Novel traits for genetic selection in Gelbvieh influenced cattle

by

Kari L White

B.S., Colorado State University, 2010
M.S., Kansas State University, 2013

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Animal Sciences & Industry
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2020

Abstract

The objective of this research is to add needed information on economically relevant traits (ERT) to the existing American Gelbvieh Association National Cattle Evaluation. Substantive pieces were added to that vision by identifying selection tools that have not previously been established for that evaluation, or by re-assessing current selection tools to include the most efficient analysis. The topics of research included are traits that are often difficult or expensive to measure, which will benefit the greatest from further research into developing efficient and effective selection tools.

The objectives of the feed energy utilization study were to estimate genetic parameters for dry matter intake (DMI), percent daily dry matter required (PDMR), residual feed intake (RFI), adjusted weaning weight (AWWT), and post weaning gain (PWG) in a multi-breed population of growing beef cattle, in addition to implementing an economic selection index identify genetically favorable animals in the complex of traits associated with feed energy utilization. Feed intake and performance data for this analysis included records on animals collected by twelve individual breeders using Growsafe® systems and were later submitted to the AGA.

Feed efficiency parameters were estimated to be moderately heritable in this data set of Gelbvieh influenced cattle, indicating producers can make genetic improvement through selection for the traits. In addition, correlations among certain feed efficiency traits indicate selection for one trait should result in a correlated response in others. Index selection is preferable for genetic improvement in feed efficiency traits because of a large unfavorable genetic correlation between feed intake and growth. Continued collection of feed efficiency phenotypes is essential to identifying animals that are profitable in feed energy utilization.

The objectives of the sustained productivity study were to calculate an estimated breeding value (EBV) for each sire for relative risk of failing to calve consecutively within 425 days from 1 to 9 parities. The EBV for relative risk could then be used as genetic selection tool for sires whose daughters are more likely to reproduce in the herd within 425 days from 1 to 9 parities. Data for this analysis were birth dates and disposal codes reported by breeders to the AGA. Every animal in the AGA database has an associated code. For the purposes of this analysis, a female was considered to have a complete record (uncensored, code "0") if she failed to calve within 425 days of the previous calving, with no reported disposal code. A female was also considered uncensored, or considered to have a complete record, if she was greater than 11 years and 60 days old at the time of data extraction without a calving interval greater than 425 days in her lifetime. A female was considered to have an incomplete record (censored, code 1) if she had a defined non-reproductive disposal code, indicating she was culled from the herd for a reason other than reproduction. Females still active and producing in the herd at the time of data extract were also considered censored, since the upper bound of their productive life was still unknown.

Analysis indicated that animals in our data set that failed to calve within 425 days of previous calving, or those who were still producing in the herd at 11 years 60 days of age (uncensored) exited the herd at an average of 2.19 years old. Animals with a defined non-reproductive disposal code, or those still active in the herd at less than 11 years 60 days of age (censored) exited the herd at an average of 2.39 years old. Younger parities had a greater culling rate that decreased at later parities. This indicates failure occurs at a higher rate at younger ages. It should be noted that while it appears younger parities have a greater risk of failure, animals most likely to be culled for reproductive failure have already left the herd by later parities. As a result, culling rate is lower in advanced parities.

Sustained reproductive success and length of productive life as indicators of cow fertility are of great economic importance to the beef industry. The current study is a prototype genetic evaluation that will allow the AGA to select for sires that have daughters with improved length of productive life.

The objectives of the tenderness study were to quantify the genetic and phenotypic relationships between various methods of tenderness evaluation for fresh and frozen samples, quantitatively estimate breed effects of tenderness, and to assess the interaction of breed with *calpastatin* (CAST) and *μ-calpain* (CAPN1) markers. Data used in this analysis included SSF predicted by visible spectroscopy (LED), visible/near-infrared hyperspectral imaging (VISNIR) predicted SSF, fresh and frozen SSF aged to approximately 14 days (SSF14), frozen SSF aged to approximately 3 and 4 days combined (SSF3), and frozen WBSF aged to approximately 14 days and 3 and 4 days combined (WBS14 and WBS3).

Predicted measures of meat tenderness (LED and VISNIR) were estimated to be highly heritable at 0.78 and 0.59, respectively. High heritability in predicted measures of tenderness indicate they may be useful as correlated traits for selection. Slice shear force 3 and WBS3 had the greatest genetic correlation of 0.93 (0.03). Genetic correlations between estimated tenderness values (LED and VIS) and measured tenderness values (SSF and WBSF) ranged from low (0.02) to moderate (0.36) for LED and from low (-0.01) to moderate (0.48) for VIS. Warner-Bratzler shear force values at different days of post-mortem aging were found to be highly genetically correlated at 0.81 (0.05). Genetic correlations between SSF and WBSF values ranged from moderate (0.39) to high (0.93) depending on age.

Breed was found to be a significant effect at $p < 0.05$ for LED, VISNIR, SSF14, SSF3, and WBS14. Individual breed effects relative to Angus suggest variation between breeds when

selecting for meat tenderness. Non-zero breed effects would be important to include in multi-breed genetic evaluations of tenderness to ensure accurate predictions of genetic merit. Multiple markers on both CAPN1 and CAST were found to be associated with each trait, indicating marker assisted selection could be employed as a selection tool for post-mortem tenderness. Our data did not indicate a significant interaction between breed and marker, which suggests markers significantly associated with tenderness phenotypes traits may possibly be used for animals from a wide variety of breed groups. Results from this study provide an opportunity to use marker data from USMARC to estimate genomic enhanced tenderness for Gelbvieh influenced cattle because there is a lack of significant interaction between breed and marker.

