

# Nutritional controls of beef cow reproduction<sup>1</sup>

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**ABSTRACT:** The livestock industry and animal scientists have long recognized the importance of proper nutrition for cattle to achieve reproductive success. Timely resumption of estrus following parturition is a major milestone that a cow must reach for optimal reproduction. Dynamic interplay among all strata of the hypothalamo-hypophyseal-ovarian axis occurs during the cow's transition from postpartum anestrus to reproductive competence. The reproductive axis integrates a milieu of nutritionally related signals that directly or indirectly affect reproduction. Directing nutritional inputs toward anabolic processes is critical to stimulating key events that promote reproductive success. Although prepartum and postpartum energy balance are the most important factors affecting duration of the

postpartum interval to first estrus in beef cows, other nutritional inputs likely impinge on the hypothalamo-hypophyseal-ovarian axis to influence reproduction. For example, feeding fat to beef cows for approximately 60 d before calving may improve pregnancy rates in the upcoming breeding season. Supplementing postpartum diets with lipids high in linoleic acid can impede reproductive performance of beef cows. Precise mechanisms through which nutritional inputs mediate reproduction have not yet been fully elucidated. Scientists investigating nutritional mediators of reproduction, or how nutritional inputs affect reproduction, must be cognizant of the interactions among nutrients and nutritional cues responsible for mediating reproduction.

Key Words: Beef Cows, Dietary Lipids, Energy Balance, Hormones, Nutrition, Reproduction

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## Introduction

Beef cattle producers are continually challenged with the need to maintain sustainable production systems. The most important factors affecting financial viability of a cow-calf enterprise are reproduction and nutrition. In reviewing several sources of information, Bellows et al. (2002) estimated that reproductive diseases and conditions cost beef cattle producers \$441 to \$502 million in lost income yearly (aggregated national cost >\$14/cow). Financial cost associated with feed (4-yr average = approximately \$205/cow) was the greatest factor influencing profit of commercial beef cow operations, accounting for over 63% of the variation in total annual cow costs (Miller et al., 2001). Of the environmental cues that influence reproduction, nutrition commands

the greatest attention because the livestock producer can control nutritional inputs (Dunn and Moss, 1992). Proper nutritional inputs may afford beef cattle managers the opportunity to produce beef cattle more efficiently and become more sustainable. One important goal for beef cattle production systems, therefore, is to develop nutritional programs based on optimal diet formulation for maintaining or enhancing reproductive efficiency of the cowherd. Of equal importance is the identification of nutritional factors that are potentially detrimental to the reproductive capability of beef cows. The primary focus of this review is to discuss the nutritional controls of beef cow reproduction.

## Historical Developments

The importance of proper nutrition for livestock to achieve reproductive success has long been recognized by the livestock industry and animal scientists. The first publication in what is known today as the *Journal of Animal Science* was a review of nutritional and endocrine controls of reproduction (Guilbert, 1942). Guilbert (1942) noted "the livestock industry is familiar with the wide and economically significant variations in reproductive output of domestic animals that result from good and poor environmental conditions." In referring

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to nutritionally induced anestrus, Guilbert (1942) suggested that there was evidence for such a phenomenon in domestic livestock, but clear-cut data were lacking regarding the degree of inanition necessary to elicit anestrus. In a more recent review of historical advances in the area of postpartum cow research, Short et al. (1990) cited nine review papers and 17 book chapters or symposia articles from a database of over 700 references, although not all of the reviews cited specifically addressed the relationships between nutrition and reproduction. However, in a review presented at the same symposium, Randel (1990) cited 10 reviews concerning nutritional influences on reproductive performance of cattle that had been published since 1960. We located 15 American Society of Animal Science-sponsored reviews on nutrition and reproduction interactions that were published from 1990 through 2004. Clearly, the topic of nutritional controls of beef cattle reproduction has been studied extensively. Nutritional effects on reproduction, however, will undoubtedly continue to be the subject of immense investigation because nutritional management can be manipulated extensively by domestic livestock producers.

### *Review Themes*

Reviews that present the complexities of biological mechanisms linking nutrition and reproduction can be categorized into three general areas: 1) physiological processes that may be involved in mediating nutritional effects on reproduction (Randel, 1990; Short et al., 1990; Schillo, 1992; Dunn and Moss, 1992; Dhuyvetter and Caton, 1996; Armstrong and Benoit, 1996; Keisler and Lucy, 1996; Hawkins et al., 2000; Wettemann and Bossis, 2000; Wettemann et al., 2003; Webb et al., 2004); 2) relationships between nutritional status and measurements that are indicative of reproductive success (Randel, 1990; Short et al., 1990; Williams, 1990; Dunn and Moss, 1992; Wettemann and Bossis, 2000; Wettemann et al., 2003); and 3) specific examples of nutritional manipulation to influence reproduction (Randel, 1990; DelCurto et al., 2000; Hawkins et al., 2000; Williams and Stanko, 2000; Funston, 2004). We elected to use the approach taken by previous reviewers as a template to guide our discussion. Thus, the remainder of the discussion will focus on physiological processes mediating nutritional effects on reproduction, relationships between nutritional status and reproductive success, and examples of nutritional manipulation to influence reproduction. The overall goal of this review was to demonstrate the advances made in the area of nutrition  $\times$  reproduction interactions and to provide suggestions for future investigation.

### **Physiological Processes Mediating Nutritional Effects on Reproduction**

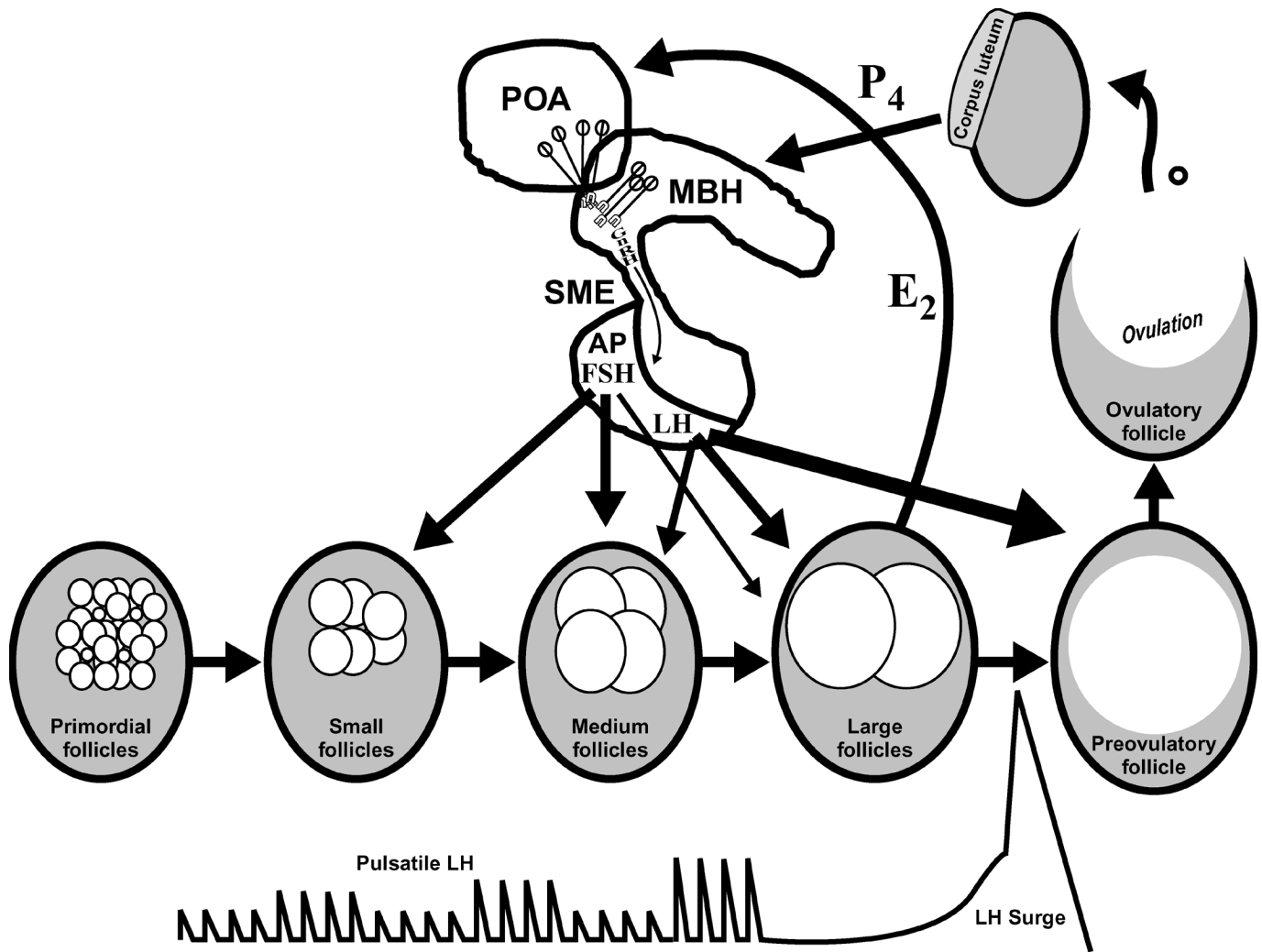
Potential mechanisms involved with nutritional modulation of reproduction have been thoroughly reviewed

