HEALTHFULNESS OF BEEF: A GENOME-WIDE ASSOCIATION STUDY USING CROSSBRED CATTLE

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Introduction

Consumers are becoming increasingly health-conscious and demand healthy and palatable meat, both of which are affected by lipid composition (Dunner et al., 2013). Red meat has relatively high levels of saturated fatty acids and beneficial oleic acid, and low concentrations of beneficial polyunsaturated fatty acids (Dunner et al., 2013). However, fats are not the only nutrients that affect the nutritional value of beef. Beef is an excellent source of iron required in the human diet, yet the consistency of iron content in beef products is highly variable (Duan et al., 2009). Considerable attention has been placed on improving the nutritional value of beef and the development of products that are beneficial to human health and disease prevention (Scollan et al., 2006).

It has been illustrated that animal nutritional regime differences can alter the nutrient profile of beef (Realini et al., 2004) and that genetic factors can also play a role (De Smet et al., 2004; Mateescu et al., 2013a,b). Identification of genetic variants that would allow producers to select for optimum nutritional values with respect to fatty acids, minerals, and vitamins, without sacrificing performance or product quality, could ultimately increase value and consumer satisfaction of beef. Genetic selection aided by genomic predictors may serve as an important and highly applicable tool in improving the nutritional value of beef given the expensive and difficult nature of phenotypic data collection. The objectives of the current study were to determine the proportion of phenotypic variation explained by the Ilumina BovineSNP50K-Bead-Chip for cholesterol (CH), polyunsaturated fatty acids (PUFA), monounsaturated fatty acids (MUFA), protein, potassium, iron and sodium, to identify chromosomal regions that harbor major genetic variants underlying the variation of these traits.

Materials and Methods

Experimental Design

Crossbred steers and heifers of unknown pedigree and breed fractions (n= 236) with varying percentages of Angus, Simmental and Piedmontese were placed in a Calan gate facility at the Agricultural Research and Development Center (ARDC) feedlot facility near Mead, NE. Prior to arrival, animals were genotyped for the Piedmontese-derived myostatin mutation (*C313Y*) to determine their myostatin genotype (MG) as either homozygous normal (*313C/313C*, 0 copy, n=83), heterozygous (*313C/313Y*, 1-copy, n=96), or homozygous for inactive myostatin (*313Y/313Y*, 2-copy, n=57). Cattle were fed in four groups over a 2-yr period. Groups 1 and 3 consisted of calf-fed steers and groups 2 and 4 consisted of yearling heifers as described by Howard et al., (2013).

Animals had *ad libitum* access to water and were fed a diet that met or exceeded National Research Council (NRC) (1996) requirements. The finishing ration for steers and heifers in year 1 included wet distillers grain with solubles, a 1:1 blend of high moisture and dry rolled corn, grass hay and supplement at 35, 52, 8, and 5 % of the diet on a dry matter basis. The finishing ration for steers and heifers in year 2 included modified distillers grain with solubles, sweet bran, a 1:1 blend of high moisture and dry rolled corn, grass hay and supplement at 20, 20, 48, 8, and 4 % of the diet on a dry matter basis. Animals were on an all-natural program and were not implanted or fed growth-promoting additives. Cattle were harvested as a group based on average body weight and external fat. Steaks were sampled from the *M. Longissimus thoracis et lumborum* (LTL) and the *M. Semitendinosus* (ST) three days post mortem. Steaks were cut to ½ inch thick and trimmed to 1/8 inch of subcutaneous fat. Steaks were shipped to Midwest Laboratories, Inc. (Omaha, NE) for further analysis. Lipid, and mineral analysis results were reported for a 113.40 gram serving size.

Statistics for carcass traits are summarized in Table 1. Fatty acids (MUFA and PUFA) and CH were analyzed as both a percentage of total lipid content

and mg/100g of whole (wet) tissue. Omega 3, 6 and 9 fatty acids were reported as MUFA or PUFA. The interpretation of these two measurement scales is dramatically different, as a sample with relatively low PUFA content as measured in mg/100g of whole (wet) tissue would likely have low total lipid content and as a consequence would have relatively high PUFA content when measured as a percentage of total lipids. Potassium, iron and sodium were analyzed as ppm of whole tissue.

