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Long Chain Fatty Acids of Diet as Factors Influencing Reproduction in Cattle

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Contents

Cattle are fed moderate amounts of long chain fatty acids (FA) with the objective to enhance lactation and growth; however, recent interest on lipid feeding to cows has focused on reproduction, immunity and health. Increasing the caloric density of the ration by fat feeding has generally improved measures of cow reproduction, but when milk yield and body weight losses were increased by fat supplementation, positive effects on reproduction were not always observed. Feeding fat has influenced reproduction by altering the size of the dominant follicle, hastening the interval to first postpartum ovulation in beef cows, increasing progesterone concentrations during the luteal phase of the oestrous cycle, modulating uterine prostaglandin (PG) synthesis, and improving oocyte and embryo quality and developmental competence. Some of these effects were altered by the type of FA fed. The polyunsaturated FA of the n-6 and n-3 families seem to have the most remarkable effects on reproductive responses of cattle, but it is not completely clear whether these effects are mediated only by them or by other potential intermediates produced during rumen biohydrogenation. Generally, feeding fat sources rich in n-6 FA during late gestation and early lactation enhanced follicle growth, uterine PG secretion, embryo quality and pregnancy in cows. Similarly, feeding n-3 FA during lactation suppressed uterine PG release, and improved embryo quality and maintenance of pregnancy. Future research ought to focus on methods to improve the delivery of specific FA and adequately powered studies should be designed to critically evaluate their effects on establishment and maintenance of pregnancy in cattle.

Introduction

Ruminant diets are supplemented with fat primarily to increase energy concentration and to enhance animal performance. Dairy and beef cattle diets, without any supplemental fat, contain approximately 2% long-chain fatty acids (LCFA) of vegetable origin that are predominantly polyunsaturated. Because of the high energy density, fats are usually incorporated into cattle rations to improve production, growth and reproduction.

During early lactation, when lactating cows undergo a period of nutrient deficit, it was initially thought that incorporating supplemental fat to the diet would enhance energy intake and energy balance, which was expected to improve reproduction. Because early lactation cows mobilize large quantities of stored triacylglycerols in adipose tissue, concentrations of fatty acids (FA) in blood are usually high during the first weeks of lactation (Drackley 1999). This has been suggested to cause an unbalance in substrate supply to the cow, which compromises appetite and overall energy intake (Drackley 1999). When fat is fed in early lactation, often cows either consume less diet or production increases, therefore fat feeding early postpartum seldom alters energy status even though a more energy dense ration is consumed. Staples et al. (1998) indicated that feeding fat did not alter the energy status of dairy cows and suggested that reproductive responses were the result of supplying LCFA and altering substrate availability to the cow rather than simply an energy effect.

As with other nutrients, certain FA are essential for mammals. In 1929, George O. Burr and his wife were the first to describe the essentiality of FA in rats (Burr and Burr 1929, 1930). They observed that growing rats fed diets low in fat ceased growing and experienced health problems and irregular ovulation, which were then reversed after feeding fat sources rich in the polyunsaturated FA C18:2 n-6 (linoleic acid) and C18:3 n-3 (α-linolenic acid) (Burr and Burr 1930). Therefore, the concept of essential FA was established and later understood that C18:2 n-6 and C18:3 n-3 could not be synthesized by mammalian cells because of lack of desaturase enzymes beyond the 9th C in the acyl chain. Because of the essentiality of FA and the role of specific FA on reproductive processes, it is possible that reproduction in cattle may be more influenced by the type of fat fed than fat feeding *per se*. This is particularly important and challenging as ruminants extensively hydrogenate polyunsaturated FA, thereby limiting the supply of dietary unsaturated FA for absorption in the small intestine.

Feeding Fat and Fatty Acids to Cattle

Lipids are important molecules that serve as a source of energy and are critical components of the physical and functional structure of cells. Lipids present in cell membranes such as FA in phospholipids play an important role in regulating the properties and activities of cell membranes. Changes in chain length, degree of unsaturation and position of the double bonds in the acyl chain of FA can have remarkable impacts on their function and may play a role in reproduction in cattle (Staples et al. 1998; Mattos et al. 2000), although the exact mechanisms are still unclear. Potential mechanisms may include improved dietary energy density (Ferguson et al. 1990), altered follicle development (Staples and Thatcher 2005), increased concentrations of progesterone (Staples et al. 1998), suppressed luteolytic signals around maternal recognition of pregnancy (Mattos et al. 2000), and improved embryo quality (Cerri et al. 2004).

