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Timing of Exposure to High-Concentrates versus High-Quality Forages on Growth and Marbling Deposition in Steers[1,2]

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Abstract: Forty Angus-cross steers (280 ± 21.4 kg BW, 8 mo.) were used to examine the effects of exposure to 2 diets [high concentrate diets (CONC) versus high quality forages (FOR)] during 2 time periods [early (EARLY; at 30-d post weaning) or late (LATE; just prior to slaughter)] on animal growth, marbling deposition and tenderness. Steers were blocked by weight and randomly assigned to four dietary treatments: 1) CONC-FOR, 2) CONC-CONC, 3) FOR-CONC, or 4) FOR-FOR. Exposure to CONC during the EARLY or LATE period increased ($P < 0.05$) growth and fat deposition compared to FOR-FOR. Hot carcass weight was greater ($P < 0.05$) for CONC-CONC and FOR-CONC steers than FOR-FOR and CONC-FOR due to changes in dressing percent. Marbling score was greater ($P < 0.05$) for CONC-CONC and CONC-FOR compared to FOR-FOR. Exposure to CONC during the EARLY period (CONC-FOR and CONC-CONC) increased ($P < 0.05$) n-6 polyunsaturated fatty acids (PUFA) deposition in longissimus muscle (LM) and subcutaneous adipose tissue (SQ); whereas, exposure to CONC during the LATE period (CONC-CONC and FOR-CONC) reduced ($P < 0.05$) n-3 PUFA, trans-11 octadecenoic acid and cis-9 trans-11 isomer of conjugated linoleic acid (CLA). Warner-Bratzler shear force at d 2 and 7 of postmortem aging in ribeye steaks from CONC-CONC and FOR-CONC was greater ($P < 0.05$) than FOR-FOR and CONC-FOR. Lipogenic gene expression was up-regulated ($P < 0.05$) and lipolytic gene expression was downregulated ($P < 0.06$) in SQ from CONC-CONC and FOR-CONC compared to FOR-FOR. Overall, exposure to CONC in both periods increased growth rate and marbling deposition but LATE exposure had the greatest impact on adipose lipogenesis and lipolysis, fatty acid composition, and tenderness.

Keywords: beef, fatty acids, lipogenesis, marbling, tenderness
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Introduction

Serial slaughter studies in finishing steers demonstrate that intramuscular fat deposition increases with time-on-feed when consuming high concentrate diets (Greene et al., 1989; Duckett et al., 1993; Bruns et al., 2004). Greene et al. (1989) reported that Angus steers graded Choice after 65 d on a high concentrate diet. Duckett et al. (1993) showed that exposure to high-concentrate diets increased intramuscular fat deposition in a nonlinear manner with gradual increases from 0 to 84 d, largest increases from 84 to 112 d, followed by a plateau out to 196 d on feed. Bruns et al. (2004) found the greatest advances in marbling were achieved at hot carcass weights less than 300 kg, when evaluating on a total carcass fat basis. Comparisons between grain- and grass-finishing systems show that steers of the similar genetics have higher quality grades when finished on grain compared to grass at the same animal age (Neel et al., 2007; Duckett et al., 2009a; Duckett et al., 2013). Little research has examined how early grain exposure followed by

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forage-finishing would alter marbling deposition and fatty acid composition of the longissimus muscle compared to only forage-finishing systems. In typical beef production systems, steer calves are placed into stocker programs on high-quality forages after weaning prior to entering into the feedlot for finishing on high-concentrate diets. We hypothesized that early exposure to high concentrate diets post-weaning would accelerate marbling deposition and alter lipid metabolism. The objective of this study was to examine how exposure to high concentrate diets versus high-quality forages at 2 time periods, early (EARLY, d 0 to 111) or late (LATE, d 209 to target slaughter weight), altered animal growth, marbling deposition and tenderness.

Materials and Methods

Experimental procedures were reviewed and approved by Clemson University Animal Care and Use Committee, 2012–052.

Animals

Forty Angus-cross steers (280 ± 21.4 kg BW, 8 mo.) were used to examine the effects of exposure to 2 diets [high concentrate diets (CONC) versus high quality forages (FOR)] during 2 time periods [early (EARLY; d 0 to 111) or late (LATE; d 209 to target slaughter weight] on animal growth, marbling deposition and tenderness. Steers were blocked by weight and randomly assigned to 4 dietary treatments: 1) CONC-FOR, 2) CONC-CONC, 3) FOR-CONC, or 4) FOR-FOR. During MID period, all steers grazed high quality forages. Steers fed CONC were stepped up to the final ration in 4 steps (Step 1: 75% corn silage, 25% concentrates; Step 2: 50% silage, 50% concentrates; Step 3: 38% silage, 62% concentrate) and then were fed the final high concentrate ration (d 0 to 111 CONC: 25% corn silage, 63% corn grain, 10% soybean meal, 2% limestone, 13% crude protein; d 209-final CONC: 25% silage, 70% corn grain, 3% soybean mean, 2% limestone; 11.5% crude protein). Steers on FOR treatments grazed high quality forages (non-toxic tall fescue, 16.3% crude protein; cereal rye/annual ryegrass, 21.3% crude protein; alfalfa, 26.3% crude protein, and cowpea, 29.1% crude protein) at a stocking rate that provided ample forage to achieve an ADG of 0.68 kg/d or greater throughout the duration of the study. At the end of EARLY period, CONC steers were fed a step-down ration for 4 d and then moved to high quality forage pastures (FOR) from d 112 to 208 (MID) period. Steers were weighed on 2-consecutive days at the beginning and end of each period. One steer died during the MID period, which was unrelated to treatment.

Real-time ultrasound measurements were collected on d 0, 28, 56, 97, 167, 208, and 251 using an Aloka 500-V ultrasound unit (Corometrics Medical Systems, Wellingford, CT) equipped with a 17-cm, 3.5-MHz linear probe over the 12/13th rib to estimate intramuscular fat content, and subcutaneous fat thickness. Additionally, LM area was also measured between the 12th and 13th ribs near the end of phase 1 (d 97). All images were interpreted using Biosoft Toolbox (Biotronics, Inc., Ames, IA) by the same ultrasound technician.

When the average target weight was achieved for each treatment group (565 kg), steers were transported (145 km) to a commercial packing plant for slaughter. Individual animal identification was maintained throughout the slaughter process and carcass data was obtained by experienced personnel at 24 h postmortem on each individual carcass. At 24 h postmortem, a rib (IMPS 107) from the left side of each carcass was identified, removed, vacuum-packed and shipped to the Clemson University Meat Laboratory. Upon arrival at the meat laboratory, ribs were maintained at 4°C and then fabricated into steaks (2.54 cm thick) at 2-d postmortem. At 48 h postmortem, ribs were removed from packaging and allowed to bloom for 15 min. Then L*, a*, and b* color measurements were taken for the LM and subcutaneous fat at the 12th rib. Ribs were then cut into individual 2.54-cm thick steaks for subsequent proximate and fatty acid composition analyses (12th rib), and postmortem aging treatments (d 2, 7, and 14) for Warner-Bratzler shear force (WBSF; 11th to 9th rib). For WBSF, steaks were randomized and assigned to postmortem aging treatments. Then the steaks were vacuum-packed, stored at 4°C for their assigned postmortem age, and frozen at –20°C.

