

# Can beef heifers and young postpartum cows be physiologically and nutritionally manipulated to optimize reproductive efficiency?

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## Abstract

Beef production efficiency from extensive rangeland systems is often compromised by negative impacts on reproduction in young cows and heifers due to the seasonal dynamics of forage quality and quantity coupled with the higher nutritional demands of these animals. Our goals are to strategically use biologically potent combinations of nutrients that relieve metabolic inefficiencies, alter the utilization of endogenous nutrients, and redirect nutrient partitioning in a manner that positively influences reproductive processes. These effects must be achieved with minimal input and labor costs in order to maintain economic viability. Specifically, the use of nutrients that alter glucose metabolism and spare endogenous protein depots is addressed here. The influence of these strategies on reproductive outcomes in heifers and young cows is discussed. A better understanding of the metabolic and physiological mediators of key reproductive events is mandatory for improving rangeland resource utilization and production efficiency of range cow-calf operations in harsh nutritional environments.

*Key Words: Supplementary Feeding, Reproductive Efficiency, Cows, Heifers*

## Introduction

Extended postpartum anestrus in young range cows and delayed heifer puberty are major impediments to biological and economic efficiency in range cow herds. Optimal use of native rangeland in the Great Plains, Arid Southwest, and Intermountain West requires use of fewer intensive inputs, including labor and capital, and increasing reliance on year-round grazing. Cow-calf producers operating under these constraints have a greater dependence on range vegetation and the loss of flexibility in nutritional management; thus, cattle become susceptible to nutrient fluctuations in diet quality by season and year.

Livestock inaccessibility due to extensive pasture area, varied topography, and inclement weather create labor and capital constraints that demand the application of simple and biologically potent nutritional strategies. Strategic supplementation becomes an applicable, if not essential, concept.

Success of management using restricted growth in heifers and weight loss before and after calving in young cows depends on periods of compensatory gain and(or) improved metabolic efficiency. Exposure to environmental stresses such as extreme weather conditions, reduced forage availability, and limited precipitation creates periods of nutritional stress. These stress periods increase maintenance energy requirements and are exacerbated by restricted caloric intake. Such uncontrolled factors, along with nutritional requirements for parturition, lactation, growth, and activity, create nutritional management challenges. A solution is to discover specific metabolic messengers that regulate key events that limit timely reproduction in young range beef cows. Detecting the pharmacological consequences of supplement ingredients and development of specific formulations that provide potent limiting intermediates or messengers is a goal for

nutrition and reproduction research in the western United States and other locations with similar environmental challenges.

## Undernutrition

In order to discover the limitations to reproduction and puberty in undernourished range beef cows or heifers, we must understand the physiology of undernutrition. An obvious solution would be to feed our way out of undernutrition. Recommendations suggest that cows (for best results) should be in a body condition score of 5 to 6 (scale of 1 to 9) at calving and breeding (Randel, 1990). Although this is a good goal, because cows with a body condition score of 6 are reproductively punctual and highly successful, the cost of achieving this body condition score in cows restricted to rangeland may increase purchased feed costs to an unprofitable level.

When cows or heifers are grazing dormant native range it can be assumed that diet quality is low, acetate is the major VFA produced via ruminal fermentation, and propionate (the preferred ruminant glucogenic substrate) is in inadequate supply. Ruminal microbial protein synthesis is minimal due to an inadequate supply of ruminal nitrogen, restricted DM intake, and slow fermentation rate of the diet, thus reducing the supply of metabolizable protein and potential glucose precursors to the animal. Concurrent with inadequate gluconeogenesis, depletion of oxaloacetate (OAA) occurs, which is a key intermediate required for gluconeogenesis (Salway et al., 1994) and acetate metabolism. The restricted supply of OAA diverts metabolism of acetate from ATP production to futile cycles increasing heat production, thus decreasing energetic efficiency while redirecting acetate carbon into ketone synthesis. This adjustment in metabolism

is attenuated by a decrease in intake, which reduces the supply of incoming acetate, and a reduction in the efficiency of energy metabolism as reflected by increases in serum  $\beta$ -hydroxybutyrate (Kaneko et al., 1989). Plasma glucose declines to a limited extent compared to other metabolites (Miner et al., 1990; Wiley et al., 1991), but it may not be highly indicative of the extent of undernutrition experienced by beef cows. Cow metabolism seems to be oriented to the maintenance of serum glucose concentrations above 48 mg/100 mL (Dhuyvetter et al., 1993). The magnitude of blood urea nitrogen elevation will exceed the decline in blood glucose when protein tissues are catabolized and amine groups are released during amino acid carbon utilization for gluconeogenesis or oxidative metabolism.

In response to negative energy balance (e.g., postpartum), growth hormone becomes elevated and stimulates tissue catabolism and gluconeogenesis, and insulin declines ( $< 0.2$  ng/mL; Tovar-Luna et al., 2000a), minimizing lipogenesis and glycolysis. Without the negative feedback of insulin, glucagon is released and stimulates gluconeogenesis, increasing weight loss. Insulin-like growth factor I (IGF-I) in the well-fed state is stimulated by growth hormone; however, this relationship with growth hormone becomes uncoupled during negative energy balance, and IGF-I is elevated only slightly, if at all (Downing et al., 1995). This sequence leads to a period of continued weight loss and most likely a suppression of reproductive function. The point at which weight loss is reversed has been recognized as the point at which metabolism becomes permissive for the initiation of events leading to estrus (Zurek et al., 1995). This is partially due to a reduction in growth hormone, increases in insulin and IGF-I, and the subsequent release of gonadotropins. In dairy cattle, Butler and Canfield (1989) determined that the time required for attainment of the weight loss nadir is an important predictor of resumption of estrous cyclicity. If these findings with dairy cattle can be extrapolated to range beef cows, then a fundamental management milestone might be to monitor and manipulate the nadir of postpartum weight loss as a means of improving reproductive success.

A variety of approaches to manipulate magnitude and duration of postpartum weight loss may exist; however, in the context of the constraints to nutritional management for range beef cattle, strategies that alter conventional ingredient formulations to achieve specific physiological results may be most applicable. One particular approach to reducing the slope or extent of the weight loss curve is to substitute a supplement rich (50% of the total CP) in ruminally undegradable intake protein (UIP) for a more traditional formulation (35% UIP) common to feeds similar to soybean meal. With the addition or substitution of 150 to 300 g of UIP  $\cdot$  animal<sup>-1</sup>  $\cdot$  d<sup>-1</sup>, cow weight loss and (or) the time until weight gain occurs is decreased (Wiley et al., 1991; Dhuyvetter et al., 1993; Triplett et al., 1995).

Weight loss includes utilization of body fat for oxidative metabolism and catabolism of protein tissues to supply amino acids for glucose production and oxidative metabolism. Utilization of amino acid carbon for glucose synthesis may be inefficient (Preston and Leng, 1987). The excessive loss of

of protein tissue may have severe consequences to animal metabolism and physiology. The importance of partitioning tissue utilization (to reduce protein catabolism) during weight loss is an unexplored concept that requires further examination.

