EFFECTS OF PROTEIN SUPPLEMENTATION ON REPRODUCTIVE PERFORMANCE OF FALL CALVING COWS, AND PRENATAL AND POSTNATAL GROWTH, AND CARCASS CHARACTERISTICS OF CALVES

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Abstract:

Fall calving cows were used to determine the effects of protein supplementation on reproduction, and growth and carcass characteristics of calves. Cows were individually supplemented from mid-November to mid-March for four years with either a control diet (Con; 1.82 kg/d of 38 % CP) or low diet (L; 0.2 kg/d of 8% CP). During each year, cows were reassigned dietary treatments according to calving date and BCS, with half of Con and L cows remaining on the same diets as the previous year and the other half assigned to the other diet. Cows were exposed to bulls for 60 d beginning December 1. Statistical analyses were performed with a 2 x 2 factorial design with PROC GLM and PROC FREQ. Cows on Con diets lost less BW from November to January compared with L cows (-29.8 ± 2.8 and -49.7 ± 2.8 kg, $P < 0.001$). Control cows had greater BCS compared with L cows in May (4.1 ± 0.1 and 3.9 ± 0.1, $P = 0.03$). Prenatal supplementation did not influence birth weight of calves ($P = 0.86$). Concentrations of IGF-I were greater in plasma of calves suckling Con cows compared with calves from L cows (21.4 ± 2.1 and 14.8 ± 2.1ng/ml, respectively; $P = 0.03$). There was a prenatal x postnatal effect for BW of calves; prenatal Low and postnatal Control (LCon) calves (186.1 ± 4.4, $P = 0.02$) had greater 205 d adjusted weaning weights compared with prenatal Low and postnatal Low (LL), prenatal Control and postnatal Low (ConL), and prenatal Control and postnatal Control (ConCon) calves (154.9 ± 4.0, 172.4 ± 4.1, and 180.1 ± 4.2 kg, respectively). Calves from cows on Con diets during prenatal and postnatal growth had greater hot carcass weights (393.6 ± 9.1 kg) compared with LL calves (362.6 ± 9.1 kg, $P = 0.02$), however, other carcass characteristics were not influenced by treatment ($P < 0.17$). Feeding supplemental protein that decreased BW loss and increased BCS, increased ADG of calves prior to weaning, increased IGF-I in plasma, and increased BW until harvest, but did not influence carcass characteristics of calves.

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CHAPTER I

INTRODUCTION

Profitability of a cow-calf producer depends on the calf to sell at weaning, thus weaning weight is the most important variable that influences efficiency of production (Dickerson, 1970). Gestation length in beef cows averages 280 d, therefore cows have approximately 85 d after parturition for involution, resumption of estrous activity, and rebreeding to produce a calf every 12 mo. Excess nutrient intake is stored as body energy reserves in adipose tissue and are utilized during periods when nutrient intake is inadequate. Body energy reserves, 1-9 scale as BCS (Wagner et al., 1988), at calving is the best indicator of the time it will take for cows to initiate estrous cycles and conceive after parturition (Richards et al., 1986; Selk et al., 1988; DeRouen et al., 1994).

As forage availability and quality decrease during late summer and winter grazing cows cannot acquire adequate protein or energy needed for maintenance. Inadequate nutrients not only influence reproductive efficiency of a cow herd but can also decrease birth weight of calves if restriction occurs during late gestation (Spitzer et al., 1995; Sletmoen-Olson et al., 2000b; Stalker et al., 2006). When nutrient restriction occurs during gestation, birth weight is decreased. Nutrient restriction that continues postnatally will alter growth and development of the neonate (Freetly et al., 2000). Reduced postnatal growth will decrease profitability of a cow-calf operation because income is based on production of maximum BW at weaning.

Evaluation of data from the Dutch Famine has led to the development of a theory known as the thrifty phenotype; the environment provided in utero will influence fetal development that may result in traits best suited for survival when exposed to adverse external environment (Roseboom et al., 2001). The increase in disease associated with prenatal nutrient restriction has led to the field of fetal origins of adult disease in humans or fetal programming in domesticated livestock (Barker et al., 1993; Godfrey and Barker, 2000; Roseboom et al., 2001).

The effects of restriction of nutrients during gestation are dependent on the time and severity of restriction. Nutrient restriction early in gestation may not influence birth weight of calves (Martin et al., 2007; Long et al., 2009) or lambs (Zhu et al., 2006; Ford et al., 2007); however, a normal phenotype does not ensure that metabolic pathways are functioning normally. Nutrient restriction of beef cattle during early to mid-gestation increases the prevalence of glucose intolerance (Long et al., 2010d), reduces organ development (Long et al., 2010c), decreases muscle mass, and increased adipocyte diameter (Long et al., 2012). Birth weight is less when nutrient restriction occurs during late gestation (Wiltbank et al., 1962; Dunn et al., 1969; Bellows and Short, 1978) and postnatal growth and weaning weight of calves will be reduced (Corah et al., 1975).

Objectives of this study were to determine the influence of protein supplementation during early gestation and mid lactation on calf growth, carcass characteristics, and reproductive performance of fall calving cows.

CHAPTER II

REVIEW OF LITERATURE

Nutritional Regulation of Reproductive Performance of Beef Cows

Nutritional regulation of reproduction is controlled through body energy reserves, nutrient intake, and suckling intensity. Nutritional status, before and after calving, is a major determinant of reproductive efficiency of a beef herd, however, uterine involution after calving are similar between cows on differing planes of nutrition (Kiracofe, 1980; Spicer et al., 1986; Perry et al., 1991). Body energy reserve at parturition is the major factor influencing duration between parturition and resumption of estrus cycles (Richards et al., 1986; Selk et al., 1988; DeRouen et al., 1994). Pre- and postpartum BW fluctuations will not influence pregnancy rates when cows are in good condition at calving (Corah et al., 1975; Dunn and Kaltenbach, 1980).

Body Condition Score:

Body energy reserves are quantified with a nine point system known as body condition score (BCS) with 1 = emaciated and 9 = obese (Wagner et al., 1988). A one BCS unit change has been related to a 33 to 51 kg change in BW (Wagner, 1985; Buskirk et al., 1992; Ferrell and Jenkins, 1996; NRC, 1996; Lalman et al., 1997). During late gestation, BW is confounded with rapid fetal and placental development, thus utilizing body fat and BCS is a more accurate indicator of condition and energy reserves (Wiltbank et al., 1962; Richards et al., 1986; Wagner et al., 1988). Pregnancy rate is dependent on BCS and maximum reproductive efficiency can be achieved when BCS at calving is greater than or equal to 5 for multiparous cows (Dziuk and Bellows, 1983; Richards et al., 1986; Selk et al., 1988) and greater than or equal to 6 for primiparous cows (DeRouen et al., 1994; Spitzer et al., 1995; Lalman et al., 1997).

Restriction of nutrient intake will result in loss of body energy stores and cessation of estrous cycles. To reinitiate estrous cycles after nutritionally induced anestrus, cows must obtain a greater BCS compared with the BCS at the onset of anestrus (Louw et al., 1988; Richards et al., 1989a). Availability of energy reserves will influence the interval from parturition to resumption of estrous activity when nutrient intake is not adequate (Rakestraw et al., 1986). Maintenance of BCS greater than or equal to 5 will allow for resumption of estrous activity sooner after parturition than if cows lose weight after calving and reproductive success can be decreased (Wettemann, 1994). When postpartum BCS is inadequate i.e. below 5, nutritional intake will influence the interval for an animal to return to estrus (Richards et al., 1986).

Nutrient Intake:

Reproductive performance is dependent on adequate nutrient intake during gestation and after calving. Visceral tissues use the majority of nutrients during maintenance and growth of body tissues (Lobley, 2003). Gestation and lactation are unique physiological states that increase nutrient requirements but do not benefit the dam. The majority of bovine fetal development occurs during the last third of gestation, after nutrient demands for lactation have ceased. Nutrient demands of the developing fetus cause nutrient requirements for cows to be similar during lactation and during late gestation (Bauman and Currie, 1980).

Body energy reserves are mobilized when nutrient intake is inadequate; BCS will decrease and the ability of cows to conceive will be reduced. Nutrition does not influence uterine involution unless nutrients are inadequate (Kiracofe, 1980). Uterine involution will occur, within 30 d of parturition, well before estrous activity resumes and will not influence resumption of estrous cycles; except when dystocia (Bellows and Short, 1978; Bellows et al., 1982) or heat stress (Lewis et al., 1984) occurs.

Energy may be the most influential nutrient for reproduction, and glucose is a precursor for milk production, fetal development, fat stores, and reproductive function. Inadequate pre- and postpartum energy consumption will decrease birth weights, milk production, and increase the interval to ovulation (Wiltbank et al., 1962; Bellows and Short, 1978; Perry et al., 1991). Reduced ovarian activity (Oxenreider and Wagner, 1971), size of dominant follicle (Lents et al., 2008), and secretion of LH (Perry et al., 1991; Grimard et al., 1995) will occur when energy intake is inadequate.

Prepartum energy intake influences the postpartum interval from parturition to ovulation and greater energy intake increases conception rates (Wiltbank et al., 1962; Dunn et al., 1969; Ciccioli et al., 2003). Fat supplementation is readily used to increase energy in diets. The ability of fat to increase energy has conflicting effects on reproduction depending on the type and source of fat, age of animal, and physiological state of supplementation (Funston, 2004).

Protein and energy requirements increase about 33% during gestation but supplementing energy will initiate estrous activity sooner after parturition than supplementing protein (Davis et al., 1977). Protein supplementation of cows grazing winter range during late gestation, will increase BCS (Stalker et al., 2006; Lents et al., 2008; Larson et al., 2009) and BW (Fleck and Lusby, 1986; Lusby et al., 1991; Marston et al., 1995; Sletmoen-Olson et al., 2000b) at calving. Influence of protein on reproductive traits may be dependent on the source of protein supplemented (Fleck and Lusby, 1986; Van Saun et al., 1993; Marston et al., 1995).

Degradable intake protein (DIP) has negative effects on reproduction in dairy cattle (Canfield et al., 1990) especially during lactation due to increases in milk production which exacerbates the negative energy balance (Butler, 1998). Conception rates and overall pregnancy rates are decreased from excessive DIP supplementation of dairy cows (Canfield et al., 1990) and heifers (Canfield et al., 1990; Elrod and Butler, 1993). Supplemental DIP did not change reproductive characteristics or endocrine function of beef cows (Wiley et al., 1991; Rusche et al., 1993). Therefore, greater amounts of milk production of dairy cattle may increase protein availability to the rumen and contribute to reduced reproductive efficiency.

Undegradable intake protein (UIP) may have beneficial effects on reproductive traits, especially, in cows with BCS of 4 or 5 (Wiley et al., 1991). Supplemental UIP does not influence BCS or BW (Rusche et al., 1993; Triplett et al., 1995; Lents et al., 2000) but may decrease postpartum weight loss (Miner et al., 1990; Dhuyvetter et al., 1993). Protein supplementation with 50 % UIP increased first service conception and overall pregnancy rates but did not influence interval to estrus compared with protein supplement containing 75 % UIP (Triplett et al., 1995). A supplement consisting of 25 % UIP of total protein decreased interval to first estrus but had no effect on pregnancy rates compared with 50 % UIP supplement (Dhuyvetter et al., 1993). Greater amounts of UIP increased BCS at calving and after calving (Van Saun et al., 1993). Supplementation of

UIP to heifers increased BW at puberty compared with energy and monesin supplementation (Lalman et al., 1993). However, energy and monesin supplementation decreased age of heifer at the onset of puberty (Lalman et al., 1993).

Suckling Effect on Reproduction:

Postpartum anestrous interval is shorter for cows not suckled or milked (Graves et al., 1968; Oxenreider, 1968; Saiduddin et al., 1968; Wagner and Oxenreider, 1971), or milked twice a day (Wiltbank and Cook, 1958) compared with regular suckling or milking four times per day (Clapp, 1937). Short et al. (1972) found that mastectomy of multiparous cows shorten the interval from parturition to estrus even more than only removal of suckling stimuli. The number of offspring suckling will also affect the duration of the interval to the first postpartum estrus. Cows suckling two calves had a longer interval to estrus compared with cows only suckling one calf and the effect was independent of BW (Wettemann et al., 1978).

Removal of calves allows ovarian activity to occur sooner after parturition compared with cows managed with calves. Weaning calves allows cows to rebreed sooner than suckled cows (Lusby and Wettemann, 1986; Bishop et al., 1994). The earlier resumption of reproductive activity after weaning is due to increased concentrations of LH in plasma which stimulate ovarian function and follicular growth (Carter et al., 1980). Early weaning of calves increased number of LH pulses and shortened the number of days to luteal activity and the response occurred sooner in cows with greater BCS (Bishop et al., 1994). Formation of a fully functional corpus luteum seldom occurs before the first behavioral estrus with a majority of first calf heifers (Ciccioli et al., 2003) and cows (Looper et al., 2003), and the first luteal cycle before estrus is usually a short luteal phase. Early regression of the corpus luteum is caused by increased concentrations of prostaglandins from the uterus prior to the time that pregnancy recognition usually occurs (Guilbault et al., 1984; Guilbault et al., 1987a; Guilbault et al., 1987b).

Postpartum Anestrus:

Production of a calf every 12 mo is essential to maximize efficiency and profitability of a cow/calf operation. The length of time required for involution of the uterus, resumption of normal ovarian activity, estrous behavior, and conception is influenced by numerous factors such as age, nutrition, BCS, and lactation. The time from calving until the first behavioral estrus is known as postpartum anestrous interval and should be less than 85 d. The corpus luteum formed during the anestrous period is smaller and secretes less progesterone (Lishman et al., 1979; Rutter and Randel, 1984; Carruthers et al., 1986).

The effects of BCS, nutrition and suckling on ovarian function and estrus were discussed previously and will only be summarized. Thin BCS (BCS < 5) at calving will increase the length of the postpartum anestrous interval in both cows and heifers (Richards et al., 1986; Spitzer et al., 1995; Lalman et al., 1997). Body condition score at calving is the best indicator of interval from parturition to resumption of estrus, thus, greater nutrient intake during gestation will reduce the anestrous period (Dunn et al., 1969; Rutter and Randel, 1984; Lalman et al., 1997). Inadequate nutrient intake after calving can have a greater effect on the duration of the interval to estrus when cows have a thin BCS. Greater nutrient intake can reduce the interval to estrus but cannot completely overcome the increase in time due to thin BCS at calving in cows (Wiltbank et al., 1962; Perry et al., 1991) and heifers (Dunn et al., 1969; Spitzer et al., 1995).

Primiparous cows have a longer interval from parturition to estrus than multiparous cows because of the increase in nutrients needed for growth (Wiltbank, 1970; Bellows et al., 1982; Triplett et al., 1995). Nutrient partitioning during gestation and lactation influences heifers more than cows because heifers are growing and have higher nutrient requirements. Bellows et al. (1982) found that sex of the offspring also influenced the resumption of estrus and both cows and heifers suckling male calves had a longer interval to estrus than those suckling female calves. Male calves will consume greater quantities of milk which results in greater gains prior to weaning and have heavier weaning weights than females (Reynolds et al., 1978).

The environment may also influence the interval from parturition to estrus by increasing stress on cows and altering nutrient availability for the resumption of reproductive function. These factors include relative humidity, wind speed, dew point, barometric pressure, radiation and photoperiod which influence an animal's ability to maintain body temperature (Christenson, 1980; Hansen, 1997; Wolfenson et al., 2000).

With a limited time for conception to occur after parturition, cow-calf producers must understand how nutrients and BCS, environmental factors, suckling, and age influence resumption of estrus to maximize profitability of their operation. An understanding of nutritional influences on reproduction will increase the efficiency of a cow herd. The ability to assess BCS, and knowledge of the different effects of nutrients, allows mangers to correctly identify areas of concern without wasting resources.

Endocrine and Metabolic Regulation of Nutritional Effects on Reproduction

The main focus of metabolism in ruminants is to control concentrations of glucose in the blood (Brockman and Laarveld, 1986). Glucose is the key energy substrate for the brain (Lindsay and Setchell, 1976) and has a role in controlling reproduction. Reproduction is one of the body processes that is influenced first by inadequate nutrients;

either directly on reproductive organs or by altered endocrine function. Secretion of LH is decreased when nutrient availability is reduced (Richards et al., 1989a; Bossis et al., 1999). This reduction in LH is mediated through a reduction in secretion of GnRH which may be influenced by altered concentrations of insulin, glucose, GH, IGF-I and NEFA in plasma (Bossis et al., 2000). Increased nutritional intake after parturition will increase BCS, number of heifers with luteal activity, and concentration of glucose in plasma (Vizcarra et al., 1998).

Glucose:

Cattle grazing forages produce acetate as the primary volatile fatty acid (VFA), whereas, propionate is the primary VFA in starch based diets (Stewart et al., 1958). When glucose is adequate, acetate is metabolized more efficiently (Cronje et al., 1991). Acetate is lost as heat due to inadequate nitrogen supply to rumen microbes when grazing dormant forages and metabolizable energy is reduced. Propionate, a more efficient glucogenic precursor, is often inadequate in cattle grazing low quality forages (Cronje et al., 1991; Hawkins et al., 2000).

The majority of fetal growth occurs during late gestation. Glucose is the primary energy substrate for the fetus which explains the linear decrease in circulating concentrations of glucose in plasma during late gestation (Sletmoen-Olson et al., 2000a). Concentrations of glucose in plasma increase in a quadratic manner during early lactation. This increase alleviates the negative energy balance and provides the glucose required for milk production. Glucose is required for lactose production in the mammary gland and to incorporate acetate for formation of long chain fatty acids in adipose and mammary tissue (Hawkins et al., 2000).

