Journal of Animal Science, 2020, Vol. 98, No. 8, 1–12

doi:10.1093/jas/skaa247
Advance Access publication August 13 2020
Received: 8 June 2020 and **Accepted:** 29 July 2020
Fetal Programming

FETAL PROGRAMMING

Supplementing Ca salts of soybean oil to late-gestating beef cows: impacts on performance and physiological responses of the offspring

Alice Poggi Brandão,[†] Reinaldo F. Cooke,[†,1] Kelsey M. Schubach,[†] Bruna Rett,[‡] Osvaldo A. Souza,[‡] Christopher L. Schachtschneider,[‖] George A. Perry,[$] Sergio A. Arispe,[¶] Donald B. Jump,[**] Ky G. Pohler,[†] David W. Bohnert,[††] and Rodrigo S. Marques[‡‡]

[†]Department of Animal Science, Texas A&M University, College Station, TX 77845, [‡]School of Veterinary Medicine and Animal Science, São Paulo State University (UNESP), Botucatu 18168-000, Brazil, [‖]Umatilla County Extension Office, Oregon State University, Pendleton, OR 97801, [$]Texas AgriLife Research, Texas A&M University System, Overton, TX 75684, [¶]Malheur County Extension Office, Oregon State University, Ontario, OR 97914, [**]Nutrition Program, School of Biological and Population Health Sciences, Linus Pauling Institute, Oregon State University, Corvallis, OR 97331, [††]Eastern Oregon Agricultural Research Center, Oregon State University, Burns, OR 97720, [‡‡]Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717

[1]Corresponding author: reinaldocooke@tamu.edu

ORCiD numbers: 0000-0002-7497-3601 (R. F. Cooke); 0000-0002-4590-2898 (R. S. Marques).

Abstract

This experiment compared the performance and physiological responses of the offspring from cows supplemented with Ca salts of soybean oil (**CSSO**) or prilled saturated fat (**CON**) during late gestation. Nonlactating, pregnant, multiparous Angus × Hereford cows (n = 104) that conceived during the same fixed-time artificial insemination protocol were assigned to this experiment. Cows were ranked by pregnancy sire (one of two sires), body weight (**BW**), and body condition score (**BCS**) on day −15 of the experiment (day 180 of gestation). Cows were then assigned to receive (dry matter basis) 415 g of soybean meal per cow daily in addition to: 1) 195 g/cow daily of CSSO (n = 52) or 2) 170 g/cow daily of CON (n = 52). Cows were maintained in two pastures (26 cows/treatment per pasture) and received daily 12.7 kg/cow (dry matter basis) of grass-alfalfa hay from day −15 to calving. Cows were segregated into 1 of 24 feeding pens three times weekly and received treatments individually from day 0 to calving. Calves were weaned on day 290 of the experiment, preconditioned for 35 d (day 291 to 325), and transferred to a feedyard, where they remained until slaughter (day 514). Cows receiving CSSO and their calves had greater (P < 0.01) plasma concentrations of linoleic acid and total ω-6 PUFA compared with CON after calving. Concentrations of immunoglobulin G in the colostrum and in calf plasma 24 h after birth were greater (P ≤ 0.02) in CSSO vs. CON cattle. Calves from CSSO cows had greater (P ≤ 0.05) expression of adipogenic (*adipocyte fatty acid-binding protein* and *stearoyl-CoA desaturase*) and myogenic (*myogenic differentiation 1* and *myogenin*) genes in the *longissimus* muscle (**LM**) compared with CON. No treatment differences in birth BW, weaning BW, and final preconditioning BW were noted (P ≥ 0.36). Average daily gain and final BW in the feedyard were greater (P ≤ 0.05) in steers from CSSO cows compared with CON. The incidence of calves diagnosed with BRD that required a second antimicrobial treatment was less (P = 0.03) in calves from CSSO cows, resulting in reduced (P = 0.05) need of treatments to regain health compared with CON. Upon slaughter, LM area was greater

(P = 0.03) in calves from CSSO cows compared with CON. Collectively, these results are indicative of programming effects on postnatal offspring growth and health resultant from CSSO supplementation to late-gestating cows. Hence, supplementing CSSO to beef cows during pregnancy might be a feasible alternative to optimize offspring productivity and welfare.

Key words: beef cows, Ca salts of soybean oil, offspring, pregnancy, supplementation

Abbreviations

ADG	average daily gain
BCS	body condition score
BRD	bovine respiratory disease
BS	blood sample
BW	body weight
CON	prilled saturated fat supplementation
CSSO	Ca salts of soybean oil
FA	fatty acid
FABP4	*adipocyte fatty acid-binding protein*
FASN	*fatty acid synthase*
HCW	hot carcass weight
IgG	immunoglobulin G
LM	*longissimus* muscle
LMB	*longissimus* muscle biopsy
MyoD	*myogenic differentiation 1*
PCR	polymerase chain reaction
PPAR-γ	*peroxisome proliferator-activated receptor gamma*
PUFA	polyunsaturated fatty acids
SCD	*stearoyl-CoA desaturase*

Introduction

Maternal nutrition is a major extrinsic factor programming nutrient partitioning and development of fetal organ systems associated with health, production, and reproduction (Long et al., 2010; Silvestre et al., 2011; Garcia et al., 2014). Accordingly, nutritional management of late-gestating beef cows has been shown to directly impact the performance of the subsequent offspring via programming effects (Funston et al., 2010; Bohnert et al., 2013; Marques et al., 2016). However, the majority of the research conducted within this subject focused on energy and protein nutrition, and limited information exists about the potential impacts of supplementing polyunsaturated fatty acids (**PUFA**) to gestating cows on offspring productivity.

Research from our group reported that supplementing Ca salts of ω-3 and ω-6 PUFA to beef cows during late gestation improved offspring performance (Marques et al., 2017). More specifically, calves born from cows supplemented with ω-3 + ω-6 PUFA had a greater average daily gain (**ADG**) in the feedlot and increased hot carcass weight (**HCW**), marbling, and *longissimus* muscle (**LM**) area compared with cohorts from nonsupplemented cows. These results were suggestive of programming effects from ω-3 + ω-6 PUFA supplementation, by enhancing fetal skeletal muscle hypertrophy and adipocyte development during gestation, which translated into increased growth and marbling when offspring were provided high-energy anabolic feedlot diets (Harper and Pethick, 2004; Du et al., 2010). Nonetheless, the mechanisms underlying the outcomes reported by Marques et al. (2017) still warrant investigation, including the specific role of ω-3 and ω-6 PUFA.

Linoleic acid and its ω-6 PUFA derivatives have been associated with cell differentiation and development in young cattle (Mangrum et al., 2016; Schubach et al., 2019). Ricks et al. (2020) recently reported that supplementing ω-6 PUFA to beef cows during the last trimester of gestation, via Ca salts of soybean oil (**CSSO**), increased offspring growth up to weaning. These authors, however, did not evaluate postweaning performance of the offspring. In contrast, supplementing Ca salts of ω-3 PUFA to gestating ewes had limited benefits to lamb preweaning and postweaning development (Coleman et al., 2018; Carranza Martin et al., 2018). Therefore, supplementing CSSO to gestating beef cows may be more advantageous than the combination of ω-6 + ω-3 PUFA used by Marques et al. (2017) and will help elucidate the specific programming roles of ω-6 PUFA. Based on this rationale, we hypothesized that CSSO supplementation to late-gestating beef cows will improve lifelong offspring productivity via programming effects. This experiment compared growth, physiological responses, and carcass characteristics of offspring from cows supplemented or not with CSSO during late gestation.

Materials and Methods

This experiment was conducted at the Oregon State University—Eastern Oregon Agricultural Research Center (Burns station). The animals utilized 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 (#4974). A summary of the experimental design is presented in Figure 1.

Cow–calf management and dietary treatments

One hundred and four multiparous, nonlactating, pregnant Angus × Hereford cows (unshrunk body weight [**BW**] = 505 ± 6 kg, age = 5.4 ± 0.3 yr, body condition score [**BCS**] = 4.88 ± 0.03 according to Wagner et al., 1988) were assigned to this experiment at the end of their second trimester of gestation. All cows conceived to the same fixed-time artificial insemination protocol using semen from two Angus sires, according to the breeding management and pregnancy diagnosis described by Cooke et al. (2014). Gestation length was 195 d for all cows on day 0 of the experiment.

Prior to the beginning of the experiment (day –15), cows were ranked by sire, BW, and BCS, and assigned to one of two groups (52 cows/group) in a manner that all these variables were equivalent between groups. Groups were maintained in individual meadow foxtail (*Alopecurus pratensis* L.) pastures from day –15 until calving. Grass-alfalfa hay was provided daily at 12.7 kg/cow (dry matter basis), and cows had ad libitum access to water and a commercial mineral + 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 D3, and 0.05 IU/g of vitamin E. No forage was available for grazing due to previous hay harvest and snow cover resultant from wintery conditions.

