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Effect of dietary restriction and compensatory growth on performance, carcass characteristics, and metabolic hormone concentrations in Angus and Belgian Blue steers

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ABSTRACT

Compensatory growth (**CG**) is the ability of an animal to undergo accelerated growth after a period of restricted feeding. However, there is a dearth of information in relation to the effect of genotype on CG response, thus the objective of this study was to evaluate CG response in two contrasting breed types, namely Aberdeen Angus (**AN**) and Belgian Blue (**BB**). Crossbred AN × Holstein-Friesian or BB × Holstein-Friesian steers were assigned to one of two treatment groups in a two (genotypes) × two (diets) factorial design. For 99 days, one group (11 AN and 12 BB) was offered a high energy control diet (**H-H**) whereas the second group (11 AN and 12 BB) was offered an energy restricted diet (**L-H**). At the end of the differential feeding period (99 days), both groups of animals were then offered a high energy control diet for a further 200 days. All animals were then slaughtered on day-299 of the study. During feed restriction, L-H had lower DM intake (**DMI**), had greater feed conversion ratio (**FCR**) and lower plasma concentrations of insulin, IGF-1, leptin, glucose, urea, betahydroxybutyrate and smaller *M. longissimus thoracis or lumborum* muscle and fat depths compared to H-H steers. During realimentation, there was no difference in DMI between diets; however, L-H had greater live weight gain compared to H-H steers. Overall, H-H consumed greater quantities on a DM basis, however, had a higher FCR compared to L-H steers. By the end of the realimentation period, there was no difference in plasma metabolite or hormone concentrations, linear body measurements, ultrasonically scanned fat depths, carcass conformation, dressing percentage or fat class between H-H and L-H steers. At slaughter, carcass weights were affected by diet with greater values for H-H compared to L-H steers. Genotype affected measures associated with body composition including pelvic width and both muscle and fat depths ($P < 0.05$). Overall, L-H had a CG (or recovery) index of 0.52 and did not make up for the loss of gains during the differential feeding period; however, *M. longissimus thoracis et lumborum*, a tissue of high economic value, recovered completely making it a target of interest for further investigation.

Implications

Compensatory growth is an accelerated growth displayed in cattle upon realimentation following a prior period of dietary restriction. However although widely utilised in beef production systems as a means to reduce feed costs, knowledge of the effect of varying breed type on compensatory growth response is lacking. Results from this study show that both Aberdeen Angus and Belgian Blue steers displayed compensatory growth following a moderate dietary restriction, however, body composition as a consequence of dietary restriction may be differentially altered dependent on breed type.

Introduction

In beef cattle production systems, feed costs account for approximately 75% of total variable costs (Kenny et al., 2018). Thus, strategies to reduce costs without compromising overall animal performance are of particular interest to the beef sector. Compensatory growth (**CG**) is the ability of an animal to undergo accelerated growth and enhanced efficiency upon realimentation

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following a prior period of restricted feeding (Hornick et al., 2000). Although this naturally occurring accelerated growth phenomenon has evolved naturally across many species, it has been extensively incorporated into animal production systems, particularly beef systems, whereby feed input costs may be reduced (Ashfield et al., 2014). This is particularly effective under pasture based production systems, whereby the exploitation of this biological phenomenon facilitates redistribution of feed supply from periods when feed is scarce and expensive (e.g. winter) to those when feed is less expensive and/or more plentiful (e.g. grased pasture in summer), while still maintaining overall production targets (Ashfield et al., 2014; Fitzsimons et al., 2017). Indeed, data have shown that clear savings in feed costs may be achieved through utilising CG (Ashfield et al., 2014).

However, although CG is employed worldwide, effective utilisation of the trait is dependent on a number of factors which may confound the resultant CG response. Reports in the published literature related to the underlying biology contributing to the accelerated growth response may be ambiguous and remain to be elucidated fully, with results typically confounded by experimental design (Lawrence and Fowler, 2002; Keogh et al., 2015a). Such conflicting results in the literature may impact successful and effective incorporation of CG into production systems. Factors impacting a successful CG response include both management factors, for example, the level or severity of dietary restriction imposed as well as the diet type offered during both restriction and realimentation phases as well as individual animal factors, including the age and stage of development of the animal, as well as the genotype and gender (Hornick et al., 2000; Lawrence and Fowler, 2002). Whilst there have been a number of studies focusing on the CG response in relation to management factors (Hornick et al., 1998a,b; Cabaraux et al., 2003; Keogh et al., 2015a,b), there is a dearth of information in relation to animal related factors. In particular there is limited information on variation in CG response between contrasting breed types, for example, breeds which differ in maturation rate (early versus late maturing breed type). As a period of dietary restriction may alter body composition (Keogh et al., 2015a), there is potential that breeds of different maturation rates may respond differently both to a period of dietary restriction and to the subsequent realimentation induced CG. Therefore, the objective of this study was to examine the response to differential diets of two genotypes, representing early and late maturing breed types and their potential to exhibit CG upon realimentation following a prior period of dietary restriction. Our study was focused on variation between Aberdeen Angus (**AN**) and Belgian Blue (**BB**) genotypes, due to the well documented differences in carcass conformation, muscle composition as well as maturation rates (Keane and Drennan, 2008; Dinh et al., 2010).

Material and methods

Animal model and management

Spring-born male progeny (n = 46) of Holstein-Friesian dams and sired through AI by either AN or BB bulls were identified and sourced from Irish commercial herds. After arrival at Grange Beef Research Centre, the calves were vaccinated against bovine respiratory syncytial virus, parainfluenza 3 virus and pasturella haemolytica using Bovipast RSP (Intervet, Schering-Plough Ltd., Wicklow, Ireland). Calves were also vaccinated against infectious bovine rhinotracheitis (Pfizer Animal Health, Cork, Ireland) as well as against the clostridial disease, Blackleg (*C. chauvoei;* Intervet, Schering-Plough Ltd., Wicklow, Ireland). The animals were treated for parasites using Closamectin (Norbrook Laboratories Ltd., Monaghan, Ireland). Within 1 month of arrival at Grange Beef Research Centre, the calves were castrated using the burdizzo method. All calves were subjected to a 3 month common feeding period of grass silage *ad libitum* plus 1 kg of concentrates per steer per day before commencing the study to acclimatise the animals to their environment, reduce latent influence of previous environment and provide recovery from castration. Mean age at the commencement of the study was 362 (SD 15.5) and 369 (SD 19.4) d for AN and BB steers, respectively, with mean weights of 295 (SD 30.0) and 287 (SD 48.6) kg for AN and BB groups, respectively. Within genotype, animals were blocked by weight and randomly assigned to one of two treatment groups in a two (genotypes) × two (diets) factorial design. For 99 days, one group (11 AN and 12 BB) was offered a high energy control diet (**H-H**) consisting of concentrates *ad libitum* (DM 825 g/kg, *in vitro* DM digestibility 862 g/kg, CP 120.9 g/kg, ash 43 g/kg, NDF 557 g/kg and ADF 351 g/kg) and 7 kg of grass silage per steer daily (DM 228 g/kg, *in vitro* DM digestibility 677 g/kg, CP 112 g/kg, ash 80 g/kg, pH 3.6, NDF 557 g/kg and ADF 351 g/kg) whereas the second group (11 AN and 12 BB) was offered an energy restricted diet (**L-H**) consisting of grass silage *ad libitum* plus 0.5 kg of concentrates per steer per day (chemical analysis as described above). This period was known as the differential feeding period. At the end of the differential feeding period, both groups of animals were then offered a total mixed ration consisting of grass silage:-concentrate ratio of 80:20 with the concentrate proportion increasing gradually over a 3 week period to H-H ration (*ad libitum* access to concentrate and 7 kg grass silage per steer per day). This period, which lasted 200 days, was known as the realimentation period, and all animals were slaughtered on day-299 of the study. Animals were individually fed in tie-up stalls during the differential feeding period and subsequently moved to individual slatted floor pens for the realimentation period. Fresh feed was offered daily and feed refusals were removed and weighed twice weekly. Animals were weighed on two consecutive days at the start of the study, at the end of the differential feeding period and again at slaughter. Additionally, throughout the study, animals were weighed at 2 week intervals. Weighing was at the same time each morning before fresh feed was offered.

