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Supplementing calcium salts of soybean oil to beef steers early in life to enhance carcass development and quality[1]

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Abstract

This study evaluated the effects of supplementing Ca salts of soybean oil (**CSSO**) to beef steers at 2 mo of age via creep-feeding, and/or during a 40-d preconditioning period on performance and carcass development responses. A total of 64 steers were enrolled in this study over 2 yr (32 steers per year), with 4 periods each year: creep-feeding (**CF**; day 0 to 60), preweaning (day 61 to weaning on day 124 and 127 of year 1 and 2, respectively), preconditioning (**PC**; day 132 to 172 in year 1 and day 135 to 175 of year 2), and feedlot (feedlot arrival to slaughter, day 173 to 378 in year 1 and day 176 to 385 in year 2). On day 0 steers were ranked by body weight (**BW**) and age (114 ± 4 kg of BW; 66.1 ± 0.9 d of age) and allocated to 1 of 16 pens. Pens were randomly assigned to receive CSSO during CF (80 g/d per steer) and/or PC (150 g/d per steer) in a 2 × 2 factorial arrangement of treatments. During CF and PC, nonsupplemented steers (**CON**) were provided an isolipidic prilled saturated fat supplement. Steer BW was recorded on day 0, 60, at weaning, and prior to feedlot shipping. Carcass traits were recorded upon slaughter. On day 0, 60, at weaning, prior to feedlot shipping, and during the feedlot period, blood samples were collected and *longissimus* muscle (**LM**) biopsies were collected. On day 60, steers that received CSSO during CF had greater ($P < 0.01$) plasma concentrations of linoleic and ω-6 compared with CON (CF treatment × day; $P \leq 0.05$). Steers that received CSSO during PC had greater ($P < 0.01$) plasma concentrations of linoleic, ω-6, and total fatty acids compared with CON at feedlot shipping (PC treatment × day; $P \leq 0.05$). A PC treatment × day interaction was also detected ($P = 0.04$) for mRNA expression of *peroxisome proliferator-activated receptor gamma* (**PPAR-γ**), which was greater ($P = 0.04$) at feedlot shipping for steers receiving CSSO during PC. Interactions between CF treatment × day were detected ($P \leq 0.01$) for mRNA expression of *adipocyte fatty acid-binding protein*, *fatty acid synthase*, PPAR-γ, and *stearoyl-CoA desaturase*, which were greater ($P \leq 0.02$) in the feedlot in steers receiving CSSO during CF. No treatment differences were detected for ($P \geq 0.18$) performance or carcass traits, including marbling and backfat thickness. Results from this study suggest that supplementing CSSO to suckled beef steers via creep-feeding upregulated mRNA expression of the adipogenic genes investigated herein later in life. These outcomes, however, were not translated into improved carcass quality.

Key words: beef cattle, Ca salts of soybean oil, carcass quality, mRNA expression, supplementation

Introduction

Metabolic imprinting, defined as biological responses to a nutritional intervention during early life that permanently alters physiological outcomes later in life (Du et al., 2010), has been shown to enhance carcass characteristics in cattle (Graugnard et al., 2009; Moriel et al., 2014). As an example, Scheffler et al. (2014) reported feeding a high-concentrate diet to early-weaned beef steers from 100 to 205 d of age increased marbling compared with forage fed-steers weaned at 205 d of age. Improved carcass quality and increased marbling benefits carcass prices (USDA, 1997) and beef palatability through greater tenderness, juiciness, and flavor (Jost et al., 1983). Therefore, nutritional management to stimulate metabolic imprinting appears to be an effective strategy to improve marbling and quality of beef carcasses.

Our research group reported that supplementation with Ca salts of soybean oil (**CSSO**) to beef steers weaned at 6 mo of age during a 28-d preconditioning period, at 0.07% of weaning body weight (**BW**), increased marbling and percent of choice carcasses upon slaughter compared with cohorts not receiving supplemental fat (Cooke et al., 2011). Similarly, Mangrum et al. (2016) reported beef steers weaned at 5 mo of age and supplemented with CSSO for 110 d after weaning, at 0.09% of weaning BW, had greater marbling upon slaughter compared with nonsupplemented cohorts. These studies suggested that CSSO supplementation stimulates metabolic imprinting events related to carcass marbling in cattle, likely due to its essential fatty acid (**FA**) content. More specifically, ω-6 FA have been shown to modify genes associated with adipose development (Azain, 2004; Benatti et al., 2004). However, Cooke et al. (2011) and Mangrum et al. (2016) evaluated steers older than 5 mo of age, whereas younger animals appear to be more responsive to metabolic imprinting events (Lucas, 1998).

One alternative to provide CSSO supplementation to younger steers in traditional cow-calf systems and stimulate metabolic imprinting events is via creep-feeding (Reis et al., 2015). Therefore, we hypothesized that inclusion of CSSO into a creep-feeding supplement provided to suckled steers, beginning at 2-mo of age would promote carcass marbling via metabolic imprinting effects beyond the outcomes reported by Cooke et al. (2011) and Mangrum et al. (2016). Moreover, we also theorized that inclusion of CSSO into both creep-feeding and preconditioning supplements would result on additive benefits to carcass marbling. To test these hypotheses, this experiment evaluated growth, physiological parameters, and carcass characteristics of beef steers receiving CSSO at 2 mo of age via creep-feeding, and/or postweaning via preconditioning supplementation.

Materials and Methods

This experiment was conducted over 2 consecutive years (2016 and 2017) at the Oregon State University – Eastern Oregon Agricultural Research Center (Burns station) and was divided into 4 periods: creep-feeding (**CF**: day 0 to 60), preweaning period (day 61 to weaning), preconditioning (**PC**; weaning to feedlot shipping), and a feedlot period (feedlot arrival to slaughter). All animals were cared for in accordance with acceptable practices and experimental protocols reviewed and approved by the Oregon State University, Institutional Animal Care and Use Committee (#4863).

Animals and Treatments

A total of 64 Angus × Hereford steers were enrolled in this study (32 steers per year). Steers were maintained on a 6,500-ha semiarid range pasture (Ganskopp and Bohnert, 2009) with their respective dams from birth until the beginning of the study (day –1). On day 0, steers were ranked by BW, age (initial BW = 114 ± 4 kg; initial age = 66.1 ± 0.9 d), as well as dam age and body condition score (**BCS**; Wagner et al., 1988) and allocated to 1 of 16 drylot pens (20 × 7 m; 2 steers per pen) in a manner that mean calf age, BW, dam age, and dam BCS were equivalent across all pens. Pens were randomly assigned to receive CSSO supplementation or not (**CON**) during the CF and/or PC periods, in a 2 × 2 factorial arrangement of treatments. As a result, 4 treatment combinations were generated (4 pens per treatment each year): 1) CSSO during CF and PC, 2) CSSO during CF and CON during PC, 3) CON during CF and CSSO during PC, and 4) CON during CF and PC.

