant livestock dams and offspring.

Introduction

Early life, or the neonatal period, is perhaps the most challenging time for ruminant livestock, including cattle, sheep, and goats. Parturition and the time immediately following it are difficult for all mammalian offspring as they adapt to the extra-uterine environment, begin to rely completely on enteral nutrition, and thermoregulate outside of the uterus.^{1,2} Although ruminant livestock species have been domesticated for centuries and are under the care of farmers and ranchers, they are often born into adverse conditions, including cold, hot, wet, windy, or muddy environments. Additionally, small ruminants are likely to gestate multiple fetuses, which increases early life challenges due to competition for pre- and postnatal nutrients and maternal care.² Ruminant neonates are precocious, standing shortly after birth and following their dams in the early hours of life, frequently across difficult terrain or in the face of possible predation. While adapting to the challenging extrauterine environment, ruminant neonates also must undergo important physiological changes, similar to neonates of other species.^{3,4}

It is well-established that ruminant livestock are programmed by the maternal environment, influenced by not only their prenatal environment, but also by maternal contributions postnatally. Maternal influences during gestation, especially nutrition, are known to alter many processes that affect the neonatal period. Despite this, developmental programming research in ruminant livestock often focuses on fetal and/or placental development^{5–8} or long-term effects on offspring,^{9–11} choosing endpoints prior to parturition or well into the post-weaning period that miss critical data from neonates. While developmental programming research data from these time periods are instrumental to our understanding of the importance of maternal nutrition and management during pregnancy, it is crucial to consider programming of the neonatal period in ruminant livestock as well. This is especially true as early life experiences have long-lasting consequences of their own.^{12,13} Most importantly, pre-weaning death losses are concentrated around birth and the neonatal periods in ruminant livestock.^{2,14} Simply put, one dramatic way that early life can program later productivity is death of offspring as neonates.

The long-term effects of maternal nutrition during gestation on offspring are commonly attributed solely to the prenatal environment, but it is critical to consider influences of early life on later productivity and health as well. The overall objective of this review is to summarize our knowledge of the major ways in which the maternal environment programs the neonatal period in ruminant livestock (Figure 1), with special focus on maternal energy and protein nutritional status during pregnancy. Small ruminants in particular are considered to be good models for human pregnancy,⁷ and ruminant livestock are a valuable source of nutrients in the human diet;¹⁵ thus, our understanding of ways to improve the ability of ruminant neonates to survive and even thrive is important to humankind.

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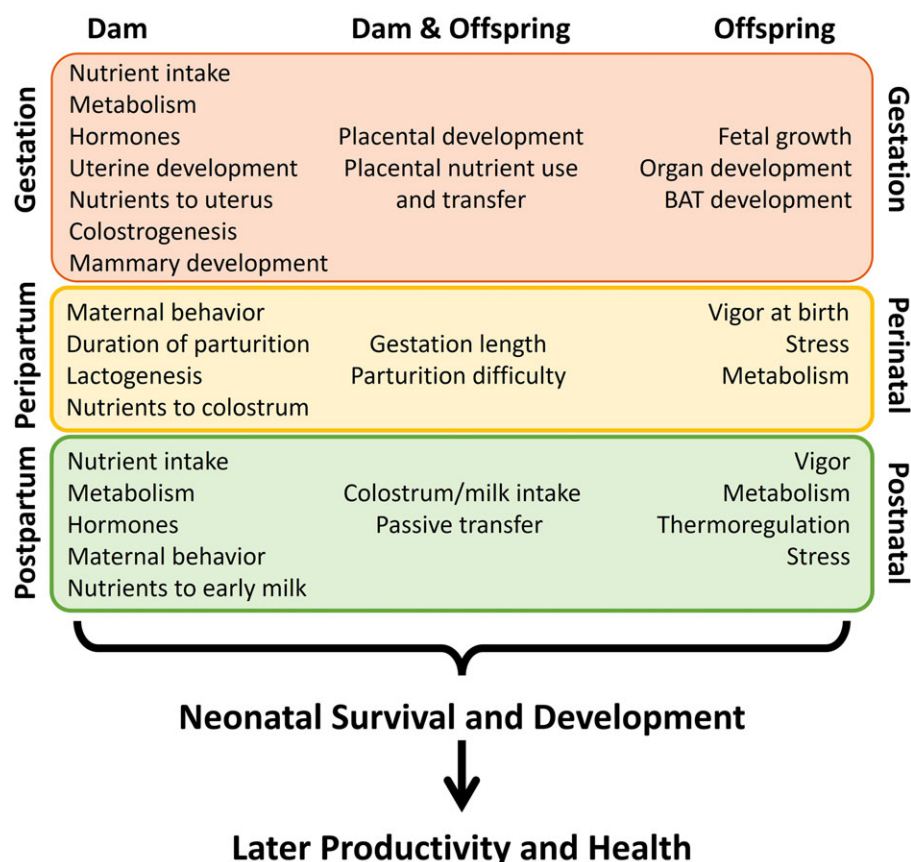


Figure 1. Overview of maternal environment's effects on neonatal development and survival, including dam and offspring factors during gestation, peripartum/perinatal, and postpartum/postnatal periods. BAT, brown adipose tissue.

Maternal nutritional status

Maternal energy and protein status during pregnancy drives many of the factors that affect neonatal outcomes shown in Figure 1 and summarized in Tables 1–6. Ruminant females that are grazing or fed harvested forage during late gestation often do not meet their nutrient requirements during this period;^{16,17} therefore, the effects of restricted energy and protein during late pregnancy have been studied for decades. More recently, overnutrition has been studied in sheep models for human pregnancy. Most data included in Tables 1–6 are from controlled nutrition experiments investigating effects of under- or overnutrition relative to nutrient requirements or supplementation of energy and/or protein relative to a basal diet of poor quality forage. Alternatively, a few datasets^{18–20} resulted from comparing body condition score of beef females at calving, which represents the energy stores of the dam prepartum but could have been set recently or much earlier in the production cycle. Maternal intake of trace minerals, vitamins, amino acids, and fatty acids has also been shown to affect neonatal ruminants.^{21,22} These effects are variable depending on the basal diet, supplemented nutrient, species, timing, and outcomes measured and are not the focus of the present review.