The use of fat in diets of dairy cattle usually increases the energy density of the ration and improves lactation and reproduction, although improvements in reproduction occur in spite of provision of calories (Staples et al. 1998). These effects might be mediated by the FA composition of the fat source; however, a

major impediment to the study of FA and reproduction in cattle is the inability to predict the delivery of specific lipids, particularly polyunsaturated FA to the small intestine for absorption, and the specific needs of different tissues for FA to modulate reproduction. Microbial activity in the rumen results in lipolysis of triacylglycerols and biohydrogenation of unsaturated FA which dramatically reduces the amount of polyunsaturated FA reaching the small intestine for absorption. In fact, Juchem (2007) demonstrated that more than 70% of the C18:2 n-6 and more than 85% of C18:3 n-3 fed to lactating cows were biohydrogenated in the rumen when fed as unprotected oils or as Ca salts of long chain FA (Ca-LCFA), respectively. Therefore, if specific unsaturated FA are important for reproduction in cattle, it is critical that future research with lipids and reproduction aim to improve the extent of delivery of unsaturated FA for absorption. In spite of the difficulties to deliver polyunsaturated FA to ruminants, studies have generally indicated that the polyunsaturated FA of the n-6 (linoleic acid) and n-3 [α-linolenic acid; eicosapentaenoic (EPA), C20:5 n-3; docosahexaenoic (DHA), C22:6 n-3] families are the most beneficial to improving reproduction in cows.

Fatty Acids and Postpartum Uterine Health

Uterine health is an important risk factor for subsequent fertility in lactating dairy cows. During the process of parturition, eicosanoids are produced in substantial amounts and play an important role in regulation and control of parturition, and expulsion of the placenta and uterine contents through opening of the cervix and contractions of the uterus. Prostaglandin $F_{2\alpha}$ is an important eicosanoid that regulates CL lifespan and might influence retention of foetal membranes and subsequent uterine health. Uterine synthesis of $PGF_{2\alpha}$ is regulated in part by substrate availability, and arachidonic acid (AA; C20:4 n-6) is the precursor for $PGF_{2\alpha}$ synthesis, so it is plausible to suggest that increments in AA content of endometrial tissue should enhance uterine $PGF_{2\alpha}$ secretion, which in turn may influence uterine health.

Burns et al. (2003) fed non-lactating beef cows n-3 FA from fish meal and reduced the endometrial concentration of AA and increased those of EPA and total n-3 FA. Similar effects have been observed with lactating dairy cows fed increasing amounts of fish meal or Ca-LCFA enriched in fish oil (Bilby et al. 2006b; Moussavi et al. 2007). Because of incorporation of n-6 and n-3 FA primarily in the phospholipid component of endometrial tissue, it is possible that changes in FA content of the endometrial tissue might modulate endometrial secretion of $PGF_{2\alpha}$ in cows. Feeding approximately 2% of the ration as fish oil rich in n-3 FA reduced the peripheral blood concentrations of $PGF_{2\alpha}$ metabolite (PGFM) indicating reduced uterine secretion of $PGF_{2\alpha}$ (Mattos et al. 2004). In contrast feeding supplemental fat pre-partum containing approximately 30% of FA as C18:2 n-6 increased uterine secretion of $PGF_{2\alpha}$ based on PGFM in blood (Cullens et al. 2004). Increased synthesis of $PGF_{2\alpha}$ when cows were supplemented with n-6 FA pre-partum might enhance the potential for uterine and immune cells to secrete eicosanoids which may influence postpartum uterine health and immuno-competence of the cow. Collectively, these data indicate that feeding fat sources differing in FA profile during the transition period can influence the natural release of $PGF_{2\alpha}$ by the uterus of the cow.