During the CF period (day 0 to 60), steers were housed with their respective dams in the aforementioned drylot pens containing a creep-feeder that allowed both steers in the pen to have simultaneous access to the supplement. Pens received (as-fed basis) 500 g per steer daily of a pelletized corn-based creep supplement + 100 g soybean meal in addition to 80 g per steer daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ; $n = 8$ pens per year), or 67 g per steer daily of prilled saturated fat (EnergyBooster, Milk Specialties, Eden Prairie, MN) + 13 g per steer daily of limestone (CON, $n = 8$ pens per year). Supplemental CSSO was provided at a rate of 0.07% of steer initial BW, which was the CSSO supplementation rate used by Cooke et al. (2011). Treatments were formulated to be isocaloric, isonitrogenous, and isolipidic, but differing in FA composition (Table 1). Limestone was added to CON to compensate for the Ca included in the CSSO source (Table 1). Pens received 25% of their supplement treatments beginning on day 0, and were offered the remaining portion in a step-up manner so that 100% of supplement was received by day 10 of the CF period (25% from day 0 to 2, 50% from day 3 to 6, and 75% from day 7 to 9). Supplement was readily consumed by steers within 24 h of being offered. Cows from both treatments received and readily consumed 20 kg per cow daily (DM basis) of alfalfa-grass hay during the CF phase. Hay consumption by steer calves was negligible given that steer height was insufficient to reach feed bunks containing hay, and milk is still the major dietary component of calves at this age (Ansotegui et al., 1991).

During the preweaning period (day 61 to weaning), cows and steers were returned to the same 6,500-ha semiarid range pasture (Ganskopp and Bohnert, 2009) and managed as a single group with no FA supplementation. Upon weaning (day 124 of year 1 and day 127 of year 2), steers were managed as a single group for 8 d in a semiarid range pasture, with ad libitum access to grass-alfalfa hay and no concentrate supplementation. This interval served as a transition period between weaning and experimental procedures to alleviate behavioral stress caused by maternal separation (Weary et al., 2008). Steers were then returned to the same drylot pens used in the CF period (16 pens; 2 steers per pen each year), for a 40-d PC period. During the PC period (day 132 to 172 of year 1 and day 135 to day 175 of year 2), steers had access to free-choice mixed alfalfa-grass hay and received a corn-based concentrate (Table 1) in addition to 150 g per steer daily of CSSO (Essentiom; Church and Dwight Co., Inc.; $n = 8$ pens per year), or 125 g per steer daily of prilled saturated fat (EnergyBooster, Milk Specialties) + 25 g per steer daily of limestone (CON, $n = 8$ pens per year). As in the CF phase, CSSO supplementation was provided at a rate of 0.07% of steer weaning BW, and limestone added to CON to compensate for the Ca included in the CSSO source (Table 1). Treatments were isocaloric, isonitrogenous, isolipidic, differed in FA composition

Table 1. Composition and nutritional profile of treatments during the 60-d creep-feeding (CF) and 40-d preconditioning (PC) periods

	CF		PC	
Item	CSSO	CON	CSSO	CON
Ingredients, as-fed basis (g/d)				
Pellet	500	500	0	0
Ground corn	0	0	1,135	1,135
Soybean meal	100	100	200	200
Essentiom[1]	80	0	150	0
EnergyBooster[2]	0	67	0	125
Limestone	0	13	0	25
Nutrient profile, dry matter basis				
Total digestible nutrients, %[3]	96.93	96.24	98.88	98.17
Net energy for maintenance, Mcal/kg[4]	2.67	2.74	2.69	2.75
Net energy for growth, Mcal/kg[4]	1.89	1.97	1.91	1.97
Crude protein, %	20.36	20.26	13.75	13.68
Neutral detergent fiber, %	9.93	9.98	7.78	7.83
Ca, %	1.23	0.78	1.06	0.68
Fatty acids, %	12.77	12.70	12.15	12.05
Palmitic (16:0), %	3.77	3.76	3.31	3.39
Stearic (18:0), %	0.49	5.03	0.42	4.30
Oleic (18:1), %	3.40	1.28	3.28	1.46
Linoleic (18:2), %	4.29	1.16	4.53	1.83
Linolenic (18:3), %	0.43	0.10	0.36	0.09

[1]Church and Dwight Co., Inc. (Princeton, NJ).
[2]Milk Specialties (Eden Prairie, MN).
[3]Calculated according to the equations described by Weiss et al. (1992).
[4]Calculated with equations described by the NRC (2000).

(Table 1). Steers were observed daily for bovine respiratory disease (**BRD**) signs according to the DART system (Zoetis, Florham Park, NJ), as detailed by Sousa et al. (2018). Throughout the CF, preweaning, and PC periods, water and a commercial mineral and vitamin mix (Cattleman's Choice; Performix Nutrition Systems, Nampa, ID) containing 14% Ca, 10% P, 16% NaCl, 1.5% Mg, 6,000 ppm Zn, 3,200 ppm Cu, 65 ppm I, 900 ppm Mn, 140 ppm Se, 136 IU/g of vitamin A, 13 IU/g of vitamin D_3, and 0.05 IU/g of vitamin E were available for ad libitum consumption.

At the end of the PC period (day 173 of year 1 and day 176 of year 2), steers were loaded onto a commercial livestock trailer, and transported for 218 km to a commercial feedlot (Lightning Feeders, Nyssa, OR), where they were managed as a single group (feedlot period). Upon feedlot arrival, steers received a hormonal implant (Component TE 200; Elanco Animal Health, Greensfield, IN) and received the same diets (Table 2) until slaughter at a commercial packing facility (day 378 of year 1 and day 385 of year 2; Tyson Fresh Meats, Inc., Pasco, WA). Steers were observed daily for BRD signs during the feedlot period based on the DART system (Zoetis), and received medication according to the management criteria of the commercial feedlot.