Brendemuhl et al. (1989) illustrated this concept using postpartum sows fed four diets in a slaughter experiment. The diets supplied high energy + high protein, high energy + low protein, low energy + high protein, or low energy + low protein. The most pertinent findings involve the comparison of the sows fed high energy + low protein to those receiving the low energy + high protein diet. Although both groups of animals lost similar amounts of body weight, the type of tissue lost differed. Sows receiving the high energy + low protein diet had the greatest reduction in protein tissue loss, and those fed the low energy + high protein diet lost less protein tissue and more adipose tissue. In a previous study (Brendemuhl et al., 1987) with gilts, these authors observed similar trends in the apparent composition of body weight loss. More importantly, gilts fed the low energy and high protein diet returned to estrus in less time after weaning than the gilts fed the high energy and low protein diet, and they were similar to those fed the high energy and high protein diet. Therefore, in swine, sparing of endogenous protein at the expense of adipose tissue was a positive influence on reproductive success during negative energy balance.

Recommendations have been made concerning the negative influences of weight and body condition loss before calving and breeding on reproduction in the beef cow (Randel, 1990). Although body condition change is an indirect measure of the magnitude of adipose depot loss, it is positively correlated with return to estrus and pregnancy (Wettemann et al., 1982). The mechanism explaining how body fat participates in regulating reproduction has yet to be elucidated (Frisch, 1994). When using body condition or body weight changes to assess adipose depot loss, the associated alterations in protein tissue mass must be considered. As discussed previously, the composition of body weight loss may be altered by specific nutrient density of the diet. Furthermore, changes in the liver, gut, and other protein tissues may influence metabolic function and requirements (Burrin et al., 1990; Ryan et al., 1993) and may alter the relationship of nutrition and reproduction (Houghton et al., 1990).

A few studies with ruminants have demonstrated that body fat used during weight loss may be used to satisfy energy needed to restore or maintain body protein. Leng et al. (1978) used overly fat lambs and fed them a barley straw-based diet formulated to promote weight loss with or without 150 g of fish meal. A portion of the lambs were slaughtered at the initiation and termination of the study to evaluate body composition changes. As expected, the lambs fed only barley straw lost weight (both adipose and protein tissue). The group fed the small amount of fish meal maintained body weight. More importantly, these lambs changed in body composition, with adipose tissue decreasing and protein tissue increasing. Thus, energy released from mobilized body fat and protein supplied by fish meal were utilized to increase lean tissue accretion, although body weight did not change.

Because additional metabolizable protein was supplied by the fish meal, utilization of endogenous energy was improved and metabolic nutrient balance was achieved. Miner et al. (1990) fed pregnant, wintering range cows 454 g/d of soybean meal with or without 150 g/d of blood meal. Cows provided with the additional ruminally undegraded protein from blood meal reduced weight loss by 300/g d, but losses in body condition score were similar. Serratos-Corona (1998) fed lactating beef cows a buffalograss straw-based diet supplemented with increasing amounts of UIP and total CP (0, 155, 311, 466, and 602 g/d CP, 50% UIP). The results of this experiment demonstrated that as metabolizable protein increased in the diet, milk production and body weight loss also increased. However, nitrogen retention in the body increased simultaneously with these responses from -2 to 154 g/d. These results imply that body fat was mobilized for milk production while body protein was being replaced. From this study and others (Fattet et al., 1984; Chowdhury et al., 1990; Triplett et al., 1995), one could speculate that cows receiving additional protein during negative energy balance are more capable of coping with nutritional stresses, due to an improvement in the efficiency of body energy depot utilization and protection of endogenous protein stores. In order for supplemental protein to have such a dramatic effect on reducing weight loss, it must be influencing nutrient metabolism.

There are two important questions suggested by these studies: 1) Is the relationship between body condition score and reproduction linked to protein tissue mass? 2) If one type of tissue (i.e., fat vs protein) is more important to reproduction than another, is it possible through diet manipulation to target specific tissues for utilization when planned weight loss occurs?

### **Metabolic Limitations of Dormant Native Range Diets for Reproduction**

Delayed puberty or conception in range cattle may be due to a state of overall inadequate nutrition (Short et al., 1990) or possibly to the lack of important rate-limiting intermediates. Absorbed digestion and fermentation products are utilized in specific metabolic pathways. Acetate and butyrate are used for fatty acid synthesis and oxidative metabolism (production of ATP) and can account for 85 to 90% of the total VFA produced. Propionate, making up 15% or less of the total VFA from low-quality forage diets (Caton et al., 1988), is the preferred precursor for glucose synthesis in the ruminant (Brockman, 1990). Ninety percent or more of propionate may be metabolized through gluconeogenesis. Glucogenic amino acids of dietary or endogenous origin may serve as an important secondary source for glucose production when propionate is limiting or glucose demand is elevated (Overton et al., 1999).

Short and Adams (1988) suggested that glucose might serve as a principle mediator of nutrition and reproduction. This hypothesis is supported by the observation that ruminants experiencing nutritional stress are often reproductively compromised, as well as being deficient in glucose. Glucose absorption from the small intestine is minute and for all prac-

tical purposes does not exist with forage diets, and the ruminant's metabolism is directed to gluconeogenesis (van der Walt and Linnington, 1990). Therefore, the supply of glucose precursors becomes increasingly important to metabolic function and reproductive competence when diet quality is low. Acetate metabolism has been enhanced when the glucogenic potential of a roughage diet was increased (Cronje et al., 1991). This enhancement of acetate metabolism (decreased acetate half-life following an acetate infusion) has also been observed when increasing amounts of UIP were provided to ewes (Tovar-Luna et al., 2000a) or primiparous cows (Appeddu-Richards, 1999). When glucose status improves in the beef cow consuming low-quality roughage, overall energy metabolism is improved because acetate is metabolized at a faster rate. If glucose precursors are not available, potential metabolic energy from acetate is lost as heat, and the availability of metabolizable energy declines. Glucose is also required for the incorporation of acetate into long-chain fatty acids in adipose tissue or the mammary gland. Fourteen NADPH are needed to couple the reaction of eight acetyl-CoA (from acetate) to form the fatty acid palmitic acid. If glucose were used to provide all of the NADPH, then 4 mol of glucose would be oxidized to synthesize 1 mol of LCFA (89 g glucose for 100 g of LCFA). It is an enormous metabolic burden for a lactating range cow to synthesize this quantity of glucose to support milk production. Glucose is also required for the production of glycerol for triglyceride synthesis. Finally, lactose is fabricated from 2 mol of glucose as the sole precursor. These are important uses of and relatively large sinks for glucose in maintenance and lactation (estimated requirement of 450 g of glucose/d). Strategic feeding of glucose precursors or compounds that can spare glucose oxidation (such as triglycerides) should reduce the demand for glucose by the mammary gland, thereby sparing glucose for other uses, especially those involved with reproduction.

There is evidence that amino acids may be preferentially used for gluconeogenesis over protein synthetic purposes when glucose is deficient (Preston and Leng, 1987). The increased glucose need and limited supply of dietary precursors thus stimulates protein catabolism in the postpartum beef cow grazing dormant forage. The results of glucose inadequacy are therefore higher rates of body weight and endogenous protein loss. Although body weight loss may be acceptable, the compromises in metabolic efficiency due to inadequate glucose exacerbate the situation and reduce the efficacy of tissue and dietary product utilization. Provision of glucose precursors can have large effects on this system. Leng et al. (1978) fed four diets to growing wethers. The basal diet was formulated to support a small rate of gain ( $\cong$  100 g/d). The other three diets supplied either 80 g of glucose via abomasal infusion, additional protein in the form of fish meal (6% DM), or a combination of the glucose and protein treatments. The glucose infusion improved gain and feed efficiency compared to the control, demonstrating that glucose was limiting growth. The protein-supplemented wethers gained more and were more feed-efficient than the glucose-infused wethers, demonstrating that the protein sup-

plementation was capable of supplying at least the same amount of glucose as well as amino acids for protein accretion. The wethers fed the combination treatment experienced the greatest gain and the greatest feed efficiency, indicating that when the glucose demand is met by nutrients other than protein, more of the protein can be used for synthesis and improvement in animal efficiency. Extrapolation of these results to the situation of postpartum beef cows suggests that part of the observed reductions in postpartum weight loss with UIP supplements is due to the glucogenic potential of the UIP fed.

