

Nutritional Management during Gestation: Impacts on Lifelong Performance

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Introduction

Effective nutritional management during gestation has long been recognized as an important component of sound livestock production practices (Bull and Carroll, 1937; Barcroft, 1946; Morrison, 1949; Maynard and Loosli, 1956; Crampton and Lloyd, 1959; NRC, 1970). Recent observation in the area of developmental programming (Barker et al., 1992; Barker et al., 1993; Godfrey and Barker, 2000; Barker, 2004) has elevated the concept of maternal onset of adult disease and lifelong performance to the forefront of investigation in several national and international laboratories. In addition, the 2007 Aspen Perinatal Biology Symposium <http://www.med.uc.edu/obgyn/aspen/index.html> and the 2007 5th International Congress on Developmental Origins of Health & Disease, which is sponsored by the International Society for Developmental Origins of Health and Disease <http://www.congresswest.com.au/dohad/index.html> both focus on developmental programming and have major sections that highlight relevance in animal agricultural. Clearly, research in these directions with livestock species (and other animal models) has and will likely continue to produce relevant data for both livestock and biomedical interests. In this report, several aspects of existing data with livestock species are reviewed and potentially relevant aspects to both livestock management and biomedicine are highlighted. The importance of nutritional management during gestation in regards to fetal programming, livestock production, and human health are addressed. Impacts of nutritional management during gestation on outcomes during the peri-conceptual period, fetal growth and development, birth to weaning, and weaning to adulthood are also discussed.

Nutritional Management During Gestation

The importance of nutritional management during pregnancy to the ruminant livestock industry is somewhat self-evident. Certainly from a production efficiency standpoint, nutritional management during gestation is of the utmost importance. Larger

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ruminants have long gestational periods and producing females that come up open are usually culled from the herd, which further emphasizes the importance of proper nutritional management during pregnancy and the peri-conceptional period.

Pregnancy is energetically costly. Data from Brody (1938) and Ferrell et al. (1976) summarized in **Figure 1** indicate that in beef cattle, energy expenditure increases by as much as fifty percent in pregnant cows during the last trimester of

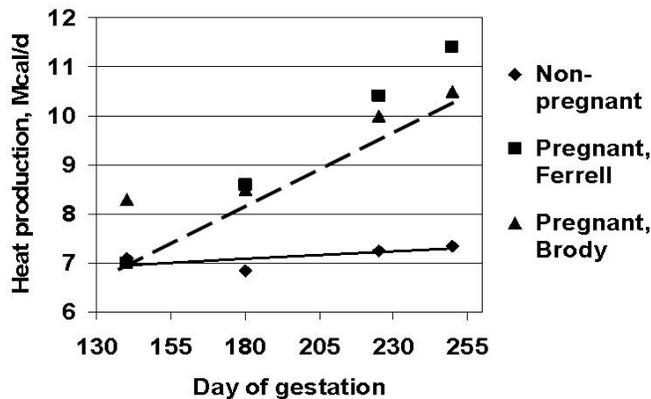


Figure 1. Energy expenditure in cows during the last half of gestation. Data adapted from Brody (1938) and Ferrell et al. (1976). Data are conceptually similar for other mammals.

gestation. Data from NRC (NRC, 1996) allows for comparing replacement heifers with mature cows. As shown in **Figure 2** (following page), in the ninth month of gestation the net energy required to support pregnancy is 38.6 percent of the total energy in cows and up to 34.9 percent of the energy demands of pregnant heifers. Increased energy demand associated with advancing gestation cannot be completely explained by increasing energy demands of the fetus. Scheaffer et al. (2003) concluded that a portion of increased energy demand associated with gestation could be accounted for by service functions associated with visceral tissues.

Ferrell and Jenkins (1985) reported that 70 to 75 percent of total annual energy requirements of typical cow types used in North American beef production were used for tissue maintenance functions. Data summarized by Webster (1989) demonstrates vast differences between ruminants and non-ruminants in the amount of energy expended on maintaining parent populations of livestock production systems. Unlike non-ruminant species, parent populations of ruminant livestock consume over 50% of the total energy associated with product formation (Webster, 1989). Total production herd energy expenditure for maintenance can range from 60 to 90% of total energy use (Caton and Dhuyvetter, 1996) depending upon location and production management systems used. Maintenance energy expenditure is defined as the energy needed for basal processes plus some minimal amount of work; or, as the amount of energy needed to maintain energy balance in the absence of product formation (Ferrell, 1988; Baldwin, 1995). While it is clear from existing data that metabolic costs associated with maintenance of cow herds are high, it should also be pointed out that the largest portion of out-of-pocket costs in beef production systems is related to total feed costs. Hughs (1998) reported that average feed costs represented 61% of total annual costs of production. Clearly most of the feed energy and, therefore, associated economic costs are partitioned towards maintenance functions. Consequently, if metabolic costs associated with whole animal maintenance (energy and other resources) are reduced

by production and management practices, then total cash outlay for maintaining the production herd would likely be reduced.