Although most discussion here includes experiments focused on protein and energy nutrition, many other factors affect maternal nutritional status during pregnancy. Anything that alters nutrient requirements or use during gestation can affect the balance of nutrient intake relative to needs, even when energy and protein intake are not changed. Good examples that occur regularly for ruminant livestock include the first parity,²³ heat stress,²⁴ cold stress,²⁵ fetal number or litter size,²⁶ and immune challenges.²⁷ As reviewed by our lab,²³ offspring of primiparous

ruminant females (dams during their first pregnancy) have similar negative effects as those born to nutrient-restricted dams, in particular when considering perinatal and neonatal periods (Table 7). It is often hypothesized that consequences of dam primiparity are due to the competition of nutrient partitioning between the growing dam (as most ruminant livestock are bred at an immature weight and physiological maturity), uteroplacenta, fetus, and mammary gland.^{28,29} Alternatively, we hypothesize that the first use of tissues (e.g., uterus and mammary gland) and first experience of parturition by the primiparous dam also plays a role.²³ Heat stress decreases nutrient intake, along with altering metabolism and physiology,^{30,31} whereas cold stress increases voluntary intake (if more feed is available) but also increases energy requirements.³² Research of heat stress during the late gestational dry (non-lactating) period of dairy cows has repeatedly demonstrated that offspring are affected pre- and postnatally.^{24,33} Not all effects of environment are negative; for example, shearing late gestation ewes in winter has mixed effects on maternal metabolism but results in greater brown adipose tissue and glycogen stores in lambs.²⁵

Methods other than nutritional treatments that induce placental insufficiency and/or intrauterine growth restriction are commonly used in small ruminant models, including hyperthermia during the height of placental growth in mid-gestation, carunclectomy, single umbilical artery ligation, and placental embolization.^{7,34} Rarely do these models report data shown in Tables 1–6, even though they generally act through reducing prenatal availability of nutrients (and oxygen) to the growing fetus and therefore have similarities with some nutrition models discussed here.^{7,34} Research models in poor maternal nutrition, dam primiparity, and maternal heat stress that mimic real-world

Table 1. Effects of maternal nutrition on parturition difficulty and maternal behavior in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Parturition effects ³	Reference
Beef cattle, primi	Last 90 d gestation	<i>Low</i> (0.5 kg/d BW loss) vs. <i>Maintenance</i> (maintain BW) vs. <i>High</i> (0.75 kg/d BW gain)	↑ abnormal fetal presentations in Low and Maintenance ↑ time of parturition in Low	Kroker and Cummins, 1979 ⁵⁰
Beef cattle, mixed	–	Body condition score at calving (1 = emaciated to 9 = obese)	↑ odds ratio for dystocia for BCS<5 or if BCS loss during mid-late pregnancy ↑ odds ratio for severe dystocia for BCS ≤ 3	Waldner, 2014 ¹⁹
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↑ abnormal fetal presentations in Nutr Res ↑ standing time for 3 d prepartum and 7 d postpartum in Nutr Res	Redifer et al., 2023 ³⁹ ; Johnson et al., 2022 ⁶⁵
Sheep, primi	wk 4 gestation to lambing	<i>High</i> vs. <i>Low</i> (65% of High) intake	↑ delivery assistance required in Low ↑ abnormal fetal presentations in Low ↑ time interval between twins in Low ↓ time grooming lambs in first 30 min postpartum by Low ↑ time spent eating in first 30 min postpartum and first 3 d postpartum by Low ↓ likelihood to be assigned high maternal behavior score or maternal attachment score in Low	Dwyer et al., 2003 ⁵¹
Sheep, primi	d 13 gestation to lambing	<i>Low</i> (gain 10 kg) vs. <i>Moderate</i> (gain 20 kg) vs. <i>High</i> (gain 30 kg)	↓ maternal behavior score in Low and Moderate ↓ bleats in response to lamb and % low bleats in Low	Corner et al., 2006 ⁶²
Sheep, multi	d 70 gestation to lambing	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) of energy and protein	↓ time spent near own lambs in Nutr Res	Olazabal Fenchio et al., 2013 ⁶³
Sheep, multi	Last 10 d of gestation	Grazing native pasture (<i>Basal</i>) vs. Grazing with energy and protein supplementation (<i>Suppl</i>)	↓ duration of parturition in Basal	Olivera-Muzante et al., 2022 ⁹⁴
Goats, multi	Last 12 d gestation	Grazing only (<i>Basal</i>) vs. Grazing with corn supplementation (<i>Suppl</i>)	↑ duration of parturition in Basal ↑ abnormal fetal presentations in Basal	Ramirez-Vera et al., 2012a ⁴⁹
Goats, multi	Last 12 d gestation	Grazing only (<i>Basal</i>) vs. Grazing with corn supplementation (<i>Suppl</i>)	↑ rejection of own kids in Basal ↑ time to amniotic fluid consumption in Basal ↓ frequency of amniotic fluid consumption in Basal ↓ frequency and duration of invitations to suckle in Basal ↓ udder acceptance toward own kids in Basal ↑ udder rejections toward own kids in Basal ↑ aggressive behaviors toward own kids in Basal ↓ low pitched bleats toward own kids in Basal ↑ low pitched bleats toward alien kids in Basal	Ramirez-Vera et al., 2012b ⁶⁴

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. ³Comparisons made to treatment most closely matched to requirements during pregnancy. BCS, body condition score.

livestock environments often reduce placental and fetal growth and development, but not necessarily to the same extent as these more dramatic models of placental insufficiency or intrauterine growth restriction.

Timing of nutritional insults

Timing of poor nutrition or nutritional interventions during pregnancy can have differential effects, especially when considering developmental windows of fetal and placental development. Placental development and organogenesis occur in early to mid-gestation, whereas the majority of fetal growth and organ maturation occur in late gestation.⁶ Even within ruminant species, there is variation in these windows. Placental growth is largely complete in the ewe and doe by mid-pregnancy, but it continues throughout pregnancy in the cow.³⁵ Moreover, the competition of pregnancy with lactation varies among the species, as beef cattle

females generally experience early gestation and commonly some of mid-gestation while lactating when maintaining a yearly calving interval. Dairy cattle females have overlap of all but very late gestation (approximately 60 days) with lactation. On the other hand, small ruminants experience pregnancy and lactation separately unless they reproduce twice per year or are maintained in lactation for dairying purposes.