Ovarian function may not be directly influenced by concentrations of glucose, although, minimal amounts are needed for steroidogenesis (Stewart et al., 1995). Treatment of cattle with a metabolic inhibitor decreased CL formation and estrus (McClure et al., 1978). Hypoglycemic states induced by a competitive glucose antagonist decreased pulse frequency but did not inhibit GnRH effects in cows (Rutter and Manns, 1987) or lambs (Bucholtz et al., 1996). When cows receive 70% of energy requirements, hypoglycemia is not induced but secretion of LH in plasma may by altered (Grimard et al., 1995). Infusion of glucose can increase follicular growth in sheep (Gallet et al., 2011) and has been linked to cholesterol uptake by the ruminant ovary (Rabiee and Lean, 2000).

Systemic infusion of lactating cows with glucose increased concentration and pulse frequency of LH, indicating direct effects on the hypothalamus and/or pituitary (Garmendia, 1986). When systemic glucose is adequate in lactating beef cows infusion of glucose did not alter basal LH or LH pulses (McCaughty et al., 1988), however propionate infusion increased pituitary sensitivity to GnRH (Rutter et al., 1983). Energy restricted heifers that were supplemented with propionate had LH concentrations similar to control heifers, but heifers supplemented with acetate had reduced LH secretion (DiCostanzo et al., 1999). Concentration of glucose in plasma cannot be used to predict reproductive performance (Vizcarra et al., 1998).

Insulin:

Glucose and energy status may be key elements to variation in secretion of hormones influential to reproductive processes (Short and Adams, 1988), however glucose uptake into cells cannot occur without glucose transporters. Glucose transporters (GLUT) 1 and 3 are involved in transport within the brain and are insulin independent transporters in cattle (Zhao et al., 1993). Dominant follicles and the CL have similar mRNA expression for GLUT 1 and 3 as the brain of cattle (Nishimoto et al., 2006). An insulin dependent transporter, GLUT 4, is expressed in the hypothalamus and pituitary of cattle (Zhao et al., 1993; Livingstone et al., 1995), and indicates that insulin may influence the ability of glucose to regulate gonadotropin secretion (Brant et al., 1993) and LH pulse frequency (Hileman et al., 1993). Insulin infusion will increase GnRH secretion from the hypothalamus when concentrations of glucose are adequate, indicating insulin facilitates GnRH secretion through regulation of glucose (Arias et al., 1992).

Insulin mediates the availability of energy to tissues by altering systemic glucose concentrations, and plasma concentrations of insulin can be used as an indicator of the nutritional status of cattle (Ciccioli et al., 2003; Lents et al., 2005). Similar to concentrations of glucose in plasma, insulin in postpartum beef cows is not indicative of luteal activity (Vizcarra et al., 1998), but plasma glucose and insulin concentration are significant predictors of days to second postpartum ovulation in dairy cows (Francisco et al., 2003). Systemic concentrations of glucose and insulin are reduced, and concentrations of NEFA are elevated, when cyclic cows receive inadequate nutrients (Richards et al., 1989b) and during early lactation in dairy cows (Butler and Smith, 1989). The ability of insulin to regulate glucose is altered during nutritional deprivation by decreased glucose clearance and increased concentrations of insulin in serum of cows (Richards et al., 1989b).

The suckling stimulus decreased concentrations of insulin and glucose in cows and may be a mechanism by which suckling inhibits the onset of postpartum estrous cycles (Rutter and Manns, 1987). Heifers on a weight loss diet and treated with glucose or propionate will exhibit increased secretion of insulin (DiCostanzo et al., 1999). Supplementation with protein (Marston et al., 1995) or lipid (Ryan et al., 1995) will increase concentrations of insulin in plasma of cows because both are gluconeogenic precursors. Concentrations of insulin in plasma increased linearly with increased BCS, when postpartum nutrition of cows is adequate (Vizcarra et al., 1998).

Insulin will also influence endocrine function of the ovary by increasing the number of follicular thecal (Stewart et al., 1995), and granulosa (Spicer et al., 1993) cells. Insulin and LH are synergistic to increase thecal cell production of progesterone and androstenedione (Stewart et al., 1995) and insulin and glucose are additive to increase steroid production (Stewart et al., 1995). Insulin stimulates granulosa cells from both large and small follicles to increase progesterone production. Exposure of differentiated granulosa cells from large follicles to increased concentrations of insulin and FSH will enhance production of estradiol (Spicer et al., 1993). Insulin will stimulate estradiol production in granulosa cells of small follicles even in the absence of IGF-I and FSH (Spicer et al., 1993).

Growth Hormone /IGF-I axis:

Insulin-like growth factor - I (IGF-I) is indicative of nutrient status (Houseknecht et al., 1988; Granger et al., 1989; Rutter et al., 1989) and is related to BCS of cows (Bishop et al., 1994; Ciccioli et al., 2003; Lents et al., 2008). Greater amounts of protein and energy in the diet of heifers increased IGF-I concentrations and follicular growth rate, but decreased oocyte quality (Armstrong et al., 2001). When adequate protein is provided neither BCS nor protein supplementation influences IGF-I concentrations (Spicer et al., 1991; Lents et al., 2008). Decreased protein concentrations due to restricted nutrient intake will decrease IGF-I concentrations in plasma (Lents et al., 2005).

The interval from parturition to first estrus is reduced when nutrient intake is increased. Therefore, IGF-I may be associated with the resumption of ovarian activity. Acute changes in IGF-I do not influence resumption of ovarian activity (Ciccioli et al., 2003). Concentrations of IGF-I in plasma, increased linearly, prior to the resumption of ovulation, in anestrous heifers (Bossis et al., 2000), non-lactating cows (Richards et al., 1995), and suckled cows (Stagg et al., 1998), and prior to the onset of puberty in heifers (Jones et al., 1991). Francisco et al. (2003) found that IGF-I was the most significant predictor of days to first postpartum ovulation in dairy cows. Yelich et al. (1996) found that heifers fed to gain more weight prior to puberty attained puberty at a younger age and had greater concentrations of IGF-I compared with heifers that had less ADG. However, heifers gaining less BW had similar IGF-I concentrations at initiation of puberty as heifers that had greater ADG before puberty. Insulin-like growth factor - I may influence the return of estrous activity in suckled or feed restricted cows but it does not influence variability in postpartum ovulations associated with genotype (Spicer et al., 2002).

Peripheral concentrations of IGF-I regulate dominant follicle growth rate and maximum diameter. Dairy cows with greater concentrations of IGF-I after parturition ovulated the first postpartum dominant follicle (Beam and Butler, 1997). Beef cows selected for increased twinning rate had greater concentrations of IGF-I in plasma. Systemic concentrations of IGF-I are indicative of concentrations of IGF-I levels within follicular fluid of large follicles (Echternkamp et al., 1990). Thecal cells (Stewart et al., 1996) and granulosa cells (Spicer et al., 1994) from large follicles have greater numbers of IGF-I receptors compared with small or immature follicles. Sensitivity of follicles to

LH is increased by IGF-I and facilitates increases binding site numbers and steroid hormone production necessary for ovulation (Stewart et al., 1995; Stewart et al., 1996). Increased concentrations of IGF-I will increase of thecal (Stewart et al., 1995) and granulosa (Spicer et al., 1993) cell proliferation and steroidogenic capabilities. Although stress may decrease ovarian activity via suppression of LH secretion (Li et al., 2003), short-term dexamethasone decreased concentrations of IGF-I and this was associated with reduced luteal progesterone secretion without affecting follicular growth (Maciel et al., 2001). In vitro, cortisol induces proliferation and steroid production in thecal cells (Spicer and Chamberlain, 1998).

Secretion of IGF-I by the liver is stimulated by GH binding to receptors. This indicates IGF-I secretion is coupled with GH activity (Thissen et al., 1994). Nutrient restriction will reduce systemic IGF-I (Richards et al., 1991; Armstrong et al., 1993; Richards et al., 1995) and increase GH in plasma of heifers (Bossis et al., 1999) and cows (Roberts et al., 1997). This coupled effect was demonstrated by Armstrong et al. (1993) through immunization against GH which decreased both GH and IGF-I in plasma of heifers. Feed restriction further depleted concentrations of IGF-I in plasma. The increase in GH associated with decreased IGF-I in plasma is due to a decrease in metabolic clearance rate of GH and decreased concentration of somatostatin in hypothalamic portal vessels (Keisler and Lucy, 1996). Increased amount (Yelich et al., 1996) and quality (Houseknecht et al., 1988) of energy intake decreased systemic GH. Protein supplementation will decrease also systemic GH in beef cows fed poor quality hay (Sletmoen-Olson et al., 2000a).

The uncoupling of GH stimulated IGF-I secretion may be detrimental to reproductive functions because hepatic IGF-I is more influential than IGF-I located within follicular fluid (Diskin et al., 2003). The effect of GH on reproductive function is not limited to stimulation of IGF-I. Severe reductions in follicular and luteal development occurs in cattle with severely reduced systemic IGF-I due to a mutation in GH, rendering GH biologically inactive (Chase et al., 1998; McCormack et al., 2009; Chase et al., 2011). Concentration and pulses of GH increase at puberty and may be influential in the onset of puberty in heifers (Yelich et al., 1996). Growth hormone receptors are located in large luteal cells, liver, muscle, and adipose tissue in greater numbers compared with follicles and small luteal cells (Lucy et al., 1993). There is also greater amounts of mRNA for GH receptor located in CL and uterine tissue compared with the hypothalamus, pituitary, and ovary (Lucy et al., 1998), and may explain why GH only influenced thecal cells of large follicles at physiological doses (Spicer and Stewart, 1996).

Nutritional Effects on Growth and Carcass Traits of Calves

The cow-calf sector of the beef industry relies on production of pounds of calf at weaning for profitability (Dickerson, 1970). There are many factors that can influence the weaning weight of calves; that range from environment to genetics (Short et al., 1996). Producers can increase lactation through supplementation of cows and increase weaning weight of calves though direct supplementation.

Birth Weight:

Late gestation and early lactation are the physiological stages of production in which nutrient requirements are the greatest. These times are when supplementation can have the greatest influence. The majority of fetal growth occurs during the last third of gestation (Winters et al., 1942; Swett et al., 1948; Bauman and Currie, 1980). Prenatal protein supplementation of cows will not only increase BCS and BW but may increase birth weight of the calves (Spitzer et al., 1995; Sletmoen-Olson et al., 2000b; Stalker et al., 2007) or may have no effect (Hough et al., 1990; Stalker et al., 2006; Martin et al., 2007). The type or quality of forage which is available may influence birth weight; improved pastures (Martin et al., 2007) or corn residues (Larson et al., 2009) provide more nutrients and can eliminate some of the need for protein or energy supplementation.

Maternal Diet:

Postpartum supplementation of cows will usually not provide nutrients for maternal tissues but nutrients will be used by the mammary gland for lactation. Nutrition of cows in early lactation must be adequate to maintain BCS (Short et al., 1996). Protein supplementation after calving will increase milk production (Furr and Nelson, 1964; Rusche et al., 1993; Short et al., 1996), quality of milk (Van Saun et al., 1993), and weaning weights of calves (Rusche et al., 1993; Stalker et al., 2006; Martin et al., 2007; Larson et al., 2009). Amount of growth from supplementation is dependent on the total diet of the cow. Increased protein (Beaty et al., 1994; Sletmoen-Olson et al., 2000b) or energy (Spitzer et al., 1995; Ciccioli et al., 2003) supplementation will usually increase weaning weights. Supplementation of UIP did not influence milk production in mature cows (Triplett et al., 1995). Supplemental energy will not alleviate the effects of feed restriction, with prenatal or postnatal restriction reducing weaning weights (Corah et al., 1975; Perry et al., 1991). Although, calves suckling energy supplemented cows exhibited more sustained growth after supplementation (Marston et al., 1995).

Nutritional Supplementation of Calves:

Access of high quality forages for calves and not cows is an option for producers to increase weaning weights with minimal inputs (Harvey and Burns, 1988). When calves grazed corn residues, BW was heavier compared with calves born on dormant native range in May (Martin et al., 2007; Larson et al., 2009). Another option is to provide direct supplementation to calves through creeping feeding. Creep feeding is usually done when milk yields are limiting (Christian et al., 1965) to increase weaning weights of calves (Bray, 1934) and the profitability of a calf crop (Peterson et al., 1989). Creep feeding calves a protein supplement will increase forage intake and digestibility when calves are grazing warm season forages (Lusby and Wettemann, 1986). However, supplementation when calves graze cool season forages does not increase efficiency of calf growth (Cremin et al., 1991).

Ad libitum creep feeding can have detrimental side effects such as decreased forage digestibility throughout the entire gastro-intestinal tract (Stricker et al., 1979; Faulkner et al., 1994). Limit fed calves are more efficient (Cremin et al., 1991) with up to 1.0 kg/d increasing ADG prior to weaning (Lusby, 1986; Lusby and Wettemann, 1986; Faulkner et al., 1994). Increasing efficiency in gain by creep feeding is more profitable when calves are sold as feeder animals but when raising replacement heifers, excess fat deposition may decrease the development of maternal traits (Holloway and Totusek, 1973). Others have indicated that creep feeding does not appear to influence fat deposition of heifers (Prichard et al., 1989) and additional weight gained was negated by one year of age in replacement heifers (Martin et al., 1981).

Preweaning Nutritional Effects on Carcass Characteristics:

Effects of prenatal and postnatal nutrition on carcass characteristics is difficult to evaluate with all of the variables in management, environment, and genetics that can influence the finished carcass. Protein supplementation during both late gestation and early lactation will increase gain before weaning and the effect may continue throughout growing and finishing (Stalker et al., 2006; Stalker et al., 2007; Larson et al., 2009). Calves from protein supplemented cows had greater ADG and DMI when placed on high concentrate finishing diets (Larson et al., 2009) or there was no influence on ADG and DMI of calves (Stalker et al., 2006). The effects of protein supplementation on weight gain may be dependent on length of supplementation and age at weaning (Ciminski, 2002). Early weaning programs allow for more recovery time for cows, calves start on finishing diets at a lighter weight, and increased quality of carcasses (Myers et al., 1999; Fluharty et al., 2000). Final body weights and carcass weights were heavier but marbling score, yield grade, 12th rib fat (Stalker et al., 2007; Larson et al., 2009), and ribeye area (Larson et al., 2009) were not influenced by maternal protein supplementation and calves grazed improved pastures or corn residues compared with calves on dormant native range which suckled cows that were not supplemented. Supplying calves with creep feed allows them to reach finish weight and greater quality grades at a younger age (Rouquette et al., 1983; Faulkner et al., 1994).

Nutritional Effects on Fetal Programming

A unique circumstance occurred during WWII in the Netherlands. After Allied forces were stalled just north of the Dutch border all food transport stopped. This severe restriction in food supply limited residents to less than 1000 calories per day, however people still had children and good records were kept. Analysis of these records sparked interest in the effects of maternal nutrition on human fetal development and risk of disease (Roseboom et al., 2011). The theory of the fetal origin of adult disease was developed from these data with the impacts varying widely between sexes, time of restriction, and severity of restriction (Barker et al., 1993). Restriction of nutrients in early gestation increased the incidence of brain damage, impaired brain function, and development of anti-social personality disorders (Stein et al., 1972). Nutrient restriction in early gestation also increased the prevalence of heart disease (Painter et al., 2006) and hypertension (Stein et al., 2006).

Nutrient restriction of humans during mid-gestation altered formation of glomeruli, overall kidney function, and airway formation (Lopuhaa et al., 2000). Exposure to famine at any time during gestation increased the chance for cardiovascular disease, metabolic disorders, breast cancer, and obesity to develop during adulthood (Painter et al., 2008a). Similar to domesticated livestock, stress to human fetuses influences each sex differently. The Dutch Famine studies indicated that women exposed to nutrient restriction in utero have increased fertility with a greater incident of twins, larger families, and reached puberty at a younger age (Lumey and Stein, 1997; Painter et al., 2008b). This may be an attempt to overcome increased mortality rates within nutrient restricted environments. In contrast fetal nutrient restriction did not influence male fertility. Nutrient restriction increases neonatal adiposity in both sexes, but male fetuses have a greater incident of this increase which results in obesity (Ravelli et al., 1976; Ravelli et al., 1999).

The placenta as well as the fetus is influenced by nutrient restriction. A major function of the placenta is nutrient exchange and severe dysfunction occurs during and after nutrient restriction (Reynolds and Redmer, 1995; Meschia, 1983). Nutrient restriction during gestation will decrease uterine blood flow and fetal growth while increasing uterine vascular resistance and the risk of complications (Trudinger et al., 1985; North et al., 1994). Results from these human studies have been extrapolated to production livestock for a better understanding of growth and development.

Bovine:

The cow-calf industry experiences periods of nutrient restriction. Forages are dormant during late summer and winter months and seldom provide adequate nutrients for gestating cows. Lack of available nutrients in spring-calving cows, in Oklahoma, occurs during mid to late gestation and in fall-calving cows restriction can occur prior to breeding through the first half of gestation. Nutrient restriction will decrease muscle mass and increase adipocyte growth and overall fatness of offspring (Zhu et al., 2006; Long et al., 2009). Supplementation of protein will have a positive associative effect to increase DMI, thus, increasing total protein and energy available to the animal.

Nutrient restriction during early to mid-gestation may not influence birth weight (Martin et al., 2007; Long et al., 2009) or may reduce birth weight (Carstens et al., 1987; Spitzer et al., 1995; Larson et al., 2009). Reduced nutrient intake in late gestation increased the weight of the placenta to compensate for less maternal nutrients (Rasby et al., 1990). In contrast to the increase in placental weight, numbers of cotelydons (Long et al., 2009) surface density, and number of capillaries within the placentome were decreased after nutrient restriction (Vonnahme et al., 2007). When postnatal nutrition was adequate BW was not affected by birth weight (Freetly et al., 2000). Postnatal supplementation or grazing improved forage will increase weaning weights (Funston et al., 2010).

Calves that were nutrient restricted during early to mid-gestation had decreased muscle mass and increased adipocyte diameter at harvest (Long et al., 2012). Nutrient restriction, in utero, may increase (Long et al., 2012) or have no effect (Stalker et al., 2007; Larson et al., 2009) on yield grades of carcasses. The decrease in muscle mass may be due to a decrease in the number of muscle fibers (Long et al., 2010c). Adipose deposition may be increased by a greater concentration of glucose in plasma of restricted vs. adequately fed calves. Prenatally nutrient restricted calves have a reduced ability to clear glucose after infusion of a glucose bolus (Long et al., 2010d). Nutrient restriction can reduce (Long et al., 2010c) or not influence (Stalker et al., 2006; Long et al., 2012) organ development depending on time and severity of restriction.

