Postweaning substitution of grazed forage with a high-energy concentrate has variable long-term effects on subcutaneous fat and marbling in Bos taurus genotypes

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Postweaning substitution of grazed forage with a high-energy concentrate has variable long-term effects on subcutaneous fat and marbling in *Bos taurus* genotypes[1]

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ABSTRACT: The objective of this study was to quantify the effects and interactions of stage of growth and genotype on commercial carcass traits and intramuscular fat (IMF) content in 5 muscles of *Bos taurus* steers (n = 165) and to test the hypothesis that substituting pasture with a high-energy concentrate during the immediate postweaning period increases IMF. Cattle of 3 genotypes (Angus, Hereford, and Wagyu × Angus; n = 55/genotype) were selected at weaning from commercial herds, targeting genotypic differences in marbling and subcutaneous fatness. Following weaning, steers were fed for 168 d within 2 different improved, temperate pasture-based nutritional systems: a forage-only system (FS) and forage with high-energy supplemented system (SS), with 2 replicates per system. The supplement was fed at a level of 1% of average BW adjusted every 2 wk to provide an estimated 50% of energy requirements for 168 d from weaning. Pasture on offer in both systems was managed to match the BW of the FS and SS steers during the postweaning treatment period to avoid confounding due to differences in growth rate during this period. Steers were then regrouped into 2 replicates and backgrounded on improved, temperate pasture for 158 d and then grain fed within 1 group for 105 d (short fed) or 259 d (long fed). Groups were slaughtered at commencement (d 0) and end of postweaning nutritional treatments (d 168), end of backgrounding (d 326), and after short (d 431) or long feedlotting (d 585). Serial slaughter stage had an effect on all traits assessed (P < 0.01). The FS steers had more rib fat (P < 0.01) and higher Meat Standards Australia marbling score (P < 0.05) and a tendency (P < 0.10) to have greater eye muscle area than the SS steers throughout the study. Genotypic differences were evident (P < 0.05) for all traits assessed except HCW, dressing percentage, rib fat depth, ossification score, ultimate pH, and IMF in the semitendinosus muscle. The results for marbling and IMF do not support the use of a high-energy feed as a substitute for an equivalent amount of energy from pasture during the immediate postweaning period to enhance development of marbling.

Key words: carcass composition, cattle, fatness, marbling, nutrition

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INTRODUCTION

In an effort to enhance profitability of beef production, attention has been directed toward manipulating fat deposition to consistently satisfy consumer requirements for eating quality while minimizing carcass waste. Cattle breeding decisions have placed selection emphasis on marbling (intramuscular fat [**IMF**] percentage) and subcutaneous fat depth (rib fat or P8 rump fat) resulting in reduced genetic capacity for subcutaneous fat and increased genetic capacity for IMF deposition (Barwick, 2010).

Nutrition becomes increasingly important for IMF development as animals age (Robinson et al., 2001; McKiernan et al., 2009), and during finishing, high-energy grain feeding promotes IMF compared with forage-based feeding systems (Johnston et al., 2003; Reverter et al., 2003). Recent evidence in Hanwoo cattle with high genetic capacity to deposit IMF suggests that increasing high-energy concentrate supplementation from weaning during a prolonged pasture-feeding (backgrounding) period enhances IMF and that this effect may persist through finishing (Hong et al., 2008). This is consistent with evidence from gene expression studies on IMF cells that also suggest a critical developmental time period for marbling from 10 mo of age or less for cattle (Wang et al., 2005, 2008; Lehnert et al., 2006).

However, information is limited on the effects of and interactions between genotype, stage of production, and nutrition during the immediate postweaning period on development of fat depots. Therefore, the objectives of this study were to evaluate, within a serial slaughter experiment, commercial carcass characteristics and IMF within 5 muscles in genotypes selected to differ in fat distribution. Steers were also subjected to different postweaning nutritional systems to test the hypothesis that a high-energy grain–based supplement during the immediate postweaning period would enhance the longer-term development of IMF.

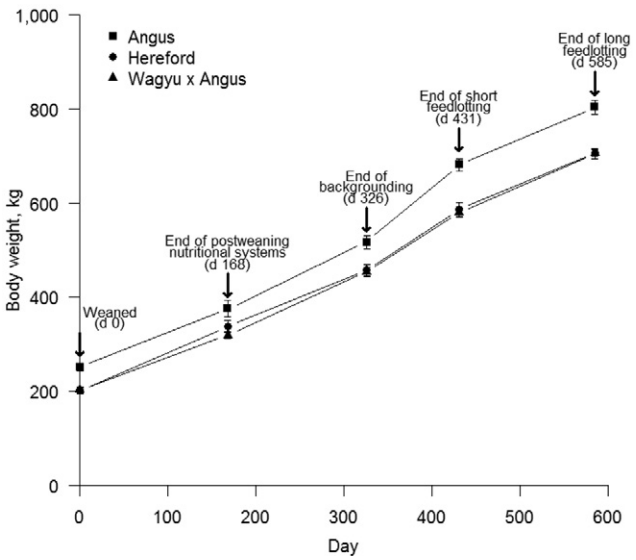

Figure 1. Mean BW ± SE for each genotype (Angus, Hereford, and Wagyu × Angus) at each of the 5 serial slaughter time points that coincided with the stages of the experiment shown by the arrows.

MATERIALS AND METHODS

Use of animals and the procedures performed in this study were approved by the New South Wales (**NSW**) Department of Primary Industries Orange Agricultural Institute Animal Ethics Committee (approval number ORA 08/005).

Experimental Design

The experimental design comprised 3 genotypes × 2 postweaning nutritional systems × 5 slaughter stages, as detailed below and shown in Fig. 1 and 2.

