Genetic parameters for sensory traits in longissimus muscle and their associations with tenderness, marbling score, and intramuscular fat in Angus cattle[1]

R. G. Mateescu,*[2] D. J. Garrick,† A. J. Garmyn,‡ D. L. VanOverbeke,§ G. G. Mafi,§ and J. M. Reecy†

*Department of Animal Sciences, University of Florida, Gainesville 32611; †Department of Animal Science, Iowa State University, Ames 50011; ‡Department of Animal and Food Sciences, Texas Tech University, Lubbock, 79409; and §Department of Animal Science, Oklahoma State University, Stillwater 74078

ABSTRACT: The objective of this study was to estimate heritabilities for sensory traits and genetic correlations among sensory traits and with marbling score (MS), Warner-Bratzler shear force (WBSF), and intramuscular fat content (IMFC). Samples of LM from 2,285 Angus cattle were obtained and fabricated into steaks for laboratory analysis and 1,720 steaks were analyzed by a trained sensory panel. Restricted maximum likelihood procedures were used to obtain estimates of variance and covariance components under a multitrait animal model. Estimates of heritability for MS, IMFC, WBSF, tenderness, juiciness, and connective tissue traits were 0.67, 0.38, 0.19, 0.18, 0.06, and 0.25, respectively. The genetic correlations of MS with tenderness, juiciness, and connective tissue were estimated to be 0.57 ± 0.14, 1.00 ± 0.17, and 0.49 ± 0.13, all positive and strong. Estimated genetic correlations of IMFC with tenderness, juiciness, and connective tissue were 0.56 ± 0.16, 1.00 ± 0.21, and 0.50 ± 0.15, respectively. The genetic correlations of WBSF with tenderness, juiciness, and connective tissue were all favorable and estimated to be –0.99 ± 0.08, –0.33 ± 0.30 and –0.99 ± 0.07, respectively. Strong and positive genetic correlations were estimated between tenderness and juiciness (0.54 ± 0.28) and between connective tissue and juiciness (0.58 ± 0.26). In general, genetic correlations were large and favorable, which indicated that strong relationships exist and similar gene and gene networks may control MS, IMFC, and juiciness or WBSF, panel tenderness, and connective tissue. The results from this study confirm that MS currently used in selection breeding programs has positive genetic correlations with tenderness and juiciness and, therefore, is an effective indicator trait for the improvement of tenderness and juiciness in beef. This study also indicated that a more objective measure, particularly WBSF, a trait not easy to improve through phenotypic selection, is an excellent candidate trait for genomic selection aimed at improving eating satisfaction.

Key words: beef, genetic parameters, marbling score, sensory traits, tenderness

J. Anim. Sci. 2015.93:21–27
doi:10.2527/jas2014-8405

INTRODUCTION

The 2011 National Beef Quality Audit assessed the status and progress made toward improving quality and consistency of U.S. cattle, carcasses, and beef products (Igo et al., 2013). The only quality category identified by packers, food service buyers, and retailers for which those sectors are willing to pay a premium was "eating satisfaction." Tenderness, juiciness, and flavor are the major determinants of beef palatability and are often used to measure eating satisfaction. Eating satisfaction is of great interest to the beef industry as improving these traits should lead to increased beef demand.

The beef industry has relied on marbling scores as a major driver to determine USDA quality grades and pricing of carcasses at wholesale level, with higher quality grades expected to correspond to more tender and palatable meat. Consumers also perceive marbling as an indicator of tenderness and overall meat quality, with consumer acceptance increasing

---

[1] This research was supported by Zoetis Animal Genetics.

[2] Corresponding author: raluca@ufl.edu

Received August 13, 2014.
Accepted October 28, 2014.

approximately 10% for each unit increase in marbling score (Platter et al., 2003). To address consumers' demand for high-quality product, more information on genetic contributions to variation in sensory traits is needed, as the ability to design effective breeding programs for genetic improvement of these traits depends on availability of genetic parameters.

