Fat Supplementation and Reproduction in Beef Females

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Fat supplementation and reproduction in beef females¹,²

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ABSTRACT: Inadequate dietary energy intake and poor body condition can negatively affect reproductive function. Supplemental lipids have been used to increase energy density of the diet and may also have direct positive effects on reproduction in beef cattle. Several fatty acid sources have been studied as they relate to reproductive function. Common sources include sunflower, safflower, cottonseed, rice bran, soybeans, fishmeal, animal tallow, and calcium salts of fatty acids. Fats have been fed before and after calving, during the breeding season, and during heifer development. Response to fat has been investigated through measuring body weight and body condition score, age at puberty, postpartum interval, first-service conception rates, pregnancy rates, calving interval, calving difficulty, and calf birth and weaning weight. Animal response seems to depend on body condition score, age (parity), nutrients available in the diet, and type of fat supplemented. To elucidate potential mechanisms of action, scientists have investigated changes in follicular and uterine development, hormonal profiles, brain function, and embryonic development. Feeding supplemental fat has resulted in varied and inconsistent effects on reproductive function. Elucidating how supplemental fat can influence reproductive function has been a difficult process. The complexity of the reproductive system and makeup of fat supplements are often confounded by management conditions and forage quality both in research and commercial feeding situations.

Key Words: Beef Cattle, Fat Supplementation, Reproduction

Introduction

Adequate nutrition is critical for successful reproductive function. Inadequate dietary energy intake and poor body condition can negatively affect reproductive function. Supplemental lipids have been used to increase the energy density of the diet and avoid negative associative effects (Coppock and Wilks, 1991) sometimes experienced with cereal grains (Bowman and Sanson, 1996) in high-roughage diets. Supplemental lipids may also have direct positive effects on reproduction in beef cattle independent of the energy contribution. Lipid supplementation has been shown to positively affect reproductive function at several important tissues, including the hypothalamus, anterior pituitary, ovary, and uterus. The target tissue and reproductive response seems to be dependent upon the types of fatty acids contained in the fat source. Fat supplementation is a common practice in dairy cattle production, primarily to increase the energy density of the diet. Associated positive and negative effects on reproduction have been reported (Grummer and Carroll, 1991; Staples et al., 1998). Due to the extreme differences in DMI and level of milk production, research may not be directly applicable to beef cattle production. The objective of this review is to examine current research findings relating to fat supplementation and reproduction in beef cattle.

Fat Sources and Metabolism

Many sources of supplemental fat have been fed to beef and dairy cattle under experimental conditions. Some of these include blends of animal and vegetable fat, tallow, yellow grease, fishmeal, cottonseeds, soybeans, rapeseeds, canola seeds, peanut hearts, safflower seeds, sunflower seeds, flaked fat, prilled fat, hydrogenated fat, calcium soaps of fat, medium-chain triglycerides, and FFA (Staples et al., 1998; Williams and Stanko, 1999). The fatty acid makeup of these fat sources varies widely. Coppock and Wilks (1991) specified the fatty acid profile of many of the commonly used fats. The major fatty acid in most seed lipid is linoleic acid (Staples et al., 1998); linolenic acid predominates in most forage lipid (Staples et al., 1998; Bellows et al., 2001). However, varietal differences

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exist among oilseeds. Bottger et al. (2002) fed safflower seeds either high in linoleic (76%) or oleic (72%) acid. The rendered fats, such as tallow and yellow grease, contain a large proportion of oleic acid (Coppock and Wilks, 1991; Staples et al., 1998). Granular fats, such as calcium soaps of palm oil, and prilled grease, contain a high percentage of the omega-3 fatty acids eicosapentaenoic acid and docosahexaenoic acid (Mattos et al., 2000; Burns et al., 2002a).

Dietary fats can undergo modification in the rumen. Bacteria of the ruminal flora digest dietary triacylglycerols, phospholipids, and galactolipids, releasing fatty acids from their glycerol backbone. Released unsaturated fatty acids have some of their double bonds reduced, and the isomer orientation changed, in a process called biohydrogenation (Mattos et al., 2000). Much of the glycerol is fermented to propionic acid (Williams and Stanko, 1999), one of the major VFA a precursor for glucose. Feeding of supplemental fat increases the proportion of propionic acid and the propionate:acetate ratio (Williams and Stanko, 1999; Howlett et al., 2003). The potential for differences in the efficiency of energy utilization and energy partitioning arises when supplemental fat is provided. Detailed reviews regarding lipid metabolism (Jenkins, 1993), and absorption and transport (Bauchart, 1993) are available.