Cattle Genotypes

Weaner steers (approximately 6–8 mo old and average ± SD BW 223 ± 33 kg; n = 165) within 3 genotypes (55 Angus, 55 Hereford, and 55 Wagyu × Angus) targeted to differ in fat distribution characteristics were sourced from 5 properties in the Northern Tablelands region of New South Wales and transported to the New South Wales Department of Primary Industries Agricultural Research and Advisory Station, Glen Innes, NSW, Australia (Glen Innes Agricultural Research & Advisory Station [**GIARAS**]; 29°44′ S, 151°42′ E, and 1,057 m altitude). The properties were

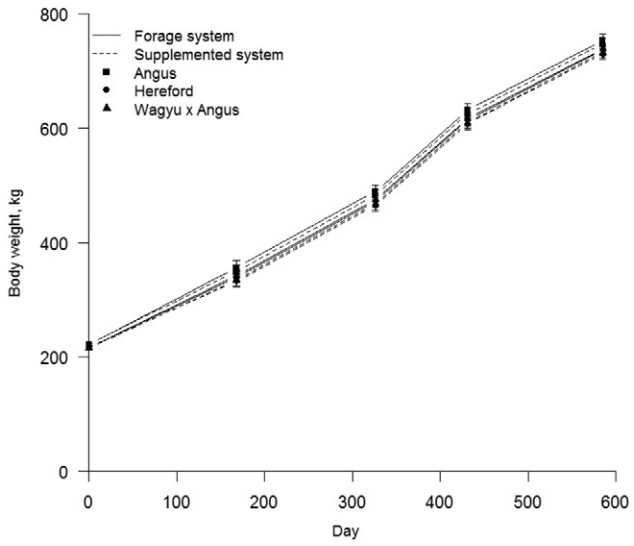

Figure 2. Least squares means of BW (adjusted for initial BW) ± SE for each genotype (Angus, Hereford, and Wagyu × Angus) and postweaning nutritional system (forage-only system or forage with high-energy supplemented system) at the 5 serial slaughter stages (see Fig. 1) from commencement of nutritional treatments when weaned to the end of long feedlotting.

all within 100 km of GIARAS. Cattle suitable for the experiment were identified in conjunction with the Animal Genetics and Breeding Unit, Armidale, NSW, Australia, using BreedPlan (Graser et al., 2005; BreedPlan, 2014) information. A combination of breed differences, within-breed EBV (Angus and Hereford), and marbling sire lines (Wagyu x Angus) were used to identify cattle suitable for the experiment. Pedigrees were known for all cattle and exact birth dates were known for the Angus and Wagyu x Angus cattle. The cattle genotypes and selection criteria were

Angus, targeting high IMF and high subcutaneous fat: 6 sires over high marbling EBV cows from 2 herds of origin, Angus BreedPlan average sire EBV of +2.0% for IMF, and approximately breed average for rib fat and P8 rump fat;

Hereford, targeting low IMF and high subcutaneous fat: 6 sires over 2 herds of origin, Hereford BreedPlan sire EBV for IMF of +0.4%, and approximately breed average for rib fat and P8 rump fat; and

Wagyu sires × Angus dams, targeting high IMF (as a breed trait for the Wagyu sires although no EBV were available) and expected lower subcutaneous fat than for Angus and Hereford: 6 Wagyu sires over the same high marbling EBV Angus genotype cows as Angus, from 1 herd of origin.

Table 1. Ingredients and nutritional composition of pelleted feed offered to steers for 168 d from weaning within the supplemented nutritional system

Component	%
Ingredient, % as fed	
Corn	58.0
Barley	25.0
Dried distillers grains	6.0
Molasses	8.0
Lime	1.0
Sodium bicarbonate	0.5
Multivitamin mix[1]	0.5
Trace mineral mix[2]	0.5
Bentonite	0.5
Nutritional value, % DM	
DM	89.5
NDF	17
ADF	8
CP	11.0
DMD[3]	85
DOMD[4]	78
Inorganic ash	9
OM	91
Predicted energy	
ME, MJ/kg DM	12.3

[1]Vitamin A 1,340,000 IU, vitamin D_3 160,000 IU and vitamin E 5,000 mg per kg multivitamin mix.

[2]Cobalt 100 mg, copper 2,400 mg, iodine 100 mg, iron 10,000 mg, manganese 8,000 mg, selenium 20 mg and zinc 8,000 mg per kg trace mineral mix.

[3]DMD = Dry matter digestibility.

[4]DOMD = Dry organic matter digestibility.

Nutritional Systems after Weaning and Management Procedures

On arrival at GIARAS, steers were vaccinated against clostridial diseases and then yard weaned for 2 wk, during which time they were fed lucerne hay ad libitum. The steers were then fed for 168 d within 2 differing pasture-based nutritional systems, with 2 replicates per nutritional system. Pasture biomass was visually assessed by a trained assessor before entry of steers to each paddock, and pasture quality was determined by laboratory analyses at the NSW Department of Primary Industries Chemical Services Laboratory (Wagga Wagga, Australia) at entry to each paddock and/or monthly to enable the criteria for each system described below to be met.

The 2 pasture-based nutritional systems were a forage-only system (**FS**), which consisted of grazing high-performance tetraploid Italian ryegrass (*Lolium multiflorum*) and Nile oats (*Avena sativa* L.), with a minimum of 3 t DM/ha on entry into grazing area (the nutritional value of these pastures were [mean ± SD] 10.0 ± 1.8 MJ ME and 12.4 ± 3.7% CP per kilogram DM during the treatment period), and a forage with high-energy supplemented system (**SS**), which consisted of high-energy pellets (Table 1) at an average of 1% of BW plus grazing of mixed improved temperate species (cocksfoot [*Dactylis glomerata*], perennial ryegrass [*Lolium perenne*], Phalaris [*Phalaris aquatica*], tall fescue [*Festuca arundinacea*], and white clover [*Trifolium repens*]), with approximately 2 t DM/ha on entry into grazing areas. Nutritional value of these pastures (mean ± SD) were 9.1 ± 1.6 MJ ME and 12.1 ± 1.9% CP per kg DM during the treatment period.

During the 168-d nutritional treatment period, the FS and SS replicates were rotated among pasture paddocks, based on average BW and ADG of the groups and the estimated pasture DM availability and quality, to minimize differences between treatment groups and any confounding in body compositional characteristics due to differences in BW and ADG (Fig. 2).