over the past 15 yr. Although the number of reviews devoted to this subject is not limited to the references cited in the previous paragraph, the ensuing discussion will concentrate on literature published in the *Journal of Animal Science* with literature published in other locations being referenced when necessary.

### *Reestablishing Estrus Following Parturition*

Resumption of estrus within a relatively short time-frame following parturition has long been recognized as a major milestone that must be reached for a cow to achieve optimal reproduction. Mechanisms associated with the acquisition and subsequent maintenance of reproductive competence in the postpartum beef cow results from functional integration of the hypothalamo-hypophyseal-ovarian axis. Figure 1 illustrates the critical physiological events necessary to initiate reproduction in the postpartum beef cow. The brain centers of the reproductive axis are structured such that neurosecretory neurons from the preoptic area and medial basal hypothalamus terminate in the stalk median eminence. These neurons deliver GnRH to the hypophyseal portal blood system, which transports GnRH to the anterior pituitary gland where synthesis and secretion of the gonadotropins, FSH and LH, is stimulated. Early follicular growth and development is initiated by FSH. Tonic secretion of GnRH from the neurosecretory cells of the medial basal hypothalamus stimulates the secretion of hypophyseal LH release with surges (due to pulsatile release of GnRH originating from neurosecretory neurons in the preoptic area) occurring once every 1 to 2 h. Luteinizing hormone assists in the final maturation of the dominant preovulatory follicle. Production of estradiol by the ovarian follicles eventually reaches a threshold level causing the preoptic area neurosecretory neurons to release a surge of GnRH, which in turn causes a high-amplitude surge release of LH leading to ovulation. The subsequently formed corpus luteum produces progesterone, which suppresses GnRH release from the hypothalamus. Luteal regression and the accompanying decrease in serum concentrations of progesterone allow the process to be repeated. Maintenance of the corpus luteum caused by maternal recognition of pregnancy results in continued negative feedback effects and anestrus throughout pregnancy and into the postpartum period.

Production of copious amounts of steroids by the placenta, especially estradiol and progesterone, during late pregnancy exerts strong negative feedback effects on the hypothalamus, resulting in a decreased release of GnRH (Short et al., 1990). In addition to steroids from the placenta, steroid production by the maternal ovaries continues throughout gestation; however, gonadotropic support is insufficient to facilitate follicular growth and development of a normal-sized dominant follicle (Lucy, 2003). Secretion of steroids during pregnancy also depletes hypophyseal reserves of LH (Williams, 1990; Wettemann et al., 2003). Pituitary stores



**Figure 1.** Mechanisms associated with estrus in the postpartum beef cow result from continued integrated function of the hypothalamo-hypophyseal-ovarian axis: POA = preoptic area of the hypothalamus; MBH = medial basal hypothalamus; SME = stalk median eminence; AP = anterior pituitary gland; E<sub>2</sub> = estradiol; and P<sub>4</sub> = progesterone. Model constructed by compiling information published by Short et al. (1990), Williams (1990), Lucy et al. (1992), Schillo (1992), Bao and Garverick (1998), Senger (1999), Lucy (2003), Wettemann et al. (2003), Inskip (2004), and Webb et al. (2004). See text for details.

and releasable pools of LH are restored relatively quickly following parturition (Moss et al., 1985; Williams, 1990). A hypersensitivity to the negative feedback effects of estradiol (Short et al., 1990), however, contributes to the continuation of postpartum anestrus. Nutritionally compromised cows also seem to remain more sensitive to the negative feedback effects of estradiol (Keisler and Lucy, 1996; Wettemann et al., 2003), and may remain acyclic for 100 d (Williams, 1990) or longer (Hunter, 1991) due to decreased amplitude and frequency of LH secretion (Schillo, 1992). Extended periods of acyclicity in beef cows are attributed to negative effects of nursing a calf (Williams, 1990; Lucy, 2003; Wettemann et al., 2003) and improper cues signaling appropriate nutritional status (as discussed in the subsequent paragraphs). Because the anterior pituitary gland contains concentrations of gonadotropins similar

to estrous-cycling cows by 30 d postpartum and responds normally to exogenous GnRH, researchers have concentrated efforts on identifying metabolic and endocrine messages that may influence centrally mediated mechanisms affecting the secretion of LH (Lemenager et al., 1991; Keisler and Lucy, 1996; Wettemann and Bossis, 2000; Lucy, 2003; Wettemann et al., 2003).

#### *Metabolites as Nutritional Mediators*

*Glucose.* Although changes in blood metabolites and metabolic hormones have been used to evaluate potential cause-and-effect relationships between nutrition and reproduction without obvious conclusions (Dhuyvetter and Caton, 1996), compelling arguments have been made suggesting that several nutritionally related signals serve as messengers fundamental to the process



metabolites generated during gluconeogenesis contributed to decreased LH secretion singly or in combination has not been determined; there is a paucity of information concerning the involvement of each metabolite in the reproductive axis.

*Nonesterified Fatty Acids and Ketones.* Several reviews (Schillo, 1992; Keisler and Lucy, 1996; Wettemann et al., 2003) discounted the role of NEFA as a negative signal based on results of Estienne et al. (1990), who reported that NEFA infusions did not alter LH secretion. However, Dhuyvetter and Caton (1996) noted that the NEFA in a similar study by Estienne et al. (1989) was not generated by adipose tissue and, therefore, may not truly represent the metabolic status of an animal in negative energy balance. Studies with sheep have also demonstrated that brains of ruminants can utilize ketone bodies irrespective of nutritional status (Kammula, 1976b) and hyperketonemia increased brain uptake of ketone bodies and simultaneously decreased uptake of glucose (Kammula, 1976a). Regardless, cerebral ketone body and acetate utilization was always negligible compared with that for glucose (Pell and Bergman, 1983). Less than 5% of cerebral-generated CO<sub>2</sub> was derived from acetate or ketone bodies (Lindsay and Setchell, 1976). Some regions of the brain could be more dependent on ketones than others (Schillo, 1992), but we are not aware of research designed specifically to test the potential sensing of ketones (or acetate) by the hypothalamo-hypophyseal region. Notwithstanding, the predominance of evidence from the literature supports the concept that derangements in metabolism associated with limited gluconeogenesis result in reduced secretion of LH.