Statistical Analysis

Myostatin genotype has been shown to have an effect on fatty acid composition. Consequently, outliers, adjusted for group and MG, classified as being > 3 SD from the mean of the residual variance (zero), were removed from the analysis. Summary statistics for fatty acid and mineral traits after editing are detailed in Table 2. A genome wide association study (GWAS) using the BovineSNP50K Bead-Chip was conducted via the GenSel platform (Version 0.9.2.045; Fernando and Garrick, 2011). A Bayes C model was employed (Habier et al., 2011) with group (concatenation of year (i.e. feeding regime) and sex; 4 classes) fitted as a fixed effect. The proportion of markers having a null effect was set to 0.95. A chain length of 150,000 iterations was run with the first 50,000 discarded as burn-in. The genomic estimated breeding value (GEBV) was estimated by summing posterior mean marker effects by marker genotype across all SNP. Phenotypic correlations were estimated using multivariate analysis of variance (MANOVA) procedures with group fitted as a fixed effect. To estimate potential GEBV re-ranking, correlations between GEBV were estimated across traits within a cut (i.e. ST or LTL) and between cuts within each trait. Additionally, the cattle genome was separated into 1 Megabase (Mb) windows and SNP variance within a window was summed to give an estimate of the total SNP variance for each window (n=2,677). The percentage of top 5% (n=134) windows in common across traits and cuts were then compared with GEBV correlations among traits and between cuts. The top 0.5% 1-Mb windows (n=13) for each trait were extended by 1-Mb in both directions and a positional candidate gene approach was conducted using *Bos taurus* build UMD_3.1 assembly (Zimin et al., 2009). Due to the limited functional annotation of the *Bos taurus* genome, human orthologs of beef cattle positional candidate genes were obtained and used for functional characterization by using Ensembl Genes 69 database and the BioMart data mining tool (http://www.ensembl.org/biomart/martview/dd0c118c99ed15210cc6e97131d873fb). Overrepresented gene ontology terms, and pathway analysis were identified using DAVID (http://david.abcc.ncifcrf.gov).

Results

Genomic Heritabilities

The posterior mean (standard deviation; SD) genomic heritability estimates (proportion of phenotypic variation explained by the markers) are presented in Table 3. For both cuts, heritability estimates for protein and mineral traits ranged from 0.05 to 0.75. The posterior mean (SD) genomic heritability estimates for CH, PUFA and MUFA as a percentage of total lipid content for both cuts ranged from 0.40 to 0.70. When analyzed as mg/100g of total wet tissue, the posterior mean (SD) genomic heritability estimates for CH, PUFA and MUFA for both cuts ranged from 0.45 to 0.85.

Mateescu et al. (2013a) estimated the heritability based on pedigree information and phenotypic data to be 0.48, 0.00, and 0.15 for LTL iron, potassium, and sodium, respectively. The proportions of phenotypic variation explained by the BovineSNP50 assay were 0.37, 0.03, and 0.09 for iron, potassium and sodium, respectively (Mateescu et al., 2013b). These results are in general agreement with the findings of the current study for the traits of iron and sodium. The vastly different estimates for potassium may be attributed to the admixed population or the small sample size, and the fact that this population was segregating the *C313Y* mutation. One SNP within one of the top 1Mb windows for potassium was in perfect LD with the myostatin mutation. Lower posterior mean estimates of genomic heritability for ST sodium is likely a function of the lower phenotypic variation of sodium content, which can be explained biological-

ly by the body highly regulating sodium levels (Hollenberg, 1980).

For LTL and ST CH, LTL PUFA and ST MUFA posterior mean estimates of genomic heritability remained the same regardless of the scale of measurement (percentage of total lipids or mg/100g of whole (wet) tissue). The genomic heritability estimate for LTL MUFA was higher when measured on mg/100g of whole (wet) tissue than on a percentage of total lipids. ST PUFA genomic heritability was lower when measured on mg/100g whole (wet) tissue basis. The coefficients of variation for ST PUFA were 0.61 and 0.34 when measured as a percentage of total lips and mg/100g, respectively. This increase in variation could partially explain the increase in the proportion of variation explained by the markers. Although the ST had lower concentrations of PUFA as measured in mg/100g of wet tissue, it also had lower values for total lipids. Consequently when PUFA was adjusted for total lipid content, the mean PUFA as a percentage of total lipid content was actually higher than the LTL. The same general trend of the ST containing a higher proportion PUFA and MUFA as a percentage of total fatty acids was also reported by Sexton et al. (2012). Estimates of heritability for fatty acids are sparse in the literature. Pitchford et al. (2002) reported low to moderate estimates of heritability for fatty acid traits in beef cattle. However, Cameron (1990) reported high (0.53-0.71) heritability estimates for palmitic, stearic, oleic, and linoleic fatty acids. This is consistent with the estimate of 0.75 for the heritability of C18:1 in a population of Japanese black cattle (Uemoto et al., 2010), and supports a moderate to high level of genetic control of fatty acids within meat.

