

Effect of Maternal Nutrition on Calf Health and Growth

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Abstract

In livestock, just as in humans, there is increasing evidence that production characteristics in livestock may be affected by maternal diet. This so-called metabolic or developmental “programming” of postnatal growth occurs during certain windows of growth characterized by plasticity of metabolic regulatory systems, namely in utero or shortly after birth. Developmental programming in mammals occurs through modification of the chromatin structure of deoxyribonucleic acid (**DNA**), which is heritable. A pregnant cow’s capacity to care for her embryo is largely determined by the way she partitions nutrients to support embryonic, placental, and fetal development together with her own growth, maintenance, and milk production. Production status and energy balance can have a significant effect on how nutrients are partitioned; however, diet during pregnancy is an important modifiable factor that can have a substantial influence on the viability and body composition of the newborn. Nutrition (inadequate or excess) during early gestation can effect development of organ systems, including the liver and pancreas, the mammary gland, gonads, and fat tissue. The effect of nutrition during early gestation on birth weight is variable, however, long-term consequences have been variable. Seventy-five percent of fetal growth occurs during the last trimester and nutrition during late gestation can further impact organ systems, birth weight, and long-term growth. The first weeks of life for a neonate

seem to also have long-lasting consequences on the physiological function of the animal. In fact, many of the effects of fetal programming can be ameliorated or exacerbated due to nutrition of the neonate. Thus, management of the cow herd not only has consequences for cow productivity but also for productivity of the next generation of cows.

Introduction

Effective nutritional management during the transition period has long been recognized as having a major impact on health and productivity of lactating dairy cows. While it is clear that the tremendous changes that occur during the transition period impact the cow, it has increasingly become apparent that nutrient supply and hormonal signaling during conception, gestation, or shortly after parturition can exert permanent changes to metabolism affecting lifetime performance, body composition, and metabolic function of the offspring. Thus, it is likely that the cow of today, with high milk yield but also reproductive and metabolic challenges, is not only a consequence of genetic selection, but also the result of the way her dam was fed and the way she was fed early after birth (Bach, 2012).

The concept that postnatal growth and production is sensitive to direct and indirect effects of maternal nutrition was first proposed by Dr. Barker and co-workers (Barker et al., 2002) based on epidemiological studies investigating low nutrient intake by pregnant mothers experienced during the

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1944 Dutch Famine of World War II and the resulting long-term health implication of their children. The hypothesis suggests that if intrauterine conditions are poor (e.g., poor nutrition), then the fetus becomes adapted through altered gene expression to maximize the uptake and utilization of the nutrients available. Such adaptations cause the progeny to exhibit a competitive advantage if exposed to a similarly poor environment in adulthood. However, favorable postnatal conditions can challenge the individual's homeostatic mechanisms and lead to development of deleterious metabolic conditions, such as obesity, insulin resistance, and type 2 diabetes (Barker et al., 2002). Since the inception of the Barker hypothesis, many terms have been used to categorize this phenomenon, including fetal programming (Barker and Clark, 2002), neonatal programming (Spencer et al., 2011), lactational programming (Hinde and Capitano, 2010), metabolic imprinting (Waterland and Garza, 1999), metabolic programming (Lucas, 2000), and developmental programming (Reynolds et al., 2010) which encompasses all of these developmental phases and concepts.

Developmental programming in mammals occurs through epigenetic changes (Wu et al., 2006). These modifications are mainly due to alterations in the chromatin structure through acetylation of histones or methylation of DNA. As a result, gene expression continues to be modified throughout life without alteration of the DNA sequence. Such a mitotically heritable alteration of gene expression induces a non-genomic tuning of phenotype through developmental plasticity (Crews and McLachlan, 2006). These effects can even be passed on to more than one succeeding generation.

In livestock, just as in humans, there is increasing evidence that production characteristics in livestock may be affected by maternal diet (Wu et al., 2006). Compromised fetal or neonatal growth in livestock has been shown to lead to increased neonatal morbidity and mortality, slow postnatal

growth, increased fat deposition, insulin resistance, and dysfunction of specific organs, including the ovaries, testes, mammary gland, liver, and small intestine (Wu et al., 2006). Potential causes and consequences in dairy cattle have been reviewed recently (Bach, 2012); however, the potential effects on metabolic, immune, and reproductive function, as well as milk performance, of pre- and early postnatal nutrition and management in dairy cattle has not been extensively studied.