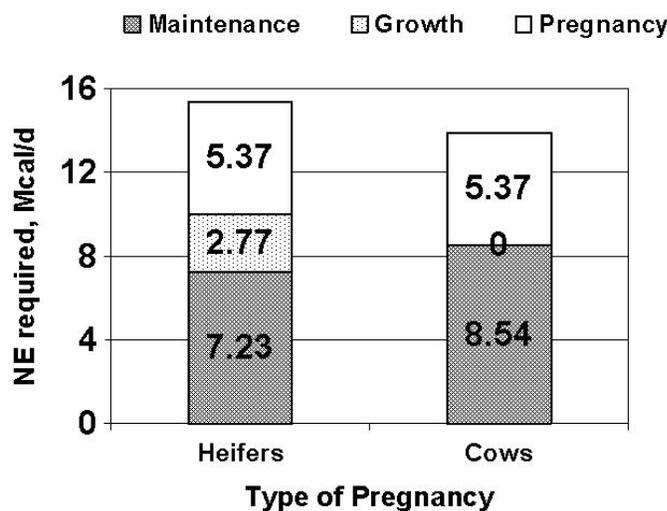


Figure 2. Energy requirements during the last month of gestation in cow. By the end of pregnancy, NE required to support the pregnancy (5.37 Mcal/d) is 38.6% (cows) to 34.9% (heifers) of daily NE requirements.

As demonstrated below and in several excellent reviews (Ferrell and Jenkins, 1985; Cant et al., 1996; Goetsch, 1998; Seal and Parker, 2000; Caton et al., 2000), visceral tissues (particularly the intestine and liver) are very metabolically active and consume large portions of whole animal energy expenditure. In addition, intestinal tissues are essential for nutrient absorption and thus for product formation. In reviewing the work of several authors (Smith and Baldwin, 1974; Ferrell, 1988; Webster, 1981; Webster, 1989; Baldwin, 1995), it can be concluded that, on the average, the viscera and internal organs (heart, kidney, digestive tract, and liver) consume 55% of total energy use in ruminant species.

This figure is impressive when one realizes that the same tissues represent only 6 to 7% of empty body mass (Ferrell, 1988). Therefore, attempts at understanding and manipulating whole animal production and metabolism towards more product formation and less maintenance cost should consider these highly active visceral tissues.

Perhaps of equal importance and even more relevant to the current review, is the fact that internal organs are subject to the effects of developmental programming. Examples of developmental programming in livestock models are evident for heart (Han et al., 2004), lung (Gnanalingham et al., 2005), pancreas (Limesand et al., 2005; 2006), kidney (Gilbert et al., 2007), placenta (Reynolds et al., 2006), perirenal fat (McMillin et al., 2004; Matsuaki et al., 2006), small intestine (Greenwood and Bell, 2003; Caton et al. unpublished), muscle (Zhu et al., 2006), and weaning weight and reproductive performance (Martin et al., 2006)

Investigation into effective nutritional management during gestation in livestock has relevance in two primary directions. First, efficient production of a high quality food supply that is both profitable to the industry and safe for consumers in both an industry and a national priority. Second, increased insight into fundamental mechanisms associated with nutritional management during gestation in large animal models can provide keen insight into fundamental mechanisms of developmental programming and fetal onset of adult disease and dysfunction. Consequently, animal experiment stations with scientists working in basic areas of biology find themselves uniquely positioned to

address both livestock production issues and mechanistic biomedical questions within common research programs that have applications across species.

The importance of animal models to addressing mechanistic and clinical aspects of relevant biomedical research questions is clearly recognized in the broader scientific community. The National Heart, Lung, and Blood Institute recently convened a working group (September 2005) entitled “The Influence of Early Programming in the Development of Cardiovascular, Lung, Blood, and Sleep Disorders.” This working group was preceded by a workshop entitled “The Intrauterine Environment: Long Term Consequences for Obesity and Metabolic Disorders” (<http://www.niddk.nih.gov/fund/other/maternalobesity/>), which was cosponsored by four NIH institutes (NIDDK, NHLBI, NICHD, and NIEHS). One of the eight recommendations (<http://www.nhlbi.nih.gov/meetings/workshops/earlyprg.htm>) arising from the discussions was to develop new animal models and refine old ones to evaluate phenotypes and development of physiological pathways. In a recent NIH RFA (RFA-DK-05-014) entitled “The Obese and Diabetic Intrauterine Environment: Long-term Metabolic or Cardiovascular Consequences in the Offspring” one of the suggested potential research topics was “Development of appropriate animal models to facilitate determination of the relative roles of the genetic, maternal in utero environment, and post-natal environment.” Clearly animal models are widely recognized as essential components of cutting edge research in developmental programming.