Sampling

Samples of hay and supplement ingredients utilized during CF and PC periods were collected before the beginning of the experiment and analyzed for nutrient concentration by a commercial laboratory (Dairy One Forage Laboratory, Ithaca, NY). All samples were analyzed by wet chemistry procedures for concentrations of crude protein (method 984.13; AOAC, 2006), acid detergent fiber (method 973.18 modified for use in an Ankom 200 fiber analyzer, Ankom Technology Corp., Fairport, NY: AOAC, 2006), neutral detergent fiber (Van Soest et al., 1991; modified for use in an Ankom 200 fiber analyzer, Ankom Technology Corp.), and FA concentrations using gas chromatography (Autosystem XL Gas Chromatograph, Perkin Elmer, Inc., Waltham, MA) according to Sukhija and Palmquist (1988). Only FA that were individually identified in the analysis are reported herein. Calculations for total digestible nutrients used the equations proposed by Weiss et al. (1992), whereas net energy for maintenance and gain were calculated with the equations proposed by the NRC (2000). Nutritional and FA concentrations of all feedstuffs utilized are described in Table 3.

Steer BW was recorded on 2 consecutive days to determine BW prior to (day –1 and 0) and at the end of the CF period (day 60 and 61) and used to calculated average daily gain (**ADG**). Steer BW was also recorded on 2 consecutive days at weaning (day 124 and 125 of year 1 and day 127 and 128 of year 2) and used to calculate ADG during the preweaning period. Individual shrunk

Table 2. Ingredient composition (as-fed basis) of diets offered to steers during the feedlot period[1]

	Diets[2]				
Ingredients, % as fed	A	B	C	D	E
Alfalfa hay	53.0	39.0	19.0	12.0	4.0
Distillers grains	0.0	0.0	2.0	2.0	4.0
Dried corn	0.0	0.0	11.0	10.0	18.0
High-moisture corn	42.0	55.0	46.0	53.3	54.5
Corn Silage	0.0	0.0	18.0	17.0	11.0
Mineral and vitamin mix[3]	5.0	6.0	4.0	4.5	6.5
Tallow	0.0	0.0	0.0	1.2	2.0

[1]Feedlot period was day 174 to slaughter (day 378) of year 1, and day 177 to slaughter (day 385) of year 2.
[2]A = offered for 5 d after arrival receiving; B = offered for 5 d after diet A; C = offered for 7 d after diet B; D = offered for 10 d after diet C; E = offered until slaughter.
[3]Customized blend of minerals, vitamins, and feed additives (Performix Nutrition Systems, Nampa, ID).

Table 3. Nutritional and fatty acid profile (dry matter basis) of feedstuffs[1]

Item	Pellet	Corn	Soybean meal	Essentiom[2]	EnergyBooster[3]	Grass-alfalfa hay
Total digestible nutrients, %	84	89	81	190	219	61
Net energy for maintenance, Mcal/kg	2.09	2.22	1.96	6.82	8.73	1.28
Net energy for growth, Mcal/kg	1.43	1.54	1.32	5.19	6.86	0.70
Crude protein, %	17.5	8.9	50.9	0.7	0.4	17.8
Neutral detergent fiber, %	10.5	7.51	14.8	0.91	1.75	44.5
Fatty acids, %	2.69	3.74	2.71	82.51	96.11	1.86
Palmitic (16:0), %	0.48	0.49	0.44	26.54	31.08	0.40
Stearic (18:0), %	0.07	0.06	0.10	3.33	46.05	0.06
Oleic (18:1), %	0.68	1.03	0.37	22.60	6.84	0.04
Linoleic (18:2), %	1.19	2.07	1.47	25.44	0.80	0.32
Linolenic (18:3), %	0.09	0.07	0.24	2.57	0.01	0.61

[1]Values obtained from a commercial laboratory wet chemistry analysis (Dairy One Forage Laboratory, Ithaca, NY). Total digestible nutrients were calculated according to the equations described by Weiss et al. (1992). Net energy for maintenance and growth was calculated with equations described by the NRC (2000).
[2]Church and Dwight Co., Inc. (Princeton, NJ).
[3]Milk Specialties (Eden Prairie, MN).

BW was recorded prior to the beginning of the PC period (day 131 of year 1 and day 134 of year 2) and prior to feedlot shipping (day 171 of year 1 and day 174 of year 2) after 16 h of feed and water withdrawal, and values were used to calculate ADG during PC. At the commercial packing plant, hot carcass weight (**HCW**) was collected upon slaughter (day 378 of year 1 and day 385 of year 2). Final BW was estimated based on HCW adjusted to a 63% dressing percentage to minimize variation associated with gut fill (Loza et al., 2010), and was used to estimate ADG during the feedlot period. After a 24-h chill, trained personnel assessed carcass backfat thickness at the 12th rib and LM area, and all other carcass measures were recorded by a USDA grader. Cow BW and BCS were also recorded on day –1, 61, and at weaning.

Supplement, hay, and total DM intake were evaluated daily during the PC period by collecting and weighing offered and nonconsumed feed. All samples were dried to 96 h at 50 °C in forced-air ovens for DM calculation. Hay, supplement, and total daily DM intake (**DMI**) of each pen were divided by the number of steers within each pen and expressed as kg per steer per day. Total BW gain and DMI of each pen during the PC period were used for feed efficiency (**G:F**) calculation. Blood samples were collected from all steers on day 0, 60, weaning (day 124 of year 1 and day 127 of year 2), prior to shipping (day 172 of year 1 and day 175 of year 2), and during the feedlot period (day 328 of year 1 and day 337 of year 2). Blood was collected via jugular venipuncture into commercial blood collection tubes (Vacutainer, 10 mL; Becton Dickinson, Franklin Lakes, NJ) containing freeze-dried sodium heparin. Immediately after blood sampling, biopsies of the *longissimus* muscle (**LM**) between the 11th and 12th rib were performed in all calves via needle biopsy (Tru-Cut biopsy needle; CareFusion Corporation, San Diego, CA) according to Meijer et al. (1995). Muscle biopsy samples were stored in 2-mL tubes containing 1 mL of RNA stabilization solution (RNAlater, Ambion, Inc., Austin, TX), and stored at –80 °C until further processing.

Laboratorial Analyses

After collection, all blood samples were immediately placed on ice, centrifuged (2,500 × *g* for 30 min; 4 °C) for plasma harvest, and stored at –80 °C on the same day of collection. Plasma samples were analyzed for FA concentration using gas chromatography (Agilent 7890, Agilent Technologies, Inc.) using the same procedures described by Tripathy et al. (2010). Only FA that were individually identified in the analysis are reported herein.