Novel traits for genetic selection in Gelbvieh influenced cattle

by

Kari L White

B.S., Colorado State University, 2010
M.S., Kansas State University, 2013

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Animal Science & Industry
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2020

Approved by:

Major Professor
Dr. Robert L. Weaber

Copyright

Abstract

The objective of this research is to add needed information on economically relevant traits (ERT) to the existing American Gelbvieh Association National Cattle Evaluation. Substantive pieces were added to that vision by identifying selection tools that have not previously been established for that evaluation, or by re-assessing current selection tools to include the most efficient analysis. The topics of research included are traits that are often difficult or expensive to measure, which will benefit the greatest from further research into developing efficient and effective selection tools.

The objectives of the feed energy utilization study were to estimate genetic parameters for dry matter intake (DMI), percent daily dry matter required (PDMR), residual feed intake (RFI), adjusted weaning weight (AWWT), and post weaning gain (PWG) in a multi-breed population of growing beef cattle, in addition to implementing an economic selection index identify genetically favorable animals in the complex of traits associated with feed energy utilization. Feed intake and performance data for this analysis included records on animals collected by twelve individual breeders using Growsafe® systems and were later submitted to the AGA.

Feed efficiency parameters were estimated to be moderately heritable in this data set of Gelbvieh influenced cattle, indicating producers can make genetic improvement through selection for the traits. In addition, correlations among certain feed efficiency traits indicate selection for one trait should result in a correlated response in others. Index selection is preferable for genetic improvement in feed efficiency traits because of a large unfavorable genetic correlation between feed intake and growth. Continued collection of feed efficiency phenotypes is essential to identifying animals that are profitable in feed energy utilization.

The objectives of the sustained productivity study were to calculate an estimated breeding value (EBV) for each sire for relative risk of failing to calve consecutively within 425 days from 1 to 9 parities. The EBV for relative risk could then be used as genetic selection tool for sires whose daughters are more likely to reproduce in the herd within 425 days from 1 to 9 parities. Data for this analysis were birth dates and disposal codes reported by breeders to the AGA. Every animal in the AGA database has an associated code. For the purposes of this analysis, a female was considered to have a complete record (uncensored, code "0") if she failed to calve within 425 days of the previous calving, with no reported disposal code. A female was also considered uncensored, or considered to have a complete record, if she was greater than 11 years and 60 days old at the time of data extraction without a calving interval greater than 425 days in her lifetime. A female was considered to have an incomplete record (censored, code 1) if she had a defined non-reproductive disposal code, indicating she was culled from the herd for a reason other than reproduction. Females still active and producing in the herd at the time of data extract were also considered censored, since the upper bound of their productive life was still unknown.

Analysis indicated that animals in our data set that failed to calve within 425 days of previous calving, or those who were still producing in the herd at 11 years 60 days of age (uncensored) exited the herd at an average of 2.19 years old. Animals with a defined non-reproductive disposal code, or those still active in the herd at less than 11 years 60 days of age (censored) exited the herd at an average of 2.39 years old. Younger parities had a greater culling rate that decreased at later parities. This indicates failure occurs at a higher rate at younger ages. It should be noted that while it appears younger parities have a greater risk of failure, animals most likely to be culled for reproductive failure have already left the herd by later parities. As a result, culling rate is lower in advanced parities.

Sustained reproductive success and length of productive life as indicators of cow fertility are of great economic importance to the beef industry. The current study is a prototype genetic evaluation that will allow the AGA to select for sires that have daughters with improved length of productive life.

The objectives of the tenderness study were to quantify the genetic and phenotypic relationships between various methods of tenderness evaluation for fresh and frozen samples, quantitatively estimate breed effects of tenderness, and to assess the interaction of breed with *calpastatin* (CAST) and *μ-calpain* (CAPN1) markers. Data used in this analysis included SSF predicted by visible spectroscopy (LED), visible/near-infrared hyperspectral imaging (VISNIR) predicted SSF, fresh and frozen SSF aged to approximately 14 days (SSF14), frozen SSF aged to approximately 3 and 4 days combined (SSF3), and frozen WBSF aged to approximately 14 days and 3 and 4 days combined (WBS14 and WBS3).

Predicted measures of meat tenderness (LED and VISNIR) were estimated to be highly heritable at 0.78 and 0.59, respectively. High heritability in predicted measures of tenderness indicate they may be useful as correlated traits for selection. Slice shear force 3 and WBS3 had the greatest genetic correlation of 0.93 (0.03). Genetic correlations between estimated tenderness values (LED and VIS) and measured tenderness values (SSF and WBSF) ranged from low (0.02) to moderate (0.36) for LED and from low (-0.01) to moderate (0.48) for VIS. Warner-Bratzler shear force values at different days of post-mortem aging were found to be highly genetically correlated at 0.81 (0.05). Genetic correlations between SSF and WBSF values ranged from moderate (0.39) to high (0.93) depending on age.