The objective of this study was to estimate heritabilities for sensory traits and genetic correlations among sensory traits and with marbling score (**MS**), Warner-Bratzler shear force (**WBSF**), and intramuscular fat content (**IMFC**) measured by chemical extraction. Associations between sensory traits and MS are particularly important, because MS is the trait used in selection breeding programs as an indicator trait of palatability and eating satisfaction, while WBSF and IMFC are objective measures of tenderness and IMFC and are obvious candidate traits for genomic selection.

MATERIALS AND METHODS

Animals and Sample Collection

The Iowa State University and Oklahoma State University Institutional Review Boards approved the experimental protocols used in this study.

A total of 2,285 Angus-sired bulls (n = 540), steers (n = 1,311), and heifers (n = 434) representing offspring of 155 sires were used in this study. All cattle were finished on concentrate diets in Iowa (n = 1,085), California (n = 360), Colorado (n = 388), or Texas (n = 452). Animals were harvested at commercial facilities when they reached typical U.S. market endpoints with an average age of 457 ± 46 d. Production characteristics and additional details regarding sample collection and preparation of these cattle were reported previously (Garmyn et al., 2011). Trained personnel obtained carcass measurements. The amount of intramuscular fat at the cut surface of the rib eye on the 12th rib surface determines MS and the scale used for data entry was 3.0 = traces, 4.0 = slight, 5.0 = small, 6.0 = modest, 7.0 = moderate, 8.0 = slightly abundant, 9.0 = moderately abundant, and 10 = abundant. Rib sections or strip loins were obtained from each carcass. All steaks were vacuum packaged, aged at 2°C for 14 d from harvest date, and then frozen at –20°C. One 1.27-cm steak was trimmed of external fat and connective tissue and analyzed at Iowa State University (Ames, IA) for nutrient composition including IMFC, determined by ether extraction using AOAC International method 960.39 (AOAC, 2007) and expressed as grams fat per 100 g of muscle tissue, that is, percent fat. Two 2.54-cm steaks were fabricated for WBSF and sensory analysis. Steaks were cooked and subjected to sensory analysis at Oklahoma State University Food and Agricultural Products Center (Stillwater, OK).

Warner Bratzler Shear Force

This test measures the force required to shear a cooked steak after postmortem ageing. The frozen steaks were allowed to thaw at 4°C for 24 h before cooking, broiled in an impingement oven (XLT Impinger, model 3240-TS [BOFI Inc., Wichita, KS] or Lincoln Impinger, model 1132-000-A [Lincoln Foodservice Products, Fort Wayne, IN]) at 200°C to an internal temperature of 68°C, and cooled at 4°C for 18 to 24 h as recommended by the American Meat Science Association (1995). Six cores, 1.27 cm in diameter, were removed parallel to muscle fiber orientation and sheared once, using a Warner-Bratzler head attached to an Instron Universal Testing Machine (model 4502; Instron Corporation, Canton, MS). The Warner-Bratzler head moved at a crosshead speed of 200 mm/min. Peak load (kg) of each core was recorded by an IBM PS2 (model 55 SX) using software provided by the Instron Corporation. Mean peak load (kg) was analyzed for each sample.

Sensory Analysis

Detailed description of the selection and training of sensory panel members and procedures were provided by Garmyn et al. (2011). Briefly, steaks were assigned a randomized number for sensory sessions and assigned to sensory panel session based on the randomized number. Steaks were thawed at 4°C for 24 h before cooking, cooked to 68°C, sliced into approximately 2.54-cm by 1.27-cm by 1.27-cm samples, and served warm for sensory evaluation by 8 trained panelists. Samples were evaluated using a standard ballot from the American Meat Science Association (1995). Panelists evaluated samples in duplicate for sustained juiciness and overall tenderness using an 8-point scale and for cooked beef flavor intensity using a 3-point scale. The average score of all panelists for each animal was used in analysis. For juiciness, the scale ranged from 1 = extremely dry to 8 = extremely juicy. The scale used for overall tenderness ranged from 1 = extremely tough to 8 = extremely tender. The scale for connective tissue ranged from 1 = abundant to 8 = none. The scale used for beef flavor intensity was 1 = not detectable, 2 = slightly detectable, and 3 = strong flavor. Sensory sessions were conducted once or twice per day and contained 12 samples each. The 12 samples were served in a randomized order according to the panelist.