Fat Supplementation and Reproductive Function

Metabolic Hormone Secretion

Documented effects of supplemental lipids on metabolic hormones have been mixed. The consumption of polyunsaturated plant oils has been shown to increase serum insulin and GH concentrations in both dairy and beef cows (Williams and Stanko, 1999). However, Bottger et al. (2002) reported no differences in serum concentrations of glucose, NEFA, GH, IGF-I, insulin, or IGF-I binding proteins in primiparous beef heifers supplemented with high linoleic or high oleic safflower seeds. Bellows et al. (2001) also found no differences in concentrations of IGF-I, glucose, or NEFA after feeding primiparous beef heifers sunflower seeds for 68 d before calving compared to a control diet without added fat. Staples et al. (1998), in a review of dairy literature on fat supplementation and reproduction, reported lower insulin levels in several studies where supplemental fat was fed. It was also reported that plasma NEFA is nearly always elevated in cows fed supplemental fat and blood glucose concentrations generally are not changed under conditions of supplemental fat. Measuring peripheral concentrations of metabolic hormones may not be an accurate measurement of metabolic status because this does not account for differences in clearance rate or cellular uptake that might occur with lipid supplementation.

Cholesterol-Progesterone Concentrations

Dietary fat supplementation increases circulating concentrations of cholesterol (Staples et al., 1998) and progesterone and the lifespan of induced corpora lutea (CL) in cattle (Williams and Stanko, 1999). Cholesterol serves as a precursor for the synthesis of progesterone by ovarian luteal cells. Progesterone prepares the uterus for implantation of the embryo and also helps maintain pregnancy. Increased concentrations of plasma progesterone have been associated with improved conception rates of lactating ruminants (Staples et al., 1998). Increased concentrations of cholesterol from fat supplementation may lead to an increase in progesterone synthesis (Staples et al., 1998) or reduced rate of clearance from the blood (Hawkins et al., 1995).

LH Secretion and Follicular Development

Secretion of LH from the pituitary and follicular growth in cattle are regulated partially by the energy status of the animal. Energy provided by fat supplementation increases LH secretion in animals deficient in energy. A mechanism independent from energy by which dietary fatty acids affect LH secretion has not been established (Mattos et al., 2000). In some studies, LH dynamics were stimulated by fat supplementation but were unchanged or decreased in others (Staples et al., 1998). The mechanism by which supplemental fat would stimulate LH release is not known unless a glucose-sparing effect occurs at the mammary gland, providing greater glucose to signal the hypothalamic-pituitary control system to secrete more LH (Staples et al., 1998). Similarly, fat supplementation may increase glucose production through increased propionate production. This increase in glucose may have a positive effect on LH release (Funston et al., 1995).

Supplemental fat stimulated programmed growth of a preovulatory follicle, increased total number of follicles, and increased the size of preovulatory follicles (Mattos et al., 2000). Increased size of preovulatory follicles may be due in part to increased concentrations of plasma LH, which stimulates the latter stage of follicular growth. The ovulation of larger follicles may result in the formation of larger corpora lutea with increased steroidogenic capacity and result in greater progesterone production, which has been associated with higher conception rates.

Prostaglandin Synthesis

Prostaglandins play an important role in reestablishing estrous cycles both immediately after parturition and thereafter, until conception occurs. Prostaglandin F₂₀ (PGF₂₀) is responsible for uterine involution after parturition. Greater postpartum PGF₂₀ concentration is associated with faster uterine involution. The uterus releases PGF₂₀ during each estrous cycle to regress each new CL if the cow is not pregnant.
and initiate a new estrous cycle. During the period of CL regression, concentrations of PGF$_{2\alpha}$ and progesterone are inversely related. If the cow conceives, release of PGF$_{2\alpha}$ from the uterus is prevented in order to preserve the CL and maintain pregnancy. Prostaglandin F$_{2\alpha}$ is important for uterine involution after parturition, but increased production and release after conception may lead to luteolysis and increased embryonic mortality.