Total RNA was extracted from muscle samples using the TRIzol Plus RNA Purification Kit (Invitrogen, Carlsbad, CA). Quantity and quality of isolated RNA were assessed via UV absorbance (NanoDrop Lite; Thermo Fisher Scientific, Wilmington, DE) at 260 nm and 260/280 nm ratio, respectively (Fleige and Pfaffl, 2006). Reverse transcription of extracted RNA and real-time reverse transcription-PCR using gene specific primers (20 pM each; Table 4) were completed as described by Rodrigues et al. (2015). A portion of the amplified products were purified with the QIAquick PCR purification kit (Qiagen Inc., Valencia, CA) and sequenced at the Oregon State University – Center for Genome Research and Biocomputing to verify the specificity of amplification. All amplified products represented only the genes of interest. Responses from the genes of interest were quantified based on the threshold cycle (C_T), the number of PCR cycles required for target amplification to reach a predetermined threshold. The C_T responses from muscle genes of interest were normalized to the geometrical mean of C_T values of *ribosomal protein S9* and *β-actin* (Vandesompele et al., 2002). The CV for the geometrical mean of reference genes across all samples was 3.6%. Results are expressed as relative fold change ($2^{-\Delta\Delta CT}$), as described by Ocón-Grove et al. (2008).

Statistical Analysis

All data were analyzed using pen as experimental unit and Satterthwaite approximation to determine the denominator degrees of freedom for tests of fixed effects. Quantitative data were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC), whereas binary data were analyzed using the GLIMMIX procedure of SAS. During the CF and preweaning periods, the model statements used for steer and cow BW, cow BCS, and steer ADG contained the effects of CF treatment. Model statements used for mRNA expression of LM genes and plasma FA concentrations contained the effects of CF treatment, day, and the CF treatment × day interaction. Data from CF and preweaning periods were analyzed using pen(CF treatment × year), steer(pen), and year as random variables. During the PC and feedlot periods, model statements for steer BW, ADG, incidence of BRD, feed efficiency, and carcass variables contained the effects of CF treatment, PC treatment, and the resultant interaction. Model statements used for mRNA expression of LM genes, plasma FA concentrations, and precondition DMI contained the effects of CF treatment, PC treatment, day, and all resultant interactions. Data from the PC and feedlot periods

Table 4. Primer sequences, accession number, and reference for all gene transcripts analyzed by real-time reverse transcription PCR

Target[1]	Primer sequence	Accession n°	Source
FABP4			
Forward	AAACTTAGATGAAGGTGCTCTGG	AJ4160220	Li et al. (2018)
Reverse	CATAAACTCTGGTGGCAGTGA		
FASN			
Forward	ATCGAGTGCATCAGGCAAGT	AF479289	Jeong et al. (2012)
Reverse	TGTGAGCACATCTCGAAAGCCA		
MyoD			
Forward	ATCCTGCGCAACGCCATCCGCTATATCGA	AF093675	Muroya et al. (2002)
Reverse	CTCGCTGTAGTAAGTGCGGTCGTAGCAGT		
Myogenin			
Forward	GAGAAGCGCAGACTCAAGAAGGTGAATGA	AF091714	Muroya et al. (2002)
Reverse	TCTGTAGGGTCCGCTGGGAGCAGATGATC		
PPAR-γ			
Forward	GCATTTCCACTCCGCACTAT	AY137204	Li et al. (2018)
Reverse	GGGATACAGGCTCCACTTTG		
SCD			
Forward	GCCAACAACTCTGCCTTTATG	GU947654	Li et al. (2018)
Reverse	CACCAATGACTGACCACCTG		
SREBP1			
Forward	ACTACCACGCCAAGTTCCTG	JN790254	Li et al. (2018)
Reverse	CGATGCCAATCTCCTCCTT		
B-*actin*			
Forward	AGCAAGCAGGAGTACGATGAGT	NM_173979	Bong et al. (2012)
Reverse	ATCCAACCGACTGCTGTCA		
Ribosomal protein S9			
Forward	CCTCGACCAAGAGCTGAAG	AF479289	Jeong et al. (2012)
Reverse	CCTCCAGACCTCACGTTTGTTC		

[1]FABP4 = adipocyte fatty acid-binding protein; FASN = fatty acid synthase; MyoD = myogenic differentiation 1; PPAR-γ = peroxisome proliferator-activated receptor-γ; SCD = stearoyl-CoA desaturase; SREBP1 = sterol regulatory element-binding protein-1.

were analyzed using pen(CF treatment × PC treatment × year), steer(pen), and year as random variables, but for DMI and feed efficiency that used pen(CF treatment × PC treatment × year) and year as random variables. For all analysis using repeated measures, the specified term was day, whereas the subject was steer(pen) for mRNA expression of LM genes and plasma FA, or pen(CF treatment × PC treatment × year) for preconditioning DMI. The covariance structure utilized was autoregressive, which provided the best fit for these analyses according to the lowest Akaike information criterion. Values obtained on day 0 were not used as independent covariate for each respective analysis given the experimental length and sampling schedule. All results are reported as least square means, and least square differences or PDIFF were used for simple or multiple mean separation, respectively. Significance was set at $P \leq 0.05$ and tendencies were determined if $P > 0.05$ and ≤ 0.10. In the text, results are reported according to main treatment effects if higher-order interactions containing treatments were nonsignificant, or according to highest-order interaction detected. Nonetheless, results are reported in tables according to sampling days to facilitate assessment and interpretation.

Results and Discussion

Creep-Feeding and Preweaning Periods

As designed, steers receiving CON and CSSO during CF were of similar age ($P = 0.63$) at the beginning of the experimental period (Table 5). No CF treatment differences were detected ($P \geq 0.69$) for BW or ADG prior to weaning (Table 5), which was expected given CF treatments were isocaloric, isonitrogenous, and isolipidic. Cow milk yield was not evaluated in the present experiment to estimate milk consumption and its contribution to steer daily nutrient intake during the CF and preweaning periods. Nevertheless, cows nursing CSSO and CON steers received the same nutritional management during lactation, and had similar age, days in milk (based on calf age), BW, and BCS at the beginning of the CF period, which are known to impact milk production in cattle (NRC, 2000). Moreover, cow BW and BCS remained similar between treatment groups throughout the CF and preweaning periods, which further mitigates potential differences in steer milk intake during the experiment (Reis et al., 2015).