Table 1. Means, SC, CV, skewedness, and kurtosis for marbling score, intramuscular fat content (%), Warner-Bratzler shear force (kg), and trained panel evaluation of tenderness, connective tissue, juiciness, and beef flavor of steaks from Angus cattle

Trait	*n*	Mean	SD	CV	Skewness	Kurtosis
Marbling score	2,285	5.96	1.04	0.17	0.71	0.50
Intramuscular fat content	2,227	5.66	2.22	0.39	1.01	3.83
Warner-Bratzler shear force	2,251	3.53	0.77	0.22	0.72	1.78
Panel tenderness[1]	1,720	5.79	0.59	0.10	–0.62	1.01
Juiciness[1]	1,720	5.00	0.50	0.10	–0.09	–0.08
Beef flavor[2]	1,720	2.50	0.23	0.09	–0.61	1.60
Connective tissue[1]	1,720	5.88	0.59	0.10	–0.73	1.03

[1] Scale: 1 = extremely dry/tough and 8 = extremely juicy/tender.

[2] Scale: 1 = not detectable and 3 = strong.

Statistical Analysis

Trait means, SD, skewedness, and kurtosis were calculated using the UNIVARIATE procedure in SAS 9.3 (SAS Inst. Inc., Cary, NC).

The generalized linear mixed model assumes that the relationship between the mean of the dependent variable *y* and the fixed and random effects can be modeled as a linear function, the variance is not a function of the mean, and that the random effects follow normal distributions. The REML procedure used in this study, the most versatile method for estimation of variance and covariance, is very robust against moderate deviation from normality. Given the categorical nature of the traits analyzed, the assumption of normality was verified.

For each sensory and carcass trait, REML procedures were used to estimate genetic and residual variances as well as heritability, based on single-trait animal models fitted to the data using WOMBAT (Meyer, 2007b; http://didgeridoo.une.edu.au/km/wombat.php).

In matrix notation, the basic model equation was

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}u + \mathbf{e},$$

in which the design matrices X and Z relate phenotypic observations in the vector y to fixed (β) and random (u) effects, respectively. The vector e contains random residual effects specific to each animal. The vectors u and e were assumed to be normally distributed with 0 means and variances $A\sigma^2_a$ and $I\sigma^2_e$, respectively, in which I is an identity matrix of order equal to the number of animals with observations, A is the additive relationship matrix, σ^2_a is the additive genetic variance, and σ^2_e is the residual variance.

Restricted maximum likelihood procedures were also used to estimate genetic and phenotypic covariances from pairwise bivariate animal models fitted to all combinations of traits using WOMBAT (Meyer, 2007b). Those models included extra variance parameters reflecting the association between elements of **u** for the 2 traits on the same animals and between elements of **e** for the 2 traits in the same animals.

Contemporary groups were defined based on gender at harvest (bull, heifer, or steer), finishing location (California, Colorado, Iowa, or Texas), and harvest date for a total of 33 groups. Contemporary groups were fit as fixed effects in all analyses.

A pedigree file with 5,907 individuals including identification of all animal, sire, and dam trios for 4 ancestral generations was used to define relationships among animals in the data set. Significance of genetic correlations was obtained as $\theta \pm Z_\alpha/2$ (sampling error), assuming normality of the estimator, θ.