The amount of pellets fed to the SS steers during the 168-d postweaning period was based on providing an average of 50% of estimated energy requirements (Freer et al., 2007) from the pellets and 50% from the pasture. To achieve this, every 2 wk, cattle were weighed and the amount of pelleted feed offered readjusted to 1% of average BW within each of the 2 replicates. The pellets were provided in open troughs with adequate space to

Table 2. Ingredients and nutritional value of feedlot rations offered to short-fed and long-fed steers

Component	Short-fed steers	Long-fed steers
Feedlot period, d	0–105	106–259
Ingredient, % as fed		
Barley	77.5	70
Grassy lucerne hay	10	10
Forage sorghum	0	10
Cottonseed meal	2.5	0
Molasses	8	8
Sodium bicarbonate	0.5	0.5
Sulfate of ammonia	0.5	0.5
Lime	1.0	1.0
Nutritional value		
DM, % as fed	87.2	87.1
NDF, % DM	22.7	26.7
ADF, % DM	8.8	11.7
Ash, % DM	7.0	8.0
CP, % DM	13.7	12.9
Predicted energy		
ME, MJ/kg DM	12.2	11.8

ensure that competition between steers for pellets was minimized to avoid any disadvantage to shy feeders.

At the completion of the nutritional treatment period, steers were randomized within 2 replicates balanced for genotype and postweaning nutritional system and backgrounded on the same improved temperate pastures as described for FS above for 158 d until feedlot entry at 18 mo of age.

Before the end of backgrounding, the steers underwent a prefeedlot entry health program including vaccination against bovine respiratory disease and clostridial diseases. The cattle were also treated for internal and external parasites and liver fluke before transport to the feedlot.

Following backgrounding, the cattle were transported to the Australian Cooperative Research Centre for Beef Genetic Technologies (Tullimba) research feedlot near Kingstown, NSW, Australia (30°20′ S, 151°10′ E, and 560 m altitude), for grain finishing. After arrival at the feedlot, they were allocated to a large open bunk pen for adaptation to a grain-based diet. Steers undertook either a short (105 d) or a long (259 d) feeding period consistent with normal industry practices (Table 2).

Serial Slaughter Stages

The serial slaughters were conducted at the following stages: baseline steers (d 0; n = 15) were slaughtered when weaned (stage 1) and other groups were subsequently slaughtered at the end of the postweaning nutritional systems (d 168; n = 30; stage 2), at the end of backgrounding period before feedlot entry (d 326; n = 30; stage 3), and after short (d 431; n = 30; stage 4) and long (d 585; n = 60; stage 5) feedlotting (Fig. 1).

Slaughter Procedures and Measurements

Transport and Slaughter Procedures. The cattle were transported to Northern Cooperative Meat Company abattoir, Casino, NSW, Australia, for slaughter from either GIARAS (225 km; 3 h; stages 1 to 3) or Tullimba (380 km; 5 h; stages 4 and 5). Groups left the research station or the feedlot midmorning and were slaughtered during the morning on the following day. They were provided with water ad libitum during lairage and there was no mixing with other cattle at any stage. After slaughter by captive bolt stunning and exsanguination, standard AUS-MEAT carcasses (AUS-MEAT, 2007) were prepared and split into 2 sides. Rump fat depths at the P8 site were measured on each untrimmed carcass, and both sides from all animals slaughtered at each stage were weighed and placed together in the same chiller.

Carcass Chiller Assessment. The carcass sides were chilled overnight and then quartered between the 10th and 11th ribs. No less than 20 min after quartering, sides were graded according to Meat Standards Australia (**MSA**) standards (Meat Standards Australia, 2009) by the same MSA assessor at each slaughter.

Intramuscular Fat Assessment. A sample of muscle tissue (approximately 40 g) was cut from the following muscles: biceps femoris muscle (outside flat), supraspinatus muscle (chuck tender), semitendinosus muscle (eye round), longissumus lumborum muscle (striploin, cranial end), and infraspinatus muscle (oyster blade). Chemical IMF was determined as described by Perry et al. (2001).

Statistical Analyses

Descriptive statistics of initial BW (**iBW**; i.e., weaning weight) taken 7 d before baseline steers were slaughtered, slaughter BW, and commercial carcass characteristics and IMF in muscles from weaning through to the end of long feedlotting are presented for the entire data set in Table 3.

The carcass data for baseline steers (stage 1, Day 0) were analyzed using a linear regression model with iBW as the covariate. These data were analyzed separately from the analyses of the other stages described below because these steers were not allocated to a postweaning nutritional treatment.

A linear mixed-effects model was fitted to the data for stages 2 to 5. Sire was included as a random term using the REML algorithm in the lmer routine (Pinheiro et al., 2008) in R (R Development Core

Table 3. Descriptive statistics for initial and slaughter BW, commercial carcass characteristics, and intramuscular fat (IMF) content (%) for 5 muscles from commencement of nutritional treatments when weaned to end of long feedlotting for all animals in the data set

Variable	No.	Mean	SD	Minimum	Maximum
Initial BW, kg	165	224	33.7	142	333
Slaughter BW, kg	165	550	189.5	176	912
HCW, kg	165	329	128.6	90	579
Dressing, %	165	58.8	4.5	50.2	71.0
P8 rump fat, mm	165	14.9	10.6	1	47
Rib fat, mm	165	9.6	6.47	1	30
EMA,[1] cm^2	165	73.2	20.9	30	124
MSA[2] marbling score, 100 to 1,200	163	408	178.1	100	1,180
Ossification score, 100 to 590	165	133	22.4	100	190
Ultimate pH	165	5.56	0.07	5.43	5.91
Biceps femoris muscle, IMF %	134	6.15	3.7	1.39	18.2
Supraspinatus muscle, IMF %	135	5.37	2.8	1.89	14.5
Semitendinosus muscle, IMF %	135	4.25	2.5	1.47	19.5
Longissimus lumborum muscle, IMF %	135	6.35	4.8	1.55	26.9
Infraspinatus muscle, IMF %	135	9.00	6.1	1.86	31.7

[1]EMA = eye muscle area.

[2]MSA = Meat Standards Australia (Meat Standards Australia, 2009).

Team, 2013). The lm routine (Chambers, 1992) was used to evaluate carcass traits and muscle IMF when sire was not significant ($P > 0.05$). No differences ($P > 0.05$) in postweaning nutritional system replicates (1 and 2) or herds of origin were found; hence, these factors were removed from the analyses. The response variables (carcass traits and IMF of 5 individual muscles) were evaluated as follows:

$$\text{variable} = \beta_0 + \beta_1 St + \beta_2 G + \beta_3 T + \beta_4 St \times G + \beta_5 St \times T + \beta_6 G \times T + \beta_7 iBW + e, \quad [1]$$

in which the fixed effects were St (serial slaughter stage: 2 to 5), G (genotype: Angus, Hereford, and Angus x Hereford), and T (postweaning nutritional treatment: FS and SS); iBW was fitted as a covariate; and e was the residual error.