*Amino Acids.* Supplementation strategies designed to increase glucogenic precursors were reviewed by Randel (1990) and Hawkins et al. (2000). In addition to increasing metabolizable AA available for gluconeogenesis (Hawkins et al., 2000), the quantity of AA available to support other metabolic functions, such as protein synthesis was increased in cows supplemented with AA protected from ruminal degradation (Hess et al., 1998). It is probable that increased supplies of metabolizable AA, or perhaps specific AA imbalances, are detected by the regions of the brain responsible for LH release. Possible effects of excitatory AA (Lemenager et al., 1991; Dunn and Moss, 1992; Keisler and Lucy, 1996), tyrosine (Schillo, 1992; Dhuyvetter and Caton, 1996; Keisler and Lucy, 1996; Wettemann and Bossis, 2000), large neutral AA (Keisler and Lucy, 1996), the ratio between tyrosine and large neutral AA (Schillo, 1992), and valine, leucine, and isoleucine (Dunn and Moss, 1992; Schillo, 1992) as metabolic mediators of nutritional status have been reviewed. Until conclusive evidence is published to the contrary, we propose that brain regions regulating reproduction integrate signals from a milieu of blood-borne metabolites that ultimately affect LH secretion. It is possible that blood-borne metabolites exert their effects indirectly by in-

fluencing hormones purported to be involved in modulating the hypothalamo-hypophyseal-ovarian axis.

### *The Role of Neurohormones*

Several neuroendocrine hormones or factors have been implicated as being mediators of reproduction. Endogenous opioid peptides can inhibit the secretion of LH (Short et al., 1990; Williams, 1990; Lemenager et al., 1991; Keisler and Lucy, 1996), but seem to be only part of the control system (Short et al., 1990). Keisler and Lucy (1996) suggested the data of McShane et al. (1993) illustrated the existence of a functional relationship between the opiates and neuropeptide Y (NPY). It was postulated that NPY acts on opioidergic neurons to alter opiate tone, or opioidergic neurons act on NPY-containing neurons to suppress the expression of NPY. Convincing evidence was presented (Keisler and Lucy, 1996; Wettemann and Bossis, 2000) supporting the contention that as NPY increased, LH decreased; however, in a study designed to evaluate interactions between plane of postpartum nutrition and time required for resumption of estrus, no relationship was identified between the length of the postpartum anestrus period and NPY in thin primiparous beef cows (Lalman et al., 2000). Mean values reported by those authors actually indicate that cerebral spinal fluid concentrations of NPY were greater in cows with shorter periods of postpartum anestrus. These findings do not preclude a role of the endogenous opioid-NPY system, but rather indicate that this system cannot be solely responsible for mediating nutritional status.

### *Metabolic Hormones as Nutritional Mediators*

*Insulin.* In the search for the signal responsible for modulating nutritional effects on reproduction, tremendous attention has been devoted to the role of the metabolic hormones. This approach seems reasonable because changes in metabolic hormones reflect the shifting metabolic status of the animal (Lucy, 2003). Due to its facilitation of glucose metabolism, insulin seems to be a logical candidate for communicating the nutritional status of the animal. A number of studies have demonstrated that insulin is an important signal mediating nutritional effects on follicle dynamics in cattle (Webb et al., 2004). Insulin combined with glucose can stimulate release of GnRH from the hypothalamus (Arias et al., 1992); however, neither intracerebroventricular infusions (Hileman et al., 1993) nor s.c. injections (Dhuyvetter and Caton, 1996) of insulin without glucose altered secretion of LH. At the ovarian level, insulin can stimulate cell proliferation and steroidogenesis (Wettemann and Bossis, 2000). Insulin may also facilitate production of IGF-I by the liver (Keisler and Lucy, 1996; Webb et al., 2004). Others (Hunter, 1991; Dhuyvetter and Caton, 1996; Hawkins et al., 2000) suggested that increased insulin and concomitant decrease in GH is an important relationship to consider when evaluat-

ing nutritional impacts on reproduction. The functional relationship between insulin and GH with respect to reproduction appears to be anabolic in nature. Thus, insulin serves an important role in directing metabolic events critical to the reproductive axis.

*The Somatotrophic Axis.* Directing nutritional inputs toward anabolic processes has tremendous connotations with regard to reproduction. In addition to insulin, the somatotrophic axis has been implicated in mediating metabolic status centrally (Keisler and Lucy, 1996). However, a central role for GH on the reproductive axis is difficult to reconcile because GH secretion is downstream from the hypothalamus and is controlled by hypothalamic secretions (Keisler and Lucy, 1996). Likewise, bovine ovarian follicles are nearly devoid of GH receptors although GH may exert direct actions on luteal cells (Lucy et al., 1999). Growth hormone regulates expression of the IGF-I gene in extrahepatic tissues (Etherton, 2004) in addition to its classical role in stimulating hepatic expression and secretion of IGF-I in nutritional modulation along the hypothalamo-hypophyseal-ovarian axis (Armstrong and Benoit, 1996; Wettemann and Bossis, 2000; Wettemann et al., 2003; Webb et al., 2004). Interestingly, insulin interacts with GH to control hepatic IGF-I production (Molento et al., 2002). Serum concentrations of IGF-I increased from wk 2 to 10 in beef cows that resumed estrus early postpartum but not in cows that remained anestrous (Roberts et al., 1997). Armstrong and Benoit (1996) suggested that IGF-I may act via autocrine, paracrine, and endocrine mechanisms because, in addition to the presence of IGF-I receptors, mRNA for IGF-I has been detected in the ovary and median eminence. Granulosa cells of selected and dominant follicles also express the highest level of mRNA for IGF-I (Bao and Garverick, 1998). Regardless of the hormone's origin, IGF-I is a positive signal to the hypothalamo-hypophyseal-ovarian axis.

*Insulin-Like Growth Factor Binding Proteins.* Discussion of IGF-I as the only mediator of the somatotrophic axis would not be appropriate because  $\geq 95\%$  of the IGF-I in circulation (Etherton, 2004) is transported by one of six IGFBP (Thissen et al., 1994). Synthesis of an acid-labile subunit by the liver sequesters most IGF-I into ternary complexes consisting of IGF-I, IGFBP-3, or IGFBP-5 and the acid-labile subunit. However, IGFBP-5 contributes  $< 10\%$  to the total complex (Boisclair et al., 2001) and may not be readily detected in serum (Roberts et al., 2001). The anabolic effects of systemic IGF-I are related to relative abundance of IGFBP-3 (Armstrong and Benoit, 1996; Boisclair et al., 2001) whereas IGFBP-2 is associated with poor nutritional status (Armstrong and Benoit, 1996). Concentrations of IGFBP-2 in serum of beef cows at 2 wk postpartum diminished, and concentrations of IGFBP-3 increased in cows that resumed estrus by 20 wk postpartum compared with anestrous cows (Roberts et al., 1997). Insulin-like growth factor binding protein-2, -3, and -5 have been detected (Funston et al., 1995)

and are produced (Roberts et al., 2001) in the anterior pituitary gland of cycling beef cows. Stalk median eminence concentrations of these IGFBP were greater in ewes maintained on a higher plane of nutrition and were positively correlated with serum concentrations of LH (Snyder et al., 1999). Ewes fed a lower plane of nutrition also tended to have greater amounts of IGFBP-2 (Snyder et al., 1999). Expression of mRNA for IGFBP also occurs in the ovary (Bao and Garverick, 1998), and IGFBP-2, -3, -4, and -5 have been detected in the ovarian follicular fluid of beef cows (Funston et al., 1996). Follicular fluid concentrations of IGFBP-2, -4, and -5 are high in small- to medium-sized and larger atretic follicles, but decrease in the dominant follicle (Armstrong and Benoit, 1996; Wettemann et al., 2003; Webb et al., 2004). Insulin-like growth factor binding protein-3 was the only IGFBP detected in fluid from the preovulatory follicle (Funston et al., 1996). Heifers consuming increased dietary energy had reduced concentrations of mRNA for IGFBP-2 and IGFBP-4 in small follicles (Armstrong et al., 2001). Based on these observations, IGFBP must be considered potential mediators of nutritional inputs into the reproductive axis.