RESULTS AND DISCUSSION

Summary statistics for WBSF, IMFC, MS, and palatability traits are shown in Table 1. Averages for WBSF and for IMFC were 3.53 kg and 5.66 g fat/100 g muscle, that is, 5.66% fat. The average MS score was 5.96, which corresponded to modest marbling. The averages for panel tenderness, connective tissue, and juiciness were 5.79, 5.88, and 5.00, respectively. These traits were scored on 8-point scale, but it should be noted that none of the samples in this study received scores below 3. Based on the scale used for tenderness, no sample in the data was found to be extremely or very tough and the average was in the upper half of the interval between slightly and moderately tender. Almost identical average scores were observed for connective tissue. Regarding juiciness, no sample in the data was found to be extremely or very dry or extremely juicy and the average corresponds to the slightly juicy class. The average for beef flavor was 2.5, half way between detectable and strong beef flavor on the 3-point scale used by the panel.

The CV is the ratio of SD to the mean, and the estimate showed that dispersion in sensory traits was 2 to 4 times less than for IMFC and WBSF and 1.5 times

Table 2. Genetic (σ^2_a) and residual (σ^2_e) variance and heritability (h^2) estimates with SE for marbling score, intramuscular fat (%), Warner-Bratzler shear force (kg), and trained panel sensory traits of steaks from Angus cattle obtained by single-trait REML analysis

Trait	σ^2_a	σ^2_e	h^2 ± SE
Marbling score	0.61	0.30	0.67 ± 0.08
Intramuscular fat	1.29	2.13	0.38 ± 0.07
Warner-Bratzler shear force	0.07	0.30	0.19 ± 0.05
Panel tenderness	0.05	0.24	0.18 ± 0.06
Juiciness	0.01	0.20	0.06 ± 0.04
Connective tissue	0.07	0.21	0.25 ± 0.07

smaller than for MS. Skewness measures the degree and direction of asymmetry, with a symmetric distribution having a skewness close to 0. Skewness was negative and to the left for all sensory traits, but the magnitude varied with juiciness being less skewed (–0.09) while tenderness, beef flavor intensity, and connective tissue were more skewed (–0.62, –0.61, and –0.73). All other traits considered (MS, IMFC, and WBSF) had positive skewness, being skewed to the right (0.71, 1.01, and 0.721). Kurtosis is a measure of the heaviness of the tails of a distribution and kurtosis close to zero indicates a nearly normal distribution. All traits except juiciness had positive kurtosis, which indicated fewer cases in the tails relative to a normal distribution, with values that ranged from 3.83 for IMFC to 0.50 for marbling. Juiciness had a negative kurtosis (–0.08) and was very close to 0, so the tails are similar to a normal distribution.

A common rule-of-thumb test for normality is based on skewness and kurtosis divided by SE (Garson, 2012). When values of these statistics are within the range –2 to +2, the trait is approximately normally distributed. Often, a more lenient range of –3 to +3 is applied when the procedure used is more robust with respect to deviations from normality. These statistics were calculated for all categorical traits and MS, tenderness, juiciness, and connective tissue did not violate the normality assumption, as both statistics for these traits are within –2 to +2 range. The only trait in this analysis that, based on this test, deviates substantially from a normal distribution was beef flavor, with 2 statistics of –2.65 and 6.95. Based on this assessment, the beef flavor trait was excluded from subsequent analysis used to estimate genetic parameters.

Heritabilities

Heritability estimates for MS, IMFC, WBSF, and trained panel sensory traits are shown in Table 2.

In a comprehensive review (Utrera and Van Vleck, 2004), the average heritability of MS from 29 studies was 0.49 and the average of 6 studies published after the review was 0.52 (Mateescu, 2014). The estimated heritability in this study (0.67 ± 0.08), somewhat larger relative to other recent estimates from Angus cattle (0.58 ± 0.05 [Meyer, 2007a], 0.445 ± 0.025 [MacNeil and Northcutt, 2008], and 0.48 ± 0.03 [MacNeil et al., 2010]), confirmed the prevailing assessment of MS as a trait with moderate to high heritability.