Linoleic acid is a substrate for the synthesis of PGF$_{2\alpha}$. Linoleic acid can be desaturated and elongated to form arachidonic acid, which is a precursor for PGF$_{2\alpha}$. Regulatory enzymes for this conversion include Δ$_{5}$-desaturase and cyclooxygenase. Linoleic acid can inhibit PGF$_{2\alpha}$ synthesis by competitive inhibition with these key enzymes (Staples et al., 1998). In contrast, Grant et al. (2003) found that supplementing beef cows postpartum with high-linoleate safflower seed increased PGF-metabolite from 25 to 80 d postpartum and tended to decrease first-service conception rates. Filley et al. (2000) also demonstrated that feeding calcium salts of palm oil increased plasma linoleic acid and PGF-metabolite in beef heifers. Arachidonic, and two fatty acids found in fishmeal, eicosapentaenoic (EPA) and docosahexanoic (DHA), have been shown to inhibit cyclooxygenase activity as well (Mattos et al., 2000). Wamsley et al. (2003) found heifers with low-luteal phase progesterone supplemented with fishmeal had lower PGF-metabolite concentrations after an oxytocin challenge. However, fishmeal had no effect in heifers with high-luteal phase progesterone. Linolenic acid was also present in the endometrial PGF$_{2\alpha}$ synthesis inhibitor isolated by Thatcher et al. (1994). Linolenic acid has also been shown to be a strong inhibitor of PGF$_{2\alpha}$ synthesis (Pace-Asciak and Wolfe, 1968). The amount and probably type of particular fatty acids reaching the target tissues likely influence whether PGF$_{2\alpha}$ synthesis is stimulated or inhibited (Thatcher and Staples, 2000). It has also been suggested that reductions in intrafollicular (Wehrman et al., 1991) and serum (Hightshoe et al., 1991) concentrations of estradiol associated with fat supplementation may play a role in modulating luteal responsiveness to prostaglandin (Staples et al., 1998).

Production and Reproductive Responses

Research with supplemental fat has been conducted on cows that have had one or more calves, and in replacement heifers. Fats have been fed before and after calving, and during the breeding season. Several response variables have been examined, including body weight and body condition score, age at puberty, postpartum interval, first-service conception rates, pregnancy rates, calving interval, calving difficulty, and calf birth and weaning weight. To determine potential mechanisms of action, scientists have investigated changes in follicular and uterine development, hormonal profiles and changes, brain function, and embryonic development. The following is a summary of several research trials investigating the effect of supplemental fat on reproductive performance in beef heifers and cows.

Fat Supplementation to Replacement Heifers

Heifers fed safflower seeds (4.4% dietary fat; Lamoglia et al., 2000) for 162 d had a tendency to have a greater percentage reaching puberty at the beginning of the breeding season than heifers fed no added dietary fat. However, there was no difference in overall pregnancy rate. A diet × sire breed interaction suggested the response to fat supplementation might be breed-dependent. Heifers fed supplemental fat had greater cholesterol and progesterone concentrations than unsupplemented heifers.

Supplementing soybean oil at 3% of the diet to a forage-based ration to prepubertal heifers for approximately 100 d increased feed efficiency in one experiment, but not in another, compared to heifers receiving a corn-based control supplement (Whitney et al., 2000). Additionally, in the second experiment, but not the first, heifers tended to conceive earlier in the breeding season. In the above experiments, supplementing at a level of 6% soybean oil decreased feed efficiency compared to 3% added oil and did not change growth or reproductive performance compared to the other diets. No improvement in pregnancy rate was found among groups.

Feeding 0.91 kg (6 to 7% total dietary fat; Funston et al., 2002) of whole sunflower seeds for either 30 or 60 d before AI did not improve estrous response, conception, or pregnancy rate in beef heifers. In this study, heifers fed sunflower seeds for 60 d had lower ADG than heifers fed a control diet without added fat. It is possible this level of added fat inhibited fiber digestion.

Garcia et al. (2003) hypothesized that diets high in linoleic acid would increase conjugated linoleic acid (CLA) tissue content, reduce adiposity and leptin production, and result in an increase in the age at puberty in heifers. Heifers were fed whole sunflower seeds (5% added fat; 70% linoleic acid) from 4 mo of age until postpubertal slaughter. It was concluded that diets high in linoleic acid fed to growing heifers beginning early in life have little or no effect on total carcass fat, circulating leptin, or age at puberty despite measurable increases in CLA accumulation.