*Leptin.* The direct perception of metabolic cues by the hypothalamo-hypophyseal-ovarian axis may not be the only level at which nutrition effects reproduction. For example, the "exquisite orchestration" of glucose partitioning related to attenuation of insulin sensitivity at the adipose tissue by GH (Etherton and Bauman, 1998) contributed to decreased adipose tissue growth (Etherton, 2004). This effect may in turn influence the expression and secretion of leptin, a protein hormone secreted from the adipocytes that may be chronically regulated by insulin (Houseknecht et al., 1998). Strong relationships have been observed between cow body fatness, adipocyte size, and plasma leptin concentrations (Delavaud et al., 2002). Plasma concentrations of leptin were also positively correlated with BCS in Zebu  $\times$  Brown Swiss heifers (León et al., 2004). The strength of the relationship was nearly twice as great ( $r = 0.47$  vs.  $0.83$ ) during periods of weight gain vs. periods of nutritional restriction. Published information utilizing nonruminant animals provides convincing evidence for leptin as a signal that links metabolic status to the activation of the reproductive system (Houseknecht et al., 1998; Barb, 1999). Although there is no evidence to suggest that nutritional restriction mediates hypothalamic or pituitary function via leptin or its receptors in the beef cow, there is evidence for such action in sheep (Wettemann et al., 2003). Delavaud et al. (2002) and León et al. (2004) suggested that increased circulating leptin is associated with increased plane of nutrition. Therefore, as a hormone produced in response to anabolic processes occurring within the adipose tissue, leptin may also serve as a messenger signaling the reproductive axis at the brain level or perhaps even at the level of the ovary (Spicer, 2001).

*Ghrelin.* The purification of the ligand for GH secretagogue receptor, ghrelin, in stomach extracts by Kojima

et al. (1999) has reinitiated scientific inquiry about how the gastrointestinal tract exerts an influence on energy homeostasis. The main source of circulating ghrelin is produced by enteroendocrine cells in the stomach and the intestine (Date et al., 2000). A large number of studies with humans and rodents have demonstrated that ghrelin is involved in the regulation of energy balance with apparent effects being opposite of leptin (Horvath et al., 2001). Although ghrelin is produced mainly in the fundic region of the stomach (Kojima et al., 2001), lower amounts are derived from the intestines, kidney, immune system, placenta, pituitary, gonads, and hypothalamus (Gnanapavan et al., 2002). Investigations into the role of ghrelin in mediating reproductive processes have been spurred by the hormone's involvement in energy balance and localization along the reproductive axis.

Ovarian levels of ghrelin mRNA were highest when the rat's corpus luteum entered its functional phase and were also higher in early pregnancy compared with the later part of gestation (Caminos et al., 2003), suggesting a potential functional autocrine-paracrine role of ghrelin in the regulation of luteal development and/or function. Ghrelin reaches its receptors in the anterior pituitary and possibly the hypothalamus through general circulation (Tschöp et al., 2000). Intracerebroventricular administration of ghrelin inhibited LH secretion in ovariectomized rats (Furuta et al., 2001; Fernández-Fernández et al., 2004). Likewise, intracerebroventricular administration of ghrelin suppressed pulsatile LH secretion in ovariectomized rats receiving estradiol treatment. Ghrelin mRNA expression in the stomach and levels of the hormone in the blood increased before feeding and by fasting, and decreased after feeding in meal-fed animals, including sheep (Sugino et al., 2002a, 2004). However, changes in plasma ghrelin concentrations are much more subtle throughout the day in sheep given ad libitum access to feed (Sugino et al., 2002b). Circulating ghrelin concentrations in humans are decreased in chronic and acute states of energy balance, but it has yet to be proven that modest changes in circulating ghrelin have physiological relevance (Horvath et al., 2001). Similarly, our laboratory reported that feeding ewes 50% of NRC recommendations from d 28 to 78 of gestation did not affect expression of messenger encoding for prepro-ghrelin in the gastrointestinal tract (Han et al., 2004). Although there is evidence for a role of ghrelin along the hypothalamo-hypophyseal-ovarian axis in rats, evidence for such action in ruminants to date is putative at best. The research indicating that insulin is a physiological and dynamic modulator of plasma ghrelin (Saad et al., 2002) lends further support for the contention that the animal construes anabolic events as part of the process of reinitiating estrus following parturition. It is also important to note that, although ghrelin is regulated acutely like a satiety factor, leptin concentrations are not regulated by meals, but rather by actual increase

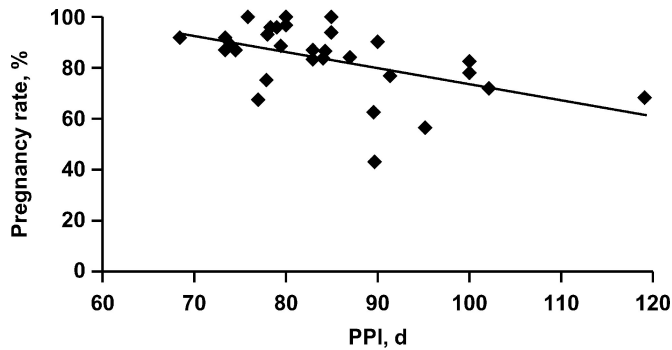
in adipose tissue (Horvath et al., 2001), which is indicative of increased energy balance.

## Nutritional Status and Reproductive Success

Although it is difficult to ascertain if specific nutrients limit reproduction through common or discrete mechanisms, appropriate quantities of the nutrients are required for optimal reproduction (Dunn and Moss, 1992). For example, "substandard" hay quality caused low reproductive performance in a commercial cow-calf operation in southwestern Colorado (Lankister et al., 1999). Under practical conditions, much of the variation in reproductive performance of beef cows may be accounted for by differences in energy intake and body condition (Lemenager et al., 1991). Reviews of the scientific literature published in the *Journal of Animal Science* within the last 15 yr demonstrated 1) prepartum nutrition is more important than postpartum nutrition in determining the length of postpartum anestrus; 2) inadequate dietary energy during late pregnancy lowers reproduction even when dietary energy is sufficient during lactation; 3) a BCS  $\geq 5$  will ensure body reserves are adequate for postpartum reproduction; and 4) further declines in reproduction occur when lactating beef cows are in negative energy balance (Randel, 1990; Short et al., 1990; Williams, 1990; Dunn and Moss, 1992; Wettemann and Bossis, 2000; Wettemann et al., 2003). The regression analyses conducted by Dunn and Kaltenbach (1980), and later refined by Short et al. (1990), clearly established the relationship between plane of nutrition  $\times$  BCS and reproduction of beef cows. These types of relationships have not been published in American Society of Animal Science-sponsored symposia format since 1990. Therefore, we reevaluated nutritional effects on beef cow reproduction using datasets constructed from studies reported in the *Professional Animal Scientist* and *Journal of Animal Science* since 1990.