Genomic Estimated Breeding Value and Phenotypic Correlations

Correlations between GEBV follow the phenotypic correlation trends as reported by Ahlberg et al., (2014). Phenotypic correlations are presented in Tables 4 and 5. Among the protein and mineral, as well as the mineral and protein with lipids, correlations were low to moderate between and within the two cuts and were varied in the direction of the correlation when measured as a percentage of fat and as mg/100g of wet tissue. Phenotypic correlations among lipid traits were moderate to strong as a percentage of fat and as mg/100g of wet tissue. The MUFA was negatively correlated with PUFA and CH within and across cuts when measured on a percentage of total fat. However, when measured as mg/100g of wet tissue, MUFA and PUFA were strong positively correlated and CH was moderate negatively correlated with MUFA and PUFA between and across cuts. Consequently, from a selection perspective, the phenotype used (percentage or mg/100g) would lead to the selection of different animals. This is primarily because increases in fat content dilute fatty acids found in membranes, notably CH and PUFA. Expression of results as mg/100g of wet tissue thus reflects overall increases in fat content.

The interpretation of results relative to fatty acids is conditional on understanding the scale of the phenotypes (percentage of total fatty acids or mg/100g of wet tissue). When the gravimetric amount of PUFA, for instance, is low the amount of PUFA relative to total fatty acids (percentage of total fatty acids) can be high simply because the amount of total fatty acids was also very low. Similarly, when PUFA content is relatively high as a percentage of total fatty acids (i.e. when the amount of total fatty acids is also low) CH would also be expected to be relatively high when measured as a percentage of total fatty acids. The expectation that with the increase in adipose tissue that CH increases, PUFA decreases and MUFA increases on a percent fat basis is challenged in the case of cattle with the double muscling genotype. Raes et al. (2001) have shown that the double muscling genotype within the Belgian Blue breed has low proportions of MUFA and high proportions of PUFA in muscle lipid compared with normal genotype animals. This is due to the low concentration of total lipid in the muscle and a high ratio of phospholipid and total lipid. Phospholipids are high in PUFA content in order to perform the function as a constituent of cellular membranes (Wood et al., 2008). However, when PUFA content is high in mg/100g of whole (wet) tissue, total fatty acid content is also likely high leading to a reduction in the proportionate amount of CH.

Significant correlations between GEBV suggest that selection for increased iron concentration in the ST would lead to increased levels of MUFA and decreased levels of both CH and PUFA as a percentage of total lipids. In both cuts, selection for

increased levels of potassium would have the opposite effects leading to increased PUFA and CH and decreased MUFA as a percentage of total lipids. On a total tissue basis, selection for increased potassium in both cuts would lead towards a correlated decrease in PUFA and MUFA and increase in CH. Selection for increased iron would lead to a correlated decrease in CH and an increase in MUFA and PUFA in the ST on a total wet tissue basis.

Sodium was lowly to moderately correlated with all traits measured, in agreement with Mateescu et al. (2013) who also reported low to moderate correlations between sodium and other mineral traits. However, correlations between GEBV between the different cuts for sodium was high despite the low proportion of variation explained by the markers. This strong GEBV correlation may be due to markers picking up breed/family relationships, which would give rise to a larger positive GEBV correlation.

Candidate Gene Annotation

Functional annotation analysis resulted in a common gene found among lipid traits was GULP1 (*Engulfment adaptor PTB domain containing 1*). GULP1 is an adaptor protein that binds and directs the trafficking of LRP1 (*Low density lipoprotein receptor-related protein 1*), which is involved in lipid homeostasis (He and Lin, 2010). ITGAV is associated with metabolic processes and negative regulation of lipid transport and storage (Kim et al., 2013).