Three studies examined the effect of feeding fat pre-partum on postpartum health of dairy cows (Cullens et al. 2004; Juchem 2007; Silvestre, unpublished data). When cows were supplemented with Ca-LCFA rich in n-6 FA pre-partum, incidence of postpartum diseases including retained placenta, metritis and mastitis was reduced (8.3% vs 42.9%) compared with cows not fed fat pre-partum (Cullens et al. 2004). Juchem (2007) supplemented the diet of 501 pre-partum dairy cows with 2% Ca-LCFA of either palm oil or a blend of C18:2 n-6 and trans-octadecenoic FA. Incidence of retained placenta did not differ between treatments (6.6%). Risk of uterine disease was similar between sources of FA, but cows fed the blend of C18:2 n-6 and trans-octadecenoic FA had reduced the odds of puerperal metritis (8.8% vs 15.1%; adjusted odds ratio = 0.53). Rate of uterine involution did not differ, and 91% of the cows had completed uterine involution at the last ultrasonography on week 6 postpartum (Juchem 2007). In a similar attempt, Silvestre (unpublished data) fed 1167 pre-partum dairy cows 1.5% of the ration as Ca-LCFA of either palm oil or safflower oil. Feeding a fat source rich in C18:2 n6 enhanced measures of innate immunity; however, incidences of retained placenta (10.1%), metritis (17.4%), and purulent cervical discharge (29%) did not differ between treatments. These data suggest that, although feeding fat sources rich in n-6 FA may enhance immune responses and have pro-inflammatory effects, its impacts on uterine health are subtle.

Fatty Acids, Follicle Development and Resumption of Postpartum Cyclicity

One of the mechanisms by which fat feeding might improve fertility in cattle is by influencing follicle growth and ovulation (Lucy et al. 1993). Lucy et al. (1991) replaced corn with Ca-LCFA in the diet fed to dairy cows beginning at parturition, and feeding Ca-LCFA increased the number of medium (6–9 mm) sized follicles within 25 days postpartum, and that of follicles >15 mm in a synchronized oestrous cycle. In addition, diameter of the largest (18.2 vs 12.4 mm) follicle was greater in cows fed Ca-LCFA. When this study was repeated with isocaloric diets, similar effects were observed (Lucy et al. 1993). Staples and Thatcher (2005) summarized the effects of supplemental fats on the size of the dominant follicle (Table 1). On average, dominant follicle diameter was 3.2 mm larger, which represents a 23% increase in fat supplemented cows. Several studies have shown that dominant follicle diameter increased in cows fed diets enriched in polyunsaturated FA compared with monounsaturated FA, suggesting differential effects of FA on follicle growth (Staples et al. 2000; Bilby et al. 2006a). Follicles from cows abomasally infused with yellow grease

Table 1. Effect of supplemental fat on the diameter of the dominant ovarian follicle of lactating dairy cows (from Staples and Thatcher 2005)

Reference	Fat source	Experimental diets	
		Control (mm)	Fat (mm)
Ambrose et al. (2006)	Rolled flaxseeds	14.1	16.9
Beam and Butler (1997)	Tallow, yellow grease	11.0	13.5
Bilby et al. (2006a)	Ca-LCFA or flaxseed oil	15.0	16.5
Lucy et al. (1991)	Ca-LCFA	12.4	18.2
Lucy et al. (1993)	Ca-LCFA	16.0	18.6
Oldick et al. (1997)	Yellow grease	16.9	20.9
Robinson et al. (2002)	Protected soybeans	13.3	16.9
Staples et al. (2000)	Soybean oil, fish oil	14.3	17.1
Average		14.1	17.3

Ca-LCFA = Ca salts of long chain fatty acids from palm oil or a blend of palm and soyabean oils.
Control vs fat was $P < 0.10$ for each study.

grew faster to a larger diameter than follicles from cows infused with tallow (Oldick et al. 1997). It appears that fat feeding, but more importantly type of fat, stimulates follicle growth in cows. The impact of larger ovarian follicles on fertility because of fat supplementation has not been defined, but cows experiencing earlier postpartum ovulation have been reported to have larger follicles (Beam and Butler 1997). Therefore, it is possible that increasing the number and size of larger follicles by feeding fat can reduce the interval from calving to first postpartum ovulation, which has been observed for postpartum beef cows (Lammoglia et al. 1996, 1997; De Fries et al. 1998).