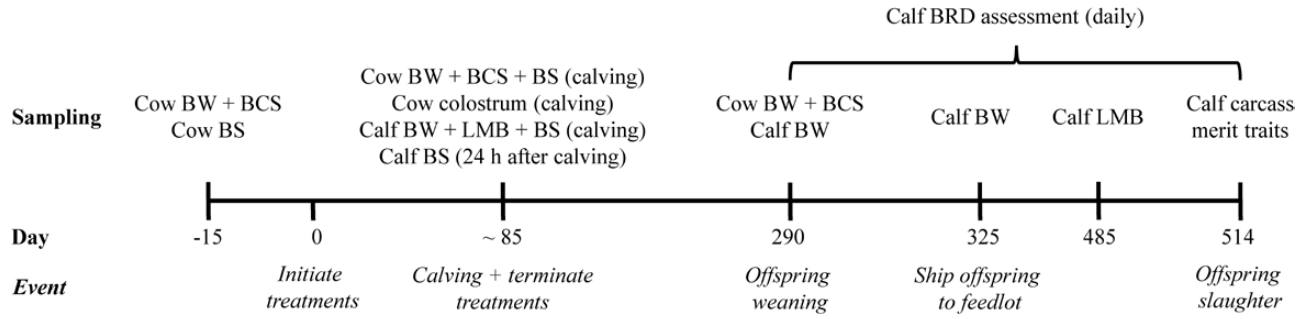

Figure 1. Experimental design assigned to beef cows receiving diets supplemented with CSSO (n = 52) or CON (n = 52) during the last trimester of gestation.

Table 1. Composition and nutritional profile of diets containing CSSO or CON

Item	CON	CSSO
Ingredients, kg/d (dry matter basis)		
Grass-alfalfa hay	12.7	12.7
Soybean meal	0.415	0.415
Essentiom[1]	0	0.195
EnergyBooster[2]	0.170	0
Limestone	0.025	0
Nutrient profile,[3] dry matter basis		
Dry matter, %	91.9	92.1
Net energy for maintenance,[3] Mcal/kg	1.28	1.28
Crude protein, %	8.3	8.3
FA, %	2.46	2.45
Palmitic (16:0), %	0.64	0.63
Stearic (18:0), %	0.61	0.08
Oleic (18:1), %	0.16	0.41
Linoleic (18:2), %	0.29	0.65
Linolenic (18:3), %	0.31	0.35

[1]Essentiom (Church and Dwight Co., Inc., Princeton, NJ).
[2]Energy Booster 100 (Milk Specialties, Eden Prairie, MN).
[3]Values obtained via wet chemistry analysis (Dairy One Forage Laboratory, Ithaca, NY).

Cows within groups were again ranked by sire, BW, and BCS, and assigned to receive (dry matter basis) 415 g of soybean meal per cow daily in addition to 1) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ; n = 52) or 2) 170 g/cow daily of prilled saturated fat (EnergyBooster, Milk Specialties, Eden Prairie, MN) + 25 g/cow daily of limestone (**CON**, n = 52). Treatments were formulated to be isocaloric, isonitrogenous, and isolipidic but differing in fatty acid (**FA**) composition. Limestone was added to CON to compensate for the Ca included in the CSSO source. From day 0 of the experiment until calving, cows from both groups were gathered three times weekly (Mondays, Wednesdays, and Fridays; Cook et al., 2017; Marques et al., 2017) and individually sorted into 1 of 24 feeding pens (1 cow/pen; 6 × 9 m pens). Cows individually received treatments (1.42 kg of treatment/feeding, dry matter basis) and returned to pasture after their treatment was completely consumed. This process was repeated until all cows had been individually sorted into pens and consumed their treatments. Diets (hay + treatments) were formulated to meet or exceed the nutrient requirements for energy, crude protein, minerals, and vitamins of late-gestating beef cows (NRC, 2000; Table 1).

Immediately after calving, cow–calf pairs were removed from their pasture and assigned to the general management of the research herd until weaning (Marques et al., 2016), which did not include supplementation with CSSO or CON. Male calves were castrated at birth using an elastic castration band. All calves were administered One Shot Ultra 7 and Bovi-Shield Gold 5 (Zoetis, Florham Park, NJ) at approximately 30 d of age.

Calf management

Preconditioning (day 290 to 325)

Calves were weaned on day 290 of the experiment and transferred to a 6-ha meadow foxtail (*Alopecurus pratensis* L.) pasture, which had been previously harvested for hay, for a 35-d preconditioning period as a single group. Calves were administered One Shot Ultra 7, Bovi-Shield Gold 5, and Dectomax (Zoetis, Florham Park, NJ) at weaning and received a booster of Bovi-Shield Gold 5 and UltraChoice 7 (Zoetis) 21 d after weaning (day 311 of the experiment). During preconditioning, calves received mixed alfalfa-grass hay, water, and the same commercial mineral and vitamin mix previously described (Cattleman's Choice; Performix Nutrition Systems) for ad libitum consumption.

Growing and finishing (day 325 until slaughter)

On day 325, all calves were loaded into a livestock trailer and transported for 215 km to a commercial feedyard (Cannon Hill Feeders LLC., Nyssa, OR), where they were managed as a single group until slaughter (day 514 of the experiment) at a commercial packing facility (Agri Beef Co., Toppenish, WA). Calves received a hormonal implant (Component TE 200; Elanco Animal Health, Greenfield, IN, USA) upon feedyard arrival and were offered diets (Table 2) that did not contain CSSO or CON.

Sampling

Feedstuffs

Samples of all ingredients fed to late-gestating cows were collected before the beginning of the experiment and analyzed for nutrient content 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. Net energy for maintenance was calculated with the equations proposed by the NRC (2000).

Table 2. Ingredient composition (as-fed basis) of feedyard diets offered to cattle

	Diets[1]				
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[2]	5.0	6.0	4.0	4.5	6.5
Tallow	0.0	0.0	0.0	1.2	2.0

[1]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 13 d after diet C; E = offered for 188 d until slaughter.
[2]Customized blend of minerals, vitamins, and feed additives (Performix Nutrition Systems, Nampa, ID, USA).

Cows and newborn calves

Prior to the beginning of the experiment (day −15), individual unshrunk BW and BCS (Wagner et al., 1988) were recorded, and a blood sample (**BS**) was collected from all cows via jugular venipuncture. Upon calving, cow unshrunk BW and BCS were recorded and a BS collected via jugular venipuncture, while a colostrum sample was collected via hand milking (50 mL) from each cow. Concurrently with cow postcalving sampling, calf birth BW and calf gender were recorded, a BS was collected via jugular venipuncture, and LM biopsy (**LMB**) was performed as in Schubach et al. (2019) in all calves. Cows and calves were sampled as soon as the calving was completed. However, cows that calved at night and their calves were sampled at first light the next morning, but within 8 h from calving. Another BS was collected from calves 24 h after birth via jugular venipuncture.

Weaning and preconditioning

Cow unshrunk BW and BCS (Wagner et al., 1988) were recorded at weaning (day 290). Calf unshrunk BW was recorded over two consecutive days after weaning (days 290 and 291) and prior to shipping to feedyard (days 324 and 325), which were averaged to calculate preconditioning ADG. Calves were observed daily for bovine respiratory disease (**BRD**) signs during the 35-d preconditioning period according to the subjective criteria described by Berry et al. (2004).

Feedyard

Calves were observed daily for BRD signs according to the DART system (Zoetis) and received medication according to the management criteria of the feedyard. LMB was again performed in all calves (Schubach et al., 2019) on day 485 of the experiment. At the commercial packing plant, HCW was collected upon slaughter. Final finishing BW was estimated based on HCW adjusted to a 63% dressing percentage (Loza et al., 2010). After a 24-h chill, trained personnel assessed carcass backfat thickness at the 12th rib and LM area, whereas a United States Department of Agriculture grader recorded all other carcass measures. Feedyard ADG was determined based on final preconditioning BW, and the final finishing BW estimated from HCW.

Laboratorial analysis

BSs were collected into commercial blood collection tubes (Vacutainer, 10 mL; Becton Dickinson, Franklin Lakes, NJ) containing either no additive or freeze-dried sodium heparin for serum and plasma collection, respectively. After collection, all BSs were placed immediately on ice, centrifuged (2,500 × *g* for 30 min; 4 °C) for plasma or serum harvest, and stored at −80 °C on the same day of collection. Colostrum samples were also stored at −80 °C on the same day of collection. All plasma samples were analyzed for FA concentration using gas chromatography (Agilent 7890, Agilent Technologies, Inc.) as in Schubach et al. (2019). Only FA that were individually identified in the analysis are reported. Colostrum and plasma samples collected from calves 24 h after birth were analyzed for immunoglobulin G (**IgG**) concentrations (E11-118; Bethyl Laboratories, Montgomery, TX).

LMB 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. 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 polymerase chain reaction (**PCR**) using gene-specific primers (20 pM each; Table 3) were completed as described by Rodrigues et al. (2015). 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. A portion of the amplified products was purified with the QIAquick PCR purification kit (Qiagen Inc., Valencia, CA) and sequenced at the Texas A&M AgriLife Genomics and Bioinformatics Service to verify the specificity of amplification. All amplified products represented only the genes of interest. 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 coefficient of variation for the geometrical mean of reference genes across all samples was 2.4%. Results are expressed as relative fold change ($2^{-\Delta\Delta CT}$), as described by (Ocón-Grove et al., 2008).