### Strategies to Alleviate Metabolic Insufficiency

An obvious solution to arrest weight loss in postpartum range cows or enhance gain in prepuberal heifers would be to feed 2.5 to 5 kg of a cereal grain or 5 kg of hay to substantially increase caloric intake and glucose precursor availability. With large herds and land areas, this approach becomes impractical and minimizes utilization of the rangeland forage resource. Feeding supplements formulated with ruminally degradable protein can result in increased acetate production, exacerbating the inefficiencies in animal metabolism due to imbalances in acetate and glucose. Such a strategy could result in increased microbial protein flow and might increase availability of glucose precursors. However, increasing ruminally undegradable nutrients will more predictably alter the composition of metabolizable nutrients.

Some interesting effects occur when ruminal escape nutrients are fed. Undegradable protein supplements stimulate a chronic elevation of serum insulin and a depression in growth hormone (Petersen et al., 1992). Insulin stimulates re-esterification of fatty acids by increasing uptake of glucose into adipose tissue and inhibits mobilization of fatty acids. By reducing circulating NEFA concentration, the glucose demand for acetyl CoA metabolism should decline and ketogenesis will be reduced. Unlike other tissues, nutrient uptake by the mammary gland is not regulated by insulin. Therefore, increased competition between maternal tissues and the mammary gland occurs when insulin increases in response to protein supplementation. By creating conditions in which milk production may decline slightly, the magnitude of negative energy balance of the dam is reduced (Hunter and Manger, 1988; Dhuyvetter et al., 1993). Concurrent with these effects is the reduction in growth hormone with a subsequent decrease in body tissue mobilization and weight loss and a reduction in the supply of nutrients for lactation. Tovar-Luna et al. (2000b) demonstrated this effect when they compared cows treated with exogenous insulin to those fed protein supplements. The insulin-treated and protein-supplemented cattle had similar serum insulin concentrations and milk production but different plasma glucose concentrations and daily gain (protein-supplemented cows gained more weight). Dhuyvetter et al. (1993) and Triplett et al. (1995) reported little or no effect of feeding higher amounts of protein to cows over 4 yr old, suggesting that sensitivity to UIP via insulin may decline with age. Similarly, Tovar-Luna et al. (2000a) demonstrated that older lactating ewes in negative

energy balance tend to be more insulin-resistant than younger ewes, based on responses to a glucose tolerance test.

Prolonged nutrient restriction reduces maintenance energy requirements (Ledger and Sayers, 1977). This reduction may be partially due to a decrease in visceral size (Ferrell et al., 1986) and metabolic rate (Drouillard et al., 1991). Visceral tissues may contribute as much as 30 to 55% of whole-body substrate oxidation (Eisemann and Nienaber, 1990). Freetly and Nienaber (1998) have observed general reductions in energy requirements (i.e., heat production) in nutrient-restricted cows. In developing Hereford heifers fed to gain at a modest rate, Burgwald-Balstad et al. (1999) found a negative linear response in gut weight and length in response to increasing intake of UIP (up to 300 g/d). The consequences of this reduction may be that heifers fed greater amounts of UIP have lower maintenance requirements due to lower gut mass, potentially improving efficiency of intake energy utilization and allowing for greater partitioning of metabolic energy to maternal tissues.

Metabolic signals that stimulate lipolysis include catecholamines (a stress response) and growth hormone. Gambill et al. (1994) and Serrato-Corona et al. (1996) have shown that feeding additional protein to lactating beef cows inhibits the release of free fatty acids in response to an exogenous challenge of epinephrine. This response may serve as a potential mechanism for reductions in weight loss occurring when higher UIP protein sources are fed. The sum of these factors is that cows are more resistant to weight loss and achieve the nadir of negative energy balance sooner (Hunter and Manger, 1988; Wiley et al., 1991; Dhuyvetter et al., 1993) when supplemented with UIP.

We have conducted a series of experiments to intensively evaluate metabolic and endocrine events associated with reproduction in postpartum beef cows. It is important to note that conditions exist in drylot trials that are not analogous to what the grazing female experiences. These include proximity of a calf to its dam, which often results in higher frequency of suckling episodes and elimination of selective grazing behavior when low-quality hay is used to simulate range conditions. Even with these limitations, the intensive studies have provided insight into responses to UIP supplementation.

To evaluate the effectiveness of UIP supplementation, with or without fat, under limited forage conditions an experiment was conducted (Albertini et al., 1996) with young, postpartum beef cows. In this study, cows were maintained on a very limited energy supply compared with NRC (1996) recommendations. Cows were fed the basal diet of hay at 1.8% of BW, and this level of hay was adjusted every week with cow BW (i.e., as cows lost BW, hay offered was decreased, or vice versa). Supplements ( $908 \text{ g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ ) consisted of control ( $363 \text{ g CP} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$  of which 115 g was UIP), UIP ( $504 \text{ g CP} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$  with 263 g of UIP) and UIP plus fat ( $504 \text{ g CP} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$  with 263 g of UIP plus  $78 \text{ g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$  of fat). Degradable intake protein was held constant at  $240 \text{ g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ . Results from this study showed that BW and backfat thickness of cows did not differ among treatments when energy was limit-

ing. The mean beginning and ending body weights in this trial (90 d) were 442 and 445 kg, respectively. Milk production in cows supplemented with either UIP or UIP with fat was greater than that of cows fed control supplements. Insulin concentrations were not affected by treatment in this study. These results may be due to the limited energy supplied to cows in the current study. No differences were observed among treatments for either area under the LH curve (AUC) or GnRH-induced LH release on d 20 or 38 postpartum.

The low energy intake (1.8% BW, 6% CP) was probably the most limiting factor influencing animal performance. Under the conditions of this study, limiting forage quantity and quality impaired positive effects of UIP supplementation previously observed. Use of supplements containing UIP with or without fat may not be the strategy to increase animal performance in those seasons of severe drought with poor quality and quantity of grass.

To ascertain the optimal level of UIP supplement for young postpartum females an additional experiment was conducted (Kane et al., 1998). Treatments consisted of three levels of UIP, fed every other day, wk 2 to 11 postpartum as follows: 1) low UIP (**L**: 908 g • cow<sup>-1</sup> • d<sup>-1</sup>; 36% CP, 108 g UIP), 2) mid UIP (**M**: 908 g • cow<sup>-1</sup> • d<sup>-1</sup>; 36% CP, 165 g UIP), and 3) high UIP (**H**: 908 g M + 243 g feather meal • cow<sup>-1</sup> • d<sup>-1</sup>; 47% CP, 335 g UIP). Cows were fed a basal diet (2% BW, as fed) of sudan grass hay (7.3% CP) to simulate late winter-early spring dormant forage conditions.