Although some studies have indicated that feeding fat hastens follicle growth, which might influence resumption of postpartum ovulation (Lammoglia et al. 1996, 1997; De Fries et al. 1998), it is unclear whether supplemental fats differing in FA profile have any differential effect on resumption of cyclicity. Juchem (2007) fed 699 multiparous cows either 400 g of FA from tallow or from Ca-LCFA containing palm and fish oils and observed no difference in proportion of cycling cows at 65 days postpartum (83.2% vs 82.2%, respectively). Subsequently, dairy cows supplemented with Ca-LCFA of palm oil or a blend of C18:2 n-6 and trans-octadecenoic FA from 25 days pre-partum to 80 days postpartum experienced a similar mean interval to first postpartum ovulation (30.5 and 32.2 days, respectively; Juchem 2007). Recently, Silvestre (unpublished data) fed cows (n = 1055) either Ca-LCFA of palm oil or of safflower oil from 2 weeks pre-partum to 4 weeks postpartum, and then half of the cows in each transition treatment group were switched to either Ca-LCFA of palm oil or fish oil (264/treatment). The proportions of cyclic cows at 63 days postpartum were 84.2%, 79.5%, 79.2% and 77.1% for cows fed palm oil/palm oil, palm oil/fish oil, safflower/palm oil, and safflower/fish oil, respectively, and they did not differ. Taken together, these data demonstrate that type of supplemental FA, whether more saturated or unsaturated does not influence resumption of postpartum cyclicity in lactating dairy cows.

Fatty Acids and Oestradiol

Oestradiol has stimulatory effects on uterine secretion of $PGF_{2\alpha}$ (Knickerbocker et al. 1986), and can increase the sensitivity of the CL to $PGF_{2\alpha}$ (Howard et al. 1990) which may enhance regression of the CL. Thus lowered plasma oestradiol may help prevent pre-mature CL regression and early embryonic mortality. Oldick et al. (1997) reported that abomasal infusion of tallow or yellow grease reduced concentrations of plasma oestradiol on days 15 to 20 of a synchronized oestrous cycle compared with cows infused with glucose, a response that also has been observed in beef cows supplemented with lipids (Hightshoe et al. 1991). Also, oestradiol concentration was reduced in the follicular fluid from beef cows fed soybean oil (Ryan et al. 1992). Although a reduction in follicular oestradiol caused by fat feeding might potentially benefit CL lifespan, it may be detrimental to expression of oestrus and uterine priming during prooestrus.

Fat and Luteal Function

Improved fertility in cattle has been associated with increased circulating concentrations of progesterone during the luteal phase before and after AI. Addition of fat to cattle diets has consistently shown to increase plasma cholesterol and cholesterol content in follicular fluid and in the CL (Staples et al. 1998; Williams 1989; Ryan et al. 1992; Hawkins et al. 1995; Lammoglia et al. 1996). Cholesterol serves as a precursor for the synthesis of progesterone by ovarian cells and both high and low density lipoproteins deliver cholesterol to ovarian tissues for steroidogenesis (Grummer and Carroll 1991). Hypercholesterolemia may increase CL steroidogenesis; however, the increased plasma progesterone concentrations in dairy and beef cows fed fat (Table 2) may be explained possibly by reduced progesterone clearance, not by increased synthesis (Hawkins et al. 1995).

Fatty Acids, Oocyte Quality and Membrane Composition

Competence of the oocyte and embryo is related to FA composition; specifically, phospholipid content of the cellular membrane plays a vital role in development during and after fertilization. The amount of lipid in the ruminant oocyte is approximately 20-fold greater than that of the mouse (76 vs 4 ng) and consists (w/w) of approximately 50% triacylglycerol, 20% phospholipid, 20% cholesterol and 10% free FA (McEvoy et al. 2000). Previous studies showed that C16:0 and C18:1 were the most abundant FA in the phospholipid fraction of oocytes from cattle and may function as an energy reserve (Kim et al. 2001; Zeron et al. 2001). Polyunsaturated FA comprised <20% of total FA, with C18:2 n-6 the most abundant of these.