Statistical analysis

All variables were analyzed with cow as the experimental unit, and cow(treatment × group) and group as random variables. Quantitative data were analyzed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC), and binary data were analyzed using the GLIMMIX procedure of SAS (SAS Inst. Inc.). All data were analyzed using gestation days receiving treatment as an independent covariate and Satterthwaite approximation to determine the denominator degrees of freedom for tests of fixed effects. Model statements for cow-related responses included the effects of treatment. Analysis of cow plasma FA profile at calving also included results from day −15 as an independent covariate. Model statements for calf-related responses analyses included the effects of treatment, calf sex, and the treatment × calf sex interaction. Incidence of BRD signs was analyzed as repeated measures using day as a fixed effect and all resultant interactions with treatment and calf sex. The subject for the repeated statement was cow (treatment × group), and the covariance structure utilized was autoregressive by providing the best fit according to the lowest Akaike information criterion. The expression of LM genes was not analyzed as repeated measures, given the substantial interval between samplings (~400 d). Results are reported as covariately adjusted least square means and separated using least square difference. Significance was set at $P \leq 0.05$ and tendencies were determined if $P > 0.05$ and ≤ 0.10.

Table 3. Primer sequences, accession number, and reference for all gene transcripts analyzed by real-time reverse transcription PCR

Target	Primer sequence	Accession no.
FABP4 (Li et al., 2018)		
Forward	AAACTTAGATGAAGGTGCTCTGG	AJ4160220
Reverse	CATAAACTCTGGTGGCAGTGA	
FASN (Jeong et al., 2012)		
Forward	ATCGAGTGCATCAGGCAAGT	AF479289
Reverse	TGTGAGCACATCTCGAAAGCCA	
MyoD (Muroya et al., 2002)		
Forward	ATCCTGCGCAACGCCATCCGCTATATCGA	AF093675
Reverse	CTCGCTGTAGTAAGTGCGGTCGTAGCAGT	
Myogenin (Muroya et al., 2002)		
Forward	GAGAAGCGCAGACTCAAGAAGGTGAATGA	AF091714
Reverse	TCTGTAGGGTCCGCTGGGAGCAGATGATC	
PPAR-γ (Li et al., 2018)		
Forward	GCATTTCCACTCCGCACTAT	AY137204
Reverse	GGGATACAGGCTCCACTTTG	
SCD (Li et al., 2018)		
Forward	GCCAACAACTCTGCCTTTATG	GU947654
Reverse	CACCAATGACTGACCACCTG	
B-*actin* (Bong et al., 2012)		
Forward	AGCAAGCAGGAGTACGATGAGT	NM_173979
Reverse	ATCCAACCGACTGCTGTCA	
Ribosomal protein S9 (Jeong et al., 2012)		
Forward	CCTCGACCAAGAGCTGAAG	AF479289
Reverse	CCTCCAGACCTCACGTTTGTTC	

Results and Discussion

Nutrient composition and profile of diets (hay + treatment) offered to CSSO- and CON-supplemented cows are described in Table 1. The CSSO was supplemented herein at the same daily amount that Marques et al. (2017) provided the mix of Ca salts of ω-3 and ω-6 PUFA to late-gestating cows. The CON treatment was included to serve as an isolipidic, isocaloric, and isonitrogenous control. Both CSSO and CON diets were formulated to represent a typical forage-based diet with limited FA content and provided adequate amounts of energy and crude protein to pregnant cows during the last trimester of gestation (NRC, 2000). Hence, results from this experiment should not be associated with differences in total FA intake, but with the potential impacts of supplemental ω-6 PUFA to late-gestating beef cows.

Cow parameters

Cow age, days receiving treatments, and gestation length did not differ ($P \geq 0.60$) between CSSO and CON cows (Table 4). As designed, CSSO and CON cows had similar ($P \geq 0.89$) initial BW and BCS (day −15), which remained similar ($P \geq 0.40$) between treatment groups at calving and weaning. These outcomes were expected given that CSSO and CON cows consumed similar amounts of energy and protein during late gestation and were managed as a single group from calving until weaning. Others have also reported similar BW and BCS responses between beef (Marques et al., 2017; Ricks et al., 2020) and dairy cows receiving supplements containing CSSO or other FA sources during late gestation (Garcia et al., 2014; Salehi et al., 2016).

Cows assigned to receive CSSO and CON had similar ($P \geq 0.15$) plasma concentrations of individual and total FA on day −15 (data not shown), hence equivalent circulating FA profile before treatment administration. Upon calving, CSSO cows had greater ($P < 0.01$) concentrations of plasma palmitic, stearic, linoleic, dihomo-γ-linolenic, arachidonic, and osbond acids, as well as total saturated FA, PUFA, ω-6 PUFA, and total FA compared with CON-supplemented cows (Table 5). Cows receiving CON had greater ($P < 0.01$) concentrations of plasma myristic, palmitoleic, oleic, and α-linolenic acids, as well as total monounsaturated and ω-3 PUFA, compared with CSSO cows (Table 5). These results corroborate the FA content and intake of treatments, given that plasma FA profile reflects the intake and intestinal flow of FA (Klusmeyer and Clark, 1991; Lake et al., 2007; Hess et al., 2008). The decrease in plasma α-linolenic acid and ω-3 PUFA concentrations in CSSO-supplemented cattle has also been reported by our group in research with mature and growing beef cattle (Brandão et al., 2018, 2020; Schubach et al., 2019).

Table 4. Performance of beef cows receiving diets supplemented with CSSO ($n = 52$) or CON ($n = 52$) during the last trimester of gestation[1,2]

Item	CON	CSSO	SEM	*P*-value =
Cow age, yr	5.33	5.39	0.41	0.93
Days receiving treatments, d	85.5	85.1	0.6	0.60
Gestation length, d	280	280	0.6	0.60
BW, kg				
Initial (day −15)	504	505	9	0.89
Calving	545	554	9	0.48
Weaning (day 290)	568	564	9	0.78
BCS				
Initial (day −15)	4.88	4.88	0.04	0.92
Calving	4.74	4.82	0.07	0.59
Weaning (day 290)	5.19	5.09	0.08	0.40

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving.
[2]Unshrunk BW and BCS (Wagner et al., 1988) were recorded prior to the beginning of the experiment (initial; day −15), within 8 h after calving, and at weaning (day 290).

Table 5. Plasma FA profile (μg/mL of plasma) at calving of beef cows receiving diets supplemented with CSSO (*n* = 52) or CON (*n* = 52) during the last trimester of gestation[1,2]

Item	CON	CSSO	SEM	P-value
Myristic (14:0)	6.34	4.76	0.17	<0.01
Palmitic (16:0)	83.0	102	3.5	<0.01
Palmitoleic (16:1, ω-7)	10.3	4.39	0.36	<0.01
Stearic (18:0)	98.7	113	4.0	0.01
Oleic (18:1, ω-9)	90.0	60.5	3.3	<0.01
Linoleic (18:2, ω-6)	145	342	12	<0.01
α-Linolenic (18:3, ω-3)	60.5	34.2	1.5	<0.01
Dihomo-γ-linolenic acid (20:3, ω-6)	8.63	12.1	0.4	<0.01
Arachidonic (20:4, ω-6)	13.3	19.2	0.7	<0.01
Osbond (22:5, ω-6)	20.3	26.9	1.1	<0.01
Docosapentaenoic (22:5, ω-3)	6.77	7.28	0.27	0.20
Total saturated FA	201	233	7	<0.01
Total monounsaturated FA	104	67	4	<0.01
Total polyunsaturated FA	270	450	15	<0.01
Total ω-3 polyunsaturated FA	67.4	41.7	1.7	<0.01
Total ω-6 polyunsaturated FA	202	408	13	<0.01
Total identified FA	575	750	25	<0.01

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving.
[2]BSs were collected from all cows on day −15 of the experiment and within 8 h after calving and analyzed for FA profile according to Schubach et al. (2019). Values form day −15 were used as an independent covariate within each individual FA analysis.

Table 6. Calving, weaning, and preconditioning responses from offspring of beef cows receiving diets containing CSSO (*n* = 52) or CON (*n* = 52) during the last trimester of gestation[1]

Item	CON	CSSO	SEM	P-value
Calving results				
Calving rate, %	100	100	—	—
% of male calves born	56.6	51.0	7.0	0.57
Calf birth weight, kg	37.0	37.7	0.6	0.42
Adjusted calf birth weight[2], kg	38.3	39.1	0.6	0.36
Colostrum IgG, mg/mL	373	423	15	0.02
Calf plasma IgG 24 h after birth, mg/mL	55.7	97.9	9.0	< 0.01
Weaning results				
Weaning rate, %	96.0	100	2.0	0.17
% of male calves weaned	56.9	51.0	7.0	0.56
Calf weaning age, d	209	209	0.1	0.91
Calf weaning weight, kg	262	264	4	0.72
Calf 205-d adjusted weaning weight[2], kg	267	270	4	0.57
Preconditioning results				
ADG, kg/d	0.68	0.67	0.05	0.84
Final BW, kg	287	289	4	0.77

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving. Calves were weaned on day 290 of the experiment, preconditioned for 35 d (day 291 to 325), and transferred to a feedyard (Cannon Hill Feeders LLC., Nyssa, OR) where they remained until slaughter (day 514). All BWs collected were unshrunk.
[2]According to BIF (2010).