Maternal Environment and Fetal Growth

In the United States, poor intrauterine conditions can occur in the cow due to: 1) competition for nutrients between maternal growth and metabolic needs and fetal growth, particularly in peripubertal dams, 2) selection for increased milk production, in which the increased energy demand of lactation competes with the increased energy demand of fetal and placental growth, 3) pregnancy occurring during periods of high environmental temperature (e.g., summer to early fall), or 4) over-nutrition of the dam during gestation during times of supplemental feeding resulting in rapid maternal growth and accumulation of maternal adipose tissue.

A pregnant cow's capacity to care for her embryo is largely determined by the way she partitions nutrients to support embryonic, placental, and fetal development together with her own growth, maintenance, and milk production (Banos et al., 2007). Development of the fetus through gestation is presented in Figure 1. The peri-conceptual period typically coincides with peak lactation in a mature cow and with development of peri-pubertal dams. Thus, the embryo must compete for nutrients with the cow's nutrient demands for lactation and the peripubertal animal's demands for growth. Changing nutrient supply during the peri-conceptual period can have profound impacts on quality of oocytes as well as development of the embryo. Although nutrient requirements for embryonic growth are low during the first trimester, critical events for normal

fetal development occur, including establishment of functional fetal and uteroplacental circulation, organogenesis, myogenesis, and adipogenesis (Robinson et al., 1999; Du et al., 2010). The first trimester typically coincides with early to mid-lactation in a mature cow and with development of peripubertal dams. A poor uterine environment during the first trimester can have a significant impact on development of the mammary gland and subsequent milk production, development of the ovaries and reproductive capability, development of fat tissue stores and ability to maintain body condition, and development of homeostatic mechanisms in the liver and pancreas, with an impact on capacity of the progeny to utilize and metabolize nutrients (Symonds et al., 2010). Examples of developmental programming in livestock models are evident for heart, lung, pancreas, kidney, placenta, perirenal fat, small intestine, muscle, weaning weight, and reproductive performance (Caton et al., 2007).

During the second trimester, the fetus continues to develop and grow, but it will only reach about 25% of the size it will be at birth (Symonds et al., 2010); therefore, the nutritional requirements of the cow do not increase substantially above lactation requirements during this period. During the second trimester, the lactating cow may be in positive energy balance and will be better able to sustain the fetus. The second trimester coincides with mid-to-late-lactation and a poor uterine environment may have an impact on further development of organ systems (Symonds et al., 2010). The majority of fetal development has already occurred by the beginning of the final trimester. However, 75% of fetal growth (increase in tissue size) occurs during this phase (Robinson et al., 1977). The final trimester coincides with late-lactation and the dry period, and a poor uterine environment during the final trimester typically impacts birth weight, with the potential to impact long-term health and growth of the offspring.

Production Status

Dam age

When pregnancy coincides with the continued growth of the first parity mother, the fetus may face intense competition for nutrients from its mother's own metabolic needs. Thus, the normal hierarchy of nutrient (i.e. protein and energy) partitioning between body growth and fetal growth may be altered (Wallace et al., 2006). Age at calving (parity) manifests the state of development of the dam during gestation regarding her own growth. For example, in sheep, progeny from first parity ewes are lighter than progeny from second parity ewes (Bradford, 1972; Bradford et al., 1974), but whether this effect continues with increasing parity (i.e. > 2 pregnancies) was not clear. Fuerst-Waltl et al. (2004) reported in Austrian dual-purpose Simmental cows that as maternal age increased, milk production and longevity were decreased and days to first service were increased in female progeny. Similarly, Banos et al. (2007) observed that daughters of older dams had lower body condition score (**BCS**), produced less daily milk, and needed more days to first service. Banos et al. (2007) also observed that daughters from late calving first parity cows (30 to 36 mo) had a 7% lower BCS, produced 4.5% less milk, and had their first service almost 3 days later than daughters from early calving first parity cows (18 to 23 mo). In contrast, cows whose first parity dams calved later needed fewer inseminations per conception and had fewer returns to estrus (i.e., a higher proportion conceived at first insemination). Early-calving cows, therefore, may produce progeny that mature early, exhibiting the characteristics of high-producing Holsteins cows, but they cannot conceive as easily as cows born to older first-calving dams. Offspring resulting from early second calvings were associated with increased production and improved BCS and fertility (Banos et al., 2007).