Interactions between CF treatment × day were detected ($P \leq 0.05$) for plasma concentrations of palmitoleic, linoleic, linolenic, ω-6, PUFA, and ω-6: ω-3 ratio (Table 6). Concentrations of linoleic, ω-6, PUFA, and ω-6: ω-3 ratio in plasma were greater ($P < 0.01$) in CSSO vs. CON steers on day 60, but similar ($P \geq 0.68$) between CF treatment groups on day 0 and at weaning (Table 6). In turn, plasma concentrations of palmitoleic and linolenic were greater ($P \leq 0.01$) in CON vs. CSSO steers on day 60, but similar ($P \geq 0.40$) between CF treatment groups on day 0 and at weaning (Table 6). No CF treatment differences were detected ($P \geq 0.22$) for plasma concentrations of palmitic, stearic, oleic, dihomo-gamma-linolenic, docosadienoic, arachidonic, docosapentaenoic, SFA, MUFA, ω-3, and total FA (data not shown). As in Brandão et al. (2018), these results corroborate the FA content and profile of treatments (Table 1), given that plasma FA concentrations reflect intake and duodenal flow of FA (Lake et al., 2007; Scholljegerdes et al., 2007; Hess et al., 2008). Previous research also reported that CSSO supplementation increased plasma concentrations of linoleic acid, ω-6 FA, and total PUFA while reducing plasma concentrations of linolenic acid and ω-3 FA in growing steers,

Table 5. Performance responses of cows and their steer calves, which were supplemented with Ca salts of soybean oil (CSSO; *n* = 16 pens) or prilled saturated fat (CON; *n* = 16 pens) via creep-feeding (day 0 to 60)[1,2]

Item	CON	CSSO	SEM	*P*-value
Steers				
Initial age, d	65.8	66.4	0.9	0.63
Body weight, kg				
Day 0, kg	115	113	4	0.74
Day 60, kg	189	193	4	0.50
Weaning, kg	229	233	4	0.47
Average daily gain, kg/d				
Day 0 to 60	1.23	1.32	0.06	0.30
Day 60 to weaning[2]	0.67	0.67	0.04	0.97
Cows				
Initial age, yr	6.09	6.31	0.45	0.73
Body weight, kg				
Day 0, kg	536	526	12	0.57
Day 60, kg	564	556	12	0.61
Weaning, kg	530	526	12	0.75
Body condition score[3]				
Day 0	5.03	5.03	0.07	0.99
Day 60	5.06	5.15	0.07	0.35
Weaning	4.75	4.60	0.07	0.14

[1]CSSO = daily supplementation (per steer) with 80 g of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone.
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2.
[3]According to Wagner et al. (1988).

Table 6. Plasma fatty acid concentrations (μg/mL of plasma) in beef steers supplemented with Ca salts of soybean oil (CSSO; *n* = 16 pens) or prilled saturated fat (CON; *n* = 16 pens) via creep-feeding (day 0 to 60)[1,2]

Item	CON	CSSO	SEM	*P*-value
Palmitoleic (16:1)				
Day 0	26.9	25.3	1.4	0.40
Day 60	26.8	17.8	1.4	<0.01
Weaning	11.7	10.9	1.4	0.70
Shipping	4.42	4.86	0.43	0.47
Finishing	7.32	7.68	0.43	0.55
Linoleic (18:2, ω-6)				
Day 0	156	152	18	0.86
Day 60	218	380	18	<0.01
Weaning	162	155	18	0.68
Shipping	255	222	15	0.13
Finishing	361	366	15	0.80
Linolenic (18:3, ω-3)				
Day 0	81.6	79.8	5.6	0.82
Day 60	104	84.2	5.6	0.01
Weaning	57.8	53.8	5.6	0.62
Shipping	50.5	49.6	2.7	0.82
Finishing	12.1	12.3	2.7	0.94
Total ω-6				
Day 0	215	221	20	0.83
Day 60	291	453	20	<0.01
Weaning	207	199	20	0.77
Shipping	298	263	16	0.12
Finishing	398	403	16	0.82
ω-6: -3 ratio				
Day 0	1.91	1.92	0.20	0.99
Day 60	2.10	4.56	0.20	<0.01
Weaning	2.97	2.93	0.20	0.89
Shipping	6.46	5.33	0.55	0.15
Finishing	24.8	24.4	0.55	0.56
Total PUFA[3]				
Day 0	317	321	25	0.91
Day 60	417	560	25	<0.01
Weaning	279	266	25	0.71
Shipping	360	324	17	0.15
Finishing	413	419	17	0.81

[1]CSSO = daily supplementation (per steer) with 80 g of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone.
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively. Blood samples were collected on day 0, 60, weaning (day 124 of year 1; day 127 of year 2), prior to shipping to the feedlot (shipping; day 172, year 1; day 175, year 2), and once during the feedlot period (finishing; day 328, year 1; day 337, year 2).
[3]PUFA = linoleic, linolenic, dihomo-gamma-linolenic, arachidonic, docosadienoic, and docosapentaenoic acids.

without immediate impacts on their growth rates (Cooke et al., 2011). Hence, supplementing 80 g of CSSO to suckled beef steers via creep-feeding effectively increased intake and circulating concentrations of linoleic and ω-6 FA.

No CF treatment differences ($P \geq 0.45$) were detected for mRNA expression of genes associated with adipogenic activities in the LM prior to and at the time of weaning (Table 7). More specifically, *peroxisome proliferator-activated receptor gamma* (**PPAR-γ**) plays a pivotal role in the regulation of adipogenesis and lipid metabolism, through induction of genes mediating the process (Houseknecht et al., 2002), and has been identified as a candidate gene related to adipogenesis of bovine intramuscular adipose tissue (Lim et al., 2011). *Adipocyte fatty acid-binding protein* (**FABP4**) is a target gene of PPAR-γ (Taniguchi et al., 2008), and is highly involved in adipocyte differentiation, lipid hydrolysis, and acts as an intracellular FA chaperone (Michal et al., 2006). *Stearoyl-CoA desaturase* (**SCD**) is a key regulatory enzyme in the lipogenic pathway (Ntambi, 1999), and increased expression is associated with adipocyte hypertrophy (Martin et al., 1999). Increased expression of *fatty acid synthase* (**FASN**), an enzyme that modulates de novo synthesis of FA, is also a marker of adipogenesis (Graugnard et al., 2009). Similar to PPAR-γ, *sterol regulatory element-binding protein-1* (**SREBP1**) is a regulator of lipid metabolism, induced during the early stages of adipogenesis binding to the response element of PPAR-γ (Du et al., 2010). Increased expression of SREBP1 indicates enhanced capacity for de novo FA synthesis, and therefore increased lipid accumulation in the muscle tissue (Zhao et al., 2010). No CF treatment differences were also detected ($P \geq 0.52$) for mRNA expression of *myogenin* or *myogenic differentiation 1* (**MyoD**), which are myogenic regulatory factors in the LM that regulate postnatal muscle growth through differentiation and fusion of satellite cells with existing muscle fibers (Perdiguero et al., 2009; Du et al., 2010). Nevertheless, the impacts of dietary FA on these LM genes are still unclear (Price et al., 2000). Collectively, CSSO supplementation during a 60-d creep-feeding did not modulate mRNA expression of genes involved with lipid accumulation or myogenesis analyzed herein in the LM of suckled beef calves.