In a recent study (Funston, unpublished data), beef heifers were fed 1.36 kg/d (4% added fat) whole soybeans in a total mixed diet approximately 110 d before AI, and fewer (81 vs. 96% for soybean and control, respectively; $P < 0.05$) heifers fed soybeans were detected in estrus through 120 h after melengestrol acetate (MGA)/PGF$_{2\alpha}$ synchronization. Estrous response (time after PGF$_{2\alpha}$) was also delayed (3.2 vs. 2.9 d for soybean and control, respectively; $P = 0.05$) in the heifers fed soybeans. Neither AI conception rates (81
2% added fat to the diet. Heifers were synchronized with soybeans, whole cottonseed, or pelleted soybean hulls to estrogens, which may have affected estrous response and time of estrus. Soybeans and cottonseeds contributed approximately 2% added fat to the diet. Heifers were synchronized with MGA/PGF₂α, and experimental diets were discontinued approximately 1 wk before the first MGA feeding. Treatment did not affect the proportion of heifers pubertal before beginning MGA feeding. First-service conception rates were also not affected by treatment. However, there was a 20% increase (P = 0.27) in first-service conception rates in the soybean fed group (57%) compared to controls (37%). In this study, 96 heifers were split into three treatments and a control group. Neither estrous response nor time of estrus was reported.

Studies are limited on the use of fat supplements in replacement heifer diets. In general, heifers in the studies cited were on a positive plane of nutrition and developed to optimum weight and age at breeding. There may have been a positive response to fat supplementation had heifers been nutritionally challenged. It appears from the studies cited here that there is limited benefit of fat supplementation in well-developed replacement females and is probably only warranted when supplements are priced comparable to other protein and energy sources.

Fat Supplementation Prepartum

Supplementing the diet of late-gestation heifers (d 230 until calving) with safflower seeds at 0.68 kg/d (approximately 4.7% fat in the diet) increased subsequent pregnancy rate by 19% compared to control diets with similar energy and protein content (Lammoglia et al., 1997).

Bellows et al. (2001) supplemented first-calf heifers with safflower seeds, soybeans, or sunflower seeds (4.7, 3.8, and 5.1% fat in diet, respectively) for the last 65 d before calving and increased subsequent pregnancy rates (94, 90, and 91%, respectively) compared to controls (79%) receiving diets with equivalent energy (2.4% fat). In a second experiment, supplementing diets with sunflower seeds (6.5% fat in diet) the last 68 d before calving did not improve subsequent pregnancy rate compared to control diet (2.2% fat). The major difference between the two studies was forage availability. It was estimated there was 71% more forage available and greater nutrient quality in the second study. Forage samples were also analyzed in the second study for protein and fat; protein ranged from 18 to 34% and fat was from 2 to 3.5% depending on forage species. The major fatty acid in the forages was linolenic. It was concluded the abundant, high-quality forage available in the second study resulted in a near-maximal, plateaued nutritional-reproduction response in these dams and this tended to mask any carryover effect resulting from supplemental fat fed in the gestation diet.

Performance of cows supplemented with safflower seeds (3.5 to 4% estimated total dietary fat) 49 d before calving on native range was influenced by calving season and cow age. Three-year-old cows calving in February and 5-yr-old cows calving in April receiving a high-fat supplement had greater pregnancy rates than those fed a low-fat supplement. The opposite was found for 3-yr-olds calving in April. There was no effect of supplemental type on cows calving in June (Grings et al., 2001). Differences in response due to calving season may be similar to research reported by Bellows et al. (2001). June calving cows would have had the opportunity to graze longer before calving and fatty acids obtained from forages may have masked any treatment effect. It is not clear why fat supplementation would decrease pregnancy rate in 3-yr-olds calving in April.

Feeding high-linoleate safflower seeds (5.3% total dietary fat) 56 d before calving had no effect on weight gain, BCS, pregnancy rate, or postpartum interval. Calf birth weight, calving difficulty, and weaning weight were not affected by treatment. However, calf vigor was greater in calves born to heifers fed the high-fat diet. Heifers were BCS 4.4 at the beginning of treatment and 5.8 at calving (Geary et al., 2002).

