Effect of Feeding Calcium Soaps to Early Postpartum Dairy Cows on Plasma Prostaglandin $F2_a$, Luteinizing Hormone, and Follicular Growth[1]

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ABSTRACT

Multiparous Holstein cows (n = 18) were fed a total mixed ration containing corn silage, corn grain, whole cottonseed, soybean meal, dried distillers grains, and chopped bermudagrass hay (control) or same diet plus Ca salts of long-chain fatty acids (2.2% of diet DM) for the first 60 d postpartum. Predicted energy balance was calculated from DM intake, milk yield and composition, and BW. On d 25 postpartum, cows were injected with 25 mg of prostaglandin Fl_a and treated for 15 d with an intravaginal device containing 1.9 g progesterone. Profiles of 15-keto-13,14-dihydro-prostaglandin $F2_a$ (d I to 21) and plasma triglycerides (d 7 to 60) were similar between groups. Average number of follicles, determined by ultrasonography prior to d 25, tended to differ between groups; controls had more 3- to 5-mm and fewer 6- to 9-mm follicles than the group of fat-fed cows. Basal, smoothed mean concentration, and average luteinizing hormone amplitude, determined by 10-min samples for 8 h on d 10, were not significantly different between groups. Increasing predicted energy balance was associated with increased pulse amplitude and diameter of the largest follicle on d 10. During the progesterone treatment period and the postprogesterone treatment estrous cycle, cows fed fat had greater numbers of 3- to 5-mm and >15-mm follicles. In conclusion, feeding fat did not influence 15-keto-13,14-dihydro-prostaglandin Fl_a or luteinizing hormone dynamics but did alter the average number of follicles within different size classes and the diameter of largest and second *largest* follicle after progesterone treatment.
(Key words: follicle, fatty acids, prostaglandin $F2_a$)

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Abbreviation key: C = control group, Ca-LCFA = Ca salts of long-chain fatty acids, CIDR-B = controlled internal drug release — bovine, LCFA = long-chain fatty acids, PBS = phosphate-buffered saline, $PGF2_a$ = prostaglandin $F2_a$, PGFM = prostaglandin $F2_a$ metabolite.

INTRODUCTION

Strategic feeding regimens (17, 26), including use of Ca salts of long-chain fatty acids (Ca-LCFA), have *been used as* a method to alleviate a portion of the dietary energy deficit experienced by early postpartum dairy cows (2, 6). The Ca-LCFA provide higher energy density without *depressing ruminal* microbial function (4, 5, 9, 16, 22, 30). Dietary ingredients used to alleviate negative energy balance may yield important benefits to the reproductive health of the cow. Postpartum anestrus, associated with extreme negative energy balance (3, 28), may be alleviated partially by feeding of energy-rich additives similar to Ca-LCFA. These may modulate the recrudescence of hypothalamic and pituitary function (and therefore ovarian activity) through effects on the overall

energy status of the cow. Furthermore, greater fat ingestion may have direct effects on ovarian structures [i.e., follicles and corpora lutea; (24, 34)].

In addition to their more obvious effects on energy balance (EB), LCFA may increase postpartum release of uterine prostaglandin Fa_x, ($PGF2_a$), which has *been implicated as an* important modulator in the initiation of estrous cycles after calving (10, 12, 19, 32). One practical method to increase $PGF2_a$ (tested in nonfarm species) is feeding dietary precursor molecules of $PGF2_a$, [linoleic acid or arachi-donic acid; (1, 7, 20)]. Augmenting postpartum PGF2, concentrations and enhancing ovarian function by feeding various forms of LCFA to cows may be possible. The objectives of this study were 1) to measure plasma PGF_{2a}, metabolite (PGFM) and triglyceride concentrations in lactating cows fed diets with or without Ca-LCFA, 2) to relate Ca-LCFA ingestion to LH secretion on d 10 postpartum, and 3) to monitor follicular populations in control and Ca-LCFA fed cows from d 7 to 60 postpartum.