Fetal Programming, Livestock Production, and Human Health

Fetal programming has also been termed the Barker Hypothesis or, more recently, developmental origins of health and disease. The concept that a maternal stimulus or insult at sensitive periods of fetal development could have long-term effects has been termed “Fetal Programming” and was originally championed by Dr. David Barker, at Southampton University in England (Barker et al., 1993; Godfrey and Barker, 2000; Barker, 2004). Barker and his colleagues studied birth records in the United Kingdom and Europe, and related different maternal stresses to infant weight and physical characteristics at birth and to subsequent health status in later life. They found maternal undernutrition in the first half of gestation, followed by adequate nutrition from mid-gestation to term, resulted in infants of normal birth weight, which were proportionally longer and thinner than normal. This early fetal undernutrition resulted in an increased incidence of health problems experienced by these individuals as adults, including obesity, diabetes, and cardiovascular disease.

The data of Godfrey and Barker (2000) demonstrates that standard mortality ratios in men and in women decline as birth weight goes up. Their data further indicates that low birth weight infants have a tendency to have a higher mortality ratio from coronary heart disease. So low birth weight infants are at greater risk from coronary heart disease compared with higher birth weight infants.

In livestock production systems it has been known for decades that adequate birth weight is related to survival and productivity. Moule et al. (1956) summarized data

in sheep that indicates that as birth weight goes from about 2 to about 4 kg the percent mortality ratio drops dramatically. In fact, in their data set lamb birth weights of approximately 1 kg results in a percent mortality ratio of almost 100. So, birth weight we know is very important in livestock species in regard to mortality ratios. In addition, most livestock producers would argue that birth weight is very important to postnatal and even lifelong performance.

Most early work investigating the effects of maternal nutrition in the cow studied the latter part of pregnancy. Since most fetal growth occurs in the latter part of gestation, researchers hypothesized that the effects of variation in nutrient intake would be greater in late compared with early pregnancy. Cow nutrition precalving has also been shown to affect calf survival. Corah et al. (1975) reported that pregnant cows fed 70% of their calculated energy requirements during the last 90 days of gestation produced calves with increased morbidity and mortality rates. Research conducted at Colorado State University (reviewed by Odde, 1988) investigated the relationship between precalving nutrition and disease susceptibility in the neonatal calf. First-calf heifers produced calves that had lower levels of serum immunoglobulins at 24 hours 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 two 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. Calves born to thin (< 5 body condition score) two-year-old heifers were less vigorous and had reduced serum immunoglobulin levels at 24 hours of age.

Undernutrition of pregnant cows during the initial stages of fetal development may appear to be unimportant because of the limited nutrient requirements of the fetus for growth and development during the first half of gestation. This is accentuated by the fact that 75% of the growth of the ruminant fetus occurs during the last two months of gestation (Robinson et al., 1977). However, it is during this early phase of fetal development that maximal placental growth, differentiation, and vascularization occurs, as well as fetal organogenesis, all of which are critical events for normal conceptus development.

Recently, Vonnahme et al. (2004) reported that multiparous beef cows bred to the same bull, carrying female fetuses, and fed to meet NRC requirements gained weight (average = + 4.25% body weight) from d 30 to d 125 of gestation and had fetuses which were heavier compared with cows fed below NRC, which lost weight (average = - 6.8% body weight). Upon realimentation, fetuses in both groups were similar in weight near term. Previous studies in sheep (Whorwood et al., 2001) and humans (Ravelli et al., 1988; Barker et al., 1993; Godfrey et al., 1996) 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 increased length and thinness of the neonate. The clinical significance of epidemiological data of fetal programming lies in the associations between transient reductions in maternal nutrition during early gestation, and the risk of abnormalities in skeletal muscle function,

mineralization of bone, liver cholesterol metabolism, insulin secretion, renal development and obesity (Godfrey and Barker, 2000; Rhind et al., 2001). Unfortunately, at present, little is known about specific nutrient induced changes in fetal programming that results in observed permanent alterations in adult structure, physiology and metabolism in either livestock or humans.