Color

Instrumental color measurements were recorded for L* (measures darkness to lightness; lower L* indicates a darker color), a* (measures redness; higher a* value indicates a redder color), and b* (measures yellowness; higher b* value indicates a more yellow color) using a Minolta chromameter (CR-310, Minolta Inc., Osaka, Japan) with a 50-mm-diameter measurement area using a D65 illuminant, which was calibrated using the ceramic disk provided by the manufacturer (American Meat Science Association, 2012). Color readings were determined at 2 d postmortem on the exposed LM at the posterior (12th rib) of the rib after a 15 min bloom time and subcutaneous (SQ) fat covering the posterior rib.

Values were recorded from three locations of exposed lean and SQ fat to obtain a representative reading.

Shear force

After aging for the assigned postmortem aging period, steaks were frozen for approximately 30 d prior to shear force analyses. Then steaks were thawed for 24 h at 4°C and broiled on Farberware (Bronx, NY) electric grills to an internal temperature of 71°C as monitored by insertion of type-T thermocouples and Digi-Sense (Cole-Parmer, Vernon Hills, IL) temperature logger (American Meat Science Association, 2015). Degree of doneness was assessed by visual inspection on each steak after cooking and used as a covariate in the shear force data analyses. Steaks were allowed to cool to room temperature before six 1.27-cm-diameter cores were removed from each steak parallel to the longitudinal orientation of the muscle fibers. All cores were sheared perpendicular to the long axis of the core using a Warner-Bratzler shear machine (G-R Manufacturing, Manhattan, KS).

Fatty acids

Longissimus muscle samples were trimmed of all external fat and epimysial connective tissue. The LM was chopped (Blixer 3 Series D, Robot Coupe Inc., Ridgeland, MS) to reduce particle size and a sample (15 g) removed for determination of moisture content. Moisture content was determined in triplicate by weight loss after drying at 100°C for 24 h. The remaining samples were frozen at –20°C, lyophilized (VirTis, SP. Scientific, Warminster, PA), ground (Blixer 3 Series D), and stored at –20°C. Total lipids from LM were extracted in duplicate using an Ankom XT15 extractor (Ankom Technology, Macedon, NY) with hexane as the solvent. Freeze dried samples were transmethylated according to the method of Park and Goins (1994). Fatty acid methyl esters (FAME) were analyzed using an Agilent 6850 (Agilent, Santa Clara, CA) gas chromatograph equipped with an Agilent 7673A (Agilent) automatic sampler. Separations were accomplished using a TRACE TR-FAME capillary column (0.25 mm i.d., 0.20 μm film thickness, 120 m; Thermo-Fisher, Waltham, MA). Column oven temperature increased from 150 to 174°C at 1°C per min, from 174 to 179°C at 0.2°C per min, from 179 to 225°C at 2°C per min, and then held at 225°C for 15 min. The injector and detector were maintained at 250°C. Sample injection volume was 1 μL. Hydrogen was the carrier gas at a flow rate of 1 mL per min. Samples were run twice with a split ratio of 100:1 for trans C18:1 and long-chain fatty acids and again at split ratio of 10:1 for conjugated linoleic acid (CLA) and omega-3 fatty acids. Individual fatty acids were identified by comparison of retention times with standards (Matreya, Pleasant Gap, PA; Larodan, Solna, Sweden). Fatty acids were quantified by incorporating an internal standard, methyl tricosanoic (C23:0) acid, into each sample during methylation and expressed as a weight percentage of total fatty acids.

Relative mRNA expression

Total RNA was extracted from subcutaneous adipose tissue (2 g/sample) using the TriZol method (Invitrogen, Carlsbad, CA) according to Duckett et al. (2009b). Further purification of RNA was performed with 0.57 mL of 2-propanol added to the supernatant and passed through a PureYield RNA Midiprep System column (Promega, Madison, WI) according to the directions of the manufacturer. Isolated RNA samples were precipitated overnight and resuspened in tris-EDTA acid. RNA concentration and quality was assessed using a NanoDrop ND-100 Spectrophotometer (NanoDrop Technologies, Wilmington, DE). The RNA samples of high quality (260:280 absorbance ratio > 1.8) were reverse transcribed using SuperScript III reverse transcriptase (Invitrogen) in duplicate to generate cDNA.

Quantitative PCR was then conducted on 2 ng of cDNA in duplicate for all samples with each primer set combination and the most stable housekeeping gene (GAPDH; Duckett et al., 2009b). Primers for genes of interest were designed using Primer3 software (http://www.bioinformatics.nl/cgi-bin/primer3plus/primer3plus.cgi) and tested for efficiency (Duckett et al., 2009b). New primers were developed for fatty acid elongase 5 (ELOVL5; Forward: GTCATCTGGCCGTGTACCTT; Reverse: GGGAAGAAAAGCTGCTGATG), fatty acid elongase 6 (ELOVL6; Forward: GGAAAGCAACGAAAGCTGAC; Reverse: TGGGTTGTGTGTTTGCTCAT), and carnitine palmitoyltransferase 1B (CPT1B; Forward: GCACCTCTTCTGCCTTTACG; Reverse: CGATCTGGCTAGTGGAGAGG). The transcript amounts for each gene were calculated at the C_T at which each fluorescent signal was first detected above background. Normalized C_T values ($\Delta C_T = C_T$, gene – C_T, GAPDH) were calculated for each sample. Relative abundance compared to FOR-FOR (control) was calculated for each treatment and analyzed to determine differences from control.

Statistics

Data were analyzed in a completely randomized block design using the MIXED procedure of SAS (SAS

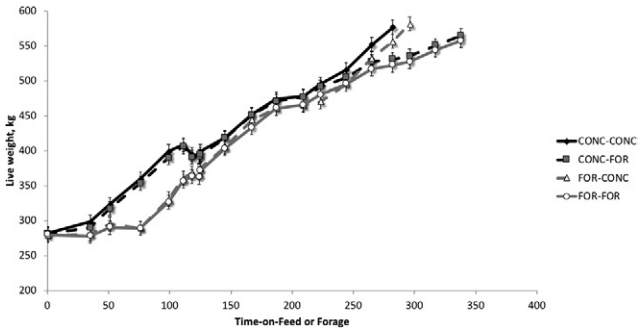

Figure 1. Changes in live weight of steers by dietary treatment during the finishing study.

Inst. Inc., Cary, NC). The model included dietary treatment and block was included as a random variable. For WBSF, postmortem aging time and the interaction with dietary treatment was also included in the model. For ultrasound and live weight measurements, repeated measures analyses were used to evaluate dietary treatment, time-on-feed/forage, and interaction. Least Squares means were generated and separated using a protected least significant difference test.