Mature crossbred cows were supplemented with safflower seeds (5 vs. 2.5% fat for control diet) in two studies from 50 to 56 d before calving. Cows consuming the high-fat diet tended to have higher intake and gain more weight throughout the trial. Body weight and condition were similar. Pregnancy rate, calf birth weight, and weaning weight were not affected by treatment. In both studies, cows were in adequate (BCS 5 to 6) condition and on a positive plane of nutrition throughout the experiment (Encinias et al., 2001).

First-calf heifers supplemented with 5% fishmeal (0.4% added fat) 25 d before and throughout a 90-d breeding season tended (P = 0.12) to have a higher first-service conception rate (76 vs. 62% for fishmeal and control, respectively) than heifers supplemented with corn gluten meal in a silage-based diet. Both plasma EPA and DHA were increased in the fishmeal-fed cows during the first 35 d of supplementation. It was hypothesized that these two fatty acids may attenuate PGF₂α synthesis and improve conception rates (Burns et al., 2002a).

In a subsequent study, Burns et al. (2002b) supplemented 2- and 3-yr-old cows with fishmeal (0.45 kg/
Fat Supplementation Postpartum

Feeding 0.23 kg/d of protected fat (calcium salts of palm oil; 4.7% fat in diet) to first-calf heifers (BCS = 5) for 30 d immediately after calving increased PGF$_{2\alpha}$ synthesis. No improvement in days to first estrus or pregnancy rate was found (Filley et al., 2000).

Supplementing rice bran (5.2% fat in the diet) from d 1 to 50 after calving tended to improve pregnancy rate in mature cows compared to cows receiving a control diet (3.7% dietary fat; De Fries et al., 1998).

Feeding 0.83 kg/d rice bran (5.2% fat in diet) or 200 mg of lasalocid to cows (BCS = 6) starting 1 d after calving increased the percentage of cows returning to estrus and decreased days to return compared to cows consuming control diets of similar energy. However, intervals from calving to CL formation, functional CL, and first progesterone level greater than 1 ng were longer in cows fed diets containing rice bran plus lasalocid (Webb et al., 2001). In this study, cows were randomly assigned within calf sex to treatment. The cows in the rice bran-lasalocid treatment were 0.7 BCS lower than the other treatments at calving. It is not clear why the combination of supplemental fat and lasalocid would negatively affect reproductive events independent of a lower BCS at the beginning of the study.

Supplementation with 1.36 kg of whole cottonseed (5.5% fat in diet) 30 d before the breeding season increased the number of cows (BCS = 4) cycling at the start of the breeding season by 18% compared to a control diet without added fat (Wehrman et al., 1991).

Supplementation with two different fat supplements (21 and 17% fat; 1.8 kg/d) improved estrous response in 2-yr-old cows and first-service conception rate in mature cows when fed for 51 and 45 d postpartum, respectively, compared with control supplement (3% fat; 1.8 kg/d; Bader et al., 2000).

First-calf heifers (BCS = 5.5) were supplemented with two types (high oleate or linoleate; 5% fat in the diet) of cracked safflower seeds and fed ad libitum native grass hay (7.8% CP, 46.3% ADF, 75.7% NDF) for 90 d postpartum. Type of supplement had no effect on length of postpartum interval, pregnancy rate, cow or calf weight change, calf weaning weight, and total or forage OM intake. Overall mean serum IGF-I was greater in heifers fed high-linoleate safflower seeds.
compared to high oleate or control. Treatment did not affect growth hormone, glucose, or NEFA concentrations (Botger et al., 2002).

Ryan et al. (1994) supplemented cows varying in body condition (BCS = 3, 4, 6, or 8) with soybean oil (0.44 kg/500 kg body weight) mixed with 2 kg of ground sorghum beginning at parturition through d 17 postpartum. It was concluded that cows calving with a BCS less than 4, and fed such that body weight and BCS do not increase, are unlikely to respond to short-term dietary fat supplementation (Ryan et al., 1994).

Supplementing fat postpartum seems to be of limited benefit from studies reported here. The majority of the studies reported approximately 5% fat in the diet supplemented with fat. It is not known whether more or less fat would have elicited a different response (either positive or negative). If supplementing fat can either increase or decrease PGF\(_{2\alpha}\) production, it seems reasonable that the amount of fat supplemented might affect which response is elicited. Titration studies are needed to determine critical amounts of fat needed to affect reproductive function.

