

Dietary fats as reproductive nutraceuticals in beef cattle¹

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Abstract

Inadequate dietary energy intake and poor body condition are two of the most pervasive factors influencing reproductive efficiency in beef cattle production systems. Therefore, an important goal has been to discover novel methods for enhancing reproductive processes in cattle that are exposed to these conditions, often on a repeated basis. This review will examine dietary fat as a reproductive “nutraceutical,” including the role of fatty acid content and minimum effective intake. Although the consumption of neutral lipids by ruminants is limited under natural conditions, the addition of digestible fats to increase caloric content or to positively modify diet physical characteristics is a long-standing practice. More recently, fat supplements have been used in attempts to influence specific metabolic pathways and, ultimately, hormones that directly modulate ovarian cellular processes. The basis for this approach lies within an array of digestive, metabolic, and reproductive sequelae that occur when cattle consume significant quantities of digestible fat. Evidence suggests that the consumption of fat by cattle, particularly polyunsaturated plant oils, can positively influence ovarian follicular growth, luteal function, and postpartum reproductive performance independent of caloric effects. Mechanistically, these effects have been attributed to a cascade of events that change rumen fermentation patterns, heighten lipoprotein-cholesterol synthesis, increase secretion of ovarian steroids, modify circulating concentrations of insulin and GH, and enhance the synthesis or accumulation of IGF-I in ovarian cells. Whole oilseeds, oil milling by-products, and some manufactured products are available to exploit these physiological concepts.

Key Words: Dietary Fat, Hormones, Metabolism, Reproduction, Cattle

Introduction

Nutrition is a major factor in the efficiency of mammalian reproduction. In cattle, the most studied aspects of the nutrition-reproduction interaction have been the effects of dietary energy, body energy reserves, and nitrogen balance on sexual maturation and postpartum rebreeding performance (Kinder et al., 1987; Randel, 1990). An important goal in beef cattle production systems has been to discover novel nutritional supplementation strategies for positively enhancing reproductive efficiency in grazing cattle maintained in less than optimal environments. In our laboratory, we have focused on the potential of dietary fat supplementation to assist in this effort. Although fat is clearly a concentrated source of energy, the objectives of our work have been to determine the reproductive sequelae of fat feeding, independent of its energy contribution per se. Hence, the purpose of this review is to describe the digestive, metabolic, and reproductive effects of fat as a “nutraceutical,” which herein is defined as a feedstuff or feed additive having physiological effects outside of its generally accepted role as a nutrient source (DeFelice, 1999). More specifically, this review will examine metabolic changes brought about by specific types and levels of fat supplementation, examine how the reproductive system responds, and suggest potential methods for incorporating fat into technologically efficient delivery systems under grazing conditions.

Discussion

High levels of digestible fatty acids do not occur in forages consumed naturally by ruminants. However, fat has been used for many years in both the beef and dairy cattle industries to increase caloric density of diets, reduce dust, and improve product palatability (Church, 1976). In order to exploit the use of significant quantities of fat in diets of cattle, several important aspects of ruminant digestion must be considered.

Metabolism of Fats in the Rumen. Ruminal microflora hydrolyze triglycerides and phospholipids that contain polyunsaturated fatty acids. Fats of plant or animal origin contain the unsaturated fatty acids palmitoleic (16:1), oleic (C18:1), linoleic (18:2 *n*-6), and α -linolenic (18:3 *n*-3) acids (Table 1), all of which are metabolized in the rumen. Linoleic acid predominates in seed and seed products, and α -linolenic predominates in forages. Fats are hydrolyzed to their polyunsaturated fatty acid constituents and to glycerol. A high proportion of the fatty acids are then partially or completely hydrogenated and much of the glycerol is fermented to propionic acid (Church, 1976; Noble, 1978). Estimates of hydrogenation efficiency of linoleic acid range from 70 to 90% (Staples et al., 1998).

The consumption of large quantities of ruminally active fat (> 5% of total dry matter intake) can markedly reduce fiber digestibility and reduce dry matter intake in ruminants (Coppock and Wilks, 1991). This occurs due to the selection against microorganisms with cellulolytic capability. However, certain types of fat-containing feedstuffs can be fed in

quantities that would contribute fat at levels greater than the 5% limit without such negative effects. For example, whole cottonseeds (approximately 23% oil) can be fed at much higher levels than would be possible if the free oil were mixed throughout the diet. Apparently, this is possible because ruminal metabolism of the oil is slowed by the fibrous seed coat, and a portion actually passes through the rumen intact (Coppock and Wilks, 1991). Due to the lack of reactive double bonds, saturated fatty acids also pass through the rumen undegraded and are considered bypass fats (Jenkins, 1993). The effects of animal tallow and other predominantly saturated fats on the metabolism and physiology of the ruminant differ somewhat because of this phenomenon. However, the fatty acid profile of a predominantly saturated fat such as tallow can vary greatly, with concentrations of linoleic acid constituting from 2 to 9% of the total (Coppock and Wilks, 1991). Table 1 summarizes the fatty acid content of three common fat sources (soybean oil, tallow, and fish oil) used in a study conducted in this laboratory (Thomas et al., 1997).