There were no differences in BW loss (mean BW loss 34 kg) among cows fed the three levels of UIP supplementation. In addition, no differences were noted among treatments in backfat and rumpfat. However, all cows lost backfat and rumpfat throughout the study. Milk components and yield were similar among treatments. Therefore, feeding UIP supplement at any of the three levels studied failed to alter weight loss and body condition loss in postpartum beef cows. The confinement conditions and number of suckling episodes may have precluded the detection of body composition changes.

There were no differences in BUN among treatments within week. Observations in postpartum dairy cows have indicated that UIP supplementation increased BUN and were associated with alterations in uterine pH on d 7 of the estrous cycle (Elrod and Butler, 1993); this has been implicated as a factor in impaired fertility with high-protein supplements. Uterine pH was not different on days supplement was offered compared to days on which it was not offered, either within or among treatments. Pituitary LH secretion in response to the GnRH, measured by the AUC, was enhanced in their H treatment. The increase in LH secretion in cows consuming UIP may reduce the time required for the resumption of postpartum ovarian activity. Resumption of pituitary function postpartum has been implicated as a primary indication of escape from postpartum anestrus (Nett, 1987; Schillo, 1992).

Although UIP supplementation has been reported to improve reproductive efficiency and minimize changes in body condition in postpartum beef cows on forage of low quantity and quality, in the above study varying levels of UIP supple-

ment did not decrease BW or body condition loss. In addition, although BUN tended to increase with increasing UIP supplementation, there was no accompanying alteration in uterine environment, even at high UIP. It is unclear how high UIP levels impair fertility as previously reported. However, changes in pituitary endocrine responsiveness, specifically LH, in cows fed high UIP may contribute to a shorter postpartum anestrus (Schillo, 1992; Jolly et al., 1995; Keisler and Lucy, 1996). Therefore, effects of UIP supplementation on reproductive traits may be mediated at the level of the level of the hypothalamus and/or anterior pituitary and seem to occur independent of body composition.

Due to the previously mentioned effects of UIP on insulin secretion we investigated the effects of UIP and exogenous insulin on endocrine events during the postpartum period in a 2 × 2 factorial arrangement of treatments (Bays et al., 1994). Crossbred postpartum cows (average of 29 ± 9 d postpartum) were used to evaluate effects of exogenous insulin and/or UIP on basal and GnRH-induced release of LH and FSH. Cows were fed either 600 g/d of supplemental crude protein (**S**), of which 300 g was UIP and/or 60 IU of exogenous daily insulin (**I**) or no supplement (**NS**) and/or no insulin (**NI**). All cows were fed a basal diet of mature buffalo grass hay (6% CP) that would mimic early spring forage conditions in the western United States. Cows fed **S** were restricted to 2% (as fed basis) of BW of hay, and **NS** cows were allowed to consume 2.3% BW to provide isoenergetic diets to account for the energy contribution of the supplement.

Cows receiving **S** had mean LH concentrations during the 6-h intensive sampling period on d 10 of supplementation similar to those of **NS** cows. Additionally, LH AUC before GnRH treatment was similar in **S**-treated and **NS**-treated cows. No difference was noted in mean LH concentration in response to insulin when compared with controls during the 360-min sampling period. Likewise, insulin had no effect on LH AUC before GnRH administration or after GnRH. However, insulin- and supplement-treated animals had higher ( $P < .05$ ) mean FSH concentrations than animals on the other treatments. Area under the curve for FSH was elevated ( $P < .05$ ) in insulin- and supplement-treated cows (442 ± 75 AUC units) compared with all other treatments (187 ± 60, 129 ± 45, and 184 ± 60 for controls, insulin, and supplement, respectively). Cows in both supplement and insulin treatments had numerically greater FSH concentrations before the GnRH challenge (0 to 120 min) compared with controls. Increased basal FSH secretion in cows consuming UIP may provide a logical explanation for the decreases in postpartum intervals previously described. However, this response may have resulted from increased insulin concentrations in supplement-treated cows. The increased FSH concentrations found in the supplement- and insulin-treated animals may be partially explained by the increased insulin concentrations; however, factors resulting in the additive effects of UIP were not identified in this study. Days to first estrus was shorter for supplemented cows (72 d) than for control cows (110 d), supporting the ability of UIP supplementation to hasten ovarian activity.

Recent studies (Kane et al., 1999) suggest that a potential mechanism involved in increased FSH secretion is enhanced mRNA for FSH in UIP-fed heifers. At present the precise mechanisms involved are not known, yet we speculate that insulin or IGF may play a role.

Collectively, the studies indicate potential for UIP supplementation to enhance pituitary release of LH and FSH. The ability of the postpartum cow to cycle ultimately is dependent on hypothalamic-hypophyseal function. It is not clear how UIP supplementation alters gonadotropin synthesis or secretion. It is plausible that these insulinogenic actions of UIP are monitored by the hypothalamic-hypophyseal axis and perceived as indicative of a positive nutritional state, resulting in increased LH and FSH. The increased LH and FSH release would stimulate folliculogenesis and resumption of postpartum ovarian activity. Preliminary data from our laboratory have demonstrated that UIP supplementation increased the mRNA for FSH $\beta$  subunit, which goes along with the findings of Bays et al. (1994), who noted that FSH secretion was greatest in UIP-supplemented postpartum cows.

#### Responses by Young Range Cows to Specific Nutrient Supplementation

Miner et al. (1990) fed .45 kg/d of a soybean meal-based 40% CP supplement during 2 yr to pregnant cows grazing native winter range in southwestern Montana with additions of 150 g/d of blood meal. In a winter when cows lost weight they reported that a soybean meal-based supplement reduced winter weight loss by 50%; however, with the addition of blood meal weight loss was negligible. These dramatic effects encouraged Wiley et al. (1991) to feed similar supplements containing UIP to postpartum 2-yr-old cows that had been fed for maintenance or below maintenance during the winter. They found that regardless of the prepartum nutrition cows initiated weight gain and pregnancy sooner when fed additional UIP. Hunter and Manger (1988) had reported similar results with treated casein fed as a protein supplement. These studies suggested that protein-mediated reductions in weight loss were associated with increases in serum insulin. Elevation in insulin is suggested to repartition nutrients to maintenance or replacement of body tissue (as discussed above) and act synergistically with gonadotropins and ovarian function.

Dietary protein has been shown to increase serum insulin concentrations depending on the type and combinations of protein fed to yearling ewes (Petersen et al., 1992). Dhuyvetter (1993) demonstrated with 2-yr-old cows that exogenous insulin reduced milk production. These two studies interpreted together support the concept that certain types of protein supplements can stimulate insulin elevation and redirect nutrient use. In order to test the value of these findings, a series of experiments have been conducted at the Corona Range and Livestock Research Center in central New Mexico. The general design has used 2-yr-old cows grazing native winter range. They are individually fed supplements that contain equal amounts of ruminally degradable intake protein

(**DIP**) and vary in UIP content and are fed only after calving (March 1) until breeding (May 10) for 60 to 100 d, depending on calving date and rainfall. Cows average less than a body condition 4 at breeding and weigh less than 425 kg at calving. In the fall, after weaning, they will have a mean body condition score of 4.5. The amount of supplement fed is dictated by cost. Our goal is to spend less than \$30 • cow<sup>-1</sup> • yr<sup>-1</sup> in total purchased feed cost. Usually cows are individually fed supplements twice per week and rotate among three pastures (320 ha each) from calving to the end of the breeding season.