The estimated heritability of IMFC in this study was 0.38 ± 0.07. Recent estimates of heritability for IMFC in Angus cattle measured by ultrasound on live animals, a practical way of measuring the trait in the field, were 0.18, 0.30, and 0.25 for bulls, heifers, and steers (MacNeil and Northcutt, 2008) and 0.31 ± 0.08 for steers (MacNeil et al., 2010). It can be concluded that IMFC, measured directly by chemical analysis or indirectly using ultrasound on live animals, is a moderately heritable trait. This is in agreement with numerous studies that report carcass traits to be moderately to highly heritable and their estimated heritabilities to be insensitive to finish end points (Utrera and Van Vleck, 2004; Dikeman et al., 2005).

Published heritability estimates for WBSF are within the range of 0.14 to 0.29 (Mateescu, 2014), spanning the estimate in this study (0.19 ± 0.05), which confirmed the perception that this objective measure of tenderness has a moderate to low heritability.

Sensory traits are affected by many factors such as carcass processing method (i.e., electrical stimulation, tenderstretching, or ageing), the specific muscle analyzed, and the subjective nature of the panel evaluation, to name a few. This is reflected in the relatively wide ranges for reported heritability estimates for these traits, which are in the moderate to low range. The average heritability from 9 studies for panel tenderness was 0.25 with a range of 0.06 to 0.46 (Mateescu, 2014) and the estimate from this study (0.18 ± 0.06) confirmed a moderate to low heritability for this trait. The heritability estimate for panel juiciness from this study (0.06 ± 0.04) is at the lower end of the 0.00 to 0.46 range of heritabilities reported in 9 studies for panel juiciness (Mateescu, 2014). The estimated heritability for connective tissue (0.25 ± 0.07) was the highest among sensory traits in this study. In general, the heritability estimates reported for panel sensory traits are moderate to low, with tenderness being the highest (Riley et al., 2003; Dikeman et al., 2005; Gill et al., 2010; Wheeler et al., 2010), similar to our study.

Correlations

The estimates of the genetic and phenotypic correlations among these traits are shown in Table 3.

The phenotypic correlations between MS and sensory traits were positive but relatively weak, in the

Table 3. Estimates of genetic (above the diagonal) and phenotypic (below the diagonal) correlations with approximate SE (in parenthesis) between marbling score (MS), intramuscular fat content (IMFC; %), Warner-Bratzler shear force (WBSF; kg), and trained panel sensory traits of steaks from Angus cattle obtained by multiple-trait REML analysis

Trait	MS	IMF	WBSF	Panel tenderness	Juiciness	Connective tissue
MS		1.00 (0.01)	–0.50 (0.12)	0.57 (0.14)	1.00 (0.17)	0.49 (0.13)
IMFC	0.72 (0.01)		–0.47 (0.14)	0.56 (0.16)	1.00 (0.21)	0.50 (0.15)
WBSF	–0.23 (0.02)	–0.23 (0.02)		–0.99 (0.08)	–0.33 (0.30)	–0.99 (0.07)
Panel tenderness	0.21 (0.03)	0.23 (0.03)	–0.58 (0.02)		0.54 (0.28)	1.00 (0.02)
Juiciness	0.23 (0.02)	0.27 (0.02)	–0.11 (0.02)	0.31 (0.02)		0.58 (0.26)
Connective tissue	0.17 (0.03)	0.19 (0.02)	–0.55 (0.02)	0.92 (0.00)	0.22 (0.02)	

range of 0.17 to 0.23, which indicated that this carcass trait, used by industry as the major driver of quality grading and often used directly by consumers as an indicator of quality, is not a reliable predictor of eating satisfaction. This is even more important considering that when a consumer purchases the product expecting superior eating satisfaction and that expectation is only seldom met, that disappointment would influence future purchasing decisions and negatively impact beef demand. The phenotypic correlations between IMFC and sensory traits were similarly weak, in the range of 0.19 to 0.27. A trait in this study that is a good indicator of eating satisfaction was WBSF, which has phenotypic correlations of –0.58, –0.11, and –0.55 with tenderness, juiciness and connective tissue, respectively. However, WBSF is difficult and expensive for routine measurement.