## Statistical Analyses

For all analyses, treatment means were used as individual observations. Treatment mean observations for length of postpartum interval to first estrus (**PPI**) were weighted (Steel and Torrie, 1980) because these means were based on differing sample size and variances. Pearson correlation coefficients were computed to determine linear associations between weighted variables. Stepwise regression using weighted variables was performed and studentized residuals were used to identify outliers. Studentized residuals exceeding 2.5 were removed and the data were reanalyzed. A similar approach was attempted for data on pregnancy rates, but authors often failed to report associated variance. Therefore, statistical inferences about pregnancy rates were suspect because the resulting relationships likely contained bias. Moreover, of the 33 instances where both PPI (67 to 119 d) and pregnancy rate (43 to 100%)

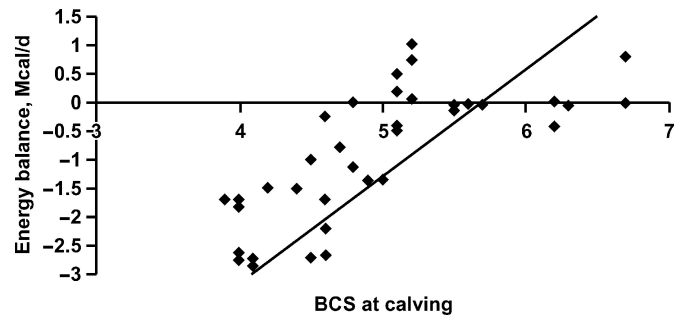


**Figure 3.** The influence of length of postpartum interval to first estrus (PPI in days) on pregnancy rate: pregnancy rate, % =  $PPI \times (-0.60 \pm 0.19) + (134.01 \pm 15.59)$ ;  $R^2 = 0.25$ .

were reported (DelCurto et al., 1990; Murphy et al., 1992; Beaty et al., 1994; Triplett et al., 1995; Reed et al., 1997; Thrift et al., 1999; Weder et al., 1999; Alderton et al., 2000; Filley, et al., 2000; Smith et al., 2001; Gunter et al., 2003), pregnancy rate was negatively correlated ( $P = 0.003$ ;  $r = -0.50$ ) with PPI. Although caution must be exercised when interpreting these results because the data are not adjusted for trial effects, the subsequent regression equation illustrated that pregnancy rate would be 100% for cows with PPI = 56.5 d, and pregnancy rate was decreased by at least 0.5% unit for each additional day a cow was anestrous (Figure 3). Dunn and Moss (1992) demonstrated that a cow with a PPI between 40 and 60 d has an 88% chance of calving within 365 d. Decreased pregnancy rates associated with longer PPI are probably related to factors that cause extended PPI rather than the effect of extended PPI per se. Extended periods of PPI would limit reproductive efficiency of the cowherd if beef cow managers used restricted breeding seasons. Therefore, length of postpartum anestrus was chosen as the reproductive outcome to assess plane of nutrition effects on reproduction. We recognize that much more robust statistical methods are available; however, our only intent was to reevaluate the relationship between plane of nutrition and PPI using more recent literature to permit comparisons with previous literature on nutrition  $\times$  reproduction interactions.

#### Plane of Nutrition During Late Gestation

Mean observations, sample size, and variance reported in the original articles were used to develop a dataset for correlation and regression analyses between late gestational (42 to 105 d before calving) plane of nutrition and subsequent measures of reproduction. Plane of nutrition was estimated from animal performance. For all cow BW measurements, weight of the conceptus both prepartum and at parturition (estimated from the equations of Ferrell et al., 1976) was deducted from the reported cow BW. Prepartum energy balance was estimated from changes in BW or BCS



**Figure 4.** The relationship between prepartum energy balance estimated from prepartum BCS change and BCS at calving. The dataset was generated using 22 observations from results of Beaty et al. (1994), Bellows et al. (1994), Sletmoen-Olson et al. (2000), Smith et al. (2001), Weidmeier et al. (2002), and Gunter et al. (2003).

using the equations of the NRC (2000). To avoid confounding the results with postpartum plane of nutrition, we limited our dataset to treatments in which cows were near maintenance after calving ( $\leq$  approximately 3% change in BW or  $\leq 0.2$  overall change in BCS). Of the 15 publications and 45 observations satisfying our criteria, only 21 observations were available for duration of postpartum anestrus. Additionally, this dataset was somewhat narrow because it only included cows with BCS ranging from 4.0 to 6.7 at calving.

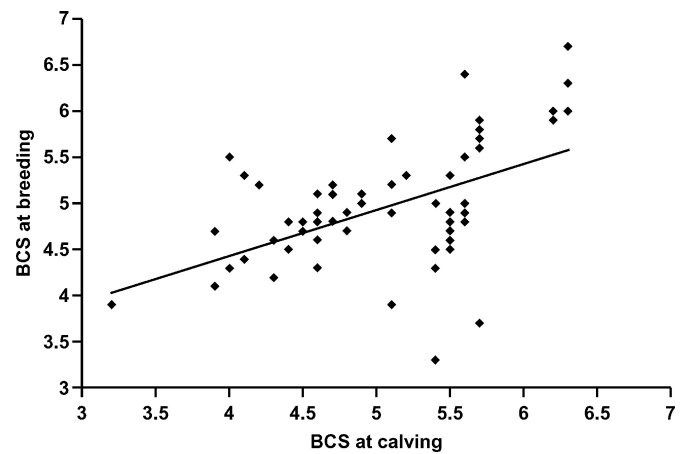
Length of PPI was correlated with BCS at calving ( $r = 0.75$ ;  $P < 0.001$ ) and prepartum energy balance estimated from changes in prepartum BCS ( $r = 0.52$ ;  $P = 0.01$ ) but not with prepartum change in BCS ( $r = 0.35$ ;  $P = 0.11$ ). Results of our stepwise regression demonstrated that BCS at calving was the only variable to consider for estimating effects of prepartum plane of nutrition on PPI ( $P < 0.001$ ;  $R^2 = 0.57$ ). However, it should be noted that cows calving with a BCS of  $< 5$  experienced negative energy balance during late gestation (Figure 4). Our laboratory demonstrated that beef cows experiencing 90 d of nutrient restriction (2.8 Mcal/d negative energy balance) during early gestation have less visceral tissue mass (Molle et al., 2004), which may decrease metabolic rate (Drouillard et al., 1991; Krehbeil and Ferrell, 1999) and energy requirements (Freetly and Nienaber, 1998). The consequences of such decreases may be that efficiency of energy utilization could be improved (Hunter, 1991; Hawkins et al., 2000) once cows that experienced negative energy balance prepartum are fed to achieve maintenance after calving.

In a study designed to evaluate how BCS at parturition (accomplished by altering prepartum dietary energy status) affected subsequent reproductive performance, Houghton et al. (1990) demonstrated that PPI was extended if beef cows calved with a BCS  $< 6$  (adjusted to a nine-point scale), but first-service conception rates and overall pregnancy rates were exceptionally high for thinner cows receiving 130% NRC-recom-

mended dietary energy postpartum. We did not evaluate effects of prepartum plane of nutrition on first-service conception rates using reports in the literature because only two studies satisfied our criteria. However, Lake et al. (2004) conducted a 2-yr study in which 3-yr-old beef cows were nutritionally managed to achieve a BCS of 4 or 6 at parturition and were then fed near maintenance levels during lactation. First-service conception rates were not affected ( $P = 0.22$ ), but overall pregnancy rates were lower ( $P = 0.01$ ) for thinner cows (BCS 4 = 36.1 and 63.9%, whereas BCS 6 = 50.0 and 88.9%, respectively), even though the thinner cows were losing less ( $P = 0.09$ ) BW and had a slight increase ( $P = 0.02$ ) in BCS during the first 60 d postpartum. In discussing the practice of supplemental feeding as a method to increase prepartum plane of nutrition, Hunter (1991) suggested that prepartum plane of nutrition affected development of follicles that mature in the subsequent breeding season. It is also possible that prepartum plane of nutrition affects oocyte quality (Krisher, 2004), size, and steroidogenic capacity of the corpus luteum, and uterine function through mechanisms that cause extended anestrus (for details, see Lucy, 2003). Our unpublished results for serum concentrations of GH and IGF-I from the study of Lake et al. (2004) would suggest that there was an uncoupling of the somatotrophic axis. Mean concentrations of serum GH (blood was drawn every 15 min for 4 h) were 18% greater ( $P = 0.002$ ) and serum IGF-I was 62.7% ( $P < 0.001$ ) less in cows with a BCS of 4 than those with a BCS of 6. Lake et al. (2004) determined that cows with a BCS of 4 had the proclivity for increased lipogenic activity, but serum insulin ( $P = 0.27$ ) did not differ between cows with BCS 4 or 6. These results may suggest that sensitivity to insulin was affected by BCS (Eherton and Bauman, 1998). Thus, our findings support the contention that several of the metabolic hormones discussed in the previous section either mediate, signal, and/or indicate the potential for successful reproduction.