The assumptions of normality and constant variance were evaluated on all models. Four diagnostic plots were evaluated: residual vs. fitted values, normal Quantile-Quantile plot, square root residual (standardized residuals) vs. fitted values, and residual values vs. leverage. The residual values vs. leverage were used to determine the existence of any outliers. The Box–Cox transformation (Box and Cox, 1964; Venables and Ripley, 2002) in R (R Development Core Team, 2013) was used to determine if the data required transformation and the optimal transformation reported in Table 4. The least squares means (**LSM**), transformed and back transformed, and a "pairwise" comparison of P-values adjusted using the Tukey method of the fixed effects of genotype and serial slaughter stage for carcass characteristics and muscle IMF content are reported in the tables. Effects of postweaning nutritional systems are presented in the figures. Direct back transformation of the LSM and upper and lower SE values are presented in the figures.

All nonsignificant ($P > 0.05$) effects were removed from the models, except for genotype effects.

RESULTS

Transformations applied to carcass traits and IMF content of muscles, the residual error, and the adjusted R^2 values for the fitted models are reported in Table 4. The effects of serial slaughter stage, iBW, genotype, and postweaning nutritional treatment for commercial carcass traits and IMF content of 5 muscles are detailed as follows.

Effects of Serial Slaughter Stage and Initial BW

The effect of serial slaughter stage was significant ($P < 0.001$) in all commercial carcass traits (Tables 5 and 6) and IMF content in the 5 muscles (Table 7).

There were no serial slaughter stage × genotype interactions ($P > 0.05$) for commercial carcass traits; however, there were genotype × serial slaughter stage interactions ($P < 0.05$) for IMF content in the biceps femoris and supraspinatus muscles. The iBW covariate was significant for HCW, P8 rump fat, and eye muscle area (**EMA**; $P < 0.01$) and for ossification score ($P < 0.05$) but did not affect IMF content in the 5 muscles ($P > 0.10$).

Table 4. Model transformations, residual error, and adjusted R^2 for commercial carcass traits and intramuscular fat (IMF) content (%) in 5 muscles

Variable	Transformation	Residual error	Adjusted R^2
Carcass traits			
HCW, kg	log(x)	0.083	0.95
Dressing, %	1	2.84	0.57
P8 rump fat, mm	$x^{1/2}$	0.55	0.85
Rib fat, mm	$x^{1/5}$	0.087	0.84
EMA,[1] cm^2	log(x)	0.10	0.85
MSA marbling score[2]	log(x)	0.25	0.58
Ossification score[3]	1/x	0.00071	0.64
Ultimate pH	1	0.065	0.11
IMF, %			
Biceps femoris muscle	log(x)	0.25	0.78
Supraspinatus muscle	log(x)	0.27	0.72
Semitendinosus muscle	$1/x^{1/2}$	0.069	0.65
Longissimus lumborum muscle	$1/x^{1/2}$	0.061	0.83
Infraspinatus muscle	$1/x^{1/2}$	0.038	0.86

[1]EMA = eye muscle area.

[2]MSA = Meat Standards Australia. Score: 100 to 1,200 (Meat Standards Australia, 2009).

[3]Ossification score: 100 to 590.

Effects of Genotype on Commercial Carcass Characteristics

The back-transformed LSM, transformed LSM, and average SED across the serial slaughter stages for commercial carcass characteristics are reported in Tables 5 and 6. Genotype had a significant effect ($P < 0.05$) on all commercial carcass characteristics in stages 2 to 5 except for HCW, dressing percentage, rib fat, ossification score, and ultimate pH (Tables 5 and 6).

The P8 rump fat depth was significantly ($P < 0.05$) greater in Hereford than Angus steers across stages 2 to 5 (Table 5). Eye muscle area was greater in Wagyu x Angus than in Hereford steers ($P < 0.01$) across stages 2 to 5 (Table 6). Meat Standards Australia marbling score was lower ($P < 0.01$) in Hereford steers than in the other genotypes across stages 2 to 5 (Table 6).

Effects of Genotype on Intramuscular Fat Percentage

The back-transformed LSM, transformed LSM, and average SED for IMF content in 5 muscles across genotypes at each stage are reported in Table 7.

Table 5. Least squares means for back-transformed (inverse of transformation) and transformed data (where required, in parentheses) and average SED for carcass traits at all 5 slaughter stages.[1] Transformed data were generated using the transformations shown in Table 4

Variable and stage	No./genotype	Genotype			Average SED
		Angus	Hereford	Wagyu × Angus	
HCW, kg					
Stage 1, 0 d	5	114.8 (4.74)	114.0 (4.74)	116.8 (4.76)	0.023
Stage 2, 168 d	10	186.7 (5.23)	183.9 (5.21)	186.8 (5.23)	0.023
Stage 3, 326 d	10	266.5 (5.59)	262.4 (5.57)	266.5 (5.59)	0.023
Stage 4, 431 d	10	382.1 (5.95)	376.3 (5.93)	382.2 (5.95)	0.023
Stage 5, 585 d	20	459.1 (6.13)	452.2 (6.11)	459.2 (6.13)	0.023
Dressing, %					
Stage 1, 0 d	5	54.4	51.8	53.6	1.08
Stage 2, 168 d	10	54.4	54.5	55.2	0.57
Stage 3, 326 d	10	55.9	56.0	56.7	0.57
Stage 4, 431 d	10	61.6	61.7	62.4	0.57
Stage 5, 585 d	20	61.8	61.9	62.6	0.57
P8 rump fat, mm					
Stage 1, 0 d	5	1.38 (1.17)	1.16 (1.08)	1.50 (1.23)	0.23
Stage 2, 168 d	10	2.67 (1.63[a])	4.87 (2.21[b])	3.22 (1.79)	0.20
Stage 3, 326 d	10	5.63 (2.38[a])	8.68 (2.95[b])	6.41 (2.53)	0.20
Stage 4, 431 d	10	17.15 (4.14[a])	22.22 (4.71[b])	18.49 (4.30)	0.20
Stage 5, 585 d	20	22.52 (4.75[a])	28.27 (5.32[b])	24.05 (4.90)	0.20
Rib fat, mm					
Stage 1, 0 d	5	1.00 (1.00)	1.53 (1.09)	1.16 (1.03)	0.038
Stage 2, 168 d	10	2.72 (1.22)	2.86 (1.23)	2.9 (1.24)	0.020
Stage 3, 326 d	10	4.84 (1.37)	5.04 (1.38)	5.12 (1.39)	0.020
Stage 4, 431 d	10	12.59 (1.66)	13.03 (1.67)	13.18 (1.67)	0.020
Stage 5, 585 d	20	14.62 (1.71)	15.11 (1.72)	15.28 (1.73)	0.020

[a,b]Within a row, means without a common superscript letter differ ($P < 0.05$).