Nutrient restriction during late prenatal growth will affect weight and growth more than development, due to the immense increase in growth rate that occurs during the last third of gestation. Nutrient restriction during the last trimester can decrease birth weight (Dunn et al., 1969; Corah et al., 1975; Bellows and Short, 1978). Energy restriction during late gestation will reduce the ability of the offspring to thrive and may result in reduced weight at weaning (Corah et al., 1975). Similar to results in human studies, nutritional restriction may not influence birth weight but can decrease BW and composition of beef cattle.

Ovine:

The ovine model has been used extensively to determine the effect of maternal nutrition on growth and development of the fetus. Birth weight is not influenced when ewes receive inadequate nutrients during early gestation (Wu et al., 2006; Ford et al., 2007; Long et al., 2010a). Nutrient restriction during late gestation decreased birth weight of lambs and subsequent milk production of ewes (Tygesen et al., 2007). Lambs that are smaller at birth have less developed GH/IGF-I axis and overall endocrine function with decreased concentrations of IGF-I and increased concentrations of insulin and GH in plasma (Greenwood et al., 2002). Similar to cattle, nutrient restriction influences the composition of skeletal muscle. The number of muscle fibers are decreased when lambs are restricted during early gestation (Zhu et al., 2006). Nutrient restriction late in gestation decreases the size of each myocyte but does not alter the number of fibers within the muscle (Greenwood et al., 2000)

Alterations in glucose metabolism occurs in lambs born to both underfed and obese ewes (Gardner et al., 2005; Ford et al., 2007; Long et al., 2010a) and probably is associated with changes in pancreatic development and insulin resistance due to early overexposure of tissues to insulin (Ford et al., 2009). Concentrate diets fed to lambs from nutrient restricted ewes exacerbates glucose intolerance and increases the amount of adipose deposition (Ford et al., 2007). Lambs born to obese ewes had restricted development of the gastro-intestinal tract at harvest (Long et al., 2010a).

Nutrient restriction during early gestation may influence peripheral organogenesis to a greater extent than brain development. Nutrient restricted lambs had a decrease in cortisol concentrations (Bispham et al., 2003) and release (Long et al., 2010b) in response to stress, but when challenged with ACTH or CRH responses were similar to control lambs. This indicates influences on the hypothalamus and/or pituitary glands rather than adrenal gland dysfunction. Nutrient restricted lambs had decreased concentrations of progesterone in plasma and overall fertility compared with non-restricted animals (Long et al., 2010b). Supplementation with selenium negated some of the effects of nutrient restriction on follicular development (Grazul-Bilska et al., 2009).

Placentome number and vascularity increases during the last two trimesters of gestation in association with increased growth (Borowicz et al., 2007). Nutrient restriction will increase placental weight (Rasby et al., 1990) and decrease placentome numbers and vascularity in cattle (Vonnahme et al., 2007; Long et al., 2009). Nutrient restriction in ewes will alter placentome formation causing the increase in cotyledon and caruncle contact to occur earlier in gestation (Vonnahme et al., 2006). Increased cotyledonary vascular density during nutrient restriction probably increases the amount of nutrients available to the fetus (Zhu et al., 2007). Decreased vascular density of cotyledons in obese or over nourished ewes may decrease growth rate (Zhu et al., 2009). Limited nutrient intake of humans, cattle, and sheep during gestation will influence the growth of offspring, organ development and endocrine function. The acquisition and understanding of the effects of nutrient restriction, or over nourishment, will allow for more efficient production of livestock and longer, healthier lives for all animals.

Conclusions

The cow-calf industry relies on weight of calves at weaning for profit. For cows to be efficient they must conceive and give birth to a calf every 12 mo. To achieve this goal a cow must complete parturition and uterine involution, resume estrous cycles, and become pregnant within approximately 85 d after calving. Nutrition has a major role in the efficiency of reproduction. Nutrient intake and body energy reserves are limiting factors for reproductive efficiency.

Completion of parturition with limited adverse effect on the reproductive tract and cow is the first step in this process. Use of bulls with genetic potential for minimal birth weight will avoid complications with small and immature cows. Adequate nutrient intake and BCS to provide energy to complete parturition is essential. Uterine involution is a process over which a producer has little influence and length is dependent on the amount of damage inflicted during parturition. Good management scenarios at parturition result in rapid involution and rebreeding is not influenced.

Three factors have roles in resumption of estrous activity: BCS, nutrient intake, and intensity of lactation. Lactation, whether from suckling or milking, may inhibit LH pulses from the anterior pituitary resulting in limited ovarian activity or anestrus. Ad libitum suckling will cause the postpartum anestrous interval to be extended compared with milking either once or twice daily. The amounts of nutrients consumed daily by a cow can have two roles in the resumption of estrus: 1) provide direct nutrients for bodily functions, and 2) excess nutrients are stored as body energy reserves. The best indicator of the length of time between parturition and resumption of estrous activity is BCS at the time of parturition, which is a direct estimate of body energy reserves that are available. Both energy and protein supplementation during the last trimester of gestation will increase BCS prior to calving which will decrease the number of days to the resumption of estrus.

Glucose is the primary energy substrate for the fetus. Ruminants produce VFA that function as gluconeogenic precursors. Propionic acid is the most efficient glucose precursor but cattle grazing forages produce acetate as the primary VFA. Insulin will decease glucose from the circulation and increase energy availability within tissues and for bodily stores, thus concentrations of insulin in plasma can be used as an indicator of nutritional status. Concentration of IGF-I in plasma is also indicative of nutrient intake and may have a vital role in ovarian activity and follicular growth. When nutrient intake is adequate, GH will stimulant secretion of hepatic IGF-I. When nutrient intake is adequate and BCS is great enough to allow for estrous activity to resume within the 85 d after calving, a cow will generally rebreed within a given breeding season.

Greater maternal nutrient intake prior to weaning will increase weaning weight of calves. A vast majority of nutrients and body reserves will be utilized for lactation, thus providing energy and protein that can be used to increase growth and weight gain of calves. Prenatal and postnatal nutrient intake can influence the quality of carcass at harvest. Diet of cattle can increase the amount of muscle or fat deposited which will influence the quality of meat.

The Dutch Famine provided direct insight into the effects caused by inadequate nutrients during gestation in humans. Greater concerns about health in developing countries, associated with malnutrition, or in developed countries due to over nutrition, have focused attention to the field of fetal programming. The effects of nutrient restriction during gestation vary from decreased BW gain to dysfunction of organs and cardiovascular disease. Over nutrition has an influence on health by influencing the prevalence of type II diabetes and obesity in humans, and increasing the fatness of carcasses in ruminants. Development of a better understanding of how prenatal nutrition will influence productivity and health of offspring throughout life will allow for increased efficiency in beef production.

CHAPTER III

EFFECTS OF PROTEIN SUPPLEMENTATION ON REPRODUCTIVE PERFORMANCE OF FALL CALVING COWS, AND PRENATAL AND POSTNATAL GROWTH, AND CARCASS CHARACTERISTICS OF CALVES

ABSTRACT

Fall calving cows grazing native dormant range were used to determine the effects of protein supplementation on reproductive performance of cows and growth and carcass characteristics of calves. Cows were individually supplemented from mid-November to mid-March for four years with either a control diet (Con; 1.82 kg/d of 38 % CP) or low diet (L; 0.2 kg/d of 8%). During each year cows were reassigned dietary treatments according to calving date and BCS, with half of Con and L cows remaining on the same diets as the previous year and the other half assigned to the other diet. Cows were exposed to bulls for 60 d beginning December 1. Statistical analyses were performed utilizing a 2 x 2 factorial design with PROC GLM and PROC FREQ. Cows on Con diets lost less BW from November to January compared with L cows (-29.8 ± 2.8 and -49.7 ± 2.8 kg, respectively, respectively; $P < 0.001$). Body condition score of Con cows at weaning was greater than that of L cows (4.1 ± 0.1 and 3.9 ± 0.1, $P = 0.03$). Protein supplementation increased insulin concentrations in plasma of Con compared with L cows during treatment (*P* < 0.003). Birth weight of calves was not influenced by prenatal treatment (*P* = 0.86). Maternal protein supplementation did not influence plasma concentrations of insulin in calves (*P* > 0.22). Concentrations of IGF-I were greater in calves suckling Con cows compared with calves from L cows (21.4 ± 2.1 and 14.8 ± 2.1ng/ml, respectively; *P* = 0.03). A prenatal x postnatal effect was detected for BW of calves; prenatal low and postnatal control calves (LCon; 186.1 ± 4.4, *P* = 0.02) had greater 205 d adjusted weaning weights compared with prenatal low and postnatal low (LL), prenatal control and postnatal low (ConL), and prenatal control and postnatal control (ConCon) calves (154.9 ± 4.0, 172.4 ± 4.1, and 180.1 ± 4.2 kg, respectively). There was a tendency (*P* = 0.06) for a prenatal x postnatal effect on ADG of calves at weaning; LCon calves gained more than LL and ConCon calves (2.1 ± 0.1, 1.7 ± 0.1, and 1.9 ± 0.1 kg/d, respectively). Calves from cows on Con diets during prenatal and postnatal growth had greater hot carcass weights (393.6 ± 9.1 kg) compared with LL calves (362.6 ± 9.1 kg, *P* = 0.02), however, other carcass characteristics were not influenced by treatment (*P* > 0.17). Supplemental protein that increased BW and BCS of cows, increased ADG of calves prior to weaning, and increased BW at harvest, but did not influence carcass characteristics of calves.

Introduction

Reproductive efficiency of a cow-calf operation is determined by adequate BCS at calving which is the most important factor that influences the postpartum anestrous interval (Richards et al., 1986; Selk et al., 1988; Morrison et al., 1999). Profitability depends on maximizing production and minimizing inputs; however, the majority of profit comes from increasing BW of calves at weaning (Dickerson, 1970). A cow must produce one calf every 12 mo to maximize this production, thus there are only 85 d after gestation to become reproductively fit and rebreed. Supplementation of cows will increase input costs but may be necessary for successful conception rates during times when forage quality is less than adequate (Lusby and Wettemann, 1988; Horney et al., 1996; DelCurto et al., 2000). Supplementation of calves, with ad libitum protein and energy, will increase weaning weights but can also decrease the amount of forages consumed (Stricker et al., 1979; Faulkner et al., 1994).

Cows will frequently be subjected to inadequate forage quality and quantity for the stage of production. When adequate nutrients are not provided to the fetus during gestation, changes may result which will alter productivity of the offspring (Barker et al., 1993). The Dutch Famine gave an opportunity to evaluate the effects of prenatal malnutrition in humans (Roseboom et al., 2001) and resulted in increased experimentation with domesticated livestock. When nutrient restriction occurs during late gestation, birth weights are reduced in cattle (Wiltbank et al., 1962; Corah et al., 1975; Bellows and Short, 1978), however, early gestational nutrient restriction may not influence birth weight (Martin et al., 2007; Long et al., 2009; Long et al., 2010c). Fetuses deprived of adequate nutrition during early gestation had decreased muscle and increase adipose development (Long et al., 2012). Inadequate prenatal nutrition of calves may cause decreased fertility (Martin et al., 2007) and carcass quality (Stalker et al., 2006; Long et al., 2010c).

The major objective of the current study was to determine the effects of protein supplementation of fall calving cows on BW, BCS, reproductive performance, and the influence of protein supplementation to cows on prenatal and postnatal growth, and carcass characteristics of calves. A second objective was to evaluate the effects of protein supplementation on plasma concentrations of insulin, glucose, IGF-I, and plasma proteins in cows and insulin, IGF-I, and plasma proteins in calves. Our hypothesis was that protein supplementation of fall calving cows will influence prenatal and postnatal growth and carcass characteristics of calves without affecting reproductive efficiency of the cows.

Materials and Methods

All experimental procedures described were approved by the Oklahoma State University Animal Care and Use Committee.

Animals

Fall calving, multiparous Angus cows were used to determine the effects of protein supplementation on BW and BCS, reproductive performance, plasma concentrations of insulin, IGF-I, plasma proteins, and glucose in cows and calves, calf growth, and carcass characteristics of calves. Cows were maintained in the same pastures, at the Range Cow Research Center, west of Stillwater, OK and diets only differed during protein supplementation. Cows were individually supplemented, from mid-November to mid-March during four consecutive years (n = 44, yr 1; n = 51, yr 2; n = 58, yr 3; n = 53, yr 4) with one of two diets.

The low diet (L) consisted of 95 % soybean hulls and 5 % molasses (as-fed) at 0.2 kg/d for an 8% crude protein supplement and control diet (Con) consisted of 81 % cottonseed meal, 11 % soybean meal, and 8 % wheat mids (as-fed) at 1.82 kg/d for a 38 % crude protein supplement. Diets were fed 4 d/wk with Con cows received 3.2 kg and L cow received 0.4 kg each feeding. During lactation the subsequent year, half of the cows on Con and L prenatal treatments were assigned to Con and the other half was assigned to L. Cows were provided premixed mineral supplement ad libitum. Grass hay was provided when forage amounts were inadequate due to snow cover or availability. Hay was also provided when ambient temperature was less than 0˚ C or 4˚ C with wet weather.

Cows were exposed to mature bulls for a 60 d commencing on December 1. Body weights and BCS were obtained for cows, after a 16 h shrink period, 4 to 19 d before calving in August, during November to March, and at weaning in May. Pregnancy rates were determined at weaning via rectal palpation and the interval from calving to conception was caclulated by subtraction of 280 d from calving dates.

Calf Growth and Carcass Traits

Protein supplementation of cows was used to alter prenatal and postnatal nutrients available to calves. Treatment combinations for calves were: Con prenatal and Con postnatal (ConCon), L prenatal and Con postnatal (LCon), Con prenatal and L postnatal (ConL), and L prenatal and L postnatal (LL). Birth weights were taken within 24 h of birth and bull calves were castrated with rubber bands. Body weights of calves were recorded in January, February, March, and at weaning in May.

Post-weaning growth was determined from BW obtained 3 to 5 times before calves entered the feedlot and adjusted ADG was calculated for 205 d and 365 d. After weaning each year calves were maintained as a single group at the Range Cow Research Center until entry into the feedlot. Calves received an implant of Component - S (yr 1; Elanco Animal Health, Greenfield, IN) or Revalor – S (yr 2; Merck Animal Health, Summit, NJ), with 120 mg of trenbolone acetate and 24 mg of estradiol-17β, upon entry into the feed lot (0 d). Calves received a high concentrate diet, during finishing, that consisted of 53 % dry rolled corn, 7 % roughage, 15 % dried distillers grains, 15 % wet corn gluten, 5 % premixed dry supplement, and 5 % premixed liquid supplement on a dry matter basis. Calves were fed until it was estimated that adipose deposition was adequate to result in at least 65 % choice carcasses with 1.25 cm back fat depth and prior to carcass weights that are penalized for being too heavy.

Each year calves were harvested on a single day at a commercial abattoir in Arkansas City, KS and carcass characteristics were determined by experienced personnel. Hot carcass weights, ribeye area, quality grade, yield grade, back fat thickness, dressing percentage, and marbling scores were obtained.

Hormone Analysis

Plasma samples were collected immediately following supplementation during yr 3 from cows via tail veinipuncture and from calves via jugular veinipuncture with Monoject vacuum tubes with 15 mg EDTA (Tyco Healthcare Group, LP; Mansfield, MA) and samples were placed on ice. Plasma was removed within 4 h via centrifugation at 1800 x g for 15 min and stored at -20˚ C. Cows were sampled in December, January, March, and May and calves were sampled in December, January, May, and the following November. Insulin and IGF-I were quantified in samples from calves and cows, and glucose was quantified in cows.

Plasma samples were thawed at room temperature for 4 h on the day of analyses. IGF-I was quantified after acid ethanol extraction (16 h at 4˚ C) using a double antibody RIA protocol (Echternkamp et al., 1990) with recombinant human IGF-I (R&D Systems; Minneapolis, MN) as the standard. Intra- and inter-assay CV's were 13 and 4 %, respectively, for mature cow plasma and 13 and 16 %, respectively, for calf plasma. Insulin was quantified by a solid-phase RIA (Bossis et al., 1999; Coat-a-Count; Siemens, Los Angelos, CA) with bovine pancreatic insulin as the standard (Sigma Chemical Co., St. Louis, MO). Intra- and inter-assay CV's were 15 and 26 %, respectively, for cow plasma, and 20 and 30 %, respectively, for calf plasma.

Concentrations of glucose were quantified with Infinity™ Glucose Hexokinase Liquid Stable Reagent (Thermo Fisher Scientific Inc., Marietta, OH) in triplicate, at a concentration of 1:150 and kept at 4˚ C via ice water, prior to addition of reagent until incubation. Immediately following vortexing, samples were incubated in a water bath at 27˚ C for 10 min; after incubation samples were placed into ice water until quantification. Intra- and inter-assay CV's were 7 and 3 %, respectively.

Statistical Analysis

The GLM procedure of SAS (SAS Institute Inc., Cary, NC), was used to analyze carcass traits, IGF-I, insulin, glucose, postpartum anestrous interval, BW and BCS. The model for cow traits included previous year treatment, current year treatment, and all interactions. The model for calf traits included prenatal treatment, postnatal treatment, year, and, when appropriate, sex and age as covariates. Chi-squared analyses were used to evaluate the effect of treatment on pregnancy rates (PROC FREQ; SAS). Year was initially in the model, without significant interactions, year was removed and means were pool. Fisher's least square difference was used to compare means when F-test for treatments was significant ($P < 0.05$).