Linear measurements and body composition

Linear body measurements (Campion et al., 2009a) were recorded on four separate occasions: start (day-0); end of differential feeding period (day-99); early in the realimentation period (day-131) and again before slaughter (day-299). Height at withers, chest depth, pelvic width, chest girth and back length were measured. These measurements were expressed relative to live weight on the day of measurement.

The steers were ultrasonically scanned five times throughout the study; start (day-0); middle of the differential feeding period (day-55); end of differential feeding period (day-99); early in the realimentation period (day-131) and again before slaughter (day-299). A Dynamic Imaging ultrasound scanner (Concept MCV Veterinary Ultrasound scanner with 3.5 MHz probe; Dynamic Imaging, Livingston, Scotland) was used to measure *M. longissimus thoracis or lumborum* depth at the third lumbar vertebra, and fat depth at the third lumbar vertebra, the 13th thoracic rib and the rump on their right side as described by Conroy et al. (2010).

Metabolic hormones and metabolites

For the analysis of plasma concentrates of IGF-1, insulin and leptin, blood samples were collected on four occasions: start (day-0), end of differential feeding period (day-99), early in the realimentation period (day-131), and again before slaughter (day-299). In addition, animals were blood sampled on seven occasions to determine plasma concentrations of the metabolites glucose, urea, betahydroxybutyrate (**BHB**) and non-esterified fatty

acids (**NEFAs**). Blood sampling times were as follows: start (day-0), middle of the differential feeding period (day-55), end of differential feeding period (day-99); during the realimentation period (day-131, day-233, day-273), and again before slaughter (day-299). Blood was collected into three (10 mL) lithium heparin and one (6 mL) sodium fluoride vacutainer tubes (Greiner Vacuette, Cruinn Diagnostics, Dublin, Ireland). Samples were centrifuged at 1 500*g* for 15 min at 4 °C. The plasma retrieved was separated in borosilicate glass scintillation vials and stored at −20 °C until further analysis. IGF-I concentrations in blood plasma were determined by radioimmunoassay after an acid–ethanol extraction procedure, as described by Spicer et al. (1988). Intra-assay CV for IGF-1 quantification were 10.8, 3.2 and 8.6% for low, medium, and high standards, respectively. Inter-assay CV for IGF-1 were 14.3, 12.7 and 13.6% for low, medium and high standards, respectively. Insulin concentrations were quantified by fluoroimmunoassay (AutoDELFIA, PerkinElmer Life and Analytical Sciences, Turku, Finland) and validated for bovine plasma (Ting et al., 2004). Intra-assay CV for insulin was 5.9, 13.4 and 7.2% for low, medium, and high standards, respectively. Inter-assay CV for insulin was 10.0, 8.8 and 9.9% for low, medium and high standards, respectively. Leptin analysis was carried out using a double antibody radioimmunoassay as described by Wylie et al. (2008). The mean intra-assay CV for leptin was 6.9 and 6.7% for high and low standards, respectively, while the mean inter-assay CV was 16.5 and 19.9% for high and low standards, respectively.

Carcass traits and non-carcass components

Animals were weighed the day before slaughter and again on the morning of slaughter. These weights were averaged to give final live weight at slaughter (**SW**). The steers were transported 130 km to Meadow Meats commercial slaughter facility in Rathdowney, Co. Laois, Ireland and all animals were slaughtered within 1 h of arrival.

After slaughter, cold carcass weight (**CW**; Hot CW × 0.98) was recorded and dressing percentage was calculated as a proportion of CW to SW. Carcass conformation and fat score were automatically recorded on a 15 point scale using video imaging analysis equipment (VBS2000, E + V, Oranienburg, Germany) as described by Hickey et al. (2007). Non-carcass components were weighed for each steer separately, namely the heart, lungs, gall bladder, liver, spleen, intestines (full), rumen excluding abomasum and omasum (full and empty), fore and hind feet, hide, kidneys, head, and perinephric-retroperitoneal fat. All and measurements were calculated relative to SW.

Linear carcass measurements (Campion et al., 2009a) were recorded at 3 h postslaughter on the right side of each carcass. Carcass length, leg length, chest depth, maximum leg width, and leg thickness (width of leg from the medial splitting surface of the symphysis pubis) were recorded. After 24 h at 4 °C, the right side of each carcass was quartered between the fifth and sixth ribs into a pistola hind quarter (without the flank) and a fore quarter that included the flank as described by Keane and Allen (1998). The pistola was separated by cutting between the 10th and 11th ribs. The *M. longissimus thoracis or lumborum* outline at the 10th rib was traced onto translucent paper and the area was subsequently measured using a digital planimeter (Placom KP-90 N, Sokkisha, Japan). The sixth to 10th rib joint (five-rib joint) was weighed and dissected into *M. longissimus thoracis et lumborum*, other muscle, muscle trim, total fat, and bone plus ligamentum nuchae/supraspinale.

Statistical analysis

Data collected from the study were checked for normality using the UNIVARIATE procedure in SAS. Where appropriate, data were transformed by raising to the power of λ using the TRANSREG procedure. Data were analysed using mixed model methodology (PROC MIXED, SAS). Within genotype, animals were blocked by weight to treatment. Block, genotype, diet (H-H or L-H) and their interaction were included as main effects and sire was included as a random effect in the statistical model. Where no interactions were observed, the data were reanalysed for main effects only. The Tukey critical difference test was performed to determine the existence of statistical differences between treatment mean values. For data with repeated measures (BW, live weight gain, blood metabolites and hormones, linear body measurements and muscle and fat scans), sample day was included as a repeated effect with an unstructured or compound symmetry covariance structure assumed among records within animal, as appropriate. The choice of residual covariance structure was based on the magnitude of the Akaike Information Criterion (lowest is better). To determine separation between genotype and dietary treatment groups, a principal component analysis was also undertaken using the PRINCOMP procedure in SAS.

Results

DM intake and feed conversion ratio

DM intake (**DMI**) and feed conversion ratio (**FCR**) as affected by both genotype and diet are presented in Table 1. A genotype × diet interaction ($P = 0.04$) was observed during the differential feeding period with AN/L-H consuming more silage on a DM basis compared to BB/L-H; however, this was not observed between AN/H-H and BB/H-H steers. As expected, there was a diet effect ($P < 0.0001$) for both silage and total DMI with L-H consuming more silage but less total DM compared to H-H steers during the differential feeding period. Interestingly, during the feed realimentation period, there was no difference ($P > 0.05$) in total DMI between groups. Overall, for the entire period, there was no effect of genotype ($P > 0.05$) on DMI; however, H-H consumed more feed on a DM basis compared to L-H steers ($P < 0.0001$). FCR was not affected by genotype ($P > 0.05$) at any time throughout the study. There was an effect of diet with L-H steers having a greater FCR ($P < 0.05$) during the differential feeding period; however, during the realimentation period, the opposite was true with H-H having a greater FCR ($P < 0.001$). Interestingly, FCR was lower ($P < 0.05$) for the entire period in L-H compared to H-H steers.

Live weight and live weight gain

Live weight changes and live weight gains as affected by both genotype and diet are reported in Table 2. A genotype × dietary period interaction ($P > 0.05$) was not observed for live weight with both genotypes expressing similar live weights throughout the study. There was no difference ($P > 0.05$) in live weight between the two dietary groups between diets observed at the start (day-0); however, H-H was heavier compared to L-H steers at the end of the differential feeding period (day-199; $P < 0.001$) which was sustained until slaughter (day-299; $P < 0.05$). There was no effect of genotype on live weight gain for any period throughout the study with the exception of between day-131 and day-195 (middle of the realimentation period) when BB had greater gains compared to AN steers ($P = 0.001$). There was an effect of diet during the differential feeding period (day-0 to 99; $P < 0.001$) with live weight gains greater in H-H compared to L-H steers; however, from the end of the differential feeding period (day-99) to day-195 in the realimentation period, live weight gain was greater ($P < 0.001$) for the L-H steers compared to the H-H animals. However, after this, no difference ($P > 0.05$) in live weight gain between dietary treatment groups was observed for the remainder of the study.

Table 1
Effect of genotype and diet on total DM intake and feed conversion ratio in Aberdeen Angus (AN) and Belgian Blue (BB) steers.

