Maternal Plane of Nutrition: Impacts on Fetal Outcomes and Postnatal Offspring Responses

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Purpose

Objectives of this review are:

1. Summarize the current information regarding effects of maternal nutrition on fetal outcomes and postnatal offspring performance.
2. Provide a platform to assist in the formation of additional hypotheses regarding relevant aspects of developmental programming in grazing ruminant livestock species.
Maternal Nutritional Plane and Developmental Programming
Maternal Nutritional Plane During Gestation

- Varies widely, especially in extensive production systems
- Importance to the livestock industry
  - Production system efficiency
  - Potential impacts on health, performance and product quality
  - Economic return
- Improved efficiency, profitability, and production of high quality healthy products.
Importance to Livestock Industry

- 70 to 75% of annual energy requirements for typical cow types are used for tissue maintenance functions.
- In ruminant livestock production systems, more energy is devoted to parent than slaughter populations.
- Feed costs represent over 60% of annual costs of production associated with cow herds.
- Most of the energy cows use and money we spend are for maintenance.
Pregnancy is Energetically Costly*

*Data of Brody (1938) and Ferrell et al. (1976) for cows – data are similar for other mammals.
Crude Protein Content of Improved Pasture and Native Range in Autumn

CP, % of DM

d 150-180 of gestation for a winter calving system

d 180-210 of gestation for a winter calving system
Body Weight Loss by Cows Grazing Summer Native Range

<table>
<thead>
<tr>
<th>BW loss, kg</th>
<th>% losing BW</th>
<th>BW loss of cows in negative energy balance, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.8</td>
<td>54.0</td>
<td>31.7</td>
</tr>
</tbody>
</table>
Fetal Nutrition

- Critical for normal healthy development and neonatal survival
- Placenta is one of the “Key Nutrient Transferring Tissues”
- Proper placental function is essential for adequate fetal nutrient supply
- Other key nutrient transferring tissues include maternal gut, fetal and perinatal gut, and mammary gland
Sheep Placentome

Fetal Placenta - Cotyledon (COT)

Maternal Placenta - Caruncle (CAR)
Adequate fetal nutrient supply is essential to proper development and a healthy start for offspring.

Many factors can alter placental function and/or fetal nutrient supply, including:
- Maternal nutrient restriction and/or excess
- Placental insufficiency
- Intrauterine growth restriction (IUGR)
- Environmental stress
- Number of fetuses

Early work clearly demonstrated that intrauterine environment impacted birth weight and adult body size.
The Classical Study of Hammond and Wallace (1938)

“maternal constraint to fetal growth.”
“Developmental Programming” is also termed the “Barker Hypothesis,” or, “Developmental Origins of Health and Disease.”

Developmental programming is the concept that perturbations during critical developmental periods may have long-term impacts on offspring outcomes.

Epidemiological evidence in humans and controlled studies in animals, indicate that poor fetal growth and development can result in problems with both the neonate and during adult life (Barker, 1994; Wilson and Grundy, 2003).

- Reduced birth weight
- Metabolic syndrome

Additional work with relevant livestock species has also provided evidence for developmental programming, which is often associated with IUGR (Wu, 1996).
Developmental Programming

- Intrauterine growth restriction (IUGR) can result from
  - External environment to dam
    - Temperature, hypoxia
  - Maternal environment
    - Gestational nutrition
    - Metabolic state
  - Intrauterine environment
    - Fetal number

- IUGR can result in impaired development and potential long-term consequences (Godfrey and Barker, 2000; Wu et al., 2006)
  - This can occur even when birth weight is unaffected (Ford et al., 2007; Martin et al., 2007; Larson et al., 2009)
Fetal Growth and Critical Windows: Opportunities for Developmental Programming
Relationship of Fetal Weight to Stage of Gestation in Sheep

*Ferrell et al., 1976

10% of fetal growth

Day of Gestation

Weight, kg

0 1 2 3 4 5

0 30 60 90 120 150

*Ferrell et al., 1976
Fetal Growth; Relationship of Fetal and Placental Weight to Stage of Gestation in Sheep*

*Ferrell et al., 1976
Placental Development and Function

- A primary role of the placenta is to provide for physiological interface, including nutrient and waste exchange (Meschia, 1983; Reynolds and Redmer, 1995; Reynolds et al., 2010).