Breed was found to be a significant effect at $p < 0.05$ for LED, VISNIR, SSF14, SSF3, and WBS14. Individual breed effects relative to Angus suggest variation between breeds when

selecting for meat tenderness. Non-zero breed effects would be important to include in multi-breed genetic evaluations of tenderness to ensure accurate predictions of genetic merit. Multiple markers on both CAPN1 and CAST were found to be associated with each trait, indicating marker assisted selection could be employed as a selection tool for post-mortem tenderness. Our data did not indicate a significant interaction between breed and marker, which suggests markers significantly associated with tenderness phenotypes traits may possibly be used for animals from a wide variety of breed groups. Results from this study provide an opportunity to use marker data from USMARC to estimate genomic enhanced tenderness for Gelbvieh influenced cattle because there is a lack of significant interaction between breed and marker.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to acknowledge the American Gelbvieh Association for their participation and support in this research.

Dedication

I dedicate this dissertation to my children. Work hard and be kind.

Chapter 1 - Literature Review

National Cattle Evaluation History and Development

Early Development

The beef cattle industry is unique among livestock species in the structure of its genetic evaluation. Poultry and swine industries formed around large commercial breeding programs that undertook their own performance recording and genetic evaluation. Dairy industry structure developed around a centralized laboratory for processing records, with genetic evaluation administered by the United States Department of Agriculture (USDA) in Beltsville, Maryland (Garrick, 2005). The beef cattle industry, in contrast, developed into multiple sectors representing cow-calf, back grounding, feedlot, processing, and ancillary sectors. The cow-calf sector developed as the component responsible for producing sires for breeding (seedstock), with the bull breeding component accounting for less than 5% of the national population of beef cows (Garrick, 2009). Another component of the cow-calf sector developed around calf producing, using sires breed by other producers (bull buyers) (Garrick, 2009). The genetic content of bull buying, or commercial herds, can be determined by the succession of sires used (Koch et al., 1986). Seedstock producers represent the primary source of genetic improvement in the beef cattle industry, and as such were the focal point of efforts to improve genetic merit (Koch et al., 1986).The seedstock component of the beef cattle industry partitioned into breed associations, with each entity being responsible for their own pedigree and data collection, as well as their own genetic evaluation (Garrick, 2005).

By 1900 livestock breeders in the Midwest United States had imported enough British stock to become breeders and provide commercial producers with the first Shorthorn and later Hereford sires. Breed associations were formed on the principle that pedigree, along with visual

appraisal, was the basis of successful breeding (Diel, 1993). By 1908, the Angus, Hereford, and Shorthorn breeds had been imported to the United States, and their breed associations began actively promoting their cattle and collecting pedigree records (Warwick, 1958). Responsibilities of these early breed associations included compliance with laws, such as the Dingley Act of July 24, 1897, which created regulations for certification of breed associations and herd books (Mohler, 1937).

The primary form of animal evaluation at this time was by phenotype. Livestock shows were well established by 1908, and breeders relied on the results to select sires for their herds (Warwick, 1958). Cattle producers began to recognize the benefit of using purebred sires on native cattle. The USDA also recognized the most rapid improvement in beef cattle came as a result of the widespread use of purebred sires who were selected by phenotype. Soon after 1908, USDA and state extension personnel embarked on "Better Sire Campaigns" (Warwick, 1958). As a result of these efforts, the number of purebred sires in the United States increased rapidly from between 60,000 and 95,000 in 1908 to between 750,000 and 860,000 in 1957 (Warwick, 1958). The increase in purebred sires by 1957 ensured enough sires to service all the nation's cows (Warwick, 1958). Breeders began to search for specific purebred sires to better fit the environment. In the gulf coast, Zebus were imported and crossed with British or indigenous cattle (Diel, 1993). In the 1920's, the King ranch of Texas developed the first American cattle breed, the Santa Gertrudis, with 3/8 Zebu and 5/8 British blood (Diel, 1993).

Increased emphasis on selection led to the first scientific papers in animal breeding on inheritance of horns in beef cattle (Bateson and Saunders 1902). The use of inbreeding to improve consistency of offspring led to the estimation of relationship and inbreeding coefficients (Wright, 1922). In 1946 Congress passed the Research Marketing Act, which provided for three

regional beef cattle breeding projects; Western, Midwest, and Southern (Baker, 1967). The purpose of these regional projects was to foster cooperation on agricultural problems too broad for single research stations alone (Warwick, 1958). Much of the early research information available in beef cattle breeding emanated from these projects. Also during this time, the first extension Beef Cattle Improvement (BCI) programs were founded in California, New Mexico, and Montana in order to pass knowledge between academics and producers (Baker, 1967).

Research from the regional projects showed that cattle varied in growth, gain, efficiency, and quality of final product. Data from the U.S. Range Livestock Experiment Station in Miles City, Montana led to the first estimates of heritability on quantitative traits by Knapp and Nordskog in 1946. Heritability estimates were made on traits such as birth and weaning weights, post weaning gain, efficiency of gain, final weight, and rib-eye area (Warwick, 1958). Also from the Miles City data, Koch and Clark (1955) performed early research on genetic correlations by investigating relationships between maternal abilities of the dam and post weaning gain of the calf. Performance and efficiency of brood cows was also explored. Koger and Knox (1947) found weight and score of calves could be used as a repeatable characteristic to assess the average performance of a cow. Information gained from the regional projects that cattle differed in inherent productivity, and that these differences were heritable, led to early performance testing programs throughout the United States (Warwick, 1958).

A large impact on the germ plasm base and beef cattle breeding in North America was the development of quarantine facilities and procedures by Agriculture Canada in the 1960s. These facilities allowed for the importation of "new" breeds of European origin into North America (Koch et al., 1986). Use of artificial insemination helped newly imported breeds to become established through three of four generations of top-crossing (Koch et al., 1986).