Table 7. Expression of *longissimus* muscle genes in beef steers supplemented with Ca salts of soybean oil (CSSO; *n* = 16 pens) or prilled saturated fat (CON; *n* = 16 pens) via creep-feeding (day 0 to 60)[1,2]

Item[3]	CON	CSSO	SEM	*P*-value
FABP4				
Day 0	21.4	17.4	7.1	0.69
Day 60	29.8	24.9	7.1	0.63
Weaning	31.2	30.1	7.1	0.91
Shipping	66.7	54.3	8.3	0.16
Finishing	38.5	72.5	8.3	0.02
FASN				
Day 0	29.8	24.4	4.3	0.37
Day 60	37.5	32.4	4.3	0.43
Weaning	14.6	21.9	4.3	0.25
Shipping	91.0	80.2	18.3	0.39
Finishing	124	210	18.6	0.02
MyoD				
Day 0	35.5	31.9	4.0	0.52
Day 60	14.6	15.5	4.0	0.87
Weaning	38.9	33.8	4.0	0.37
Shipping	12.9	13.8	1.0	0.55
Finishing	8.02	9.00	1.05	0.39
Myogenin				
Day 0	43.5	43.8	4.7	0.95
Day 60	29.3	22.7	4.7	0.32
Weaning	61.2	49.9	4.7	0.11
Shipping	39.9	42.2	4.4	0.80
Finishing	7.42	8.58	4.5	0.77
PPAR-γ				
Day 0	4.39	3.91	0.46	0.45
Day 60	4.40	3.97	0.46	0.49
Weaning	3.67	3.71	0.46	0.95
Shipping	7.18	6.11	0.73	0.13
Finishing	5.01	8.20	0.74	0.01
SCD				
Day 0	26.6	22.7	3.9	0.48
Day 60	28.6	22.6	3.9	0.28
Weaning	10.6	17.9	3.9	0.19
Shipping	65.8	61.8	17.1	0.68
Finishing	96.5	202	17.4	<0.01
SREBP1				
Day 0	2.76	2.84	0.14	0.68
Day 60	2.67	2.54	0.14	0.51
Weaning	1.93	1.93	0.14	0.98
Shipping	3.25	3.59	0.19	0.31
Finishing	3.07	3.22	0.20	0.59

[1]CSSO = daily supplementation (per steer) with 80 g of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone.

[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively. Samples of the *longissimus* muscle were taken via needle biopsy on day 0, 60, weaning (day 124 of year 1; day 127 of year 2), prior to shipping to the feedlot (shipping; day 172, year 1; day 175, year 2), and once during the feedlot period (finishing; day 328, year 1; day 337, year 2). Values are expressed as relative fold change compared with threshold cycle of reference genes analyzed within the same sample (Ocón-Grove et al., 2008).

[3]FABP4 = adipocyte fatty acid-binding protein; FASN = fatty acid synthase; MyoD = myogenic differentiation 1; PPAR-γ = peroxisome proliferator-activated receptor-γ; SCD = stearoyl-CoA desaturase; SREBP1 = sterol regulatory element-binding protein-1.

Preconditioning and Feedlot Periods

During the PC period, a CF × PC treatment interaction was detected for hay and total DMI. These variables were greater ($P \leq 0.03$) in steers receiving CON during both CF and PC compared with steers receiving CON during CF and CSSO during PC (Table 8). No other CF or PC treatment differences were detected ($P \geq 0.12$) for preconditioning hay, supplement, and total DMI (Table 8). Addition of CSSO to preconditioning diets has been shown to reduce forage and total DMI in cattle naïve to CSSO supplementation (Araujo et al., 2010; Cooke et al., 2011). In turn, lack of similar results in steers that received CSSO during CF suggest that these animals may have been previously adapted to this FA source, preventing substantial hay and total DMI depression when supplemented during the PC period. Nonetheless, these outcomes were not sufficient to impact ($P \geq 0.53$) BW, ADG, or feed efficiency during preconditioning (Tables 8 and 9). These results support previous studies indicating CSSO supplementation to preconditioning cattle did not affect ADG or feed efficiency measures, compared to cohorts offered isocaloric, isonitrogenous, and isolipidic control diets (Araujo et al., 2010; Cooke et al., 2011). It also should be noted that BRD signs were not observed during the PC period, despite this experiment not being specifically designed to assess this response.

Interactions between PC treatment × day were detected ($P \leq 0.05$) for plasma concentrations of palmitic, palmitoleic, linoleic, linolenic, arachidonic, MUFA, PUFA, ω-6, ω-3, total FA, and ω-6: ω-3 ratio (Table 10). Plasma concentrations of palmitic, linoleic, arachidonic, ω-6, PUFA, total FA, and ω-6: ω-3 ratio were greater ($P \leq 0.04$) in steers receiving CSSO compared with CON during PC prior to feedlot shipping, but similar ($P \geq 0.24$) between PC treatment groups during the feedlot period (Table 10). In turn, plasma concentrations of palmitoleic, linolenic, ω-3, and MUFA were greater ($P \leq 0.05$) in steers receiving CON compared with CSSO during PC prior to feedlot shipping, and similar ($P \geq 0.12$) between PC treatment groups during the feedlot period (Table 10). No PC treatment differences were noted ($P \geq 0.12$) for plasma concentrations of stearic, oleic, dihomo-gamma-linolenic, docosadienoic, docosapentaenoic, and SFA (data not shown). Moreover, no CF treatment effects were detected ($P \geq 0.12$) for plasma FA profile prior to feedlot shipping and during the feedlot period (Table 6). Similar to treatment differences noted during the CF period, these outcomes corroborate the FA content and profile of PC treatments (Table 1; Hess et al., 2008), and also implicate that there are no long-term carryover effects of CSSO supplementation during the CF period on plasma FA profile. Hence, supplementing 150 g of CSSO to beef steers during preconditioning had immediate effects on circulating concentration of linoleic and ω-6 FA, as previously reported by others (Araujo et al., 2010; Cooke et al., 2011; Mangrum et al., 2016).