Results and Discussion

Changes in steer growth over time are shown in Fig. 1. There was an interaction ($P < 0.05$) between dietary treatment and time-on-feed/forage for live weight. Steers started at a similar ($P = 0.80$) live weight (280 kg). At d 51, steers fed CONC during the early period (CONC-CONC and CONC-FOR) had heavier ($P < 0.01$) live weights than FOR-FOR or FOR-CONC, which remained heavier throughout the end of EARLY period (d 51- 111). Steers fed CONC during the early period (CONC-CONC and CONC-FOR) had heavier ($P < 0.05$) live weights from d 112 to 125 when all steers were grazing high quality forages (MID); however from d 145 to end of MID period (d 208), live weight did not differ ($P > 0.05$) among steers by treatment. At the beginning of LATE period (d 209), live weight for CONC-CONC and CONC-FOR did not differ ($P > 0.05$) compared to FOR-FOR or FOR-CONC. On d 265, CONC-CONC and FOR-CONC steers tended ($P = 0.07$) to have heavier live weights than did FOR-FOR or CONC-FOR. On d 282, steers fed concentrates during the LATE period (CONC-CONC and FOR-CONC) had heavier ($P < 0.001$) live weights than FOR-FOR or CONC-FOR, which remained higher ($P < 0.05$) throughout the end of LATE period when they reached target slaughter weight. In both the EARLY and LATE periods, differences in live weight for CONC-fed steers were not observed until after 50 d (EARLY) or 73 d (LATE) on feed. Steers fed CONC-CONC had the shortest number of days to slaughter at the target weight (282 d). Steers that received FOR-CONC had the second shortest number of days to reach slaughter weight (296 d). Steers that were finished on FOR-FOR or CONC-FOR took the longest number of days to reach slaughter weight (338 d). Similarly, others (Crouse et al., 1984; Bennett et al., 1995; Duckett et al., 2009a) have reported increases in animal performance for animals consuming a high-concentrate based diet compared to those grazing forages.

Animal performance measures are shown in Table 1. Average daily gain was increased ($P < 0.001$) for CONC-CONC and CONC-FOR by 0.41 kg/d compared to FOR-FOR or FOR-CONC. Others (Crouse et al., 1984; Duckett et al., 2009a; Pordomingo et al., 2012) have also shown that increasing the plane of nutrition with grain feeding improves animal performance. Feeding CONC-CONC and CONC-FOR reduced ($P < 0.001$) ADG in MID period by 0.36 kg/d compared to steers that grazed FOR-FOR or FOR-CONC. Similarly, Scheffler et al. (2014) reported decreases in body weight gain when transitioning steers from a high-concentrate based diet to forages during finishing. Average daily gain was also greater ($P < 0.001$) for CONC-CONC and FOR-CONC than FOR-FOR or CONC-FOR during the LATE finishing period by 0.57 kg/d. Overall ADG was greater ($P < 0.001$) for steers fed CONC-CONC and FOR-CONC during the LATE finishing period compared to CONC-FOR or FOR-FOR.

Subcutaneous fat thickness (SQ) and intramuscular fat percentage (IMF) were collected over time using real-time ultrasound. There was an interaction ($P < 0.05$) between dietary treatment and time-on-feed/forage for SQ fat thickness (Fig. 2). Subcutaneous fat thickness did not differ ($P > 0.05$) between treatments at d 0 and 28. By d 56, SQ fat thickness was greater ($P < 0.01$) for CONC-CONC and CONC-FOR compared to FOR-FOR or FOR-CONC and remained greater ($P < 0.01$) through d 167 (MID). At d 208 (MID) and d 251 (LATE), SQ fat thickness was similar ($P > 0.05$) among treatment. Others (Hersom et al., 2004; Sharman et al., 2013b) have reported that increasing plane of nutrition through forage quality and stocking density during the winter grazing period increased gains and fat thickness deposition prior to feedlot entry. Sharman et al. (2013a) found that steers with greater subcutaneous fat deposition due to higher plane of nutrition also had greater deposition in other fat depots including mesenteric, KPH, and marbling when harvested at an intermediate time point. Correlations between the ultrasound 12th rib fat thickness at the beginning of LATE (d 251) and carcass

Table 1. Performance and days to target final weight for steers fed high concentrate (CONC) diets or high quality forages (FOR) after weaning (EARLY) or before slaughter (LATE)

Time-on-feed/forage	Dietary treatment					
EARLY, d 0- 111	CONC	CONC	FOR	FOR		
LATE, d 209- target	CONC	FOR	CONC	FOR		
n	10	10	9	10	SE	*P*-level
ADG, kg/d						
d 0- 111	1.14[a]	1.10[a]	0.74[b]	0.69[b]	0.41	0.0001
d 112- 208	0.71[b]	0.75[b]	1.07[a]	1.11[a]	0.35	0.0001
d 209- slaughter	1.28[a]	0.66[b]	1.21[a]	0.69[b]	0.31	0.0001
Overall ADG, kg/d	1.03[a]	0.83[b]	1.01[a]	0.81[b]	0.23	0.0001
Days to target slaughter wt, 568 kg	282	338	296	338		

[ab]Means in the same row with uncommon superscripts differ ($P < 0.05$) between treatments.

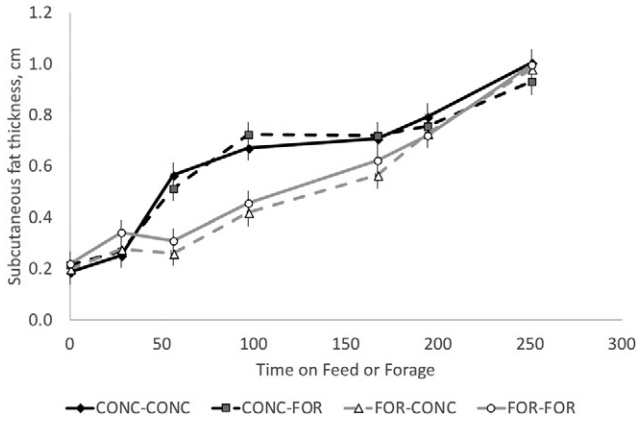

Figure 2. Deposition of subcutaneous fat thickness as estimated by real time ultrasound during by dietary treatment during the finishing study.

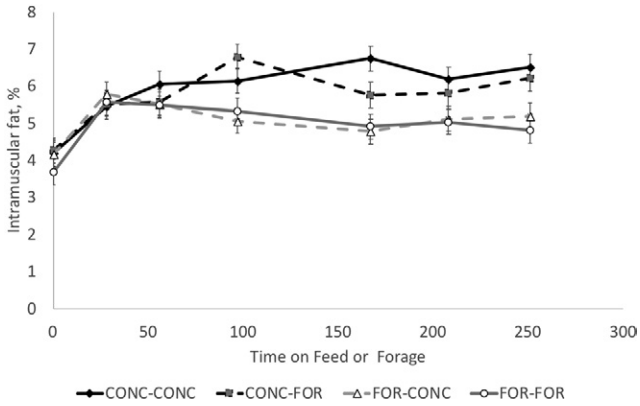

Figure 3. Deposition of intramuscular fat (IMF) as estimated by real time ultrasound by dietary treatment during the finishing study.