Dam age can also impact progeny immunity. Research conducted at Colorado State University (reviewed by Odde, 1988) investigated the relationship between pre-calving nutrition in beef cows and disease susceptibility in the neonatal calf. First-calf heifers produced calves that had lower levels of serum immunoglobulins at 24 hr of age than calves born to cows greater than or equal to 3 years of age. This occurred even though colostrum immunoglobulin concentrations were similar for these 2 age groups. The increased disease susceptibility observed in calves born to first-calf heifers was likely due to lower volumes of colostrum produced by first-calf heifers, although decreased calf vigor as a result of dystocia may have also contributed.

Dam milk production

Milk yield is the key competitor to the fetus for nutrients during gestation and may influence progeny development indirectly in early gestation, when fetal nutrient requirements are low, and then directly later in gestation when they are high. Banos et al. (2007) reported no significant effects of maternal milk production during pregnancy on subsequent offspring milk production in the first lactation. However, Berry et al. (2008) found a negative relationship between milk production of the dam and lactation performance of the offspring in the first and third, but not second, lactations and concluded that the majority of the maternal effects in progeny performance were due to factors other than maternal milk production. The lack of an association between milk production and long-term effects on the offspring may be related to the fact that cows could have been in various states of energy balance (i.e. negative, neutral, or positive). Thus, it may be energy balance, rather than milk yield, that impacts metabolic function of the offspring (Bach, 2012).

The BCS of a pregnant cow is associated with the amount of energy available to her to sustain

growth, maintenance, milk production, and fetal development. A cow's BCS level and change during gestation can be associated with energy balance and her ability to meet the needs of maintenance, lactation, and fetal growth, which can potentially affect the offspring's future performance as a milk-producing cow. Calves born to thin (<5 body condition score) two-year-old beef heifers were less vigorous and had reduced serum immunoglobulin levels at 24 hr of age (Odde, 1988). Banos et al. (2007) observed that as dam BCS increased, daughter BCS and fertility increased, but milk production was slightly reduced. Thus, it is important to avoid BCS losses of the dam or rapid increases in BCS, especially during the second and third trimesters of gestation. Appropriate nutritional strategies in late lactation and the dry period become crucial factors in this respect.

Nutritional Status

Diet during pregnancy is one important modifiable factor that can have a substantial influence on the viability and body composition of the newborn (Symonds et al., 2010). Significant research in livestock has demonstrated that maternal energy under- and over-nutrition can impact adiposity, insulin response, and development of progeny. Protein status of the mother can also impact progeny development but has not been as well studied. With the exception of selenium, which can increase blood flow in key nutrient-transferring tissues, including intestine, placenta, and mammary gland (Grazul-Bilska et al., 2009; Meyer et al., 2010), information concerning the effect of individual nutrients, such as amino acids, fatty acids, vitamins, and minerals, in the maternal diet and their impact on progeny development is scarce.

Early gestation

It is possible that developmental programming of offspring begins as early as the peri-conceptual period. Nutritional status has been

correlated with oocyte quality and embryo survival and are key factors influencing reproductive efficiency (Papadopoulos et al., 2001; Armstrong et al., 2003; Webb et al., 2004). Conflicting results have been reported for the effects of dietary energy density on oocyte quality and early embryonic development in ruminants. A higher proportion of ova from ewes on low energy diets were considered viable compared with those from ewes on high energy diets (McEvoy et al., 1995). However, sheep fed low energy diets had embryos with decreased cleavage rates compared with high energy diets (Papadopoulos et al., 2001). Grazul-Bilska et al. (2006) observed no differences in the number of healthy oocytes collected from superovulated ewes fed at maintenance energy requirements, ewes fed at 60% of maintenance energy requirements, and ewes overfed energy. However, at fertilization, both the overfed and the restricted ewes had reduced successful fertilizations, morulas, and blastocysts, indicating that maternal nutrition (both inadequate and excess) before mating can have profound impacts on oocyte quality and fertilization rates. These observations suggest that nutritional status during the peri-conceptual period is highly important to fertility and that some fetal programming may actually begin in the oocyte before mating occurs. In fact, lambs of ewes fed at 70% of nutritional requirements from 30 days prior to mating until 100 days of pregnancy had higher neonatal mortality rates, were lighter at birth, and grew more slowly after weaning than those fed at 100% of estimated requirements (Nordby et al., 1986, 1987). For cows, positive (Kendrick et al., 1999; Boland et al., 2001), negative (Armstrong et al., 2001), or no effects (Tripp et al., 2000) of plane of nutrition (high vs. low energy diets) on oocyte quality, fertilization rate, and early embryonic development have been reported.