A PC treatment × day interaction was detected ($P = 0.05$) for PPAR-γ mRNA expression, which was greater ($P = 0.04$) in steers receiving CSSO vs. CON during PC prior to shipping but similar ($P = 0.42$) during the feedlot period (Table 11). Dietary fat may regulate PPAR-γ mRNA expression in a ligand-dependent manner (Houseknecht et al., 2002). Polyunsaturated FA, specifically ω-6 such as linoleic acid, are known to stimulate PPAR-γ function (Kliewer et al., 1997; Xu et al., 1999; Thoennes et al., 2000), and PPAR-γ mRNA expression is upregulated with dietary supplementation of such FA (Spurlock et al., 2000). No additional effects of PC treatment were noted for mRNA expression of genes associated with lipogenesis or myogenesis in the LM after weaning ($P \geq 0.27$; Table 11). Interactions between

Table 8. Preconditioning feed intake and efficiency in beef steers supplemented with Ca salts of soybean oil (CSSO) or prilled saturated fat (CON) during the creep-feeding period (CF; day 0 to 60, top row; *n* = 16 pens) and/or a 40-d preconditioning period (PC; bottom row; *n* = 16 pens)[1,2,3]

	CON		CSSO			*P*-values		
Item	CON	CSSO	CON	CSSO	SEM	CF	PC	CF × PC
Hay, kg/d	6.11[a]	5.40[b]	5.70[ab]	5.87[ab]	0.22	0.89	0.23	0.05
Supplement, kg/d	1.15	1.08	1.03	1.05	0.04	0.11	0.52	0.82
Total, kg/d	7.07[a]	6.29[b]	6.54[a]	6.73[a]	0.22	0.84	0.19	0.03
Feed efficiency, kg/kg	0.138	0.137	0.135	0.143	0.011	0.88	0.74	0.68

[1]CSSO = daily supplementation (per steer) with 80 g (CF) and/or 150 g (PC) of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone (CF) and/or 125 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 25 g of limestone (PC). Within rows, means with different superscripts (a, b) differ ($P \leq 0.05$).
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively.
[3]Feed intake was recorded daily during preconditioning by measuring offer and refusals from each pen, divided by the number of calves within each pen, and expressed as kg per calf per day. Feed efficiency was calculated using total feed intake and body weight gain of each pen during preconditioning.

Table 9. Postweaning performance and carcass traits in beef steers supplemented with Ca salts of soybean oil (CSSO) or prilled saturated fat (CON) during the creep-feeding period (CF; day 0 to 60, *n* = 8 pens per year) or a 40-d preconditioning period (PC; *n* = 8 pens per year)[1,2,3]

	CF main effect				PC main effect			
Item	CON	CSSO	SEM	*P*-value	CON	CSSO	SEM	*P*-value
Body weight, kg								
Preconditioning	224	227	3	0.53	226	226	3	0.97
Shipping	262	265	4	0.61	264	263	4	0.87
Slaughter[4]	570	578	9	0.54	580	567	9	0.31
Average daily gain, kg/d								
Preconditioning to shipping	0.926	0.925	0.063	0.99	0.935	0.916	0.063	0.84
Shipping to slaughter[4]	1.48	1.51	0.04	0.62	1.52	1.46	0.04	0.26
Incidence of respiratory disease,[5] %	57.6	49.1	10.2	0.56	60.9	45.8	10.2	0.30
Carcass[6]								
Hot carcass weight, kg	359	364	6	0.54	366	357	6	0.31
Longissimus muscle area, cm^2	80.0	79.3	1.4	0.72	80.4	78.9	1.4	0.45
Yield grade	3.48	3.55	0.09	0.62	3.56	3.48	0.09	0.57
Marbling	493	470	16	0.32	479	484	16	0.80
Backfat, cm	1.50	1.52	0.05	0.69	1.56	1.46	0.05	0.18

[1]CSSO = daily supplementation (per steer) with 80 g (CF) and/or 150 g (PC) of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone (CF) and/or 125 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 25 g of limestone (PC).
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively.
[3]Shrunk body weight was recorded after 16 h of feed and water withdrawal on day 131 (year 1) and 134 (year 2), and prior to shipping (day 171, year 1; day 174, year 2). Average daily gain during preconditioning was calculated using initial and final shrunk body weights. Feed intake was recorded daily during preconditioning by measuring offer and refusals from each pen, divided by the number of calves within each pen, and expressed as kg per calf per day. Feed efficiency was calculated using total feed intake and body weight gain of each pen during preconditioning.
[4]Calculated based on HCW (assuming 63% dressing; Loza et al., 2010).
[5]Observed at the commercial feedlot, according to the DART system (Zoetis, Parsippany, NJ).
[6]Backfat thickness measured at the 12th rib. Marbling score: 400 = Small^{00}; 500 = Modest^{00}; 600 = Medium^{00}.

CF treatment × day were detected ($P \leq 0.01$) for mRNA expression of FABP4, FASN, PPAR-γ, and SCD in the LM (Table 7). Expression of these genes did not differ ($P \geq 0.13$) between CF treatment groups prior to feedlot shipping, but were greater ($P \leq 0.02$) in samples collected during the feedlot period in steers receiving CSSO during CF. No CF treatment effects ($P \geq 0.28$) were noted for mRNA expression of MyoD, *myogenin*, and SREBP1 in the LM after weaning (Table 7). Collectively, CSSO supplementation during CF elicited alterations in mRNA expression of adipogenic genes, which were noted during the feedlot period when lipogenesis is substantial (Pethick et al., 2004). These outcomes are suggestive of a metabolic imprinting effect (Du et al., 2010), given CF treatments were offered to steers during a period of elevated epigenetic susceptibility (Lucas, 1998). One could also attribute upregulated mRNA expression of adipogenic genes in calves that received CSSO during CF due to a potential increased DMI during the finishing period, as dietary fat may also epigenetically modulate appetite (Gupta et al., 2009). Conversely, PC treatments had no major impacts on the LM genes after weaning besides an immediate increase in PPAR-γ mRNA expression, whereas

Table 10. Postweaning plasma fatty acid concentrations (μg/mL of plasma) in beef steers supplemented with Ca salts of soybean oil (CSSO; *n* = 16 pens) or prilled saturated fat (CON; *n* = 16 pens) during a 40-d preconditioning period[1,2,3]