Some significant SNP from the top 0.5% 1-Mb windows that were on BTA2 for each trait were in high LD with the myostatin *C313Y* alleles. Consequently, these SNP may simply be an artifact of the importance of the myostatin mutation for some for the traits analyzed. Between all traits and cuts there was a wide range in the number of 1-Mb windows that were on BTA2, ranging from 1 to 9 windows. Traits with few top windows on BTA2 are likely not impacted as much by *C313Y*. Previous work by Aldai et al. (2005) showed significant differences between animals of the Asturiana de los Valles breed of cattle that were homozygous for the myostatin deletion and those that were homozygous normal for protein percentage. The authors also showed that homozygous myostatin animals had lower proportions of MUFA and higher proportions of PUFA illustrating that this mutation has a measureable impact on these traits. This is supported by Wiener et al. (2009) who showed a significant effect of the myostatin mutation in South Devon cattle for both PUFA and MUFA concentrations. Outside of the myostatin mutation, Mateescu et al. (2013c) reported 16 SNP in a single Mb region (103-104 Mb) on BTA2 to explain 1.33% of the phenotypic variation of iron content, although the region reported by Mateescu et al. (2013) does not overlap with the regions reported in the current study.

Conclusions

In general, the mean estimates of the posterior heritability were moderate to high for fatty acids, suggesting that significant progress could be made through selection with the aid of genomics. The proportion of variation for mineral traits was more variable, although a moderate proportion of variation was explained by the markers for iron and potassium content. Differences did exist for fat traits depending on the scale of measurement (mg/100g or percentage of total lipid content), in terms of relationships between traits, chromosomal regions underlying genetic variation, and in some cases the proportion of variation explained by the markers. The choice between these two scales would impact the ranking of animals. Further investigation of fatty acid and mineral concentrations need to be conducted in other populations to fully understand the proportion of variation explained by markers and better predict candidate genes. Potential candidate genes, GULP1 and ITGAV located on BTA2 in close proximity to C313Y, were identified and involve regulation of lipids. Further analysis of expression of these genes will allow for better understanding of lipid transport and regulation in muscle and their subsequent role in determining meat quality of livestock.

Table 1. Summary statistics for carcass traits.

Trait	n	0 copy[a]	1 copy[a]	2 copy[a]	Minimum	Maximum	Mean	Standard Deviation
HCW, kg.								
Group 1[c]	59	19	28	12	253.55	372.85	305.88	25.42
Group 2[c]	60	25	26	9	265.80	385.55	319.85	24.96
Group 3[c]	58	20	22	16	268.52	400.98	332.19	26.84
Group 4[c]	59	19	20	20	271.25	434.00	346.24	34.19
Back Fat, cm.								
Group 1	59	19	28	12	0.10	1.40	0.73	0.37
Group 2	60	25	26	9	0.10	2.03	0.84	0.41
Group 3	58	20	22	16	0.25	2.29	0.86	0.55
Group 4	59	19	20	20	0.25	3.05	1.02	0.68
Marbling Score[b]								
Group 1	59	19	28	12	100	470	294.92	100.75
Group 2	60	25	26	9	100	860	373.00	118.40
Group 3	58	20	22	16	250	880	533.79	166.97
Group 4	59	19	20	20	270	730	426.78	114.75

[a] Refers to the number of copies of the inactive Myostatin allele.

[b] Marbling score units: 400 = Sm^{00}, 500 = $Modest^{00}$

[c] Group 1 refers to year 1 steers, group 2 refers to year 1 heifers, group 3 refers to year 2 steers and Group 4 refers to year 2 heifers.

Table 2. Summary statistics for nutrient traits.

Trait	Units	n	Mean	Minimum	Maximum	Standard Deviation
LD[a] MUFA	(% of fat)	224	46.25	33.2	55.00	4.31
LTL MUFA	(mg/100g)	227	6087.70	270.97	13849.38	3233.42
ST[b] MUFA	(% of fat)	223	45.11	26.6	56.70	5.55
ST MUFA	(mg/100g)	227	2461.14	37.24	10308.06	1977.84
LTL PUFA	(% of fat)	223	5.27	2.66	15.30	2.21
LTL PUFA	(mg/100g)	224	572.60	149.86	1197.99	180.07
ST PUFA	(% of fat)	222	8.50	1.14	25.60	5.20
ST PUFA	(mg/100g)	227	378.87	36.24	735.02	132.31
LTL Cholesterol	(% of fat)	222	0.50	0.14	2.84	0.45
LTL Cholesterol	(mg/100g)	225	45.76	33.00	59.00	4.48
ST Cholesterol	(% of fat)	223	1.94	0.22	17.10	2.48
ST Cholesterol	(mg/100g)	225	46.26	32.00	58.00	4.73
LTL Sodium	(ppm)	226	418.69	336.50	491.20	32.14
ST Sodium	(ppm)	227	393.92	317.40	478.60	29.02
LTL Potassium	(ppm)	227	3015.18	2283.00	3614.00	268.71
ST Potassium	(ppm)	226	3484.30	2867.00	4087.00	227.99
LTL Iron	(ppm)	224	13.65	8.99	19.56	2.06
ST Iron	(ppm)	226	13.92	7.50	25.50	2.62
LTL Protein	(%)	225	21.69	17.34	27.44	1.86
ST Protein	(%)	227	22.91	18.58	26.17	1.33