12th rib fat thickness at slaughter also showed positive relationships ($P < 0.001$; $r = 0.55$).

There was a trend for an interaction ($P = 0.07$) between treatment and time-on-feed/forage for ultrasound intramuscular fat (IMF) content (Fig. 3). Intramuscular fat content did not differ ($P > 0.05$) for CONC-CONC and CONC-FOR compared to FOR-FOR or FOR-CONC from d 0 to 56 time-on-feed/forage. Near the end of EARLY period (d 97), IMF content was greater ($P < 0.01$) for CONC-CONC and CONC-FOR than FOR-FOR or FOR-CONC. Intramuscular fat content remained greater ($P < 0.01$) for CONC-CONC and CONC-FOR compared to FOR-FOR or FOR-CONC from d 97 to 251. Sharman et al. (2013a) reported that steers harvested at an intermediate time point (d 138) on a higher plane of nutrition had greater marbling scores but these differences were not always detectable using real time ultrasound. Simple correlation coefficients showed positive relationships between ultrasound IMF measures taken at the beginning of LATE period (d 251) and LM total lipid at slaughter ($P < 0.01$; $r = 0.47$). Peña et al. (2014) reported that ultrasound explained 57% of the variation in IMF for scans taken within 7 d of slaughter for 300 bulls. These results are similar to those reported by Wall et al. (2004) for ultrasound measurements of fat thickness ($r = 0.58$) and IMF ($r = 0.63$) taken at 96 to 100 d prior to slaughter compared to carcass values.

Ribeye area estimated by real time ultrasound was larger ($P < 0.05$) for CONC-CONC and CONC-FOR compared to FOR-FOR and FOR-CONC when measured near the end of EARLY finishing period (d 97; 61.37 cm^2 vs. 53.49 cm^2). However when adjusted for differences in body weight, ribeye area did not differ ($P > 0.05$) between among treatments indicating that the increased muscle mass was related to the heavier body weight for the CONC-CONC and CONC-FOR fed steers during the EARLY finishing period.

Hot carcass weight was greater ($P < 0.05$) for CONC-CONC and FOR-CONC compared to CONC-FOR and FOR-FOR. Others (Crouse et al., 1984; Bennett et al., 1995; Duckett et al., 2013) have reported that forage finished steers have lighter hot carcass weights in comparison to high-concentrate finishing when finished at the same chronological age endpoint. Dressing percentage was higher ($P < 0.05$) for CONC-CONC compared to

all other treatments. Dressing percentage was also higher for CONC-FOR and FOR-CONC steers compared to FOR-FOR. Previous research (Neel et al., 2007; Pavan and Duckett, 2008; Duckett et al., 2013) has shown that there are differences in dressing percentage when steers are finished on forages versus concentrates likely due to rumen mass and/or gut fill. Sharman et al. (2013b) reported differences in total viscera and liver weights in steers from different stocker programs prior to and at the end of feedlot finishing due to forage type and stocking rate to alter rate of gain.

Ribeye area was greater ($P < 0.05$) for CONC-CONC compared to CONC-FOR and FOR-FOR; however when adjusted for HCW, REA did not differ ($P > 0.05$) among treatments. Steers finished on concentrates versus forages are typically reported as having larger ribeye sizes and heavier carcass weights (Duckett et al., 2013; Sharman et al., 2013a). Fat thickness was greatest ($P < 0.05$) for FOR-CONC and lowest ($P < 0.05$) for CONC-FOR and FOR-FOR with CONC-CONC being intermediate. The percentage of kidney, pelvic and heart fat was higher ($P < 0.05$) for FOR-CONC than CONC-FOR and FOR-FOR. Marbling score was greater ($P < 0.05$) for steers fed CONC-CONC compared to FOR-CONC and FOR-FOR with CONC-FOR being intermediate. Skeletal maturity was more advanced ($P < 0.05$) for CONC-FOR and FOR-FOR than FOR-CONC or CONC-CONC; however, all carcasses were in A maturity classification regardless of dietary treatment. Percentage of carcasses grading US Choice was higher ($P < 0.01$) for CONC-CONC and CONC-FOR compared to FOR-CONC and FOR-FOR. Percent Choice was also greater ($P < 0.05$) for FOR-CONC than FOR-FOR. The percentage of carcasses grading Certified Angus Beef (CAB) was highest ($P < 0.01$) for CONC-CONC. Similarly, Scheffler et al. (2014) and Moisá et al. (2014) reported that feeding high-concentrate diets after weaning increased marbling scores in early-weaned steers. Duckett et al. (2007) found that higher stocker growth rate increased intramuscular lipid deposition in steers finished on concentrates. In contrast, supplementation of corn (< 1% of body weight) on pasture (Pavan and Duckett, 2008; Greenwood et al., 2015; Wright et al., 2015) does not appear to alter marbling deposition. Smith and Crouse (1984) found that glucose provided the majority of acetyl units for intramuscular fat deposition; whereas acetate provided the majority of acetyl units for subcutaneous adipose deposition. Nayananjalie et al. (2015) evaluated acetate kinetics in early weaned steers fed concentrates and found that acetate utilization was not responsible for the increased marbling deposition. Early exposure to high concentrate feeding would likely increase propionate production in the rumen, which would be available for gluconeogenesis. Thus, results from this study show that exposure to high concentrate diets fed ad libitum during the early post-weaning finishing period appears to stimulate marbling deposition in normal weaned steers that result in greater numbers grading US Choice. Steers that were exposed to high concentrate diets both at the beginning and end of the finishing period had greater percentages making the CAB brand, which could possibly be a strategy for getting more Angus steers to reach the modest level of marbling required for CAB.

Longissimus muscle color measurements differed ($P < 0.05$) among finishing systems (Table 2). Redness (a*) values of the LM were higher ($P < 0.05$) for CONC-FOR and FOR-FOR compared to CONC-CONC and FOR-CONC. Yellowness (b*) values were highest ($P < 0.05$) for FOR-FOR compared to CONC-FOR, which was higher ($P < 0.05$) than CONC-CONC or FOR-CONC. In subcutaneous fat, FOR-FOR had the highest ($P < 0.05$) a* value and CONC-CONC had the lowest ($P < 0.05$). Yellowness (b*) values of subcutaneous fat was higher ($P < 0.05$) for steers finished during LATE period on FOR (CONC-FOR and FOR-FOR) compared to CONC (CONC-CONC and FOR-CONC). Lightness (L*) values did not differ ($P > 0.05$) among treatments for LM or SQ. Previous research (Duckett et al., 2007, 2013) found higher L* and b* values in subcutaneous fat from FOR finished steers. Others (Crouse et al., 1984; Bennett et al., 1995; Yang et al., 2002) have also reported increased yellowness (higher b*) in subcutaneous fat from forage-finished cattle due to higher β-carotene values from the forages (Simonne et al., 1996; Yang et al., 2002; Duckett et al., 2009a). These results show that the LATE finishing treatment had the greatest impact on the color of the LM and SQ.