Item[3]	CON	CSSO	SEM	*P*-value
Palmitic (16:0)				
Shipping	85.4	102	4.1	0.04
Finishing	90.7	89.6	4.1	0.79
Palmitoleic (16:1)				
Shipping	5.58	3.70	0.43	<0.01
Finishing	8.07	7.02	0.43	0.12
Linoleic (18:2, ω-6)				
Shipping	177	301	15	<0.01
Finishing	364	364	15	0.94
Linolenic (18:3, ω-3)				
Shipping	63.9	36.2	2.7	<0.01
Finishing	12.5	11.9	2.7	0.47
Arachidonic (20:40, ω-6)				
Shipping	12.8	16.6	0.7	<0.01
Finishing	14.9	15.8	0.7	0.24
Total ω-6				
Shipping	216	344	15	<0.01
Finishing	401	399	15	0.97
Total ω-3				
Shipping	74.8	47.8	3.0	<0.01
Finishing	16.5	16.5	2.9	0.98
ω-6: ω-3 ratio				
Shipping	2.90	8.90	0.55	<0.01
Finishing	24.6	24.6	0.55	0.98
Total MUFA				
Shipping	68.7	58.3	3.8	0.05
Finishing	107.3	99.9	3.8	0.13
Total PUFA				
Shipping	291	392	17	<0.01
Finishing	417	416	17	0.97
Total FA				
Shipping	593	713	29	0.01
Finishing	831	811	29	0.58

[1]CSSO = daily supplementation (per steer) with 80 g (CF) and/or 150 g (PC) of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone (CF) and/or 125 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 25 g of limestone (PC).
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively. Blood samples were collected prior to shipping to the feedlot (shipping; day 172, year 1; day 175, year 2) and once during the feedlot period (finishing; day 328, year 1; day 337, year 2).
[3]MUFA = palmitoleic and oleic acids; PUFA = linoleic, linolenic, dihomo-gamma-linolenic, arachidonic, docosadienoic, and docosapentaenoic acids.

providing CSSO during both CF and PC also failed to yield additive benefits on these variables.

No CF or PC treatment differences were noted ($P \geq 0.18$) for performance responses during the feedlot period, not carcass traits upon slaughter (Table 9). No CF or PC treatment effects were also detected ($P \geq 0.30$) for BRD incidence during the feedlot period (Table 9), which was not a major variable of interest herein despite the potential immune benefits of CSSO (Cooke et al., 2011). Lack of LM area and HCW differences

Table 11. Postweaning mRNA expression of *longissimus* muscle genes in beef steers supplemented with Ca salts of soybean oil (CSSO; *n* = 16 pens) or prilled saturated fat (CON; *n* = 16 pens) during a 40-d preconditioning period[1,2]

Item[3]	CON	CSSO	SEM	*P*-value
FABP4				
Shipping	65.3	68.1	45.7	0.25
Finishing	41.2	35.9	77.2	0.58
FASN				
Shipping	87.8	94.3	75.0	0.53
Finishing	134	113	243	0.23
MyoD				
Shipping	12.5	13.2	13.1	0.53
Finishing	9.46	6.58	9.37	0.22
Myogenin				
Shipping	46.3	33.4	38.4	0.79
Finishing	6.83	8.02	8.60	0.66
PPAR-γ				
Shipping	6.37	8.00	5.48	0.04
Finishing	4.71	5.31	9.54	0.42
SCD				
Shipping	64.6	67.0	54.5	0.42
Finishing	101	91.7	222	0.44
SREBP1				
Shipping	3.63	2.87	3.56	0.28
Finishing	3.15	2.99	3.29	0.37

[1]CSSO = daily supplementation (per steer) with 80 g (CF) and/or 150 g (PC) of Ca salts of soybean oil (Essentiom, Church and Dwight Co., Inc., Princeton, NJ); CON = daily supplementation (per steer) with 67 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 13 g of limestone (CF) and/or 125 g of prilled saturated fat (EnergyBooster 100, Milk Specialties, Eden Prairie, MN) + 25 g of limestone (PC).
[2]Weaning occurred on day 124 of year 1 and on day 127 of year 2. Calves were preconditioning from day 132 to 172 and day 135 to day 175 of year 1 and 2, respectively. Steers were shipped to the feedlot and remained there from day 173 to slaughter (day 378) and day 176 to slaughter (day 385) of year 1 and 2, respectively. Samples of the *longissimus* muscle were taken via needle biopsy prior to shipping to the feedlot (shipping; day 172, year 1; day 175, year 2) and once during the feedlot period (finishing; day 328, year 1; day 337, year 2). Values are expressed as relative fold change compared with threshold cycle of reference genes analyzed within the same sample (Ocón-Grove et al., 2008).
[3]FABP4 = adipocyte fatty acid-binding protein; FASN = fatty acid synthase; MyoD = myogenic differentiation 1; PPAR-γ = peroxisome proliferator-activated receptor-γ; SCD = stearoyl-CoA desaturase; SREBP1 = sterol regulatory element-binding protein-1.

corroborate similar MyoD and *myogenin* mRNA expression (te Pas et al., 1999), as well as similar performance between CF and PC treatment groups throughout the experimental period. However, differential mRNA expression of FABP4, FASN, PPAR-γ, and SCD during the feedlot period did not translate into greater marbling in steers receiving CSSO during CF. Increased mRNA expression may not be supported by equivalent final phenotypic differences (Clancy and Brown, 2008). Graugnard et al. (2010) also reported altered PPAR-γ and FASN mRNA expression in the *longissimus lumborum*, but similar carcass marbling scores, in beef steers receiving high- or low-starch diets for 112 d after weaning at 5 mo of age. Reis et al. (2015) reported increased FASN and PPAR-γ mRNA expression, but similar backfat thickness in heifers provided concentrate ad libitum via creep-feeding for 50 d or not. Urrutia et al. (2015) also reported differential mRNA expression of SCD in the *longissimus thoracis* muscle of lambs fed a 10% linseed compared to a control diet for 5 wk but found

no differences in *longissimus thoracis* fat content. Nonetheless, the lack of PC treatment effects on marbling score do not corroborate with Cooke et al. (2011) or Mangrum et al. (2016), who reported increased marbling score in steers supplemented with CSSO after weaning for 28 and 110 d, respectively. However, treatments offered in these previous experiments (Cooke et al., 2011; Mangrum et al., 2016) were not isonitrogenous or isolipidic as utilized herein; hence, their results may also be related to the energy contribution of CSSO supplementation rather than the specific treatment FA profile.

In summary, supplementing CSSO to beef steers at 2 mo of age via creep-feeding stimulated mRNA expression of some genes involved in lipid metabolism later in life compared with cohorts receiving an isocaloric, isonitrogenous, and isolipidic supplement based on prilled saturated fat. However, increased mRNA expression of these genes, which included FABP4, FASN, PPAR-γ, and SCD, did not translate into improved carcass characteristics. Research is still warranted to investigate the effects of CSSO supplementation to nursing beef cattle during the period of epigenetic susceptibility on lipogenic gene expression, growth, and carcass characteristics. Nonetheless, CSSO supplementation to young cattle appears to be a nutritional alternative to upregulate mRNA expression of LM genes associated with lipogenesis during the finishing period.

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