Lipoprotein-Cholesterol Metabolism. Maynard et al. (1931) were the first to describe the unique features of lipoprotein metabolism in lactating cows. During lactation, homeostatic mechanisms regulating intestinal synthesis of α -low-density (LDL) and high-density (HDL) lipoproteins seem to undergo a unique adaptation. Nonlactating cows consuming primarily forage-based diets exhibit serum lipoprotein-cholesterol concentrations of approximately 100 to 150 mg/dL, whereas peak lactation produces plasma concentrations often approaching 300 mg/dL in dairy (Maynard et al., 1931; Noble, 1978) and beef cattle (Williams, 1989). The evolutionary and physiological significance of this phenomenon is not clearly understood. However, it seems to be the consequence of mammary gland activity and the hepatic production of triglycerides for synthesis of milk fat (Puppione, 1978). Fat supplementation also stimulates the synthesis and accumulation of lipoprotein-cholesterol and cholesterol esters in tissues and body fluids, including the ovary. Increased dietary fat consumption and lactation synergize to produce even greater synthesis and accumulation of these products than either one alone. The predominant species of circulating lipoprotein in blood of ruminants is HDL, and it is the only lipoprotein with access to the intrafollicular compartment, regardless of species (Caravaglios and Cilotti, 1957). Detailed recent reviews regarding lipid metabolism (Jenkins, 1993), absorption and transport (Bauchart, 1993), and metabolism (Chilliard, 1993; Grummer, 1993) are available.

Historical Basis of Fat as a Reproductive Nutraceutical: Cholesterol-Progesterone Relationships

Dietary fat supplementation increases circulating concentrations of progesterone and lifespan of induced CL in cattle (Table 2). In our original studies relating dietary fat metabolism to ovarian function, the main focus was on lipoprotein metabolism (Talavera et al., 1985). We examined the rela-

tionship between plasma cholesterol and luteal function because of a previously published experiment conducted in miniature swine (Lussier-Cacan et al., 1977). In the swine study, serum cholesterol concentrations varied inversely and dramatically in relation to circulating progesterone during the luteal phase of the estrous cycle. Whether this occurred as a result of luteal tissue scavenging cholesterol from blood or as a consequence of progesterone negative feedback on lipoprotein-cholesterol metabolism was unknown. Circulating cholesterol is the primary substrate for luteal progesterone synthesis in mammals. De novo synthesis from acetate within luteal tissue is inadequate to sustain normal luteal function. Therefore, we hypothesized that dietary-mediated increases in plasma cholesterol could potentially modulate luteal function. When dairy heifers were provided high-fat supplements via whole sunflower seeds, serum cholesterol increased dramatically, and mid- to late-luteal phase concentrations of progesterone also increased (Talavera et al., 1985). We concluded that hyperlipidemia/hypercholesterolemia either changed the rate of synthesis of progesterone by the corpus luteum or changed its metabolism or clearance rate.

Reproductive Effects of Fat Supplementation

Subsequent studies with beef cattle focused on various aspects of lipoprotein-cholesterol metabolism, both in vivo and in vitro, and its effects on ovarian physiology and ovarian cells. Our initial work addressed the pattern of lipoprotein-cholesterol concentrations in grazing cattle during early lactation and examined the effect of oilseed supplementation on induced luteal function during the early postpartum period (Williams, 1989). Supplemental fat fed during the early postpartum period enhanced induced luteal function by reducing the incidence of short cycles. Mechanisms associated with the enhancement of mean serum progesterone concentrations in cyclic cattle, and the prolongation of corpora lutea destined to be short-lived, have not been definitively determined. However, the enhancement of luteal lifespan may be related to the ability of fat supplementation to modify growth and physiology of the preovulatory follicle before ovulation (Wehrman et al., 1991; Ryan et al., 1992). As discussed later, this phenomenon could also be related to the effects of linoleic acid on uterine prostaglandin synthesis. Effects observed on serum progesterone during normal cycles may involve a decrease in metabolic half-life of progesterone in plasma or increased availability of cholesteryl esters in luteal cells (Hawkins et al., 1995). Based on dose-response studies of luteal cells to nonesterified cholesterol (Carroll et al., 1992), it is possible that the supply of HDL-cholesterol within the ovary can be marginally limiting under conditions of extreme nutritional restriction (Ryan et al., 1994). Table 2 summarizes the collective effects of dietary fat supplementation on luteal progesterone secretion and luteal lifespan.