Results

Control cows lost less BW (-29.8 ± 2.8 kg; $P < 0.001$; Table 1) during November to January, compared with L cows (-49.7 ± 2.8 kg). Protein supplementation increased BW ($P = 0.05$) and BCS ($P = 0.03$; Table 2) of Con cows (576.2 ± 7.0 kg and 4.2 ± 0.1, respectively) compared with L cows (556.1 ± 7.0 kg and 4.0 ± 0.1, respectively) in February. Control cows had greater BW compared with L cows in March (545.4 ± 7.6

and 522.3 ± 7.6 kg, respectively; *P* = 0.03). Control cows had greater BW (548.1 ± 6.0 kg; *P* = 0.03) and BCS (4.1 ± 0.1; P = 0.03) compared with L cows (529.0 ± 5.9 kg and 3.9 ± 0.1, respectively) in May. Calving date, pregnancy rate, and postpartum interval to conception were not influenced by protein supplementation (*P* > 0.22, Table 3).

Concentrations of insulin in plasma of Con cows were greater (*P* < 0.001) in December, January, and March (1.49, 1.43, and 1.50 ± 0.06 ng/mL, respectively) compared with L cows (1.16, 1.04, and 1.15 ± 0.06 ng/mL, respectively). Insulin in plasma of cows at weaning, was not influenced by treatment (*P* = 0.35, Fig. 1). Concentrations of glucose in plasma were not influenced by protein supplementation at any sampling period (*P* > 0.22, Fig. 2). Concentrations of IGF-I (Fig. 3) were greater in Con cows compared with L cows in December (26.5 ± 3.0 and 17.1 ± 3.0 ng/mL, respectively; *P* = 0.04) but were not influenced in January, March, and May.

Birth weight of calves was not influenced by prenatal protein supplementation of cows (*P* = 0.86, Table 4). There was a prenatal x postnatal treatment effect (*P* = 0.04) on BW of calves in January; LL calves weighed less than calves on other treatments (Table 4). Calves that were LL gained less weight from birth until January (0.69 ± 0.03 kg/d; *P* = 0.04) compared with ConCon, ConL, and LCon calves (0.83, 0.78, and 0.85 ± 0.02 kg/d, respectively, Fig. 5). Adjusted weaning weights (205 d) were less for LL calves (*P* < 0.003) compared with all other groups. LCon calves weighed more than ConL calves (186.1 ± 4.4 and 172.4 ± 4.1 kg, respectively, *P* = 0.02) and ConCon calves did not differ in BW compared with LCon and ConL calves (Table 4). Gains of LCon calves were greater from January to weaning (0.70 ± 0.02 kg/d) compared with ConL calves (0.63 ±

0.02 kg/d, *P* = 0.007); LL calves had the least gain compared with all treatments (0.56 ± 0.02 kg/d; *P* < 0.01, Fig. 4).

There were no interactions between prenatal and postnatal treatments after weaning. Postnatal supplementation increased yearling weights (Table 4) of calves regardless of prenatal treatment. Calves that suckled Con cows had greater BW (301.1 ± 8.8 kg) compared with calves which suckled L cows (278.5 ± 8.8 kg, *P* = 0.01). Postnatal Con calves tended to have greater ADG from weaning to one year of age compared with L calves (0.59 ± 0.02 and 0.56 ± 0.01 kg/d, respectively; *P* = 0.10). There was a tendency for ConCon calves to weigh more than LL calves (405.0 ± 10.4 and 381.4 ± 10.4 kg, respectively, *P* = 0.09) at entry to the feed yard (Table 4), at approximately 19 mo of age. During the feedlot phase LCon calves had greater ADG (Fig. 5) than all other treatments (2.1 ± 0.1 kg/d, *P* = 0.03) and ConCon calves had a tendency to gain more compared with LL calves (1.9 ± 0.1 and 1.7 ± 0.1 kg/d, respectively, *P* = 0.06).

Final BW was greater (Table 5; *P* = 0.02) for ConCon calves (642.6 ± 14.7 kg) compared with LL calves (601.4 ± 14.7 kg). Hot carcass weight was greater (*P* = 0.02) for ConCon (393.6 ± 9.0 kg) and LCon (398.3 ± 9.0 kg) compared with LL calves (362.6 ± 9.0 kg). Treatments did not influence dressing percentage (*P* = 0.17), ribeye area (*P = 0.56*), yield grade (*P = 0.34*), or marbling score (*P = 0.92*; Table 5).

Concentrations of insulin (Fig. 6) in plasma of calves were not influenced (*P > 0.43*) by prenatal and postnatal treatment. IGF-I concentrations were greater in January (*P* = 0.03) and tended to be greater in November (*P* = 0.07) in the postnatal Con calves (21.4 ± 2.1 and 23.1 ± 1.6 ng/mL, respectively; Fig. 7) compared with calves on postnatal L (14.8 ± 2.1 and 18.7 ± 1.6 ng/mL, respectively). Steers tended to have greater concentrations of IGF-I at weaning compared with heifers (29.8 ± 2.6 and 22.1 ± 2.9 ng/mL, respectively, $P = 0.06$).

Discussion

Body weight and BCS at weaning were decreased by inadequate protein for L cows compared with adequate protein for Con cows. Body weight and BCS of cows at calving the subsequent fall was not influenced by protein supplementation the previous winter because good quality summer forages were available and cows gained weight. Fall calving cows grazing dormant pastures are usually exposed to inadequate nutrients during the 1st trimester of gestation if supplemental protein is not fed. Supplementation of lactating beef cows can influence reproductive traits (Wiltbank et al., 1962; Wiltbank et al., 1964; Dunn et al., 1969), however, milk production has a greater priority for nutrients than BW gain and endocrine functions associated with reproduction (Bauman and Currie, 1980). Body condition score at calving is the best indicator of reproductive performance of beef cows (Richards et al., 1986; Selk et al., 1988; DeRouen et al., 1994). The interval from parturition to conception and overall pregnancy rates were not influenced by treatments because cows in this study were maintained with the minimal BCS that would allow onset of estrus and pregnancy to occur within a 60 d breeding season (Rakestraw et al., 1986).

Supplementing protein to cows grazing dormant, low quality forages will increase dry matter intake and available energy (Fleck et al., 1988; Ovenell et al., 1991). The supplementation program for L cows resulted in a good model to determine if prenatal nutrient restriction results in long term effects on calves. Concentrations of insulin in plasma were greater in Con compared with L cows during protein supplementation due to increased nutritional status. Similarly, Marston et al. (1995) found that protein supplementation increased insulin in lactating cows consuming dry forage.

Concentrations of glucose in plasma were not influenced by treatment. The lack of effect of treatment on plasma concentrations of glucose, although concentrations of insulin were greater in Con cows, could be caused by one or more of four possible mechanisms: 1) increased insulin caused glucose entry into tissues, 2) excess glucose was utilized by the developing fetus and placenta, 3) excess glucose was used for lactose production in the mammary gland and/or 4) increased dry matter intake from protein supplementation increased the amount of acetate produced which is an inefficiency precursor for gluconeogenesis. The fourth possibility is not that probable since concentrations of insulin in plasma were increased.

Concentrations of IGF-I were greater in December in plasma of Con cows compared with L cows. Insulin and IGF-I are both indicative of nutritional status (Rutter et al., 1989; Ciccioli et al., 2003; Lents et al., 2005). Increased concentrations of insulin and IGF-I in plasma indicate that protein supplementation increased available nutrients. These differences in maternal environment indicate Con cows can provided greater concentrations of nutrients to the developing fetus, or suckling calf, due to repartitioning of nutrients toward fetal growth and milk production (Bauman and Currie, 1980).

The lack of effect of prenatal protein supplementation of cows on birth weight of calves was most likely caused by the stage of gestation that protein and energy were limited. The absence of an effect of nutrient deficiency during early gestation on birth weight of calves has also been observed by Martin et al. (2007) and Long et al. (2009). Even without an influence of prenatal treatment on birth weight, postnatal growth of calves was reduced. Reduced postnatal growth after prenatal nutrient restriction agrees with studies with humans and the development of a “thrifty phenotype” (Barker et al., 1993). Reduced availability of nutrients in utero may program the fetus for survival when exposed to nutrient restriction after birth. Animals that are prenatally programmed to survive with limited postnatal nutrients have increased efficiency when adequate nutrients are available after birth (Larson et al., 2009). Calves that were restricted both prenatally and postnatally gained less from birth in September and October to January, and had less BW compared with other treatments. During the first few months before weaning, calves rely more on milk production, thus calves suckling L cows gained less due to decreased milk availability, in agreement with Reynolds et al. (1978). The interaction between prenatal and postnatal treatments resulted in reduced BW and ADG for LL calves and intermediate growth for ConL and ConCon calves compared with LCon calves existed until weaning.

Prenatal protein supplementation of cows did not influence concentrations of IGF-I in plasma of calves. Calves that suckled Con cows had greater concentrations of IGF-I compared with calves suckling L cows in January. Greater concentrations of IGF-I in plasma of calves indicates increased nutritional status through increased milk consumption and may explain why differences between Con and L cows diminished after December.

Nutrient restriction can reduce organ development and function depending on severity and time of restriction (Long et al., 2010c). Concentrations of insulin in plasma of calves were not influenced by treatments indicating normal development of the pancreas and liver, which agrees with results of Stalker et al. (2006) and Long et al.

(2012). In agreement with the effect of nutrient restriction in sheep (Greenwood et al., 2002), prenatal and postnatal protein supplementation tended to decrease concentrations of insulin in ConCon calves compared with LL calves in December. Severe restriction of nutrients of dams altered concentrations of glucose and insulin in plasma of cattle (Long et al., 2010d) and sheep (Gardner et al., 2005; Ford et al., 2007). Maternal obesity reduced the ability of lambs to remove glucose from plasma similar to lambs from nutrient restricted ewes (Ford et al., 2009; Long et al., 2010a) indicating pancreatic malfunction and decreased insulin sensitivity of offspring from obese and under nourished mothers.

Calves grazed forage for almost 12 mo after weaning and the effects of prenatal and preweaning nutrition on BW were minimal. Adjusted yearling weight was influenced by postnatal supplementation of cows and ConCon and LCon calves were heavier compared with LL calves. Concentrate diets fed in the finishing stage of beef production increase concentrations of propionate in plasma, which could exacerbate insulin insensitivity (Ford et al., 2007; Long et al., 2010a). Prenatal L and postnatal Con calves had greater growth than other treatment groups when fed rations to maximize gain. Conclusions on the influence of maternal protein supplementation on growth when calves consume high concentrate diets will be finalized when calves from the final two years are fed and harvested.

Reduced BW and altered body composition occur in humans (Ravelli et al., 1999), sheep (Ford et al., 2007; Zhu et al., 2007), and cattle (Zhu et al., 2006; Long et al., 2009; Long et al., 2010c) due to prenatal nutrient restriction. Restricted pre-weaning protein supplementation reduced final BW and hot carcass weight of calves, and the effect was greatest in calves exposed to low prenatal and low postnatal protein supplementation of cows. Although BW was increased by maternal protein supplementation, ribeye area, dressing percentage, yield grade, or marbling score were not influenced.

Nutrient restriction decreased muscle mass in cattle (Long et al., 2010c) and sheep (Zhu et al., 2006) and increased the area of muscle fibers. Nutrient restriction in sheep increased adiposity of carcasses by 18 wk of age (Ford et al., 2007). Quality grades are given to assess the amount of marbling and maturity of carcasses; marbling scores are directly related to quality grade. Quality grades were not influenced by protein supplementation of dams. Carcasses from prenatal L and postnatal L calves had slightly reduced marbling scores, and with a limited number of carcasses that have been harvested quality grade differences were not adequately evaluated.

In conclusion, prenatal protein supplementation of fall calving cows, that did not influence reproductive efficiency of cows or birth weight of calves, increased growth of calves when postnatal nutrition was adequate. Overall, postnatal protein supplementation of cows increased ADG and BW of calves but neither prenatal nor postnatal nutrition influenced the quality of the carcass.

Table 1. Influence of protein supplementation (Control) during breeding and the 1st trimester of gestation, mid-November to mid-March, compared with low supplementation on BW of fall calving cows

BW, kg	Treatment		SE	*P* value
	Control	Low		
No. of cows	75	75	-	-
November	622.4	629.8	6.9	0.45
November to January	-29.8	-49.7	5.6	< 0.001
January	594.4	580.3	7.4	0.18
February	576.2	556.1	7.0	0.05
March	545.4	522.3	7.6	0.03
January to May	-48.0	-51.1	2.9	0.45
May	548.1	529.0	6.0	0.03
August	656.6	660.3	7.1	0.71

Table 2. Influence of protein supplementation (Control) during breeding and the 1st trimester of gestation, mid-November to mid-March, compared with low supplementation on BCS of fall calving cows

BCS [a]	Treatment		SE	*P* value
	Control	Low		
No. of cows	75	75	-	-
November	4.8	4.8	0.1	0.56
November to January	-0.54	-0.59	0.05	0.47
January	4.4	4.3	0.1	0.49
February	4.2	4.0	0.1	0.03
March	3.9	3.9	0.1	0.30
January to May	-0.29	-0.40	0.05	0.13
May	4.1	3.9	0.1	0.03
August	5.3	5.2	0.1	0.37

[a] BCS: 1 = emaciated; 9 = obese (Wagner et al., 1988)

Table 3. Effect of protein supplementation during breeding and the 1st trimester of gestation, mid-November to mid-March, on calving date, postpartum interval (PPI), and pregnancy rates in fall calving cows

Trait	Treatment				SE	*P* value
	ConCon [a]	LCon	ConL	LL		
No. of Cows	38	37	38	37	-	-
Calving Date [b]	268	269	271	268	3	0.30
Pregnancy Rate, %	95.5	90.6	86.0	88.0	4.9	0.49
PPI to conception, d	83.9	90.6	89.7	87.2	3.7	0.22

[a] ConCon = previous year dietary control treatment and current year dietary control treatment
[b] Julian date

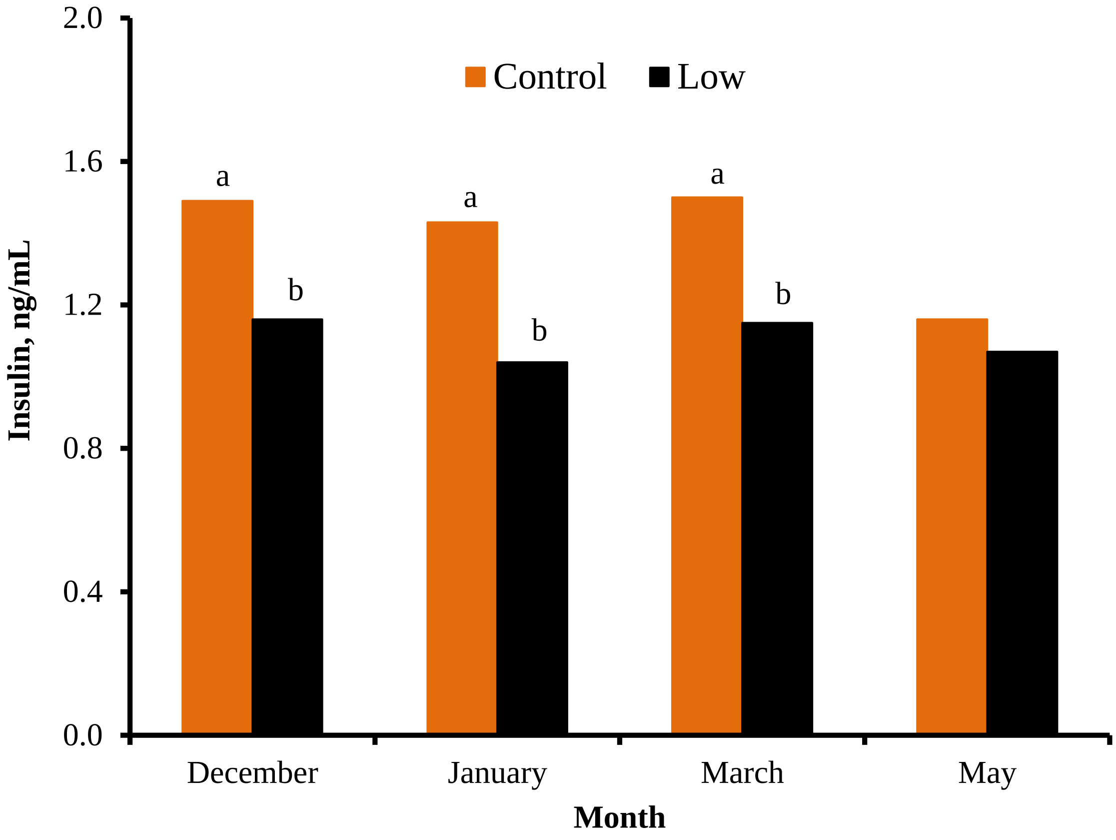

Figure 1. Effect of protein supplementation (Control) on concentrations of insulin in plasma compared with low supplementation of fall calving cows. [a,b] Within month means without a common letter differ (*P* < 0.001). SE were 0.1, 0.1, 0.1, and 0.1 for December, January, March and May, respectively (n = 58).