[a] *M. Longissimus dorsi* (LTL)

[b] *M. Semitendinosus* (ST)

Table 3. Genomic heritabilities

Trait	Units	Heritability (SE)
LTL[a] MUFA	(% of fat)	0.40 (0.10)
LTL MUFA	(mg/100g)	0.85 (0.04)
ST[b] MUFA	(% of fat)	0.60 (0.07)
ST MUFA	(mg/100g)	0.60 (0.10)
LTL PUFA	(% of fat)	0.70 (0.06)
LTL PUFA	(mg/100g)	0.70 (0.08)
ST PUFA	(% of fat)	0.65 (0.06)
ST PUFA	(mg/100g)	0.45 (0.04)
LTL Cholesterol	(% of fat)	0.50 (0.09)
LTL Cholesterol	(mg/100g)	0.50 (0.06)
ST Cholesterol	(% of fat)	0.45 (0.10)
ST Cholesterol	(mg/100g)	0.45 (0.11)
LTL Sodium	(ppm)	0.15 (0.08)
ST Sodium	(ppm)	0.05(0.05)
LTL Potassium	(ppm)	0.75 (0.08)
ST Potassium	(ppm)	0.65 (0.09)
LTL Iron	(ppm)	0.35 (0.13)
ST Iron	(ppm)	0.35 (0.09)
LTL Protein	(%)	0.70 (0.08)
ST Protein	(%)	0.75 (0.06)

[a] *M. Longissimus dorsi* (LTL)

[b] *M. Semitendinosus* (ST)

Table 4. Phenotypic correlations with lipid traits measured as a percent of total fat[abcdef].

Trait[abc]	STPR	STI	STS	STPO	STCH	STMUFA	STPUFA	LTLPR	LTLI	LTLS	LTLPO	LTLCH	LTLMUFA	LTLPUFA
STPR	-	-0.32 (0.01)	-0.09 (0.19)	0.64 (0.01)	0.35 (0.06)	-0.53 (0.01)	0.59 (0.01)	0.59 (0.01)	-0.05 (0.46)	0.15 (0.03)	0.49 (0.01)	0.45 (0.01)	-0.44 (0.01)	0.48 (0.01)
STI	-	-	0.30 (0.01)	-0.16 (0.02)	-0.31 (0.01)	0.32 (0.01)	-0.39 (0.01)	-0.34 (0.01)	0.35 (0.01)	-0.06 (0.36)	-0.30 (0.01)	-0.27 (0.01)	-0.32 (0.01)	-0.36 (0.01)
STS	-	-	-	0.24 (0.01)	0.02 (0.78)	-0.09 (0.16)	-0.03 (0.70)	-0.05 (0.45)	0.02 (0.73)	0.25 (0.01)	0.02 (0.82)	0.03 (0.83)	-0.07 (0.27)	-0.008 (0.91)
STPO	-	-	-	-	0.24 (0.01)	-0.48 (0.01)	0.44 (0.01)	0.39 (0.01)	-0.06 (0.37)	0.12 (0.07)	0.46 (0.01)	0.28 (0.01)	-0.37 (0.01)	0.28 (0.01)
STCH	-	-	-	-	-	-0.59 (0.01)	0.68 (0.01)	0.50 (0.01)	-0.12 (0.07)	0.17 (0.01)	0.29 (0.01)	0.75 (0.01)	-0.50 (0.01)	0.56 (0.01)
STMUFA	-	-	-	-	-	-	-0.85 (0.01)	-0.61 (0.01)	0.20 (0.01)	-0.21 (0.01)	-0.52 (0.01)	-0.66 (0.01)	0.74 (0.01)	-0.65 (0.01)
STPUFA	-	-	-	-	-	-	-	0.68 (0.01)	-0.21 (0.01)	0.19 (0.01)	0.47 (0.01)	0.74 (0.01)	-0.58 (0.01)	0.71 (0.01)
LTLPR	-	-	-	-	-	-	-	-	-0.08 (0.22)	0.25 (0.01)	0.64 (0.01)	0.71 (0.01)	-0.60 (0.01)	0.70 (0.01)
LTLI	-	-	-	-	-	-	-	-	-	0.20 (0.01)	0.18 (0.01)	-0.11 (0.11)	0.15 (0.02)	-0.20 (0.01)
LTLS	-	-	-	-	-	-	-	-	-	-	0.50 (0.01)	0.23 (0.01)	-0.24 (0.01)	0.20 (0.01)
LTLPO	-	-	-	-	-	-	-	-	-	-	-	0.49 (0.01)	-0.55 (0.01)	0.51 (0.01)
LTLCH	-	-	-	-	-	-	-	-	-	-	-	-	-0.63 (0.01)	0.82 (0.01)
LTLMUFA	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.71 (0.01)
LTLPUFA	-	-	-	-	-	-	-	-	-	-	-	-	-	-