#### *Plane of Nutrition Following Parturition*

Similar to our prepartum plane of nutrition evaluations, the effects of postpartum energy status (estimated from animal performance) on reproduction were evaluated. There were 19 publications with a total of 65 observations in our dataset. Body condition score at breeding ( $r = -0.41$ ;  $P < 0.001$ ), but not BCS at calving ( $r = 0.10$ ;  $P = 0.41$ ), was correlated with PPI. Both BCS change ( $r = 0.47$ ;  $P < 0.001$ ) and energy balance estimated from BCS change ( $r = 0.43$ ;  $P < 0.001$ ) were also correlated with PPI. Results of a stepwise regression analysis, however, indicated that BCS at breeding was the only predictor of PPI. A large portion (47%) of the variation in BCS at breeding was explained by BCS at calving (Figure 5). From a practical perspective, BCS at breeding is less useful as a management tool than BCS at calving because it would be difficult if not impos-



**Figure 5.** The relationship between BCS at calving and BCS at breeding. The dataset included 65 observations from the literature (DelCurto et al., 1990; Murphy et al., 1992; Simpson et al., 1992; Beaty et al., 1994; Triplett et al., 1995; Lalman et al., 1997, 2000; Reed et al., 1997; Thrift et al., 1999; Weder et al., 1999; Alderton et al., 2000; Filley et al., 2000; Lents et al., 2000; Sletmoen-Olson et al., 2000; Smith et al., 2001; Webb et al., 2001; Weidmeier et al., 2002; Gunter et al., 2003; Strauch et al., 2003).

sible to improve BCS of cows once the breeding season has begun.

Overall, our results are consistent with the volumes of previously cited literature indicating that dietary energy is critically important to beef cow reproduction.

### **Nutritional Manipulation to Influence Reproduction**

#### *Supplemental Lipids as an Example*

Dietary manipulations designed to enhance reproduction of beef cows have often focused on the net effect of increased energy status because of the aforementioned importance of dietary energy to the process of reproduction. Dietary fats, which contain the most energy-dense nutrient, stimulate follicular growth when fed to increase energy balance (Lucy et al., 1992). However, DelCurto et al. (2000) indicated that the benefits of dietary lipid from vegetable sources were apparently different from the value of fat as a source of energy because lipid-containing diets were formulated to deliver the same quantity of energy as control treatments. The use of dietary fat as a nutraceutical to positively influence reproductive events (Williams and Stanko, 2000) has piqued the interest of several researchers (Hess et al., 2002; Hess, 2003; Funston, 2004).

*Prepartum Lipid Supplementation.* Feeding supplemental fat to beef cows during late gestation has been evaluated as a method to alleviate the negative effects of prepartum nutritional inadequacy on reproductive performance. Experiments published in *The Professional Animal Scientist*, wherein researchers fed fat to

**Table 1.** Effects of feeding supplemental fat to beef cows during gestation on subsequent cow reproduction

Reference	Feeding period	Basal diet	Supplements	Response <sup>a</sup>			
				Postpartum interval	Detected estrus	First-service conception	Pregnancy rate
Bellows et al. (2001)	Exp. 1 65d prepartum	Corn silage + grass hay	Barley/soybean meal	NR	68%	NR	79%
			High-linoleate safflower seeds		85%		97%↑
			Soybean seeds		76%		93%↑
			Sunflower seeds		76%		92%↑
Exp. 2 68d prepartum	Corn silage + alfalfa hay	Barley/soybean meal	NR	66%	NR	90%	
		Sunflower seeds		55%		80%	
Alexander et al. (2002)	Exp. 1 62d prepartum	Bromegrass hay	Corn/soybean meal	NS	83%	55%	73%
			Sunflower seeds/soybeans	avg 66d	50%	38%	100%
			Soapstocks		60%	71%	100%
	Exp. 2 59 d preparutm	Bromegrass hay	Corn/soybean meal	NR	NR	60%	88%
			Sunflower seeds/soybeans			67%	91%
			Soapstocks			71%	92%

<sup>a</sup>Response variables with ↑ beside them were greater than the value reported for the other treatment(s) within each study. NR = not reported; NS = not significant.

beef cows before calving, are summarized in Table 1. The length of the supplemental fat period ranged from 59 to 68 d before calving. Duration of the postpartum interval was only determined in one (Alexander et al., 2002) of the four experiments and was not affected by prepartum dietary fat. Likewise, the percentage of cows detected in estrus and first-service conception rates were not affected by feeding fat to cows during late gestation. In only one experiment (Bellows et al., 2001) did more cows become pregnant as a result of feeding fat prepartum. Numerical trends for pregnancy rates favored the nonfat supplement in one trial (Bellows et al., 2001), whereas prepartum supplemental fat numerically increased pregnancy rates in the two experiments of Alexander et al. (2002). Because of the limited number of reports and limited number of animals used in each of these experiments, results from these two manuscripts were combined to conduct  $\chi^2$  analyses. This dataset had 140 control cows and 274 fat-supplemented cows. Results revealed an improvement ( $P = 0.02$ ) in pregnancy rates when beef cows were supplemented with fat (91.6%) during late gestation compared with control cows (82.9%).

Other reports in the nonrefereed literature showed similar improvements in reproduction with prepartum supplementation of fat to beef cows. Graham et al. (2001) reported that feeding whole soybeans to mature beef cows for either 30 or 45 d before calving increased first-service conception rates (62.8 vs. 85.7% and 62.5 vs. 75%, respectively). In a summarization of data from the two studies wherein high-linoleate safflower seeds were fed to primiparous beef cows 53 or 55 d prepartum (Lammoglia et al., 1999a,b), Bellows (1999) noted that pregnancy rates increased from 56% for the 89 control cows to 70% for 179 fat-supplemented cows. Likewise, feeding high-oleate and high-linoleate safflower seeds to primiparous beef cows approximately 55 d prepartum increased subsequent pregnancy rates from 57 to 75 and 77%, respectively (Lammoglia et al., 1997). Thus,

our proposed 10.5% enhancement in pregnancy rates may be a conservative estimate of the potential to improve reproduction by supplementing the diets of beef cows with fat before calving. We conclude that supplementing fat to beef cows during late gestation is an effective means to improve reproductive success in the upcoming breeding season; however, the magnitude of this response may depend on dietary factors during the supplementation period as well as following supplementation (Bellows et al., 2001). Small et al. (2004) recently reported that prepartum lipid supplementation to cows in adequate condition at calving (BCS = 5.1) that exhibited an 0.31 unit increase in BCS for the first 60 d of lactation did not increase the number of cows exhibiting estrus 60 d postpartum ( $93.5 \pm 2.9$ ) or improve AI first-service conception rates ( $67.3 \pm 5.5\%$ ) or final conception rates ( $97.4 \pm 1.8\%$ ). The positive response to supplementing fat to cows during late gestation diminished slightly when Hess (2003) added data of Small et al. (2004) to the dataset reported in Table 1; the overall pregnancy rate increased ( $P = 0.05$ ) from 86.3 to 91.8%. Therefore, it would seem reasonable to suggest that feeding fat to beef cows for approximately 60 d before calving may result in a 6.4% improvement in pregnancy rates in the upcoming breeding season for beef cow herds with pregnancy rates  $\leq 90\%$ .

*Pre- and Postpartum Lipid Supplementation.* Espinoza et al. (1995) increased pregnancy rates (first 95 d of breeding) of range beef cows fed a fat supplement containing more energy than the control supplement. Fat supplementation from the third trimester of gestation through the third postpartum estrous cycle caused the postpartum anestrous interval to be prolonged, but decreased the incidence of short estrous cycles (Oss et al., 1993). It is difficult to draw definitive conclusions based on the limited reports available; however, beef cow responses to supplemental fat pre- and postpartum seem to be comparable to responses observed when feeding fat to postpartum beef cows.