MATERIALS AND METHODS

Animals

Eighteen multiparous Holstein cows were assigned to one of two diets. These are the same cows from diets 3 and 4 from the companion paper (18). The control (C) group was fed a totally mixed diet consisting of corn silage, corn *grain, soybean* meal, whole cottonseed, dried distillers grains, and chopped bermudagrass hay (1.70 Mcal NEI/kg of DM). The experimental cows were fed the same diet as C cows, except that Ca salts of palm oil (Ca-LCFA; 44% palmitic, 5% stearic, 40% oleic, 9.5% linoleic acids; Megalac; Church and Dwight Co., Inc., Princeton, NJ) were included at 2.2% of diet DM (1.75 Mcal NE/kg DM). Daily predicted EB was determined for all cows (18).

Reproductive Management and Ultrasound

On d 25, all cows were injected with 25 mg of $PGF2_a$ (Lutalyse; Upjohn Co., Kalamazoo, MI) to *induce* corpus luteum regression. On the same day, an intravaginal device [controlled internal drug release—bovine (CIDR-B); Eazi-Breed, AHI Plastic Co., New Zealand) containing a total of 1.9 g of progesterone was inserted into the vagina of each cow to prevent subsequent ovulation. On d 40 postpartum (15 d after initial insertion), CIDR-B devices were removed, and a synchronous ovulation was anticipated.

Ovaries were examined by ultrasonography on d 7, 16, 18, 20, 22, and 25 after calving (pre-CIDR-B); d 30, 35, and 40 after calving (during ClDR-B), and d 6, 12, and 18 of the first estrous cycle after CIDR-B removal. Ultrasonic examination *was* performed as previously described (18).

Blood Collection and Analyses

Ten milliliters of blood were collected by coccygeal venipuncture from all cows on d 1 through 21 postpartum (calving = d 0). On the morning of d 10 postpartum, 16 cows were fitted with a jugular cannula (16-gauge, 13.3-cm Angiocath, Becton Dickinson, Rutherford, NJ), and 10 ml of blood were collected every 10 min for 8 h. Individual samples were mixed with 50 U of sodium heparin (Sigma Chemical Co., St Louis, MO), and plasma was processed as described previously (18).

Plasma PGFM was measured on d 1, every other day until d 21, and on d 25, 30, 35, and 40. Competitive binding radioimmunoassay was performed on nonextracted samples as described previously (11). Intraassay and inter-assay CV were 7.9 and 10.9%, respectively. Plasma estradio1-170 was measured on d 7, 16, 20, 25, 30, 35, and 40 postpartum by radioimmunoassay (12). Interassay and intraassay CV were 2.4 and 8.2%, respectively.

Plasma LH was measured by radioimmunoassay in samples collected during the frequent bleeding on d 10 postpartum. Plasma (200 µI) was diluted in phosphate-buffered saline (PBS) and incubated with 100 µI anti-LH (USDA-309-684p; 1:75,000 dilution in PBS) for 24 h at 23°C. On d 2, 100 µ.1 of PBS containing approximately 20,000 cpm [^{1}u1]LH (USDA-bLH-I-1) were added and the incubation continued for an additional 24 h at 23°C. Precipitation of the antibody complexes was performed on d 3 with addition of 200 µI of sheep anti-rabbit gamma globulin serum (1:5 dilution) and 1 ml of 6% (wt/vol) polyethylene glycol-6000. After a 15-min incubation, assay tubes were *centri-*

fuged for 30 min at 3000 x *g*. Supernatant was decanted, and gamma emissions from the precipitate were counted for 1 min. Concentration of LH in unknown samples was estimated from a standard curve (.02, .03, .06, .13, .25, .5, 1, 2, and 4 ng/tube) using bLH (USDA-bLH-B5). Cross reactivities were: 1.0% for USDA-bFSH-Bl; 1.1% for USDA-bGH-B1; .002% for USDA-bPRL-B1; and .5% for USDA-bTSH-Il. Increasing volume of cow plasma (50, 100, 200, and 300 µI) resulted in a displacement curve that was parallel to the standard curve (tested by heterogeneity of regression (P>.10)). Addition of different masses (X = 31.2, 125, 500, 1000, and 2000 pg) of bLH resulted in linear recovery of mass (Y; R^2 = .98) at assay volumes of 50 µI (Y = .20 + 1.08X), 100 µI (Y = .29 + .92X), 200 µ1 (Y = .33 + .93X), and 300 µI (Y = .44 + .92)Q. Concentration of LH in unknown samples represented the average of two replicates. Intraassay and interassay CV were 10.9 and 13.4%, respectively.