Follicular Growth. Fat supplementation affects follicular growth dynamics in cattle by increasing the number of follicles in the medium-sized classification by 1.5- to 5-fold

within 3 to 7 wk (Wehrman et al., 1991; Ryan et al., 1992; Thomas et al., 1997). This effect occurs independent of dietary metabolizable energy or weight gain of cattle in moderate to obese condition. Changes in the medium-sized follicle pool occur coincident with a tendency for small follicle populations (≤ 3 mm) to decline (Wehrman et al., 1991). The greatest increase in medium follicle populations has been measured in response to plant oil, which is high in linoleic acid (Figure 1). Sources of plant oil have included whole cottonseed (Wehrman et al., 1991; Ryan et al., 1995), soybean oil (Ryan et al., 1992; Thomas and Williams, 1996; Thomas et al., 1997), and rice bran (Lammoglia et al., 1996). In the latter case, follicles 8 mm in size were classified as large; therefore, the number of large follicles were also considered to increase.

Maximum follicular growth responses to plant oil supplementation were found to occur in response to fat additions of at least 4% of estimated total dry matter intake, with lesser increases noted with lower levels of added fat (Thomas and Williams, 1996; Stanko et al., 1997). Animal tallow (Thomas and Williams, 1996; Thomas et al., 1997), calcium salts of predominantly saturated fatty acids (Hightshoe et al., 1991; Lucy et al., 1991), or fish oil (Thomas et al., 1997) have been shown to have less robust effects on follicular growth than plant-derived oils. We believe that this effect is due mainly to the abundance of linoleic acid (C18:2) in plant-derived oils, as discussed later. Further work is warranted to determine whether extended feeding periods can benefit follicular development in cows in very low body condition, but it is not reasonable to expect fat supplementation alone to obviate the effects of severe energy deprivation and(or) suckling on the hypothalamic-pituitary-ovarian axis (Randel, 1990; Williams, 1990). Table 3 summarizes the effects of dietary fat supplementation in cattle on follicular growth and steroidogenic potential of follicle cells as reported by various laboratories.

Superovulation Regimens. Because prolonged fat supplementation increases the number of follicles in the medium-sized pool, it was hypothesized that regimens of FSH would be able to recruit a greater number of follicles into the superovulatory pool. However, this did not occur, nor was the number of viable embryos affected (Ryan et al., 1992; Table 1). Based on our current understanding of follicle growth and atresia, it is possible that the dominance effects of the largest follicle at the onset of FSH treatment prevents the recruitment of additional medium-sized follicles. However, if the largest follicle is aspirated transvaginally on d 4 of the cycle, FSH-induced superovulation remains unimproved (Thomas and Williams, 1996). Further work is needed to overcome the limitations imposed by the dominant follicle.

Postpartum Reproduction. Duration of the postpartum anovulatory interval in beef cattle is controlled by several interacting factors, including recovery of pituitary gonadotrophs from the effects of high circulating concentrations of placental-derived estradiol (Williams et al., 1982; Nett, 1987), body condition or body energy reserves at parturition

(Randel, 1990; Short et al., 1990), and the suckling calf (Williams, 1990; Williams and Griffith, 1995). These factors markedly influence the pace at which the hypothalamic-pituitary axis is able to generate the pattern of pulsatile GnRH and LH release necessary for development of an estrogen-active, preovulatory follicle (Ryan et al., 1994; Gazal et al., 1998). Does increased intake of fat, aside from its obvious contribution to caloric density of the diet, contribute to postpartum recovery? The answer seems to be yes. Although there have been some reports indicating that fat supplementation influences pituitary function, the mechanisms through which fat supplementation improves reproductive performance seem to involve mainly an increased functional capability at the ovarian level. Physiological and endocrine candidates that could mediate this increased functionality are discussed in more detail below.

Field Trials. Supplementation of postpartum, lactating beef cows with .36 kg fat via whole cottonseed, beginning 30 d before the start of the breeding season, increased the number of cows cycling at the start of the breeding season by up to 18% (Wehrman et al., 1991; Purina Mills, 1998, unpublished observations). This response was most evident when environmental conditions resulted in a loss of body condition during the postpartum period, despite supplementation (Table 4). Work at other locations (Hightshoe et al., 1991; Espinoza et al., 1995) has confirmed that fat supplementation reduces the postpartum anovulatory interval and enhances rebreeding performance. The latter trials were conducted with fats containing predominantly saturated fatty acids, which tend to bypass the rumen unmetabolized. We can only speculate that performance would have been further enhanced if polyunsaturated plant oils had been used, because ovarian responses to saturated fats seem less robust than responses to polyunsaturated fats. Studies to confirm this speculation have not been reported. Dose-response studies indicate that the amounts of added plant oil necessary to maximize positive ovarian effects is not less than 4% (Stanko et al., 1997). As is the case for any technology or management strategy that improves specific aspects of ovarian physiology and cyclic activity, actual improvements in pregnancy rates, weaned calf crop, or total weight of calf produced are dependent on an array of interactive management practices and environmental conditions.