[a] *M. Longissimus thoracis et lumborum* (LTL) [b] *M. Semitendinosus* (ST)

[c]ST protein (STPR), ST iron (STI), ST sodium (STS), ST potassium (STPO), ST cholesterol (STCH), ST monounsaturated fatty acids (STMUFA), ST polyunsaturated fatty acids (STPUFA), LTL protein (LTLPR), LTL iron (LTLI), LTL sodium (LTLS), LTL potassium (LTLPO), LTL cholesterol (LTLCH), LTL monounsaturated fatty acids (LTLMUFA), and LTL polyunsaturated fatty acids (LTLPUFA)

[d]STCH, STMUFA, STPUFA, LTLCH, LTLMUFA and LTLPUFA units as percent of total fat

[e]Phenotypic correlations (P value). [f]Standard errors for correlations were 0.067.

Table 5. Phenotypic correlations with lipid traits measured as mg/100g of total (wet) tissue[abcdef].

Trait[abc]	STPR	STI	STS	STPO	STCH	STMUFA	STPUFA	LTLPR	LTLI	LTLS	LTLPO	LTLCH	LTLMUFA	LTLPUFA
STPR	-	-0.32 (0.01)	-0.09 (0.19)	0.64 (0.01)	0.40 (0.01)	-0.48 (0.01)	-0.43 (0.01)	0.59 (0.01)	-0.05 (0.46)	0.14 (0.03)	0.49 (0.01)	0.31 (0.01)	-0.65 (0.01)	-0.47 (0.01)
STI	-	-	0.20 (0.01)	-0.16 (0.02)	-0.33 (0.01)	0.22 (0.01)	0.19 (0.01)	-0.34 (0.01)	0.35 (0.01)	-0.06 (0.36)	-0.30 (0.01)	-0.29 (0.01)	0.40 (0.01)	0.31 (0.01)
STS	-	-	-	0.24 (0.01)	0.02 (0.78)	0.05 (0.47)	0.02 (0.81)	-0.05 (0.45)	0.02 (0.73)	0.25 (0.01)	0.02 (0.82)	0.01 (0.84)	0.04 (0.56)	0.03 (0.63)
STPO	-	-	-	-	0.29 (0.01)	-0.36 (0.01)	-0.29 (0.01)	0.39 (0.01)	-0.06 (0.37)	0.12 (0.07)	0.46 (0.01)	0.28 (0.01)	-0.46 (0.01)	-0.27 (0.01)
STCH	-	-	-	-	-	-0.27 (0.01)	-0.21 (0.01)	0.41 (0.01)	-0.07 (0.29)	0.15 (0.02)	0.33 (0.01)	0.34 (0.01)	-0.45 (0.01)	-0.27 (0.01)
STMUFA	-	-	-	-	-	-	0.82 (0.01)	-0.47 (0.01)	0.06 (0.35)	-0.15 (0.02)	-0.36 (0.01)	-0.24 (0.01)	0.53 (0.01)	0.46 (0.01)
STPUFA	-	-	-	-	-	-	-	-0.39 (0.01)	0.16 (0.02)	-0.11 (0.12)	-0.24 (0.01)	-0.19 (0.01)	0.42 (0.01)	0.45 (0.01)
LTLPR	-	-	-	-	-	-	-	-	-0.08 (0.22)	0.25 (0.01)	0.64 (0.01)	0.46 (0.01)	-0.82 (0.01)	-0.76 (0.01)
LTLI	-	-	-	-	-	-	-	-	-	0.20 (0.01)	0.18 (0.01)	-0.03 (0.67)	0.09 (0.20)	0.08 (0.22)
LTLS	-	-	-	-	-	-	-	-	-	-	0.50 (0.01)	0.23 (0.01)	-0.24 (0.01)	-0.28 (0.01)
LTLPO	-	-	-	-	-	-	-	-	-	-	-	0.39 (0.01)	-0.70 (0.01)	-0.62 (0.01)
LTLCH	-	-	-	-	-	-	-	-	-	-	-	-	-0.45 (0.01)	-0.35 (0.01)
LTLMUFA	-	-	-	-	-	-	-	-	-	-	-	-	-	0.83 (0.01)
LTLPUFA	-	-	-	-	-	-	-	-	-	-	-	-	-	-