Temperature modulates the physical properties of lipids in cell membranes and changes in lipid composition of the membrane. Zeron et al. (2001) reported that oocyte membrane fluidity and FA composition were affected by season. Furthermore, a relationship was documented between decreased polyunsaturated FA

Table 2. Effect of supplemental fat on plasma progesterone concentrations in dairy and beef cattle

Measurement	Progesterone, ng/ml		p <	Reference
	Control	Fat		
Dairy cows				
Peak concentration	6.0	8.1	0.08	Garcia-Bojalil et al. (1998)
Week 2 to 12 postpartum	4.2	4.8	0.05	Son et al. (1996)
Week 5 to 12 postpartum	4.5	6.0	0.05	Spicer et al. (1993)
Day 1 to 12 of oestrous cycle	4.2	5.2	0.05	Lucy et al. (1993)
Day 9 to 15 of oestrous cycle	6.6	7.7	0.05	Carroll et al. (1990)
Beef cows and heifers				
Peak concentration	15.5	14.2	NS	De Fries et al. (1998)
Days 12 to 13 of the EC	5.8	11.8	0.02	Hawkins et al. (1995)
Day 5 of the second EC	< 2.6	> 4.0	0.01	Lammoglia et al. (1997)
Weekly samples	7.6	10.3	0.01	Lammoglia et al. (1996)
Day 5 of FSH-induced EC	21.5	24.1	NS	Thomas and Williams (1996)

NS, not significant; EC, oestrous cycle.

content, a change in biophysical behaviour of oocytes, and low fertility of dairy cows during summer. Zeron et al. (2001) documented that monounsaturated and polyunsaturated FA contents were reduced in oocytes and granulosa cells in the summer compared with those from cattle in the winter season. The number of high quality oocytes increased in ewes fed polyunsaturated FA compared with those not fed fat (74.3% and 57.0%, respectively), and polyunsaturated FA supplementation increased the proportion of LCFA in the plasma and cumulus cells (Zeron et al. 2002). However, these FA changes were relatively small indicating that uptake of polyunsaturated FA by the oocyte is either selective or highly regulated, which might limit potential impacts of nutrition on FA composition of oocytes.

Fatty Acids and Embryo Quality and Development

Few studies have investigated the effects of fat supplementation on embryo quality and development in lactating dairy cattle. Fouladi-Nashta et al. (2007) fed lactating dairy cows either 200 or 800 g/day of Ca-LCFA of palm oil, and follicles were transvaginally aspirated, then matured, fertilized and cultured *in vitro*. A greater percentage of oocytes developed into blastocysts from cows fed the high fat diet and those blastocysts had more total cells, because of increased trophectoderm cell population. Although *in vitro* studies have shown an improvement in embryo development with dietary fat supplementation, it is not clear which particular FA is most beneficial. Bilby et al. (2006a) were unable to demonstrate differential effects of dietary FA on embryo quality after IVM and IVF with lactating cows in the summer. *In vitro* systems may not necessarily mimic *in vivo* responses, which might mask potential effects of source of FA on subsequent embryo development. Furthermore, cows were exposed to heat stress, which might compromise oocyte and subsequent embryo quality, thereby limiting potential benefits from different sources of FA (Bilby et al. 2006a).

When super-stimulated lactating cows were fed fat sources rich in saturated, n-6 or n-3 FA, fertilization rate and number of transferable embryos did not differ; however, embryo development was enhanced in cows fed the unsaturated compared with saturated FA (Thangavelu et al. 2007). Embryos from non-super-stimulated lactating cows had increased number of accessory spermatozoa and cells, percentage of live cells, and they were of better quality when cows were fed Ca-LCFA rich in C18:2 n-6 and trans-octadecenoic FA compared with cows fed Ca-LCFA of palm oil (Cerri et al. 2004). Embryos from gilts supplemented with a high-fat diet rich in C18:2 n-6 had increased number of nuclei after cryopreservation compared with gilts fed a low-fat diet (Kojima et al. 1996). Therefore, *in vivo* studies suggest that supplementing cows with unsaturated FA may improve embryo quality and development.