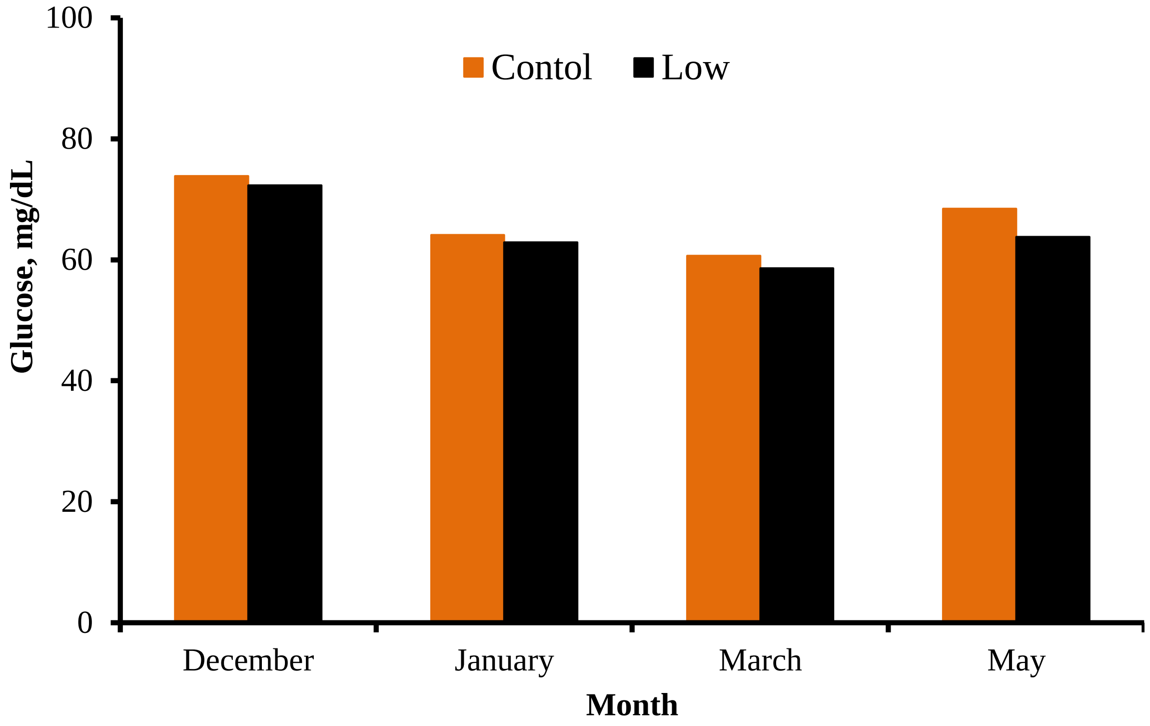

Figure 2. Effect of protein supplementation (Control) on plasma concentrations of glucose compared with low supplementation in fall calving cows. SE were 1, 2, 2, and 3 for December, January, March and May, respectively (n = 58).

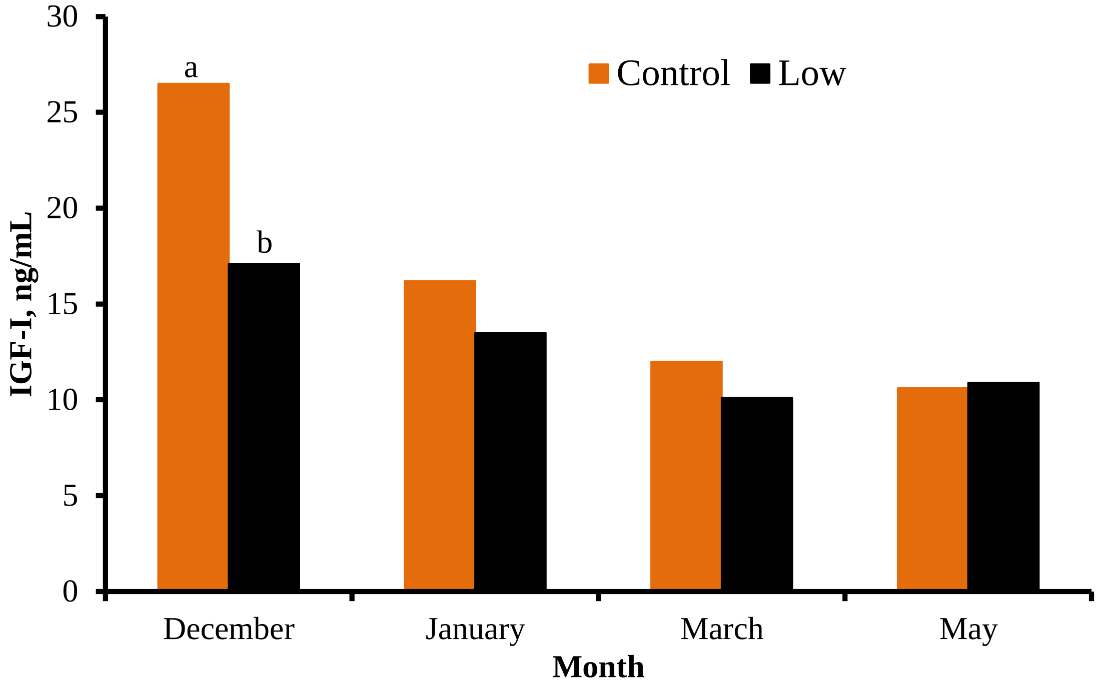

Figure 3. Effect of protein supplementation (Control) in fall calving cows on concentrations of IGF-I in plasma compared with low supplementation. [a,b] Within month means without a common letter differ (*P* = 0.04). SE were 3.0, 1.3, 0.9, and 0.7 for December, January, March and May, respectively (n = 58).

Table 4. Effects of prenatal [2] and postnatal [3] maternal protein supplementation on growth of calves fall born calves

Trait	Treatment				S.E.	Number of Years
	ConCon [1]	ConL	LCon	LL		
Birth Weight, kg	37.8		38.1		0.6	4
BW January, kg	126.2^{a}	122.6^{a}	128.3^{a}	111.5^{b}	3.2	4
Weaning Weight, kg	180.1^{ab}	172.4^{b}	186.1^{a}	154.9^{c}	4.2	4
Yearling Weight, kg	303.1^{a}	287.7^{ab}	299.0^{a}	269.2^{b}	8.8	3
Feedlot Entry BW, kg	405.0^{g}	395.1^{gh}	384.4^{gh}	381.4^{h}	10.4	2

[a,b,c] Means within row without a common letter differ ($P < 0.05$).

[g,h] Means within row without a common letter differ ($P < 0.10$).

[1] ConCon = prenatal control diet and postnatal control diet

[2] prenatal treatments during conception and the 1st trimester of gestation

[3] postnatal treatments during early to mid-lactation

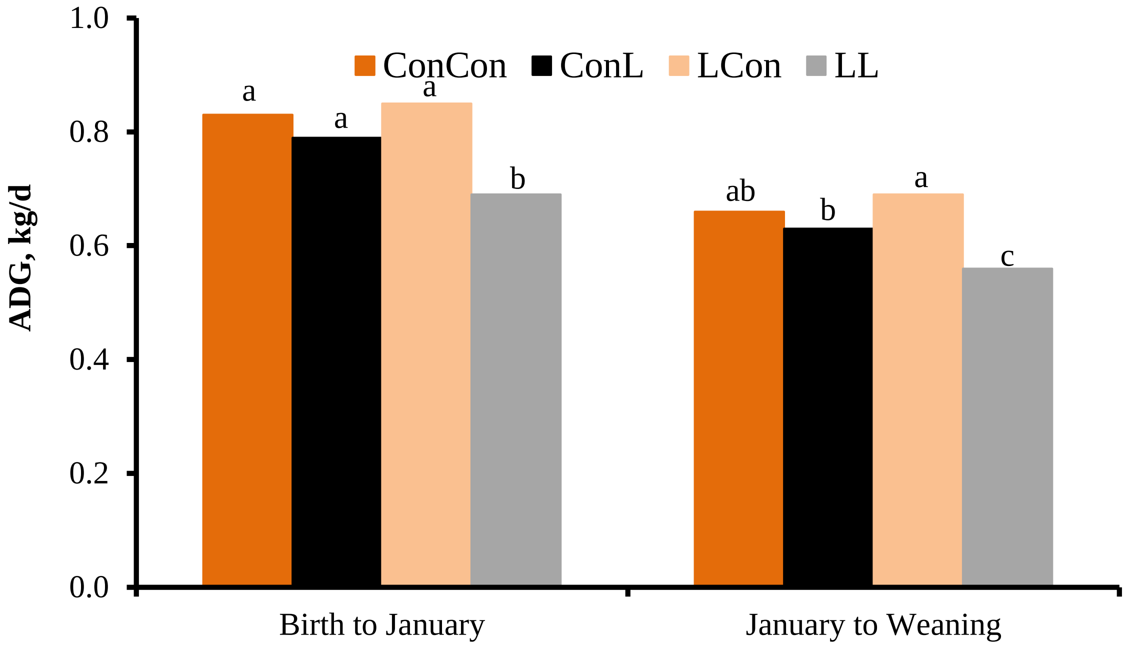

Figure 4. Effects of maternal protein supplementation during early gestation and early lactation on ADG of calves prior to weaning. ^{a,b,c} Within growth period, means without a common letter differ ($P < 0.01$). SE were 0.06 and 0.04 for birth to January and January to weaning, respectively (n = 151).

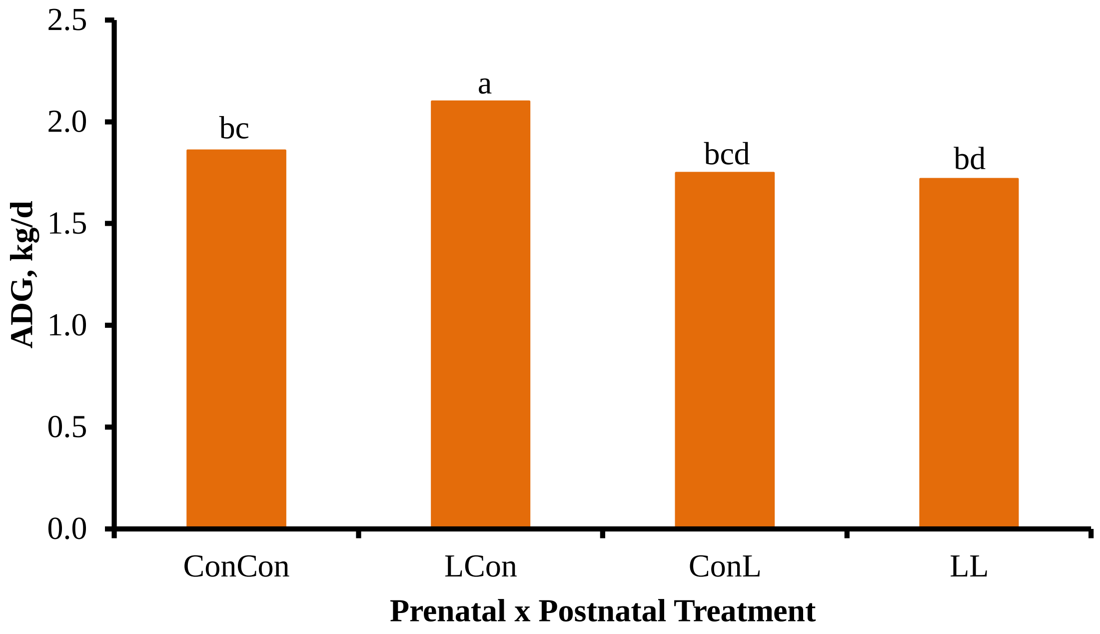

Figure 5. Effect of prenatal and postnatal maternal protein supplementation on ADG of steers on high concentrate diets (2 yr; n = 35). [a,b] Means without a common superscript differ ($P < 0.05$). [c,d] Means without a common superscript tend to differ ($P < 0.10$). SE between treatments was 0.06.

Table 5. Effect of prenatal [2] and postnatal [3] maternal protein supplementation on carcass characteristics during years 1 and 2

Trait	Treatment				S.E.
	ConCon [1]	ConL	LCon	LL	
Steers, n	10	6	11	8	--
Final BW, kg	642.6[a]	616.4[ab]	650.7[ab]	601.4[b]	14.7
Hot Carcass Weight, kg	393.6[a]	376.0[ab]	398.3[a]	362.6[b]	9.0
Dressing Percentage, %	62.5	63.9	64.0	62.3	0.7
Ribeye Area, in^2	13.7	14.1	13.5	13.4	0.6
Final Yield Grade	3.4	2.9	3.1	3.2	0.3
Marbling Score[c]	332	325	309	295	28.6

[a,b] Within row means without a common letter differ ($P < 0.05$).

[c] Small = 300-399; Slight = 200-299

[1] ConCon = prenatal control diet and postnatal control diet

[2] prenatal treatments during conception and the 1st trimester of gestation

[3] postnatal treatments during early to mid-lactation

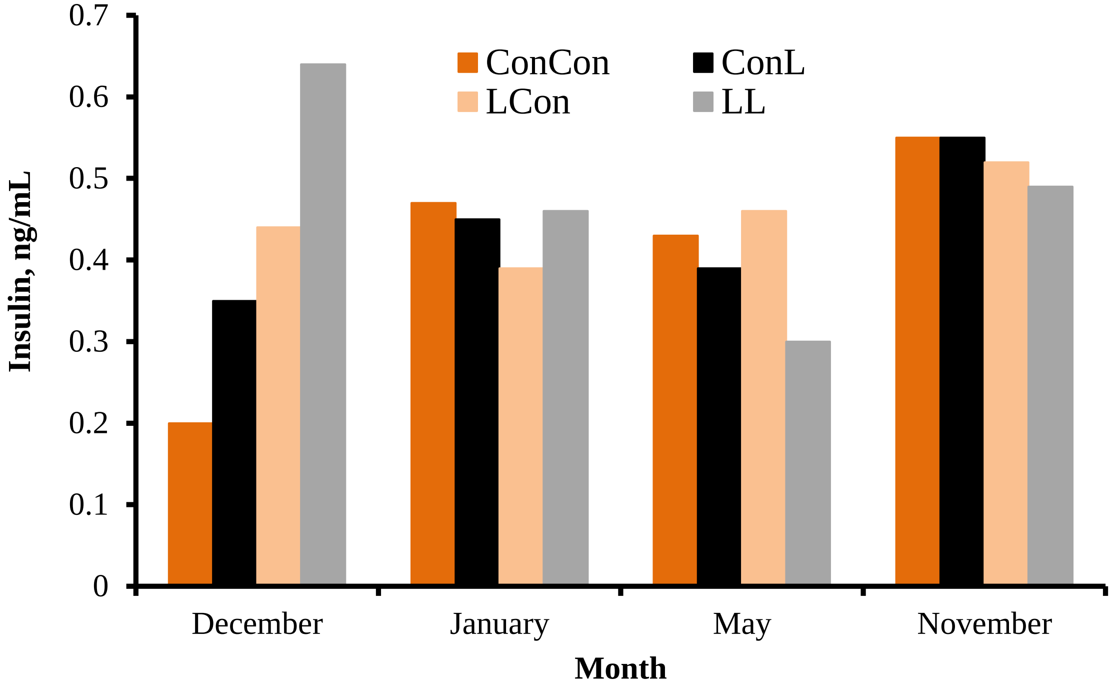

Figure 6. Effect of prenatal and postnatal protein supplementation of cows during early gestation and early lactation on concentrations of insulin in plasma of fall born calves (n = 43). SE were 0.2, 0.1, 0.1, and 0.1 before weaning in December, January, May, and in November at 13 mo of age, respectively.

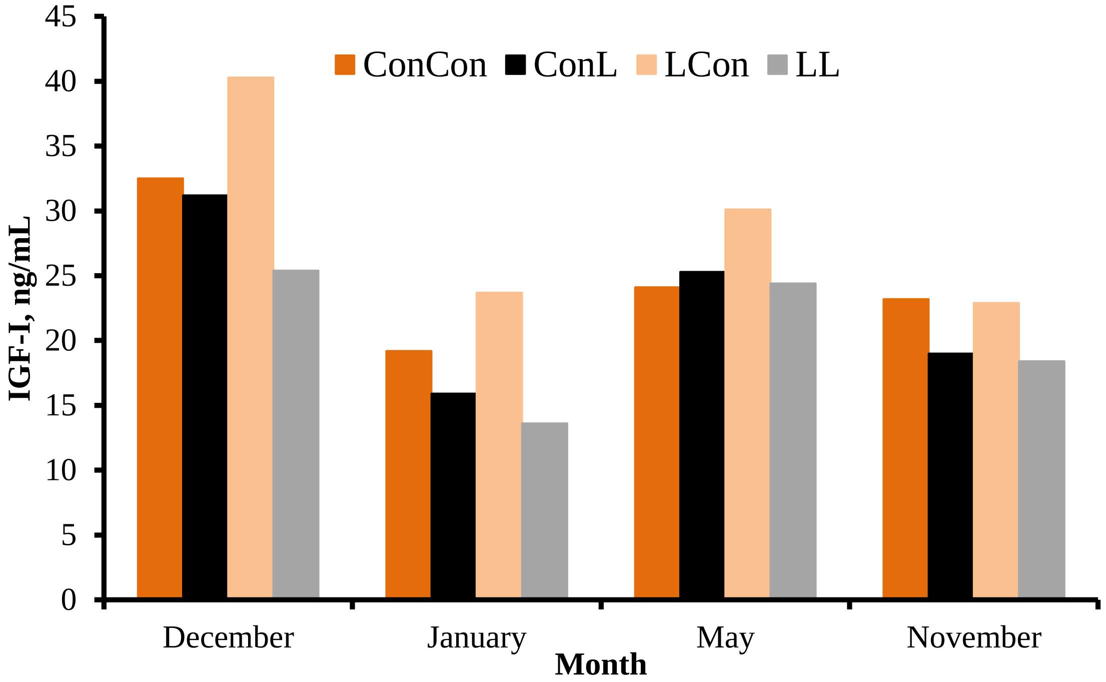

Figure 7. Effect of prenatal and postnatal protein supplementation of cows during early gestation and early lactation on plasma concentrations of IGF-I in fall born calves (n = 43). SE were 6.4, 2.9, 3.9, and 2.3 before weaning in December, January, May, and in November at 13 mo of age, respectively.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Fall calves born (Sept/Oct.) during four consecutive years (n = 196) were used to determine the effects of protein supplementation on cow performance and calf growth and carcass characteristics. The major objective of this study was to determine the effects of maternal protein supplementation on prenatal and postnatal growth and carcass characteristics of calves, and BW, BCS, and reproductive performance of cows. A secondary objective was to evaluate the effects of maternal protein supplementation on plasma concentrations of insulin, IGF-I, and proteins in calves and insulin, glucose, IGF-I, and proteins in cows. Our hypothesis was that protein supplementation of fall calving cows will influence prenatal and postnatal growth and carcass characteristics of calves without effecting reproductive efficiency of the cows.