[1]Stages: 0 d = weaned and start of nutritional treatment; 168 d = end of nutritional treatment; 326 d = end of backgrounding; 431 d = end of short feedlotting; 585 d = end of long feedlotting.

Table 6. Least squares means for back-transformed data (inverse of transformation) and transformed data (where required, in parentheses) and average SED for carcass traits at all 5 slaughter stages.[1] Transformed data were generated using the transformations shown in Table 4

Variable and stage	No./genotype	Genotype			Average SED
		Angus	Hereford	Wagyu × Angus	
EMA,[2] cm^2					
Stage 1, 0 d	5	33.0 (3.50)	37.7 (3.63)	40.8 (3.71)	0.103
Stage 2, 168 d	10	50.2 (3.92)	48.7 (3.89^A)	53.7 (3.98^B)	0.032
Stage 3, 326 d	10	63.8 (4.16)	61.7 (4.12^A)	68.1 (4.22^B)	0.032
Stage 4, 431 d	10	82.9 (4.42)	80.2 (4.38^A)	88.5 (4.48^B)	0.032
Stage 5, 585 d	20	90.1 (4.50)	87.3 (4.47^A)	96.3 (4.57^B)	0.032
MSA marbling score[3]					
Stage 1, 0 d	5[4]	130 (4.87)	119 (4.78)	114 (4.73)	0.180
Stage 2, 168 d	10	307 (5.73^A)	234 (5.45^B)	299 (5.70^A)	0.061
Stage 3, 326 d	10	346 (5.84^A)	263 (5.57^B)	335 (5.82^A)	0.061
Stage 4, 431 d	10	493 (6.20^A)	375 (5.93^B)	479 (6.17^A)	0.061
Stage 5, 585 d	20	580 (6.36^A)	441 (6.09^B)	563 (6.33^A)	0.061
Ossification score[5]					
Stage 1, 0 d	5	111 (0.0090)	104 (0.0096)	102 (0.0098)	0.00008
Stage 2, 168 d	10	109 (0.0092^{ab})	108 (0.0092^a)	114 (0.0088^b)	0.00027
Stage 3, 326 d	10	120 (0.0083^{ab})	120 (0.0084^a)	126 (0.0079^b)	0.00027
Stage 4, 431 d	10	132 (0.0076^{ab})	132 (0.0076^a)	139 (0.0072^b)	0.00027
Stage 5, 585 d	20	148 (0.0067^{ab})	147 (0.0068^a)	157 (0.0064^b)	0.00027
Ultimate pH					
Stage 1, 0 d	5	5.5	5.6	5.5	0.028
Stage 2, 168 d	10	5.6	5.6	5.6	0.013
Stage 3, 326 d	10	5.5	5.5	5.5	0.013
Stage 4, 431 d	10	5.5	5.6	5.6	0.013
Stage 5, 585 d	20	5.6	5.6	5.6	0.013

^{a,b}Within a row, means without a common superscript letter differ ($P < 0.05$).

^{A,B}Within a row, means without a common superscript letter differ ($P < 0.01$).

[1]Stages: 0 d = weaned and start of nutritional treatment; 168 d = end of nutritional treatment; 326 d = end of backgrounding; 431 d = end of short feedlotting; 585 d = end of long feedlotting.

[2]EMA = eye muscle area.

[3]MSA = Meat Standards Australia. Score: 100 to 1,200 (Meat Standards Australia, 2009).

[4]MSA marbling score: Angus; stage 1, 0 d; $n = 3$.

[5]Ossification score: 100 to 590.

The biceps femoris muscle IMF content was greater at stage 3 in Wagyu x Angus ($P < 0.01$) and Angus ($P < 0.05$) than in Hereford steers and greater at stage 4 in Angus than Hereford steers ($P < 0.01$). Significant differences were not evident ($P = 0.08$) in this muscle at stage 5. The supraspinatus muscle IMF content was lower in Hereford than in Angus and Wagyu x Angus steers at stage 3 ($P < 0.05$) and stages 4 and 5 ($P < 0.01$). The semitendinosus muscle IMF content did not differ significantly ($P > 0.05$) due to genotype at any stage. The longissimus lumborum muscle and infraspinatus muscle IMF contents were lower ($P < 0.01$) in Hereford than in Angus and Wagyu x Angus steers at stages 2 to 5.

Effects of Postweaning Nutritional System

Rib fat depth was significantly ($P < 0.01$) greater in FS than in SS steers across stages 2 to 5 (Fig. 3a). Results for P8 rump fat (Fig. 3b) are also presented for comparative purposes but did not differ significantly ($P = 0.06$) between FS and SS steers. The MSA marbling score was significantly greater ($P < 0.05$) in FS than SS steers across stages 2 to 5 (Fig. 3c). Results for EMA indicated a tendency ($P = 0.05$) to be greater in FS than SS steers for stages 2 to 5 (Fig. 3d). At stage 5, FS steers tended to have higher IMF in the longissimus lumborum muscle ($P = 0.06$) at stage 5 (Fig. 4a). However, SS steers tended to have higher IMF in the semitendinosus muscle ($P = 0.22$) and infraspinatus muscle ($P = 0.16$) than the FS steers (Fig. 4b and 4c). The differences between treatment effects are shown in Fig. 4a, 4b, and 4c, with *P*-values reported for pairwise differences between nutritional treatments at conclusion of the study at the end of long feedlotting at stage 5.