Nutrient requirements of the dam increase dramatically during late pregnancy,³² as rapid fetal growth occurs. Because most ruminant production systems are timed to have the high nutrient requirements of lactation coincide with plentiful forage availability, late gestation is frequently a time of poor nutrient availability in production settings despite this increase in nutrient needs. Additionally, most investigations of peripartum and perinatal outcomes in ruminants utilized nutritional treatments that occur during late gestation, regardless of their initiation time. For these reasons, this review will focus on the effects of maternal

Table 2. Effects of maternal nutrition on offspring vigor at birth in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Vigor effects ³	Reference
Beef cattle, primi	Last 90 d gestation	<i>Low</i> (0.5 kg/d BW loss) vs. <i>Maintenance</i> (maintain BW) vs. <i>High</i> (0.75 kg/d BW gain)	↑ time to stand in Low vs. High ↑ time to suckle in Low vs. Maintenance and High	Kroker and Cummins, 1979 ⁵⁰
Beef cattle, primi	d 190 gestation to calving	55% (<i>Low protein</i>) vs. 91% (<i>Adequate</i>) protein	↑ time to stand in Low protein	Odde, 1988 ²⁰
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↑ time to attempt to stand and time to stand in Nutr Res ↓ vigor score at 20 min of age in Nutr Res	Wichman et al., 2023 ⁷¹
Sheep, primi	d 13 gestation to lambing	<i>Low</i> (gain 10 kg) vs. <i>Moderate</i> (gain 20 kg) vs. <i>High</i> (gain 30 kg)	↑ in time to bleat and ↓ in bleats in response to dam in Low ↓ % contact with dam in Low and Moderate	Corner et al., 2006 ⁶²
Sheep, multi	d 70 of gestation to lambing	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) of energy and protein	↑ high pitch bleats at 24 h of age in Nutr Res ↓ time near their own dam in Nutr Res	Olazabal Fenochio et al., 2013 ⁶³
Sheep, primi	Throughout gestation	<i>Maintenance</i> (<i>Control</i>) vs. <i>High</i> nutrient intake (<i>Over</i>)	↑ number of assisted feedings in Over ↓ proportion with no assistance or minimal assistance during first 24 h in Over	Wallace et al., 2021 ⁸⁴
Goats, multi	Last 12 d gestation	<i>Grazing only</i> (<i>Basal</i>) vs. <i>Grazing with corn supplementation</i> (<i>Suppl</i>)	↓ low pitch bleats within 90 min of birth in Basal ↓ frequency of teat seeking within 1 h of birth in Basal ↓ suckling frequency and time from 30 to 90 min after birth in Basal	Ramirez-Vera et al., 2012a ⁴⁹

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. BW, body weight. ³Comparisons made to treatment most closely matched to requirements during pregnancy.

nutrition in late gestation. Some experiments include the entirety of pregnancy, whereas others focus on mid and late, late only, or even the last days of gestation. Timing of these treatments should be considered when interpreting results. It is well established that early and mid-pregnancy can affect placental and fetal development in ruminant species, even if birth weight is unchanged.^{6,17,36,37} From a review of sheep literature, it is clear nutrient intake during early or mid-gestation alone can also influence maternal and offspring behavior, passive transfer, thermoregulation, and lamb survival;²² thus, more research is likely necessary to determine carryover effects from earlier in pregnancy.

Effects of maternal nutrition on neonatal ruminants

Fetal growth and gestation length

Fetal growth, measured as birth weight in most of the studies cited in Tables 1–6, or as fetal weight in terminal or Cesarean section studies, is generally decreased by substantial (e.g., 30% or more reduction in nutrients) nutrient restriction in sheep^{36,38} but is not always affected by nutrient restriction in cattle.^{14,39} Overnutrition of pregnant young primiparous ewes,³⁸ heat stress during mid-gestation in ewes,^{40,41} and heat stress of dairy cows in late gestation²⁴ also generally cause intrauterine growth restriction, although likely by differing mechanisms. Birth weight is a major variable of interest because it affects postnatal survival, especially through three mechanisms: (1) being an indicator of fetal development and maturity, (2) ensuring a newborn ruminant is large enough to survive cold conditions or nutrient deficiency by having the body mass and presence of energy stores and protein for mobilization, and (3) allowing ruminant offspring to be small enough to not cause dystocia at birth due to fetopelvic

disproportion.^{42,43} Birth weight often serves as a crude proxy for development or maturity at birth that is possible to assess without euthanasia and dissection. It is a poor proxy, however, due to asymmetric fetal growth (e.g., brain sparing) and differential timing of growth, development, and maturation among tissues. Several tissues, such as the gastrointestinal tract, lungs, brain, brown adipose tissue, energy stores (glycogen and adipose), muscle, and many others are known to be affected by maternal nutrition during pregnancy.^{6,25,44}

Gestation length is one determinant of birth weight and controlled by both the dam and fetus to some degree.⁴⁵ Ruminant models of altered gestational nutrition are variable in their effects on gestation length. Overnourished adolescent ewes seem to most consistently have shortened gestation lengths by 5 d on average (145 d in controls).³⁸ Nutrient restriction,³⁹ dam primiparity,²³ and dry period heat stress²⁴ are inconsistent in decreasing gestation length, with the majority of papers reporting no difference. In many of the studies cited here or in the references given, birth weight differences do not appear to be due completely to altered days of fetal growth. Given the importance of not only size at birth but also the final maturation of organs prior to birth,⁶ change in gestation length caused by maternal nutrition or other stress is an important factor affecting neonatal survival.

Parturition difficulty and maternal behavior

One of the most common reasons for neonatal death loss in livestock species is dystocia or difficult parturition.^{46–48} Experiments investigating effects of maternal nutrition are rarely powered to observe statistical differences in dystocia rates. Despite this, data suggest that even though poor maternal nutrition during pregnancy often decreases birth weight, dystocia can increase after nutrient restriction or for animals with poor body condition score