*Postpartum Lipid Supplementation.* Studies in which researchers reported luteal activity and/or PPI of beef cows in response to consumption of fat postpartum are summarized in Table 2. The incidence of luteal activity increased in three of the six experiments, but only one (Webb et al., 2001) of 14 supplemental fat regimens decreased the duration of postpartum anestrus. Moreover, although Williams (1989) and Hightshoe et al. (1991) reported dietary fat increased the number of cows exhibiting normal estrus, six other studies demonstrated an equivocal effect of postpartum dietary fat. Of the 11 dietary fat treatments summarized, only one (Webb et al., 2001) decreased the percentage of cows exhibiting normal estrous cycles. The summary of results from Table 2 also indicated that feeding fat to postpartum beef cows did not consistently decrease the postpartum anovulatory period. First-service conception rates were not affected by feeding fat to postpartum beef cows. Likewise, none of these studies reported a detrimental effect on overall pregnancy rates, and only one of the 11 dietary fat treatments improved pregnancy rates. Because the greatest number of cattle used in any of the experiments was 24 per treatment, a number that may have been insufficient to obtain statistically meaningful results, we conducted  $\chi^2$  analysis of the pregnancy rate data from these studies. This dataset had 324 individual observations with 170 cows given fat for 4 to 90 d during the postpartum period. Pregnancy rate was not affected ( $P = 0.84$ ) by diet, and was 82.9% when cows consumed fat and 83.8% when cows did not consume supplemental fat postpartum. Results of this summary are consistent with the review of Funston (2004), who demonstrated that responses to postpartum fat supplementation have been inconsistent. It is, however, equally important to point out that feeding fat to postpartum beef cows did not elicit deleterious effects on reproduction. Therefore, we agree with Funston (2004), who concluded that producers should utilize fat supplementation if cost-effective fat sources are available.

*Supplementing High-Linoleate Safflower Seeds to Postpartum Cows.* Reviews that have concentrated on the beneficial effects of feeding cows fat have attributed many positive responses to the high linoleic acid content of the supplementary lipids (Staples et al., 1998; Williams and Stanko, 2000). We conducted a series of experiments to elucidate mechanisms by which dietary lipids high in linoleate, supplemented postpartum, influence reproduction of beef cows. In all cases, supplemental cracked safflower seeds (oleate or linoleate content ranges from 67 to 76%) formulated to provide 5% of total DMI as fat were compared with a control supplement formulated to provide beef cows with similar quantities of dietary energy throughout early lactation. In a study using primiparous cows for the first 90 d postpartum, Bottger et al. (2002) reported that feeding high-linoleate safflower seeds permitted cows to maintain greater BCS, whereas feeding high-oleate safflower seeds increased milk fat synthesis. This apparent abil-

ity for cows fed high-linoleate safflower seeds to partition nutrients away from milk fat toward body energy reserves prompted Grant et al. (2003) to evaluate the influence of supplemental high-linoleate safflower seeds on reproductive endocrine dynamics in young, postpartum beef cows. Serum concentrations of the gonadotropins in response to a GnRH challenge at 45 d postpartum were similar among treatments, but mean concentrations of progesterone peaked 2 d later in cows fed high-linoleate safflower seeds (d 4 vs. 6 after GnRH administration) and fewer of the fat-supplemented cows formed a functional corpus luteum. The  $\chi^2$  analysis of data from experiments in which we fed safflower seeds to young beef cows revealed that first-service conception rate decreased from 50.0% for control to 28.8% for cows receiving supplemental fat (Hess, 2003). Although it would seem that the level of fat provided to cows in our studies was somewhat high (approximately 480 g/d of supplemental lipid), it is important to note that Webb et al. (2001) included other dietary ingredients (such as corn) that contributed substantially to total dietary fat intake (total fat intake was approximately 470 g/d). There is currently insufficient evidence to definitively conclude that level of fat was the major factor contributing to the response, and fatty acid composition or other components of the fat source cannot be ruled out as factors that contributed to the negative response on first service conception rates. Overall pregnancy rates ( $80.2 \pm 3.4\%$ ) were not affected by supplemental safflower seeds, but the cows were not fed supplemental fat throughout the breeding season. Additional research is necessary to determine whether the influence of feeding lipids high in linoleic acid persist throughout the postpartum period.

The aforementioned effects of supplemental fat on reproduction may be exerted at least partially on the uterine tissue. The endometrium is a major site of  $\text{PGF}_{2\alpha}$  in the postpartum cow (Short et al., 1990). Plasma or serum concentrations of 13,14-dihydro-15-keto- $\text{PGF}_{2\alpha}$  metabolite (**PGFM**), a metabolite produced when the lungs and uterus metabolize  $\text{PGF}_{2\alpha}$ , have been used to assess the role of  $\text{PGF}_{2\alpha}$  in reproductive processes (Staples et al., 1998). Our laboratory reported that supplemental fat increased serum concentrations of PGFM from d 25 to 90 postpartum (Grant et al., 2002). Moreover, the fatty acid composition of the lipid supplement evoked differential effects on PGFM. Serum concentrations of PGFM were greater in cows fed high-linoleate safflower seeds ( $647 \pm 62$  pg/mL) than in cows fed either high-oleate safflower seeds ( $371 \pm 68$  pg/mL) or the control supplement ( $452 \pm 68$  pg/mL). Our results (Grant et al., 2002) contrast with the mechanism that Staples et al. (1998) proposed as the way in which supplemental fat affects prostaglandin synthesis. Those authors suggested that increasing delivery of linoleate and eicosapentanoate to the uterus inhibited the secretion of  $\text{PGF}_{2\alpha}$ . In a companion study to our lactating cow experiments, Scholljegerdes et al. (2004a) demonstrated that intestinal supply of linoleic acid was

**Table 2.** Ovarian follicular dynamics, apparent luteal function, and reproductive performance of beef cows consuming fat-supplemented diets during the postpartum period

Reference	Feeding period	Supplements	Ovarian follicles	Luteal activity and postpartum interval	Response <sup>a</sup>			
					Reproductive hormones	Normal estrus	First-service conception	Pregnancy rate
Williams (1989)	~48d	Whole corn	NR	38%	36%	NR	NR	NR
Hightshoe et al. (1991)	~45d	Whole cottonseed		81%↑	↑			
		Grain sorghum	0.25 at 10–15 mm	NS	33%	NR	NR	NR
Wehrman et al. (1991)	30d	Ca fatty acids	0.92 at 10–15 mm↑		↑LH & P <sub>4</sub> , ↓E <sub>2</sub>			
		Corn + milo grain	NR	44%	NR	NR	NR	NR
Carr et al. (1994) Exp. 1	100d	Whole cottonseed		62%↑				
		Corn	NR	100% and 61 d	=P <sub>4</sub>	NR	NR	NR
Exp. 2		Whole cottonseed (4.3% fat)		100% and 63 d				
		Whole cottonseed (5.3% fat)		92% and 56 d				
		Whole cottonseed (6.3% fat)		100% and 57 d				
		Cottonseed meal	NR	86% and 54 d	=P <sub>4</sub>	NR	NR	NR
		Whole cottonseed (5.5% fat)		77% and 56 d				
Ryan et al. (1995)	28d	Whole cottonseed (8.3% fat)	NR	86% and 54 d				
		Grain sorghum	NR	53%	NR	NR	NR	NR
De Fries et al. (1998)	45d	Whole cottonseed		80%↑				
		Corn + soybean meal	58% w/L	NS	=P <sub>4</sub>	NR	NR	71%
Tjardes et al. (1998)	79d	Rice bran	80% w/L↑, ↑M and L					
		Corn	NR		NR	NR	NR	91%↑
Filley et al. (1999)	d 7–11	Yellow grease						75%
		1 L saline i.v.	NR					100%
		1 L 20% soybean oil i.v.	NR	133 d				75%
		1 L 50% dextrose i.v.	NR	130 d				80%
		0.5 L 20% soybean oil i.v.	NR	126 d				100%
Filley et al. (2000)	30d	Barley		120 d				
		Ca fatty acids		115 d				68%
Webb et al. (2001)	~48d	Corn + soybean meal	2.5 M↑	111 d	↑PGFM d-7 and 9	NR	72%	
		Rice bran	1.88 M=	54 d	NS for P <sub>4</sub> and PGFM	71%	76%	
		Corn + lasalocid	1.41 M↓	44 d↓		60%	60%	
		Rice bran + lasalocid	1.38 M↓	42 d↓		50%	50%	
Bottger et al. (2002)	90d	Corn + soybean meal	NR	52 d		73%	67%	
		High-linoleate safflower seeds		NS	NR	NS	100%	100%
Lloyd et al. (2002)	54d	High-oleate safflower seeds						92%
		Corn + inorganic minerals	NR	NR				100%
		Corn + chelated minerals						94%
		Ca fatty acids + inorganic minerals						88%
		Ca fatty acids + chelated minerals						92%
								90%