Proximate composition of the LM is presented in Table 3. Moisture, total lipid, and ash content of the LM did not differ ($P > 0.05$) between dietary treatments. Crude protein content was lower ($P < 0.01$) for CONC-CONC and FOR-CONC compared to FOR-FOR and CONC-FOR. Similarly, Duckett et al. (2009a) also reported a tendency for reduced protein content with high concentrate versus to forage-finishing. Concentrations of P, K, Mg, and Fe were greater ($P < 0.05$) in LM from steers grazing FOR during LATE period (CONC-FOR and FOR-FOR) compared to CONC (CONC-CONC and FOR-CONC). Calcium content of the LM was highest ($P < 0.05$) for CONC-FOR than CONC-CONC and FOR-CONC. Sodium and zinc content did not differ ($P > 0.05$) among treatments. Duckett et al. (2009a) found reduced Ca, Mg, and K in the LM from concentrate-finished versus grass-finished steers; whereas, other minerals (Fe, Na, and Zn) were similar among finishing systems.

Table 2. Carcass characteristics and objective color values of LM and subcutaneous fat for steers fed high concentrate (CONC) diets or high quality forages (FOR) after weaning (EARLY) or before slaughter (LATE)

Time-on-feed/forage	Dietary treatment					
EARLY, d 0- 111	CONC	CONC	FOR	FOR		
LATE, d209- target	CONC	FOR	CONC	FOR		
n	10	10	9	10	SE	*P*-level
HCW, kg	326.4[a]	304.7[b]	323.4[a]	297.2[b]	20.78	0.0081
Dressing percent, %	60.35[a]	58.05[b]	59.08[b]	56.64[c]	1.21	0.0001
Fat thickness, cm	1.08[ab]	0.89[b]	1.31[a]	0.80[b]	0.41	0.0499
Ribeye area (REA), cm^2	82.39[a]	71.75[b]	76.58[ab]	75.75[b]	6.62	0.01
REA/HCW	0.253	0.236	0.238	0.255	0.13	0.068
KPH, %	2.20[ab]	1.90[b]	2.39[a]	1.60[bc]	0.47	0.0046
Skeletal maturity	155[c]	174[a]	167[b]	174[a]	6.21	0.0001
Marbling score[1]	580[a]	531[ab]	508[bc]	472[c]	64.98	0.0064
Quality grade[2]	5.3[a]	4.8[ab]	4.4[bc]	3.8[c]	0.92	0.0073
Percent Choice, %	80[a]	70[a]	44[b]	20[c]	46	0.029
Percent Certified Angus Beef, %	50[a]	10[b]	11[b]	0[b]	35	0.016
Yield grade	2.64	2.74	3.17	2.34	0.63	0.053
LM L*	43.91	42.07	42.18	42.28	2.16	0.207
LM a*	24.99[b]	28.71[b]	25.51[a]	29.56[a]	1.30	0.0001
LM b*	10.58[c]	11.60[b]	10.90[c]	12.24[a]	0.64	0.0001
SQ[3] L*	75.87	77.75	75.06	78.06	3.34	0.16
SQ a*	9.62[c]	12.16[ab]	10.19[bc]	12.46[a]	2.42	0.030
SQ b*	18.91[b]	22.0[a]	19.37[b]	22.86[a]	2.77	0.0066

[a–c]Means in the same row with uncommon superscripts differ ($P < 0.05$) between treatments.

[1]Marbling score code: 300 = traces, 400 = slight, 500 = small, 600 = modest.

[2]Quality grade code: 3 = Select-, 4 = Select+, 5 = Choice-, 6 = Choice°, 7 = Choice+.

[3]SQ = subcutaneous fat.

Table 3. Proximate composition of the longissimus muscle of steers fed high concentrate diets (CONC) or high quality forages (FOR) during EARLY (d 0 -111) or during LATE (d 209 to slaughter) finishing period

Time-on-feed/forage	Dietary treatment					
EARLY, d0- 111	CONC	CONC	FOR	FOR		
LATE, d 209- target	CONC	FOR	CONC	FOR		
n	10	10	9	10	SE	*P*-level
Moisture, %	72.56	72.77	72.95	73.10	0.94	0.61
Crude protein, %	21.28[b]	22.36[a]	21.64[b]	22.45[a]	0.62	0.0003
Total lipid, %	4.66	4.16	3.82	3.73	1.15	0.29
Ash, %	1.24	1.16	1.44	1.18	1.25	0.14
Minerals (mg/100g LM)						
P	184.9[b]	200.5[a]	188.6[b]	202.4[a]	5.13	0.0001
K	345.4[c]	395.8[a]	356.7[b]	405.5[a]	11.58	0.0001
Ca	4.23[b]	5.87[a]	4.21[b]	4.85[ab]	1.31	0.026
Mg	21.14[b]	23.01[a]	21.75[b]	23.02[a]	0.82	0.0001
Fe	1.76[b]	2.22[a]	1.75[b]	2.07[a]	0.204	0.0001
Na	35.75	37.18	36.61	36.55	2.08	0.50
Zn	3.20	3.58	3.48	3.45	0.31	0.055

[ab]Means in the same row with uncommon superscripts differ ($P < 0.05$) between treatments.

Fatty acid composition of the longissimus muscle is shown in Table 4. Concentrations of pentadecylic (C15:0) acid were higher ($P < 0.05$) for CONC-FOR and FOR-FOR than CONC-CONC and FOR-CONC. Trans-10 octadecenoic acid concentration was higher ($P < 0.05$) for CONC-CONC than other finishing systems (CONC-FOR,

Table 4. Fatty acid composition of longissimus muscle of steers fed high concentrate (CONC) or high quality forage (FOR) during EARLY (30 d post-weaning (d 0) to d 111) or LATE (d 209 to slaughter) finishing period