In humans there is considerable drama and a growing body of data associated with concepts of fetal programming and nutritional management during pregnancy. Perceptions, risks, and benefits of nutritional modulation during pregnancy and developmental origins of adult disease have caught the eye of popular press as evident in the fairly recent Newsweek report (1999) “Where Health Begins – Obesity, Cancer and Heart Attacks – How Your Odds Are Set in the Womb,” or if you look at a Time special report from November 11, 2002, “Inside the Womb – An Amazing Look At How We All Begin, Plus The Latest Science On How Healthy Babies Are Born,” you can see how the popular press and general public is very aware of concepts surrounding nutritional perturbations during pregnancy and lifelong health and wellbeing. In addition, Roberts et al. (2000) indicated that, in humans, compromised fetal or neonatal growth leads to an increased risk of developing “Syndrome X” in adulthood. Syndrome X is defined as a combination of clinical issues, which are interrelated and include insulin resistance, dyslipemia, obesity, and cardiovascular disease.

Many or all of these post-natal problems, as I mentioned before, occur in livestock and likely in humans and they likely contribute substantially to reduced productivity in livestock and reduced health and well being in humans. The hidden cost of reduced productivity in livestock may be a real disconnect between the genotype being select for, and the phenotype actually use for selection.

The Peri-conceptual Period

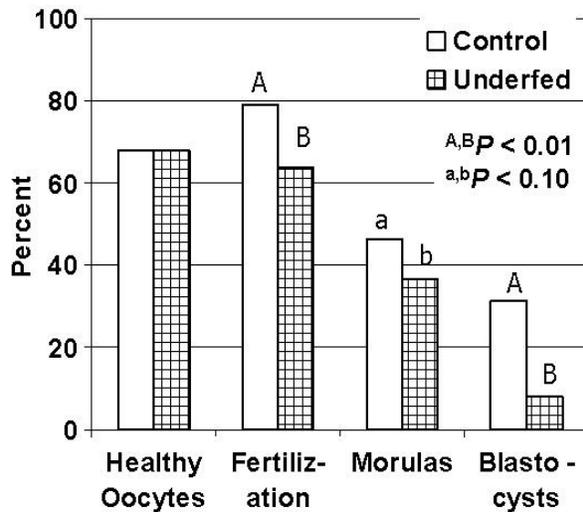


Figure 3. Effects of maternal nutrition before mating on oocyte quality (Borowczyk et al., 2006). Underfed ewes were provided 60% of the nutrients offered controls.

Nutritional status is a major factor influencing an animal’s ability to reproduce (Robinson, 1990; Webb et al., 1999; O’Callaghan et al., 2000). Nutrition has a significant impact on numerous reproductive functions including hormone production, fertilization and early embryonic development (Boland et al., 2001; Armstrong et al., 2003; Boland and Lonergan, 2005). Changing nutrient supply during the peri-conceptual period can have profound impacts on reproduction. Nutritional status has been correlated with embryo survival and is a key factor influencing efficiency in assisted reproductive technologies (Armstrong et al., 2003; Webb et al.,

2004). Conflicting results have been reported for the effects of low or high energy diets on oocyte quality and early embryonic development in ruminants (Kendrick et al., 1999; Boland et al., 2001; Papadopoulos et al., 2001). For example, sheep fed low energy diets have embryos with decreased cleavage rates compared with high energy diets (Papadopoulos et al., 2001). In contrast, 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). For cows, positive (Nolan et al., 1998; Kendrick et al., 1999; Boland et al., 2001), negative (Yaakub et al., 1999; 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.

Recent studies (Borowczyk et al., 2006; Grazul-Bilska et al., 2006) at North Dakota State University have investigated the effects of maternal plane of nutrition prior to superovulation and in vitro fertilization on oocyte quality and embryonic development. In the first study (Borowczyk et al., 2006) control ewes were fed at maintenance and an underfed group was fed at 60% of controls. After eight weeks ewes were superovulated, oocytes collected and evaluated, in vitro fertilization rates of oocytes determined, and viability to morula and blastocysts states of embryos determined (**Figure 3**). There were no differences in the number of healthy oocytes collected from control and restricted ewes. However, at fertilization, restricted ewes produced oocytes that fertilized more poorly. In addition, morulas and blastocysts, were less in the underfed group.