Putative Mechanisms Through Which Fat Supplementation Could Enhance Reproduction

Ruminal Fermentation. Studies related to effects of fat supplementation on reproductive processes have for the most part been careful to use isoenergetic and isonitrogenous control diets. However, the consumption of reactive fats by ruminants results in effects on fermentation patterns. Therefore, the potential for differences in the efficiency of energy utilization and local energy partitioning cannot be eliminated from consideration. Changes in ruminal volatile fatty acid production occur in response to increments in dietary fat, and

the proportion of change is dependent on the degree of saturation of the fatty acids consumed (e.g., polyunsaturated > saturated and highly polyunsaturated) and quantity fed (Jenkins, 1993). As already noted, consumption of polyunsaturated fatty acids increases ruminal propionate production and decreases the acetate:propionate ratio. Highly polyunsaturated and saturated fats tend to bypass the rumen unaltered and have fewer effects on ruminal fermentation. Other effects on serum cholesterol and triglycerides are generally similar among the three types of fats, although tallow tends to increase serum triglycerides to a greater extent than the other fats, and fish oil (highly polyunsaturated fatty acids) tends to produce a lesser increase in both total and HDL-cholesterol (Thomas et al., 1997).

Metabolic Hormone Secretion. Dietary fat supplementation causes an array of metabolic effects in cattle (Figure 2). The consumption of polyunsaturated plant oils increases basal serum insulin concentrations in both dairy (Palmquist and Moser, 1981) and beef cows (Thomas and Williams, 1996; Ryan et al., 1995). This phenomenon has been observed in cycling cattle (Figure 3) and in response to feeding during the postpartum period (Figure 4). Therefore, it is possible that increased serum concentrations of insulin occurring in response to polyunsaturated plant oils play a role in mediating increased follicular growth, either directly through its own receptor or indirectly by modulating granulosa cell IGF-I production (Yoshimura et al., 1994). Mean serum concentrations of insulin also increase gradually in response to fats in which either saturated (animal tallow) or highly polyunsaturated fatty acids (fish oil) predominate (Figure 3), with correspondingly modest increases in populations of medium-sized follicles. We speculate that this may be due to the presence of either linoleic acid or palmitoleic acid (16:1) in tallow and fish oil, respectively.

All of the fats we have tested increased serum concentrations of GH in beef cattle (Ryan et al., 1995; Thomas and Williams, 1996; Thomas et al., 1997). However, during the postpartum period of beef cows, the effect of fat consumption seemed to be mainly to prevent a postpartum decline in serum GH (Figure 4). Studies conducted during later lactation have demonstrated a similar phenomenon in high-producing dairy cows (Grum et al., 1996a,b). Increases in serum GH seem to occur coincident with an increase in the accumulation of follicular fluid IGF-I, but without effects on peripheral circulating IGF-I (Grum et al., 1996a,b; Thomas et al., 1997). The basis for this rather confusing observation has not been determined. However, a recent report indicates that moderate doses of porcine somatotropin do not increase growth rate, serum IGF-I, or IGF-I binding proteins in suckling pigs. Growth hormone receptors, while rare, are present in bovine follicles and are abundant in corpora lutea (CL; Lucy et al., 1993); therefore, mechanisms involving IGF-I as a mediator of local GH effects may or may not be operative. In either case, we have observed increases in follicular fluid IGF-I of fat-supplemented cattle, regardless of type of fat consumed, and a heightened ability of fresh luteal tissue from

these animals to secrete IGF-I in vitro (Ryan et al., 1995; Thomas et al., 1997). In rats, GH has been shown to directly stimulate IGF-I mRNA within granulosa cells and to enhance the production of IGF-I (Yoshimura et al., 1994). Table 5 summarizes the effects of dietary fat supplementation on circulating concentrations of GH and insulin, intrafollicular concentrations of IGF-I, and luteal tissue production of IGF-I as reported by various laboratories.

Availability of Lipoprotein-Cholesterol. In vitro studies with granulosa, theca, and luteal cells suggest that our original hypothesis relating high-fat diets, lipoprotein-cholesterol metabolism, and ovarian cellular physiology could be at least partially correct. High-density lipoprotein constitutes approximately 80% of the total lipoprotein mass in serum of cattle, and both HDL and LDL have been shown to differentially regulate certain aspects of bovine theca, granulosa, and luteal cell metabolism and growth (Bao et al., 1995, 1997). We found that both HDL and LDL promoted granulosa cell viability in vitro regardless of follicle type, and they increased in vitro proliferation of theca-derived cells from preovulatory follicles. One of the more dramatic effects was the ability of both HDL and LDL to stimulate IGF-I production by granulosa and luteal cells. However, in bovine cells, HDL is more potent in its ability to stimulate progesterone (granulosa, theca) and androstenedione (theca cells) production, which is in keeping with the fact that only HDL is contained within follicular fluid. Moreover, LDL seemed to attenuate HDL-stimulated progesterone production (Bao et al., 1995).