Appeddu-Richards (1999) reported a study in which 2-yr-old cows were supplemented after calving with 1,136 g of supplement per day. Supplements were low protein (182 g CP, 128 g DIP, 54 g UIP; **LP**), moderate protein (477 g CP, 344 g DIP, 143 g UIP; **MP**), and high protein (613 g CP, 307 g DIP, 306 g UIP; **HP**). Body condition scores in February (prepartum) ranged from 4.6 for LP to 5.0 for MP; by breeding in May they ranged from 4.3 to 4.4, and they were 4.8 to 5 at weaning in October. Cow and calf body weight change was unaffected by type of supplement fed, although all cows started to gain weight by 63 to 84 d postpartum. Cows produced 1,070, 1,128, or 1,099 g ( $\pm$  181) of milk per 4 h when fed LP, MP, or HP, respectively. Partially through the 72-d breeding season, on June 11, 92% of the cows fed HP had exhibited luteal activity, whereas only 67 and 83% of the cows fed MP and LP had cycled ( $P < .11$ ). Average calving dates the following year were March 7, 6, and 5, and calving rates were 100, 92, and 92% for LP, MP, and HP, respectively. The type of protein supplement fed had little effect on important economic traits, although the HP supplement tended ( $P < .14$ ) to be used more efficiently as measured by grams of gain per gram of intake (0.21, 0.17, and 0.23 for LP, MP, and HP, respectively). The cost of supplementation per cow varied from \$15.40 to \$19.00 to \$23.30 ( $P < .01$ ) for LP, MP, and HP, respectively.

In a subsequent study, Appeddu-Richards (1999) fed three supplements that were slightly different from those in the previous experiment. An unsupplemented group was used as a negative control, because the previous study did not definitively demonstrate that supplementation was required. The quantity of supplement (751 g/d) was reduced because there had been previous feed refusals. The three treatments consisted of 1) no supplement (**NS**); 2) low protein 233 g CP, 181 g DIP, 52 g UIP (**LP**), and 3) moderate protein 405 g CP, 203 g DIP, 202 g UIP (**MP**). Body condition scores ranged from 4.3 to 4.5 in April (immediately postpartum) to 3.3, 3.8, and 3.8 for NS, LP, and MP, respectively, in June (during breeding) and were 4.2, 4.4, and 4.5 at weaning (NS, LP, and MP, respectively). Cows calving after March 12 continued to lose weight until June 30, when precipitation began to improve forage quality (45 d later than the previous year). Cows fed MP lost less ( $P < .01$ ) weight than the LP- and NS-treated cows, which had a similar amount of weight loss. Milk production was 616, 706, and 885 ( $\pm$  94) g per 4 h for NS, LP, and MP, respectively, demonstrating that the additional nutrients from the supplements were diverted to milk production rather than maternal tissues. However, cows

fed MP lost less weight and produced more milk. Calves from protein-supplemented cows gained at a faster rate ( $P < .03$ ), but not as fast as might be anticipated because forage quality was limiting. On June 10, 36, 43, and 47% of the NS, LP, and MP cows had initiated estrous cycles during the 77-d breeding season. Average calving dates the following year were March 23, 24, and 20, and calving rates were 100, 100, and 93.3% for NS-, LP-, and MP-treated cows, respectively. The cost of supplementation was \$11.00 and \$14.10 per cow ( $P < .01$ ) for those fed LP or MP. Due to drought conditions, all cows received .9 kg/d of a low-protein supplement during the first 30 d of the breeding season at a cost of \$4.50 per cow. In conclusion from this study, the MP supplement was used more efficiently for reduction of weight loss from April to June (-.57 and -.26 g daily weight loss per gram of supplement consumed for LP- and MP-fed cows).

In a third study, Knox et al. (1998) supplied two supplements fed at a rate of  $908 \text{ g} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ . Both supplements were formulated to contain 36% CP but contained differing amounts of UIP, either 212 g DIP plus 114 g UIP (low UIP) or 163 g DIP plus 163 g UIP (moderate UIP) and were fed from March 4 to May 12. Average body condition scores remained below 4 until July, with both groups being similar. The cows in both groups lost weight until May. Milk production (grams per 4 h) and calf weaning weights (kg) were 1,033 or 1,004 ( $\pm 133$ ) and 230 or 233 kg for low UIP- and moderate UIP-supplemented cows, respectively. After calving, the low- and moderate-UIP treated-cows required an average of 101 or 99 d until the onset of estrus, respectively. Fall pregnancy rates from the 63-d breeding season were affected by the type of supplement fed ( $P < .11$ ). Of the cows fed low UIP, 73% were pregnant, and of those that received moderate UIP 91% were pregnant. The cost of supplementation was \$24.44 and \$25.00 for low UIP and moderate UIP.

In these three studies, conducted in sequential years, the cost of supplementation ranged from \$15.40 to \$25.00 per cow with seven out of eight treatment groups achieving a 90% or better pregnancy or subsequent calving rates. Five of the eight treatment groups entered the breeding season with an average body condition score below 4. In general, any of the supplementation treatments were acceptable in regard to cost and reproductive performance. However, these studies do expose some advantages to utilizing greater UIP in protein supplements. These three experiments suggest that a nutrient plane (i.e., forage quality)  $\times$  protein source interaction may exist. When energy intake was limiting (as demonstrated by late June initiation of weight gain in experiment 2), the supplemental UIP was utilized to increase milk production without increasing weight loss, and calf gain was improved with no improvement in any aspect associated with reproduction. If energy is adequate (as demonstrated by weight gain occurring before May 15 in Exp. 1 and 3), it seems that a tendency to improve reproduction exists, as shown by earlier estrous cyclicity in Exp. 1 and higher pregnancy rates in Exp. 3.

## Fats and the Postpartum Beef Female

Numerous studies have evaluated the relationships between serum concentrations of cholesterol, the precursor for steroids. Collectively, these studies provide evidence suggesting that diets containing supplemental fat increase serum concentrations of cholesterol, thereby enhancing the delivery of substrate for synthesis of progesterone. The resulting increase in luteal progesterone synthesis and secretion occurs by decreasing the disappearance rate of progesterone, increasing amounts of luteal lipid, or by enhancing the life span of corpora lutea (Hawkins et al., 1995; Williams, 1996, 1998).

Different sources of fat alter ovarian functions differently. Studies using fat supplements derived from plant products (e.g., sunflower seed, cotton seed, or soybean oil) have shown that the onset of postpartum ovarian activity was shortened, the recruitment of medium-sized (4 to 9.9 mm) populations of ovarian follicles was enhanced, and metabolic hormones were different in postpartum cows of various body conditions (Talavera et al., 1985; Wehrman et al., 1991; Ryan et al., 1992, 1994, 1995). Moreover, studies that used calcium soaps of fatty acids (i.e., Megalac; Church & Dwight Co.) as supplements reported an increase in the number of large follicles (10 to 15 mm) and an increase in mean serum concentration of LH, but differences in the postpartum interval were not detected (Hightshoe et al., 1991; Hawkins et al., 1995).