Table 3. Effects of maternal nutrition on colostrum yield and composition in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Effect on colostrum yield ³	Other colostrum effects ³	Reference
Beef cattle, primi	d 190 gestation to calving	55% (<i>Low protein</i>) vs. 91% (<i>Adequate</i>) protein	↓ in Low protein	↑ IgG ₁ concentration in Low protein	Odde, 1988 ²⁰
Beef cattle, multi	Last 15 d gestation	Grass silage (<i>High</i>) vs. straw (<i>Low</i>)	No difference	↓ total IgG ₁ , IgM, and combined Ig in Low	McGee et al., 2006 ⁸⁶
Beef cattle, multi	d 201 to 271 of gestation	Non-supplemented low quality forage (<i>Basal</i>) vs. Forage with DDGS supplementation (<i>Suppl</i>)	↓ in Basal	No difference in IgG concentration or total	Kennedy et al., 2019 ⁸⁵
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↓ in Nutr Res	↓ total lactose in Nutr Res ↑ protein, IgG, IgA concentration in Nutr Res	Redifer et al., 2023 ³⁹
Sheep, multi	d 105 gestation to lambing	High plane (<i>High</i>) vs. Low plane (<i>Low</i>) vs. Low d 105-139 then High d 140-lambing (<i>Low-High</i>)	↓ in Low and Low-High	–	Mellor and Murray, 1985 ⁷⁵
Sheep, multi	d 105 gestation to lambing	High plane (<i>High</i>) vs. Low plane (<i>Low</i>) vs. Low d 105-139 then High d 140-lambing (<i>Low-High</i>)	↓ in Low and Low-High	–	Mellor et al., 1987 ⁷⁶
Sheep, primi	Throughout gestation	Maintenance (<i>Control</i>) vs. High nutrient intake (<i>Over</i>)	↓ in Over	↓ lactose, fat concentration in Over ↑ IgG concentration in Over ↓ total lactose, fat, protein, IgG in Over	Wallace et al., 2001 ⁸²
Sheep, multi	d 85 gestation to lambing	100% (<i>Control</i>) vs. 140% (<i>High Protein</i>) protein	↓ in High Protein	–	Ocak et al., 2005 ⁸³
Sheep, multi	d 80 gestation to lambing	70% (<i>Nutr Res</i>) vs. 110% (<i>Control</i>) of metabolizable energy	↓ in Nutr Res	↓ lactose concentration in Nutr Res ↑ protein concentration in Nutr Res	Banchero et al., 2006 ⁷⁷
Sheep, multi	Last 14 d of gestation	Hay only to meet requirements (<i>Basal</i>) vs. Hay with corn (<i>Corn</i>) vs. Hay with barley (<i>Barley</i>)	↑ in Corn and Barley	↑ in lactose concentration in Corn and Barley ↓ in protein concentration in Corn and Barley	Banchero et al., 2007 ⁹⁵
Sheep, primi	d 50 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↓ in Nutr Res and Over	↑ IgG concentration in Nutr Res ↓ total lactose, fat, protein, IgG in Nutr Res and Over	Swanson et al., 2008 ⁷⁸
Sheep, multi	Last 8 wk gestation	<i>High</i> vs. <i>Low</i> (50% metabolizable energy of High)	↓ in Low	No difference in colostrum leptin	Tygesen et al., 2008 ⁷⁹
Sheep, primi	d 40 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↓ in Nutr Res and Over	↑ fat concentration in Nutr Res ↓ total lactose, protein in Nutr Res and Over ↓ total fat in Over	Meyer et al., 2011 ⁸⁰
Sheep, primi	Throughout gestation	Maintenance (<i>Control</i>) vs. 0.75x Control (<i>Nutr Res</i>) vs. High nutrient intake (<i>Over</i>)	↓ in Nutr Res and Over	↑ IgG concentration in Nutr Res and Over ↓ total IgG in Over ↓ lactose concentration in Nutr Res ↓ total lactose, fat, crude protein, energy content in Nutr Res and Over	Wallace et al., 2012 ⁸¹
Sheep, primi	Throughout gestation	Maintenance (<i>Control</i>) vs. High nutrient intake (<i>Over</i>)	↓ in Over	↑ in proportion with inadequate colostrum or <50 mL colostrum in Over	Wallace et al., 2021 ⁸⁴
Sheep, multi	Last 10 d of gestation	Grazing native pasture (<i>Basal</i>) vs. Grazing with energy and protein supplementation (<i>Suppl</i>)	↓ in Basal	↑ viscosity in Basal ↓ total lactose, fat, and protein in Basal	Olivera-Muzante et al., 2022 ⁹⁴
Goats, multi	Last 12 d gestation	Grazing only (<i>Basal</i>) vs. Grazing with corn supplementation (<i>Suppl</i>)	↓ in Basal	No difference in lactose, protein, or fat concentrations	Ramirez-Vera et al., 2012a ⁴⁹

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. DDGS, dried distillers grains with solubles. ³Comparisons made to treatment most closely matched to requirements during pregnancy. Ig, immunoglobulin.

Table 4. Effects of maternal nutrition on offspring transfer of passive immunity in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Passive transfer effects ³	Reference
Beef cattle, primi	–	Body condition score at calving (1 = emaciated to 9 = obese)	↓ serum IgG ₁ in BCS 3 and 4	Odde, 1988 ²⁰
Beef cattle, primi	d 190 gestation to calving	55% (<i>Low protein</i>) vs. 91% (<i>Adequate</i>) protein	↑ serum IgG ₁ and IgM at 24 h of age in Low protein	Odde, 1988 ²⁰
Beef cattle, multi	last 15 d gestation	Grass silage (<i>High</i>) vs. straw (<i>Low</i>)	↓ serum IgG ₁ and combined Ig at 8 and 48 h of age for Low	McGee et al., 2006 ⁸⁶
Beef cattle, mixed	–	Body condition score <5 vs. ≥ 5	↑ serum IgG at 2 to 8 d of age for BCS <5	Waldner and Rosengren, 2009 ¹⁸
Beef cattle, mixed	last 14 d gestation	Low quality hay only (<i>Basal</i>) vs. 1 kg protein supplementation (<i>Suppl</i>)	↓ serum IgG at 48 h of age in Basal	Silva et al., 2022 ⁹⁸
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↑ serum IgG at 48 h of age in Nutr Res	Wichman et al., 2023 ⁷¹
Sheep, primi	d 40 or 50 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↑ serum IgG at 24 h of age in Nutr Res	Hammer et al., 2011 ¹⁰⁰
Sheep, multi	d 30 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↓ serum IgG at 7 d of age in Nutr Res and Over (ewe lambs only)	Tillquist et al., 2025 ⁹⁹

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. ³Comparisons made to treatment most closely matched to requirements during pregnancy. Ig, immunoglobulin; BCS, body condition score.