Serum Concentrations of LH. Increases in basal concentrations of LH before, but not after, calf removal in anestrous beef cows have been observed in response to polyunsaturated fat supplementation (Morgan and Williams, 1989; Table 5). However, these changes were relatively modest. Others have reported positive effects on basal LH concentrations in range beef cows fed calcium soaps of palm oil fatty acids (Hightshoe et al., 1991). Anterior pituitary responsiveness to GnRH was not affected by high-fat diets (Johnson et al., 1987; Morgan and Williams, 1989), and we have observed no effect of high-fat diets on the number or affinity of receptors for LH in induced CL (Ryan et al., 1995). Hence, although dietary fat supplementation does seem to have some effect on basal concentrations of LH, it is not clear at this time what role these rather subtle changes might play in the context of previously observed ovarian changes. High-fat diets would be more likely to influence the secretion of FSH, because modifications in follicle growth seem to occur primarily as an increase in numbers of medium-sized follicles. The pattern of FSH secretion in animals fed high-fat diets has not been examined.

Uterine Prostaglandin Synthesis. The effects of fat supplementation in beef cattle have focused primarily on changes in lipoprotein-cholesterol metabolism and on metabolic hormones and growth factors that seem to mediate responses at the ovarian level. However, another approach has been to consider the effects of fat-supplemented diets on

uterine prostaglandin synthesis and secretion. Linoleic acid has inhibitory effects *in vivo* and *in vitro* on uterine prostaglandin synthesis (Kaduce et al., 1982; Staples et al., 1998) through inhibition of the enzyme cyclooxygenase. Linoleic acid actually competes with arachidonic acid for binding with this enzyme. Based on these observations, it has been speculated that changes in prostaglandin synthesis may help explain how dietary fat supplementation enhances luteal function and pregnancy rates (Staples et al., 1998). Oxytocin-mediated release of PGF_{2α} metabolites (PGFM) was reduced in dairy cows infused abomasally with yellow grease (Oldick et al., 1997). 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). Inclusion of fish meal in dairy cow diets improved conception rates, which was speculated to have occurred as a result of the presence of docosahexanoic acid (22:6 *n*-3). However, in contrast to the above studies, intravenous infusion of soybean oil or olive oil actually increased PGFM concentrations in ewes (Burke et al., 1996). Moreover, in a recent study, rumen bypass fat fed to postpartum beef heifers failed to alter circulating PGFM or conception rates (Filley et al., 2000). In summary, studies in dairy cattle, beef cattle, and sheep suggest the potential for fat supplementation to affect reproduction (either negatively or positively) through changes in prostaglandin synthesis and metabolism; however, no cause and effect relationships have been established to date.

Fat Supplementation Strategies

The majority of the early work studying fat supplementation effects on reproduction employed either whole oilseeds (Talavera et al., 1985; Williams, 1989), soybean oil (Ryan et al., 1992), or Megalac (Hightshoe et al., 1991), which contains calcium salts of palm oil. Depending on oil content, oilseeds were fed at a rate of 15 to 30% of the diet on a dry matter basis and supplied 4 to 8% added fat. Oilseeds, particularly cottonseed, provide a unique blend of energy, protein, fiber, and fat and make an excellent supplemental feed when fed at .9 to 2.2 kg per animal daily. An issue that has been raised regarding the use of whole cottonseed is that of gossypol toxicity. Beef cows consuming up to 20 g daily of dietary free gossypol for up to 2 mo, via diets containing direct solvent-extracted cottonseed meal (high gossypol) and whole cottonseed, exhibited no effects on reproductive endocrine function, estrous cycles, or pregnancy rates (Gray et al., 1993). Although high levels of gossypol produce increased red blood cell fragility, this effect does not seem to create a clinically significant pathology in beef cows under normal management conditions. Moreover, the levels of gossypol present in typically fed quantities of whole cottonseed for protein or fat supplementation (as described above) provided only a fraction of the amount of gossypol fed in the study by Gray et al. (1993). In mature female cattle, the only reports

of gossypol toxicity have been in the dairy industry involving diets containing up to 45% direct solvent cottonseed meal for 14 wk (Lindsey et al., 1980). The reader is referred to a complete treatise on the subject of gossypol-containing feeds and gossypol toxicity in beef cattle (Jones et al., 1991).