Thomas and Williams (1996) and Thomas et al. (1997) designed a series of studies to determine effects of different sources of fats (i.e., differing fatty acid composition) on metabolism and reproductive processes. To summarize the results of these studies, all fat sources (animal tallow, soybean oil, and fish oil) were cholesterologenic; however, these fat sources differentially influenced serum concentrations of metabolic hormones and follicular growth patterns when fed on an isocaloric and isonitrogenous basis relative to a control diet. More specifically, soybean oil, which is rich in linoleic acid, produced abrupt changes in serum concentrations of insulin and in medium-sized follicle populations after only 3 wk of feeding. These effects were maximal after 7 wk of feeding relative to the diets that contained both saturated fats (i.e., animal tallow) and highly polyunsaturated fats (i.e., fish oil). All of these fat sources yielded similar changes in serum concentrations of growth hormone and follicular fluid IGF-I relative to the control diet. The work that has been published to date (Miner and Peterson, 1989; Miner et al., 1990; Lam-moglia et al., 1997; Oldick et al., 1997; Staples et al., 1998) suggests that most fat supplements can alter metabolism and subsequently influence luteal progesterone synthesis and secretion and follicular growth. However, it seems that fat sources that contain high percentages of linoleic acid, such as in plant oils, seem to yield the most beneficial influence on metabolic and reproductive traits.

Palmquist (1976) suggested that a ruminant's diet should contain less than 5% unprotected fat and less than 10% protected fat. In the studies reviewed by Williams (1996, 1998) in which fat was added to the diet to evaluate metabolic and

reproductive alterations, consumption of polyunsaturated fat sources fed at a level of 4% or greater of DM intake was effective at shifting metabolic hormones to influence reproductive traits. This was also the conclusion from a fat consumption experiment in which levels of polyunsaturated fat intake of 4.21, 2.87, and 1.41% were compared (Stanko et al., 1997). Reports of these types of incremental intake or titration studies with other fat sources targeted to enhance reproductive performance are limited at this time. Also, reports evaluating the influence of the fat on actual cow-herd performance is limited. Wehrman et al. (1991) reported that cows supplemented with whole cottonseed for 1 mo before a breeding season exhibited greater luteal activity than cows consuming isocaloric-isonitrogenous control supplements (62 vs 44%). These data are supported by the recent work of De Fries et al. (1998) in which Brahman cows supplemented with rice bran tended to have higher pregnancy rates (94.1 vs 71.4%) and enhanced calf weight gain relative to cows supplemented with isocaloric and isonitrogenous control.

Two studies have been conducted with fat formulated in range supplements supplied to 2-yr-old postpartum cows. In both studies a processed fat, either Megalac or Alifet, was fed because each can be incorporated into manufactured supplements. The first study was conducted in the Chihuahuan desert in southern New Mexico at the USDA Jornada Experimental Range (Gambill et al., 1995) with self-fed molasses blocks formulated with 10% CP (**LP**), 10% CP and 10% added fat (**F**), or 27% CP with 60% UIP (**HP**). Calving started February 22. Cows began to gain weight in April; the weight gain was 4, 26, and 37 kg ( $P < .1$ ) from April 15 to June 15 for cows fed LP, F, and HP, respectively. Body condition scores were 4.6 prior to calving and in June decreased to 4.2, 4.2, and 4.5 ( $P < .1$ ) for LP, F, and HP, respectively. Calf body weights were similar on June 15 and at weaning. Pregnancy rates in the fall were improved by F (83%) supplementation compared to LP (76%) and HP (66%). Appeddu-Richards (1999) fed Alifet in protein supplement to 2-yr-old cows at the Corona Range and Livestock Center and found no changes in reproductive measurements. They did show nearly a 1-kg increase in milk production and an increase in cow weight loss that was realized as a 15-kg increase in calf weaning weight. A follow-up study was conducted by Serrato-Corona (1998), who fed 100 g of tallow in 908 g of a molasses-based supplement for 30 d to midlactation range cows. The addition of tallow increased ( $P < .1$ ) milk production 800 g/d compared to that of cows receiving the same mix without tallow added.

### Summary and Recommendations

Metabolically, reproduction in females might best be considered a luxury event. This implies that reproduction occurs only when life-supporting metabolism is maintained, so that additional nutrients can be diverted toward reproductive processes. Factors related to nutritional involvement of ovulation, age at first estrus, and duration of postpartum anestrus interval have been thoroughly researched. These data indicate the importance of energy and protein in estab-

lishing and maintaining ovarian events and pregnancy. However, in the western United States the nutrient needs of young females are seldom, if ever, achieved without supplementation.

### Implications

Supplementing conservative amounts of undegradable intake protein to heifers and young range beef cows may initiate alterations in metabolism. A reduction in weight loss or slight improvements in winter gains can be anticipated. These responses are partially due to enhanced energetic efficiency. Metabolic alterations enhance the glucose pool, which positively affects utilization of acetate, increases serum insulin concentrations, reduces responsiveness from signals that initiate lipolysis, and partitions body nutrient utilization to reduce maintenance requirements and spare protein tissue. This series of metabolic changes allows postpartum cows to lose less weight, or developing heifers to gain slightly more weight, which may result in earlier pregnancy and greater conception rates due to earlier initiation of the release of gonadotropins. In a harsh environment, the sum of these changes might allow cows in marginal body condition or underdeveloped heifers to become pregnant sooner.

### Literature Cited

- Albertini, H. L., D. E. Hawkins, M. K. Petersen, D. M. Hallford, T. T. Ross, R. A. Renner, K. K. Kane, and L. A. Appeddu. 1996. Undegradable intake protein (UIP) and fat on reproductive and endocrine function of young beef cows. *Proc. West. Sect. Am. Soc. of Anim. Sci.* 47:197-199.
- Appeddu-Richards, L. 1999. Utilization of undegradable intake protein in young range beef cows and ewes for modification of metabolism, weight loss or reproduction. Ph. D. dissertation. New Mexico State Univ., Las Cruces.
- Bays, T. R., D. E. Hawkins, M. K. Petersen, I. Tovar, and D. M. Hallford. 1994. Protein and exogenous insulin in postpartum beef cows. 1. Effects on metabolic hormones and pituitary stores of LH and FSH. *Proc. West. Sect. Am. Soc. of Anim. Sci.* 45:263-265.
- Brendemuhl, J. H., A. J. Lewis, and E. R. Peo, Jr. 1987. Effect of protein and energy intake by primiparous sows during lactation on sow and litter performance and sow serum thyroxine and urea concentrations. *J. Anim. Sci.* 64:1060-1069.
- Brendemuhl, J. H., A. J. Lewis, and E. R. Peo, Jr. 1989. Influence of energy and protein intake during lactation on body composition of primiparous sows. *J. Anim. Sci.* 67:1478-1488.
- Brockman, R.P. 1990. Effect of insulin on the utilization of propionate in gluconeogenesis in sheep. *Br. J. Nutr.* 64:95-101.
- Butler, W. R., and R. W. Canfield. 1989. Interrelationships between energy balance and postpartum reproduction. In: *Proc. Cornell Nutrition Conf. for Feed Manufacturers*, Ithaca, NY. pp 66-74.
- Burgwald-Balstad, L. A., C. R. Krehbiel, G. D. Pulsipher, M. K. Petersen, K. K. Kane, D. E. Hawkins, B. M. Capitan, S. A. Soto-Navarro, S. E. Sawyer, and R. C. Waterman. 1999. Effect of increasing undegradable intake protein on visceral organ mass, digesta pH and enzyme activity in heifers fed sudan grass hay. *Proc. West. Sect. Am. Soc. Anim. Sci.* 50:280-284.