Colostrum IgG concentration was greater (*P* = 0.02) in CSSO vs. CON cows (Table 6). Ricks et al. (2020) also reported increased colostrum IgG concentrations in cows supplemented with CSSO during the last trimester of gestation compared with cows receiving an isocaloric and isonitrogenous diet containing corn gluten feed. Supplementing CSSO and other ω-6 PUFA sources regulates immune responses in cattle, including proinflammatory reactions that stimulate humoral responses (Hess et al., 2008; Schmitz and Ecker, 2008; Garcia et al., 2016). The majority of the IgG in the colostrum of cows is derived from their systemic synthesis and circulatory reserves (Hurley and Theil, 2011). Perhaps the increased colostrum IgG concentrations in beef cows receiving CSSO noted herein and by Ricks et al. (2020) are a resultant from heightened humoral immunity. Nonetheless, research investigating the impacts of supplementing CSSO or other ω-6 PUFA sources to late-gestating cows on colostrum quality is limited and deserves further investigation given its importance to lifelong offspring development (Besser and Gay, 1994; Wittum and Perino, 1995).

Calf birth, weaning, and preconditioning parameters

All cows assigned to the experiment on day −15 gave birth to a live calf; hence, the calving rate was 100% across treatments (Table 6). No treatment effects were detected (*P* ≥ 0.36) for calf birth BW and proportion of male calves born (adjusted or not; BIF, 2010), whereas calf sex influences birth BW and subsequent growth responses (Koger and Knox, 1945; Table 6). Calves from CSSO cows had greater (*P* < 0.01) concentrations of plasma linoleic, dihomo-γ-linolenic, and arachidonic acids, as well as total PUFA and ω-6 PUFA, compared with calves from CON-supplemented cows (Table 7). Calves from CON cows had greater (*P* ≤ 0.05) concentrations of plasma palmitoleic and α-linolenic acids, as well as total monounsaturated and ω-3 PUFA, compared with CSSO cohorts (Table 7). These results corroborate differences noted in plasma FA profile of CSSO and CON cows at calving, given that maternal circulating FA are transferred to the fetus via the placenta (Noble et al., 1978; Garcia et al., 2014). These differences could also be associated with the colostrum FA profile as a few calves may have nursed cows before sample collection, particularly those born at night. Accordingly, Ricks et al. (2020) reported greater concentrations of linoleic acid and PUFA in colostrum from CSSO-supplemented cows, and colostrum FA content reflects cow prepartum FA intake and circulating FA profile (Long et al., 2009; Leiber et al., 2011; Garcia et al., 2014). Nonetheless, Ricks et al. (2020) also collected BSs from calves immediately after birth and before calves were capable of standing and suckling. These authors also reported greater serum concentrations of linoleic and arachidonic acid in calves born from CSSO-supplemented cows, corroborating the differences in calf plasma FA profile noted herein (Table 7).

Calves from CSSO cows had greater (*P* ≤ 0.05) mRNA expression in the LM of *adipocyte fatty acid-binding protein* (**FABP4**) and *stearoyl-CoA desaturase* (**SCD**) at birth, as well as tendency for the same outcome for *peroxisome proliferator-activated receptor gamma* (**PPAR-γ**) compared with CON cohorts (Table 8). No treatment effect was noted (*P* = 0.36) for mRNA expression of *FA synthase* in the LM at birth (Table 8). The C_T values of housekeeping genes, analyzed individually or as geometrical mean, did not differ (*P* ≥ 0.95) between CSSO and CON calves at birth (22.66 vs. 22.69 for *B-actin*, SEM = 0.14; 19.41 vs. 19.45 for *ribosomal protein S9*, SEM = 0.10; 20.99 vs. 20.99 for the geometrical mean, SEM = 0.11), corroborating the validity of these mRNA expression analyses. All genes of interest analyzed in this experiment are associated with adipogenic

Table 7. Plasma FA profile (μg/mL of plasma) at birth from offspring of beef cows receiving diets supplemented with CSSO (n = 52) or CON (n = 52) during the last trimester of gestation[1,2]

Item	CON	PUFA	SEM	P-value
Myristic (14:0)	12.9	12.7	1.5	0.92
Palmitic (16:0)	96.5	96.9	6	0.96
Palmitoleic (16:1, ω-7)	15.9	3.6	0.8	0.04
Stearic (18:0)	36.5	36.6	1.6	0.98
Oleic (18:1, ω-9)	91.4	83.6	3.7	0.14
Linoleic (18:2, ω-6)	24.5	41.9	4.2	<0.01
α-Linolenic (18:3, ω-3)	1.23	0.100	0.285	<0.01
Dihomo-γ-linolenic acid (20:3, ω-6)	3.63	5.69	0.39	<0.01
Arachidonic (20:4, ω-6)	7.98	11.6	0.69	<0.01
Osbond (22:5, ω-6)	0.912	0.379	0.328	0.25
Docosapentaenoic (22:5, ω-3)	0.621	0.233	0.279	0.32
Total saturated FA	150	150	9	0.99
Total monounsaturated FA	121	107	5	0.05
Total polyunsaturated FA	40.1	60.6	4.6	<0.01
Total ω-3 polyunsaturated FA	2.50	1.05	0.50	0.05
Total ω-6 polyunsaturated FA	37.6	59.5	4.4	<0.01
Total identified FA	311	319	15	0.73

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving.
[2]BSs were collected from all cows within 8 h after calving and analyzed for FA profile as in Schubach et al. (2019).

Table 8. Expression of LM genes in the offspring of beef cows receiving diets containing CSSO (n = 52) or CON (n = 52) during the last trimester of gestation[1,2]

Item	CON	CSSO	SEM	*P-value*
FABP4				
Birth	35.0	73.9	14	0.03
Feedyard	6.09	6.97	0.80	0.44
FASN				
Birth	1.77	1.92	0.11	0.36
Feedyard	4.36	4.61	0.44	0.69
MyoD				
Birth	13.3	22.6	3.0	0.02
Feedyard	3.76	3.89	0.30	0.76
Myogenin				
Birth	7.03	9.77	1.00	0.04
Feedyard	2.45	2.60	0.18	0.55
PPAR- γ				
Birth	3.16	4.55	0.56	0.07
Feedyard	2.66	3.00	0.28	0.38
SCD				
Birth	3.43	4.54	0.34	0.05
Feedyard	3.16	3.60	0.31	0.33

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving. Calves were weaned on day 290 of the experiment, preconditioned for 35 d (day 291 to 325), and transferred to a feedyard (Cannon Hill Feeders LLC., Nyssa, OR) where they remained until slaughter (day 514).
[2]Samples of the LM were taken via needle biopsy within 8 h after birth and on day 485 of the experiment. Values are expressed as relative fold change compared with the threshold cycle of reference genes analyzed within the same sample (Ocón-Grove et al., 2008).

activities in the LM (Schubach et al., 2019). More specifically, PPAR-γ regulates adipogenesis and lipid metabolism through the induction of genes mediating these processes (Houseknecht et al., 2002) and has been identified as a candidate gene related to adipogenesis of bovine intramuscular adipose tissue (Lim et al., 2011). The FABP4 is a target gene of PPAR-γ (Taniguchi et al., 2008), involved in adipocyte differentiation, lipid hydrolysis, and acts as an intracellular FA chaperone (Michal et al., 2006). The SCD is a key regulatory enzyme in the lipogenic pathway modulated by PPAR-γ (Ntambi, 1999), and increased expression is associated with adipocyte hypertrophy (Martin et al., 1999). Linoleic acid and ω-6 PUFA regulate PPAR-γ mRNA expression in a ligand-dependent manner (Houseknecht et al., 2002), stimulating PPAR-γ function and mRNA expression (Xu et al., 1999; Thoennes et al., 2000; Spurlock et al., 2000). Hence, CSSO supplementation to late-gestation cows increased the supply of ω-6 PUFA to the fetus, resulting in the increased expression of LM genes within the PPAR-γ lipogenic pathway at birth.

Calves from CSSO cows also had greater ($P \leq 0.04$) mRNA expression in the LM of *myogenic differentiation 1* (**MyoD**) and *myogenin* at birth compared with CON cohorts (Table 8). *Myogenin* and MyoD are regulatory factors expressed by myocytes that regulate postnatal muscle growth, through differentiation and fusion with existing muscle fibers (Le Grand and Rudnicki, 2007; Perdiguero et al., 2009). Increased mRNA expression of these genes may indicate a greater proliferation of myocytes in the LM of CSSO offspring at birth, which terminally develop into muscle fibers upon *myogenin* expression (Du et al., 2010, 2011). The mechanisms by which ω-6 PUFA upregulates these genes deserve further investigation, as ω-3 PUFA are typically associated with increased expression of LM genes that regulate muscle development and function (Hiller et al., 2012). Perhaps, the increased supply of ω-6 PUFA during gestation to CSSO offspring promoted the differentiation and development of muscle cells via proinflammatory pathways (Cooke, 2019). Arachidonic acid is a precursor of prostaglandin E2 via the cyclooxygenase-2 pathway, which promotes myogenesis in skeletal muscle by stimulating myoblast proliferation (Bondesen et al., 2004; Mo et al., 2015; Ho et al., 2017). Accordingly, calves from CSSO cows had greater concentrations of arachidonic acid compared with CON cohorts after birth, although research is warranted to validate this rationale in beef cattle.