Plasma triglyceride concentration was measured by a calorimetric Hantzsch condensation reaction as described initially by Foster and Dunn (8). Concentration of plasma triglyceride in samples was estimated by comparing light absorbance at 405 nm with a triolein standard curve (Sigma Chemical Co., St. Louis, MO).

Statistical Analysis

Plasma concentration of PGFM, estradiol-1713, and triglyceride were analyzed using the general linear models procedure (PROC GLM) of SAS (25). The statistical model included treatment (diet), animal within treatment, day postpartum, treatment by day interaction, and residual. Plasma PGFM concentration during the first 21 d postpartum were analyzed by tests for heterogeneity of regression for third-order fitted curves (33). Plasma LH on d 10 was subjected to the PULSAR algorithm (21) for determination of number of LH peaks, magnitude of peaks, and smoothed basal concentration. These responses were analyzed using PROC GLM in a model that included the main effect of treatment. Ovarian follicles were grouped into four size (diameter) classes. Total number of follicles in class 1 (3 to 5 mm), class 2 (6 to 9 mm), class 3 (10 to 15 mm), and class 4 (>15 mm) were analyzed in models that included treatment, cow within treatment, class, day postpartum, all second- and third-order interactions, and residual. Data were analyzed separately for measurements made before CIDR-B insertion (<d 25), during CIDR-B usage (d 25 to 40 postpartum), and during the post-CIDR-B estrous cycle on d 6, 12, and 18. Size of the largest and second largest follicles and difference between the two were analyzed using a model containing the main effects of treatment, animal within treatment, day postpartum, treatment by day interaction, and residuaL Significance was P<.10 unless otherwise noted.

RESULTS

Plasma Hormones and Metabolites

Concentration of plasma triglyceride across all sampling days was not different between cows fed Ca-LCFA (24.2 mg/100 ml [SE = 2.4]) and control cows (20.6 mg/100 ml [SE = 2.1]). Across treatments, plasma triglyceride increased with day postpartum (P<.001) from a minimum of 14.8 mg/100 ml (SE = 2.4) on d 16 to a maximum of 28.4 mg/100 ml (SE = 3.1) on d 60. Mean plasma PGFM concentration was highest on d 3 postpartum (2209.5 pg/ ml [SE = 172.5]) and declined (P<.001) thereafter to 78.4 pg/ml (SE = 168.6) on d 21. Average concentrations of PGFM on d 1 to 21 was not different between Ca-LCFA and C cows. Mean concentration of PGFM from d 25 to 40 was similar between Ca-LCFA (298.3 pg/ ml [SE = 116.4]) and C (102.6 pg/ml [SE = 12.8]) cows. A treatment by day interaction was detected (P<.07) because of an apparent rise in PGFM concentration in Ca-LCFA cows (738 pg/ml) compared with C cows (84.4 pg/ ml) on d 35. This was caused by high PGFM values in two of nine Ca-LCFA-fed cows.

As determined by the PULSAR algorithm, no difference was noted on d 10 postpartum between C cows and Ca-LCFA-fed cows in average LH concentration (406 [SE = 94] vs. 576 [SE = 109] pg/ml; C vs. Ca-LCFA, respectively), baseline LH concentration (264 [SE = 71] vs. 443 [SE = 104] pg/ml), the number of LH peaks per 8 h (9.5 [SE = 1.1] vs. 8.4 [SE = .8]), amplitude of LH peaks (331 [SE = 81] vs. 448 [SE = 78] pg,/m1), or residual variance for LH secretion. Across treatments, increasing predicted EB was associated with an increase in