The phenotypic correlations among sensory traits were all positive with strong correlation between tenderness and connective tissue (0.92) and moderate correlations of juiciness with tenderness (0.31) or connective tissue (0.22).

The genetic correlation between MS and IMFC was 1, which is to be expected as they are alternative measures of the same trait with MS determined through visual observation of the carcass whereas IMFC is the chemically measured fat content of the same muscle in the same carcass. This indicates that MS is a good selection trait if the breeding goal is to modify IMFC in finished cattle.

Of specific interest in this study were the genetic correlations of MS, IMFC, and WBSF with sensory traits. The genetic correlations of MS with tenderness, juiciness, and connective tissue were 0.57 ± 0.14, 1.00 ± 0.17, and 0.49 ± 0.13, all positive and strong. Although it is a general consensus that the degree of marbling is associated with palatability, how muscle fat content contributes to sensory traits is still under debate. Hocquette et al. (2010) suggested that IMFC has a direct effect on juiciness and an indirect effect on tenderness by changing the structure of the connective tissue. The estimated genetic correlations of IMFC with tenderness, juiciness, and connective tissue were 0.56 ± 0.16, 1.00 ± 0.21, and 0.50 ± 0.15, respectively, and these estimates seem to support the above hypothesis.

The genetic correlations of WBSF with tenderness, juiciness, and connective tissue were all favorable and estimated to be –0.99 ± 0.08, –0.33 ± 0.30, and –0.99 ± 0.07, respectively. These estimates are consistent with estimates from other studies (Riley et al., 2003; Wheeler et al., 2010). The very high genetic correlations of WBSF with panel tenderness and connective tissue is expected as they are different measures of the same trait and the lower genetic correlation with juiciness support the hypothesis that WBSF has an indirect effect on juiciness.

The perfect genetic correlation observed between test panel measure of tenderness and connective tissue is difficult to interpret but, combined with very high phenotypic correlation between these 2 test panel measures (0.92), confirmed the expectation that the amount of connective tissue in a steak is strongly associated with tenderness perceived by trained test panels and, perhaps, consumers.

Strong and positive genetic correlations were estimated between panel tenderness and juiciness (0.54) and between connective tissue and juiciness (0.58), larger than phenotypic correlations between these traits (0.31 and 0.22, respectively). Previous studies reported high genetic correlations among palatability traits assessed through sensory panels (Van Vleck et al., 1992; Gregory et al., 1995; Riley et al., 2003), and the effect of tenderness on the perceived juiciness of a steak has been referred as the "halo" effect (Shorthose and Harris, 1991; Meilgaard et al., 1999).

These strong correlations among sensory panel traits are not surprising given the interdependency among these traits, where the score for one trait is likely to influence the score for the other traits (i.e., steaks with at least 1 negative attribute being likely to be scored lower for the other traits and vice versa).

There are close relationships between marbling, juiciness, and tenderness, whereby meat samples that readily release fat and maintain juiciness are also perceived as tender. This is supported by the strong and favorable phenotypic correlations between both measures of intramuscular fat and both measures of tenderness (WBSF and tenderness assessed by the taste panelists). The genetic correlations between WBSF and MS or IMFC were –0.50 and –0.47, respectively, which indicated that a lower WBSF (more tender steaks) is genetically correlated with higher IMFC. Similarly, the panel tenderness was strongly and favorably correlated with both MS and IMFC (0.57 and 0.56, respectively). These correlations are very similar to those reported by Reverter et al. (2003) and Wheeler et al. (2010). In these reports, genetic correlations between intramuscular fat and tenderness in temperate breeds were moderate and favorable: 0.40 and 0.61 for intramuscular fat and consumer panel tenderness and –0.52 and –0.38 for intramuscular fat and tenderness evaluated by WBSF, respectively.