The placenta plays a major role in the regulation of fetal growth. Establishment of functional fetal and uteroplacental circulation is one of the earliest events during embryonic and placental

development (Patten, 1964; Ramsey, 1982). It has been shown that the large increase in transplacental exchange, which supports the exponential increase in fetal growth during the last one-half of gestation, depends primarily on the dramatic growth of the uteroplacental vascular beds during the first one-half of pregnancy (Meschia, 1983; Reynolds and Redmer, 1995). In beef cattle, under-nutrition of ~75% of recommended allowance during early stages of pregnancy compromises placental angiogenesis, cotyledon weight, and thus, fetal development (Vonnahme et al., 2007). Upon realimentation, Vonnahme et al. (2007) observed that fetuses in both groups were similar in weight near term. Previous studies with sheep have demonstrated that an extended period of maternal nutrient restriction during the first half of gestation results in relatively normal birth weights but leads to increases in the length and thinness of the neonate, increases in adiposity, and suppressed glucose tolerance (Whorwood et al., 2001; Bispham et al., 2003; Ford et al., 2007). Gardner et al. (2005) demonstrated that increased adiposity as a result of early fetal restriction can persist to 1 year of age.

Overnutrition can also impact placental development and development of progeny. It has been reported that over nourishing singleton-bearing adolescent ewes results in rapid maternal growth and accumulation of maternal adipose tissue (Wallace et al., 2006). As a result, placental growth was restricted 30 to 40%, and ewes delivered lambs prematurely that were 20 to 30% lighter at birth compared with moderately nourished adolescents of similar age. Furthermore, over-nourished ewes produced less colostrum and progeny had lower growth from birth to weaning (Da Silva et al., 2001).

The first trimester of fetal life coincides with the peak in the number of follicles and oocytes in fetal ovaries (Erickson, 1966), although ovarian folliculogenesis in the bovine fetus is not completed until late gestation (Rhind et al., 2001). Borwick et al. (1997) reported retarded ovarian development

in fetuses from ewes fed 50% of energy requirements from breeding through mid-gestation when compared with dams fed 150% of energy requirements during that same period. Similarly, Grazul-Bilska et al. (2009) identified that fetuses collected at 135 days of gestation from ewes that were nutritionally restricted from 50 to 135 days of gestation had reduced proliferation of ovarian primordial follicles when compared to fetuses of adequately nourished ewes. This compliments data in beef cattle which have illustrated a reduced number of antral follicles present in heifers born to nutritionally restricted dams during the first trimester of gestation (Mossa et al., 2009; Echterkamp et al., 2012). While reproductive development and efficiency may be influenced in the offspring of nutritionally altered dams, we know that epigenetic modifications to the genome are heritable, and therefore, alterations in reproductive capacity may not be relegated to the first generation. Blair et al. (2010) reported a trans-generational effect of maternal nutrition during early pregnancy on reproductive capacity of descendants. Fewer grand-offspring resulting from over-nourished, lightweight ewes reached puberty prior to their first breeding season when compared with limit-fed, lightweight grand-dams or heavyweight grand-dams regardless of nutrition.

Studies investigating protein supplementation of cows during early gestation have reported alterations in the placental environment that can impact embryonic development. Research in dairy cattle has reported that high protein diets increased concentrations of blood urea nitrogen (**BUN**) and milk urea nitrogen (**MUN**), resulting in decreased pregnancy rates, conception rates, and embryonic development (Blanchard et al., 1990; Butler et al., 1996; Rajala-Schultz et al., 2001). Specifically, a BUN above 19 mg/dL decreased preimplantation embryo development and survival in sheep (Butler et al., 1996); whereas, BUN concentrations below 10 mg/dL did not (Rajala-Schultz et al., 2001). Sullivan et al. (2009) identified