	Genotype (G)			Diet[1] (D)			*P*-value	
Trait	AN	BB	SEM	H-H	L-H	SEM	G	D
DM intake, kg/d								
Differential feeding period, days 0–99								
Silage[2]	3.07	3.04	0.021	2.14	3.96	0.026	0.09	<0.0001
Total	6.92	6.96	0.061	9.48	4.41	0.085	0.99	<0.0001
Early realimentation period, days 99–131								
Total	10.27	10.32	0.092	10.34	10.25	0.091	0.99	0.89
Final period to slaughter, days 131–253								
Total	10.24	10.21	0.095	10.12	10.33	0.092	0.99	0.20
Entire period, days 0–253								
Total	8.91	8.92	0.073	9.93	7.89	0.195	0.82	<0.0001
Feed conversion ratio[3]								
Differential feeding period, days 0–99	7.44	6.99	0.586	6.51	7.92	0.561	0.45	0.02
Early realimentation period, days 99–131	6.92	7.42	0.627	8.72	5.63	0.614	0.44	<0.0001
Final period to slaughter, days 131–253	6.29	5.78	0.342	6.45	5.61	0.338	0.14	0.01
Entire period, days 0–253	6.44	6.15	0.181	6.65	5.94	0.187	0.13	0.0005

[1] H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.
[2] There was a Genotype × Diet interaction ($P = 0.04$) with values for AN/H-H, AN/L-H, BB/H-H and BB/L-H 2.14[a], 3.99[b], 2.15[a] and 3.93[b] kg/day, respectively (superscripts indicate significant difference between values)
[3] Live weight gain ÷ total DM intake.

Table 2
Effect of genotype and diet on mean live weight and live weight gain in Aberdeen Angus (AN) and Belgian Blue (BB) steers.

	Genotype (G)			Diet[1] (D)			*P*-value	
Trait	AN	BB	SEM	H-H	L-H	SEM	G	D
Live weight, kg								
Start, day-0	307	288	7.0	296	298	6.9	0.79	1.00
End of differential feeding period, day-99	404	390	7.0	438	356	6.9	0.99	<0.0001
Realimentation, day-131	452	438	7.0	474	416	6.9	0.99	<0.0001
Slaughter, day-299	655	644	7.1	669	630	6.9	1.00	0.04
Live weight gain, kg/d								
Differential feeding period, days 0–99	1.06	1.12	0.052	1.55	0.63	0.050	0.28	<0.0001
Realimentation period, days 99–131	1.50	1.50	0.097	1.26	1.74	0.093	0.98	<0.0001
Realimentation period, days 131–195	1.65	1.90	0.070	1.63	1.91	0.060	0.0007	0.0001
Realimentation period, days 195–253	1.34	1.33	0.090	1.34	1.33	0.090	0.89	0.87
Realimentation period, days 253–299	0.91	0.64	0.180	0.84	0.71	0.170	0.14	0.47
Entire period, days 0–299	1.25	1.26	0.038	1.33	1.18	0.036	0.81	0.0004

[1] H-H = *ad libitum* access to feed; L-H = restricted access to feed for 99 days followed by *ad libitum* access to feed until slaughter.

Linear measurements and body composition

The effect of genotype and diet on linear measurements and ultrasonically scanned muscle and fat depths are reported in Table 3. No genotype × dietary interactions ($P > 0.05$) were evident for any linear measurements. However, there was evidence for an effect of genotype on pelvic width, which was greater in BB at the end of the differential feeding period ($P < 0.05$), as well as on day-131 of realimentation ($P = 0.06$). There was also an effect ($P < 0.05$) of dietary intake on all linear measurements recorded, whereby measurements were greater in L-H compared to H-H at the end of the differential feeding period as well as during realimentation on day-131. There were no genotype × diet interactions observed for muscle or fat depth recordings throughout the trial ($P > 0.05$). A genotype effect was apparent for both muscle and fat depths, with muscle depth greater in BB on days 131 and 299, whilst fat depth was greater in AN from mid-way of the differential feeding period through to slaughter on day-299 ($P < 0.05$). Additionally, diet effects were also evident during both the mid-point and end of the differential feeding period ($P < 0.05$) for muscle depth, and at the end of the differential feeding period for fat depth, with depths being greater in H-H steers.

Metabolic hormones and metabolites

Genotype × diet interactions were not detected for any of the plasma analytes measured ($P > 0.05$). Concentrations of IGF-1, leptin and insulin were greater ($P < 0.001$) in H-H steers compared to L-H on day-99 (end of differential feeding), but were not different for each other time-point analysed. Metabolic hormone profiles for the duration of the trial are presented in Fig. 1. There was no effect of genotype on either IGF-1 or insulin concentrations, with similar concentrations for AN and BB steers throughout the trial. However, there was an effect of genotype on leptin concentrations ($P < 0.05$), whereby leptin concentrations were greater in AN at slaughter (day-299) with no difference apparent between AN and BB earlier in the trial.

Metabolite profiles for the duration of the trial are presented in Fig. 2. A genotype effect was evident for plasma urea concentrations ($P < 0.01$) with AN having greater concentrations compared to BB (5.46 mmol/l vs. 4.34 mmol/l, respectively) on day-233 of the study, but similar values ($P > 0.05$) at all other times throughout the study. There was no effect ($P > 0.05$) of genotype on glucose, BHB or NEFA concentrations. Diet affected glucose concentrations, with values greater in H-H at the mid-point and end of the differential feeding period, subsequently greater in L-H on day-131 ($P < 0.01$), with all other time-points similar between H-H and L-H groups ($P > 0.05$). On days 55 and 131 of the trial, blood urea concentrations were greater ($P < 0.05$) in H-H steers, with no significant difference ($P > 0.05$) in urea concentration between H-H and L-H groups for the remaining sampling time-points. BHB concentrations were greater ($P < 0.05$) in H-H steers on days 55, 99 and 131 of the trial with no difference evident across

Table 3
Effect of genotype and diet on linear body measurements, muscle and fat depth in Aberdeen Angus (AN) and Belgian Blue (BB) steers.

	Genotype (G)			Diet[1] (D)			*P*-value	
Trait	AN	BB	SEM	H-H	L-H	SEM	G	D
Linear body measurements								
Height at withers, mm/kg								
Start, day-0	3.69	3.86	0.102	3.73	3.82	0.101	0.76	0.99
End of DFP[2], day-99	3.03	3.11	0.056	2.79	3.34	0.055	0.81	<0.0001
Realimentation, day-131	2.65	2.69	0.050	2.55	2.79	0.049	0.97	<0.0001
Slaughter, day-299	2.01	2.06	0.039	1.98	2.09	0.038	0.85	0.08
Chest girth, mm/kg								
Start, day-0	4.78	4.72	0.082	4.75	4.75	0.081	0.99	1.00
End of DFP[2], day-99	4.34	4.39	0.059	4.13	4.59	0.059	0.99	<0.0001
Realimentation, day-131	3.91	3.90	0.053	3.79	4.02	0.052	1.00	0.0014
Slaughter, day-299	3.29	3.24	0.103	3.26	3.27	0.102	0.99	1.00
Length of back, mm/kg								
Start, day-0	3.27	3.45	0.063	3.38	3.31	0.063	0.22	0.94
End of DFP[2], day-99	2.71	2.72	0.044	2.50	2.93	0.044	1.00	<0.0001
Realimentation, day-131	2.27	2.33	0.045	2.23	2.37	0.044	0.94	0.03
Slaughter, day-299	1.81	1.88	0.048	1.78	1.90	0.048	0.75	0.21
Chest depth, mm/kg								
Start, day-0	1.85	1.93	0.039	1.87	1.90	0.039	0.47	0.99
End of DFP[2], day-99	1.56	1.59	0.026	1.47	1.69	0.026	0.94	<0.0001
Realimentation, day-131	1.37	1.39	0.022	1.33	1.43	0.022	0.93	<0.0001
Slaughter, day-299	1.10	1.13	0.021	1.10	1.14	0.021	0.88	0.63
Pelvic width, mm/kg								
Start, day-0	1.29	1.44	0.079	1.43	1.29	0.079	0.63	0.71
End of DFP[2], day-99	1.08	1.13	0.015	1.04	1.17	0.015	0.01	<0.0001
Realimentation, day-131	0.94	0.99	0.018	0.93	1.01	0.017	0.06	0.0008
Slaughter, day-299	0.82	0.85	0.049	0.82	0.84	0.023	0.21	0.98
Ultrasound measurements								
Muscle depth[3], mm								
Start, day-0	44.2	46.7	1.378	45.90	45.01	1.317	0.78	0.99
Middle of DFP[2], day-55	49.5	51.9	1.389	53.12	48.25	1.367	0.81	0.02
End of DFP[2], day-99	50.9	54.2	1.397	56.02	49.05	1.365	0.38	<0.0001
Realimentation, day-131	55.6	60.4	1.401	59.04	57.04	1.377	0.03	0.90
Slaughter, day-299	58.7	67.1	1.417	62.49	63.33	1.393	<0.0001	0.99
Fat Depth[4], mm								
Start, day-0	0.79	0.61	0.065	0.74	0.67	0.065	0.15	0.97
Middle of DFP[2], day-55	1.06	0.70	0.085	0.98	0.79	0.085	0.0013	0.48
End of DFP[2], day-99	1.41	0.79	0.136	1.53	0.67	0.136	0.0004	<0.0001
Realimentation, day-131	3.51	2.51	0.287	3.42	2.60	0.286	0.021	0.12
Slaughter, day-299	7.41	5.14	0.481	6.77	5.78	0.48	0.0002	0.55