Oilseeds are not universally available or economically practical under all conditions in which beef cattle supplementation is employed. Therefore, other alternatives are needed. One of these alternatives is molasses-based liquid supplements containing soybean oil soapstocks (Stanko et al., 1997). Technology to maintain fat in a homogenous suspension for long periods continues to be the major challenge, and optimization of blends containing urea, sugars, fat, and other constituents to promote consistent intake will be required. Recently, dry fat supplements containing 18 to 20% plant oil have been marketed for grazing beef (CONCEPT; Purina Mills, St. Louis, MO) and dairy cattle (High Fat Product; ADM, Decatur, IL) to exploit the benefits of fat supplementation on reproductive performance. Animal tallow has been used in supplements designed to enhance reproductive performance; however, there are marked palatability problems associated with high feedstuff concentrations of tallow. Therefore, it seems that plant-derived oils, when recommended for use at levels shown to maximize ovarian physiological responses, will continue to be the source of choice. Alternative commercial supplements or other by-products containing up to 20% plant oils are needed. Yellow grease, a by-product of the restaurant trade (20 to 25% linoleic acid), can be used as one of those alternatives.

Implications

Increased consumption of dietary fat affects an array of ovarian and reproductive end points in cattle. This review has attempted to present the current status of knowledge concerning those effects, as well as research that presents plausible physiological, metabolic, and hormonal explanations to account for them. Further studies are required to define how dietary fat consumption by cattle and other ruminants may influence ovarian physiology and reproductive efficiency and to develop methods to optimize this influence under field conditions.

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Notes

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Table 1. Fatty acid composition (%) of saturated (animal tallow), polyunsaturated (soybean oil), and highly polyunsaturated (fish oil) fats (From Thomas et al., 1997 with permission)

Fatty acid	Type of fat		
	Saturated	Polyunsaturated	Highly polyunsaturated
12:0	—	—	—
14:0	4.4	—	11.1
14:1	0.6	—	0.2
15:0	0.7	—	0.7
16:0	26.6	11.3	26.9
16:1	2.4	—	12.7
17:0	1.7	—	2.1
17:1	0.8	—	1.2
18:0	21.0	3.9	4.1
18:1	39.8	23.8	11.4
18:2	2.0	53.5	1.8
18:3	1.0	7.5	3.1
20:0	—	—	0.4
20:1	—	—	1.6
20:4	—	—	0.9
20:5	—	—	13.0
22:5	—	—	—
22:6	—	—	8.8

Table 2. Summary of effects of dietary fat supplementation on luteal characteristics and circulating concentrations of progesterone in cattle

Source	Characteristics affected
Talavera et al., 1985; Williams, 1989; Hightshoe et al., 1991; Spicer et al., 1993; Hawkins et al., 1995; Lammoglia et al., 1996	Increased serum concentrations of progesterone
Williams, 1989; Morgan and Williams, 1989; Ryan et al., 1995	Increased lifespan of induced CL; increased number ovulating
Hawkins et al., 1995	Decreased metabolic clearance rate of progesterone
De Fries et al., 1998	No effect on serum progesterone

Table 3. Summary of effects of dietary fat supplementation in cattle on ovarian follicular growth and steroidogenic potential of follicle cells in vitro

Source	Characteristics affected
Wehrman et al., 1991; Ryan et al., 1992; Hightshoe et al., 1991; Lucy et al., 1991; Thomas and Williams, 1996; Thomas et al., 1997; Lammoglia et al., 1996; Stanko et al., 1997; De Fries., et al., 1998	Increased number of medium-sized follicles (polyunsaturated fat > saturated and highly polyunsaturated fat effects)
Wehrman et al., 1991; Ryan et al., 1992	Increased granulosa cell progesterone production in vitro; increased follicular fluid progesterone
Ryan et al., 1992; Thomas and Williams, 1996	No effect on superovulation rate
De Fries et al., 1998	Increased number of large follicles; increased size of largest follicle

Table 4. Effects of feeding high-fat supplements to suckled, postpartum beef cows for 1 mo prior to the start of breeding on incidence of luteal activity at the start of the breeding season in grazing beef cows (from Wehrman et al., 1991 with permission)

Group ^a	Year	No. of cows	Luteal activity, %
High fat	1	61	72.0
Control	1	59	57.6
High fat	2	31	42.0
Control	2	32	18.8
High fat	Both	92	61.9 ^b
Control	Both	91	43.9 ^c

^aHigh fat and control supplements were isocaloric and isonitrogenous

^{b,c}Means with differing superscripts differ ($P < .05$).