in *Bos indicus*-cross beef cows that high crude protein (**CP**) concentrations during mid-gestation reduced primordial and primary follicle density in female progeny at 23 months of age. Furthermore, Sullivan et al. (2010) reported that excess maternal dietary CP during the first trimester of gestation resulted in decreased follicle stimulating hormone (**FSH**) concentrations, seminiferous tubule diameter, and testicular volume in male offspring at 5 months of age. This decrease in fertility may be mediated through changes in the uterine environment. Research by Elrod et al. (1993) and Elrod and Butler (1993) found that excess protein decreased uterine pH on day 7 of the estrous cycle compared to those fed a balanced diet. Changes in uterine pH are important due to the effect pH has on embryo development and survival. Ocon and Hansen (2003) reported that in vitro culture of bovine embryos below a pH of 7.0 resulted in decreased cleavage rates and development to blastocyst stage.

Although excess protein may negatively impact early embryonic development, moderate increases in protein during the later stages of early gestation may be beneficial. The amino acid arginine is the substrate for nitric oxide (**NO**) synthesis (Flynn et al., 2002), which is a known vasodilator, and when used as a therapeutic agent, has increased birth litter weight in pigs (Mateo et al., 2007) and birth weight in humans (Vosatka et al., 1998). Therefore, it is conceivable that increased dietary protein could result in greater amounts of arginine in the diet, resulting in increased uteroplacental blood flow and subsequent birth weights. In fact, Sullivan et al. (2009) reported that increased dietary protein during the first 2 trimesters of gestation increased the number of placental cotyledons in first-parity *Bos indicus* heifers, and Vonnahme et al. (2011) reported increased uterine blood flow in protein supplemented ewes when compared with a control.

Late gestation

Energy demand by the gravid uterus is greatest during the last trimester (Ferrell et al., 1976), and supply of glucose and amino acids to the gravid uterus are important substrates for fetal growth. Providing an adequate supply of nutrients to the fetus has the potential to increase birth weights and has significant implications for subsequent growth, as birth weights are positively correlated with calf growth rate to weaning and live weight at weaning when calves are reared on their dams (reviewed in Greenwood et al., 2010). Energy deficiency (70% of recommendations) in primiparous beef cows during the last 100 days of pregnancy in beef cattle was reported to decrease calf birth weight, weaning weight, and delayed age at puberty of the progeny compared to heifers from dams adequately fed during the last 100 days (Corah et al., 1975). Furthermore, Corah et al. (1975) observed that progeny born to energy-restricted cows had increased rates of morbidity and mortality. In sheep, energy restriction during the last trimester has been generally shown to decrease birth weights, but a reduction in postnatal growth may or may not persist through weaning and 1 year of age, depending on adequacy of postnatal diets (reviewed in Greenwood et al., 2010). When ewes are undernourished during lactation, growth restriction of progeny persists, but when ewes are adequately nourished during lactation, growth restriction of progeny does not persist. Thus, it appears that direct prenatal effects on capacity for growth of the progeny are somewhat ameliorated or exacerbated depending upon the postnatal environment into which they are born (Greenwood et al., 2010).

As lactation and gestation progresses in the dairy cow, she moves from a negative to a positive energy balance. Excess energy during this period has the potential to increase glucose supply to the fetus and lead to increased risk of glucose intolerance and obesity in the offspring, as seen in other species (Buchanan and Kjos, 1999).

Increased maternal body weight (**BW**) and plasma triglycerides have been linked to an increased fatty acid transfer to the fetus in humans, thereby inducing increased birth weight and adiposity (Heerwagen et al., 2010). In sheep, decreased glucose effectiveness and insulin sensitivity, increased appetite and gain, increased carcass adiposity, and increased weight at 19 months of age were observed in progeny from gestating ewes fed 150% of energy requirements to an obese body mass index (Long et al., 2010).

Source of energy in late-gestation beef cow diets also appears to impact fetal growth and development. Loerch (1996) reported that limit feeding a high grain diet to beef cows during late gestation resulted in heavier birth weight calves compared to cows fed an isocaloric hay based diet; however, inconsistent results were reported for weaning weight (Loerch, 1996). In contrast, Susin et al. (1995) reported similar birth weights and postnatal growth of lambs from ewes limit-fed a corn-based gestation diet similar to the studies conducted in cows (Loerch, 1996).