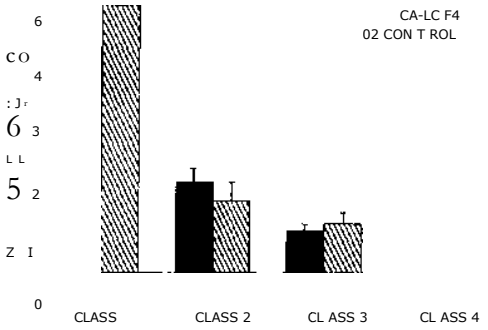

Figure 1. Average number of follicles within different follicle size classes (class 1, 3 to 5 mm; class 2, 6 to 9 mm; class 3, 10 to 15 mm; class 4, >15 mm) before d 25 postpartum for lactating dairy cows fed diets with and without calcium salts of long-chain fatty acids (Ca-LCFA).

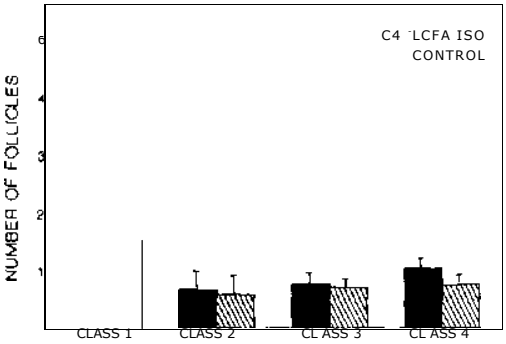

Figure 2. Average number of follicles within different follicle size classes (class 1, 3 to 5 mm; class 2, 6 to 9 mm; class 3, 10 to 15 mm; class 4, >15 mm) during the controlled internal drug release period (d 25 to 40 postpartum) for lactating dairy cows fed diets with and without calcium salts of long-chain fatty *acids* (Ca-LCFA).

the average pulse amplitude on d 10 (ampl = 339.9 + 25.3 x EB, R^2 = .23; P<.06). In addition, diameter of the largest follicle increased with LH pulse amplitude on d 10 (diameter = 7.1 + .0085 x ampl, R^2 = .34; P<.02) and increasing EB on d 10 was associated with an increase in the diameter of the largest follicle (diameter = 9.24 + .56 x *EB,* R^2 = .48; P<.004). Furthermore, day of detection of the first corpus luteum occurred earlier as average predicted EB (before d 25) increased (corpus luteum d = 19.2 — .30 x EB, R^2 = .31, P<.06).

Plasma estradio1-1715 before d 40 postpartum increased with day postpartum (day, P<.001) but was not different between control cows and cows *fed* Ca-LCFA. For all cows, plasma es-tradio1-1713 increased from a minimum of 7.4 pg/ml (SE = .7) on d 7 to 11.1 pg/ml (SE = .7) on d 35. Maximum estrogen secretion on d 35 apparently was associated with follicular dynamics (e.g., increased size of largest follicle during CIDR-B period; Table 1).

Follicle Development

Daily average number of class 1 to 4 follicles per cow from d 7 to 25 are given in Figure 1. Prior to d 25, the diet by follicular size class interaction approached significance *(P* = .13). Control cows had more class 1 and fewer class 2 and 4 follicles. The number of cows ovulating before insertion of the CIDR-B was equivalent (7 of 9) for each treatment group. The relationship among average number of follicles with size classes was reversed partially during the CIDR-B period (d 25 to 40; Figure 2) with Ca-LCFA cows having more *class* 1 and 4 follicles (treatment by class, *P* = .03). After removal of the CIDR-B, seven Ca-LCFA cows and five C cows had an ovulation. A significant treatment by class interaction (P<.03) was noted, with Ca-LCFA-fed cows having more class 1 and 4 and fewer class 2 follicles (Figure 3). Average number of class 4 follicles was 3.4 times higher (.71 vs. .21) in Ca-LCFA-fed cows during the estrous cycle after CIDR-B removal.

The average diameter of the largest and second largest follicles and size *difference between* them before, during, and after the CIDR-B is presented in Table 1. Before the CIDR-B, the average size of the largest and second largest follicle increased with day postpartum (P<.01) and was not different between cows fed C or Ca-LCFA diets. Size difference was not influenced by day postpartum. For all days prior to C1DR-B insertion, the largest, second largest, and size difference were 11.0, 6.5, and 4.6 mm, respectively, for C cows and 12.5, 7.3, and 5.3 nun, respectively, for Ca-LCFA-fed cows.