Table 5. Effects of maternal nutrition on offspring neonatal thermoregulation and metabolic rate in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Thermoregulation effects ³	Reference
Beef cattle, primi	d 190 gestation to calving	55% (<i>Low protein</i>) vs. 91% (<i>Adequate</i>) protein	↓ thermoneutral metabolic rate in Protein Res	Carstens et al., 1987 ¹¹³
Beef cattle, primi	d 190 gestation to calving	70% then 40% (<i>Energy Res</i>) vs. 100% (<i>Control</i>) metabolizable energy	↓ thermoneutral metabolic rate in Energy Res	Ridder et al., 1991 ¹¹⁴
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↓ rectal temperature post-standing but pre-suckling for Nutr Res ↑ rectal temperature at 24 h of age for Nutr Res	Wichman et al., 2023 ⁷¹
Sheep, multi	Last 1–2 mo gestation	<i>High</i> (gained 0.1 kg/d) vs. <i>Medium</i> vs. <i>Low</i> nutrition (lost 0.1 kg/d)	↓ survival time after starvation at thermoneutral in Low ↓ survival time after starvation in cold conditions in Low	Alexander, 1962 ¹¹⁵
Sheep, multi	wk 13 gestation to lambing	<i>Ad libitum</i> vs. Restricted (<i>Res</i>) feeding	↓ brown adipose tissue depots in d 125 fetuses from Res	Alexander, 1978 ¹⁰⁷
Sheep, multi	d 80 to 143 gestation	100% (<i>Control</i>) vs. 150% (<i>Over</i>) metabolizable energy	↓ perirenal fat (g/kg BW) at d 143 fetuses in Over ↑ UCP1 and thermogenic activity in brown adipose tissue of d 143 fetuses in Over	Budge et al., 2000 ¹⁰⁸
Sheep, multi	period 1: d–60 relative to breeding to d 8 post-breeding; period 2: d 8 to 144 gestation	70% energy (<i>Res</i>) vs. 100% energy (<i>Con</i>) during each period: <i>Res-Res</i> , <i>Res-Con</i> , <i>Con-Res</i> , <i>Con-Con</i>	↑ perirenal fat (g/kg BW) in d 144 fetuses in Con-Res ↓ UCP1 in perirenal adipose in d 144 fetuses in Res-Res	Budge et al., 2004 ¹⁰⁹
Sheep, multi	d 105 to 143 gestation	50% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) of requirements	↓ perirenal fat (g/kg BW) in d 143 fetuses in Nutr Res ↑ UCP1 in perirenal adipose in d 143 fetuses in Nutr Res	Budge et al., 2004 ¹⁰⁹
Sheep, mixed	d 110 gestation to lambing	<i>Control</i> vs. 50% of Control (<i>Nutr Res</i>)	↑ perirenal fat (g/kg BW) at birth in Nutr Res ↓ hepatic GH receptor mRNA at 1 d of age in Nutr Res born to primi	Hyatt et al., 2007 ¹¹⁰

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. ³Comparisons made to treatment most closely matched to requirements during pregnancy. BW, body weight; UCP1, uncoupling protein 1; GH, growth hormone.

Table 6. Effects of maternal nutrition on offspring neonatal metabolism, blood chemistry, and hormones in ruminant livestock

Species, parity ¹	Treatment timing	Maternal nutritional treatment ²	Metabolism effects ³	Reference
Beef cattle, multi	Last 90 d gestation	57% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↑ cortisol during first 48 h in <i>Nutr Res</i> ↓ T ₃ during first 48 h in <i>Nutr Res</i>	Hough et al., 1990 ¹¹¹
Beef cattle, multi	Last 100 d gestation	<i>Control</i> (maintain BCS) vs. <i>Nutr Res</i> (lose 1 to 1.5 BCS) vs. <i>Nutr Res</i> + <i>Protein</i>	↓ plasma glucose at birth in <i>Nutr Res</i> and <i>Nutr Res</i> + <i>Protein</i> ↑ plasma cortisol at birth in <i>Nutr Res</i> and <i>Nutr Res</i> + <i>Protein</i> ↑ plasma cortisol on d 1 of age in <i>Nutr Res</i> ↑ plasma leptin at birth in <i>Nutr Res</i> + <i>Protein</i>	LeMaster et al., 2017 ¹¹⁶
Beef cattle, multi	d 134 gestation to calving	<i>Low protein</i> vs. <i>High protein</i>	↑ serum insulin at birth in <i>Low protein</i>	Maresca et al., 2018 ¹¹⁸
Beef cattle, multi	d 201 to 271 of gestation	Non-supplemented low quality forage (<i>Basal</i>) vs. Forage with DDGS supplementation (<i>Suppl</i>)	↓ plasma glucose at 24 h of age in <i>Basal</i> ↑ base excess at 24 h in <i>Basal</i> ↓ hemoglobin in <i>Basal</i>	Kennedy et al., 2019 ⁸⁵
Beef cattle, primi	d 160 gestation to calving	70% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) energy and protein	↑ serum aspartate aminotransferase and creatine kinase in <i>Nutr Res</i> ↓ red blood cells in <i>Nutr Res</i>	Wichman et al., 2023 ⁷¹
Dairy cattle, mixed	Last 2 mo gestation	<i>Maintenance</i> (<i>Maint</i>) vs. <i>High</i>	↓ hematocrit and hemoglobin in <i>Maint</i>	Kume et al., 1998 ¹¹⁷
Sheep, multi	d 115 gestation to lambing	<i>Control</i> vs. 50% of <i>Control</i> (<i>Nutr Res</i>)	↓ hepatic GH receptor and IGF-1 mRNA at 1 day of age in <i>Nutr Res</i>	Hyatt et al., 2008 ¹²⁰
Sheep, primi	d 40 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↓ circulating T ₃ at birth in <i>Nutr Res</i> ↓ circulating T ₄ at 24 h of age in <i>Over</i>	Camacho et al., 2012 ¹¹²
Sheep, primi	Throughout gestation	<i>Maintenance</i> (<i>Control</i>) vs. 0.75x <i>Control</i> (<i>Nutr Res</i>) vs. <i>High nutrient intake</i> (<i>Over</i>)	↑ plasma cholesterol and LDL at birth in <i>Over</i>	Wallace et al., 2012 ⁸¹
Sheep, multi	Last 10 d of gestation	Grazing native pasture (<i>Basal</i>) vs. Grazing with energy and protein supplementation (<i>Suppl</i>)	↑ % of lambs with blood glucose <20 mg/dL at birth	Olivera-Muzante et al., 2022 ⁹⁴
Sheep, multi	d 30 gestation to lambing	60% (<i>Nutr Res</i>) vs. 100% (<i>Control</i>) vs. 140% (<i>Over</i>) of energy and protein	↑ leptin at birth in <i>Over</i>	Tillquist et al., 2023 ¹¹⁹

¹Primi, primiparous (first); multi, multiparous; mixed, both. ²Treatment names italicized. BCS, body condition score. ³Comparisons made to treatment most closely matched to requirements during pregnancy. T₃, triiodothyronine; GH, growth hormone; IGF-1, insulin-like growth factor 1; T₄, thyroxine; LDL, low density lipoprotein.