Puberty and lifetime reproductive efficiency may also be altered by maternal energy because ovarian folliculogenesis in the bovine fetus is not completed until late gestation (Rhind et al., 2001). Da Silva et al. (2002; 2003) observed a decrease in antral follicle counts of ewe lambs resulting from dams fed a high plane of nutrition during late gestation. Long et al. (2010) reported that ewes born to dams that were nutrient restricted during mid-gestation had reduced circulating concentrations of progesterone during the luteal phase of their estrous cycles, and fewer of those offspring gave birth to a lamb during their first parturition. Cushman et al. (2012) demonstrated that heifers born to mature cows (≥ 3 years of age) fed 125% of nutritional maintenance requirements during the third trimester of gestation conceived earlier in their first breeding season than those born to dams fed either 75 or 100% of nutritional maintenance requirements during that period.

Studies investigating protein supplementation of cows during late gestation have reported long-term impacts on their progeny. In a recent review, Vonnahme and Lemley (2012) reported that providing protein supplementation to cows beginning on day 190 of gestation resulted in a doubling of uterine blood flow when compared with non-supplemented cows. It is hypothesized that increased uterine blood flow may increase progeny performance, owing to increased nutrient transfer to the fetus. Gestating ewes fed a diet high in urea had progeny who went on to exhibit increased rates of metabolism and growth compared to progeny from those ewes not supplemented with urea (McEvoy et al., 1997). Singleton fetuses from ewes consuming a high-protein diet during late gestation were heavier on day 130 of gestation compared with fetuses from ewes consuming the low-protein diet, with no differences in placental weight (Camacho et al., 2010). Heifer progeny from the dams supplemented with protein had heavier BW at weaning and breeding compared with progeny from dams not supplemented with protein (Martin et al., 2007).

With regard to maternal protein and reproductive development of the progeny, maternal protein supplementation during late gestation has been shown to increase the probability of female progeny reaching puberty prior to the first year of breeding (Funston et al., 2010). Specifically, more heifers born to cows that grazed winter range and were supplemented with a 28% CP supplement during late gestation were pubertal at initiation of the first year of breeding when compared with progeny of cows not receiving a supplement. In another study, protein supplementation to cows grazing winter range during late gestation produced heifer progeny that had greater pregnancy rates during their first year of breeding and calved earlier during their first year of calving (Martin et al., 2007). Collectively, these results provide evidence that an individual component of the maternal diet, such as protein, can impact heifer progeny reproductive

development as well as steer progeny growth and body composition.

Distillers dried grains with solubles (**DDGS**), a byproduct of ethanol fermentation, contains elevated concentrations of fat and protein and is an alternative energy source used by beef cow producers. Although feeding fat as an energy source to beef cows in the form of sunflower or soybean oil (1.87 lb/day) did not impact progeny birth weights or performance (Alexander et al., 2002). Research that we have conducted at Purdue University (Gunn et al., 2011a), as well as research conducted by others (Radunz et al., 2010; Radunz et al., 2012; Wilson et al., 2012) have demonstrated that when DDGS is fed to gestating (third trimester) and lactating beef cows to meet energy requirements, increased progeny birth weights result compared to beef cows fed hay-based or corn-based diets with similar energy concentrations. However, problems with dystocia have been observed (Gunn et al., 2011a). The effect of maternal DDGS on postnatal progeny weight gain has been variable. In male progeny fed in the feedlot, weaning and yearling weights did not differ (Radunz et al., 2010; Gunn et al., 2012a; Radunz et al., 2012), however, female progeny from DDGS treated dams tended to be heavier than progeny from corn silage/hay treated dams throughout the developmental post-weaning period (Gunn et al., 2012b). In addition, DDGS progeny had a greater frame score than control progeny throughout the developmental period. Progeny from DDGS fed cows have not differed in blood glucose or insulin concentrations, glucose clearance, morbidity, or immunoglobulin concentrations (Radunz et al., 2010; Gunn et al., 2012a; Radunz et al. 2012).

The effect of DDGS on reproduction is similar to the effect that protein has had on reproduction. Gunn et al. (2011b) observed that ovarian size, antral follicle count, follicular growth parameters, and age at puberty in progeny did not differ due to maternal supplementation of DDGS.