Time-on-feed/forage	Dietary treatment					
EARLY, d 0- 111	CONC	CONC	FOR	FOR		
LATE, d 209- target	CONC	FOR	CONC	FOR		
n	10	10	9	10	SE	*P*-level
Fatty acid, %						
C14:0	2.84	2.79	3.29	2.94	0.36	0.19
C14:1 cis-9	0.70	0.70	0.82	0.69	0.16	0.98
C15:0	0.37^{b}	0.44^{a}	0.38^{b}	0.42^{a}	0.053	0.013
C16:0	27.99	27.36	29.23	27.52	1.40	0.11
C16:1 cis-9	3.95	3.70	4.04	3.95	0.44	0.27
C17:0	1.04	1.05	0.85	0.99	0.12	0.095
C18:0	13.64	14.57	14.14	14.66	1.18	0.24
C18:1 trans-10	0.49^{a}	0.00^{b}	0.019^{b}	0.00^{b}	0.37	0.010
C18:1 trans-11	0.84^{b}	1.49^{a}	1.17^{a}	1.43^{a}	0.36	0.0026
C18:1 cis-9	39.99^{a}	38.18^{b}	38.59^{ab}	38.08^{b}	1.59	0.042
C18:1 cis-11	1.44^{a}	1.42^{a}	1.33^{b}	1.29^{b}	0.090	0.0005
C18:2 cis-9,12	2.36^{a}	2.41^{a}	2.04^{ab}	1.84^{b}	0.44	0.032
C18:2 cis-9, trans-11	0.35^{c}	0.47^{a}	0.36^{bc}	0.46^{ab}	0.083	0.015
C18:3 cis-9,12,15	0.49^{c}	0.97^{a}	0.43^{b}	1.04^{a}	0.22	0.0001
C20:4 cis-5,8,11,14	0.84	0.87	0.66	0.64	0.24	0.17
C20:5 cis-5,8,11,14,17	0.12^{b}	0.17^{b}	0.24^{a}	0.28^{a}	0.063	0.0001
C22:5 cis-7,10,13,16,19	0.33^{c}	0.40^{bc}	0.53^{a}	0.48^{ab}	0.11	0.0030
C22:6 cis-6,9,12,15,18,21	0.036^{b}	0.030^{b}	0.071^{a}	0.030^{b}	0.018	0.018
SFA	44.47	44.72	46.67	45.12	1.85	0.19
OCFA	1.41	1.48	1.24	1.42	0.17	0.067
MUFA	44.64^{a}	42.59^{b}	43.46^{ab}	42.72^{b}	0.95	0.020
PUFA, n-6	3.20^{a}	3.28^{a}	2.84^{ab}	2.48^{b}	0.66	0.040
PUFA, n-3	0.98^{b}	1.57^{a}	1.56^{a}	1.82^{a}	0.33	0.0001
Ratio n-6:n-3	3.28^{a}	2.18^{b}	1.83^{c}	1.36^{d}	0.053	0.0001
Total fatty acids, g/100g	4.02	3.94	3.82	3.59	0.96	0.77

$^{a–c}$Means in the same row with uncommon superscripts differ ($P < 0.05$) between treatments.

FOR-CON or FOR-FOR). Trans-10 octadecenoic acid is formed during ruminal biohydrogentation when high concentrate diets with low forage levels are fed to cattle suggesting a shift in biohydrogenation when ruminal pH is lower (Duckett et al., 2002; Sackmann et al., 2003; Ventto et al., 2017). Our results indicate that these changes in ruminal biohydrogenation with increased trans-10 octadecenoic acid tissue accumulation occurred only in the steers that were fed CONC in both the EARLY and LATE periods (CONC-CONC). Concentrations of trans-11 vaccenic (C18:1) acid were greater for steers fed FOR during EARLY or LATE periods (FOR-CONC, CONC-FOR, or FOR-FOR) than CONC-CONC. In contrast, concentrations of cis-9 trans-11 conjugated linoleic acid (CLA) were higher ($P < 0.05$) in LM of steers fed FOR during the LATE period (CONC-FOR and FOR-FOR) compared to CONC-CONC. These results show that early exposure to CONC followed by FOR finishing does not alter trans-11 vaccenic acid or CLA concentrations in the LM.

Oleic acid and total monounsaturated fatty acid (MUFA) concentrations were greater ($P < 0.05$) for CONC-CONC than CONC-FOR and FOR-FOR with FOR-CONC being intermediate. Duckett et al. (2009b) has shown that feeding high concentrate diets up-regulates stearoyl-CoA desaturase (SCD1) gene expression, which converts saturated fatty acids to monounsaturated fatty acids (MUFA) by inserting a double bond in the cis-9 position. Thus, increases in MUFA are commonly observed with exposure to high grain diets (Duckett et al., 1993; Duckett et al., 2009b). Concentrations of cis-11 vaccenic (C18:1) acid in LM muscle tissues were higher for CONC-CONC and CONC-FOR compared to FOR-CONC and FOR-FOR. Cis-11 vaccenic acid can be produced through elongation of palmitoleic acid (Burns et al., 2012). Linoleic (C18:2) acid and total n-6 polyunsaturated fatty acid (PUFA) percentages were greater ($P < 0.05$) for CONC-CONC and CONC-FOR than FOR-FOR. Linoleic acid is an essential fatty acid

that can be elongated and desaturated to produce other n-6 polyunsaturated fatty acids (PUFA) like arachidonic acid (FAO, 2008). Linolenic (C18:3) acid concentration was greater ($P < 0.05$) in LM of steers grazing FOR during LATE period (CONC-FOR and FOR-FOR) compared to CONC (CONC-CONC or FOR-CONC). Eicosapentaenoic (C20:5 n-3; EPA) concentration was greater ($P < 0.05$) for FOR-CONC and FOR-FOR than for CONC-CONC and CONC-FOR. Docosapentaenoic (C22:5 n-3; DPA) and docosahexaenoic (C22:6 n-3; DHA) acid concentrations were higher ($P < 0.05$) for FOR-CONC than CONC-CONC. Docosahexaenoic acid is present in the lowest levels (≤ 0.10% of total fatty acids) of the n-3 polyunsaturated fatty acids in beef muscle tissues regardless of finishing system (Duckett et al., 2009a, 2013). In comparisons between forage-only or high-concentrate only finishing (Duckett et al., 2009a, 2013), DHA concentrations are typically reduced with concentrate finishing. The increase in DHA for FOR-CONC may suggest that the elongases, desaturases, and/or enzymes involved in β-oxidation that are responsible for the conversion from α-linolenic acid to DHA (FAO, 2008) were altered with exposure to high concentrates only during the LATE feeding period. Exposure to high grain diets is known to up-regulate stearoyl-CoA desaturase (SCD1), fatty acid synthase (FASN), and long-chain fatty-acyl elongases (Duckett et al., 2009b; Joseph et al., 2010) but less is known about timing of grain exposure on the specific desaturases (FADS1 and FADS2) or elongases (ELOVL) involved in conversion of α-linolenic acid to DHA.

Total n-3 PUFA concentration was greater ($P < 0.05$) for CONC-FOR, FOR-CONC and FOR-FOR compared to CONC-CONC. The ratio of n-6 to n-3 PUFA was greatest ($P < 0.05$) for CONC-CONC and lowest ($P < 0.05$) for FOR-FOR. This ratio was also higher ($P < 0.05$) for CONC-FOR than FOR-CONC. Others (Daley et al., 2010; Duckett et al., 2009a, 2013) have also shown that finishing cattle on forages increases the concentration of n-3 PUFA and lowers the ratio of n-6 to n-3 fatty acids in LM tissues. It is important to note, that despite the differences in n-6 to n-3 PUFA ratio observed in this study, the level of this ratio was below the level generally recommended by health professionals based on the Lyon Heart Study (4:1; de Lorgeril et al., 1994) for all 4 finishing systems. This is related to the fact that the CONC-FOR and FOR-CONC groups were only exposed to grain for 30% of the total time in this finishing study. The CONC-CONC steers spent 66% of their time in the feedlot versus 34% on forages. These mixed grain-forage finishing systems appear to mediate some of the changes in fatty acid composition due to shorter time periods on grains or extended time of grazing forages.