Table 7. Effects of maternal primiparity on ruminant livestock offspring

Outcome	Parity	
	1	≥3
Placenta size	↓	↑
Fetal growth	↓	↑
Gestation length	↓	↑
Dystocia incidence	↑	↓
Maternal behavior	Altered	
Colostrum yield	↓	↑
Vigor at birth	↓	↑
Neonatal stress	↑	↓
Neonatal metabolism	Altered	
Passive transfer	↓	↑

From data reviewed by Meyer and Redifer, 2024.²³

at parturition (Table 1). This occurred concurrently with birth weight that was either unchanged^{39,49} or decreased^{50,51} in the controlled experimental studies shown in Table 1. Fetopelvic disproportion is likely a contributing cause of dystocia during undernutrition of primiparous females.^{23,50,52} Although the mechanisms are unknown, maternal weakness or energy status probably plays a role in greater duration of labor or need for human assistance for normally-presented offspring. Abnormal fetal presentations were also increased^{39,49–51} in undernourished cattle, sheep, and goats, suggesting that altered maternal and/or fetal physiology hinders the ability of fetuses to obtain the appropriate birth position. Poor uterine tone is associated with incomplete fetal righting,⁵³ which has been suggested to occur after nutrient restriction.⁵⁰ Lack of fetal muscle tone may also influence this, as fetal kinesis appears to have the end result of obtaining the birth posture.⁵⁴ Given that prolonged labor or dystocia requiring human intervention is known to decrease vigor after birth,^{55,56} increase perinatal stress,⁵⁷ decrease transfer of passive immunity,⁵⁸ and ultimately increase neonatal mortality,⁵⁹ difficulty of parturition is a major effect of maternal nutrition that can program the neonatal period and beyond.

Maternal behavior during labor and especially postpartum is critical for neonates to thrive in their new extra-uterine environment.^{2,60} Although this is not commonly reported in cattle maternal nutrition studies, impaired mothering behavior of ewes and does following poor gestational nutrition was observed in four experiments shown in Table 1. Dwyer et al. hypothesized that altered circulating estradiol:progesterone affects maternal behavior after nutrient restriction⁵¹ and that priming effects on the brain may differ in first parity ewes.⁶¹ Some of these maternal behavioral changes appear to be associated with slower or less responsiveness to offspring,^{51,62,63} possibly due to exhaustion from prolonged labor or energy substrate depletion.^{51,64} Dams with poor nutrition also have more time and/or attention diverted away from offspring in the early postnatal period, sometimes toward eating,⁵¹ which is logical given the metabolic status of nutrient-restricted dams at parturition. For example, our lab observed that late gestational nutrient restriction decreased circulating glucose and triglycerides in primiparous beef females at 1 h postpartum,³⁹ and Ramirez-Vera et al.⁶⁴ observed that feeding corn supplement during only the last 12 d prepartum increased blood glucose from kidding to 4 h postpartum. Additionally, we observed that late gestationally nutrient-restricted heifers stood more in the peripartum period, indicating more restless behavior.⁶⁵ Together, these data suggest that nutrient-restricted females may be more focused on seeking feed than caring for their offspring after birth. Amniotic fluid is an important olfactory signal that encourages maternal behavior,⁶⁶ so altered consumption of amniotic fluid and grooming behavior of offspring (Table 1) may also lead to the other maternal behaviors observed, including poorer attachment to offspring,⁵¹ increased aggressiveness,⁶⁴ and less receptivity to suckling.⁶⁴ It is unclear if reduced amniotic fluid consumption in dams with poor maternal nutrition⁶⁴ is due to poor maternal responsiveness to and grooming of offspring, increased searching for feed, or other altered states in the dam. Overall, these datasets suggest that more research investigating effects of gestational nutrition on maternal peripartum behavior is warranted given its important role in neonatal survival.

Vigor at birth

Ruminant offspring behavior immediately after birth, often referred to as “vigor,” is especially important for these precocious species that need to stand, walk, and suckle quickly to obtain transfer of passive immunity.⁴³ Vigor is influenced by many perinatal factors that are negatively affected by poor maternal nutrition during pregnancy, including fetal growth and development, gestation length, size at birth, difficulty and length of parturition, and maternal behavior.² Thus, it is not surprising that neonatal vigor is affected by maternal nutrition, as shown in Table 2. Vigor can be difficult to quantify, as many experiments not cited used subjective vigor scores with a limited range (e.g., 1–3), usually without clear definitions such as “very vigorous” or “weak.” More useful objective measures include: (1) behavioral latency times to important milestones such as attempting to stand, successfully standing, and suckling; (2) vigor scores that are taken at specific times and have specific definitions (e.g., Matheson et al.⁶⁷); (3) documentation of occurrences of normal or abnormal behaviors or interventions (as proportion of time, number of behaviors, proportion of offspring displaying, etc.); or (4) physiological indicators of vigor such as those similar to the APGAR score in humans (e.g., Homerosky et al.⁶⁸). These can be very difficult to measure in extensive environments due to lack of

proximity of researchers to animals, but these also can be challenging to obtain without human obstruction of normal behavior in intensive research environments where humans and livestock are in close proximity. This likely explains the relative lack of robust datasets in ruminants, especially beef cattle. Moreover, more artificial environments usually necessary for intensive perinatal data collection may actually lessen or negate vigor differences observed in the farm or ranch setting, as improved management, ambient temperatures, housing, and other aspects of intensive research are inconsistent with many conditions in the field.