Availability of "new" breeds also stimulated interest in the current breeds available as sires, and added impetus to increased crossbreeding (Koch et al., 1986). By the 1970s, performance competition offered by recently imported breeds motivated breed associations to accept leadership roles for genetic improvement as a service to members (Koch et al., 1986). Competition of the "new" breeds provided a stimulus to the adoption of performance recording and changes in breeding goals of existing breeds in the United States (Koch et al., 1986).

Performance Program Era

Performance testing on economically relevant traits (ERT) in cattle was first implemented in the dairy industry with the Babcock fat test, which moved the industry into recording milk weight and test (Diehl, 1993). Performance testing in the beef industry began with a handful of breeders and academics from 1940 to 1960 (Diel, 1993). In 1930, the U. S. Department of Agriculture initiated research in developing methods of measuring performance in beef herds (Warwick, 1958). Central bull testing began in Balmorhea, Texas in 1941, which initiated competition among breeders based on performance of sires (Baker, 1967). The first Beef Cattle Improvement Association (BCIA) run by breeders with extension help was formed in Virginia in 1955 (Baker 1967). Performance Registry International (PRI), created in Texas in 1955, was the first performance program with standards for certification (Diel, 1993). The program was novel in that it required specific weight standards for certification. PRI expanded to begin a certified meat sire program in 1961, in which 10 of a sire's progeny were compared to standards for carcass excellence (Diel, 1993). On March 25, 1954, the Red Angus Association of America was founded in Ft. Worth, Texas as the first breed association that required weaning performance data for registered animals (Baker, 1967). The American Angus Association followed in performance programs shortly afterward with the beginning of the Angus Herd

Improvement Record program in 1959 (Baker, 1967). By 1964, five breeds announced breed association sponsored performance programs (Diel, 1993).

Throughout the late 1950's and early 1960's, Regional Testing Stations, BCIAs, and Extension BCI programs continued to grow (Baker, 1967). Breed associations were historically reluctant to adopt new technologies in performance recording (Golden et al., 2008). In 1959, the Red Angus Association of America implemented a policy that required reporting of weaning weight to register an animal. U. S. beef improvement recording was still relatively fragmented compared with other species (e. g., the Dairy Herd Improvement Program) and with that of other countries (e. g., Australian national Breedplan program or the Canadian national Record of Performance program) (Middleton and Gibb, 1991). Fragmentation of this nature had one advantage: the diversity and competition lead to extensive creativity in program design (Middleton and Gibb, 1991).

Breeders and academics began to organize conferences centered around breed improvement, such as the First Coordinated Beef Improvement Conference sponsored by the American Society of Animal Science and American National Cattlemen's Association in 1961 (Baker, 1967). Large-scale data collection by several independent performance programs led to the necessity for standardizing performance criteria. In 1965, the Extension Beef Improvement Committee of the American Society of Animal Science published the "United States Beef Cattle Records Committee Report", which recommended standardized procedures for the measurement of traits. (Diel, 1993). Assigning animals to contemporary groups, adjusting records for known sources of variation such as age of dam, and standardized measurement of weaning and yearling weights were all defined (Diel, 1993). Shortly after the Beef Cattle Records Committee report, The

United States Beef Improvement Federation (BIF) was formed and published the first complete guidelines for uniform beef improvement programs in 1970 (Diel, 1993).

Rapid Growth

Major developments in cattle evaluation in the 1970s and 1980s were largely statistical and computational in nature (Garrick, 2005). Pedigree and performance data recorded by breed associations on animals in a contemporary group were prerequisites for accurate genetic evaluation developed in this era (Garrick, 2009). Artificial Insemination became unrestricted in most breed association herd books, which increased the use of sires in more than one herd (Koch et al., 1986). Early performance testing compared the performance of a sire to a designated standard (Willham, 1979). The contemporary group average became the means for comparing individuals with others in similar groups using the ratio (Willham, 1979). Early improvement programs were based on individual performance and the calculation of ratios using the animal's own record. These expressions of merit were only useful for within-herd selection (Middleton and Gibb, 1991), and were not useful in between-herd comparisons where major genetic decisions were usually made (Willham, 1979). Progeny tests involving progeny from a common set of sires, in contrast, could yield breed value difference that could be fairly compared between sires (Willham, 1979). Breed associations began evaluating sires using the contemporary group sire model on designed data that assumed sires were mated to random dams (Diel, 1993). Willham (1979) defined national sire evaluation programs as ones designed and conducted by one organization having no direct interest in the test bulls. The purpose of such programs was to enhance the effectiveness of sire selection in the breeding programs of producers (Willham, 1979). Initially, breed association sire evaluations were based on progeny data from designed tests with reference sires for comparison (Koch et al., 1986). Reference sires usually had 100 or

more offspring in ten or more herd groups in comparison with five or more other reference sires (Koch et al., 1986). Large numbers of progeny spread over many contemporary groups allowed for comparisons among reference sires, making the prediction errors a function of progeny numbers of the test bull and progeny numbers of the reference sires (Willham, 1979). Standards for reference sires changed over time and eventually progressed to any sire with progeny in two or more reference groups being considered a reference sire (Koch et al., 1986). The value of an animal as a reference sire and his contribution to the national sire summary depended on his number of progeny and the number of contemporary groups containing his offspring (Koch et al., 1986). Direct sire comparisons were later used as a modification of the old predicted difference, as in the traditional reference sire comparisons superior sires amassed large numbers of progeny in many contemporary groups, making it difficult for young bulls with few progeny to compare in breeding value to the highly selected sires (Willham, 1979).