During the CIDR-B period, no effect of day or dietary treatment was found on the diameter of the largest follicle, or second largest follicle, or the size difference. These measures averaged 16.9, 8.4, and 8.6 mm, respectively, for C cows and 19.1, 9.9, and 9.3 mm, respectively, for Ca-

LCFA-fed cows. In contrast, during the first estrous cycle after CIDR-B removal, the average size of the largest (18.2 vs. 12.4 mm) and second largest (10.9 vs. 7.4 mm) follicle was greater (P<.04, P<.07, respectively) in cows fed Ca-LCFA compared with C cows. Size difference was not influenced by treatment during this period (5.0 vs. 7.3 mm; C vs. Ca-LCFA).

DISCUSSION

Profiles of plasma PGFM were not different between the two groups. This suggests that LCFA in the proportions given did not influence PGF production or metabolism. This could be a result of the relatively low concentration of linoleic acid (9.5%; arachidonic acid precursor) in the Ca-LCFA mixture. Other feeds (including fish meal and fish oils; 27) contain high concentration of arachidonic acid and may be more effective in altering PGF dynamics. Possibly, $PGF2_a$ secretion in early postpartum cattle is at a maximum for each individual cow, and changes in dietary precursors may be ineffective at this time. However,

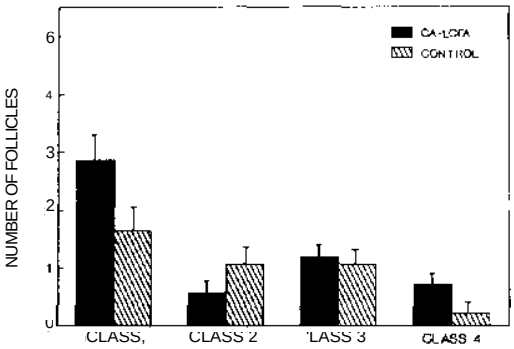

Figure 3. Average number of follicles within different follicle size classes (class 1, 3 to 5 mm; class 2, 6 to 9 mm; class 3, 10 to 15 mm; class 4, >15 mm) during an estrous cycle (d 6, 12, and 18) after removal of the controlled internal drug release device for lactating dairy cows fed diets with and without calcium salts of long-chain fatty acids (Ca-LCFA).

an interaction (treatment by day) for plasma PGFM concentration in the CIDR-B period (d 25 to 40) was detected. This could indicate that when basal intake of LCFA is *greater,* PGF

TABLE 1. Average diameter (mm) of the largest follicle (largest), second largest follicle, and difference between the largest and second largest follicle (difference) determined by ultrasound in lactating dairy cows fed diets without (control; C) or with calcium salts of long-chain fatty acids (Ca-LCFA).

		Largest		Second largest		Difference	
Period	Day	C	Ca-LCFA		Ca-LCFA		Ca-LCFA
Pre-CIDR-B							
	7	6.1	9.0	4.2	5.7	1.9	3.3
	10	9.8	11.9	5.5	7.6	4.3	4.3
	16	13.2	112	5.9	6.1	7.3	5.1
	18	12.9	13.0	5.9	8.3	7.0	4.7
	20	12.2	13.1	6.8	6.9	5.3	62
	22	11.6	13.6	8.7	7.3	2.9	6.4
	25	11.4	15.6	8.1	8.9	3.3	6.7
Pooled SE		1.5		1.1		1.6	
CIDR-B							
	30	17.3	18.3	7.2	82	10.1	10.1
	35	15.9	19.1	7.8	102	8.1	8.9
	40	17.7	19.9	10.1	11.1	7.6	8.8
Pooled SE		1.4		15		1.9	
Post-CIDR-B							
Cycle day	6	11.6	15.4	6.4	10.1	52	5.3
	12	12.1	21.0	8.8	9.5	3.3	11.4
	18	13.4	18.3	7.0	13.1	6.4	5.1
Pooled SE		15		12		1.8	