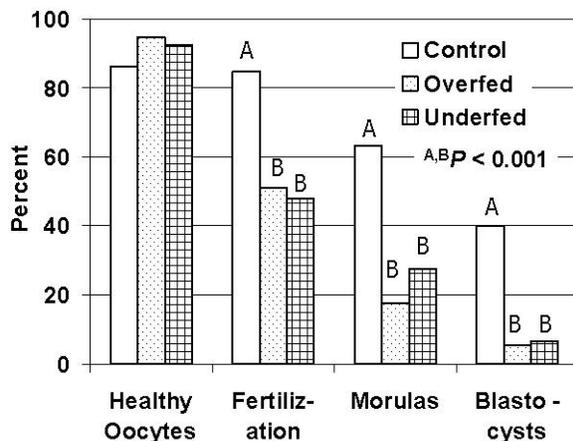


Figure 4. Effects of maternal nutrition before mating on oocyte quality (Grazul-Bilska et al., 2006). Underfed ewes were provided 60% of the nutrients offered controls. Overfed ewes were offered diets ad libitum.

To follow-up on this study (**Figure 4**), the same group of researchers added an additional treatment (Grazul-Bilska et al., 2006). In the second study, which was also with ewes, these researchers had a control group, which maintained body weight and condition score (adiposity) through an 8 week pre-superovulation period, an overfed group that increased adiposity, and a restricted group that lost weight. The overfed group was fed ad libitum and the restricted group was fed 60 percent of controls. After 8 weeks ewes were superovulated and oocytes collected. As we can see in **Figure 4**, there was no difference in the number of characterized healthy oocytes in control, overfed, and

restricted ewes. 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 nutritional status during the peri-conceptual period is highly important to fertility and, perhaps, to fetal programming. Certainly their data begs the question, "Where does fetal programming begin?" Much of the work that is published in the literature looks at various stages of gestation and impacts of nutrition; but their work suggests that some fetal programming may actually begin in the oocyte before mating occurs.

Maternal Nutrition and Fetal Growth

Maternal nutritional status is one of the factors programming nutrient partitioning and ultimately growth, development, and function of the major fetal organ systems (Wallace, 1948; Wallace et al., 1999a; Godfrey and Barker, 2000; MOD, 2002b, Barker, 2004). Prenatal growth trajectory is sensitive to the direct and indirect effects of maternal dietary intake from the earliest stages of embryonic life when requirements for conceptus growth are negligible (Robinson et al., 1999). This is relevant because pre-term delivery and fetal growth restriction are associated with greater risk of neonatal mortality and morbidity (MOD, 2002a; NLM, 2002a,b). Growth-restricted human infants are not only at risk of immediate postnatal complications, but also may be 'programmed' to exhibit poor growth and productivity, and develop significant diseases later in life (Barker et al., 1993; Godfrey and Barker, 2000).

Exposure of pregnant sheep to severe maternal undernutrition at all stages of pregnancy, and particularly during late gestation, reduces fetal growth by varying degrees (Mellor, 1983; Robinson, 1983; Vincent et al., 1985; Parr et al., 1986). However, the historical notion remains that during pregnancy nutrient partitioning favors the conceptus at the expense of the dam (Barcroft, 1946).

Although the effects of nutrient restriction during pregnancy in adult sheep are inconsistent, and may depend on the level and(or) length of restriction, it has been recently shown, that when ewes are restricted to 50% of energy intake requirements from day 28 to 80 of gestation, fetal weights at day 80 are reduced by 32% (Vonnahme et al., 2003). However, Vonnahme et al. (2004) also demonstrated that realimentation after nutrient restriction during early gestation results in fetal weight at near term being similar between control and restricted cows. Additional research has also demonstrated that high maternal dietary Se reduces placentome weights and number at day 130 of gestation (Ward et al., 2004). The precise role of the uteroplacental unit in mediating nutritional effects in the adult sheep is inconclusive (Kelly, 1992), but may depend on interactions between maternal live weight at the time of conception and body fat status or nutrient reserves at the onset of nutrient restriction (Russell et al., 1981).

Scheaffer et al. (2004a) investigated the impact of maternal intake on fetal body weight at day 90 and day 130 of gestation and reported that animals restricted to 60 percent of controls had reduced fetal body weight at day 130. Reed et al. (2007) also report that nutrient restriction from d 50 to 130 of gestation in ewes resulted in decreased day 130 fetal body weights. However, in their study they factorialized supranutritional levels of selenium (3 ppm) with nutrient restriction (60% of controls) and

reported that supranutritional levels of selenium increased fetal body weight. In fact, the increase in fetal body weight was greater in restricted animals than it was in controls, suggesting that selenium in this study may have provided a sparing effect on fetal body weight.