An almost perfect genetic correlation (–0.99) was identified between the 2 measures of tenderness: the objective WBSF and the subjective measure of tenderness assessed by the taste panelists. The negative sign of this correlation is a consequence of higher WBSF, which indicates a greater force needed for the steak to be sheared. Although a strong genetic correlation was expected between these 2 measures, it is important to note the strength of this correlation given the taste panel tenderness is a subjective measure data from taste panels, having the potential to vary greatly from panelist to panelist and/or from one taste session to another, which resulted in low consistency and reproducibility. Nevertheless, the similar heritabilities for the 2 traits and the estimated genetic correlation of –0.99 in this study indicated that the 2 measures of tenderness are, in fact, equally informative and evaluate the same trait.

A genetic correlation indicates that, if selection is exercised on 1 trait, the correlated trait is expected to also change proportional to the size of the correlation and in the direction of its sign. Regarding tenderness and juiciness, which represent the most important attributes determining eating satisfaction, substantial positive genetic correlation indicates that both traits can be simultaneously improved through selection. Unfortunately, using these traits directly in selection is not practical given their low heritability and great difficulties in measurement and collection of these phenotypes from sensory panels as well as substantial measurement error variability typical for these traits. In contrast, WBSF and IMFC are 2 phenotypes that can be measured objectively and have higher heritability and essentially perfect genetic correlations with the target traits tenderness and juiciness. The genetic correlation between WBSF and IMFC is also favorable and of similar magnitude to the genetic correlation between target traits, which makes them perfect proxy traits for selection to improve eating satisfaction.

Conclusion

This study found that WBSF, panel tenderness, and panel connective tissue had moderate heritabilities (0.18–0.22) while juiciness assessed by the taste panelists showed almost no genetic variation and therefore near zero heritability. Genetic correlations were strong and favorable, which indicated that a strong relationships exists and that similar gene and gene networks control MS, IMFC, and juiciness or WBSF, panel tenderness, and connective tissue.

The results from this study confirm that MS currently used in selection breeding programs has favorable genetic correlations with tenderness and juiciness and, therefore, is an effective indicator trait for improvement of tenderness and juiciness in beef. This study also indicates that more objective measure, particularly WBSF, is an excellent candidate trait for genomic selection aimed at improvement of eating satisfaction.

LITERATURE CITED

American Meat Science Association. 1995. Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of fresh meat. National Live Stock and Meat Board, Chicago, IL.

AOAC. 2007. Official Methods of Analysis, 18th ed. AOAC Int., Gaithersburg, MD.

Dikeman, M. E., E. J. Pollak, Z. Zhang, D. W. Moser, C. A. Gill, and E. A. Dressler. 2005. Phenotypic ranges and relationships among carcass and meat palatability traits for fourteen cattle breeds, and heritabilities and expected progeny differences for Warner-Bratzler shear force in three beef cattle breeds. J. Anim. Sci. 83:2461–2467.

Garmyn, A. J., G. G. Hilton, R. G. Mateescu, J. B. Morgan, J. M. Reecy, R. G. Tait Jr., D. C. Beitz, Q. Duan, J. P. Schoonmaker, M. S. Mayes, M. E. Drewnoski, Q. Lui, and D. L. Vanoverbeke. 2011. Estimation of relationships between mineral concentration and fatty acid composition of longissimus muscle and beef palatability traits. J. Anim. Sci. 89:2849–2858.

Garson, G. D. 2012. Testing statistical assumptions. www.statisticalassociates.com/assumptions.pdf. (Accessed 5 Aug. 2014.)