- Adequate placental circulation is imperative to successful pregnancy and is exemplified by observed close relationships among fetal weight, placental size, and uterine and umbilical blood flows during normal pregnancies (Reynolds et al., 2005a, 2005b, 2006; 2010).

- In the ewe, cotyledonary growth is exponential during the first 10 to 11 wk of pregnancy, with significant slowing until term (Stegeman, 1974: Ferrell et al., 1976).

- In the cow, the cotyledonary growth progressively increases throughout gestation (Reynolds et al., 1990; Vonnahme et al., 2007).
Placental Development and Function

- Uterine and umbilical blood flows, which represent the circulation to maternal and fetal portions of the placenta, respectively (Ramsey, 1982; Mossmann, 1987), increase exponentially throughout gestation, essentially keeping pace with fetal growth (Reynolds and Redmer, 1995; Magness, 1998).

- In sheep the absolute rate of uterine blood flow increases by approximately 3-fold throughout the last half of pregnancy (Meschia, 1983). Over a similar interval of gestation, uterine blood flow in cows increase by 4.5-fold (Reynolds et al., 1986).

- As summarized in the following slide, in sheep studied during late gestation, uterine or umbilical blood flows, or both, are reduced in every model of compromised pregnancy in which they have been evaluated.
# Changes in fetal and placental weights, uterine and umbilical blood flows, and placental vascularity in various models of compromised pregnancy in sheep

<table>
<thead>
<tr>
<th>Model</th>
<th>Day of Gestation</th>
<th>Fetal Wt</th>
<th>Placental Wt</th>
<th>Uterine Blood Flow</th>
<th>Umbilical Blood Flow</th>
<th>Vascularity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overfed Adolescent</td>
<td>130-134</td>
<td>↓20-28%</td>
<td>↓45%</td>
<td>↓36%</td>
<td>↓37%</td>
<td>↓31%</td>
</tr>
<tr>
<td>Underfed Adolescent</td>
<td>130</td>
<td>↓17%</td>
<td>NSE[^4]</td>
<td>---</td>
<td>---</td>
<td>↓20%</td>
</tr>
<tr>
<td>Underfed Adult</td>
<td>130-144</td>
<td>↓12%</td>
<td>---</td>
<td>↓17-32%</td>
<td>NSE</td>
<td>↓14%</td>
</tr>
<tr>
<td>Adolescent vs. Adult</td>
<td>135</td>
<td>↓11%</td>
<td>↓29%</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Genotype</td>
<td>130</td>
<td>↓43%</td>
<td>↓47%</td>
<td>---</td>
<td>---</td>
<td>↑36%</td>
</tr>
<tr>
<td>Heat-stressed Adult</td>
<td>133-135</td>
<td>↓42%</td>
<td>↓51%</td>
<td>↓26%</td>
<td>↓60%</td>
<td>---</td>
</tr>
<tr>
<td>Multiple Pregnancy</td>
<td>140</td>
<td>↓30%</td>
<td>↓37%</td>
<td>↓23%</td>
<td>---</td>
<td>↓30%</td>
</tr>
<tr>
<td>High Dietary Se</td>
<td>135</td>
<td>NSE</td>
<td>↓24%</td>
<td>---</td>
<td>---</td>
<td>↑20%</td>
</tr>
<tr>
<td>Hypoxic Stress</td>
<td>140</td>
<td>NSE</td>
<td>---</td>
<td>↓35%</td>
<td>---</td>
<td>↑(cap. Area)</td>
</tr>
</tbody>
</table>