Fatty Acid Receptors and Intracellular Responses

Peroxisome proliferator-activated receptors (PPAR) are a family of nuclear receptors activated by selected LCFA, eicosanoids and peroxisome proliferators. Three PPAR isoforms, encoded by separate genes, have been identified thus far: PPARγ, PPARα and PPARδ which upon ligand binding, can affect transcription of target genes. The PPARδ is expressed in a wide range of tissues and cells including the endometrium, which is vital for normal fertility serving as a regulator of PG production and required for implantation in rodent models (Lim et al. 1999). MacLaren et al. (2006) reported similar expression of PPARα and PPARδ mRNA in bovine endometrium from cyclic and pregnant Holstein cows. Agonists of PPARδ/α had a dramatic stimulatory effect on PGH synthase (PGHS-2) mRNA levels and synthesis of $PGF_{2\alpha}$ and PGE_2, which appeared to be mediated at least in part through PPARδ (MacLaren et al. 2006). The authors hypothesized that PPARδ is involved in the pregnancy recognition process of cattle and that it mediates at least some of the beneficial effects of n-3 FA on fertility. Also, Balaguer et al. (2005) reported an inverse relationship between endometrial PPARδ mRNA concentration and that of oestrogen receptor-α and PGHS-2 in lactating dairy cows. The inverse relationship between these genes spawned further speculation that PPAR, PPARδ in particular, are mediators of uterine $PGF_{2\alpha}$ biosynthesis in dairy cattle. Therefore, it is possible that feeding FA that influence PPAR may regulate $PGF_{2\alpha}$ synthesis and possibly implantation owing to the beneficial effects of certain fat supplements on cattle fertility.

Uterine Prostaglandin Synthesis and Conceptus Interactions

Appropriate cross-talk of hormonal signals between maternal and conceptus tissues are required for successful establishment and maintenance of pregnancy. The endometrium plays a critical role in regulating the oestrous cycle and establishment of pregnancy primarily through processing of AA and synthesis of $PGF_{2\alpha}$.

Feeding n-3 FA can attenuate endometrial $PGF_{2\alpha}$ production. Feeding fish meal to dairy cows attenuated the decrease in plasma progesterone concentrations 2 days after $PGF_{2\alpha}$ injection suggesting changes in CL regression because of fish oil FA (Burke et al. 1996). Mattos et al. (2002) demonstrated that FA from fish meal reduced plasma PGFM concentrations compared with unsupplemented cows after an oestradiol/oxytocin challenge. Dairy cows fed fish oil during the transition period had greater EPA and DHA concentrations in caruncular tissues and reduced postpartum concentrations of PGFM compared with cows fed olive oil (Mattos et al. 2004). Conversely, feeding fat sources rich in n-6 FA increased plasma PGFM after an oxytocin challenge (Robinson et al. 2002; Petit et al. 2004). Thus supplemental lipids can either inhibit or stimulate PG secretion depending upon the specific FA.

Incubation of bovine endometrial cells with AA stimulated $PGF_{2\alpha}$ production compared with cells not supplemented with FA. On the other hand, cells supplemented with n-3 FA had reduced secretion of $PGF_{2\alpha}$ (Mattos et al. 2003). The mechanism by which n-3 FA inhibit $PGF_{2\alpha}$ secretion may involve decreasing the availability of AA precursor, increasing the concentration of FA that compete with AA for processing by PGHS-2, or inhibition of PGHS-2 (Mattos et al. 2000). Bilby et al. (2006b) concluded that n-3 FA supplementation to lactating dairy cows had little effect on the endometrial components that regulate the PG cascade. Instead EPA and DHA exerted their regulatory effects as alternative substrates that reduced the lipid pools of AA. In support of these conclusions, Burns et al. (2003) demonstrated that feeding fish meal reduced the endometrial concentration of AA and increased those of EPA and total n-3 FA. Therefore, different FA can alter $PGF_{2\alpha}$ secretion by influencing FA availability in the endometrial tissue, and supplying FA that inhibit $PGF_{2\alpha}$ release by the uterus might improve the mechanism of embryo preservation, which may benefit embryonic survival in cattle.

Fatty Acids and Fertility of Cows

Studies evaluating the effects of supplemental fat on reproductive performance of beef cattle are limited. To our knowledge, no controlled trials have been conducted with adequate number of animals to evaluate the potential for fat supplementation to impact establishment and maintenance of pregnancy of beef cows. De Fries et al. (1998) observed a tendency ($p = 0.09$) for increased pregnancy in Brahman cows fed 5.2% fat compared with cows fed 3.7% fat in the diet; however, the number of cows used in this study was limited to only 20 per treatment.