Gill, J. L., O. Matika, J. L. Williams, H. Worton, P. Wiener, and S. C. Bishop. 2010. Consistency statistics and genetic parameters for taste panel assessed meat quality traits and their relationship with carcass quality traits in a commercial population of Angus-sired beef cattle. Animal 4:1–8.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. J. Anim. Sci. 73:1920–1926.

Hocquette, J. F., F. Gondret, E. Baeza, F. Medale, C. Jurie, and D. W. Pethick. 2010. Intramuscular fat content in meat-producing animals: Development, genetic and nutritional control, and identification of putative markers. Animal 4:303–319.

Igo, J. L., D. L. Vanoverbeke, D. R. Woerner, J. D. Tatum, D. L. Pendell, L. L. Vedral, G. G. Mafi, M. C. Moore, R. O. McKeith, G. D. Gray, D. B. Griffin, D. S. Hale, J. W. Savell, and K. E. Belk. 2013. Phase I of The National Beef Quality Audit-2011: Quantifying willingness-to-pay, best-worst scaling, and current status of quality characteristics in different beef industry marketing sectors. J. Anim. Sci. 91:1907–1919.

MacNeil, M. D., J. D. Nkrumah, B. W. Woodward, and S. L. Northcutt. 2010. Genetic evaluation of Angus cattle for carcass marbling using ultrasound and genomic indicators. J. Anim. Sci. 88:517–522.

MacNeil, M. D., and S. L. Northcutt. 2008. National cattle evaluation system for combined analysis of carcass characteristics and indicator traits recorded by using ultrasound in Angus cattle. J. Anim. Sci. 86:2518–2524.

Mateescu, R. G. 2014. Genetics of meat quality. In: D. J. G. A. Ruvinsky, editor, The genetics of cattle. CAB International, Wallingford, UK. p. 544–570.

Meilgaard, M. C., B. Thomas Carr, and G. Vance Civille. 1999. Sensory evaluation techniques, 2nd ed. CRC Press, Boca Raton, FL.

Meyer, K. 2007a. Multivariate analyses of carcass traits for Angus cattle fitting reduced rank and factor analytic models. J. Anim. Breed. Genet. 124:50–64.

Meyer, K. 2007b. WOMBAT: A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). J. Zhejiang Univ. Sci. B 8:815–821.

Platter, W. J., J. D. Tatum, K. E. Belk, P. L. Chapman, J. A. Scanga, and G. C. Smith. 2003. Relationships of consumer sensory ratings, marbling score, and shear force value to consumer acceptance of beef strip loin steaks. J. Anim. Sci. 81:2741–2750.

Reverter, A., D. J. Johnston, D. Perry, M. E. Goddard, and H. M. Burrow. 2003. Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 2. Abattoir carcass traits. Aust. J. Agric. Res. 54:119–134.

Riley, D. G., C. C. Chase Jr., A. C. Hammond, R. L. West, D. D. Johnson, T. A. Olson, and S. W. Coleman. 2003. Estimated genetic parameters for palatability traits of steaks from Brahman cattle. J. Anim. Sci. 81:54–60.

Shorthose, W. R., and P. V. Harris. 1991. Effects of growth and composition on meat quality. In: A. M. Pearson and T. R. Dutson, editors, Growth regulation in farm animals: Advances in meat research. Vol. 7. London, UK. p. 520-522.

Utrera, A. R., and L. D. Van Vleck. 2004. Heritability estimates for carcass traits of cattle: A review. Genet. Mol. Res. 3:380–394.

Van Vleck, L. D., A. F. Hakim, L. V. Cundiff, R. M. Koch, J. D. Crouse, and K. G. Boldman. 1992. Estimated breeding values for meat characteristics of crossbred cattle with an animal model. J. Anim. Sci. 70:363–371.

Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2010. Characterization of biological types of cattle (Cycle VIII): Carcass, yield, and longissimus palatability traits. J. Anim. Sci. 88:3070–3083.