[1] H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.
[2] DFP = Differential feeding period.
[3] *M. longissimus thoracis et lumborum*.
[4] Average 13th rib and lumber fat measurements.

other time-points. There was no effect of dietary treatment on NEFA concentrations.

Carcass traits and non-carcass components

The effect of genotype and diet on carcass traits, 5-rib joint weight, *M. longissimus thoracis et lumborum* area, rib joint dissection and non-carcass components are summarised in Table 4. No genotype × diet interaction ($P > 0.05$) was recorded for any of these traits. Genotype affected ($P < 0.05$) cold carcass weight, dressing percentage, carcass conformation, and fat score, with values greater in BB for all traits with the exception of fat score which was greater in AN steers. *M. longissimus thoracis et lumborum* total area was greater ($P < 0.01$) in BB, similarly *M. longissimus thoracis et lumborum* and total muscle rib joint were both greater in BB compared to AN ($P < 0.001$). Conversely though, fat rib joint composition was greater in AN compared to BB ($P < 0.001$). Dietary treatment also affected carcass composition, whereby cold carcass weight, perinephric-retroperitoneal fat, five-rib joint and fat rib joint composition were all greater ($P < 0.05$) in H-H steers compared to L-H. There was also a tendency for total muscle in rib joint composition to be greater in L-H steers ($P = 0.06$). Linear carcass measurements were affected by both genotype and dietary treatment, however, there was no evidence for an interaction in any of the measurements recorded. Carcass length, depth and the leg length were all greater in AN compared to BB ($P < 0.05$). Whilst all linear carcass measurements (carcass length and depth; leg width, length and thickness) were greater in L-H treatment compared to H-H ($P < 0.05$).

The weight of the intestines, hide and head were all significantly different ($P < 0.05$) between AN and BB groups (Table 4). Intestinal weight and hide weight were both heavier in AN, whereas head weight was greater in BB steers. The dietary treatment also affected non-carcass composition including the rumen (both full and empty) and head which were all heavier in L-H group ($P < 0.05$). Similarly, kidney weight also tended towards significance between the two dietary groups ($P = 0.09$). All remaining non-carcass component weights were unaffected by both genotype and dietary treatment.

Principal component analysis

Principal component analysis revealed that 88.6% of the variance was explained within the first two principal components. The most important variables or loadings for the first principal component were IGF-1, cold carcass weight and hot carcass

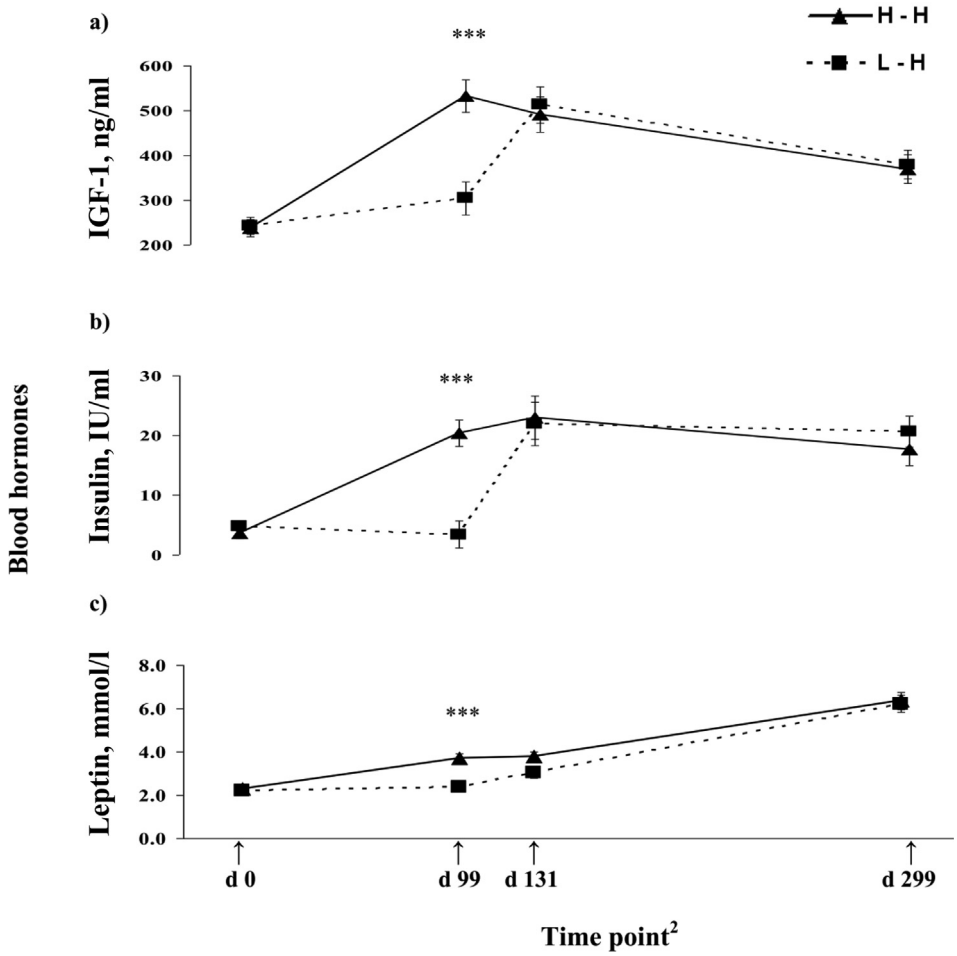

Fig. 1. Effect of diet[1] on plasma concentrations of metabolic hormones in steers. [1]H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter. [2]day-0 = Start; day-99 = end of differential feeding period; day-131 = realimentation period; day-299 = slaughter. ***$P < 001$.

weight, whilst total muscle, chest circumference, insulin and hide comprised the most important variables in the second principal component. Evidence for separation amongst data based on genotype was apparent across component 2 (Fig. 3), however, the same was not observed for the effect of diet.

Discussion

The objective of this study was to examine the response to differential diets of two genotypes, representing early and late maturing breed types, and their potential to exhibit CG after feed restriction. The AN and BB genotypes were selected because of their documented differences in carcass conformation, muscle composition and maturation rates (early vs. late; Keane and Drennan, 2008; Dinh et al., 2010). This study offers revealing insights into the CG phenomena in cattle while further elucidating the mechanisms regulating its control.

DM intake and feed conversion ratio

Although AN consumed greater quantities of silage compared to BB, when allocated to the L-H dietary regimen, this difference was not observed between the genotypes maintained on a high plane of nutrition. However, animals in the H-H group were offered concentrates *ad libitum* with silage offered restrictively to ensure higher consumption of concentrations and therefore this genotype effect may not have been observed. Additionally, the tendency for AN to consume more forage on a DM basis compared to BB was not observed by Campion et al. (2009a) or Keane et al. (2011). Sainz et al. (1995) and Keogh et al. (2015a) both reported that *ad libitum* feeding following feed restriction in beef steers and bulls, respectively, resulted in greater feed intakes during the realimentation period. However, this was not observed in the current study, with no difference in DMI between diets during the realimentation period. This is however consistent with Hornick et al. (1998a) who reported no difference in DMI during feed realimentation in BB double muscled bulls following feed restriction, compared to their contemporaries maintained on a high plane of nutrition. Although no difference was observed in feed intakes between diets during the differential feeding period, live weight gains were increased in L-H compared to H-H steers which resulted in a lower FCR. During feed realimentation, L-H steers were more feed efficient than during the differential feeding period and compared to H-H steers during both the differential feeding and realimentation periods. An overall improved efficiency has been consistently observed in CG models (Yambayamba et al., 1996a; Keogh et al., 2015a; Fitzsimons et al., 2017).