- Burrin, D. G., C. L. Ferrell, R. A. Britton, and M. Bauer. 1990. Level of nutrition and visceral organ size and metabolic activity in sheep. *Br. J. Nutr.* 64:439-448.
- Caton, J. S., A. S. Freeman, and M. L. Galyean. 1988. Influence of protein supplementation on forage intake, in situ forage disappearance, ruminal fermentation, and digesta passage rates in steers grazing dormant blue grama rangeland. *J. Anim. Sci.* 66:2262-2271.
- Chowdhury, S. A., E. R. Orskov, and N. A. MacLeod. 1990. Protein utilization during energy undernutrition in steers. *Proc. Nutr. Soc.* 49(3):208 (Abstr.).
- Cronje, P.B., J.V. Nolan, and R. A. Leng. 1991. Acetate clearance rates as a potential index of the availability of glucogenic precursors in ruminants fed on roughage based diets. *Br. J. Nutr.* 66:301-312.
- De Fries, C. A., D. A. Neuendorff, and R. D. Randel. 1998. Fat supplementation influences postpartum reproductive performance in Brahman cows. *J. Anim. Sci.* 76:864-870.
- Downing, J. A., J. Joss, P. Connell, and R. J. Scaramuzzi. 1995. Ovulation rate and the concentrations of gonadotropic and metabolic hormones in ewes fed lupin grain. *J. Reprod. Fertil.* 103:137-145.
- Dhuyvetter, D. V. 1993. Exogenous insulin effects on reproduction and nutrient partitioning in postpartum beef cows and effects of methionine or natural protein on digestion for cows fed a low quality forage. Ph.D. dissertation. New Mexico State Univ., Las Cruces.
- Dhuyvetter, D. V., M. K. Petersen, R. P. Anstotegui, 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.
- Drouillard, J.S., T.J. Klopfenstein, R. A. Britton, M. L. Bauer, S. M. Gramlich, T. J. Wester, and C. L. Ferrell. 1991. Growth, body composition, and visceral organ mass and metabolism in lambs during and after metabolizable protein or net energy restrictions. *J. Anim. Sci.* 69:3357-3375.
- Eisemann, J. H., and J. A. Nienaber. 1990. Tissue and whole body oxygen uptake in fed and fasted steers. *Br. J. Nutr.* 64:399-411.
- Elrod, C. C., and W. R. Butler. 1993. Reduction of fertility and alteration of uterine pH in heifers fed excess ruminally degradable protein. *J. Dairy Sci.* 71:694-701.
- Fattet, I., F. D. D. Hovell, E. R. Orskov, D. J. Kyle, K. Pennie, and R. I. Smart. 1984. Undernutrition in sheep. The effect of supplementation with protein on protein accretion. *Br. J. Nutr.* 52:561-574.
- Ferrell, C. L., L. J. Koong, and J. A. Nienaber. 1986. Effect of previous nutrition on body composition and maintenance energy costs of growing lambs. *Br. J. Nutr.* 56:595-605.
- Freetly, H. C., and J. A. Nienaber. 1998. Efficiency of energy and nitrogen loss and gain in mature cows. *J. Anim. Sci.* 76:896-905.
- Frisch, R. E. 1994. The right weight: body fat, menarche and fertility. *Proc. Nutr. Soc.* 53:113-129.
- Gambill, M. D., M. K. Petersen, D. V. Dhuyvetter, M. Ward, D. M. Hallford, and J. D. Wallace. 1994. Abomasal nutrient flow in postpartum beef cows receiving different sources and quality of dietary protein. *Proc. West. Sect. Am. Soc. Anim. Sci.* 45:133-136.
- Gambill, D. M., M. K. Petersen, D. E. Hawkins, I. Tovar-Luna, J. S. Serrato-Corona, D. Dunlap, and K. M. Havstad. 1995. Postpartum anestrus and fall pregnancy in two year old range cows supplemented with protein and fat. *J. Anim. Sci.* 73(Suppl. 1):255 (Abstr.).
- Hawkins, D. E., K. D. Niswender, G. M. Oss, C. L. Moeller, K. G. Odde, H. R. Sawyer, and G. D. Niswender. 1995. An increase in serum lipids increases luteal lipid content and alters the disappearance rate of progesterone in cows. *J. Anim. Sci.* 73:541-545.
- Hightshoe, R. B., R. C. Cochran, L. R. Corah, G. H. Kiracofe, D. L. Harmon, and R. C. Perry. 1991. Effects of calcium soaps of fatty acids on postpartum reproductive function in beef cows. *J. Anim. Sci.* 69:4097-4103.
- Houghton, P. L., R. P. Lemenager, L. A. Horstman, K. S. Hendrix, and G. E. Moss. 1990. Effects of body composition, pre- and postpartum energy level and early weaning on reproductive performance of beef cows and preweaning calf gain. *J. Anim. Sci.* 68:1438-1446.
- Hunter, R. A., and T. Magner. 1988. The effects of formaldehyde-treated casein on the partitioning of nutrients between cow and calf in lactating *Bos Indicus* × *Bos taurus* heifers fed a roughage diet. *Aust. J. Agric. Res.* 39:1151-1162.
- Jolly, P. D., S. McDougall, L. A. Fitzpatrick, K. L. Macmillan, and K.W. Entwistle. 1995. Physiological effects of undernutrition on postpartum anoestrus in cows. *J. Reprod. Fertil.* 49:477-492.
- Kane, K. K., K. W. Creighton, A. M. Encinias, D. E. Hawkins, M. K. Petersen, D. M. Hallford, and T. T. Ross. 1998. Effects of varying levels of undegradable intake protein on endocrine and metabolic function of postpartum beef cows. *Proc. West. Sect. Am. Soc. Anim. Sci.* 49:193-196.
- Kane, K. K., G. D. Pulsipher, L. A. Balstad, C. R. Krehbiel, M. G. Thomas, D. D. Denniston, B. J. Gardner, M. K. Petersen, D. M. Hallford and D. E. Hawkins. 1999. Effects of increasing levels of undegradable intake protein (UIP) on metabolic and endocrine factors in cycling beef heifers. *Proc. West. Sect. Am. Soc. Anim. Sci.* 50:214-217.
- Kaneko, J. J. 1989. Carbohydrate metabolism and its disease. In: J. J. Kaneko (ed.) *Clinical Biochemistry of Domestic Animals*. Academic Press, San Diego, CA.
- Keisler, D. H., and M. C. Lucy. 1996. Perception and interpretation of the effects of undernutrition on reproduction. *J. Anim. Sci.* 74 (Suppl. 3):1-17.
- Knox, L. A. 1998. The response of beef cattle grazing native rangeland to management decisions. M.S. thesis. New Mexico State Univ., Las Cruces.
- Lammoglia, M. A., S. T. Willard, D. M. Hallford, and R. D. Randel. 1997. Effects of dietary fat on follicular development and circulating concentrations of lipids, insulin, progesterone, estradiol-17 $\beta$ , 13,14-dihydro-15-keto-prostaglandin F<sub>2a</sub>, and growth hormone in estrous cyclic Brahman cows. *J. Anim. Sci.* 75:1591-1600.
- Ledger, H. P., and A. R. Sayers. 1977. The utilization of dietary energy by steers during periods of restricted food intake and subsequent realimentation. *J. Agric. Sci.* 88:11-26.
- Leng, R. A., S. Economides, and F. M. Ball. 1978. The effects on growth supplying glucose continuously into the duodenum of lambs on low protein diets. *Proc. Aust. Soc. Anim. Prod.* 12:134-135.
- Miner J. L., and M. K. Petersen. 1989. The effects of ruminal escape protein or fat on ruminal characteristics of pregnant winter-grazing beef cows. *J. Anim. Sci.* 67:2782-2791.
- 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.
- Nett, T. M. 1987. Function of the hypothalamic-hypophyseal axis during the post-partum period in ewes and cows. *J. Reprod. Fertil. Suppl.* 34:201-213.