The process of predicting genetic merit is known as genetic evaluation and involves partitioning observed performance of animals into effects according to model equations that describe factors that influence performance for a particular trait (Garrick, 2009). In 1972, Richard Willham presented a paper to the BIF on computing estimated breeding values (EBVs) featuring American Angus and Litton Charolais programs (Diel, 1993). Implemented quickly by several breed associations, including Angus, Hereford and Simmental breeds, this approach would become the foundation on which the modern National Cattle Evaluation (NCE) was built (Golden et al., 2009). By 1974, EBVs were considered for replacing performance data in performance programs. Breeding value is determined by the sum (or half the sum for Expected Progeny Difference or EPD) of all the average effects of the genes an individual carries (Garrick, 2006). This analysis made several assumptions, including that dams were randomly allotted to

sires (Golden et al., 2009). In 1973, Henderson proposed a statistical approach that would be adopted from that time forward as the standard approach to predict additive genetic merit in livestock (Golden et al., 2009). The mixed model procedures, which provided Best Linear Unbiased Prediction (BLUP) of breeding values, allowed for substantial improvement in the accuracy of prediction because they improved the quality of predictions made, particularly between contemporary groups, and allowed all available data to be used (Henderson, 1975). BLUP equations also allowed fixed effects and breeding values to be simultaneously estimated (Mrode, 2005). The general form of a BLUP model is

$$\mathbf{Y = Xb + Zu + e}$$

where Y is a vector of observations, X is a matrix relating fixed effects in vector b to observations in Y, Z is a matrix relating random effects in vector u to observations in y, and e are the random errors (Golden et al., 2009). The random additive genetic effects in u have variance-covariance $A\sigma_a^2 G_0$, where A is Wright's numerator relationship matrix and G_0 is a matrix of additive genetic variance-covariance with an order equal to the number of genetic components affecting the traits in Y (Golden et al., 2009).

A representation of the linear system to be solved for continuously observed traits, also known as Henderson's mixed model equations, is

$$\begin{bmatrix} \boldsymbol{X'X} & \boldsymbol{X'Z} \\ \boldsymbol{Z'X} & \boldsymbol{Z'Z + A^{-1}\alpha} \end{bmatrix} \begin{bmatrix} \boldsymbol{\hat{b}} \\ \boldsymbol{\hat{a}} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X'y} \\ \boldsymbol{Z'y} \end{bmatrix}$$

where A^{-1} represents the inverse numerator relationship matrix, and α is a function of heritability (Mrode, 2005). Solutions for breeding values or EPDs are obtained by solving the mixed model equations (Garrick, 2009). These equations involve a coefficient matrix, also known as the Left Hand Side, which equal the Right Hand Side when multiplied by the solution vector (Garrick, 2009). Formulations of the mixed model equations require three kinds of data.

Each animal with a record needs herd, contemporary group, sex, birth date, and age of dam information (Garrick, 2009). This information accounts for non-genetic effects that influence construction of the mixed model equations. Pedigree information included in the data dictates the nature of genetic relationships between animals in the equations (Garrick, 2009). Together, these non-genetic effects and animal relationships determine the coefficient matrix. Performance records on animals form the major determinant of the Right Hand Side, or solution matrix (Garrick, 2009).

Early methods for predicting breeding values used records on animals and close relatives, ignoring the information which could be provided by other relatives (Henderson 1952, 1973). Henderson later suggested methods to utilize all relationships in animal evaluation, which is of fundamental importance in the prediction of breeding values (Mrode, 2005). The matrix which indicates the additive genetic relationship among individuals is called the numerator relationship matrix, or A matrix (Mrode, 2005). The matrix is symmetric with a diagonal element for animal i(a_{ii}) equal to $1 + F_i$, where F_i is the inbreeding coefficient of the ith animal (Wright, 1922). The $1+F_i$ element equals twice the probability that two gametes randomly taken from animal i carry identical alleles by decent (Mrode, 2005). The off-diagonal element a_{ij} represents the numerator of the coefficient of relationship between animals i and j (Wright, 1922). The A matrix can be computed through path coefficients but a method more appropriate for computerization was described by Henderson (1976). Methods to use the relationship matrix to solve for breeding values required either inversion of the numerator relationship matrix, or transformation of the BLUP equations by pre- and post- multiplying by the relationship matrix (Henderson, 1976). Inversion was impractical because in matrixes of large size, and pre- and post- multiplying reduced the efficiency of an iterative solution (Henderson, 1976). Both routines were not suitable

for utilizing A matrices in animal breeding applications involving hundreds of thousands of animals (Henderson, 1976).