Table 7. Least squares means for back-transformed data (inverse of transformation) and transformed data (in parentheses) and average SED for intramuscular fat (IMF) content (%) at all 5 slaughter stages.[1] Transformed data were generated using the transformations shown in Table 4

Variable and stage	No./genotype	Genotype			Average SED
		Angus	Hereford	Wagyu × Angus	
Biceps femoris muscle, IMF %					
Stage 1, 0 d	5	1.90 (0.64)	2.13 (0.75)	2.16 (0.77)	0.145
Stage 2, 168 d	10	3.06 (1.12)	3.12 (1.14)	3.36 (1.21)	0.115
Stage 3, 326 d	10	4.97 (1.60^{a})	3.56 (1.27^{b,A})	6.80 (1.92^{c,B})	0.115
Stage 4, 431 d	10	7.36 (2.00^{A})	5.04 (1.62^{B,a})	6.95 (1.94^{b})	0.116
Stage 5, 585 d	10[2]	12.6 (2.53)	9.80 (2.28)	11.6 (2.45)	0.117
Supraspinatus muscle, IMF %					
Stage 1, 0 d	5	2.40 (0.88)	2.20 (0.79)	2.57 (0.94)	0.116
Stage 2, 168 d	10	2.74 (1.01)	2.47 (0.91)	3.30 (1.19)	0.126
Stage 3, 326 d	10	5.36 (1.68^{a})	3.81 (1.34^{b})	5.64 (1.73^{a})	0.128
Stage 4, 431 d	10	7.16 (1.97^{A})	4.28 (1.45^{B})	7.51 (2.02^{A})	0.129
Stage 5, 585 d	10	8.91 (2.19^{A})	5.79 (1.76^{B})	9.57 (2.26^{A})	0.127
Semitendinosus muscle, IMF %					
Stage 1, 0 d	5	1.85 (0.74)	1.97 (0.71)	2.02 (0.70)	0.053
Stage 2, 168 d	10	2.34 (0.65)	2.32 (0.66)	2.52 (0.63)	0.017
Stage 3, 326 d	10	3.69 (0.52)	3.64 (0.52)	4.05 (0.50)	0.017
Stage 4, 431 d	10	3.98 (0.50)	3.93 (0.50)	4.39 (0.48)	0.017
Stage 5, 585 d	10	6.44 (0.39)	6.34 (0.40)	7.29 (0.37)	0.017
Longissimus lumborum muscle, IMF %					
Stage 1, 0 d	5	1.93 (0.72)	1.9 (0.72)	2 (0.71)	0.027
Stage 2, 168 d	10	2.75 (0.60^{A})	2.1 (0.69^{B})	2.78 (0.60^{A})	0.017
Stage 3, 326 d	10	4.68 (0.46^{A})	3.32 (0.55^{B})	4.75 (0.46^{A})	0.017
Stage 4, 431 d	10	7.57 (0.36^{A})	4.95 (0.45^{B})	7.72 (0.36^{A})	0.017
Stage 5, 585 d	10	14.7 (0.26^{A})	8.31 (0.35^{B})	15.1 (0.26^{A})	0.017
Infraspinatus muscle, IMF %					
Stage 1, 0 d	5	2.89 (0.59)	3.24 (0.56)	3.03 (0.57)	0.057
Stage 2, 168 d	10	4.63 (0.46^{A})	3.38 (0.54^{B})	4.82 (0.46^{A})	0.009
Stage 3, 326 d	10	7.12 (0.37^{A})	4.85 (0.45^{B})	7.49 (0.37^{A})	0.009
Stage 4, 431 d	10	11.8 (0.29^{A})	7.27 (0.37^{B})	12.6 (0.28^{A})	0.009
Stage 5, 585 d	10	18.0 (0.24^{A})	10.1 (0.32^{B})	19.5 (0.23^{A})	0.009

$^{a–c}$Within a row, means without a common superscript letter differ ($P < 0.05$).

^{A,B}Within a row, means without a common superscript letter differ ($P < 0.01$).

[1]Stages: 0 d = weaned and start of nutritional treatment; 168 d = end of nutritional treatment; 326 d = end of backgrounding; 431 d = end of short feedlotting; 585 d = end of long feedlotting.

[2]Biceps femoris muscle: Stage 5, 585 d; Wagyu × Angus; $n = 9$.

DISCUSSION

The results of this study show that substituting grazed forage with a high-energy concentrate at a level equivalent to 1% of BW or approximately 50% of estimated dietary energy requirements of *Bos taurus* steers had a suppressive effect on subcutaneous rib fat depth that persisted throughout the study but little or no effect on the capacity to produce IMF. These findings are independent of effects specific to differences in size and/or growth rates, which were managed within the present experiment to minimize or eliminate confounding due to these factors. The present study also provides phenotypic data on development of commercially important fat depots in different *Bos taurus* genotypes over the 585-d period from weaning to the end of long feedlotting.

Although differences in the development of marbling in the present study were generally consistent with expectations in selecting the genotypes, subcutaneous fat depths were less so, with the Wagyu ×Angus steers having similar or more subcutaneous (rib fat and P8 rump fat) fat than their Angus counterparts. These findings, coupled with other data and samples obtained, will enable more detailed studies of fat depot development and beef quality and allow for the development and refinement of phenotypic prediction models (e.g., Walmsley et al., 2014). In regard to the latter, this experiment has been used to determine total body fatness and the relative proportions of fat in subcutaneous, in-