Feeding Considerations

As stated, the amount of supplemental fat needed to elicit a positive or, in some cases, a negative effect on reproductive function is largely unknown and titration studies are needed in all situations in which supplemental fat has been fed. Dose-response studies indicate that the amount of added plant oil necessary to maximize positive ovarian effects is not less than 4% (Stanko et al., 1997; Thomas et al., 1997). Staples et al. (1998) indicated 3% added dietary fat (DM basis) has often positively influenced the reproductive status of the dairy cow. Lower levels of added dietary fat (2%) have also been shown to elicit a positive reproductive response (Bellows et al., 2001) and, in studies with fishmeal, less than 1% added fat produced a positive reproductive response (Burns et al., 2002a), indicating that both the amount and types of fatty acids are important. Feeding large quantities of fat (>5% of total DMI) has not been recommended due to potential negative effects on fiber digestibility and reduction in DMI (Coppock and Wilks, 1991). The duration and time (pre- or postpartum) of supplement feeding needed to elicit a positive response is not precisely known; many of the studies have supplemented fat at least 30 d. The period of supplementation has varied from different times before breeding in heifer development, parturition, postpartum, and/or prebreeding periods. The young, growing cow appears to be the most likely to respond to supplemental nutrients. An appropriate situation for fat supplementation may occur when pasture or range conditions are limiting or are likely to be limiting before and during the breeding season. Feeding supplemental fat to well-developed heifers or cows in adequate body condition on adequate pasture or range resources may not provide any benefit beyond energy contribution to the diet.

The majority of fat supplementation in beef cattle diets has been in the form of oilseeds added to a total mixed diet or fed as a supplement. A challenge has been to make a supplement high in fat that can be pelleted or blocked and fed on the ground. Levels above 8% fat have resulted in pellets and blocks that are soft and of poor quality (R. A. Bellows, Bozeman, MT, personal communication). Whole soybeans, sunflower, and cottonseeds have been fed without processing; it seems that safflower seeds need to be processed to improve digestibility. Seeds should be processed (rolled) with enough pressure to crack about 90% of the seed hulls without extracting the oil (Lamoglia et al., 1999). Gossypol levels may be a concern when high levels of whole cottonseed are fed. However, levels of gossypol present in typically fed quantities of whole cottonseed for protein or fat supplementation provide only a fraction of the amount of gossypol fed in studies in which gossypol toxicity has been reported (Williams and Stanko, 1999). Other factors, such as phytoestrogens, may be present in some oilseeds (legumes in particular) and have been shown to negatively affect reproduction in cattle (Adams, 1995). The precise effect of these factors and possibly others on reproductive function has not been fully elucidated and is probably dependent on the level of inclusion, the basal diet, and the stage of physiological maturity of the female being supplemented.

Currently, research is inconclusive on exactly how to supplement fat to improve reproductive performance beyond the energy contribution. Most studies have tried to achieve isocaloric and isonitrogenous diets. However, this can be challenging. Some studies only have sufficient animal numbers to detect very large differences in reproductive parameters, such as conception and pregnancy rates. Research on feeding supplemental fat has resulted in varied and inconsistent results as it relates to reproductive efficiency, including positive, negative, and no apparent effect.

Elucidating how supplemental fat can influence reproductive function has been a difficult process. Animal response appears to be dependent on body condition score, age (parity), nutrients available in the basal diet, and type of fat supplement. The complexity of the reproductive system and makeup of fat supplements are often confounded by management conditions and forage quality both in research and in commercial feeding situations; this confounding has contributed to inconsistencies in research findings.

Implications

Improvements in reproduction reported in some studies may be a result of added energy in the diet or direct effects of specific fatty acids on reproductive processes. As is the case for any technology or management strategy that improves specific aspects of ovar-
ian physiology and cyclic activity, actual improvements in pregnancy rates, weaned calf crop, or total weight of calf produced depend on an array of interactive management practices and environmental conditions. Until these interrelationships are better understood, producers are advised to strive for low cost and balanced rations. If a source of supplemental fat can be added with little or no change in the ration cost, producers would be advised to do so. Research investigating the role of fat supplementation on reproductive responses has been variable. Therefore, adding fat when significantly increasing ration cost would be advised when the risk of low reproduction is greatest.

**Literature Cited**