Live weight and live weight gain

Greater mature live weight and live weight gain in late maturing compared to early maturing cattle breeds have been reported in some (Coleman and Evans, 1986) but not all (Cuvelier et al., 2006; Albertí et al., 2008) studies, with both traits dependent on

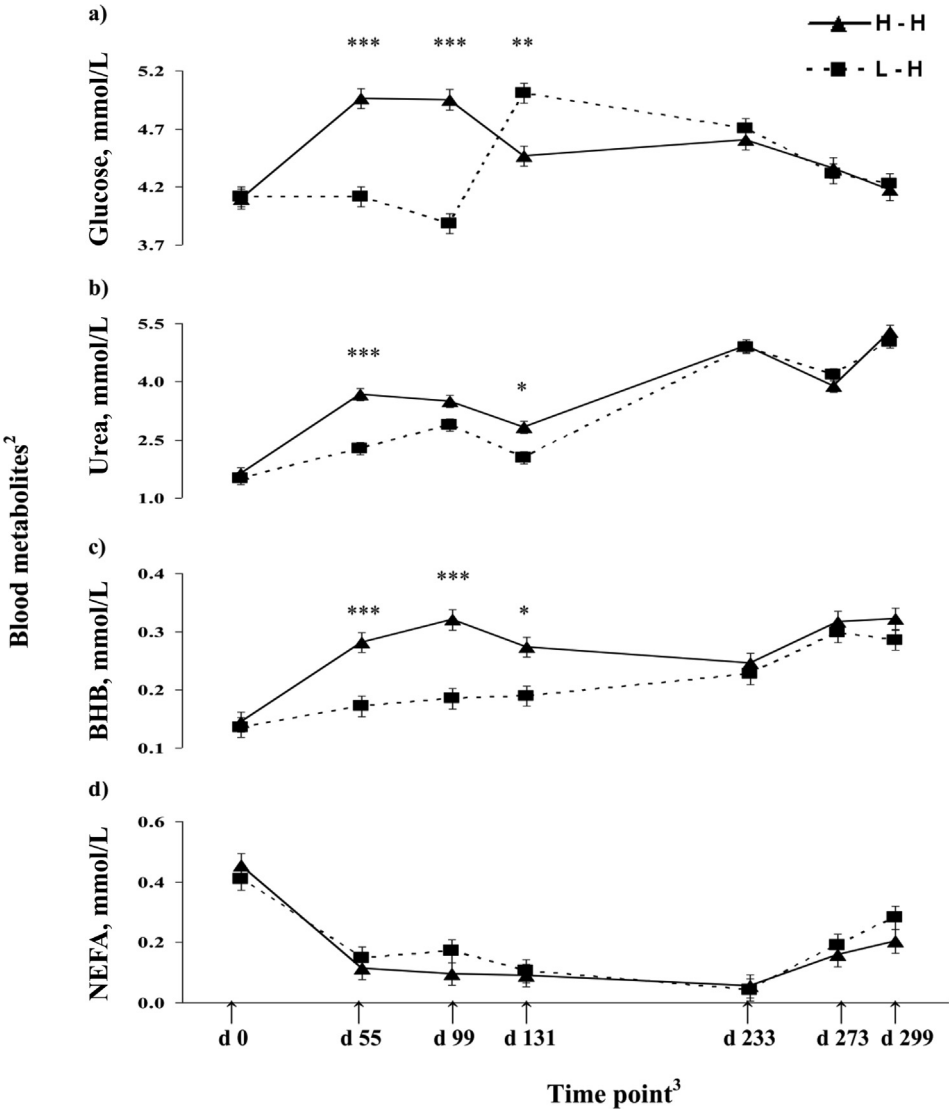

Fig. 2. Effect of diet[1] on plasma concentrations of blood metabolites in steers. *P < 0.05, **P < 0.01, ***P < 0.001. [1]H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter. [2]BHB = Betahydroxybutyrate, NEFA = non-esterified fatty acids. [3]day-0 = Start; day-55 = middle of differential feeding period; day-99 = end of differential feeding period; day-131 = realimentation period; day-233 = realimentation period; day-273 = realimentation period; day-299 = slaughter.

feeding intensity and age (Coleman and Evans, 1986). In the current study, all steers were crossbred animals, born to Holstein-Friesian cows and therefore the degree of expected difference in live weight was diluted as reflected by both genotypes having similar live weights throughout the trial. In fact, both Campion et al. (2009a) and Keane et al. (2011) reported no effect of genotype on daily gains for crossbred AN and BB steers supporting our findings. Both AN and BB steers responded similarly to feed restriction and feed realimentation with a difference only observed in live weight gains during the middle of the realimentation period (day-131 to day-195 of the study). A similar study involving the response of early and late maturing breeds to differential feeding patterns followed by realimentation to a high energy diet was undertaken by Coleman and Evans (1986) who reported CG in spring-born Charolais steers; however, CG was not evident in Angus steers during the finishing period. This may be due to the lighter weight of the Angus steers at the start of that study and also the differential feeding period being too long, as Hornick et al. (2000) state that CG is enhanced when the duration of the growth restriction is short. In our study, CG was observed early into the realimentation period in L-H compared to H-H steers. This is consistent with the literature which states that CG is at its greatest between day 30 and day 60 after feed realimentation and adaptation to a new diet (for review see Hornick et al., 2000). Although compensatory gain was observed in the L-H animals, it did not make up for the loss in potential gain during the differential feeding period. This may be due to the level of feed restriction not being severe enough, as Neel et al. (2007) reported greater compensatory gains during the finishing period in crossbred steers growing at a live weight gain of 0.23 kg/d compared to steers growing at 0.45 and 0.68 kg/d during the restriction period. However, the realimentation period was sufficiently long to ensure that CG was complete and that all animals were adequately finished for market, when slaughtered. The imposed dietary treatments in the current study resulted in a compensatory (or recovery) index (Hornick et al., 2000) of 52%. However, results for this index vary across different experiments, for example Yambayamba et al. (1996a) observed a 100% recovery in beef heifers following 92 days of maintenance feeding, whereas Keogh et al. (2015a) reported an index of 48% in just 55 days of realimentation, following 125 days of moderate dietary restriction. According to Hornick et al. (2000), the CG index typically lies between 50% and 100%. However, the compensatory

Table 4
Effect of genotype and diet on slaughter traits, 5-rib joint weight, *M. longissimus thoracis et lumborum* area, rib joint dissection and selected non-carcass components and carcass measurements in Aberdeen Angus (AN) and Belgian Blue (BB) steers.