A milestone to the implementation of sophisticated mixed models on field data sets was achieved by the discovery of methods for computing the elements of the inverse relationship matrix without computing the relationship matrix itself (Henderson, 1975; Quaas, 1976). In 1976, Henderson published a method that allowed for direct computation of the inverse relationship matrix (A^{-1}) from pedigree information without computing the A matrix itself (Henderson, 1976). The method was based on the fact that a vector of additive genetic values can be written as the product of a triangular matrix and a vector of uncorrelated random variables with equal variances (Henderson, 1976). The relationship matrix can be written (Mrode, 2005) as:

$$\mathbf{A = TDT'}$$

where T is a lower triangular matrix and D is a diagonal matrix. The matrix T traces the flow of genes from one generation to the other, and accounts only for direct parent-offspring relationships (Mrode, 2005). The matrix D contains the variance and covariance for Mendelian sampling (Mrode, 2005). The inverse relationship matrix can be written (Mrode, 2005) as:

$$\mathbf{A^{-1} = (T^{-1})'D^{-1}T^{-1}}$$

where the diagonal elements of D^{-1} are reciprocals of the diagonal elements of D (Mrode, 2005). T^{-1} is a lower matrix with ones on the diagonal, and non-zero elements to the left of the diagonal in the row for animal I are -0.5 for columns corresponding to parents. T^{-1} can be derived as I – M, where I is an identity matrix of the order of animals on the pedigree and M is a matrix of the contributions of gametes from parents to progeny (Mrode, 2005).

The first sire models did not account for relationships between sires (Golden et al., 2009). Not until the 1980s was A^{-1} computed in NCEs, accounting for relationships among animals. The first implementations of A^{-1} did not account for inbreeding of animals during construction, however, methods to determine inbreeding on all animals in large data sets were resolved (Golden et al., 1991: Meuwissen and Luo, 1992). By the mid-1990s most NCEs had evolved to account for inbreeding in the construction of A^{-1} (Golden et al., 2009). Utilizing the additional information provided by A^{-1} reduced the prediction error variance and in turn lead to an increase in the accuracy of selection (Henderson, 1976).

In addition to improved statistical procedures, important discoveries and technological developments were being made in other disciplines that would allow for implementation of increasingly sophisticated models (Golden et al., 2009). Performance limitations of computers posed a particular challenge from 1972 through 1995 (Golden et al., 2009). The first NCE predictions were generated using computers housed at university computer centers or owned by companies offering time-sharing service (Golden et al., 2009). Computers at this time were expensive and relatively slow with small memory and storage capacity (Golden et al., 2009). Compromises were often made to a model to make analysis possible. The first BLUP models used from 1974 to 1979 in cattle evaluations for Angus, Hereford, Polled Hereford, Shorthorn, Limousin, and Red Angus breeds in the United States were univariate and had only contemporary group and sire effects included (Benyshek et al., 1991). Over time, additions to the models were made in attempt to reduce the effect of unequal treatment of progeny, such as a sire x contemporary group interaction effect (Golden et al., 2009). Analysis of this nature resulted in predictions of performance of the progeny of a sire equivalent to one-half the breeding value of the sire. These predictions were labeled EPD (Golden et al., 2009).

Data from most breed association sire evaluation programs were analyzed using the mixed model procedures developed by Henderson (Willham, 1979). Contemporary group equations were first absorbed into the sire equations and then the lead diagonal of the reduced normal sire equations was augmented by the ratio of the error variance to the sire variance to create a unique solution for the random sire effects (Willham, 1979). The random sire effects were regressed for number and distribution of progeny and incomplete heritability (Willham, 1979). Originally, it was of interest to find the percentage of herd differences that were genetic (Willham, 1979). This percentage could be applied in general to include herd differences with within herd differences so animals could be compared over herds (Willham, 1979). Solving for herd and contemporary groups with herds as fixed effects and random animal effects simultaneously provided a better way to evaluate environmental differences (Willham, 1979).

The first BLUP-based NCE of the Limousin breed was the first to use field data collected from members of the North American Limousin Foundation (Golden et al., 2009). BLUP equations were steadily applied to field data in most breed association sire evaluations from 1974 to 1976 (Diel, 1993), until all NCE conducted by the mid-1980s were predominantly from field data (Golden et al., 2009). Evolution of BLUP models resulted in improvements in predictions by overcoming approximations and assumptions that created bias and decreased accuracy (Golden et al., 2009). The Animal Model was developed by Quaas and Pollak in late 1979/early 1980, which provided breeding values on the entire pedigree (Quaas and Pollak, 1980). Due to the computational complexity of this model, they quickly developed the reduced animal model (RAM) in 1980. This model provided equivalent solutions to the animal model, but the overall number of equations to solve was greatly reduced by absorbing equations for non-parent animals. The evolution from the use of univariate sire models to multivariate animal models in the NCE

occurred in a series of steps driven by improvements in computer power and developments in computational methods (Golden et al., 2009). In 1984, direct additive effects for the dams were included in the model for several breeds along with direct effects for sires (Benyshek, 1991). Including the dam allowed for pedigree connections to be made to account for nonrandom mating of dams but increased the computing required to form the inverse numerator relationship matrix (Golden et al., 2009). Including dams in the analysis would later allow for inclusion of an additive effect due to the dam, or the additive maternal effect (Willham, 1972). Breed associations would begin including one-half of the value of additive maternal predictions in their publications, calling them milk or maternal milk (Golden et al., 2009). A prediction of weaning weight called total maternal was eventually included in breed association publications, which represented one-half the direct weaning weight EPD of a sire plus its maternal milk EPD. This calculation reflected the impact of the daughters of a sire on the weaning performance of its grand-offspring (Golden et al., 2009). Researchers at Cornell University chose to implement a multivariate model in 1983 that included birth weight, weaning weight, and postweaning body weight gain to yearling age, with maternal effects for both weaning weight and birth weight (Golden et al., 2009). The multivariate approach allowed for an increase in accuracy and the ability to account for some of the selection bias that resulted from culling animals at previous ages (Golden et al., 2009). In 1985 and 1986, the previously discussed reduced animal models (RAM: Quaas and Pollak, 1980) were implemented by researchers at both the University of Georgia and Colorado State University in the form of multivariate models. Each of the four institutions that were preforming this generation of NCE migrated their analysis to multivariate animal models as computer capacity and power increased in the late 1980s and early 1990s (Golden et al., 2009).