Feeding fat to dairy cattle might improve pregnancy per AI (Table 3), although responses have not been consistent. When fat feeding increased postpartum body weight loss, primiparous cows fed fat had reduced pregnancy at first AI (Sklan et al. 1994). However, Ferguson et al. (1990) observed a 2.2-fold increased odds (odds ratio = 2.2) of becoming pregnant at first and all AI in lactating cows fed 0.5 kg/day of fat, which tended ($p = 0.08$) to enhance the proportion of pregnant cows at the end of the study (93% vs 86.2%). In grazing cows, supplementation with 0.35 kg of FA improved pregnancy after the first postpartum AI, although the proportion of cows pregnant at the end of the study did not differ (McNamara et al. 2003). Feeding Ca-LCFA of palm oil improved pregnancy of dairy cows (Schneider et al. 1988; Sklan et al. 1991), but the authors did not report statistical significance. On the other hand, others did not observe improvements on fertility of dairy cows supplemented with Ca-LCFA (Sklan et al. 1994; Scott et al. 1995) or oilseeds (Schingoethe and Casper 1991), which might be attributed to increased milk yield and body weight losses (Sklan et al. 1991, 1994).

Table 3. Effect of fat supplementation on pregnancy at first postpartum AI in lactating dairy cows

Reference	Cows	Fat source and amount	Pregnancy per AI, %	
			Control	Fat
Ferguson et al. (1990)	253	0.5 kg of saturated free FA	42.6	59.1*
McNamara et al. (2003)	201	0.32 to 0.36 kg of FA from Ca-LCFA	35.5	51.1*
Schingoethe and Casper (1991)	153	Oilseeds	46.5	42.0
Schneider et al. (1988)	181	0.5 kg of Ca-LCFA	43.1	60.5
Scott et al. (1995)	443	0.45 kg of Ca-LCFA	49.3	45.7
Sklan et al. (1991)	99	2.6% of ration as Ca-LCFA	41.5	39.2
Sklan et al. (1994)	102	2.5 of ration as Ca-LCFA		
		Primiparous	73.7*	33.3
		Multiparous	42.1	33.3

FA = fatty acid; Ca-LCFA = Ca salts of long chain fatty acids from palm oil.
*Within a row, effect of supplemental fat ($p < 0.05$).

Because the benefits of feeding fat may originate from specific FA (Staples et al. 1998; Staples and Thatcher 2005), and absorption of unsaturated FA is limited in ruminants because of microbial biohydrogenation in the rumen (Juchem 2007), studies have evaluated whether feeding FA differing in the degree of saturation might influence fertility of dairy cows (Table 4). When cows were fed 0.75 kg of fat from flaxseed, a source rich in C18:3 n-3, or sunflower seed, a source rich in C18:2 n-6, pregnancy tended ($p = 0.07$) to be greater for cows fed n-3 FA (Ambrose et al. 2006). However, a similar response to flaxseed was not observed by others (Petit and Twagiramungu 2006; Fuentes et al. 2008). Similarly, feeding n-3 FA from fish oil as Ca-LCFA did not improve pregnancy at first postpartum AI when compared with feeding beef tallow (Juchem 2007) or with Ca-LCFA of palm oil (Silvestre, unpublished data), although pregnancy at second postpartum AI was greater for cows fed n-3 FA (Silvestre, unpublished data). Juchem (2007) evaluated the effect of feeding pre- and postpartum cows Ca-LCFA of palm oil or a blend of C18:2 n-6 and trans-octadecenoic FA. Cows fed unsaturated FA were 1.5 times more likely to be pregnant at 27 or 41 days after AI compared with cows fed palm oil. Improvements in pregnancy when cows were fed Ca salts of a mix of C18:2 n-6 and *trans*-octadecenoic FA were supported by increased fertilization and embryo quality in non-superovulated lactating dairy cows (Cerri et al. 2004).