	Genotype (G)			Diet[1] (D)			*P*-value	
Trait	AN	BB	SEM	H-H	L-H	SEM	G	D
Cold carcass weight, kg	354	369	5.9	373	350	5.5	0.02	0.0003
Dressing percentage,%	52.7	56.6	0.41	54.7	54.6	0.39	<0.0001	0.75
Carcass conformation[2]	7.25	9.08	0.411	8.33	8.02	0.402	<0.0001	0.44
Fat covering[3]	10.39	7.96	0.478	9.59	8.75	0.466	<0.0001	0.08
Perinephric-retroperitoneal fat, kg	11.69	11.41	0.798	12.45	10.65	0.778	0.72	0.03
Perinephric-retroperitoneal fat[4], g/kg	34.24	31.20	2.246	34.24	31.20	2.191	0.18	0.17
5-rib joint, kg	8.39	8.58	0.232	8.91	8.06	0.219	0.42	0.0006
M. longissimus area[4], cm^2/kg	0.24	0.28	0.012	0.25	0.27	0.012	0.004	0.29
Rib joint composition[5], g/kg								
M. longissimus	226.82	275.30	10.869	245.52	256.60	10.590	<0.0001	0.31
Other muscle	278.12	284.49	14.205	271.83	290.78	13.610	0.66	0.18
Muscle trim	76.48	91.10	8.160	86.74	80.85	7.957	0.08	0.47
Bone and other tissue	236.89	236.31	5.811	232.62	240.58	5.535	0.92	0.16
Fat	185.70	115.84	13.070	166.59	134.96	12.740	<0.0001	0.02
Total muscle	569.64	641.95	11.866	594.41	617.18	11.570	<0.0001	0.06
Non-carcass components[6]								
Heart, g/kg	4.27	4.05	0.167	4.03	4.28	0.163	0.21	0.13
Lungs, g/kg	11.48	11.01	0.551	11.11	11.38	0.529	0.40	0.61
Gall bladder, g/kg	1.14	1.16	0.088	1.14	1.16	0.088	0.75	0.74
Liver, g/kg	10.56	10.58	0.383	10.45	10.69	0.373	0.95	0.53
Spleen, g/kg	2.00	1.70	0.199	1.96	1.74	0.169	0.15	0.21
Intestines, g/kg	41.76	38.54	1.330	40.63	39.67	1.290	0.02	0.46
Rumen full, g/kg	58.41	54.39	2.627	53.88	58.90	2.468	0.14	0.05
Rumen empty, g/kg	17.44	16.66	0.637	16.34	17.75	0.622	0.23	0.03
Fore feet, g/kg	9.21	9.61	0.263	9.34	9.48	0.257	0.13	0.61
Hind feet, g/kg	9.77	9.94	0.234	9.68	10.03	0.222	0.48	0.13
Hide, g/kg	96.77	81.55	1.865	88.47	89.85	1.818	<0.0001	0.45
Kidney, g/kg	1.98	1.99	0.059	1.93	2.03	0.058	0.85	0.09
Head, g/kg	28.95	30.23	0.548	28.94	30.24	0.534	0.03	0.02
Linear carcass measurements[6]								
Length of carcass, mm/kg	3.84	3.64	0.068	3.65	3.82	0.064	0.006	0.01
Carcass depth, mm/kg	1.39	1.32	0.030	1.31	1.40	0.029	0.04	0.004
Leg width, mm/kg	1.22	1.21	0.023	1.17	1.25	0.022	0.75	0.001
Leg thickness, mm/kg	0.83	0.82	0.014	0.80	0.84	0.014	0.49	0.005
Leg length, mm/kg	2.07	1.98	0.038	1.97	2.08	0.036	0.03	0.006

[1] H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.
[2] Scaled 1 (poorest) to 15 (best).
[3] Scaled 1 (leanest) to 15 (fattest).
[4] Expressed per kilogram carcass weight.
[5] Expressed per kilogram of total 5-rib joint weight.
[6] Expressed per kilogram slaughter weight.

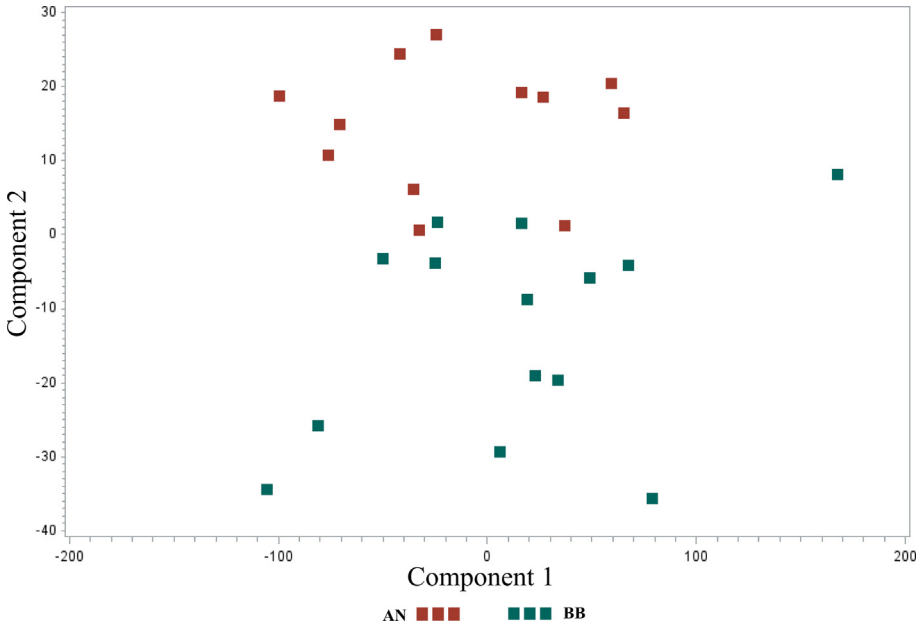

Fig. 3. Plot of the first two principal component loading vectors based on separation of Aberdeen Angus (AN) and Belgian Blue (BB) cattle by genotype.

index may be confounded by a number of factors including the diet type offered during restricted and realimentation phases, the level of the imposed dietary restriction as well as additional animal factors including the age of the animal, gender and genotype (Hornick et al., 2000; Lawrence and Fowler, 2002).

Linear body measurements and ultrasonically scanned muscle and fat depth

Campion et al. (2009a) reported an effect of genotype on chest girth, back length and chest depth with BB having lower scaled measurements throughout their lifetime compared to AN steers. In the current study, and contradictory to those findings, no difference was observed between genotypes for chest girth, back length and chest depth. According to Albertí et al. (2008), a narrow pelvis indicates slow skeletal development and low muscularity. This observation in respect of muscling is confirmed in the present study in which AN had a relatively smaller pelvic width than BB at the end of the differential feeding period (day-99) and early in the realimentation period (day-131) in addition to a lower *M. longissimus thoracis et lumborum* depth, smaller *M. longissimus thoracis et lumborum* area and a lower proportion of total muscle in the five-rib joint. By slaughter, the differences in scaled body measurements between diets were absent which is consistent with studies involving sheep (Kamalzadeh et al., 1998). As no genotype × diet interaction existed for linear body measurements at slaughter, it would appear that feed restriction followed by CG has no latent effects on skeletal development. Scanned *M. longissimus thoracis et lumborum* depth was greater for BB animals from early in the realimentation period up until slaughter, which reflects the well documented greater muscularity and better carcass conformation of this breed (Hickey et al., 2007; Keane and Moloney, 2010; Keane et al., 2011). Ultrasonically scanned *M. longissimus thoracis et lumborum* depth was greater as expected in H-H group during the differential feeding period compared to L-H animals. However, as L-H experienced CG, this difference in muscle depth between dietary groups disappeared over time with no difference in scanned *M. longissimus thoracis et lumborum* depth between diets at slaughter. This supports the findings of Schoonmaker et al. (2004) who also reported a difference in ultrasonically scanned muscle depth between steers offered different planes of nutrition but no difference in ultrasonically scanned muscle depth at slaughter after a period of feed realimentation. Importantly, it can be concluded that a CG-based feeding regime, like that employed here, has no negative effect on the economically important *M. longissimus thoracis et lumborum.*

The lower fat depth measurement for BB animals compared with AN was expected as late maturing breeds, and especially BB animals deposit less fat compared to early maturing beef breeds when compared at the same age or stage of maturity (Sadkowski et al., 2009). Greater fat depth was observed for H-H at the end of the differential feeding period (day-99) compared to L-H steers which supports the findings of Vasconcelos et al. (2009) who also detected greater ultrasonically scanned subcutaneous fat depths in steers offered a high energy compared to low energy ration. However, it is noteworthy that although both groups were offered the same diet during the realimentation period, the greater daily gain of L-H was accompanied by increased fat deposition with the result that by slaughter the difference in fat depth was no longer evident. Again, this was also observed by Vasconcelos et al. (2009) in that scanned fat depths were similar for steers offered a low compared to a high energy ration before the finishing period. Thus, it appears that the degree of feed restriction applied here facilitated CG in both *M. longissimus thoracis or lumborum* and subcutaneous fat.