This study (Reed et al., 2007) also produced some very interesting fetal muscle DNA responses to high selenium and nutrient restriction. In this study, dams fed control nutrition and selenium at adequate or supranutritional levels had similar concentrations of fetal muscle DNA. Whereas in restricted dams, those fed high selenium had approximately 60 to 70 percent greater concentrations of fetal muscle DNA. Taken at face value, this would indicate considerably more DNA and nuclei in the fetal muscle from restricted animals that were fed high selenium. This certainly raises some interesting questions regarding the role of selenium in developmental programming, particularly during periods of maternal nutrient restriction.

In applied livestock production settings, undernutrition can often occur during gestation, particularly during the first two trimesters. This results from either low feed reserves and(or) management practices that result in cows losing weight during late fall and early winter (Sletmoen-Olsen et al., 2000a,b). However, current data indicate that health and growth of offspring born from undernourished mothers are diminished (Godfrey and Barker, 2000; Vonnahme et al., 2003). In addition, livestock can be exposed to periods of high or low intakes of specific nutrients. For example, selenium (Se) intakes can be high or low in grazing or pen-fed situations (McDowell, 2003; Hintze et al., 2002). High Se intakes are particularly likely in grazing settings where forages are high in Se or when Se accumulator plant species are present (Hintze et al., 2001).

Basic information regarding the underlying mechanisms that support and encourage growth, development and nutrient utilization in large animal species are limited. Information in this regard is critical to improving livestock productivity and will provide considerable impacts on human health and wellness. Evidence suggests (Godfrey and Barker, 2000) that biological mechanisms regulating normal growth, development, and nutrient utilization are programmed in utero for postnatal growth and adult function. In addition, maternal nutritional perturbations during gestation may alter biological functions during adult life. Consequently, multiple laboratories on both the national and international arena are focusing attention in this direction.

Birth to Weaning

The nutritionally-modulated ovine model (both over and under supply) (Wallace et al., 2004; Luther et al., 2005; Luther, 2006; Ward, 2006; Ford et al., 2007; Caton et al., 2007) is unique, robust, and a highly relevant approach for investigating developmental programming (Scheaffer et al., 2004a,b; Vonnahme et al., 2004; Wallace et al., 2005; Luther et al., 2005; Reynolds et al., 2005a,b,c; Reynolds et al., 2006; Wallace et al., 2006). It has been shown that overnourishing the singleton-bearing adolescent ewe results in rapid maternal growth, and most particularly of maternal adipose tissue, at the expense of the nutrient requirements of the gravid uterus

(Wallace et al., 1996; 1999b; 2001). Therefore this model reflects not only overfeeding to promote rapid maternal growth but also maternal obesity. This also results in major placental growth restriction (30 to 40%), leading to the premature delivery of low birth weight lambs (25 to 30% reduction in birth weight) when compared with moderately nourished adolescents of similar age. Thus, in the still growing adolescent, dietary intake, and maternal nutrient partitioning during pregnancy have a major influence on pregnancy outcomes.

Wallace et al. (2004) reported that in an over-nourished adolescent pregnant ewe model a high level of nutrition creates an obese situation where maternal obesity increases from about 2.5 body condition score at conception to over 3.5 at parturition. In contrast, the moderate nutrition (control) group maintained visceral adiposity and maternal adiposity as measured by body condition score from 2.5 all the way through gestation. Both placental and birth weights were reduced in the high compared with the moderate fed ewes.

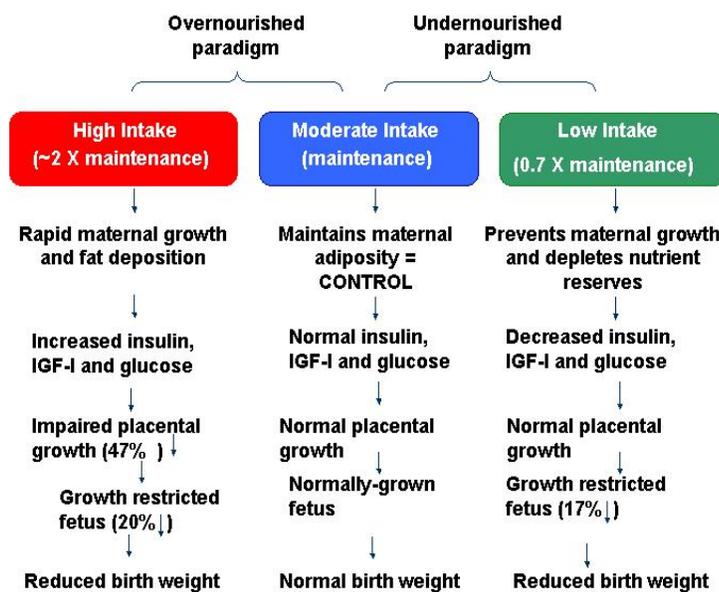


Figure 5. Effect of maternal dietary intake on pregnancy outcome in adolescent sheep. Data from Wallace et al., 2002, 2004 and Luther et al., 2005 (Adapted from Luther et al., 2005, 2006).