Calves from CSSO cows had greater plasma concentrations of IgG at 24 h after birth compared with CON cohorts (Table 6). These outcomes are partially resultant from increased colostrum IgG concentration in CSSO cows, given that circulating IgG concentration in nursing calves are positively correlated with colostrum IgG when the colostrum intake is not limited (Devery-Pocius and Larson, 1983; Morin et al., 1997). Moreover, calves from CSSO cows likely had greater ability to absorb colostrum IgG, as PUFA incorporated into intestinal cells upregulates IgG receptors (e.g., neonatal Fc receptor) responsible for IgG absorption in neonates (Israel et al., 1997; Mayer et al., 2002). Ricks et al. (2020) also reported greater serum IgG concentrations 24 h after birth in calves born from CSSO-fed cows in their study and stated that increased passive transfer of IgG due to CSSO supplementation could help mitigating subsequent calf morbidity and mortality.

No treatment differences were noted herein ($P \geq 0.17$) for the weaning rate and proportion of male calves weaned, as well as preconditioning ADG and final BW (Table 7). No BRD signs were observed in calves during the preconditioning period. Alternatively, Ricks et al. (2020) reported greater preweaning growth in calves from cows receiving CSSO during gestation.

This response, however, was mostly noted in primiparous cows and associated with improved milk production from supplementing fat to growing females (Bellows, 1999), whereas the current experiment used multiparous cows only. Supporting our results, others have also reported similar birth and weaning BW, as well as preconditioning performance in calves from multiparous cows supplemented or not with ω-6 PUFA during gestation (Banta et al., 2006, 2011 Marques et al., 2017). Collectively, calving to preconditioning results indicate that supplementing CSSO to late-gestating beef cows did not impact offspring birth BW and subsequent growth rates compared with CON-supplemented cohorts, despite differences noted in calf plasma FA profile, mRNA expression of LM genes, and IgG concentrations near birth.

Calf feedyard and carcass parameters

All calves were shipped to the packing plant on day 513 and slaughtered on day 514 of the experiment; hence, days on feed for both treatments was 188 d. A treatment × day interaction was detected for the incidence of BRD signs in the feedyard ($P = 0.03$). A greater ($P \leq 0.05$) proportion of CON cattle were observed with BRD signs from day 333 to 337 of the experiment (day 8 to 12 after feedyard arrival; Figure 2), although cumulative BRD incidence did not differ ($P = 0.16$) between treatments (Table 9). No BRD signs were noted beyond 3 wk of feedyard arrival until slaughter. Nonetheless, the incidence of calves diagnosed with BRD that required a second antimicrobial treatment was less ($P = 0.03$) in calves from CSSO cows, resulting in reduced ($P = 0.05$) need of treatments compared with CON (Table 5). These results indicate improved immunocompetence of calves from CSSO-supplemented cows upon feedyard entry, when BRD incidence is typically elevated (Snowder et al., 2006). Such outcomes may be associated with supplemental ω-6 PUFA during gestation, as these FA play critical roles in immune system development, maturation, and function (Schmitz and Ecker, 2008; Cooke, 2019). Improved immunity of calves from CSSO cows should also be attributed to their greater plasma IgG concentrations 24 after birth, which positively impact calf immunity later in life (Wittum and Perino, 1995).

No treatment effects were detected ($P \geq 0.33$) for mRNA expression of LM genes during the feedyard phase (Table 8). The C_T values of housekeeping genes also did not differ ($P \geq 0.55$) between CSSO and CON calves on day 485 (21.73 vs. 21.80 for B-*actin*, SEM = 0.08; 20.58 vs. 20.58 for *ribosomal protein S9*, SEM = 0.06; 21.15 vs. 21.19 for the geometrical mean, SEM = 0.04), further validating these mRNA expression analyses. Therefore, CSSO supplementation to late-gestating cows appears to modulate mRNA expression of adipogenic and myogenic genes in the calf LM at birth, without continuing effects later in life when supplemental CSSO or ω-6 PUFA are not provided to offspring. Treatment × sex interactions were detected ($P \leq 0.03$) for feedyard ADG, final BW, and HCW (Table 9). These responses were greater ($P \leq 0.05$) in steers from CSSO cows compared with CON and did not differ ($P \geq 0.59$) between heifers (Table 9). The proportion of male calves slaughtered did not differ among treatments ($P = 0.56$) and were equal to the proportion of male calves weaned (Table 7) given that no calf mortality was observed in the feedyard. A treatment effect was detected ($P = 0.03$) for carcass LM area, which was greater in calves from CSSO cows compared with CON across sexes (Table 9). Different than ADG and HCW, the treatment × sex interaction was not significant for this latter variable ($P = 0.31$). The LM area was greater ($P = 0.02$) in steers and tended to be greater ($P = 0.10$) in heifers from CSSO cows compared with CON cohorts (82.0 vs. 78.5 cm^2 in steers and 82.9 vs. 80.7 cm^2 in heifers, respectively; SEM = 1.1). No treatment differences were detected ($P \geq 0.43$) for the remaining carcass traits evaluated, including marbling and proportion of carcasses graded as Choice (Table 9). Feedyard results indicate that CSSO supplementation to late-gestating beef cows improved BW gain in the male offspring only, but increased LM development across offspring sexes.

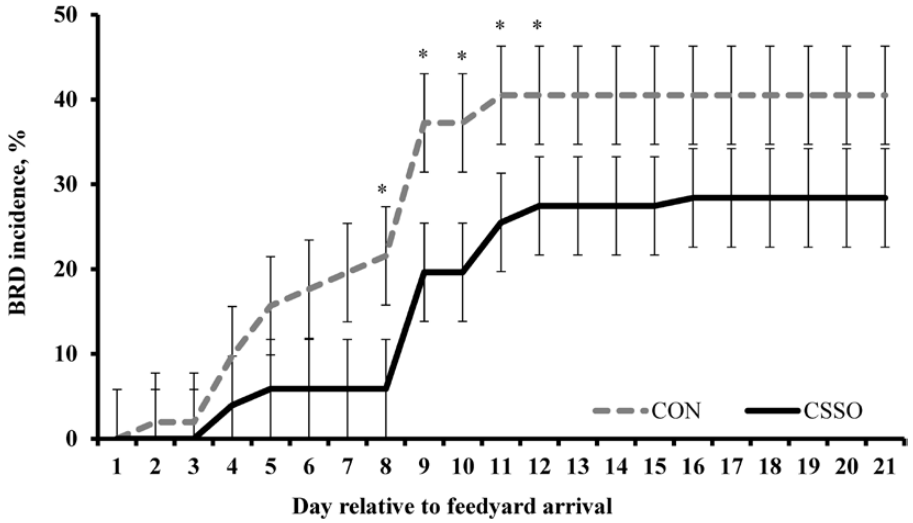

Figure 2. Cumulative incidence of BRD, during the initial 3 wk after feedyard arrival, from the offspring of beef cows receiving diets containing CSSO ($n = 52$) or CON ($n = 52$) during the last trimester of gestation. Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving. Calves were weaned on day 290 of the experiment, preconditioned for 35 d (day 291 to 325), and transferred to a feedyard where they remained until slaughter (day 514). Calves were observed daily for respiratory disease signs based on the DART system (Zoetis, Florham Park, NJ) and received medication according to the management criteria of the commercial feedyard. A treatment × day interaction was detected ($P = 0.03$), whereas no BRD incidence was noted beyond 21 d relative to feedyard arrival. Within days, *$P \leq 0.05$.

Table 9. Feedyard performance and carcass characteristics from offspring of beef cows receiving diets containing CSSO (n = 52) or CON (n = 52) during the last trimester of gestation[1]

Item	CON	CSSO	SEM	*P-value*
Cattle treated for respiratory disease[2], %				
Once	40.5	28.4	6.7	0.16
Twice	19.2	5.64	4.79	0.03
Number of antimicrobial treatments required	1.49	1.18	0.10	0.05
ADG, kg/d				
Steers	1.39	1.52	0.06	0.05
Heifers	1.54	1.50	0.06	0.59
Final BW, kg				
Steers	553	579	9	0.02
Heifers	575	570	9	0.66
Carcass characteristics[3]				
HCW, kg				
Steers	349	365	6	0.02
Heifers	362	359	6	0.66
Backfat, cm	2.46	2.40	0.14	0.76
LM area, cm^2	79.6	82.4	1.1	0.03
Marbling score	526	510	15	0.47
Yield grade	3.76	3.68	0.07	0.43
Carcasses grading choice or above, %	85.9	88.0	4.9	0.77

[1]Cows received (dry matter basis) 195 g/cow daily of CSSO (Essentiom; Church and Dwight Co., Inc., Princeton, NJ) or 170 g/cow daily of CON (Energy Booster 100; Milk Specialties, Eden Prairie, MN). Treatments were provided from day 0 (day 195 of gestation) to calving. Calves were weaned on day 290 of the experiment, preconditioned for 35 d (day 291 to 325), and transferred to a feedyard (Cannon Hill Feeders LLC., Nyssa, OR) where they remained until slaughter (day 514).
[2]Calves were observed daily for respiratory disease signs based on the DART system (Zoetis, Florham Park, NJ) and received medication according to the management criteria of the commercial feedyard.
[3]Backfat thickness measured at the 12th rib; marbling score: 400 = $Small^{00}$, 500 = $Modest^{00}$, 600 = $Medium^{00}$; yield grade calculated as reported by Lawrence et al. (2010).