Table 5. Summary of effects of dietary fat supplementation on circulating concentrations of LH, GH, IGF-I, and insulin, intrafollicular concentration of IGF-I, and luteal tissue production of IGF-I

Source	Characteristics affected
Morgan and Williams, 1989; Hightshoe et al., 1991	LH: increased serum baseline
Ryan et al., 1995; Thomas and Williams, 1996; Thomas et al., 1997	GH: increased serum baseline
Palmquist and Moser, 1981; Thomas and Williams, 1996; Thomas et al., 1997	Insulin: increased serum baseline
Ryan et al., 1995; Thomas and Williams, 1996; Thomas et al., 1997	IGF-I: No effect on serum IGF-I; increased follicular fluid concentrations; increased luteal tissue production in vitro

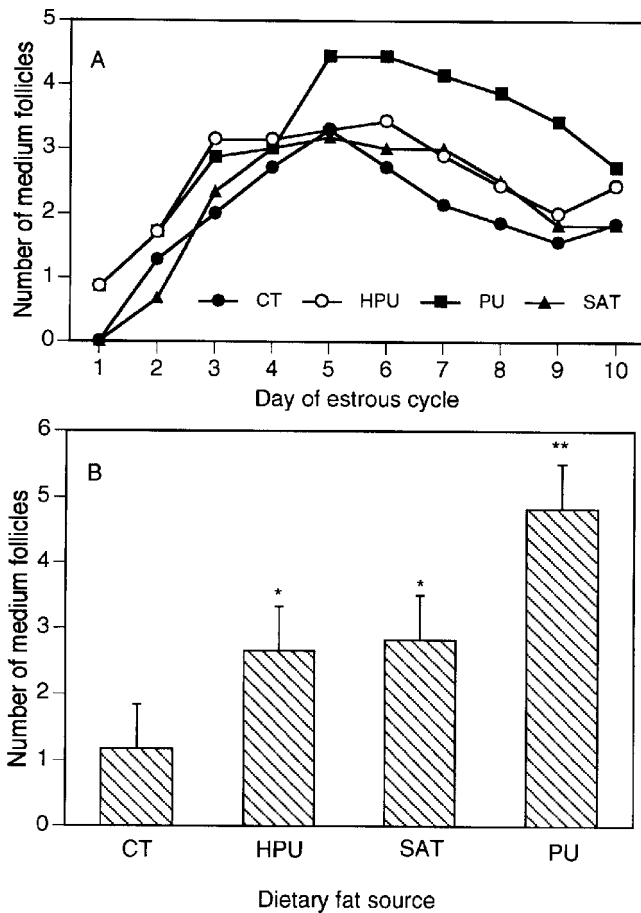


Figure 1. Numbers of medium-sized follicles in mature beef cows having normal estrous cycles and fed supplements containing no added fat (CT), highly polyunsaturated fat (HPU; fish oil), saturated fat (SAT; tallow), or polyunsaturated fat (PU; soybean oil) for 7 wk. All diets were isocaloric and isonitrogenous. Panel A depicts the pattern of follicular growth during a synchronized estrous cycle after 3 wk of feeding. The number of medium-sized follicles was determined by daily transrectal ultrasonography and was greater ($P < .05$) in cows fed PU during d 5 through 10 of the cycle. Panel B shows follicle populations determined at ovariectomy at wk 7. Cows receiving PU had a fourfold increase ($P < .01$) in medium-sized follicles compared to controls. Medium follicles in cows receiving SAT and HPU-supplemented diets also tended ($P < .1$) to increase after 7 wk (from Thomas et al., 1997 with permission).

Metabolic and Hormonal Effects of High Fat Diets

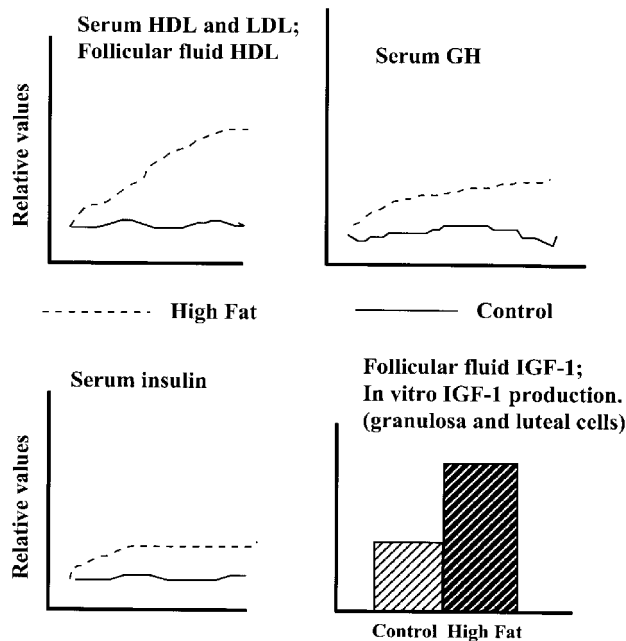


Figure 2. Schematic illustration of the effects of high-fat diets on serum concentrations of lipoprotein-cholesterol, GH, insulin, follicular fluid concentrations of HDL-cholesterol, IGF-I, and on granulosa and luteal cell production of IGF-I in vitro. See Table 5 and text for references.