Strong motivation to develop methods allowing comparisons of breeding merit between breeds arose as a result of opportunities to market composite seedstock to commercial producers, some of whom were crossbreeding (Golden et al., 2009). Many breed associations also had grading-up programs that resulted in a significant part of their pedigree records being from animals of other breeds, and their performance data resulting from animals with mixed breed composition (Golden et al., 2009). Willham (1979) predicted the direction on breeds would be toward animals that can perform well in rotational crossbreeding systems in commercial production. Technical solutions to allow comparisons of genetic prediction between breeds that used combined data sets or data sets with multibreed data were presented by researchers such as Elzo and Famula (1985) and Elzo and Bradford (1985) for sire-maternal grandsire models. These methods were extended to animal models by Arnold et al., (1992). Data structures commonly found in field data were not suited to these techniques due to confounding, particularly between breed additive direct effects, additive maternal effects, heterosis effects, and contemporary group effects (Golden et al., 2009). Reluctance to combine different breed organization data processing duties so that uniform procedures could be used to eliminate duplicate records and have consistent definitions of effects was also problematic (Golden et al., 2009). Issues in analyzing data on the same breed from multiple countries were often functions of multiple breed organizations cooperating on integration of data (Golden et al., 2009). Other factors that reinforced the reluctance of breed associations to adopt multibreed analysis included the issue that the combinations of data sets would result in substantial changes in base and scale that would be concerning to members (Golden et al., 2009). Methods were developed for comparing EPD from multiple breeds that did not require significant cooperation from the breed associations (Notter and Cundiff, 1991; Nunez-Dominguez et al., 1993). The method resulted in

tables that contained factors for adjusting EPD from different breed associations to values that were comparable (Golden et al., 2009).

The effect of a gene is not expected to be the same in every population, due to dominance effects and differences in gene frequencies between populations (Garrick, 2006). EPDs often perform reasonably well in predicting differences in performance, even in different populations and different breeds, with two exceptions (Garrick, 2006). The first is when environmental circumstances differ in nutritional, climatic, or disease stress. The second occurs when bulls or their mates represent more than one distinct breed or cross (Garrick, 2006). EPDs do not perform well with such crossbreeding for several reasons (Garrick, 2006). EPDs from each breed may be on a different base (Garrick, 2006). Heterosis or hybrid vigor in crossbred animals provides a second explanation (Garrick, 2006). Finally, the average effect of an allele substitution depends on genetic background (Garrick, 2006).

Heterosis must be taken into account in order to predict progeny performance in across-breed settings (Garrick, 2006). Heterosis values may be different for each trait and may illustrate genetic distance between breeds, as heterosis recovers losses in performance from inbreeding (Garrick, 2006). Heterosis among similar breeds is expected to be more similar than among breeds of different backgrounds (Garrick, 2006).

New Era

Quickly changing methods and great computing complexity led breed associations aligned with land grant universities for cattle evaluation. By the 1980's, four universities were responsible for the entire U. S. cattle evaluation (Garrick, 2005). Competition between the four land grant universities encouraged development of new algorithms that allowed more rapid

computations, providing for larger data sets with more animals, more correlated traits, or more appropriate models to describe phenotypic performance (Garrick, 2009).

Evaluations throughout this time became increasingly sophisticated to include maternal effects, threshold traits, heterosis, and genomic information (Garrick, 2005). Threshold traits Gianola and Foulley, 1983) were first implemented by Cornell University to predict additive genetic direct and maternal effects on calving ease in the 1985 publication of the American Simmental Association NCE. This method was later used to analyze categorically observed traits such as stayability (Snelling et al., 1995) and heifer pregnancy rate (Evans et al., 1999), which were originally published in the 1995 and 1997 NCE of the Red Angus Association of America. The North American Limousin Foundation was the first to publish and EPD for docility score in 1998 (Kuehn et al., 1998). Other breed associations quickly integrated these calculations into their own NCE (Golden et al., 2009).

Changes in structure and funding later dictated that genetic evaluation by universities was no longer sustainable. Over time with the support of the National Beef Cattle Genetic Evaluation Consortium, researchers were in a position to reduce their role in servicing NCE and focus on technological and scientific developments (Golden et al., 2009).

Computational aspects of producing genetic evaluations migrated from land-grand universities to breed associations (Garrick, 2009). Producing meaningful and accurate genetic predictions and supplying quality services to manage data from which predictions are approved became an important role of the associations (Golden et al., 2009). Several breed associations developed the capability to complete routine genetic evaluation analysis in their own in-house systems (Golden et al., 2009). Analysis routinely began with collection of raw performance data from seedstock producers (Middleton and Gibb, 1991). Data was then submitted to a breed

association, which performed within-herd analysis, including the calculation of adjusted measures and within-herd ratios (Middleton and Gibb, 1991) which were returned to the producer. Breed associations, at intervals, would take the accumulated data and conduct a national across-herd genetic evaluation (Middleton and Gibb, 1991). The results of this analysis were used in improving the performance program by providing updated predictors of genetic merit for the breed (Middleton and Gibb, 1991).