Cows were individually supplemented with protein to meet requirements when grazing dormant native range (Con; 1.82 kg/d of 38 % CP) or inadequate protein (L; 0.2 kg/d of 8 % CP). During lactation half of the cows on the Con and L prenatal treatments were assigned to the Con treatment the other half was assigned to the L treatment. Protein supplementation did not influence pregnancy rate or calving interval. Negative energy balance associated with early lactation results in BW loss, however, protein supplementation decreased the amount of BW lost from November to January. Cows that were supplemented had a greater BCS and BW at weaning (May) compared with L cows. Cows receiving L supplementations from November to March regained BW over the summer and BW and BCS were not different from Con cows prior to calving. Concentrations of insulin in plasma were increased during supplementation, while concentrations of IGF-I were increased in plasma of Con cows compared with L cows in December. The Con cows had greater nutrients available due to supplementation. This increase in nutritional status indicates an increase in nutrient uptake by the mammary gland or by the placenta/fetus.

Birth weight was not influenced by prenatal protein supplementation. Prenatal and postnatal treatments influenced growth of calves. Calves that were born to L prenatal cows, and received C diets postnatally, gained more BW from birth (Sept./Oct.) to January compared with calves from other treatments. These prenatal x postnatal interactions for ADG and overall BW remained throughout suckling with LCon calves having greater BW in January and 205 d adjusted weaning weights. Postnatal maternal protein supplementation increased concentrations of IGF-I in plasma of calves in January. This increase in IGF-I concentrations indicates that Con calves received greater nutrients compared with L calves.

Postnatal supplementation increased 365 d adjusted yearling weights and tended to influence BW of calves at entry to the feedlot. Ad libitum nutrient availability from high concentrate finishing diets resulted in LCon outgaining all other treatment groups. The onset of a thrifty phenotype was facilitated by prenatal nutrient restriction, which programmed the fetus for exposure to postnatal nutrient restriction. Control prenatal and Con postnatal calves tended to gain more than L prenatal and L postnatal calves. When calves from the final two years of this study are harvested, final conclusions will be made. Independent of prenatal treatment, calves that suckled Con cows had greater BW at harvest and hot carcass weight compared with LL calves. The BW increase with protein supplementation did not influence quality of carcasses with approximately 70 % of all carcasses grading choice. Neither prenatal nor postnatal protein supplementation influenced yield grade, ribeye area, marbling score, or dressing percentage.

In conclusion, protein supplementation of cows, during prenatal growth of calves in early gestation and postnatal supplementation, will alter the growth of calves prior to weaning and in the feedlot. The increase in BW resulted in heavier carcasses but did not influence characteristics of the carcasses. Further research is needed to fully elucidate the effects of prenatal nutrition on carcass characteristics of fall born calves.

LITERATURE CITED

Arias, P., M. Rodriguez, B. Szwarcfarb, I. R. Sinay, and J. A. Moguilevsky. 1992. Effect of insulin on LHRH release by perifused hypothalamic fragments. Neuroendocrinology 56: 415-418.

Armstrong, D. G., T. G. McEvoy, G. Baxter, J. J. Robinson, C. O. Hogg, K. J. Woad, R. Webb, and K. D. Sinclair. 2001. Effect of dietary energy and protein on bovine follicular dynamics and embryo production in vitro: associations with the ovarian insulin-like growth factor system. Biol. Reprod. 64: 1624-1632.

Armstrong, J. D., W. S. Cohick, R. W. Harvey, E. P. Heimer, and R. M. Campbell. 1993. Effect of feed restriction on serum somatotropin, insulin-like growth factor-I-(IGF-I) and IGF binding proteins in cyclic heifers actively immunized against growth hormone releasing factor. Domest. Anim. Endocrinol. 10: 315-324.

Barker, D. J., C. N. Martyn, C. Osmond, C. N. Hales, and C. H. Fall. 1993. Growth in utero and serum cholesterol concentrations in adult life. BMJ 307: 1524-1527.

Bauman, D. E., and W. B. Currie. 1980. Partitioning of nutrients during pregnancy and lactation: a review of mechanisms involving homeostasis and homeorhesis. J. Dairy Sci. 63: 1514-1529.

Beam, S. W., and W. R. Butler. 1997. Energy balance and ovarian follicle development prior to the first ovulation postpartum in dairy cows receiving three levels of dietary fat. Biol. Reprod. 56: 133-142.

Beaty, J. L., R. C. Cochran, B. A. Lintzenich, E. S. Vanzant, J. L. Morrill, R. T. Brandt, and D. E. Johnson. 1994. Effect of frequency of supplementation and protein concentration in supplements on performance and digestion characteristics of beef cattle consuming low-quality forages. J. Anim. Sci. 72: 2475-2486.

Bellows, R. A., and R. E. Short. 1978. Effects of precalving feed level on birth weight, calving difficulty and subsequent fertility. J. Anim. Sci. 46: 1522-1528.

Bellows, R. A., R. E. Short, and G. V. Richardson. 1982. Effects of sire, age of dam and gestation feed level on dystocia and postpartum reproduction. J. Anim. Sci. 55: 18-27.

Bishop, D. K., R. P. Wettemann, and L. J. Spicer. 1994. Body energy reserves influence the onset of luteal activity after early weaning of beef cows. J. Anim. Sci. 72: 2703-2708.

Bispham, J., G. S. Gopalakrishnan, J. Dandrea, V. Wilson, H. Budge, D. H. Keisler, F. Broughton Pipkin, T. Stephenson, and M. E. Symonds. 2003. Maternal endocrine adaptation throughout pregnancy to nutritional manipulation: consequences for maternal plasma leptin and cortisol and the programming of fetal adipose tissue development. Endocrinology 144: 3575-3585.

Borowicz, P. P., D. R. Arnold, M. L. Johnson, A. T. Grazul-Bilska, D. A. Redmer, and L. P. Reynolds. 2007. Placental growth throughout the last two thirds of pregnancy in sheep: vascular development and angiogenic factor expression. Biol. Reprod. 76: 259-267.

Bossis, I., R. P. Wettemann, S. D. Welty, J. A. Vizcarra, and L. J. Spicer. 2000. Nutritionally induced anovulation in beef heifers: ovarian and endocrine function during realimentation and resumption of ovulation. Biol. Reprod. 62: 1436-1444.

Bossis, I., R. P. Wettemann, S. D. Welty, J. A. Vizcarra, L. J. Spicer, and M. G. Diskin. 1999. Nutritionally induced anovulation in beef heifers: ovarian and endocrine function preceding cessation of ovulation. J. Anim. Sci. 77: 1536-1546.

Brant, A. M., T. J. Jess, G. Milligan, C. M. Brown, and G. W. Gould. 1993. Immunological analysis of glucose transporters expressed in different regions of the rat brain and central nervous system. Biochem. Biophys. Res. Comm. 192: 1297-1302.

Bray, C. I. 1934. Creep feeding beef calves. J. Anim. Sci. 1934: 96-98.

Brockman, R. P., and B. Laarveld. 1986. Hormonal regulation of metabolism in ruminants; a review. Livest. Prod. Sci. 14: 313-334.

Bucholtz, D. C., N. M. Vidwans, C. G. Herbosa, K. K. Schillo, and D. L. Foster. 1996. Metabolic interfaces between growth and reproduction. V. Pulsatile luteinizing hormone secretion is dependent on glucose availability. Endocrinology 137: 601-607.

Buskirk, D. D., R. P. Lemenager, and L. A. Horstman. 1992. Estimation of net energy requirements (NEm and NE delta) of lactating beef cows. J. Anim. Sci. 70: 3867-3876.

Butler, W. R. 1998. Review: effect of protein nutrition on ovarian and uterine physiology in dairy cattle. J. Dairy Sci. 81: 2533-2539.

Butler, W. R., and R. D. Smith. 1989. Interrelationships between energy balance and postpartum reproductive function in dairy cattle. J. Dairy Sci. 72: 767-783.

Canfield, R. W., C. J. Sniffen, and W. R. Butler. 1990. Effects of excess degradable protein on postpartum reproduction and energy balance in dairy cattle. J. Dairy Sci. 73: 2342-2349.

Carruthers, T. D., J. G. Manns, and L. M. Rutter. 1986. Failure of human chorionic gonadotropin injections to sustain gonadotropin releasing hormone induced corpora lutea in postpartum beef cows. Biol. Reprod. 35: 846-849.

Carstens, G. E., D. E. Johnson, M. D. Holland, and K. G. Odde. 1987. Effects of prepartum protein nutrition and birth weight on basal metabolism in bovine neonates. J. Anim. Sci. 65: 745-751.

Carter, M. L., D. J. Dierschke, J. J. Rutledge, and E. R. Hauser. 1980. Effect of gonadotropin releasing hormone and calf removal on pituitary-ovarian function and reproductive performance in postpartum beef cows. J. Anim. Sci. 51: 903-910.

Chase, C. C., T. H. Elsasser, L. J. Spicer, D. G. Riley, M. C. Lucy, A. C. Hammond, T. A. Olson, and S. W. Coleman. 2011. Effect of growth hormone administration to mature miniature Brahman cattle treated with or without insulin on circulating concentrations of insulin-like growth factor-I and other metabolic hormones and metabolites. Domest. Anim. Endocrinol. 41: 1-13.

Chase, C. C., C. J. Kirby, A. C. Hammond, T. A. Olson, and M. C. Lucy. 1998. Patterns of ovarian growth and development in cattle with a growth hormone receptor deficiency. J. Anim. Sci. 76: 212-219.

Christenson, R. K. 1980. Environmental influences on the postpartum animal. J. Anim. Sci. 51: 53-67.

Christian, L. L., E. R. Hauser, and A. B. Chapman. 1965. Association of preweaning and postweaning traits with weaning weight in cattle. J. Anim. Sci. 24: 652-659.

Ciccioli, N. H., R. P. Wettemann, L. J. Spicer, C. A. Lents, F. J. White, and D. H. Keisler. 2003. Influence of body condition at calving and postpartum nutrition on endocrine function and reproductive performance of primiparous beef cows. J. Anim. Sci. 81: 3107-3120.

Ciminski, L. A. 2002. Weaning date and protein supplementation effects on cow/calf productivity. MS Thesis, University of Nebraska, Lincoln.

Clapp, H. 1937. A factor in breeding efficiency of dairy cattle. Proc. Am. Soc. Anim. Prod. 37: 259-265.

Corah, L. R., T. G. Dunn, and C. C. Kaltenbach. 1975. Influence of prepartum nutrition on the reproductive performance of beef females and the performance of their progeny. J. Anim. Sci. 41: 819-824.

Cremin, J. D., D. B. Faulkner, N. R. Merchen, G. C. Fahey, R. L. Fernando, and C. L. Willms. 1991. Digestion criteria in nursing beef calves supplemented with limited levels of protein and energy. J. Anim. Sci. 69: 1322-1331.

Cronje, P. B., J. V. Nolan, and R. A. Leng. 1991. Acetate clearance rate as a potential index of the availability of glucogenic precursors in ruminants fed on roughage-based diets. Br. J. Nutr. 66: 301-312.

Davis, D., R. R. Schalles, G. H. Kiracofe, and D. L. Good. 1977. Influence of winter nutrition on beef cow reproduction. J. Anim. Sci. 45: 430-437.

DelCurto, T., B. W. Hess, J. E. Huston, and K. C. Olson. 2000. Optimum supplementation strategies for beef cattle consuming low-quality roughages in the western United States. J. Anim. Sci. 77(E-Suppl): 1-16.

DeRouen, S. M., D. E. Franke, D. G. Morrison, W. E. Wyatt, D. F. Coombs, T. W. White, P. E. Humes, and B. B. Greene. 1994. Prepartum body condition and weight influences on reproductive performance of first-calf beef cows. J. Anim. Sci. 72: 1119-1125.

Dhuyvetter, D. V., M. K. Petersen, R. P. Ansotegui, R. A. Bellows, B. Nisley, R. Brownson, and M. W. Tess. 1993. Reproductive efficiency of range beef cows fed different quantities of ruminally undegradable protein before breeding. J. Anim. Sci. 71: 2586-2593.

Dickerson, G. 1970. Efficiency of animal production—molding the biological components. J. Anim. Sci. 30: 849-859.

DiCostanzo, A., J. E. Williams, and D. H. Keisler. 1999. Effects of short- or long-term infusions of acetate or propionate on luteinizing hormone, insulin, and metabolite concentrations in beef heifers. J. Anim. Sci. 77: 3050-3056.

Diskin, M. G., D. R. Mackey, J. F. Roche, and J. M. Sreenan. 2003. Effects of nutrition and metabolic status on circulating hormones and ovarian follicle development in cattle. Anim. Reprod. Sci. 78: 345-370.

Dunn, T. G., J. E. Ingalls, D. R. Zimmerman, and J. N. Wiltbank. 1969. Reproductive performance of 2-year-old Hereford and Angus heifers as influenced by pre- and post-calving energy intake. J. Anim. Sci. 29: 719-726.

Dunn, T. G., and C. C. Kaltenbach. 1980. Nutrition and the postpartum interval of the ewe, sow, and cow. J. Anim. Sci. 51: 29-39.

Dziuk, P. J., and R. A. Bellows. 1983. Management of reproduction of beef cattle, sheep and pigs. J. Anim. Sci. 57: 355-379.

Echternkamp, S. E., L. J. Spicer, K. E. Gregory, S. F. Canning, and J. M. Hammond. 1990. Concentrations of insulin-like growth factor-I in blood and ovarian follicular fluid of cattle selected for twins. Biol. Reprod. 43: 8-14.

Elrod, C. C., and W. R. Butler. 1993. Reduction of fertility and alteration of uterine pH in heifers fed excess ruminally degradable protein. J. Anim. Sci. 71: 694-701.

Faulkner, D. B., D. F. Hummel, D. D. Buskirk, L. L. Berger, D. F. Parrett, and G. F. Cmarik. 1994. Performance and nutrient metabolism by nursing calves supplemented with limited or unlimited corn or soyhulls. J. Anim. Sci. 72: 470-477.

Ferrell, C. L., and T. G. Jenkins. 1996. Relationships between body condition score and empty body weight, water, fat, protein, and energy percentages in mature beef cows of diverse breeds. J. Anim. Sci. 74(Suppl. 1): 245 (Abstr).

Fleck, A. T., and K. S. Lusby. 1986. Corn gluten feed or soybean meal as winter supplements for pregnant beef cows grazing native range. Oklahoma Agric. Exp. Sta. MP-118: 196-201.

Fleck, A. T., K. S. Lusby, F. N. Owens, and F. T. McCollum. 1988. Effects of corn gluten feed on forage intake, digestibility and ruminal parameters of cattle fed native grass hay. J. Anim. Sci. 66: 750-757.

Fluharty, F. L., S. C. Loerch, T. B. Turner, S. J. Moeller, and G. D. Lowe. 2000. Effects of weaning age and diet on growth and carcass characteristics in steers. J. Anim. Sci. 78: 1759-1767.

Ford, S. P., B. W. Hess, M. M. Schwope, M. J. Nijland, J. S. Gilbert, K. A. Vonnahme, W. J. Means, H. Han, and P. W. Nathanielsz. 2007. Maternal undernutrition during early to mid-gestation in the ewe results in altered growth, adiposity, and glucose tolerance in male offspring. J. Anim. Sci. 85: 1285-1294.

Ford, S. P., L. Zhang, M. Zhu, M. M. Miller, D. T. Smith, B. W. Hess, G. E. Moss, P. W. Nathanielsz, and M. J. Nijland. 2009. Maternal obesity accelerates fetal pancreatic β-cell but not α-cell development in sheep: prenatal consequences. Am. J. Phys. Reg. Int. Com. Phys. 297: R835-R843.

Francisco, C. C., L. J. Spicer, and M. E. Payton. 2003. Predicting cholesterol, progesterone, and days to ovulation using postpartum metabolic and endocrine measures. J. Dairy Sci. 86: 2852-2863.

Freetly, H. C., C. L. Ferrell, and T. G. Jenkins. 2000. Timing of realimentation of mature cows that were feed-restricted during pregnancy influences calf birth weights and growth rates. J. Anim. Sci. 78: 2790-2796.

Funston, R. N. 2004. Fat supplementation and reproduction in beef females. J. Anim. Sci. 82: E154-E161.

Funston, R. N., J. L. Martin, D. C. Adams, and D. M. Larson. 2010. Winter grazing system and supplementation of beef cows during late gestation influence heifer progeny. J. Anim. Sci. 88: 4094-4101.

Furr, R. D., and A. B. Nelson. 1964. Effect of level of supplemental winter feed on calf weight and on milk production of fall-calving range beef cows. J. Anim. Sci. 23: 775-781.

Gallet, C., J. Dupont, B. K. Campbell, D. Monniaux, D. Guillaume, and R. J. Scaramuzzi. 2011. The infusion of glucose in ewes during the luteal phase increases the number of follicles but reduces oestradiol production and some correlates of metabolic function in the large follicles. Anim. Reprod. Sci. 127: 154-163.

Gardner, D. S., K. Tingey, B. W. M. Van Bon, S. E. Ozanne, V. Wilson, J. Dandrea, D. H. Keisler, T. Stephenson, and M. E. Symonds. 2005. Programming of glucose-insulin metabolism in adult sheep after maternal undernutrition. Am. J. Phys. Reg. Int. Com. Phys. 289: R947-R954.

Garmendia, J. C. 1986. Energy metabolites in blood, luteinizing hormone secretion and reproductive performance of beef cows. Ph.D. Dissertation, Oklahoma State University, Stillwater.

Godfrey, K. M., and D. J. Barker. 2000. Fetal nutrition and adult disease. Am. J. Clin. Nutr. 71: 1344s-1352s.

Granger, A. L., W. E. Wyatt, W. M. Craig, D. L. Thompson Jr, and F. G. Hembry. 1989. Effects of breed and wintering diet on growth, puberty and plasma concentrations of growth hormone and insulin-like growth factor-1 in heifers. Domest. Anim. Endocrinol. 6: 253-262.