[^1]: Table adapted from Reynolds et al. (2006; 2010).
[^2]: Length of gestation = approximately 145 d.
[^3]: cap. = capillary; CAR = caruncle (maternal placenta); COT = cotyledon (fetal placenta/villus).
[^4]: NSE = no significant effect.
Perturbations of Fetal Development: Offspring Responses in Ruminant Livestock
Developmental Programming: Windows of Opportunity

- Periconceptional
- Implantation and Placental Growth
- Organogenesis
- Rapid Fetal Growth
- Perinatal
- Postnatal

Adapted from Fowden et al., 2006
Maternal Nutrition Before Mating (Peri-Conceptional Period)

Grazul-Bilska et al., 2006
Effects of Maternal Nutrition Before Mating on Oocyte Quality

Grazul-Bilska et al., 2006
<table>
<thead>
<tr>
<th>Day</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Ovulation</td>
</tr>
<tr>
<td>9-11</td>
<td>Hatching from the zona pellucida</td>
</tr>
<tr>
<td>15-18</td>
<td>Critical period for maternal recognition of pregnancy</td>
</tr>
<tr>
<td>18-22</td>
<td>Time of conceptus attachment to the uterine wall</td>
</tr>
<tr>
<td>21-22</td>
<td>Heart beat apparent</td>
</tr>
<tr>
<td>28</td>
<td>Gonadal ridge formed</td>
</tr>
<tr>
<td>25-30</td>
<td>Limb development</td>
</tr>
<tr>
<td>40-50</td>
<td>Differentiation of the rumen stomach; formation of the rumen, reticulum, and omasum</td>
</tr>
<tr>
<td></td>
<td>Cellular differentiation and growth of the pancreas, liver, adrenals, lungs, thyroid, muscle and kidneys</td>
</tr>
<tr>
<td>45</td>
<td>Testicular development</td>
</tr>
<tr>
<td>50-60</td>
<td>Bone ossification begins</td>
</tr>
<tr>
<td></td>
<td>Limbs are increasing in length</td>
</tr>
<tr>
<td></td>
<td>Ovarian development</td>
</tr>
<tr>
<td>70</td>
<td>Completion of rumen differentiation</td>
</tr>
<tr>
<td></td>
<td>Orientation of stomach is complete</td>
</tr>
<tr>
<td>80</td>
<td>First detection of adipose cells</td>
</tr>
<tr>
<td>120</td>
<td>Marked increase in caruncular vascularization and blood flow</td>
</tr>
<tr>
<td>150</td>
<td>Completion of caruncular arterial vascularization</td>
</tr>
<tr>
<td>190</td>
<td>Brown fat is detectable</td>
</tr>
<tr>
<td>Last third of gestation</td>
<td>Further cellular differentiation and growth of all tissues</td>
</tr>
</tbody>
</table>
Nutrient restriction to the developing conceptus, regardless of the reason often results in impaired fetal organogenesis and/or development. More severe with increasing extremes of nutrient restriction. Timing of nutrient deprivation can also result in differential effects on fetal organ systems because of differing growth trajectories and maturation time points. Data indicate that both low and high planes of maternal nutrition can impact growth of numerous fetal organs (Reed et al., 2007; Caton et al., 2009; Neville et al., 2010).
Inappropriate Maternal Nutrition Impacts Fetal Organogenesis

- Responsive tissues include:
  - Small intestine (Trahair and Sangild 2002; Greenwood and Bell, 2003; Reed et al., 2007; Neville et al., 2007, 2010)
  - Pancreas (Osgerby et al., 2002; Limesand et al., 2005, 2006; Moberg et al., 2006; Effertz et al., 2007)
  - Heart (Hawkins et al., 2000; Osgerby et al., 2002; Han et al., 2004: Gilbert et al., 2005; O’Rourke et al., 2007)
  - Lung (Gnanalingham et al, 2005)
  - Kidney (Gilbert et al., 2007)
  - Others
Inappropriate Maternal Nutrition Impacts Fetal Organogenesis

- Our laboratories have a particular interest in intestinal development, growth, and function (Reed et al., 2007; Carlson et al., 2008; Caton et al., 2009; Neville et al., 2010, and Meyer et al., 2010).