The reason for the treatment × sex interaction on ADG and HCW is unclear, as steers and heifers were equally managed as a single group in the feedyard.

Treatment differences noted in LM area were observed without an equivalent response in MyoD and *myogenin* mRNA expression on day 485 (te Pas et al., 1999). However, myogenic factors are downregulated as cattle mature and muscle fibers are fully developed (Picard et al., 2002; Du et al., 2010; Schubach et al., 2019). Improved feedyard ADG and carcass LM area should also be associated with enhanced immunocompetence of calves from CSSO cows, given that the number of BRD treatments is negatively associated with feedlot performance and carcass merit (Blakebrough-Hall et al., 2020). Maternal dietary fat content appears to impact appetite regulation in the offspring (Gupta et al., 2009), and greater feed intake of calves from CSSO cows may have contributed to their improved feedyard growth and immunity responses (Cooke, 2017). Collectively, treatment differences noted in the feedyard support our hypothesis, at least partially, as supplemental CSSO during gestation had beneficial impacts on offspring development via programming effects. Increased marbling was also expected from CSSO supplementation, given the ω-6 PUFA effects on adipocyte development (Houseknecht et al., 2002; Mangrum et al., 2016; Schubach et al., 2019) and treatment effects on adipogenic genes at birth. The major benefits of CSSO supplementation during late gestation, however, were limited to muscle growth. Accumulation of ω-6 PUFA into fetal tissues during gestation appears to have enhanced the development of muscle fibers, which translated into increased carcass and LM growth when offspring were provided anabolic feedlot diets (Harper and Pethick, 2004).

Overall conclusions

Supplementing forage-fed beef cows during late gestation with CSSO did not impact cow performance, calving rate, or calf birth BW. After calving, plasma concentrations of ω-6 PUFA were greater in CSSO cows and their offspring, as well as IgG concentrations in the colostrum and in calf plasma, compared with CON cohorts. Calves from CSSO cows were also born with upregulated mRNA expression of adipogenic and myogenic genes in the LM. No treatment differences in offspring growth were observed from birth to weaning and subsequent 35-d preconditioning period. Upon feedyard arrival, offspring from CSSO cows had improved response to BRD antimicrobial treatment, whereas ADG was improved in male offspring and LM area were increased across sexes compared with CON cohorts. These results are indicative of programming effects on postnatal offspring growth and health resultant from CSSO supplementation to late-gestating cows (Funston et al., 2010; Marques et al., 2017), although CSSO impacts on muscle development vs. adipogenesis and carcass marbling warrant further investigation. Nevertheless, these outcomes indicate that supplementing CSSO to beef cows during pregnancy might be a feasible alternative to optimize offspring productivity, welfare, and carcass merit in beef systems.

Acknowledgments

Financial support for this research was provided by Church & Dwight Co., Inc. (Princeton, NJ), the Oregon Beef Council, and the National Institutes of Health (# DK112360 to Donald B. Jump). Alice P. Brandão is supported by CAPES, Brazil (#88881.128327/2016-01).

Conflicts of interest statement

The authors declare no conflict of interest.

Literature Cited

AOAC. 2006. *Official methods of analysis*. 18th ed. Arlington (VA): Association of Official Analytical Chemists.

Banta, J. P., D. L. Lalman, F. N. Owens, C. R. Krehbiel, and R. P. Wettemann. 2006. Effects of interval-feeding whole sunflower seeds during mid to late gestation on performance of beef cows and their progeny. *J. Anim. Sci.* **84**:2410–2417. Doi:10.2527/jas.2005-400

Banta, J. P., D. L. Lalman, F. N. Owens, C. R. Krehbiel, and R. P. Wettemann. 2011. Effects of prepartum supplementation of linoleic and mid-oleic sunflower seed on cow performance, cow reproduction, and calf performance from birth through slaughter, and effects on intake and digestion in steers. *J. Anim. Sci.* **89**:3718–3727. Doi:10.2527/jas.2011-3937

Bellows, R. A. 1999. Some effects of feeding supplemental fat to beef cattle. In Proceedings of the Range Beef Cow Symposium; December 14 to 16, 1999; Greely, CO. Lincoln (NE): University of Nebraska.

Berry, B. A., A. W. Confer, C. R. Krehbiel, D. R. Gill, R. A. Smith, and M. Montelongo. 2004. Effects of dietary energy and starch concentrations for newly received feedlot calves: II. Acute-phase protein response. *J. Anim. Sci.* **82**:845–850. Doi:10.2527/2004.823845x

Besser, T. E., and C. C. Gay. 1994. The importance of colostrum to the health of the neonatal calf. *Vet. Clin. North Am. Food Anim. Pract.* **10**:107–117. Doi:10.1016/s0749-0720(15)30591-0

BIF (Beef Improvement Federation). 2010. *Guidelines for Uniform Beef Improvement Programs*. 9th ed. Raleigh (NC): BIF, North Carolina State University.

Blakebrough-Hall, C., J. P. McMeniman, and L. A. González. 2020. An evaluation of the economic effects of bovine respiratory disease on animal performance, carcass traits, and economic outcomes in feedlot cattle defined using four BRD diagnosis methods. *J. Anim. Sci.* **98**:skaa005. Doi:10.1093/jas/skaa005

Bohnert, D. W., L. A. Stalker, R. R. Mills, A. Nyman, S. J. Falck, and R. F. Cooke. 2013. Late gestation supplementation of beef cows differing in body condition score: effects on cow and calf performance. *J. Anim. Sci.* **91**:5485–5491. Doi:10.2527/jas.2013-6301

Bondesen, B. A., S. T. Mills, K. M. Kegley, and G. K. Pavlath. 2004. The COX-2 pathway is essential during early stages of skeletal muscle regeneration. *Am. J. Physiol. Cell Physiol.* **287**:C475–C483. Doi:10.1152/ajpcell.00088.2004

Bong, J. J., J. Y. Jeong, P. Rajasekar, Y. M. Cho, E. G. Kwon, H. C. Kim, B. H. Paek, and M. Baik. 2012. Differential expression of genes associated with lipid metabolism in *longissimus dorsi* of Korean bulls and steers. *Meat Sci.* **91**:284–293. Doi:10.1016/j.meatsci.2012.02.004

Brandão, A. P., R. F. Cooke, K. M. Schubach, E. A. Colombo, G. N. Scatolin, B. Rett, D. B. Jump, and K. G. Pohler. 2020. Using low-moisture molasses-based blocks to supplement Ca salts of soybean oil to forage-fed beef cows. *Transl. Anim. Sci.* **4**:txaa061. Doi:10.1093/tas/txaa061

Brandão, A. P., R. F. Cooke, K. M. Schubach, R. S. Marques, D. W. Bohnert, R. S. Carvalho, N. W. Dias, C. L. Timlin, S. Clark-Deener, J. F. Currin, *et al.* 2018. Supplementing Ca salts of soybean oil after artificial insemination increases pregnancy success in *Bos taurus* beef cows. *J. Anim. Sci.* **96**:2838–2850. Doi:10.1093/jas/sky156

Carranza Martin, A. C., D. N. Coleman, L. G. Garcia, C. C. Furnus, and A. E. Relling. 2018. Prepartum fatty acid supplementation in sheep. III. Effect of eicosapentaenoic acid and docosahexaenoic acid during finishing on performance, hypothalamus gene expression, and muscle fatty acids composition in lambs. *J. Anim. Sci.* **96**:5300–5310. Doi:10.1093/jas/sky360

Coleman, D. N., K. C. Rivera-Acevedo, and A. E. Relling. 2018. Prepartum fatty acid supplementation in sheep I. Eicosapentaenoic and docosahexaenoic acid supplementation do not modify ewe and lamb metabolic status and performance through weaning. *J. Anim. Sci.* **96**:364–374. Doi:10.1093/jas/skx012

Cook, E. K., M. E. Garcia-Ascolani, R. E. Ricks, S. K. Duckett, G. C. Lamb, N. DiLorenzo, and N. M. Long. 2017. The effect of frequency of supplementing rumen-protected unsaturated fatty acids on blood serum fatty acid profiles in beef heifers and lactating cows. *J. Anim. Sci.* **95**:2977–2985. Doi:10.2527/jas.2016.1275

Cooke, R. F. 2017. Nutritional and management considerations for beef cattle experiencing stress-induced inflammation. *Prof. Anim. Sci.* **33**:1–11. Doi:10.15232/pas.2016-01573

Cooke, R. F. 2019. Effects on animal health and immune function. *Vet. Clin. North Am. Food Anim. Pract.* **35**:331–341. Doi:10.1016/j.cvfa.2019.02.004

Cooke, R. F., D. W. Bohnert, B. I. Cappellozza, R. S. Marques, T. DelCurto, and C. J. Mueller. 2014. Incorporation of sexed semen into reproductive management of range cow-calf operations. *Livest. Sci.* **163**:165–171. Doi:10.1016/j.livsci.2014.02.015