[a] *M. Longissimus thoracis et lumborum* (LTL) [b] *M. Semitendinosus* (ST)

[c]ST protein (STPR), ST iron (STI), ST sodium (STS), ST potassium (STPO), ST cholesterol (STCH), ST monounsaturated fatty acids (STMUFA), ST polyunsaturated fatty acids (STPUFA), LTL protein (LTLPR), LTL iron (LTLI), LTL sodium (LTLS), LTL potassium (LTLPO), LTL cholesterol (LTLCH), LTL monounsaturated fatty acids (LTLMUFA), and LTL polyunsaturated fatty acids (LTLPUFA)

[d]STCH, STMUFA, STPUFA, LTLCH, LTLMUFA, LTLPUFA units as mg/100g of total wet tissue.

[e]Phenotypic correlations (P value). [f]Standard errors for correlations were 0.067.

Literature Cited

Ahlberg, C. M., L. N. Schiermiester, J. T. Howard, C. Calkins, M. L. Spangler. 2014. Genome wide association study of cholesterol and poly- and monounsaturated fatty acids, protein, and mineral content of beef from crossbred cattle. *Meat Sci.,* (under review).

Aldai, N., B. E Murray, M. Olivan, A. Martinez, D.J. Troy, K. Osoro, & A. I. Najera. 2005. The influence of breed and *mh*-genotype on carcass conformation, meat physic-chemical characteristics, and the fatty acid profile of muscle from yearling bulls. *Meat Sci.* 72: 486-495.

Cameron N.D. 1999. Genetic and phenotypic parameters for fatty acid composition of subcutaneous fat, meat quality, carcass composition and eating quality traits in pigs. Proc. 4th WCGALP, Edinburgh, UK, XV: 549–552.

De Smet, S., K. Raes, & D. Demeyer. 2004. Meat fatty acid composition as affected by fatness and genetic factors: a review. *Anim. Res.* 53: 81-98.

Duan, Q., J. M. Reecy, R. Tait, J. P. Schoonmaker, D. C. Beitz, A. L. Van Eenennam, R. Mateescu, & A. Garmyn. 2009. Phenotypic variation of mineral contents in beef. *Fed. Am. Soc. Exp. Biol. J.* 23: LB412.

Dunner, S., N. Sevane, D. Garcia, H. Leveziel, J. L. Williams, B. Mangin, A. Valentini, & GeMQual Consortium. 2013. Genes involved in muscle lipid composition in 15 European *Bos taurus* breeds. *Animal Genetics* 44: 493-501.

Fernando, R. L., & D. J. Garrick. 2009. GenSel User manual for a portfolio of genomic selection related analysis. *Animal Breeding and Genetics*, Iowa State University, Ames.

Habier, D., R. L. Fernando, K. Kizilkaya, & D. J. Garrick. 2011. Extension of the Bayesian alphabet for genomic selection. *BMC Bioinformatics* 12:186.

He, Q., & D. Lin. 2010. A variable selection method for genome-wide association studies. *J. Bioinformatics* 27: 1-8.

Hollenberg, N. K. 1980. Set point for sodium homeostasis: Surfeit, deficit, and other implications. *Kidney Int.* 17: 423-429.

Howard, J. T., S. D. Kachman, M. K. Nielsen, T. L. Mader, & M. L. Spangler. 2013. The effect of myostatin genotype on body temperature during extreme temperature events. *J. Anim. Sci.* 91: 3051-3058.

Illumina, Inc. 2010. Technical Note: DNA Analysis, Infinium® Genotyping Data Analysis. San Diego (CA). *Illumina, Inc*., 9 p. Pub. No. 970-2007-005.