This research group has taken their over-nourished paradigm and coupled it with an under-nourished paradigm that is similar to that used by other groups (Scheaffer et al., 2004a; Ward et al., 2005). Combining these models into a single study they investigated maternal high intake (Figure 5), which is about 2 times maintenance, moderate intake which is at maintenance, and low intake which is about 0.7 times maintenance. Their high intake treatment results in a rapid maternal growth and a rapid fat deposition. Their maintenance level (moderate intake) maintains maternal adiposity so body condition score stays flat; however, there is a moderate level of maternal body weight gain

associated with pregnancy. The low intake prevents maternal growth and depletes nutrient reserves resulting in body condition score decreasing from 2.5 down to approximately 1.5 from day 0 to day 130 of gestation (Luther et al., 2005; Luther 2006).

Within this model (Figure 5) the overnourished group had increased insulin, increased IGF and glucose concentrations; the moderate (control) nutrition group had normal insulin, IGF, and glucose, and the low nutrition ewes had decreases in insulin, IGF, and glucose concentrations. The high nutrition group had impaired placental

growth, while the other treatments did not. Interesting, both overnutrition and undernutrition groups had restricted fetal growth, with the under-nutrition group having 17 percent smaller fetuses and the over-nutrition group having 20 percent smaller fetuses when compared with controls. There was a premature delivery in the over-nourished group with gestation being approximately 143 days of age. There were normal gestation lengths and normal deliveries in the control group at 147 days and the undernourished group at 147 days. The overnourished group had reduced colostrum yield, which was 63 percent less and the under-nourished group had reduced colostrum yield which was 50 percent less when compared with controls.

Researchers at North Dakota State University have also looked at an overnourished and an undernourished maternal first parity ewe models compared with controls (**Figure 6**). In addition, they have coupled the overnourished and undernourished model with both high selenium and normal selenium. Therefore, they have combined three maternal nutrition models together in their most recent approaches to investigating developmental programming. In addition, all lambs were removed from their dams immediately at birth and placed on identical nutrition schemes until slaughter.

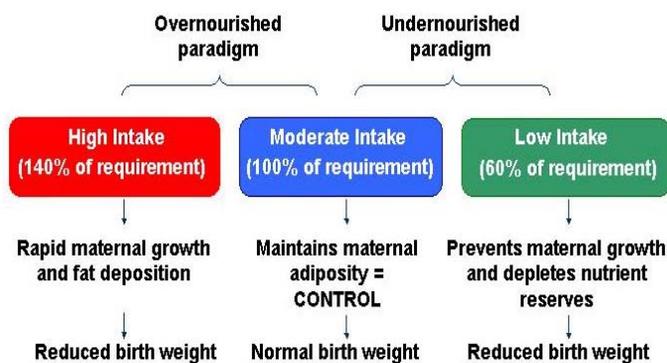


Figure 6. Schematic of ovine under- and over-nutrition models currently used by COBRE project investigators (Caton et al., 2007).

By design maternal intake had a large impact on final ewe body weight, with body weight being lower in the under-fed and higher in the overfed group compared with controls. Body condition score in the controls was approximately 2.5 at parturition, 1.5 in the restricted group, and 3.5 in the overfed group. Mammary gland weight was similar between the restricted and control group, but reduced in the 140 percent or overfed group. Colostrum weight of pregnant ewe lambs was lower in the over-fed

and under-fed groups and expressed as grams per kilogram of empty body weight. Maternal intake did have a major impact in this study on birth weight of the lambs with lambs being smaller in the restricted group and in the over-fed group when compared with controls. Weaning weights were less in lambs from mothers that were fed 60 percent restricted compared with controls, while those fed over-nutrition or 140 percent of the requirements were intermediate. Average daily gain from birth to weaning was not effected by plane of nutrition. In this study, selenium did not affect birth weight and did not interact with plane of nutrition.

Weaning to Adult

Carcass quality and rate of gain in the feedlot may also be programmed in utero. Recently, Greenwood et al. (2004) demonstrated that steers from cows which were nutritionally restricted during gestation had lower live and carcass weights compared to steers from adequately fed cows at 30 months of age. Interestingly, retail yield on the carcasses, based on indices of fatness, were greater in steers from nutritionally restricted cows, indicating that while growth was hindered in offspring from cows receiving low nutrition during pregnancy, ability to accumulate fat was not.