Devery-Pocius, J. E., and B. L. Larson. 1983. Age and previous lactations as factors in the amount of bovine colostral immunoglobulins. *J. Dairy Sci.* **66**:221–226. Doi:10.3168/jds.S0022-0302(83)81780-9

Du, M., J. Tong, J. Zhao, K. R. Underwood, M. Zhu, S. P. Ford, and P. W. Nathanielsz. 2010. Fetal programming of skeletal muscle development in ruminant animals. *J. Anim. Sci.* **88**(13 Suppl):E51–E60. Doi:10.2527/jas.2009-2311

Du, M., J. X. Zhao, X. Yan, Y. Huang, L. V. Nicodemus, W. Yue, R. J. McCormick, and M. J. Zhu. 2011. Fetal muscle development, mesenchymal multipotent cell differentiation, and associated signaling pathways. *J. Anim. Sci.* **89**:583–590. Doi:10.2527/jas.2010-3386

Fleige, S., and M. W. Pfaffl. 2006. RNA integrity and the effect on the real-time qRT-PCR performance. *Mol. Aspects Med.* **27**:126–139. Doi:10.1016/j.mam.2005.12.003

Funston, R. N., D. M. Larson, and K. A. Vonnahme. 2010. Effects of maternal nutrition on conceptus growth and offspring performance: implications for beef cattle production. *J. Anim. Sci.* **88**:E205–E215. Doi:10.2527/jas.2009-2351

Garcia, M., L. F. Greco, M. G. Favoreto, R. S. Marsola, L. T. Martins, R. S. Bisinotto, J. H. Shin, A. L. Lock, E. Block, W. W. Thatcher, *et al.* 2014. Effect of supplementing fat to pregnant nonlactating cows on colostral fatty acid profile and passive immunity of the newborn calf. *J. Dairy Sci.* **97**:392–405. Doi:10.3168/jds.2013-7086

Garcia, M., L. F. Greco, A. L. Lock, E. Block, J. E. P. Santos, W. W. Thatcher, and C. R. Staples. 2016. Supplementation of essential fatty acids to Holstein calves during late uterine life and first month of life alters hepatic fatty acid profile and gene expression. *J. Dairy Sci.* **99**:7085–7101. Doi:10.3168/jds.2015-10472

Gupta, A., M. Srinivasan, S. Thamadilok, and M. S. Patel. 2009. Hypothalamic alterations in fetuses of high fat diet-fed obese female rats. *J. Endocrinol.* **200**:293–300. Doi:10.1677/JOE-08-0429

Harper, G. S., and D. W. Pethick. 2004. How might marbling begin? *Aust. J. Exp. Agric.* **44**:653–662. Doi:10.1071/EA02114

Hess, B. W., G. E. Moss, and D. C. Rule. 2008. A decade of developments in the area of fat supplementation research with beef cattle and sheep. *J. Anim. Sci.* **86**(14 Suppl):E188–E204. Doi:10.2527/jas.2007-0546

Hiller, B., J. F. Hocquette, I. Cassar-Malek, G. Nuernberg, and K. Nuernberg. 2012. Dietary *n*-3 PUFA affect lipid metabolism and tissue function-related genes in bovine muscle. *Br. J. Nutr.* **108**:858–863. Doi:10.1017/S0007114511006179

Ho, A. T. V., A. R. Palla, M. R. Blake, N. D. Yucel, Y. X. Wang, K. E. G. Magnusson, C. A. Holbrook, P. E. Kraft, S. L. Delp, and H. M. Blau. 2017. Prostaglandin E2 is essential for efficacious skeletal muscle stem-cell function, augmenting regeneration and strength. *Proc. Natl. Acad. Sci. U. S. A.* **114**:6675–6684. Doi:10.1073/pnas.1705420114

Houseknecht, K. L., B. M. Cole, and P. J. Steele. 2002. Peroxisome proliferator-activated receptor gamma (PPARgamma) and its ligands: a review. *Domest. Anim. Endocrinol.* **22**:1–23. Doi:10.1016/s0739-7240(01)00117-5

Hurley, W. L., and P. K. Theil. 2011. Perspectives on immunoglobulins in colostrum and milk. *Nutrients* **3**:442–474. Doi:10.3390/nu3040442

Israel, E. J., S. Taylor, Z. Wu, E. Mizoguchi, R. S. Blumberg, A. Bhan, and N. E. Simister. 1997. Expression of the neonatal Fc receptor, FcRn, on human intestinal epithelial cells. *Immunology* **92**:69–74. Doi:10.1046/j.1365-2567.1997.00326.x

Jeong, J., E. G. Kwon, S. K. Im, K. S. Seo, and M. Baik. 2012. Expression of fat deposition and fat removal genes is associated with intramuscular fat content in *longissimus dorsi* muscle of Korean cattle steers. *J. Anim. Sci.* **90**:2044–2053. Doi:10.2527/jas.2011-4753

Klusmeyer, T. H., and J. H. Clark. 1991. Effects of dietary fat and protein on fatty acid flow to the duodenum and in milk produced by dairy cows. *J. Dairy Sci.* **74**:3055. Doi:10.3168/jds.S0022-0302(91)78491-9

Koger, M., and J. H. Knox. 1945. The effect of sex on weaning weight of range calves. *J. Anim. Sci.* **4**:15–19. Doi:10.2527/jas1945.4115

Lake, S. L., T. R. Weston, E. J. Scholljegerdes, C. M. Murrieta, B. M. Alexander, D. C. Rule, G. E. Moss, and B. W. Hess. 2007. Effects of postpartum dietary fat and body condition score at parturition on plasma, adipose tissue, and milk fatty acid composition of lactating beef cows. *J. Anim. Sci.* **85**:717–730. Doi:10.2527/jas.2006-353

Lawrence, T. E., N. A. Elam, M. F. Miller, J. C. Brooks, G. G. Hilton, D. L. VanOverbeke, F. K. McKeith, J. Killefer, T. H. Montgomery, D. M. Allen, *et al.* 2010. Predicting red meat yields in carcasses from beef-type and calf-fed Holstein steers using the United States Department of Agriculture calculated yield grade. *J. Anim. Sci.* **88**:2139–2143. Doi:10.2527/jas.2009-2739

Le Grand, F., and M. A. Rudnicki. 2007. Skeletal muscle satellite cells and adult myogenesis. *Curr. Opin. Cell Biol.* **19**:628–633. Doi:10.1016/j.ceb.2007.09.012

Leiber, F., R. Hochstrasser, H. Wettstein, and M. Kreuzer. 2011. Feed-ing transition cows with oilseeds: effects on fatty acid composition of adipose tissue, colostrum and milk. *Livest. Sci.* **138**:1–12. Doi:10.1016/j.livsci.2010.11.016

Li, X. Z., C. G. Yan, Q. S. Gao, Y. Yan, S. H. Choi, and S. B. Smith. 2018. Adipogenic/lipogenic gene expression and fatty acid composition in chuck, loin, and round muscles in response to grain feeding of Yanbian Yellow cattle. *J. Anim. Sci.* **96**:2698–2709. Doi:10.1093/jas/sky161

Lim, D., N. K. Kim, H. S. Park, S. H. Lee, Y. M. Cho, S. J. Oh, T. H. Kim, and H. Kim. 2011. Identification of candidate genes related to bovine marbling using protein-protein interaction networks. *Int. J. Biol. Sci.* **7**:992–1002. Doi:10.7150/ijbs.7.992

Long, N. M., M. J. Nijland, P. W. Nathanielsz, and S. P. Ford. 2010. The effect of early to mid-gestational nutrient restriction on female offspring fertility and hypothalamic-pituitary-adrenal axis response to stress. *J. Anim. Sci.* **88**:2029–2037. Doi:10.2527/jas.2009-2568

Long, N. M., A. B. Uthlaut, D. C. Rule, P. W. Nathanielsz, and S. P. Ford. 2009. The effects of maternal obesity and high nutrient intake on ovine colostrum nutrient composition. *Proc. West. Sect. Am. Soc. Anim. Sci.* **60**:183–185.