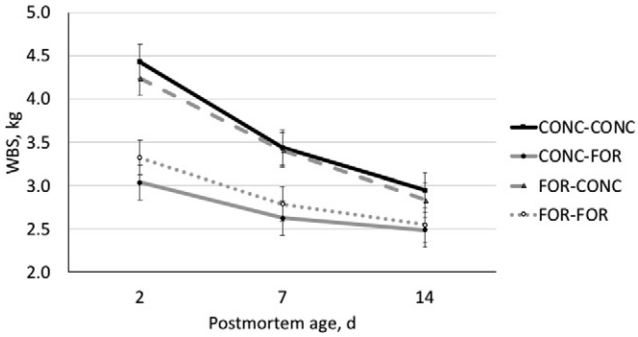

Figure 4. Warner-Bratzler shear force (WBSF) values for ribeye steaks aged for 2, 7, or 14 d postmortem by dietary treatment.

Warner-Bratzler shear force (WBSF) was measured at 2, 7, and 14 d of postmortem aging (Fig. 4). Exposure to CONC during the LATE period (CONC-CONC and FOR-CONC) increased ($P < 0.05$) WBSF in LM at d 2 and 7 postmortem compared to LM from steers that grazed FOR during the LATE period (CONC-FOR and FOR-FOR). Warner-Bratzler shear force values did not differ ($P > 0.05$) among treatments at 14 d of postmortem aging. In previous research, Duckett et al. (2009a, 2013) found that WBSF was similar between forage-only and concentrate-only finished steers when finished at the same chronological age. The increase in shear force for CONC fed steers during late period (CONC-CONC and FOR-CONC) may be related to increases in muscle fiber hypertrophy with ribeye area enlargement or connective tissue strength and solubility (Girard et al., 2012). Ebarb et al. (2016) reported that muscle fiber cross-sectional area for all fiber types (Type I, IIA, IIX) was positively correlated ($r = 0.45$ to 0.57) to d 14 Warner-Bratzler shear force in heifers given different growth promotants (none, anabolic implant, anabolic implant + β-agonist). Roy et al. (2015) found differences in perimysium collagen cross-link content in muscle of steers receiving anabolic implants but not in β-agonist fed steers. Purslow (2018) suggests that the intramuscular connective tissue quantity and thermal stability are related to cooked meat tenderness. Further investigation into the changes with LATE CONC exposure and increased WBSF at early postmortem aging is warranted.

Fatty acid composition of subcutaneous adipose tissues is shown in Table 5. Pentadecylic acid and total odd-chain fatty acid concentrations were lower ($P < 0.001$) for CONC-CONC and FOR-CONC compared to FOR-FOR and CONC-FOR. Trans-10 octadecenoic acid concentration was greater ($P < 0.05$) in SQ from steers fed CONC during the LATE period (CONC-CONC and FOR-CONC; whereas, trans-11 vaccenic acid and cis-9 trans-11 CLA concentrations were greater ($P < 0.05$) in

Table 5. Fatty acid composition of subcutaneous fat of steers fed high concentrate (CONC) or high quality forage (FOR) during EARLY (30 d post-weaning (d 0) to d 111) or LATE (d 209 to slaughter)

Time-on-feed/forage	Dietary treatment					
EARLY	CONC[3]	CONC	FOR	FOR		
LATE	CONC	FOR[4]	CONC	FOR		
n	10	10	9	10	SE	*P*-level
Fatty acid, g/100g fat						
C14:0	3.72	3.57	3.96	3.73	0.46	0.34
C14:1 cis-9	1.53	1.55	1.60	1.33	0.37	0.41
C15:0	0.52^{b}	0.63^{a}	0.49^{b}	0.62^{a}	0.07	0.0001
C16:0	27.36	26.50	28.14	27.17	1.32	0.076
C16:1 cis-9	5.45	5.79	5.31	5.40	0.75	0.52
C17:0	0.99	1.04	0.90	1.09	0.15	0.057
C18:0	11.02	11.74	11.39	12.25	1.70	0.43
C18:1 trans-10	2.02^{a}	0^{b}	2.17^{a}	0^{b}	0.47	0.0001
C18:1 trans-11	0.15^{b}	1.88^{a}	0.00^{b}	2.04^{a}	0.28	0.0001
C18:1 cis-9	39.81	38.93	38.75	38.49	1.54	0.27
C18:1 cis-11	1.62^{a}	1.51^{ab}	1.34^{bc}	1.23^{c}	0.23	0.0029
C18:2 cis-9,12	1.27^{a}	1.24^{a}	0.86^{b}	0.83^{b}	0.11	0.0001
C18:2 cis-9 trans-11	0.63^{b}	0.92^{a}	0.62^{b}	0.97^{a}	0.18	0.0001
C18:3 cis-9,12,15	0.33^{c}	0.63^{b}	0.29^{c}	0.74^{a}	0.07	0.0001
SFA	42.10	41.82	43.49	43.15	2.32	0.34
OCFA	1.50^{b}	1.67^{a}	1.39^{b}	1.71^{a}	0.19	0.0026
MUFA	46.79	46.27	45.66	45.22	1.92	0.30
PUFA, n-6	1.30^{a}	1.24^{a}	0.89^{b}	0.83^{b}	0.11	0.0001
PUFA, n-3	0.39^{c}	0.66^{b}	0.35^{c}	0.77^{a}	0.08	0.0001
Ratio n-6:n-3	3.47^{a}	1.89^{c}	2.59^{b}	1.08^{d}	0.43	0.0001
Total fatty acids, g/100g	82.63^{c}	92.70^{a}	88.82^{b}	91.69^{a}	2.94	0.0001

$^{a–c}$Means in the same row with uncommon superscripts differ ($P < 0.05$) between treatments.

SQ from steers fed FOR during the LATE period (CONC-FOR and FOR-FOR). Changes in the trans-octadecenoic acid concentrations with increased trans-10 octadecenoic acid and lower trans-11 vaccenic acid are also commonly observed with feeding of high concentrate diets (Duckett et al., 2009a, 2013). Concentrations of cis-11 vaccenic acid were greatest ($P < 0.05$) for CONC-CONC and lowest ($P < 0.05$) for FOR-FOR. Linoleic acid and n-6 PUFA concentrations were greater ($P < 0.05$) in SQ of steers fed CONC during early period (CONC-CONC and CONC-FOR) than FOR (FOR-FOR and FOR-CONC). Linolenic acid and n-3 PUFA concentrations were greater ($P < 0.05$) in SQ of steers fed FOR-FOR compared to CONC-FOR, which was greater ($P < 0.05$) than CONC-CONC and FOR-CONC. The ratio of n-6 to n-3 fatty acids was highest ($P < 0.05$) for CONC-CONC and lowest ($P < 0.05$) for FOR-FOR. Additionally, the ratio of n-6 to n-3 fatty acids was also higher ($P < 0.05$) for FOR-CONC than CONC-FOR. The reductions in n-3 fatty acid deposition and increase in the n-6 to n-3 PUFA ratio with CONC feeding during the LATE period agree with others who also reported that n-3 PUFA decline in subcutaneous adipose tissues of steers fed CONC compared FOR (Duckett et al., 2009a, 2013). Total fatty acid content of the SQ was highest ($P < 0.05$) for FOR-FOR and CONC-FOR, and lowest ($P < 0.05$) for CONC-CONC. The reduction in total fatty acid content of the SQ adipocyte observed with CONC feeding may be related to changes in adipocyte hypertrophy and an apparent dilution of fatty acids as adipocyte size increased. Robelin (1981) reported that when subcutaneous adipocytes were filled with lipids that this stimulated another wave of hyperplasia to provide more adipocytes for additional lipid filling.