Kim, T., S. Shin, J. Park, & C. Park. 2013. Genome wide identification and expression profile in epithelial cells exposed to TiO_2 particles. *J. Environ.Toxicol.* 29: 4.

Mateescu, R. G., A. J. Garmyn, R. G. Tait, Jr., Q. Duan, Q. Liu, M. S. Mayes, A. L. Van Eenennaam, D. L. VanOverbeke, G. G. Hilton, D. C. Beitz, & J. M. Reecy. 2013a. Genetic parameters for concentrations of minerals in longissimus muscle and their associations with palatability traits in Angus cattle. *J. Anim. Sci*. 91: 1067-1075.

Mateescu, R. G., A. J. Garmyn, R. G. Tait, Jr., Q. Duan, Q. Liu, M. S. Mayes, A. L. Van Eenennaam, D. L. VanOverbeke, G. G. Hilton, D. C. Beitz, & J. M. Reecy. 2013b. Genetic parameters for concentrations of minerals in longissimus muscle and their associations with palatability traits in Angus cattle. *J. Anim. Sci*. 91: 1067-1075.

Mateescu, R. G., A. J. Garmyn, R. G. Tait, Jr., Q. Duan, Q. Liu, M. S. Mayes, A. L. Van Eenennaam, D. L. VanOverbeke, G. G. Hilton, D. C. Beitz, & J. M. Reecy. 2013c. Genome-wide association study of concentrations of iron and other minerals in longissimus muscle of Angus cattle. *J. Anim. Sci*. 91: 3593-3600.

NRC. 1996. Nutrient Requirements of Beef Cattle. 7th Revised Edition, 1996: Update 1996. *National Academy Press*, Washington, D. C.

Pitchford, W. S., M. P. B. Deland, B. D. Siebert, A. E. O. Malau-Aduli, & C. D. K. Bottema, 2002. Genetic variation in fatness and fatty acid composition of crossbred cattle. *J. Anim. Sci.* 80: 2825–2832.

Raes, K., S. De Smet, & D. Demeyer, 2001. Effect of double-muscling in Belgian Blue young bulls on the intramuscular composition with emphasis on conjugated linoleic acid and polyunsaturated fatty acids. *Animal Science* 73: 253-260.

Realini, C. E., S. K. Duckett, G. W. Brito, M. D. Rizza, D. De Mattos, 2004. Effect of pasture vs. concentrate feeding with or without antioxidants on carcass characteristics, fatty acid composition, and quality of Uruguayan beef. *Meat Sci.* 74: 567-577.

Scollan, N. D., J. Hocquette, K. Nuernberg, D. Dannenberger, I. Richardson, & A. Moloney. 2006. Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality. *Meat Sci.* 74: 17-33.

Sexten, A. K., C. R. Krehbiel, J. W. Dillwith, R. D. Madden, C. P. McMurphy, D. L. Lalman,R. G. Mateescu. 2012. Effect of muscle type, sire breed, and time of weaning on fatty acid composition of finishing steers. *J. Anim. Sci.* 90: 616-625.

Uemoto, Y., T. Abe, N. Tameoka, H. Hasebe, K. Inoue, H. Nakajima, N. Shoji, M. Kobayashi, and E. Kobayashi. 2011. Whole-genome association study for fatty acid composition of oleic acid in Japanese Black cattle. *Animal Genetics*, 42: 141–148.

Wiener, P., J. A. Wooliams, A. Frank-Lawale, M. Ryan, R. I. Richardson, G. R. Nute, & J. D. Wood. 2009. The effects of a mutation in the myostatin gene on meat and carcass quality. *Meat Sci.* 83: 127-134.

Wood, J.D., M. Enser, A.V. Fisher, G. R. Nute, P. R. Sheard, R. I. Richardson, S. I. Hughes, F. M. Whittington. 2008. Fat deposition, fatty acid composition and meat quality: A review. *Meat Sci.* 78: 343-358.

Zimin, A. V., A. L. Delcher, L. Florea, D. R. Kelley, M. C. Schatz, D. Puiu, F. Hanrahan, G. Pertea, C. P. van Tassell, T. S. Sonstegard, G. Marcais, M. Roberts, P. Subramanian, J. A. Yorke, & S. L. Salzberg. 2009. A whole-genome assembly of the domestic cow, Bos taurus. *Genome Biol*. 10(4): R42.