Despite this, poorer vigor after birth in ruminant livestock is likely to exist and contribute to reduced neonatal survival caused by poor maternal nutrition (Table 2) and resembles differences observed between offspring born to primiparous and multiparous dams (Table 7²³). Latency times to stand and suckle are generally related,⁶⁹ and prolonged latency times are associated with increased mortality.⁷⁰ Small size at birth is often associated with poorer vigor, especially in small ruminants.⁵¹ Not all reduced vigor observed appears to be caused by intrauterine growth restriction, as our lab reported increased latency time to attempt to stand and stand, along with poorer vigor scores at 20 min of age, in a study in which late gestational nutrient restriction did not reduce calf birth weight.^{39,71} Dwyer et al.^{51,72} hypothesized that poorer vigor of small lambs is caused by developmental differences, including impaired neurodevelopment, but this is not well known in ruminants. Because many factors other than fetal growth and development play a role in neonatal vigor, it is also important to consider dystocia, duration of parturition, maternal behavior, and perinatal metabolism when investigating vigor as well. Unfortunately, few researchers study vigor in this area in a meaningful way or measure all of these variables at once. Overall, it is clear that vigor of neonatal ruminants is affected by maternal nutrition, which is likely to impact the ability of compromised offspring to obtain adequate nutrients and immunoglobulins postnatally.

Colostrum production and transfer of passive immunity

The most studied aspect of neonatal ruminant programming other than birth weight and gestational length is colostrum production. This is likely due to colostrum's importance in providing transfer of passive immunity, concentrated initial nutrients, substrates for heat production, and hydration. As shown in Table 3 and previously reviewed by others,^{58,73,74} maternal nutrition during gestation generally alters yield of colostrum in non-dairy ruminant livestock. In general, both undernutrition^{75–81} and overnutrition^{78,80–84} decreased colostrum yield in sheep, and nutrient restriction predominantly decreased colostrum yield in cattle.^{20,39,85} In many datasets, this decreased yield is associated with a greater concentration of immunoglobulins (Ig) and/or total protein,^{20,39,77,78,81,82} resulting in less colostrum that is more concentrated. Despite this, total Ig masses were decreased by nutrient restriction^{78,86} and overnutrition^{78,81,82} in some studies. When it is measured, nutrient yield is decreased by poor nutrition,^{39,78,80–82} whether nutrient concentrations are affected or not. These are similar trends to those observed when comparing primiparous and multiparous ruminant dams (Table 7,²³) although our lab observed that parity differences are more dramatic in nature than those caused by peripartum body condition score.⁸⁷ Many of these studies suggest that colostrogenesis, the transfer of Ig from circulation to the mammary gland, is less affected than lactogenesis by gestational nutrition.

Colostrum yield and composition differences observed are likely a culmination of several physiological and metabolic changes due to gestational nutrition, such as mammary gland development and blood flow, endocrine signaling for colostrogenesis and lactogenesis, and substrate availability for lactogenesis. Mammary development, colostrogenesis, and lactogenesis are controlled through the intricate coordination of hormones affected by gestational nutrition, including progesterone, estradiol, prolactin, and glucocorticoids.^{74,88,89} Progesterone and estradiol were both increased by nutrient restriction in late gestation ewes,^{38,51,90,91} whereas prolactin and cortisol were decreased.^{77,91} Placental size may play a role in mammary development and subsequent colostrum and milk yield, as mammary:fetal growth appear to be consistent based on litter size,⁹² and placental lactogen may be the link for this relationship.^{92,93} Reduced placental growth is hypothesized to be the major cause of poor colostrum production in overnourished ewes,³⁸ although these ewes were able to increase milk production shortly postpartum in one study.⁸⁰ Additionally, lactose production depends on the substrate glucose, which is often decreased in circulation for nutrient-restricted females.^{39,76,77} As reviewed by Banchero et al.,⁷⁴ even short-term starch-based supplementation (e.g., cereal grains) can increase colostrum yield, likely through provision of additional propionate for gluconeogenesis or post-ruminal starch for glucose absorption, although greater progesterone clearance associated with increased nutrient intake may also be involved. As shown in Table 3, both type of nutrients supplemented and species affect if short-term diet changes alter colostrum production in ruminants.^{49,86,94,95}

Ruminant neonates are born agammaglobulinemic, and they rely on transfer of passive immunity via colostrum.⁹⁶ Serum Ig or total protein concentrations are used to determine success or failure of this passive transfer,⁹⁷ although thresholds are not universally agreed upon. Colostrum is generally the focus of passive transfer studies, but neonates must have dams with good maternal behavior and adequate udder morphology, and they also must be vigorous enough to stand and successfully suckle while small intestinal Ig absorption is possible. As shown in Table 4 and previously reviewed,⁵⁸ serum Ig concentrations were both decreased^{20,86,98,99} and increased^{19,20,71,100} by poor maternal nutrition. When serum Ig was increased, this was concomitant with greater colostrum Ig concentrations in two studies.^{20,71} This is likely because neonates were able to consume more Ig quickly in the first meal after birth when small intestinal Ig absorption potential is greatest.¹⁰¹ Colostrum Ig may not be the only reason for this, as Hammer et al.¹⁰⁰ observed that lambs born to nutrient-restricted ewes had elevated serum IgG at 24 h even after consuming artificial colostrum relative to body weight. Because small intestinal development is affected by maternal nutrition,⁴⁴ it is possible that Ig transport capacity was enhanced, as was observed previously for intrauterine growth restricted neonates.¹⁰² Conversely, both maternal primiparity²³ and heat stress during the dry period¹⁰³ appear to have more consistent negative effects on transfer of passive immunity.

Neonatal thermoregulation and metabolism

Neonatal ruminants are often born into ambient conditions that are outside of their thermoneutral zone, which is more narrow and at higher temperatures than adults.^{104,105} Thermoregulation is accomplished through both shivering and non-shivering thermogenesis, as ruminants are born with brown adipose tissue to provide the latter for use early in life.¹⁰⁶ Most research investigating

the effects of maternal nutrition on the ruminant neonate's ability to thermoregulate has evaluated brown adipose tissue masses (predominantly perirenal fat) and its expression of uncoupling protein 1 (UCP1), which allows for heat production in mitochondria of brown adipose tissue, as reviewed by Symonds et al.¹⁰⁶ and shown in Table 5. Effects of nutrient restriction during late pregnancy are inconsistent,^{107–110} likely based on timing and other factors such as cold stress of the dam.^{25,106} Moreover, lower circulating triiodothyronine (T₃) in neonates born to nutrient-restricted dams^{111,112} suggests that these animals may have more shivering thermogenesis than brown adipose tissue use, as brown adipose tissue must produce T₃ to perform nonshivering thermogenesis.¹⁰⁵

Given the main goal of thermoregulation is to maintain neonatal body temperature, it is surprising that few studies investigated the effect of maternal nutrition on body temperatures of neonates in normal production environments. Our lab observed subtle differences in rectal temperatures of beef calves born to nutrient-restricted dams, but this occurred in a fall-calving experiment in which conditions were closer to thermoneutral.⁷¹ It was previously observed that calves born to both protein¹¹³ and energy¹¹⁴ restricted dams had decreased metabolic rate in thermoneutral conditions. Moreover, lambs born to nutrient-restricted ewes had decreased survival time during starvation in both cold and thermoneutral conditions.¹¹⁵ This is likely due to less brown adipose tissue as well as less white adipose presence at birth.¹¹⁵ Temperature must be regulated and basal metabolism must be maintained before a neonate can grow or develop; thus, it is critical to better understand the effects of maternal nutrition on thermoregulation and its subsequent effects on metabolism.