However, BW at puberty and pregnancy rates to artificial insemination (AI) were greater in DDGS progeny compared to non-DDGS fed progeny (70.6 vs. 33.3%). Overall breeding season pregnancy rate did not differ. Rate of dystocia in female progeny at first parturition and grand-offspring birth BW did not differ due to treatment. It is unclear if source of energy or overfeeding of protein caused these effects.

Neonatal Programming

The first weeks of life for a neonate seem to also have long-lasting consequences on the physiological function of the animal. In fact, many of the effects of fetal programming can be ameliorated or exacerbated due to nutrition of the neonate. In beef cows, Freetly et al. (2000) demonstrated that effects of variable nutrition during mid and/or late pregnancy on weight at birth are overcome when adequate, high quality postnatal nutrition is available and resulted in no differences in calf BW at 58 days of age. Right after birth, the first nutrients consumed by calves are from colostrum. In addition to nutrients, colostrum is also rich in immunoglobulins (Ig), growth factors, and hormones. DeNise et al. (1989) demonstrated a positive and significant relationship between plasma IgG concentrations and future milk production of calves that were allowed to suckle their dams for the first 24 hr of life. Other factors in colostrum could also influence subsequent production. Hough et al. (1990) observed that although maternal under nutrition did not affect colostral IgG concentrations, calves born to nonrestricted cows that received colostrum from restricted dams tended to have lower serum IgG concentrations at 24 hr of life than those receiving colostrum from well-nourished cows.

In modern dairy calf rearing systems, the restricted feeding of milk replacer and the early weaning of calves are practiced to lower costs. There is increasing evidence, however, that intensified

early nutrition may not only improve the health, well-being, and growth of the calf in the short term, but may also have a long-term positive impact on performance (Jasper and Weary, 2002). Findings of Tudor and O'Rourke (1980) with calves reared on milk replacer, coupled with studies in which calves are reared on their dams (Café et al., 2006), show that the postnatal maternal contribution to preweaning growth of calves is substantial. A positive relationship between milk intake and dry feed intake exists when considering the entire preweaning period, indicating that the influence is through increasing the capacity of the calf to consume feed (Christian et al., 1965). In fact, some have reported that increased gain in dairy calves during the first 2 mo of life results in significantly greater BW at 24 mo of age (Robelin and Chilliard, 1989; Moallem et al., 2010), reduced breeding age (Raeth-Knight et al., 2009), and higher milk yield when the calf matures (Moallem et al., 2010). One possible explanation for increased milk yields could be the influence of early feeding levels on the development of the mammary gland. A high feeding level during the first 8 weeks of life was accompanied by an intensified development of the mammary parenchymal mass, DNA, and RNA of Holstein heifer calves compared to moderately fed controls (Brown et al., 2005). Interestingly, the first weeks of life were found to be most influential because a higher feeding intensity between weeks 8 and 14 of life did not affect the development of the mammary gland (Brown et al., 2005). Composition of milk has also been suggested as an important source of variation in calf performance. Christian et al. (1965) observed that maternal milk composition accounted for more of the variability in weaning weight and pre-weaning gain than total milk intake during this period. With respect to body composition, increasing the percentage of milk replacer protein has been demonstrated to increase body protein and decrease adiposity compared with lower levels of protein (Donnelly and Hutton, 1976; Diaz et al., 2001). Additionally, decreasing milk replacer fat content decreases body fat percentage with no effect on protein (Tikofsky et al., 2001).

Research conducted at Purdue University (Shee et al., 2012) has demonstrated that feeding DDGS to cows from calving to mid lactation (129 DIM) increased male progeny gain and weight at weaning (219 DIM) compared to male progeny from cows fed a corn silage based diet. The diets were isocaloric but differed in fat and protein contents. As a result, milk composition of the cows was altered and may have been responsible for changes in growth. Feeding DDGS to cows from calving to mid lactation did not affect milk production but decreased milk fat and protein, increased the percentage of long-chain, monounsaturated and polyunsaturated fatty acids (FA) in milk, including conjugated linoleic acid (CLA), and decreased the percentage of medium-chain and saturated FA. Specific FA and level of unsaturation of the FA in maternal milk can impact growth of progeny. In rats, maternal consumption of a highly unsaturated or highly saturated FA diet results in lower birth weights and decreased postnatal weight gain (Siemelink et al., 2002). Shee et al. (2012) observed that the weight advantage for male progeny whose dams were fed DDGS was not maintained through slaughter; however, intramuscular fat content was decreased in the male progeny of DDGS-fed cows, indicating that maternal DDGS could impact progeny body composition.