Loza, P. L., C. D. Buckner, K. J. Vander Pol, G. E. Erickson, T. J. Klopfenstein, and R. A. Stock. 2010. Effect of feeding combinations of wet distillers grains and wet corn gluten feed to feedlot cattle. *J. Anim. Sci.* **88**:1061–1072. Doi:10.2527/jas.2009-2190

Mangrum, K. S., G. Tuttle, S. K. Duckett, G. S. Sell, C. R. Krehbiel, and N. M. Long. 2016. The effect of supplementing rumen undegradable unsaturated fatty acids on marbling in early-weaned steers. *J. Anim. Sci.* **94**:833–844. Doi:10.2527/jas.2015-9809

Marques, R. S., R. F. Cooke, M. C. Rodrigues, A. P. Brandão, K. M. Schubach, K. D. Lippolis, P. Moriel, G. A. Perry, A. Lock, and D. W. Bohnert. 2017. Effects of supplementing calcium salts of polyunsaturated fatty acids to late-gestating beef cows on performance and physiological responses of the offspring. *J. Anim. Sci.* **95**:5347–5357. Doi:10.2527/jas2017.1606

Marques, R. S., R. F. Cooke, M. C. Rodrigues, P. Moriel, and D. W. Bohnert. 2016. Impacts of cow body condition score during gestation on weaning performance of the offspring. *Livest. Sci.* **191**:174–178. Doi:10.1016/j.livsci.2016.08.007

Martin, G. S., D. K. Lunt, K. G. Britain, and S. B. Smith. 1999. Postnatal development of stearoyl coenzyme A desaturase gene expression and adiposity in bovine subcutaneous adipose tissue. *J. Anim. Sci.* **77**:630–636. Doi:10.2527/1999.773630x

Mayer, B., A. Zolnai, L. V. Frenyó, V. Jancsik, Z. Szentirmay, L. Hammarström, and I. Kacskovics. 2002. Redistribution of the sheep neonatal Fc receptor in the mammary gland around the time of parturition in ewes and its localization in the small intestine of neonatal lambs. *Immunology* **107**:288–296. Doi:10.1046/j.1365-2567.2002.01514.x

Michal, J. J., Z. W. Zhang, C. T. Gaskins, and Z. Jiang. 2006. The bovine fatty acid binding protein 4 gene is significantly associated with marbling and subcutaneous fat depth in Wagyu × Limousin F2 crosses. *Anim. Genet.* **37**:400–402. Doi:10.1111/j.1365-2052.2006.01464.x

Mo, C., R. Zhao, J. Vallejo, O. Igwe, L. Bonewald, L. Wetmore, and M. Brotto. 2015. Prostaglandin E2 promotes proliferation of skeletal muscle myoblasts via EP4 receptor activation. *Cell Cycle* **14**:1507–1516. Doi:10.1080/15384101.2015.1026520

Morin, D. E., G. C. McCoy, and W. L. Hurley. 1997. Effects of quality, quantity, and timing of colostrum feeding and addition of a dried colostrum supplement on immunoglobulin G1 absorption in Holstein bull calves. *J. Dairy Sci.* **80**:747–753. Doi:10.3168/jds.S0022-0302(97)75994-0

Muroya, S., I. Nakajima, and K. Chikuni. 2002. Related expression of MyoD and Myf5 with myosin heavy chain isoform types in bovine adult skeletal muscles. *Zoolog. Sci.* **19**:755–761. Doi:10.2108/zsj.19.755

Noble, R. C., J. H. Shand, J. T. Drummond, and J. H. Moore. 1978. "Protected" polyunsaturated fatty acid in the diet of the ewe and the essential fatty acid status of the neonatal lamb. *J. Nutr.* **108**:1868–1876. Doi:10.1093/jn/108.11.1868

NRC. 2000. *Nutrient requirements of beef cattle*. 7th ed. Washington (DC): National Academy Press.

Ntambi, J. M. 1999. Regulation of stearoyl-CoA desaturase by polyunsaturated fatty acids and cholesterol. *J. Lipid Res.* **40**:1549–1558.

Ocón-Grove, O. M., F. N. T. Cooke, I. M. Alvarez, S. E. Johnson, T. L. Ott, and A. D. Ealy. 2008. Ovine endometrial expression of fibroblast growth factor (FGF) 2 and conceptus expression of FGF receptors during early pregnancy. *Domest. Anim. Endocrinol.* **34**:135–145. Doi:10.1016/j.domaniend.2006.12.002

te Pas, M. F., A. Soumillion, F. L. Harders, F. J. Verburg, T. J. van den Bosch, P. Galesloot, and T. H. Meuwissen. 1999. Influences of myogenin genotypes on birth weight, growth rate, carcass weight, backfat thickness, and lean weight of pigs. *J. Anim. Sci.* **77**:2352–2356. Doi:10.2527/1999.7792352x

Perdiguero, E., P. Sousa-Victor, E. Ballestar, and P. Muñoz-Cánoves. 2009. Epigenetic regulation of myogenesis. *Epigenetics* **4**:541–550. Doi:10.4161/epi.4.8.10258

Picard, B., L. Lefaucheur, C. Berri, and M. J. Duclos. 2002. Muscle fibre ontogenesis in farm animal species. *Reprod. Nutr. Dev.* **42**:415–431. Doi:10.1051/rnd:2002035

Ricks, R. E., E. K. Cook, and N. M. Long. 2020. Effects of supplementing ruminal-bypass unsaturated fatty acids during late gestation on beef cow and calf serum and colostrum fatty acids, transfer of passive immunity, and cow and calf performance. *Appl. Anim. Sci.* **36**:271–284. Doi:10.15232/aas.2019-01900

Rodrigues, M. C., R. F. Cooke, R. S. Marques, S. A. Arispe, D. H. Keisler, and D. W. Bohnert. 2015. Effects of oral meloxicam administration to beef cattle receiving lipopolysaccharide administration or vaccination against respiratory pathogens. *J. Anim. Sci.* **93**:5018–5027. Doi:10.2527/jas.2015-9424

Salehi, R., M. G. Colazo, M. Oba, and D. J. Ambrose. 2016. Effects of prepartum diets supplemented with rolled oilseeds on calf birth weight, postpartum health, feed intake, milk yield, and reproductive performance of dairy cows. *J. Dairy Sci.* **99**:3584–3597. Doi:10.3168/jds.2015-10186

Schmitz, G., and J. Ecker. 2008. The opposing effects of *n*-3 and *n*-6 fatty acids. *Prog. Lipid Res.* **47**:147–155. Doi:10.1016/j.plipres.2007.12.004

Schubach, K. M., R. F. Cooke, A. P. Brandão, O. A. de Sousa, T. F. Schumaher, D. B. Jump, K. G. Pohler, D. W. Bohnert, and R. S. Marques. 2019. Supplementing calcium salts of soybean oil to beef steers early in life to enhance carcass development and quality[1]. *J. Anim. Sci.* **97**:4182–4192. Doi:10.1093/jas/skz272

Silvestre, F. T., T. S. M. Carvalho, N. Francisco, J. E. P. Santos, C. R. Staples, T. C. Jenkins, and W. W. Thatcher. 2011. Effects of differential supplementation of fatty acids during the peripartum and breeding periods of Holstein cows: I. Uterine and metabolic responses, reproduction, and lactation. *J. Dairy Sci.* **94**:189–204. Doi:10.3168/jds.2010-3370

Snowder, G. D., L. D. Van Vleck, L. V. Cundiff, and G. L. Bennett. 2006. Bovine respiratory disease in feedlot cattle: environmental, genetic, and economic factors. *J. Anim. Sci.* **84**:1999–2008. Doi:10.2527/jas.2006-046

Spurlock, M. E., K. L. Houseknecht, C. P. Portocarrero, S. G. Cornelius, G. M. Willis, and C. A. Bidwell. 2000. Regulation of PPARgamma but not obese gene expression by dietary fat supplementation. *J. Nutr. Biochem.* **11**:260–266. doi:10.1016/s0955-2863(00)00076-0

Sukhija, P. S., and D. L. Palmquist. 1988. Rapid method for determination of total fatty acid content and composition of feedstuffs and feces. *J. Agric. Food Chem.* **36**:1202–1206. doi:10.1021/jf00084a019

Taniguchi, M., L. L. Guan, B. Zhang, M. V. Dodson, E. Okine, and S. S. Moore. 2008. Adipogenesis of bovine perimuscular preadipocytes. *Biochem. Biophys. Res. Commun.* **366**:54–59. doi:10.1016/j.bbrc.2007.11.110

Thoennes, S. R., P. L. Tate, T. M. Price, and M. W. Kilgore. 2000. Differential transcriptional activation of peroxisome proliferator-activated receptor gamma by omega-3 and omega-6 fatty acids in MCF-7 cells. *Mol. Cell. Endocrinol.* **160**:67–73. doi:10.1016/s0303-7207(99)00254-3

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* **74**:3583–3597. doi:10.3168/jds.S0022-0302(91)78551-2

Vandesompele, J., K. De Preter, F. Pattyn, B. Poppe, N. Van Roy, A. De Paepe, and F. Speleman. 2002. Accurate normalization of real-time quantitative RT-PCR data by geometric averaging of multiple internal control genes. *Genome Biol.* **3**:RESEARCH0034. doi:10.1186/gb-2002-3-7-research0034

Wagner, J. J., K. S. Lusby, J. W. Oltjen, J. Rakestraw, R. P. Wettemann, and L. E. Walters. 1988. Carcass composition in mature Hereford cows: estimation and effect on daily metabolizable energy requirement during winter. *J. Anim. Sci.* **66**:603–612. doi:10.2527/jas1988.663603x

Wittum, T. E., and L. J. Perino. 1995. Passive immune status at postpartum hour 24 and long-term health and performance of calves. *Am. J. Vet. Res.* **56**:1149–1154.

Xu, H. E., M. H. Lambert, V. G. Montana, D. J. Parks, S. G. Blanchard, P. J. Brown, D. D. Sternbach, J. M. Lehmann, G. B. Wisely, T. M. Willson, *et al.* 1999. Molecular recognition of fatty acids by peroxisome proliferator-activated receptors. *Mol. Cell* **3**:397–403. doi:10.1016/s1097-2765(00)80467-0