Nutrient availability to ruminant neonates may be of greater concern than passive transfer following poor maternal nutrition due to lack of colostrum nutrients, challenges of thermoregulation, and altered body stores or metabolic rate. Despite this, neonatal metabolism is not consistently studied in ruminant models of maternal nutrition, especially in those relevant to production agriculture or when whole animal measures shown in Tables 1–5 are considered. When investigated, the metabolites, hormones, and other blood chemistry studied are somewhat conflicting (Table 6; reviewed by Meyer and Redifer²³ for maternal parity). Nevertheless, the data support that maternal nutrition during pregnancy can alter neonatal metabolism, showing decreased nutrients in circulation,^{85,94,116} increased markers of stress,^{71,85,117} and altered circulating hormones^{111,112,116,118,119} or endocrine-related gene expression.¹²⁰ This is likely due to a combination of factors, including fetal nutrient supply and development, parturition difficulty, colostrum yield and quality, and energy stores for mobilization. Overall, potential negative effects of maternal nutrition are additive, resulting in altered metabolism and stress, but rarely are these factors measured concurrently.

Energy substrate use to thermoregulate is an important portion of metabolism for many ruminant neonates. Because ruminant neonates have a glucose deficit in the first hours of life while consuming and digesting colostrum, they mobilize glycogen, begin gluconeogenesis, and mobilize non-esterified fatty acids from adipose to support basal metabolism.¹²¹ Amino acids are also deaminated and used for gluconeogenesis or energy pathways during this period.¹²¹ Ambient temperature is of course less affected by the dam but more influenced by location, climate, season, and management factors (e.g., housing and bedding). These make it necessary to consider the non-nutritional aspects of studies when interpreting results. For example, our lab observed

that neonatal calf metabolism is affected by season of birth, where spring-born calves showed greater energy mobilization and more indicators of stress, but fall-born calves had more signs of dehydration.¹²² In fact, we observed that calves born to first parity dams in a cold environment (spring-born) had greater circulating non-esterified fatty acids from adipose mobilization and urea nitrogen from amino acid deamination, likely to make up for their lower serum glucose while attempting to maintain body temperature.¹²³ In calves born into a more thermoneutral environment (fall-born), circulating glucose and triglycerides were less for calves born to primiparous dams, likely due to colostrum nutrient availability, but without the increase in non-esterified fatty acids or urea nitrogen (Meyer et al., unpublished). This is a good example of why it is especially important to report parturition location, timing (e.g., month or season at minimum), ambient temperatures, and housing or pasture conditions to allow for interpretation of neonatal data.

In addition to considering these factors, timing of sampling of neonatal ruminants is inconsistent and can even vary within an experiment. Our lab reported that beef calf blood chemistry¹²⁴ as well as complete blood cell count⁷¹ change dramatically during the first 48 h of life, and these differ from adult reference intervals. In general, we observe patterns to vary widely from pre-suckling ("0 h") to 24 h of age across multiple datasets, and these patterns diverge between dam nutritional planes⁷¹ and parities¹²³ as well as seasons of birth.¹²² For these reasons, it is critical to establish consistent sampling times, consider using multiple sampling times, select sampling times based on study objectives, and compare neonates to a control population or similar animals in the literature rather than adult reference values.

Neonatal and pre-weaning survival

The ultimate reason to study measures in Tables 1–6 is that all contribute to the neonatal ruminant's ability to survive.¹⁴ As reviewed for sheep by Rooke et al.,²² nutrient restriction at various stages of gestation can result in reduced pre-weaning survival. Despite this, many studies cited there and within this review observed no differences in neonatal or pre-weaning mortality, as many of the experiments were not adequately powered for binomial measures such as morbidity or mortality. Additionally, many studies had intensive or improved management as part of study design or to facilitate data collection, which likely prevented some normal health challenge and death. It is not unusual to need additional disease pressure or challenge to realize differences in mortality. For example, Corah et al.¹²⁵ observed 10% calf death at birth when beef cows were nutrient restricted for 100 d prepartum, but only 3% calf death loss for dams nutrient restricted and then fed a high plane of nutrition for 30 d pre-calving. Results were even more dramatic at weaning, where 19% of remaining calves died pre-weaning for the continuously restricted group, but no death losses occurred for the refed group. This was likely due to scours affecting the herd during this experiment. Although calves born to both groups were affected by scours (52% vs. 33%), this disease presence likely was necessary to cause pre-weaning mortality differences.

Conclusion and future directions

Overall, it is clear that maternal nutrition during pregnancy affects ruminant neonates through a myriad of physiological, metabolic, and behavioral mechanisms. Although improving survival of

ruminant livestock to weaning has long been of interest, more research is needed to understand the mechanisms that cause these neonatal insults. As much of the current focus of developmental programming research remains in the prenatal and later postnatal periods, incorporation of data from the neonatal period in these same studies would improve our understanding of the relationships among production stages. In addition, more integration of the various factors affecting neonates (Figure 1) is needed within individual experiments to establish the major challenges of each ruminant species. Better understanding of the mechanisms underlying negative effects on neonates can allow for improved management practices for both the dam and offspring, which ultimately can improve ruminant livestock neonatal survival.

Neonatal ruminant research is difficult and time-consuming, but this goal can be achieved through the creativity of current and future generations of scientists if they have adequate funding support. Greater collaboration among scientists in this area would allow for increased data collection from individual studies, including adoption of methodologies from other species and disciplines. Additionally, standardization of research approaches and data collection methods would allow for creation of larger datasets and meta-analysis. Together, these approaches can build upon our understanding of ruminant neonates and help them to thrive.

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