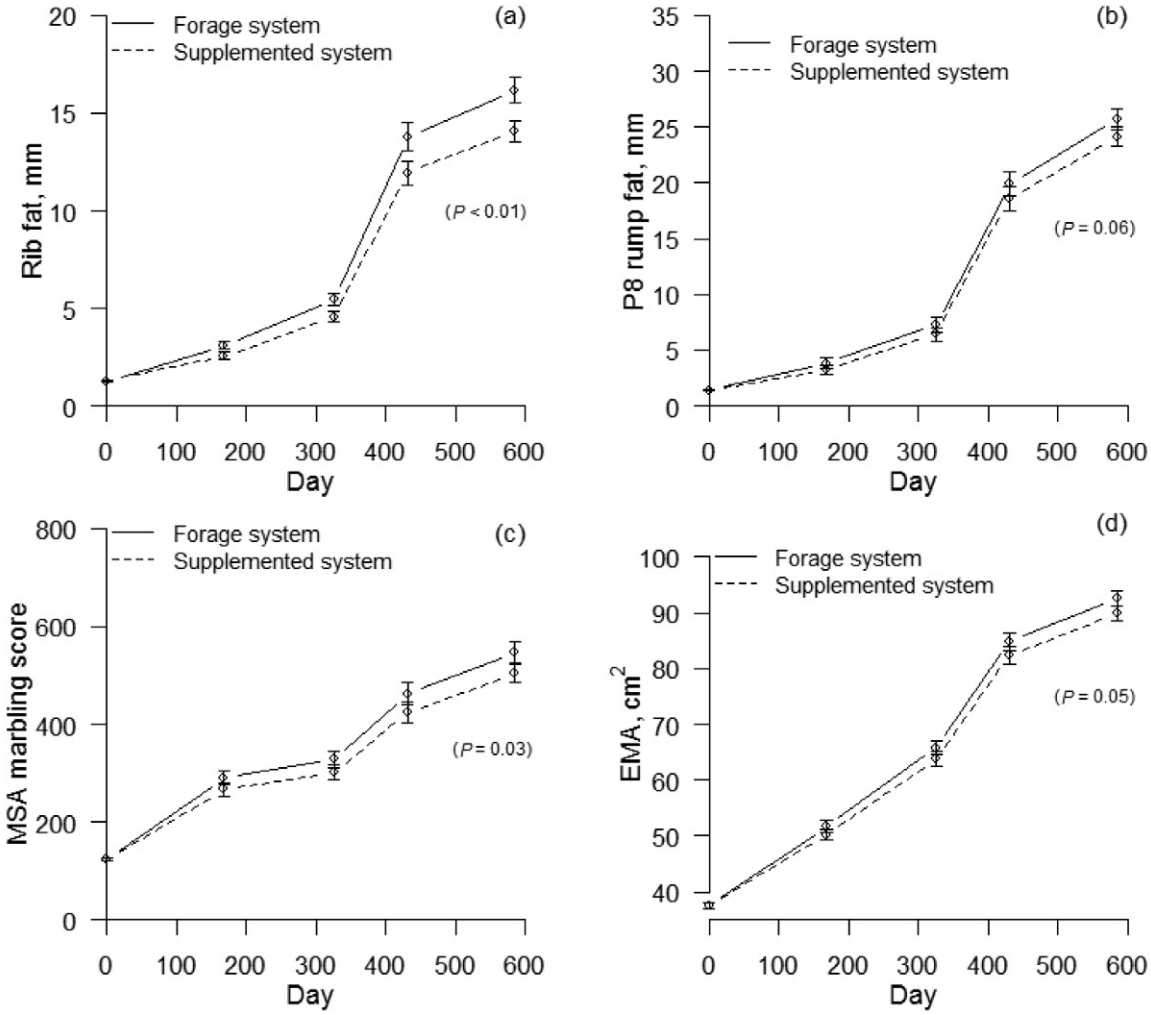

Figure 3. Least squares means and the SE directly back transformed from the final statistical model for (a) rib fat (mm), (b) P8 rump fat, (c) Meat Standards Australia (MSA) marbling score (Meat Standards Australia, 2009), and (d) eye muscle area (EMA; cm^2) for the postweaning nutritional system (forage-only system or forage with high-energy supplemented system) at the 5 serial slaughter stages (see Fig. 1) from commencement of the nutritional systems when weaned to the end of long feedlotting. The *P*-values are for the conclusion of the study at stage 5 (end of long feedlotting).

termuscular, intramuscular, and visceral fat depots during animal development from weaning to the end of a long feedlotting period (McPhee et al., 2013).

The stages of development at which the amount of marbling at market weights can be influenced by nutrition, either by earlier effects on adipogenesis and/or by the persistence of effects on lipogenesis, has been the subject of numerous studies. Within pasture-based nutritional systems similar to the present study, neither birth weight or varying maternal nutrition at pasture during pregnancy affected rib fat depth, P8 rump fat depths, MSA marbling score, or LM IMF content in *Bos taurus* cattle at heavy market weights (380 kg average carcass weight; Greenwood et al., 2006; Greenwood and Cafe, 2007; Robinson et al., 2013). These findings are at odds with the suggestion, based largely on more mechanistic evidence within fetal life and in species other than cattle, that nutrition during gestation may alter fatness and marbling at market weights (Du et al., 2013). In contrast, better maternal nutrition from birth to weaning within pasture-based systems resulted in more rapid growth of offspring and a small but persistent increase in carcass fatness, but not in marbling (Greenwood et al., 2006, 2009; Robinson et al., 2013), consistent with lack of effect of initial BW (which is indicative of growth and nutrition to weaning) on marbling score or on IMF content of the 5 muscles in the present study.

Nutrition during the immediate postweaning period can influence fatness and marbling; however, results are variable, as discussed by Meteer et al. (2013) in relation to early compared with conventional weaning systems. Within production systems with a prolonged backgrounding period similar to that of the present study, early weaning coupled with provision of high-energy supplements after weaning reduced carcass weight and did not significantly affect marbling or other carcass traits compared with conventional weaning (Wolcott et al., 2010). By contrast,