Graves, W. E., J. W. Lauderdale, E. R. Hauser, and L. E. Casida. 1968. Relation of postpartum interval to pituitary gonadotropins, ovarian follicular development, and fertility in beef cows (effect of suckling and interval to breeding). Wisconsin Ag. Exp. St. Res. Bul. 270: 23-26.

Grazul-Bilska, A. T., J. S. Caton, W. Arndt, K. Burchill, C. Thorson, E. Borowczyk, J. J. Bilski, D. A. Redmer, L. P. Reynolds, and K. A. Vonnahme. 2009. Cellular proliferation and vascularization in ovine fetal ovaries: effects of undernutrition and selenium in maternal diet. Reproduction 137: 699-707.

Greenwood, P. L., A. S. Hunt, J. W. Hermanson, and A. W. Bell. 2000. Effects of birth weight and postnatal nutrition on neonatal sheep: II. Skeletal muscle growth and development. J. Anim. Sci. 78: 50-61.

Greenwood, P. L., A. S. Hunt, R. M. Slepetis, K. D. Finnerty, C. Alston, D. H. Beermann, and A. W. Bell. 2002. Effects of birth weight and postnatal nutrition on neonatal sheep: III. Regulation of energy metabolism. J. Anim. Sci. 80: 2850-2861.

Grimard, B., P. Humblot, A. A. Ponter, J. P. Mialot, D. Sauvant, and M. Thibier. 1995. Influence of postpartum energy restriction on energy status, plasma LH and oestradiol secretion and follicular development in suckled beef cows. J. Reprod. Fert. 104: 173-179.

Guilbault, L. A., W. W. Thatcher, M. Drost, and G. K. Haibel. 1987a. Influence of a physiological infusion of prostaglandin F2α into postpartum cows with partially suppressed endogenous production of prostaglandins. 1. Uterine and ovarian morphological responses. Theriogenology 27: 931-946.

Guilbault, L. A., W. W. Thatcher, D. B. Foster, and D. Caton. 1984. Relationship of 15-keto-13,14-dihydro-prostaglandin F2 alpha concentrations in peripheral plasma with local uterine production of F series prostaglandins and changes in uterine blood flow during the early postpartum period of cattle. Biol. Reprod. 31: 870-878.

Guilbault, L. A., W. W. Thatcher, and C. J. Wilcox. 1987b. Influence of a physiological infusion of prostaglandin F2α into postpartum cows with partially suppressed endogenous production of prostaglandins. 2. Interrelationships of hormonal, ovarian and uterine responses. Theriogenology 27: 947-957.

Hansen, P. J. 1997. Effects of environment of bovine reproduction. In: W. B. Saunders (ed.) Current Therapy in Large Animal Theriogenology. p 403-415. R.S. Youngquist (Ed.), Philadelphia, PA.

Harvey, R. W., and J. C. Burns. 1988. Creep grazing and early weaning effects on cow and calf productivity. J. Anim. Sci. 66: 1109-1114.

Hawkins, D. E., M. K. Petersen, M. G. Thomas, J. E. Sawyer, and R. C. Waterman. 2000. Can beef heifers and young postpartum cows be physiologically and nutritionally manipulated to optimize reproductive efficiency. J. Anim. Sci. 77(E-Suppl): 1-10.

Hileman, S. M., K. K. Schillo, and J. B. Hall. 1993. Effects of acute, intracerebroventricular administration of insulin on serum concentrations of luteinizing hormone, insulin, and glucose in ovariectomized lambs during restricted and ad libitum feed intake. Biol. Reprod. 48: 117-124.

Holloway, J. W., and R. Totusek. 1973. Relationship between preweaning nutritional management and subsequent performance of Angus and Hereford females through Three calf crops. J. Anim. Sci. 37: 807-812.

Horney, M. R., T. DelCurto, M. M. Stamm, R. K. Bailey, and S. D. Brandyberry. 1996. Early-vegetative tall fescue hay vs alfalfa hay as a supplement for cattle consuming low-quality roughages. J. Anim. Sci. 74: 1959-1966.

Hough, R. L., F. D. McCarthy, H. D. Kent, D. E. Eversole, and M. L. Wahlberg. 1990. Influence of nutritional restriction during late gestation on production measures and passive immunity in beef cattle. J. Anim. Sci. 68: 2622-2627.

Houseknecht, K. L., D. L. Boggs, D. R. Campion, J. L. Sartin, T. E. Kiser, G. B. Rampacek, and H. E. Amos. 1988. Effect of dietary energy source and level on serum growth hormone, insulin-like growth factor-1, growth and body composition in beef heifers. J. Anim. Sci. 66: 2916-2923.

Jones, E. J., J. D. Armstrong, and R. W. Harvey. 1991. Changes in metabolites, metabolic hormones, and luteinizing hormone before puberty in Angus, Braford, Charolais, and Simmental heifers. J. Anim. Sci. 69: 1607-1615.

Keisler, D. H., and M. C. Lucy. 1996. Perception and interpretation of the effects of undernutrition on reproduction. J. Anim. Sci. 74: 1-17.

Kiracofe, G. H. 1980. Uterine involution: its role in regulating postpartum intervals. J. Anim. Sci. 51: 16-28.

Lalman, D. L., D. H. Keisler, J. E. Williams, E. J. Scholljegerdes, and D. M. Mallett. 1997. Influence of postpartum weight and body condition change on duration of anestrus by undernourished suckled beef heifers. J. Anim. Sci. 75: 2003-2008.

Lalman, D. L., M. K. Petersen, R. P. Ansotegui, M. W. Tess, C. K. Clark, and J. S. Wiley. 1993. The effects of ruminally undegradable protein, propionic acid, and monensin on puberty and pregnancy in beef heifers. J. Anim. Sci. 71: 2843-2852.

Larson, D. M., J. L. Martin, D. C. Adams, and R. N. Funston. 2009. Winter grazing system and supplementation during late gestation influence performance of beef cows and steer progeny. J. Anim. Sci. 87: 1147-1155.

Lents, C. A., D. L. Lalman, C. Vermeulen, J. S. Wheeler, G. W. Horn, and R. P. Wettemann. 2000. Effects of supplemental undegradable protein during early lactation on the performance of beef cows grazing native range. Prof. Anim. Sci. 16: 21-29.

Lents, C. A., R. P. Wettemann, F. J. White, I. Rubio, N. H. Ciccioli, L. J. Spicer, D. H. Keisler, and M. E. Payton. 2005. Influence of nutrient intake and body fat on concentrations of insulin-like growth factor-I, insulin, thyroxine, and leptin in plasma of gestating beef cows. J. Anim. Sci. 83: 586-596.

Lents, C. A., F. J. White, N. H. Ciccioli, R. P. Wettemann, L. J. Spicer, and D. L. Lalman. 2008. Effects of body condition score at parturition and postpartum protein supplementation on estrous behavior and size of the dominant follicle in beef cows. J. Anim. Sci. 86: 2549-2556.

Lewis, G. S., W. W. Thatcher, E. L. Bliss, M. Drost, and R. J. Collier. 1984. Effects of heat stress during pregnancy on postpartum reproductive changes in holstein cows. J. Anim. Sci. 58: 174-186.

Li, X. F., J. C. Mitchell, S. Wood, C. W. Coen, S. L. Lightman, and K. T. O'Byrne. 2003. The effect of oestradiol and progesterone on hypoglycaemic stress-induced suppression of pulsatile luteinizing hormone release and on corticotropin-releasing hormone mRNA expression in the rat. J. Neuroendocrinol. 15: 468-476.

Lindsay, D. B., and B. P. Setchell. 1976. The oxidation of glucose, ketone bodies and acetate by the brain of normal and ketonaemic sheep. J. Phys. 259: 801-823.

Lishman, A. W., S. M. J. Allison, R. L. Fogwell, R. L. Butcher, and E. K. Inskeep. 1979. Follicular development and function of induced corpora lutea in underfed postpartum anestrous beef cows. J. Anim. Sci. 48: 867-875.

Livingstone, C., H. Lyall, and G. W. Gould. 1995. Hypothalamic GLUT 4 expression: a glucose- and insulin-sensing mechanism? Mol. Cell. Endocrinol. 107: 67-70.

Lobley, G. E. 2003. Protein turnover- what does it mean for animal production. Can. J. Anim. Sci. 83: 327-340.

Long, N. M., L. A. George, A. B. Uthlaut, D. T. Smith, M. J. Nijland, P. W. Nathanielsz, and S. P. Ford. 2010a. Maternal obesity and increased nutrient intake before and during gestation in the ewe results in altered growth, adiposity, and glucose tolerance in adult offspring. J. Anim. Sci. 88: 3546-3553.

Long, N. M., M. J. Nijland, P. W. Nathanielsz, and S. P. Ford. 2010b. The effect of early to mid-gestational nutrient restriction on female offspring fertility and hypothalamic-pituitary-adrenal axis response to stress. J. Anim. Sci. 88: 2029-2037.

Long, N. M., M. J. Prado-Cooper, C. R. Krehbiel, U. DeSilva, and R. P. Wettemann. 2010c. Effects of nutrient restriction of bovine dams during early gestation on postnatal growth, carcass and organ characteristics, and gene expression in adipose tissue and muscle. J. Anim. Sci. 88: 3251-3261.

Long, N. M., M. J. Prado-Cooper, C. R. Krehbiel, and R. P. Wettemann. 2010d. Effects of nutrient restriction of bovine dams during early gestation on postnatal growth and regulation of plasma glucose. J. Anim. Sci. 88: 3262-3268.

Long, N. M., C. B. Tousley, K. R. Underwood, S. I. Paisley, W. J. Means, B. W. Hess, M. Du, and S. P. Ford. 2012. Effects of early- to mid-gestational undernutrition with or without protein supplementation on offspring growth, carcass characteristics, and adipocyte size in beef cattle. J. Anim. Sci. 90: 197-206.

Long, N. M., K. A. Vonnahme, B. W. Hess, P. W. Nathanielsz, and S. P. Ford. 2009. Effects of early gestational undernutrition on fetal growth, organ development, and placentomal composition in the bovine. J. Anim. Sci. 87: 1950-1959.

Looper, M. L., C. A. Lents, and R. P. Wettemann. 2003. Body condition at parturition and postpartum weight changes do not influence the incidence of short-lived corpora lutea in postpartum beef cows. J. Anim. Sci. 81: 2390-2394.

Lopuhaa, C. E., T. J. Roseboom, C. Osmond, D. J. Barker, A. C. Ravelli, O. P. Bleker, J. S. van der Zee, and J. H. van der Meulen. 2000. Atopy, lung function, and obstructive airways disease after prenatal exposure to famine. Thorax 55: 555-561.

Louw, B. P., C. R. Thomas, and A. W. Lishman. 1988. The influence of loss and gain of body mass on ovarian activity in beef cows. S. Afr. J. Anim. Sci. 18: 1-7.

Lucy, M. C., C. K. Boyd, A. T. Koenigsfeld, and C. S. Okamura. 1998. Expression of somatotropin receptor messenger ribonucleic acid in bovine tissues. J. Dairy Sci. 81: 1889-1895.

Lucy, M. C., R. J. Collier, M. L. Kitchell, J. J. Dibner, S. D. Hauser, and G. G. Krivi. 1993. Immunohistochemical and nucleic acid analysis of somatotropin receptor populations in the bovine ovary. Biol. Reprod. 48: 1219-1227.

Lumey, L. H., and A. D. Stein. 1997. In utero exposure to famine and subsequent fertility: The Dutch Famine Birth Cohort Study. Am. J. Public Health 87: 1962-1966.

Lusby, K. S. 1986. Comparison of limit-fed high protein creep feed and free-choice grain creep for spring-born calves on native range. Oklahoma Agric. Exp. Sta. MP-118: 207-209.

Lusby, K. S., and R. P. Wettemann. 1986. Effects of limit-fed high protein creep feed or early weaning on performance of fall-born calves and their dams. Oklahoma Agric. Exp. Sta. MP-118: 202-206.

Lusby, K. S., and R. P. Wettemann. 1988. Wheat middlings vs soybean meal and corn/soybean meal supplements at two protein levels for wintering spring calving beef cows. Oklahoma Agric. Exp. Sta. MP 125: 72-75.

Lusby, K. S., R. P. Wettemann, K. H. Ovenell, and D. A. Cox. 1991. Effects of lactation on performance of grazing beef cows wintered with supplements containing soybean meal, wheat middlings, or soybean meal-wheat middlings mixtures. Prof. Anim. Sci. 7: 30-34.

Maciel, S. M., C. S. Chamberlain, R. P. Wettemann, and L. J. Spicer. 2001. Dexamethasone influences endocrine and ovarian function in dairy cattle. J. Dairy Sci. 84: 1998-2009.

Marston, T. T., K. S. Lusby, R. P. Wettemann, and H. T. Purvis. 1995. Effects of feeding energy or protein supplements before or after calving on performance of spring-calving cows grazing native range. J. Anim. Sci. 73: 657-664.

Martin, J. L., K. A. Vonnahme, D. C. Adams, G. P. Lardy, and R. N. Funston. 2007. Effects of dam nutrition on growth and reproductive performance of heifer calves. J. Anim. Sci. 85: 841-847.

Martin, T. G., R. P. Lemenager, G. Srinivasan, and R. Alenda. 1981. Creep feed as a factor influencing performance of cows and calves. J. Anim. Sci. 53: 33-39.

McCaughty, W. P., L. M. Rutter, and J. G. Manns. 1988. Effect of glucose infusion on metabolic and reproductive function in postpartum beef cows. Can. J. Anim. Sci. 68: 1079-1087.

McClure, T. J., C. D. Nancarrow, and H. M. Radford. 1978. The effect of 2-deoxy-D-glucose on ovarian function of cattle. Aus. J. Biol. Sci. 31: 183-186.

McCormack, B. L., C. C. Chase Jr, T. A. Olson, T. H. Elsasser, A. C. Hammond, T. H. Welsh Jr, H. Jiang, R. D. Randel, C. A. Okamura, and M. C. Lucy. 2009. A miniature condition in Brahman cattle is associated with a single nucleotide mutation within the growth hormone gene. Domest. Anim. Endocrinol. 37: 104-111.

Meschia, G. 1983. Circulation to female reproductive organs Handbook of Physiology No. Sect. 2, Vol. III, part 1. p 241-269. Shepherd JT & Abboud FM, American Physiological Society, Bethesda, MD.

Miner, J. L., M. K. Petersen, K. M. Havstad, M. J. McInerney, and R. A. Bellows. 1990. The effects of ruminal escape protein or fat on nutritional status of pregnant winter-grazing beef cows. J. Anim. Sci. 68: 1743-1750.

Morrison, D. G., J. C. Spitzer, and J. L. Perkins. 1999. Influence of prepartum body condition score change on reproduction in multiparous beef cows calving in moderate body condition. J. Anim. Sci. 77: 1048-1054.

Myers, S. E., D. B. Faulkner, F. A. Ireland, L. L. Berger, and D. F. Parrett. 1999. Production systems comparing early weaning to normal weaning with or without creep feeding for beef steers. J. Anim. Sci. 77: 300-310.

Nishimoto, H., R. Matsutani, S. Yamamoto, T. Takahashi, K.-G. Hayashi, A. Miyamoto, S. Hamano, and M. Tetsuka. 2006. Gene expression of glucose transporter (GLUT) 1, 3 and 4 in bovine follicle and corpus luteum. J. Endocrinol. 188: 111-119.

North, R. A., C. Ferrier, D. Long, K. Townend, and P. Kincaid-Smith. 1994. Uterine artery doppler flow velocity waveforms in the second trimester for the prediction of preeclampsia and fetal growth retardation. Obstet. Gynecol. 83: 378-386.

NRC. 1996. In: N. A. Press (ed.) Nutrient Requirements of Beef Cattle (7th Ed.), Washington, DC.

Ovenell, K. H., K. S. Lusby, G. W. Horn, and R. W. McNew. 1991. Effects of lactational status on forage intake, digestibility, and particulate passage rate of beef cows supplemented with soybean meal, wheat middlings, and corn and soybean meal. J. Anim. Sci. 69: 2617-2623.

Oxenreider, S. L. 1968. Effects of suckling and ovarian function on postpartum reproductive activity in beef cows. Am. J. Vet. Res. 29: 2099.

Oxenreider, S. L., and W. C. Wagner. 1971. Effect of lactation and energy intake on postpartum ovarian activity in the cow. J. Anim. Sci. 33: 1026-1031.

Painter, R. C., S. R. de Rooij, P. M. Bossuyt, T. A. Simmers, C. Osmond, D. J. Barker, O. P. Bleker, and T. J. Roseboom. 2006. Early onset of coronary artery disease after prenatal exposure to the Dutch famine. Am. J. Clin. Nutr. 84: 322-327.

Painter, R. C., C. Osmond, P. Gluckman, M. Hanson, D. I. Phillips, and T. J. Roseboom. 2008a. Transgenerational effects of prenatal exposure to the Dutch famine on neonatal adiposity and health in later life. BJOG 115: 1243-1249.

Painter, R. C., R. G. Westendorp, S. R. de Rooij, C. Osmond, D. J. Barker, and T. J. Roseboom. 2008b. Increased reproductive success of women after prenatal undernutrition. Hum. Reprod. 23: 2591-2595.

Perry, R. C., L. R. Corah, R. C. Cochran, W. E. Beal, J. S. Stevenson, J. E. Minton, D. D. Simms, and J. R. Brethour. 1991. Influence of dietary energy on follicular development, serum gonadotropins, and first postpartum ovulation in suckled beef cows. J. Anim. Sci. 69: 3762-3773.

Peterson, E. B., D. R. Strohbehn, G. W. Ladd, and R. L. Willham. 1989. Effects of preconditioning on performance of beef calves before and after entering the feedlot. J. Anim. Sci. 67: 1678-1686.

Prichard, D. L., T. T. Marshall, D. D. Hargrove, and T. A. Olson. 1989. Effects of creep feeding, zeranol implants and breed type on beef production: II. Reproductive development and fat deposition in heifers. J. Anim. Sci. 67: 617-623.

Rabiee, A. R., and I. J. Lean. 2000. Uptake of glucose and cholesterol by the ovary of sheep and cattle and the influence of arterial LH concentrations. Anim. Reprod. Sci. 64: 199-209.