- Intestinal tissues are important to livestock production because of their role in nutrient uptake, immuno-competence, and their disproportional use of energy (and other nutrient resources) in relation to their contribution to overall body mass.

- A detailed discussion of fetal organ responses to perturbations during gestation are beyond the scope of this presentation.
Nutrient Supply in First Parity Ewes: Maternal Responses and Birth Weight

- **Overnourished adolescent paradigm**
  - **High Intake (~2 X maintenance)**
    - Rapid maternal growth and fat deposition
  - **Moderate Intake (maintenance)**
    - Maintains maternal adiposity = CONTROL
- **Undernourished adolescent paradigm**
  - **Low Intake**
    - Prevents maternal growth and depletes nutrient reserves

Luther, Wallace, Redmer, Reynolds, et al., 2006
Adiposity Score

**Impaired placental growth (47%)**
- Increased insulin, IGF-I and glucose
- Growth restricted fetus (20%)
- Premature delivery (~143 days)
- Reduced colostrum yield (63%)

**Normal placental growth**
- Normal insulin, IGF-I and glucose
- Normal gestation length (~147 days)
- Normal colostrum yield

**Decreased insulin, IGF-I and glucose**
- Reduced colostrum yield (50%)
- Growth restricted fetus (17%)
- Normal gestation length (~147 days)
Low Birth Weight: Postnatal Implications in Livestock

- Low (2.3 kg) and normal birth weight (4.8 kg) lambs selected and reared separately from dams on milk replacer.
- Lambs were not allowed to suckle dams and were individually housed and fed for either low or rapid growth rates.
- Data were collected until lambs were approximately 20 kg BW.
- Lambs were necropsied and tissues collected.

Greenwood et al., 1998; 2000, 2002, 2004
Low Birth Weight: Postnatal Implications in Livestock

- Low birth weight lambs had less body N and more ash.
- Low birth weight lambs had more fat and less lean at any given empty BW likely because maintenance energy requirements were 30% lower and intakes were relatively greater.
- Myonuclei proliferation may be influenced by fetal nutrition during late pregnancy.
- Reduced myonuclei number in very low birth weight lambs may impact postnatal skeletal muscle growth capacity.

Greenwood et al., 1998; 2000; 2002; 2004
Protein Turnover of Bovine Fetal Skeletal Muscle

Du et al., 2004

Du et al., 2005
## Selected Fat and Muscle Weights of 8-Month Old Lambs

Zhu et al., 2006

<table>
<thead>
<tr>
<th>Item</th>
<th>Control</th>
<th>Restricted</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live BW, kg</td>
<td>56.8</td>
<td>61.7</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Carcass wt, kg</td>
<td>28.8</td>
<td>31.6</td>
<td>&lt; 0.10</td>
</tr>
<tr>
<td>KPH, kg</td>
<td>0.46</td>
<td>0.68</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>KPH, % carcass</td>
<td>1.66</td>
<td>2.18</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Left LD muscle, % carcass</td>
<td>2.71</td>
<td>2.46</td>
<td>&lt; 0.10</td>
</tr>
</tbody>
</table>
Muscle Fiber Number and Diameter of 8-month old Offspring

Zhu et al., 2006
Influence of maternal dietary selenium and nutritional intake during pregnancy on offspring body weight from birth through weaning at 57 d of age (Adapted from Neville et al., 2010)