Relative abundance levels of key lipogenic and lipolytic genes are shown in Fig. 5. Feeding CONC during the LATE period (CONC-CONC and FOR-CONC) up-regulated ($P < 0.05$) fatty acid synthase (FASN), stearoyl-CoA desaturase (SCD1), elongase 5 (ELOVL5), elongase 6 (ELOVL6) and glycerol-3-phosphate acyltransferase (GPAT) compared to FOR-FOR. Acetyl-CoA carboxylase (ACC) expression did not differ ($P > 0.05$) among treatments. Both ACC and FASN are involved in *de novo* fatty acid synthesis. Acetyl CoA carboxylase converts acetyl CoA to malonyl-CoA and fatty acid synthase continues to add two carbon units to malonyl CoA until palmitic (C16:0) acid, the end-product is formed.

Palmitic acid can be elongated (ELOVL5 or ELOVL6) or desaturated (stearoyl-CoA desaturase, SCD) to produce other longer chain fatty acids. ACC is considered the rate-limiting step in *de novo* fatty acid synthesis but is regulated by post-translational phosphorylation at Ser79 by AMP-activated protein kinase (Davies et al., 1990). Glycerol-3-phophate acyltransferase is the rate-limiting step in triacylglycerol biosynthesis. Up-regulation of FASN and GPAT with exposure to concentrates during LATE finishing would be associated with greater *de novo* lipogenesis for incorporation into adipose tissues, which is in agreement with the increased fat thickness of subcutaneous adipose tissues. Duckett et al. (2009b) reported up-regulation of FASN and lack of change in ACC in subcutaneous adipose tissues from steers fed high-concentrate diets or corn grain supplementation on grass compared to grass-only finishing systems. Key et al. (2013) also observed up-regulation of FASN mRNA expression in subcutaneous adipose tissue of heifers fed grain versus grass. The up-regulation of mRNA expression of SCD in adipose tissues from cattle consuming high concentrate diets is in agreement with the literature (Duckett et al., 2009b; Key et al., 2013; Kern et al., 2014). Wang et al. (2009) found SCD and FASN to have strong correlations with marbling deposition at 20 and 25 mo of age.

Carnitine palmitoyltransferase 1b (CPT-1b) mRNA expression was lower ($P = 0.04$) for CONC-CONC and FOR-CONC compared to FOR-FOR. This enzyme, CPT-1b, is important in β-oxidation of fatty acids as it shuttles fatty acids into the mitochondria for oxidation. The downregulation of CPT-1b in steers exposed to CONC during the LATE period suggests that lipid oxidation rates are lower, and that this may allow for greater lipid accumulation during finishing. Cesar et al. (2016) found that lower CPT-1b expression was related to high oleic acid content in the skeletal muscle. Exposure to CONC during the EARLY period (CONC-CONC and CONC-FOR) increased ($P < 0.05$) mRNA expression of lipoprotein lipase (LPL) compared to FOR-FOR. Fatty acid binding protein 4 (FABP4) mRNA levels were up-regulated ($P < 0.05$) for CONC-FOR compared at FOR-FOR. Both LPL and FABP4 are involved in the uptake of dietary fatty acids from circulation and transport into the adipocyte. Lipoprotein lipase hydrolyzes the release of fatty acids from triacylglycerides in circulating chylomicrons and very low density lipoproteins (Mead et al., 2002). Fatty acid binding protein 4 transports the fatty acid into the adipocyte, which is important in regulation of energy metabolism (Syamsunarno et al., 2013). The up-regulation of LPL and FABP4 would suggest enhanced uptake of dietary fatty acids into subcutaneous adipose tissue of steers fed CONC in the EARLY period.

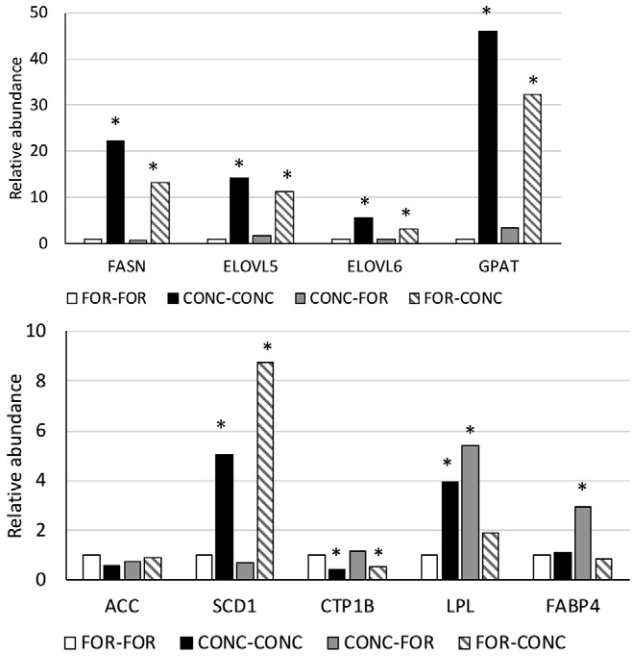

Figure 5. Lipogenic gene expression of subcutaneous adipose tissues collected at slaughter by dietary treatment. The asterisk (*) denotes treatment differs ($P < 0.05$) from FOR-FOR.

This appears to be a long-term effect from early exposure to corn grain that was maintained throughout finishing regardless of finishing system. In contrast, Buchanan et al. (2013) observed that FABP4 was up-regulated in adductor muscle of heifers that were forage-finished in comparison to concentrates. Wang et al. (2009) reported that FABP4 was elevated in Wagyu x Hereford heifers in the early weaning period and suggested that up-regulation of FABP4 in early development may help to maximize marbling deposition during later time periods.

Exposure to CONC versus FOR during the EARLY or LATE period enhanced growth, marbling deposition and percentage grading Choice. However, LATE exposure to CONC (CONC-CONC and FOR-CONC) increased WBSF values during early postmortem aging (d 2 and 7) but WBSF values did not differ among treatments at d 14. Early exposure to CONC (CONC-FOR and CONC-CONC) increased n-6 PUFA deposition in LM and SQ; whereas, LATE exposure to CONC (CONC-CONC and FOR-CONC) reduced n-3 PUFA, trans-11 octadecenoic acid and cis-9 trans-11 isomer of conjugated linoleic acid (CLA). Lipogenic gene expression was up-regulated and lipolytic gene expression was downregulated in SQ from CONC-CONC and FOR-CONC compared to FOR-FOR. Overall, exposure to CONC in both EARLY and LATE periods increased growth rate and marbling deposition but LATE exposure had the greatest impact on adipose lipogenesis and lipolysis, fatty acid composition, and tenderness.

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