'Largest follicle, Ca-LCFA > control, P<.04. Second largest follicle, Ca-LCFA > control, P<.07. CIDR-B = controlled internal drug release-bovine.

secretion will increase at certain times in certain cows, perhaps through enhanced production. This increased concentration corresponded to a period of maximal estradiol secretion in these cows and estradiol is a potent releaser of $PGF2_a$ (31). Lower overall requirements for turnover of body LCFA stores found in Ca-LCFA-fed cows (26) potentially could conserve precursors for $PGF2_a$ synthesis leading to higher $PGF2_a$ between 25 to 40 d postpartum.

Plasma LH concentrations on d 10 were not influenced significantly by diet, but were influenced apparently by overall predicted EB among cows. Generally, increasing predicted EB was associated with increasing LH pulse amplitude and increasing diameter of the largest follicle on d 10 postpartum. This finding supports work by others (29) who related plasma LH concentration in early postpartum cows to differences in milk production (a less accurate indicator of energy status). We found that although feeding Ca-LCFA altered our estimation of EB (18), its effect on LH secretion was not detectable by d 10 postpartum. However, because basal LH secretion seems to be dependent on predicted EB, feeding regimens aimed at increasing EB early postpartum could be beneficial in terms of restoring ovarian function. Examination of LH profiles of a greater number of cattle and later postpartum (e.g., d 15) will be necessary to clarify the relationship between LH, EB, and Ca-LCFA.

Feeding Ca-LCFA influenced the number of follicles within each size class at all times during the experiment. During the early postpartum period (<d 25), changes in follicle numbers were consistent with the theory that a more positive EB causes movement of follicles from smaller to larger size classes (18). Indeed, prior to d 25, cows fed Ca-LCFA had more class 2 and fewer class 1 follicles. This movement probably is responsible for earlier ovulation in cows having more positive energy status. After d 25 (C1DR-B and post-CIDR-B), effects of Ca-LCFA feeding were consistent in that cows fed Ca-LCFA had more class 1 and 4 follicles. This suggests that once estrous cycles have been initiated, effects of Ca-LCFA are quite different in that Ca-LCFA influences the number of follicles in all classes. Of interest was the higher proportion of class 4 follicles and the greater size of largest and second largest follicles found in cows fed Ca-LCFA during the post-CIDR-B period. This was seen even when cows fed Ca-LCFA were compared with a much larger group of cows (n = 50; 18). Increased incidence of follicles greater than 15 mm (class 4) may be a result of slower follicular turnover or enhanced follicular growth. Cholesterol-LCFA esters are a critical component of follicular steroidogenesis associated with the maturation of dominant follicles (13). Therefore, LCFA may influence these events. Alternatively, insulin, growth hormone, or other metabolic hormones possibly altered by Ca-LCFA feeding may be involved. Recent evidence relating circulating and intrafollicular growth factors and insulin to changes in ovarian dynamics suggests the importance of these peripheral signals (14, 23).

Finally, class 4 follicles in these cows apparently were physiologically active, because class 2 follicle frequency was reduced within the Ca-LCFA group (see d 48 to 60; d 6, 12, and 18 of the estrous cycle; Figure 3). The ability of larger follicles to influence the growth of smaller follicles is a phenomenon known as follicular dominance and is characteristic of physiologically functional follicles (15). This phenomenon seems to be operative in large dominant follicles of cows fed Ca-LCFA in this trial, and this may have caused a reduction in the number of medium-sized follicles that we observed.

In conclusion, feeding Ca-LCFA did not alter plasma PGFM concentration early postpartum. The LH pulse amplitude on d 10 was not higher in cows fed Ca-LCFA but was related positively with predicted EB and size of the largest follicle. Feeding of Ca-LCFA altered number of follicles within size classes and increased the average size of largest and second largest ovarian follicles later postpartum. These large follicles apparently were active based on their ability to influence the average number of class 2 follicles during the estrous cycle after the CIDR-B. Whether this stimulation in follicular growth is complementary or antagonistic to reproductive events after the restoration of estrous cycles in the postpartum period warrants further detailed investigation.

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