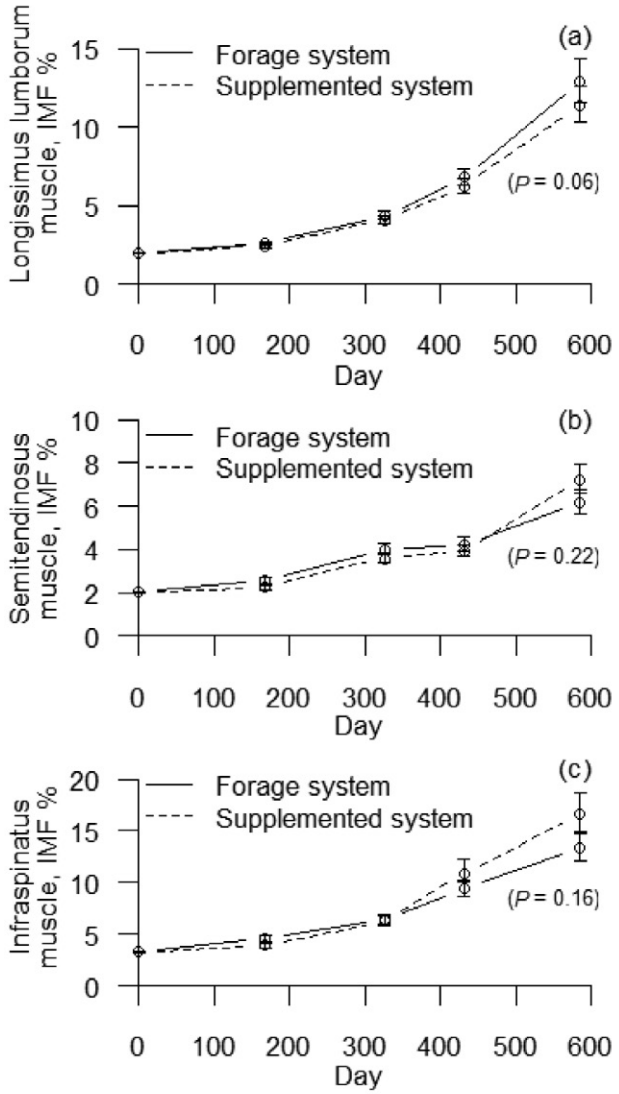

Figure 4. Least squares means and the SE directly back transformed from the final statistical model for (a) longissimus lumborum muscle intramuscular fat (IMF) content (%), (b) semitendinosus muscle IMF percent, and (c) infraspinatus muscle IMF percent for the postweaning nutritional system (forage-only system or forage with high-energy supplemented system) at the 5 serial slaughter stages (see Fig. 1) from commencement of the nutritional systems when weaned to the end of long feedlotting. The *P*-values are for the conclusion of the study at stage 5 (end of long feedlotting).

recent evidence shows that marbling (Meteer et al., 2013; Scheffler et al., 2014) and fatness (Meteer et al., 2013) at market weight can be increased by provision of high-energy concentrate feed to early-weaned and creep-fed compared with conventionally weaned calves, and marbling was increased in the early-weaned compared with creep-fed calves within a more accelerated production system (Meteer et al., 2013). However, these effects are most likely due to intake of additional energy at lighter weights rather than substrate-specific effects; within early-weaned and creep-fed calves, significant differences in marbling and fatness between calves fed starch- or forage-based diets were not evident (Meteer et al., 2013).

Modest effects of postweaning nutrition and growth rates on marbling and fatness following feedlot finishing within production systems similar to that of the present study have been observed (Robinson et al., 2001; McKiernan et al., 2009; McPhee et al., 2012). However, several growth rate studies (Harper et al., 1999; Robinson et al., 2001; Sharman et al., 2013) have found that nutrition during the finishing phase can have a more profound effect on marbling and fatness and may mask any changes in partitioning of fat during the stocker or backgrounding phase. In the present study, the effect of nutritional system on fatness during the immediate postweaning period persisted, at least for MSA marbling score and rib fat depth, independent of growth rate.

The greater rib fat depths throughout the present study in the pasture-only-fed cattle compared with those receiving concentrate after weaning provide some support for the notion that adipogenic and/or lipogenic potential may have been affected by the postweaning nutritional treatments, independent of growth-rate-related effects. It has been suggested that different fat depots have preferences for different substrates to support lipogenesis and/or adipogenesis, although empirical evidence for effects on carcass characteristics independent of the amount of NE supplied is lacking (Pethick et al., 2004; Hocquette et al., 2010). Acetate is the major carbon source for fatty acid synthesis in ruminants' fat depots (Bauman, 1976); however, it has been suggested that IMF (as opposed to other depots) preferentially utilizes glucose/lactate for fatty acid synthesis (Smith and Crouse, 1984; Rhoades et al., 2007; Smith et al., 2009; Hocquette et al., 2010). Diets based on cereal grain would potentially generate additional glucose either via gluconeogenesis from propionate or via direct absorption of glucose from the small intestine (Rowe et al., 1999). Other factors have also been implicated in regulating adipogenesis and/or lipogenesis. These include the energy cost associated with digestion of forage compared with concentrates; the visceral content of the body and the amount of energy remaining for utilization by peripheral tissues (Sainz et al., 1995); metabolism of fatty acids in the rumen, resulting in specific long-chain fatty acid isomers of the conjugated linoleic acid family that may inhibit triglyceride synthesis (Kennedy et al., 2010; Bauman et al., 2011); the relative amounts of *n*-6 and *n*-3 fatty acids in the diet (Ailhaud et al., 2006), which vary between forage and concentrate diets; and the amount of energy relative to protein in the diet and available for utilization by the tissues (Hocquette et al., 2010), coupled with the changing nutritional requirements for energy relative to protein as the animal grows and matures (Freer et al., 2007). All these mechanisms would suggest lower total adiposity in pasture-fed animals. However, this was not

observed in this study and points to total energy balance as the key driver.

The results show that within postweaning nutritional systems that produce equivalent growth rates of steers, the period from approximately 8 to 14 mo of age does not represent an early window where grain feeding stimulates adiposity, either in the immediate or longer terms. The finding that rib fat depth was greater in the FS is generally consistent with the subcutaneous depot utilizing acetate as the major substrate for fatty acid synthesis and, hence, lipogenesis. Furthermore, the difference in the direction of the trends for effects of nutritional system on IMF in the semitendinosus and infraspinatus muscles supports some variation in substrate-specific utilization between fat depots. However, the overall lack of effect of substituting high-energy supplement for pasture on IMF content during the immediate postweaning period indicates that it did not enhance development and accumulation of intramuscular adipocytes. As in later stages of growth and development, and consistent with the findings of Meteer et al. (2013) and Nayananjalie et al. (2015), it is likely that total energy supply is more important for adipocyte development and/or adipogenesis within IMF during the immediate postweaning phase than are substrate-specific effects.

In conclusion, the results of the present study provide some further insights into diet-specific effects on adipogenesis and subsequent capacity to synthesize and deposit fat in different depots. Overall, however, they do not support the use of high-energy feed as a substitute for an equivalent amount of energy from pasture to support similar growth rates during the immediate postweaning period to enhance development of marbling. The findings provide a basis for further study of development of fat depots from weaning through to long feedlotting in cattle varying in their fat depot distributional characteristics and in the development of phenotypic prediction models.

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