Rakestraw, J., K. S. Lusby, R. P. Wettemann, and J. J. Wagner. 1986. Postpartum weight and body condition loss and performance of fall-calving cows. Theriogenology 26: 461-473.

Rasby, R. J., R. P. Wettemann, R. D. Geisert, L. E. Rice, and C. R. Wallace. 1990. Nutrition, body condition and reproduction in beef cows: fetal and placental development, and estrogens and progesterone in plasma. J. Anim. Sci. 68: 4267-4276.

Ravelli, A. C., J. H. van der Meulen, C. Osmond, D. J. Barker, and O. P. Bleker. 1999. Obesity at the age of 50 y in men and women exposed to famine prenatally. Am. J. Clin. Nutr. 70: 811-816.

Ravelli, G. P., Z. A. Stein, and M. W. Susser. 1976. Obesity in young men after famine exposure in utero and early infancy. N Engl J Med 295: 349-353.

Reynolds, L. P., and D. A. Redmer. 1995. Utero-placental vascular development and placental function. J. Anim. Sci. 73: 1839-1851.

Reynolds, W. L., T. M. DeRouen, and R. A. Bellows. 1978. Relationships of milk yield of dam to early growth rate of straightbred and crossbred calves. J. Anim. Sci. 47: 584-594.

Richards, M. W., L. J. Spicer, and R. P. Wettemann. 1995. Influence of diet and ambient temperature on bovine serum insulin-like growth factor-I and thyroxine: relationships with non-esterified fatty acids, glucose, insulin, luteinizing hormone and progesterone. Anim. Reprod. Sci. 37: 267-279.

Richards, M. W., J. C. Spitzer, and M. B. Warner. 1986. Effect of varying levels of postpartum nutrition and body condition at calving on subsequent reproductive performance in beef cattle. J. Anim. Sci. 62: 300-306.

Richards, M. W., R. P. Wettemann, and H. M. Schoenemann. 1989a. Nutritional anestrus in beef cows: body weight change, body condition, luteinizing hormone in serum and ovarian activity. J. Anim. Sci. 67: 1520-1526.

Richards, M. W., R. P. Wettemann, and H. M. Schoenemann. 1989b. Nutritional anestrus in beef cows: concentrations of glucose and nonesterified fatty acids in plasma and insulin in serum. J. Anim. Sci. 67: 2354-2362.

Richards, M. W., R. P. Wettemann, L. J. Spicer, and G. L. Morgan. 1991. Nutritional anestrus in beef cows: effects of body condition and ovariectomy on serum luteinizing hormone and insulin-like growth factor-I. Biol. Reprod. 44: 961-966.

Roberts, A. J., R. A. Nugent, J. Klindt, and T. G. Jenkins. 1997. Circulating insulin-like growth factor-I, insulin-like growth factor binding proteins, growth hormone, and resumption of estrus in postpartum cows subjected to dietary energy restriction. J. Anim. Sci. 75: 1909-1917.

Roseboom, T. J., R. C. Painter, A. F. M. van Abeelen, M. V. E. Veenendaal, and S. R. de Rooij. 2011. Hungry in the womb: What are the consequences? Lessons from the Dutch famine. Maturitas 70: 141-145.

Roseboom, T. J., J. H. Van Der Meulen, A. C. Ravelli, C. Osmond, D. J. Barker, and O. P. Bleker. 2001. Effects of prenatal exposure to the Dutch famine on adult disease in later life: an overview. Twin Res. 4: 293-298.

Rouquette, F. M., R. R. Riley, and J. W. Savell. 1983. Electrical stimulation, stocking rate and creep feed effects on carcass traits of calves slaughtered at weaning. J. Anim. Sci. 56: 1012-1020.

Rusche, W. C., R. C. Cochran, L. R. Corah, J. S. Stevenson, D. L. Harmon, R. T. Brandt, and J. E. Minton. 1993. Influence of source and amount of dietary protein on performance, blood metabolites, and reproductive function of primiparous beef cows. J. Anim. Sci. 71: 557-563.

Rutter, L. M., and J. G. Manns. 1987. Hypoglycemia alters pulsatile luteinizing hormone secretion in the postpartum beef cow. J. Anim. Sci. 64: 479-488.

Rutter, L. M., and R. D. Randel. 1984. Postpartum nutrient intake and body condition: effect on pituitary function and onset of estrus in beef cattle. J. Anim. Sci. 58: 265-274.

Rutter, L. M., R. D. Randel, G. T. Schelling, and D. W. Forrest. 1983. Effect of abomasal infusion of propionate on the GnRH induced luteinizing hormone release in prepuberal heifers. J. Anim. Sci. 56: 1167-1173.

Rutter, L. M., R. Snopek, and J. G. Manns. 1989. Serum concentrations of IGF-I in postpartum beef cows. J. Anim. Sci. 67: 2060-2066.

Ryan, D. P., B. Bao, M. K. Griffith, and G. L. Williams. 1995. Metabolic and luteal sequelae to heightened dietary fat intake in undernourished, anestrous beef cows induced to ovulate. J. Anim. Sci. 73: 2086-2093.

Saiduddin, S., I. W. Riesen, W. J. Tyler, and L. E. Casida. 1968. Relation of postpartum interval to pituitary gonadotropins, ovarian follicular development and fertility in dairy cows (effect of suckling, feeding level, breeding management, and genetic level of milk production). Wisconsin Ag. Exp. St. Res. Bul. 270: 15-22.

Selk, G. E., R. P. Wettemann, K. S. Lusby, J. W. Oltjen, S. L. Mobley, R. J. Rasby, and J. C. Garmendia. 1988. Relationships among weight change, body condition and reproductive performance of range beef cows. J. Anim. Sci. 66: 3153-3159.

Short, R. E., and D. C. Adams. 1988. Nutritional and hormonal interrelationships in beef cattle reproduction. Can. J. Anim. Sci. 68: 29-39.

Short, R. E., R. A. Bellows, E. L. Moody, and B. E. Howland. 1972. Effects of suckling and mastectomy on bovine postpartum reproduction. J. Anim. Sci. 34: 70-74.

Short, R. E., E. E. Grings, M. D. MacNeil, R. K. Heitschmidt, M. R. Haferkamp, and D. C. Adams. 1996. Effects of time of weaning, supplement, and sire breed of calf during the fall grazing period on cow and calf performance. J. Anim. Sci. 74: 1701-1710.

Sletmoen-Olson, K. E., J. S. Caton, K. C. Olson, D. A. Redmer, J. D. Kirsch, and L. P. Reynolds. 2000a. Undegraded intake protein supplementation: II. Effects on plasma hormone and metabolite concentrations in periparturient beef cows fed low-quality hay during gestation and lactation. J. Anim. Sci. 78: 456-463.

Sletmoen-Olson, K. E., J. S. Caton, K. C. Olson, and L. P. Reynolds. 2000b. Undegraded intake protein supplementation: I. Effects on forage utilization and performance of periparturient beef cows fed low-quality hay. J. Anim. Sci. 78: 449-455.

Spicer, L. J., E. Alpizar, and S. E. Echternkamp. 1993. Effects of insulin, insulin-like growth factor-I, and gonadotropins on bovine granulosa cell proliferation, progesterone production, estradiol production, and(or) insulin-like growth factor I production in vitro. J. Anim. Sci. 71: 1232-1241.

Spicer, L. J., E. Alpizar, and R. K. Vernon. 1994. Insulin-like growth factor-I receptors in ovarian granulosa cells: Effect of follicle size and hormones. Mol. Cell. Endocrinol. 102: 69-76.

Spicer, L. J., and C. S. Chamberlain. 1998. Influence of cortisol on insulin and insulin-like growth factor-1 (IGF-1)-induced steroid production and on IGF-1 receptors in cultured bovine granulosa cells and thecal cells. Endocrine 9: 153-161.

Spicer, L. J., C. C. Chase, and L. M. Rutter. 2002. Relationship between serum insulin-like growth factor-I and genotype during the postpartum interval in beef cows. J. Anim. Sci. 80: 716-722.

Spicer, L. J., W. J. Enright, M. G. Murphy, and J. F. Roche. 1991. Effect of dietary intake on concentrations of insulin-like growth factor-I in plasma and follicular fluid, and ovarian function in heifers. Domest. Anim. Endocrinol. 8: 431-437.

Spicer, L. J., K. Leung, E. M. Convey, J. Gunther, R. E. Short, and H. A. Tucker. 1986. Anovulation in postpartum suckled beef cows. I. Associations among size and numbers of ovarian follicles, uterine involution, and hormones in serum and follicular fluid. J. Anim. Sci. 62: 734-741.

Spicer, L. J., and R. E. Stewart. 1996. Interaction among bovine somatotropin, insulin, and gonadotropins on steroid production by bovine granulosa and thecal cells. J. Dairy Sci. 79: 813-821.

Spitzer, J. C., D. G. Morrison, R. P. Wettemann, and L. C. Faulkner. 1995. Reproductive responses and calf birth and weaning weights as affected by body condition at parturition and postpartum weight gain in primiparous beef cows. J. Anim. Sci. 73: 1251-1257.

Stagg, K., L. J. Spicer, J. M. Sreenan, J. F. Roche, and M. G. Diskin. 1998. Effect of calf isolation on follicular wave dynamics, gonadotropin and metabolic hormone changes, and interval to first ovulation in beef cows fed either of two energy levels postpartum. Biol. Reprod. 59: 777-783.

Stalker, L. A., D. C. Adams, T. J. Klopfenstein, D. M. Feuz, and R. N. Funston. 2006. Effects of pre- and postpartum nutrition on reproduction in spring calving cows and calf feedlot performance. J. Anim. Sci. 84: 2582-2589.

Stalker, L. A., L. A. Ciminski, C. A. Don, T. J. Klopfenstein, and R. T. Clark. 2007. Effects of weaning date and prepartum protein supplementation on cow performance and calf growth. Rangel. Ecol. Manage. 60: 578-587.

Stein, A. D., P. A. Zybert, K. van der Pal-de Bruin, and L. H. Lumey. 2006. Exposure to famine during gestation, size at birth, and blood pressure at age 59 y: evidence from the Dutch famine. Eur. J. Epidemiol. 21: 759-765.

Stein, Z., M. Susser, G. Saenger, and F. Marolla. 1972. Nutrition and mental performance: prenatal exposure to the Dutch famine of 1944-1945 seems not related to mental performance at age 19. Science 178: 708-713.

Stewart, R. E., L. J. Spicer, T. D. Hamilton, and B. E. Keefer. 1995. Effects of insulin-like growth factor-I and insulin on proliferation and on basal and luteinizing hormone-induced steroidogenesis of bovine thecal cells: involvement of glucose and receptors for insulin-like growth factor I and luteinizing hormone. J. Anim. Sci. 73: 3719-3731.

Stewart, R. E., L. J. Spicer, T. D. Hamilton, B. E. Keefer, L. J. Dawson, G. L. Morgan, and S. E. Echternkamp. 1996. Levels of insulin-like growth factor (IGF) binding proteins, luteinizing hormone and IGF-I receptors, and steroids in dominant follicles during the first follicular wave in cattle exhibiting regular estrous cycles. Endocrinology 137: 2842-2850.

Stewart, W. E., D. G. Stewart, and L. H. Schultz. 1958. Rates of volatile fatty acid production in the bovine rumen. J. Anim. Sci. 17: 723-736.

Stricker, J. A., A. G. Matches, G. B. Thompson, V. E. Jacobs, F. A. Martz, H. N. Wheaton, H. D. Currence, and G. F. Krause. 1979. Cow-calf production on tall fescue-ladino clover pastures with and without nitrogen fertilization or creep feeding: spring calves. J. Anim. Sci. 48: 13-25.

Swett, W. W., C. A. Matthews, M. H. Fohrman, and 1948. Development of the fetus in the dairy cow. . US Agri. Dept. Tech. Bull.: No. 964.

Thissen, J. P., J. M. Ketelslegers, and L. E. Underwood. 1994. Nutritional regulation of the insulin-like growth factors. Endo. Rev. 15: 80-101.

Triplett, B. L., D. A. Neuendorff, and R. D. Randel. 1995. Influence of undegraded intake protein supplementation on milk production, weight gain, and reproductive performance in postpartum Brahman cows. J. Anim. Sci. 73: 3223-3229.

Trudinger, B. J., W. B. Giles, and C. M. Cook. 1985. Uteroplacental blood flow velocity-time waveforms in normal and complicated pregnancy. BJOG 92: 39-45.

Tygesen, M. P., M. O. Nielsen, P. Norgaard, H. Ranvig, A. P. Harrison, and A.-H. Tauson. 2007. Late gestational nutrient restriction: Effects on ewes' metabolic and homeorhetic adaptation, consequences for lamb birth weight and lactation performance. Arch. Anim. Nutr. 62: 44-59.

Van Saun, R. J., S. C. Idleman, and C. J. Sniffen. 1993. Effect of undegradable protein amount fed prepartum on postpartum production in first lactation holstein cows. J. Dairy Sci. 76: 236-244.

Vizcarra, J. A., R. P. Wettemann, J. C. Spitzer, and D. G. Morrison. 1998. Body condition at parturition and postpartum weight gain influence luteal activity and concentrations of glucose, insulin, and nonesterified fatty acids in plasma of primiparous beef cows. J. Anim. Sci. 76: 927-936.

Vonnahme, K. A., B. W. Hess, M. J. Nijland, P. W. Nathanielsz, and S. P. Ford. 2006. Placentomal differentiation may compensate for maternal nutrient restriction in ewes adapted to harsh range conditions. J. Anim. Sci. 84: 3451-3459.

Vonnahme, K. A., M. J. Zhu, P. P. Borowicz, T. W. Geary, B. W. Hess, L. P. Reynolds, J. S. Caton, W. J. Means, and S. P. Ford. 2007. Effect of early gestational undernutrition on angiogenic factor expression and vascularity in the bovine placentome. J. Anim. Sci. 85: 2464-2472.

Wagner, J. J. 1985. Carcass composition in mature hereford cows: estimation and influence on metabolizable energy requirements for maintenance during winter. PhD Dissertation, Oklahoma State University, Stillwater.

Wagner, J. J., K. S. Lusby, J. W. Oltjen, J. Rakestraw, R. P. Wettemann, and L. E. Walters. 1988. Carcass composition in mature Hereford cows: estimation and effect on daily metabolizable energy requirement during winter. J. Anim. Sci. 66: 603-612.

Wagner, W. C., and S. L. Oxenreider. 1971. Endocrine physiology following parturition. J. Anim. Sci. 32: 1-16.

Wettemann, R. P. 1994. Management of nutritional factors affecting the prepartum and postpartum cow. In: M. J. Fields and R. S. Sand (eds.) Factors afftecting calf crop. p 155-165. CRC Press, Inc, Boca Raton, FL.

Wettemann, R. P., E. J. Turman, R. D. Wyatt, and R. Totusek. 1978. Influence of suckling intensity on reproductive performance of range cows. J. Anim. Sci. 47: 342-346.

Wiley, J. S., M. K. Petersen, R. P. Ansotegui, and R. A. Bellows. 1991. Production from first-calf beef heifers fed a maintenance or low level of prepartum nutrition and ruminally undegradable or degradable protein postpartum. J. Anim. Sci. 69: 4279-4293.

Wiltbank, J. N. 1970. Research needs in beef cattle reproduction. J. Anim. Sci. 31: 755-762.

Wiltbank, J. N., and A. C. Cook. 1958. The comparative reproductive performance of nursed cows and milked cows. J. Anim. Sci. 17: 640-648.

Wiltbank, J. N., W. W. Rowden, J. E. Ingalls, K. E. Geegoey, and R. M. Koch. 1962. Effect of energy level on reproductive phenomena of mature Hereford cows. J. Anim. Sci. 21: 219-225.

Wiltbank, J. N., W. W. Rowden, J. E. Ingalls, and D. R. Zimmerman. 1964. Influence of post-partum energy level on reproductive performance of Hereford cows restricted in energy intake prior to calving. J. Anim. Sci. 23: 1049-1053.

Winters, L. M., W. W. Green, and R. E. Comstock. 1942. Prenatal development of the bovine. Tech. Bull. Minn. Agri. Exp. St. No. 151.

Wolfenson, D., Z. Roth, and R. Meidan. 2000. Impaired reproduction in heat-stressed cattle: basic and applied aspects. Anim. Reprod. Sci. 60–61: 535-547.

Wu, G., F. W. Bazer, J. M. Wallace, and T. E. Spencer. 2006. BOARD-INVITED REVIEW: Intrauterine growth retardation: Implications for the animal sciences. J. Anim. Sci. 84: 2316-2337.

Yelich, J. V., R. P. Wettemann, T. T. Marston, and L. J. Spicer. 1996. Luteinizing hormone, growth hormone, insulin-like growth factor-I, insulin and metabolites before puberty in heifers fed to gain at two rates. Domest. Anim. Endocrinol. 13: 325-338.

Zhao, F.-Q., D. R. Glimm, and J. J. Kennelly. 1993. Distribution of mammalian facilitative glucose transporter messenger RNA in bovine tissues. . Int. J Biochem. 25: 1897−1903.

Zhu, M. J., M. Du, B. W. Hess, P. W. Nathanielsz, and S. P. Ford. 2007. Periconceptional nutrient restriction in the ewe alters MAPK/ERK1/2 and PI3K/Akt growth signaling pathways and vascularity in the placentome. Placenta 28: 1192-1199.

Zhu, M. J., M. Du, M. J. Nijland, P. W. Nathanielsz, B. W. Hess, G. E. Moss, and S. P. Ford. 2009. Down-regulation of growth signaling pathways linked to a reduced cotyledonary vascularity in placentomes of over-nourished, obese pregnant ewes. Placenta 30: 405-410.

Zhu, M. J., S. P. Ford, W. J. Means, B. W. Hess, P. W. Nathanielsz, and M. Du. 2006. Maternal nutrient restriction affects properties of skeletal muscle in offspring. J. Phys. 575: 241-250.

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