Metabolic hormones and metabolites

Through interaction with IGF receptors, circulating IGF-1 is critical in regulating postnatal growth, development and differentiation of skeletal muscle (Duan and Xu, 2005). Yambayamba et al. (1996b) reported a reduction in circulating levels of IGF-1 in heifers during a dietary restriction period with IGF-1 concentrations rising to the same level as control animals upon realimentation to a greater energy ration. A similar outcome was observed in the current study with L-H steers exhibiting lower plasma levels of IGF-1 during the restricted period. Upon realimentation, however, plasma concentrations of IGF-1 in L-H rose to, but did not exceed those of H-H animals, suggesting that CG is not a direct consequence of elevated systemic availability of IGF-1. A similar trend was also reported by Keogh et al. (2015a) in Holstein-Friesian bulls undergoing CG. However, in our study, although L-H did not achieve IGF-1 concentrations greater than H-H animals, local production of IGF-1 within tissues or variation in expression levels of key genes in the somatotropic axis, for example IGF-1 receptors, may have induced tissue centred CG and therefore this warrants further investigation. Indeed, the increased IGF-1 concentrations in L-H cattle during CG may have contributed to the greater *M. longissimus thoracis et lumborum* area evident in these cattle by the end of the trial.

In ruminants, the absorption of amino acids and volatile fatty acids after feeding triggers the secretion of insulin from the pancreas (de Jong,1982). Insulin stimulates facilitative glucose transport activity in skeletal muscle and adipocytes (Sasaki, 2002). Both Keogh et al. (2015b) and Yambayamba et al. (1996b) reported that insulin concentrations decreased in cattle offered a restricted ration, before increasing to similar concentrations of control animals during the realimentation period. A comparable trend was observed in the current study with no difference in insulin concentrations evident between dietary groups by day-131 of the study, 32 days postcommencement of realimentation. The greater intake of energy and protein of H-H animals during the differential feeding period resulted in greater plasma glucose and potentially greater portal plasma amino acid and therefore greater concentrations of insulin (Hornick et al., 1998b). In the L-H steers, the increase in insulin concentrations during the realimentation period may be associated with the consumption of the greater energy ration. Whereas glucose declined linearly during the realimentation period, insulin concentrations remained high during this period and were maintained through to slaughter. Indeed, the increased glucose and insulin concentrations in L-H cattle during CG may have contributed to the greater muscle content in these cattle by the end of the trial. Additionally, although insulin promotes lipogenesis and inhibits lipolysis (Beeby et al., 1988), and differences in fat deposition were apparent between AN and BB genotypes, a genotype effect was not observed for insulin concentrations in the current study, which may have been due to the lack of difference in DMI between genotypes throughout the study.

In ruminants, research has shown a positive correlation between circulating concentrations of leptin and fat accumulation (Geary et al., 2003). The results in the current study support this statement in that leptin concentrations were lower in L-H animals at the end of restriction which corresponds with lower ultrasonically scanned fat depths. Following realimentation, leptin concentrations rose to similar values as H-H which coincided with increases in scanned fat depths. However, leptin concentrations did not correspond with fat reserves across genotype in that AN had greater scanned fat depths early into the study, however, a difference in leptin concentrations was only noted at slaughter and consequently this warrants further investigation.

Reduced plasma concentrations of glucose for L-H compared to H-H steers during the differential feeding period was expected due

to the lower availability of substrates in the diet. Consistent with our results, Yambayamba et al. (1996b), Hornick et al. (1998b) and Keogh et al. (2015b) all reported lower blood glucose concentrations in restricted cattle compared to those offered a high energy ration. It is unclear why glucose concentrations dropped in the H-H steers at day-131 of the study, 32 days postcommencement of realimentation. Perhaps, the switch to a total mixed ration diet consisting of greater proportions of grass silage compared to concentrates for the first three weeks of the realimentation period may have had some residual effects on glucose concentrations at this time. Similarly, Thorp et al. (1999) and Cummins et al. (2009) both reported that animals offered a silage-based diet had both lower glucose and BHB concentrations, the latter of which was also lower in the current study during dietary restriction. Following realimentation, glucose concentrations in L-H increased considerably with values greater than H-H steers during this period. In fact, concentrations were equal to values for the H-H steers during the differential feeding period. Similarly, other studies (Yambayamba et al., 1996b; Hornick et al., 1998b; Keogh et al., 2015b) all reported that plasma glucose levels rose in cattle during similar realimentation periods. As glucose concentrations in L-H never exceeded values observed for H-H animals during the differential feeding period, it appears that greater systemic availability of glucose is not a major driver of CG; however, greater utilisation potential at a local tissue level must be considered and warrants further investigation.

Both Yambayamba et al. (1996b) and Keogh et al. (2015b) reported a decrease in urea concentrations during feed restriction and in the current study, L-H animals had greater urea concentrations during the differential feeding period, whilst a period of dietary restriction has resulted in no difference in blood urea nitrogen in other studies (Ellenberger et al., 1989; Fiems et al., 2007). The greater urea concentrations observed for L-H in the current study may be attributed to the difference in both forage and concentrate intake for the two groups during the differential feeding period, with L-H consuming more rumen degradable protein in the form of greater grass silage intake. A similar lack of agreement across studies is also apparent for NEFA concentrations which were unaffected by diet in the current study. However, other studies have reported an increase in NEFA concentrations during a period of dietary restriction (Yambayamba et al., 1996b; Keogh et al., 2015b). In the current study, animals were in a positive energy balance and not metabolising body tissue. Therefore, NEFA concentrations were not altered by genotype or diet. Overall, AN had greater urea concentrations compared to BB animals throughout the trial. Campion et al. (2009b) similarly observed greater systemic levels of urea in crossbred AN compared to BB steers at slaughter. In addition, Beeby et al. (1988) reported greater urea concentrations in early maturing steers compared to late maturing. The authors attributed this result to the early maturing steers requiring less of their protein intake for muscle growth with the excess being deaminated.

Carcass traits and non-carcass components

As expected, BB had greater CW compared to AN, which was a contribution of their greater SW and greater dressing percentage. Keane and Moloney (2010) reported a similar result with crossbred BB steers having greater carcass weights and dressing percentages compared to AN animals. Although compensatory gain was evident in the L-H animals, it did not make up for the initial loss of potential gain during the differential feeding period, with an average difference between H-H and L-H of 40 kg and 23 kg in SW and CW, respectively. The absence of a difference in dressing percentage between diets was surprising as dressing percentage generally increases with increasing weight (Patterson et al., 1994). This lack of a difference, in the current study, between diets suggests that mild feed restriction followed by CG does not affect dressing percentage in steers after 200 days of feed realimentation. The superior carcass conformation of BB compared with AN agrees with many reports in the literature (Keane and Drennan, 2008; Campion et al., 2009a; Keane and Moloney, 2010). Due to the association of carcass conformation and carcass weight (Keane et al., 2006), the absence of a difference between the two diets was surprising as carcass weight was heavier for H-H compared to L-H. Schiavon et al. (2010) reported that diet before slaughter had no effect on conformation scores as CG was evident in their study. In addition, Keane (2010) reported no difference in carcass conformation scores in steers, with a live weight of 620 kg, following differential diets before slaughter. Thus, it may be concluded that a period of mild feed restriction followed by a sufficient period of CG does not affect carcass conformation in cattle of either early or late maturing genotypes.

As BB is a late maturing breed type which accumulates fat more slowly and muscle more rapidly compared to their early maturing counterparts (Campion et al., 2009a,b; Sadkowski et al., 2009; Keane, 2010), and especially as BB in particular has low carcass fat, the difference in fat cover was not surprising. Interestingly, Hornick et al. (1998a) and Keogh et al. (2015a) both reported greater fat deposition in cattle undergoing CG compared to control groups. However, in a study carried out by Keane (2010), crossbred BB steers offered grass silage for 84 d followed by *ad libitum* concentrates had similar carcass fat class values to steers offered concentrates *ad libitum* throughout. The absence of an effect of diet on carcass fat class suggests that mild energy restriction for a relatively short period followed by an adequate realimentation period does not affect carcass fat class in either AN or BB genotypes. This is further supported by a lack of difference between diets in either ultrasonically scanned fat depth or perinephric-retroperitoneal fat scaled for carcass weight. Once scaled for carcass weight, the difference in weight of perinephric-retroperitoneal fat between the dietary treatments disappeared. Yambayamba et al. (1996a) reported that abdominal fat was lower in animals subjected to a feed restriction period compared to animals offered *ad libitum* access to feed. Similarly, Keogh et al. (2015a) observed less kidney and channel fat in bulls that had underwent a period of dietary restriction when compared to their *ad libitum* counterparts. However, Moloney et al. (2008) reported that growth pattern before slaughter did not affect either the weight of perinephric-retroperitoneal fat or weight of perinephric-retroperitoneal fat proportional to carcass weight in Friesian steers, in support of our findings. Additionally, there was no effect of genotype on perinephric-retroperitoneal fat between crossbred AN and BB steers which is in line with similar findings from Keane and Moloney (2010) and Keane et al. (2011). In contrast, however, Keane and Drennan (2008) reported a greater proportion of perinephric-retroperitoneal fat in crossbred AN compared to BB animals, however, differences between studies may be due to different diets and experimental parameters employed.