<table>
<thead>
<tr>
<th>Item</th>
<th>Selenium Treatment&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Nutrition Treatment&lt;sup&gt;2&lt;/sup&gt;</th>
<th>P-Values&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ASe</td>
<td>HSe</td>
<td>SEM</td>
</tr>
<tr>
<td>BW, kg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>4.49</td>
<td>4.06</td>
<td>0.25</td>
</tr>
<tr>
<td>Females</td>
<td>4.11</td>
<td>4.43</td>
<td>0.12</td>
</tr>
<tr>
<td>Combined</td>
<td>4.25</td>
<td>4.37</td>
<td>0.10</td>
</tr>
<tr>
<td>Weaning, 57 d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>19.52</td>
<td>19.45</td>
<td>0.95</td>
</tr>
<tr>
<td>Females</td>
<td>19.60</td>
<td>19.72</td>
<td>0.64</td>
</tr>
<tr>
<td>Combined</td>
<td>19.61</td>
<td>19.55</td>
<td>0.49</td>
</tr>
<tr>
<td>180 d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>53.04</td>
<td>52.61</td>
<td>1.43</td>
</tr>
<tr>
<td>Females</td>
<td>49.41</td>
<td>51.47</td>
<td>1.73</td>
</tr>
<tr>
<td>Combined</td>
<td>51.23</td>
<td>51.98</td>
<td>1.11</td>
</tr>
</tbody>
</table>

<sup>1</sup>Selenium treatments were daily intake of organically bound Se, adequate Se (ASE; 9.5 µg/kg BW) vs. high Se (HSe; 81.8 µg/kg BW).

<sup>2</sup>Nutritional treatments were RES (fed at 60% of CON), CON (control; 100% requirements for gestating ewe lambs), and HIGH (fed at 140% of CON).

<sup>3</sup>Probability values for effects of selenium (Se), nutrition (Nut), and the interaction.

<sup>ab</sup>Means within a row having differing superscripts differ ($P < 0.10$).
Low Birth Weight: Postnatal implications in Livestock

- Low birth weight lambs appear less mature in terms of metabolic and endocrine development.
- All new born lambs exhibited the fetal characteristic of high rates of amino acid oxidation during the early postnatal period.
- Low birth weight lambs had increased insulin when fed for moderate or high rates of growth.
- Both low birth weight and postnatal nutrient supply altered internal organ growth.

Greenwood et al., 1998; 2000, 2002, 2004
Effect of Ewe Plane of Nutrition on Lamb Response to Glucose Challenge at 250 Days of Age

Ford et al., 2007
Effects of Cow Plane of Nutrition on Fetal Renal Characteristics

Fetal kidneys harvested at d 250

Absolute glomerular number

- Total glomerular numbers
- Glomeruli per gram tissue

Ford et al., 2005
Postnatal Hypertension of Lambs at 245 Days of Age

Mean arterial pressure, mmHG

Renal glomeruli, 10^4

Control Restricted

Gilbert et al., 2005
Fetal Cardiac Development of 78-day Lambs Fetuses

Vonnahme et al., 2003
Protein Supplementation During Pregnancy
Effect of Gestational Plane of Nutrition and Supplemental RUP on Cow BW Change

Price et al., 2007
Postnatal Offspring Responses
# Effects of Supplemental Protein During the Last Third of Gestation on Performance of Heifer Calves

<table>
<thead>
<tr>
<th>Item</th>
<th>No Sup.</th>
<th>Sup.</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth Weight, kg</td>
<td>35</td>
<td>36</td>
<td>0.25</td>
</tr>
<tr>
<td>Actual Weaning Wt, kg</td>
<td>207</td>
<td>212</td>
<td>0.14</td>
</tr>
<tr>
<td>Adjusted Weaning Wt, kg</td>
<td>218</td>
<td>226</td>
<td>0.02</td>
</tr>
<tr>
<td>Prebreeding BW, kg</td>
<td>266</td>
<td>276</td>
<td>0.04</td>
</tr>
<tr>
<td>Preg Check BW, kg</td>
<td>386</td>
<td>400</td>
<td>0.03</td>
</tr>
<tr>
<td>Calving in 21 d, %</td>
<td>49</td>
<td>77</td>
<td>0.01</td>
</tr>
<tr>
<td>Overall Pregnancy Rate, %</td>
<td>80</td>
<td>93</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Martin et al., 2007
# Effects of Supplemental Protein During the Last Third of Gestation on Steer Offspring Performance