<sup>a</sup>Response variables with ↑ or ↓ beside them were greater or less than the value reported for the other treatment(s) within each study. NR = not reported; NS = not significant; P<sub>4</sub> = progesterone; E<sub>2</sub> = estradiol; PGFM = prostaglandin F<sub>2α</sub> metabolite; ovarian follicles may have been classified as small (S), medium (M), or large (L).

2.85 times greater in cows fed high-linoleate safflower seeds (9.7, 8.4, and 27.8 g/d for control, high-oleate, and high-linoleate, respectively). As expected, eicosapentaenoate was not increased by feeding high-linoleate safflower seeds. Feeding fat sources with relatively high linoleate content also increased plasma concentrations of linoleic acid (Whitney et al., 2000; Alexander et al., 2002). Linoleic acid, once desaturated and elongated to arachidonic acid, may serve as a precursor to  $\text{PGF}_{2\alpha}$  (Funston, 2004). Taken together, results from our laboratory lead to the conclusion that feeding supplements high in linoleic acid results in an increase in circulating concentrations of  $\text{PGF}_{2\alpha}$ . Elevated concentrations of  $\text{PGF}_{2\alpha}$  during d 4 to 9 of the estrous cycle not only caused luteolysis, but also had direct embryotoxic effects (Inskeep, 2004). Thus, increased production of  $\text{PGF}_{2\alpha}$  may explain the decrease in first-service conception rates in beef cows fed supplemental lipids high in linoleic acid during the postpartum period.

It is also likely that portions of the hypothalamo-hypophyseal-ovarian axis are affected by feeding high-linoleate safflower seeds to beef cows during the early postpartum period. Using primiparous beef cows, Scholljegerdes et al. (2003) reported supplementing with high-linoleate safflower seeds for the first 33 d postpartum increased ( $P = 0.02$ ) hypophyseal concentrations of FSH and tended ( $P = 0.14$ ) to decrease hypophyseal LH concentrations. These same cows had lower concentrations of IGF-I in the preoptic area and medial basal hypothalamus, but not in the stalk median eminence or anterior pituitary gland (Scholljegerdes et al., 2004b). Secretion and release of GnRH from the hypothalamus may be responsive to IGF-I (Figure 2). Because hypophyseal receptors for GnRH were similar between treatments, we speculate that greater concentrations of FSH and lower LH in the anterior pituitary glands of cows fed high-linoleate safflower seeds were related to decreased GnRH release from the hypothalamus. Decreased stimulation by GnRH could lead to increased storage of FSH and decreased synthesis of LH.

Changes in hypothalamic and hypophyseal hormones could reduce gonadotropic support of ovarian follicular growth and development; however, Scholljegerdes et al. (2003) observed that the distribution of follicles among the four size classifications outlined by Lucy et al. (1992), as well as average follicular size, did not differ between cows fed high-linoleate safflower seeds or control supplements. Despite similar weight change among cows fed the two dietary treatments, serum IGF-I concentrations were lower for cows fed high-linoleate safflower seeds (Scholljegerdes et al., 2004b). Webb et al. (2004) noted that follicular fluid IGF-I was mostly systemic in origin. Consequently, it was not surprising that follicular fluid concentrations of IGF-I were less for cows fed high-linoleate safflower seeds than cows fed the control supplement (Scholljegerdes et al., 2004b). Unpublished results from this experiment revealed that IGF-BP-1 in the follicular fluid also increased ( $P = 0.09$ ) in cows fed high-linoleate safflower seeds. In a

review of the literature, Keisler and Lucy (1996) noted that IGF-BP-1 is inhibitory to IGF-I action. An aberration in follicular fluid IGF-I action could ultimately impair follicular cell proliferation and survival to maturation (Quirk et al., 2004). Therefore, perturbations in the IGF-I system as a result of feeding high-linoleate safflower seeds may also contribute to decreased early reproductive events affecting beef cow reproduction.

## Conclusions

Although numerous reviews have unequivocally demonstrated that nutritional inputs affect reproduction, exact mechanisms by which nutrition mediates the reproductive process remain to be elucidated. The timely resumption of estrous cycles within a defined breeding season is a hallmark event that initially dictates whether a beef cow will produce a calf on an annual basis. Return to estrus is orchestrated via an integration of multiple signals within the hypothalamo-hypophyseal-ovarian axis. Energy balance, which is perceived by the reproductive axis as a variety of nutritionally induced cues, has a profound effect on the duration of postpartum anestrus. Evidence is also beginning to emerge that indicates other nutritional factors, such as lipids high in linoleic acid, influence reproduction by affecting critical components of the reproductive axis.

## Future Directions

Nutritional mediation of reproduction is extremely complex. Therefore, extrapolating results from investigations that focus on single mediators or systems involved with a specific reproductive event can lead to erroneous conclusions regarding ultimate reproductive success. This is not intended to imply that fundamental research designed to elucidate specific mechanisms that regulate unique aspects of reproduction is not essential, but rather that investigators should be encouraged to develop research protocols that permit individual components of models designed to discover nutrition  $\times$  reproduction interactions that can be integrated with physiological processes in a holistic manner. Such an approach for the beef cow will undoubtedly require strong collaborations among fundamental and applied reproductive biologists, ruminant nutritionists, as well as scientists in other fields to optimize reproduction and management of resources. Moreover, precautions need to be taken to ensure future investigations are not compromised or biased by associative rather than causative regulators of reproduction. For example, BCS at calving is an important predictor of length of the postpartum anestrus period, and as such, investigators have imposed poor nutritional regimens to induce negative energy balance prepartum to reduce BCS at calving. The underlying question one must ask then becomes, "Which is the determining factor: body energy reserves at parturition or prepartum energy balance,

or do these two factors interact?" From a practical perspective, BCS at calving serves as a functional indicator of energy balance; however, assessing BCS at calving alone could not be used to determine duration or magnitude of prepartum energy balance. Whether investigating nutritional mediators of reproduction or how nutritional inputs affect reproduction, scientists must be cognizant of the interactions among the nutrients and nutritional cues responsible for mediating reproduction.

### Implications

The exact mechanism by which nutrition mediates effects on reproduction remains an enigma because nutritional controls on beef cow reproduction are not mediated by a single nutrient, metabolite, or hormone. A multitude of factors must be considered to understand the complex coordination of the nutrition–reproduction interface. Feed managers should offer completely balanced rations to beef cows throughout late gestation and early lactation to prevent poor reproductive performance. Decisions to include specific dietary ingredients should be made on the basis of cost effectiveness to decrease the financial burden associated with maintaining sustainable beef cow production systems.

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