Table 4. Effect of fatty acid (FA) supplementation on pregnancy per AI in lactating dairy cows

			FA source – Pregnancy per AI, %		
Reference	Cows	Amount/day	Saturated	n-6 FA	n-3 FA
Ambrose et al. (2006)	121	0.75 kg of fat	–	32.2	48.4**
Fuentes et al. (2008)	356	0.40 kg of fat	–	39.2	38.8
Juchem (2007)	699	0.40 kg of FA	40.7	–	35.9
Juchem (2007)	323	0.40 kg of FA	22.8	–	24.8
Juchem (2007)	344	2% of ration	28.6	37.9**	–
Petit and Twagiramungu (2006)	110	0.6–0.8 kg of FA	55.9	40.0	44.4
Silvestre (unpublished data) – first AI	1055	1.5% of ration			
		Transition	39.0	35.9	–
		> 30 d postpartum	37.3	–	37.6
Silvestre (unpublished data) – second AI	604	1.5% of ration			
		Transition	29.0	34.5	–
		> 30 d postpartum	27.2	–	37.0*

Saturated = mostly saturated and monounsaturated FA; n-6 FA = source rich in C18:2 n-6; n-3 FA = source rich in C18:3 n-3 or C20:5 n-3 + C22:6 n-3.
*Within a row, effect of source of FA ($p < 0.05$).
**Within a row, effect of source of FA ($p < 0.07$).

Table 5. Effect of fatty acid (FA) supplementation on pregnancy losses after first postpartum AI in lactating dairy cows

			FA source – Pregnancy loss, %		
Reference	Pregnancies	Amount/day	Saturated	n-6 FA	n-3 FA
Ambrose et al. (2006)	77	0.75 kg of fat	–	27.3	9.8*
Juchem (2007)	257	0.40 kg of FA	20.4	–	23.5
Juchem (2007)	77	0.40 kg of FA	5.4	–	10.0
Juchem (2007)	114	2% of the ration	9.8	6.3	–
Petit and Twagiramungu (2006)	51	0.6–0.8 kg of FA	21.1	12.5	0*
Silvestre (unpublished data)	388	1.5% of ration			
		Transition	8.3	12.1	–
		> 30 d postpartum	13.6	–	6.3*

Saturated = mostly saturated and monounsaturated FA; n-6 FA = source rich in C18:2 n-6; n-3 FA = source rich in C18:3 n-3 or C20:5 n-3 + C22:6 n-3.
*Within a row, effect of source of FA ($p < 0.05$).

Because n-3 FA can suppress uterine secretion of $PGF_{2\alpha}$ (Mattos et al. 2002, 2003, 2004), it may improve embryonic survival in cattle (Mattos et al. 2000). In three of five experiments, feeding the n-3 FA C18:3 n-3 (Ambrose et al. 2006; Petit and Twagiramungu 2006) or EPA and DHA (Silvestre, unpublished data) reduced pregnancy losses in lactating dairy cows (Table 5). On the other hand, when n-6 FA were fed as Ca-LCFA, pregnancy losses were similar to those observed for cows fed Ca-LCFA of palm oil (Juchem 2007; Silvestre, unpublished data).

Collectively, these data suggest that feeding fat to dairy cows generally improves fertility and responses are observed with the energy increment in the diet; also, these data suggest that fertility responses to fat feeding are altered according to the type of dietary FA, although responses are not always consistent. Feeding n-3 FA from flaxseeds or as Ca-LCFA improved pregnancy per AI in some, but not all studies. Similarly, feeding Ca-LCFA rich in n-6 FA improved pregnancy per AI in one of two experiments with lactating dairy cows. Although feeding n-3 FA has not consistently increased the risk of pregnancy, it has reduced pregnancy losses in dairy cows.

Conclusions

Fat is recommended to be incorporated into dairy cattle diets at moderate amounts. Feeding fat to cattle generally improved establishment and maintenance of pregnancy, but benefits to fertility can be negated when weight losses are exacesbated by fat feeding. Potential improvements in fertility of cows caused by fat feeding have generally been associated with enhanced follicle development postpartum, increased diameter of the ovulatory follicle, increased progesterone concentrations during the luteal phase of the cycle, altered uterine/embryo cross-talk by modulating PG synthesis, and improved oocyte and embryo quality. Some of these effects have been more influenced by the type of fatty acid than by fat feeding *per se*. Differential responses *in vivo* to FA feeding suggest that unsaturated FA of the n-6 and n-3 families were most beneficial.

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