As there was a difference in carcass weight between genotypes, a variation between the genotypes in the weight of the five-rib joint would be expected also. However, only a numerical difference in rib joint weight proportional to the difference in carcass weight was observed. This is in agreement with Keane and Moloney (2010) who also found a numerical but non-significant difference in the weight of the rib joint between crossbred AN and BB steers. Generally, the literature shows that crossbred BB animals have greater *M. longissimus thoracis et lumborum* area compared to AN animals (Keane and Drennan, 2008; Campion et al., 2009b; Keane and Moloney, 2010; Keane et al., 2011). Additionally, crossbred BB animals heterozygous for the double muscling myostatin mutation have increased muscle mass compared to their conventional

counterparts (Casas et al., 2004). Our results support these findings with greater proportions of muscle observed in BB compared to AN carcasses. *M. longissimus thoracis et lumborum* and total muscle values in the five-rib joint were greater in BB steers compared to AN with no difference in bone plus ligamentum nuchae/supraspinale proportions between genotypes which is consistent with Keane et al. (2011), who found similar results for these genotypes. In the current study, other muscle was not affected by genotype; however, Keane et al. (2011) reported a difference. Typically, an increase in total fat proportion of the rib joint for AN animals compared to BB is observed (Keane and Moloney, 2010; Keane et al., 2011) as AN is an early maturing breed which lay down fat at an earlier age and lighter weight. The current study supports this with AN having a greater proportion of fat compared to BB.

Steen and Kilpatrick (2000) reported no difference in *M. longissimus thoracis et lumborum* area at slaughter between steers offered either a restricted or *ad libitum* access to feed before finishing. This is consistent with the findings of the present study, with no difference in *M. longissimus thoracis et lumborum* area evident between H-H and L-H animals. The difference in the weight of the five-rib joint between H-H and L-H steers, with greater values for the former, is broadly proportional to the difference in carcass weight between the diets. Additionally, total fat proportion was greater in H-H compared to L-H carcasses, which is contrary to Hornick et al. (1998a) who reported greater percentages of connective and adipose tissue at slaughter in bulls exhibiting CG compared to bulls offered a high energy diet throughout the study. However, in that study, animals were younger and exposed to a longer restriction period and shorter realimentation period. Yambayamba and Price (1991) reported that heifers experiencing CG after a period of feed restriction had similar fat proportions compared to animals offered *ad libitum* feed throughout the study. Again, these animals were younger which may account for similar fat proportions in that study, not observed in the present study. Alternatively, it may be due to the use of heifers in Yambayamba and Price (1991) and steers in the current study, with heifers known to acquire more fat at a younger age compared to males. In the current study, differences relating to fat proportions in the five-rib joint between diets may be due to ration rather than dietary treatment group as the H-H animals had access to the greater energy diet for a longer period of time which is consistent with Wilkinson and Prescott (1970).

Belgian Blue had lighter intestinal weight when scaled for slaughter weight which contributed to their greater dressing percentage. This supports the findings of McPherron and Lee (1997) who reported that a myostatin null mutation in cattle (BB breed) is associated with a reduction in size of internal organs. Interestingly, L-H animals showed greater rumen (empty and full) proportions compared to H-H animals. The greater full rumen weight would suggest greater feed intakes in L-H animals, however, this was not observed with no difference in DMI between diets during the realimentation period. Empty rumen scaled measurements were greater in L-H compared to H-H steers which is in agreement with Yambayamba et al. (1996a) who reported that beef heifers undergoing CG during a realimentation period also had greater empty stomach proportions. They suggested that this indicated a greater metabolic activity in that organ as a consequence of enhanced dietary intake during realimentation and CG, resulting in a greater capacity for recovery. However, a larger empty rumen would consume more energy and reduce feed efficiency which may contribute to the gradual decline in feed efficiency typically observed following sustained CG (Keogh et al., 2015a). Both the liver and gastrointestinal tract have the capacity to increase and decrease size proportional to feed intake and consequently the energy required to sustain these organs fluctuates proportionally also (Johnson et al., 1990). Together this suggests that metabolically active organs such as the rumen and liver undergo CG ahead of other tissues as a direct response to processing the additional nutrients associated with realimentation. Indeed, this has been documented previously in other studies (Fitzsimons et al., 2017).

The greater hide weight for AN compared to BB animals when expressed per unit of live weight supports the findings of Campion et al. (2009a) for animals of the same genotype. The difference may be attributed to breed effects in skin thickness (Tulloh, 1961). Ansay and Hanset (1979) reported that hide plus internal organ weights from double muscled cattle were only 81% of the corresponding value for their conventional counterparts. Although the present BB animals were not homozygous for the double muscling myostatin mutation, the presence of one myostatin allele contributes a proportion of the effect witnessed when the two alleles are present (Casas et al., 2004). Genotype and diet effects were observed for head weight with BB and L-H animals showing greater head weight proportional to SW compared to AN and H-H animals, respectively. Absolute head weight in the current study did not differ across genotype or diet (data not shown) with significant results observed resulting from differences in body weight. Lack of interactions indicates CG influenced carcass traits and non-carcass components similarly across both genotypes.

Keane and Moloney (2010) reported that carcass length and carcass depth (scaled for carcass weight) were greater in crossbred AN steers compared to crossbred BB with no difference found between genotypes for leg width and leg thickness. In support of these findings, AN animals in the current study had greater scaled carcass length and depth and similarly no difference in leg width and leg thickness. Additionally, Campion et al. (2009a) and Keane et al. (2011) found that crossbred AN steers had greater relative leg length compared to BB steers supporting the current results. Greater carcass measurements relative to live weight for AN indicate a greater body size which parallels their poorer carcass conformation. The smaller linear carcass values for BB (leg length, carcass depth and length) indicate greater carcass compactness in this genotype (Keane et al., 2011). Patterson and Steen (1995) reported that plane of nutrition before finishing did not affect carcass measurements in Friesian steers; however, diet had an effect on all carcass measurements in the current study with H-H having reduced carcass proportions compared to L-H animals. Greater length/depth of the carcass per unit of weight in the H-H animals was observed although this was not reflected in carcass conformation (Hickey et al., 2007) with, as discussed earlier, no difference observed in carcass conformation between H-H and L-H animals.

Conclusions

It can be concluded that the mild feed restriction applied in this study followed by CG during a 200 days realimentation period has no lasting effects (positive or negative) at slaughter on plasma metabolite or hormone concentrations, linear body measurements, ultrasonically scanned fat depth, carcass conformation, dressing percentage or fat class in crossbred AN and BB steers. Although L-H animals had a compensatory index of 52% and did not compensate completely, *M. longissimus thoracis et lumborum*, a tissue of high economic value, had the capacity to recover completely as evident from the ultrasonically scanned muscle depth analysis. The processes regulating CG in this tissue may also offer revealing insight into CG in the animal as a whole. Therefore, the underlying biochemical mechanisms regulating CG in economically important tissues within cattle warrant further investigation.

Ethics approval

All animal procedures performed in this study were conducted under experimental licence from the Department of Health and

Children, in accordance with the Cruelty of Animals Act 1876 and the European Communities Regulation 2002 and 2005. Animals were slaughtered in an EU licensed abattoir, Meadow Meats, Rathdowney, Co. Laois, Ireland.

Data and model availability statement

None of the data were deposited in an official repository.

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Author contributions

DAK and **MGK** conceived the study and oversaw the statistical analysis and manuscript preparation. **SK** managed the animals, conducted much of the statistical and laboratory analysis and drafted the manuscript. **SMW** and **EO'R** secured funding and assisted with manuscript preparation. **KK** assisted with statistical analysis and manuscript preparation. **ARW** conducted the leptin radioimmunoassays.

Declaration of interest

None.

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