Table 1. Effects of maternal protein supplementation on postnatal performance of beef heifers (adapted from Martin et al., 2006).

Item	Con	Sup	P-value
Birth weight, kg	35	36	0.25
Actual weaning weight, kg	207	212	0.14
Adjusted weaning weight, kg	218	226	0.02
Prebreeding BW, kg	266	276	0.04
Pregnancy diagnosis BW, kg	386	400	0.03
Calving in 21 d, %	49	77	0.01
Overall pregnancy rate, %	80	93	0.05

weight at pregnancy diagnosis. In addition, number of animals calving in 21 days was increased, and the overall pregnancy rate in heifers was increased by protein supplementation of the dams.

Zhu et al. (2006) recently reported data in wethers that were from control or nutrient restricted ewes (**Table 2**). Nutrient restriction was 50% of controls and implemented from 28 to 78 days of gestation at which time ewes were fed similarly. After parturition lambs stayed with their mothers and were raised under similar conditions up to about 8 months of age at which time lambs were slaughtered and necropsied. Live lamb body weight at necropsy was increased by maternal nutrient restriction (**Table 2**). Carcass weight and kidney, pelvic, and heart fat were also increased in lambs from nutrient restricted dams. Kidney, pelvic, and heart fat as a percent of carcass was also increased. Left

Table 2. Effects of maternal nutrient restriction on postnatal performance of wethers (adapted from Zhu et al., 2006).

Item	Cont	Res	P-value
Live BW, kg	56.8	61.7	< 0.05
Carcass wt, kg	28.8	31.6	< 0.10
KPH, kg	0.46	0.68	< 0.05
KPH, % carcass	1.66	2.18	< 0.05
Left LD muscle, % carcass	2.71	2.46	< 0.10

Martin et al. (2006) reported that protein supplementation during the last trimester of cows consuming low quality forage altered growth and reproductive performance of heifer calves (**Table 1**). In their study supplementation did not alter birth weight; however, adjusted weaning weight in heifer calves was increased by increased protein supplementation of the dam. Pre-breeding weight in heifers was increased, as was body

longissimus dorsi muscle was decreased as a percent of carcass in lambs that were from nutrient restricted compared with those that were from control fed dams. These researchers also looked at muscle fiber number, and diameter and concluded that nutrient restricted animals had muscle fibers that were greater in diameter (**Figure 7**). Lambs from nutrient restricted dams also had a lower percentage of muscle fiber number.

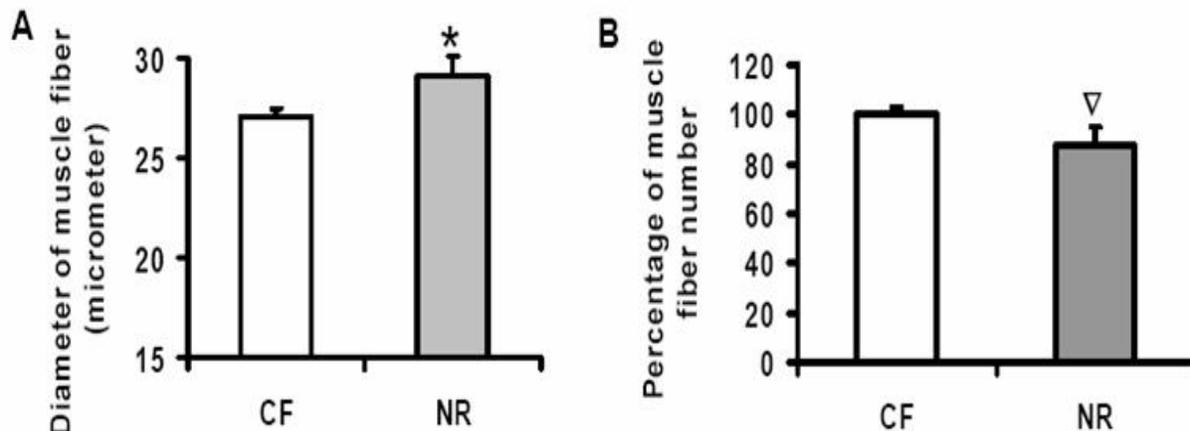


Figure 7. Effects of maternal nutrient restriction (NR) vs. control feeding (CF) on postnatal muscle fiber diameter (A) and number (B) in 8 month old wethers (adapted from Zhu et al., 2006).

Summary

In summary, nutritional management during breeding and gestation results in measurable peri-conceptual, fetal, post-natal, and adult functional responses. These responses provide both food for thought and fertile ground for research, particularly in the directions of understanding biological mechanisms, enhancing livestock production efficiency, and improving human health.

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