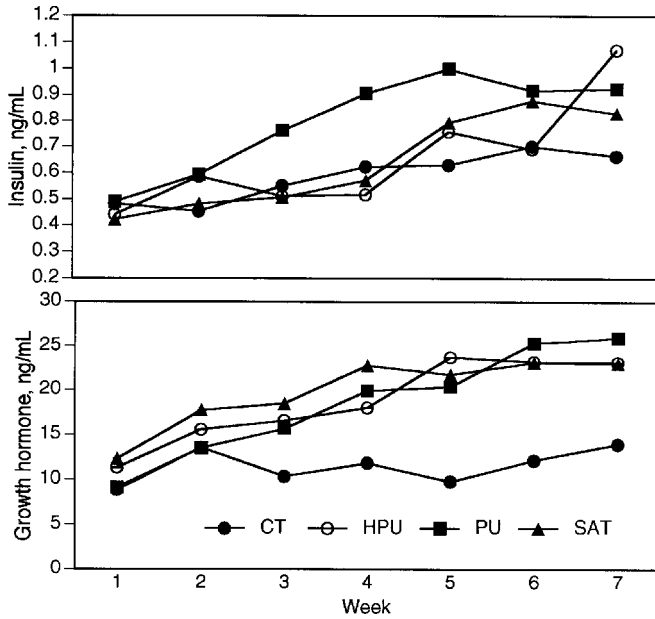


Figure 3. Serum concentrations of insulin (top panel) and GH (bottom panel) in estrous cycling beef cows fed a control diet (CT) or diets containing saturated (SAT), highly polyunsaturated (HPU), or polyunsaturated (PU) fat at 4% of total dry matter intake. Diets were isocaloric and isonitrogenous. Insulin was increased ($P < .05$) within 3 wk in cows fed PU but only after 7 wk ($P < .05$) in other fat-supplemented groups. All fat supplements increased ($P < .05$) serum concentrations of GH (From Thomas et al., 1997 with permission).

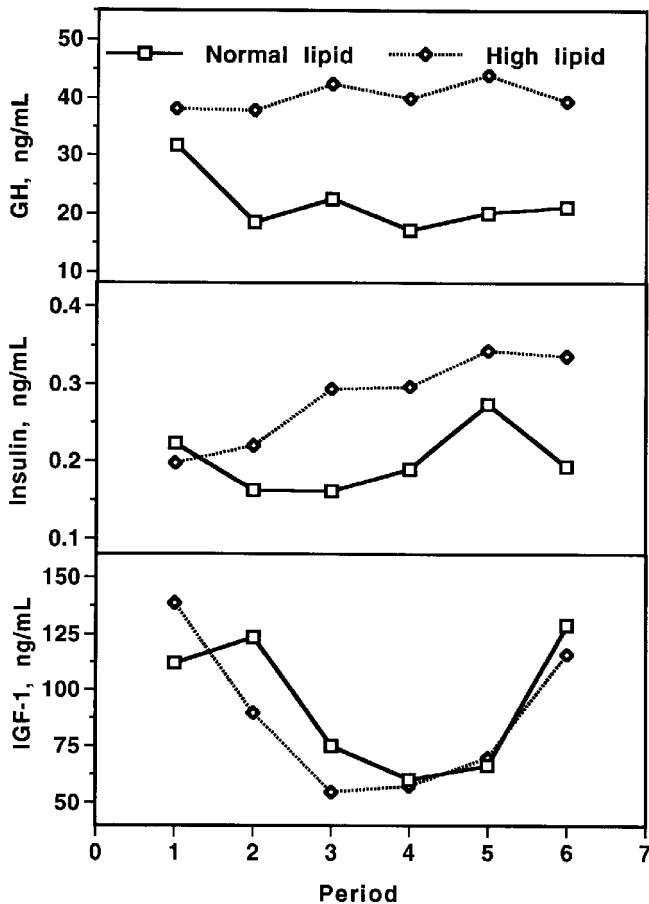


Figure 4. Circulating concentrations of growth hormone (GH), insulin, and IGF-I in undernourished (body condition score 4 on a 1–9 scale) postpartum beef cows fed control (Normal lipid) or high-fat (High lipid) diets beginning at parturition. Growth hormone was greater ($P < .05$) throughout and the postpartum increase of insulin secretion was modified from cubic to linear ($P < .05$) in the High Lipid compared to the Normal Lipid group. Serum IGF-I was not affected by diet but increased during period 5 when all cows were induced to ovulate. Each period represents 5 d. All diets were isocaloric and isonitrogenous (from Ryan et al., 1995 with permission).