<table>
<thead>
<tr>
<th>Item</th>
<th>No Sup.</th>
<th>Sup.</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birth Weight, kg</td>
<td>36.6</td>
<td>38.0</td>
<td>NS</td>
</tr>
<tr>
<td>Actual Weaning Wt, kg</td>
<td>225</td>
<td>247</td>
<td>0.05</td>
</tr>
<tr>
<td>Adjusted Weaning Wt, kg</td>
<td>219</td>
<td>231</td>
<td>0.10</td>
</tr>
<tr>
<td>Initial Feedlot BW, kg</td>
<td>222</td>
<td>243</td>
<td>0.05</td>
</tr>
<tr>
<td>Reimplant BW, kg</td>
<td>422</td>
<td>456</td>
<td>0.05</td>
</tr>
<tr>
<td>Final BW, kg</td>
<td>591</td>
<td>622</td>
<td>0.05</td>
</tr>
<tr>
<td>ADG, %</td>
<td>166</td>
<td>171</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Larson et al., 2008
### Effects of Supplemental Protein During the Last Third of Gestation on Steer Offspring Carcass Characteristics

<table>
<thead>
<tr>
<th>Item</th>
<th>No Sup.</th>
<th>Sup.</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>HCW, kg</td>
<td>357</td>
<td>376</td>
<td>0.05</td>
</tr>
<tr>
<td>Marbling Score</td>
<td>457</td>
<td>503</td>
<td>0.01</td>
</tr>
<tr>
<td>Empty Body Fat, %</td>
<td>28.7</td>
<td>29.9</td>
<td>0.06</td>
</tr>
<tr>
<td>LM area, cm²</td>
<td>88.4</td>
<td>88.5</td>
<td>NS</td>
</tr>
<tr>
<td>Yield Grade</td>
<td>2.69</td>
<td>2.94</td>
<td>NS</td>
</tr>
<tr>
<td>Quality Grade, %Md &gt;</td>
<td>26.6</td>
<td>43.2</td>
<td>0.03</td>
</tr>
<tr>
<td>12th Rib Fat, cm</td>
<td>1.16</td>
<td>1.71</td>
<td>NS</td>
</tr>
</tbody>
</table>

Larson et al., 2008
Effect of Gestational Plane of Nutrition and Supplemental RUP on Average Milk Production (d 50 & 70)

kg/d

CON: 7.6
NR: 7.6
NRP: 5.9
Effect of Gestational Plane of Nutrition and Supplemental RUP on Calf ADG from d 50 to 70

- CON: 1.11 kg/d
- NR: 1.03 kg/d
- NRP: -7.1 kg

kg/d
Calf Weights at Weaning

CON: 273.2 kg
NR: 276.1 kg
NRP: 264.4 kg
Interaction Between Severity of Restriction and Calf Age at the Start of the Restriction

A summary of 74 experiments (Berge, 1991)
Summary and Conclusions

- Maternal nutritional perturbations impact fetal nutrient supply and result in measurable impacts on fetal and postnatal outcomes.
- Developmental programming is real in relevant livestock species.
- This is an emerging area of research interest in animal agriculture that has potential to shape our understanding of the long term consequences of fetal nutrition on offspring performance.
- Degree of impact on livestock production responses, underlying mechanisms, and methods to mitigate potential negative consequences or capitalize on positive attributes remains to be determined.
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- Ms. Allison Meyer
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- Dr. Justin Luther
- Dr. Kasey Carlin
- Dr. Marc Bauer

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- Dr. Meijun Zhu
- Dr. Nathan Long
- Dr. Steve Paisley
- Dr. Gary Moss
- Dr. Brenda Alexander
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