Conclusion

Unfortunately, there is a lack of studies in dairy cattle that demonstrate direct effects of maternal nutrition on postnatal performance of offspring; however, numerous studies in beef cattle and sheep demonstrate that both energy and protein (inadequate or excess) can effect long-term productivity of progeny. Thus, management of the cow herd not only has consequences for cow productivity but also for productivity of the next generation of cows. Fortunately, management of the neonatal calf can ameliorate many of the negative consequences of poor fetal nutrition. Data are lacking on the effect of specific nutrients (FA, amino

acids, vitamins, and minerals) on long-term performance of offspring and further research is needed to determine these effects and understand the underlying mechanisms.

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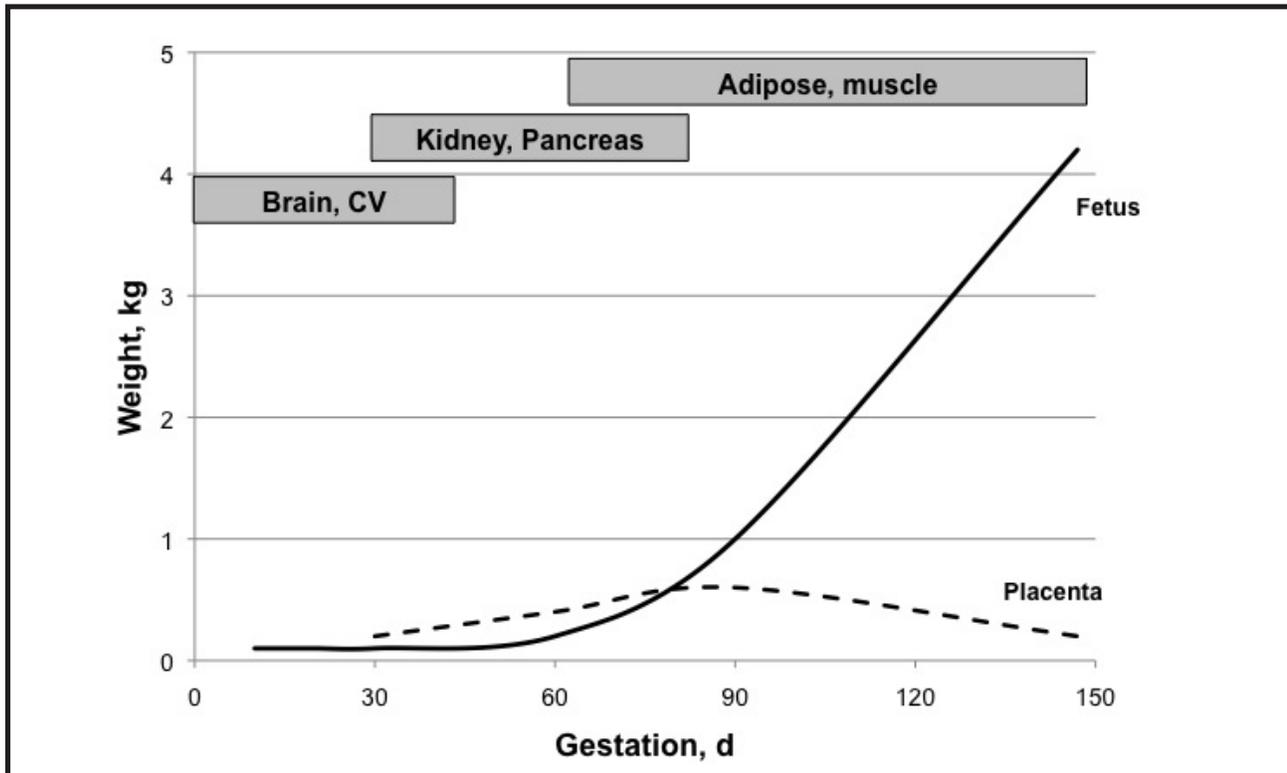


Figure 1. Sheep conceptus growth and development in gestation and periods of specific organ development that can be influenced by maternal nutrition (CV = cardiovascular system; Symonds et al., 2010).