- NRC. 1996. Nutrient Requirements of Beef Cattle. 7th ed. National Academy Press, Washington, DC.
- Oldick, B. S., C. R. Staples, W. W. Thatcher, and P. Gyawu. 1997. Abomasal infusion of glucose and fat - effect on digestion, production, and ovarian and uterine function in cows. *J. Dairy Sci.* 80:1315-1328.
- Overton, T. R., J. K. Drackley, C. J. Ottemann-Abbamonte, A. D. Beaulieu, L. S. Emmert, and J. H. Clark. 1999. Substrate utilization for hepatic gluconeogenesis is altered by increased glucose demand in ruminants. *J. Anim. Sci.* 77:1940-1951.
- Palmquist, D. L. 1976. A kinetic concept of lipid transport in ruminants: A review. *J. Dairy Sci.* 59:355-363.
- Petersen, M. K., D. M. Hallford, D. V. Dhuyvetter, D. Gambill, M. Ward, J. Cambell, E. Perez-Eugua, J. Rubio, and J. D. Wallace. 1992. The effects of supplemental feather, blood and/or cottonseed meal on metabolic hormones and serum metabolites in ewe lambs fed blue grama hay. *Proc. West. Sect. Am. Soc. Anim. Sci.* 43:560-654.
- Preston, T. R., and R. A. Leng. 1987. Matching Ruminant Production Systems with Available Resources in the Tropics and Subtropics. Penambul Books, Armidale, New South Wales, Australia.
- Randel, R. D. 1990. Nutrition and postpartum rebreeding in cattle. *J. Anim. Sci.* 68:853-862.
- Ryan, D. P., B. Bao, M. K. Griffith, and G. L. Williams. 1995. Metabolic and luteal sequelae to heightened dietary fat intake in undernourished, anestrus beef cows induced to ovulate. *J. Anim. Sci.* 2086-2093.
- Ryan, D. P., R. A. Spoon, M. K. Griffith, and G. L. Williams. 1994. Ovarian follicular recruitment, granulosa cell steroidogenic potential, and growth hormone/insulin-like growth factor-I relationships in beef cows consuming high lipid diets: Effects of graded differences in body condition maintained during the periparturition. *Domest. Anim. Endocrinol.* 11:161-174.
- Ryan, D. P., R. A. Spoon, and G. L. Williams. 1992. Ovarian follicular characteristics, embryo recovery, and embryo viability in heifers fed high-fat diets and treated with follicle-stimulating hormone. *J. Anim. Sci.* 70:3505-3513.
- Ryan, W. J., I. H. Williams, and R. J. Moir. 1993. Compensatory growth in sheep and cattle. II. Changes in body composition and tissue weights. *Aust. J. Agric. Res.* 44:1623-1633.
- Salway, J. G. 1994. Metabolism at a glance. Blackwell Science Ltd., Cambridge, MA.
- Schillo, K. K. 1992. Effects of dietary energy on control of luteinizing hormone secretion in cattle and sheep. *J. Anim. Sci.* 70:1271-1282.
- Serrato-Corona. 1998. Supplemental undegradable intake protein and fat effects on blood metabolites, fatty tissue mobilization, apparent digestibility, nitrogen retention and milk production in beef cows fed low quality forages. Ph.D. dissertation. New Mexico State Univ., Las Cruces.
- Serrato-Corona, J. S., I. Tovar-Luna, L. A. Appeddu, M. K. Petersen, H. Albertini, J. E. Sawyer, and A. Gomez. 1996. Plasma glucose and nonesterified fatty acids responses to glucose and epinephrine in protein supplemented beef heifers. *Proc. West. Sect. Am. Soc. Anim. Sci.* 47:310-313.
- 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, R. B. Staigmiller, J. G. Berardinelli, and E. E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. *J. Anim. Sci.* 68:799-816.
- Stanko, R. L., P. Fajersson, L. A. Carver, and G. L. Williams. 1997. Follicular growth and metabolic changes in beef heifers fed incremental amounts of polyunsaturated fat. *J. Anim. Sci.* 75(Suppl. 1):223 (Abstr.).
- Staples, C. R., J. M. Burke, and W. W. Thatcher. 1998. Influence of supplemental fats on reproductive tissues and performance of lactating cows. *J. Dairy Sci.* 81:856-871.
- Talavera, F., C. S. Park, and G. L. Williams. 1985. Relationships among dietary lipid intake, serum cholesterol, and ovarian function in holstein heifers. *J. Anim. Sci.* 60:1045-1051.
- Thomas, M. G., B. Bao, and G. L. Williams. 1997. Dietary fats varying in their fatty acid composition differentially influence follicular growth in cows fed isoenergetic diets. *J. Anim. Sci.* 75:2512-2519.
- Thomas, M. G., and G. L. Williams. 1996. Metabolic hormone secretion and FSH-induced superovulatory responses of beef heifers fed dietary fat supplements containing predominantly saturated or polyunsaturated fatty acids. *Theriogenology* 45:451-458.
- Tovar-Luna, I. and M. K. Petersen. 2000a. Effect of escape protein supplementation on body weight change, milk yield, metabolic hormones, blood metabolites, and intravenous glucose and acetate tolerance tests in ewes. *J. Anim. Sci.* (In press).
- Tovar-Luna, I., M. K. Petersen, D. E. Hawkins, and T. R. Bays. 2000b. Protein supplementation and exogenous insulin in postpartum beef cows. Effects on nutrient partitioning and days to first estrus. *J. Anim. Sci.* (In press).
- 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.
- van der Walt, J. G., and M. J. Linnington. 1990. A review of energy metabolism in producing ruminants: II. Control of nutrient partitioning. *J. S. Afr. Vet. Med. Assoc.* 61:77-79.
- Wehrman, M. E., T. H. Welsh, and G. L. Williams. 1991. Diet-induced hyperlipidemia in cattle modifies the intrafollicular cholesterol environment, modulates ovarian follicular dynamics, and hastens the onset of postpartum luteal activity. *Biol. Reprod.* 45:514-522.
- Wettemann, R. P., K. S. Lusby, and E. J. Turman. 1982. Relationship between changes in prepartum weight and condition and reproductive performance in range cows. *Oklahoma Agric. Exp. Sta.* 112:12-17. Stillwater, OK.
- Williams, G. L. 1996. Influence of dietary fat intake and metabolism on follicular growth in cattle. *Reprod. Domest. Anim.* 31:539-542.
- Williams, G. L. 1998. Fat, follicles, and fecundity. In: W. Hansel, G. Bray, and D. Ryan (ed.) *Nutrition and Reproduction* pp 163-179. Louisiana State University Press, Baton Rouge.
- Wiley, J. S., M. K. Petersen, R. P. Anotegui, 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.
- Zurek, E., G. R. Foxcroft, and J. J. Kennelly. 1995. Metabolic status and interval to first ovulation in postpartum dairy cows. *J. Dairy Sci.* 78:1909-1920.

## Notes

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