Economically Relevant Traits

The focus of animal breeding research shifted in recent years to ERT versus indicator traits being included in genetic evaluations (Golden et al., 2009). Motivation for development of BCI systems throughout the 1900s was the belief that knowledge of breeding values and heterosis effects allowed for determining the consequences of different mating options (Garrick, 2009). Information on the breeding values of animals was used to shift populations of cattle toward a breeding goal (Garrick, 2009). Foundation principles for a sound breeding program are animal performance for ERT and the incorporation of that performance into a single index of aggregate economic merit (Garrick, 2009). Development of a breeding program can be divided into 3 steps. The first step is defining traits that influence the breeding goal. The second step is determining the relative emphasis to put on each trait influencing the breeding goal. Finally, value and cost of using pedigree, phenotypic and molecular information to predict each trait in the list must be quantified (Garrick, 2009). This step involves determining which animals need measured for which traits at what stage of life, what to do with elite animals, determining a mating plan, and performing an economic analysis of total breeding program costs and benefits (Garrick, 2009).

Instead of adopting this approach to genetic evaluation, industry has often undertaken a data driven approach that has led to the overemphasis of evaluation on productive traits, disregarding true ERT such as reproduction, animal health, and feed requirements (Garrick, 2009). Beef performance has traditionally been categorized into three areas: growth/efficiency, reproductive/maternal, and carcass/end-product (Middleton and Gibb, 1991). Products of evaluation programs of these areas are descriptive rather than directional (Willham, 1979). Expected progeny differences are evaluated for several traits and sires are ranked into categories for each trait (Willham, 1979). This is done rather than defining direction and rewarding superior sires in overall merit (Willham, 1979). No well-defined breeding goal exists for national beef cattle improvement, with different breeders in different sectors of the industry having different goals for selection (Garrick, 2009). In the cow-calf sector, principal determinants of income are number of sale animals and value per animal. Number of sale animals in this sector is dictated by the number of breeding females, reproductive performance, calf survival, and replacement rate (Garrick, 2009). Value of each sale animal is dictated by gender, body weight at time of sale, and age. (Garrick, 2009). Expenses in this sector include feed costs, veterinary and animal health costs, and labor (Garrick, 2009). The feedlot sector, in contrast, determines revenue by number of sale animals, body weight at time of sale, and survival rate to sale (Garrick, 2009). Expenses in this sector include feed, yardage, labor, and animal health (Garrick, 2009). In the processing sector, income is the total of saleable meat and by-products (Garrick, 2009). Purchase body weight, dressing percentage, and meat yield are important factors of income (Garrick, 2009).

By the year 2000, the number of EPD published by each breed association had expanded to the point where some NCE had more than 15 different EPD (Golden et al., 2009). Many of the EPD were predictions used to influence the same trait in the breeding objective (Golden et al.,

2009). Examples include carcass EPD and direct ultrasound EPD, birth weight EPD and calving ease EPD, or scrotal circumference EPD and heifer pregnancy rate EPD (Golden et al., 2009). The volume and sometimes contradictory predictions of EPD lead to concerns by breeders and breed associations alike (Golden et al., 2009).

A solution proposed to BIF stated that EPD should only be published for a trait that was directly associated with a cost of production or revenue source. In other words, EPD should only be published on ERT (Golden et al., 2009). For example, scrotal circumference has no direct economic value, but was used as an indicator for age at puberty of a sire's daughters (Golden et al., 2009), which is an indicator for heifer pregnancy. As the true ERT, only heifer pregnancy rate should be published (Golden et al., 2009). If scrotal circumference EPD and heifer pregnancy EPD were both used in a breeding objective, the accuracy of selection would decrease compared with only using the heifer pregnancy EPD (Golden et al., 2009). Data for indicator traits should be incorporated into the analysis that produced the EPD for the ERT but should not be individually published (Golden et al., 2009). As the amount of performance information increases, the problem of managing the data and using them effectively will intensify (Middleton and Gibb, 1991). Tools that can customize delivery to a particular cattle producer's needs and integrate genetic management with health, nutritional, and financial management are needed (Middleton and Gibb, 1991).

The focus on breed associations in genetic prediction has had its drawbacks: the connection between registry and performance programs has contributed to the problem of selective reporting of data, because unregistered calves often remain unrecorded (Middleton and Gibb, 1991). Genetic evaluations going breed association centered also delayed the introduction of national across-breed evaluations for all breeds and breed crosses of cattle (Garrick, 2009).

Estimation of breed and heterosis require data that include pure and crossbred animals in the same contemporary groups. While the U. S. Meat Animal Research Center has data of this nature in the Germ Plasm Evaluation Program for Across Breed Evaluation (Notter and Cundiff, 1991) breed associations traditionally did not record this type of data (Garrick, 2009). The National Beef Cattle Evaluation Consortium promotes a vision of a single across breed data base and a single entity to undertake genetic evaluation in the future (Garrick, 2009). Computer platforms used by the breed associations for database activities are also not the same as those that are optimal for numerical analysis, making genetic evaluation challenging for certain traits (Garrick, 2009).

An important aspect of a breed association program for collecting data is the recording of a reason code when an animal is removed from a breeder's inventory (Middleton and Gibb, 1991). A breeder may choose from among 20 codes that indicate death or culling for reasons such as injury, disease, prolapse, unsoundness, infertility, pinkeye, genetic abnormality, and inferior production (Middleton and Gibb, 1991). Though many associations have broad programs for the collection of fitness data, they represent only a limited subset of possible traits (Middleton and Gibb, 1991).

In the future, ERTs could include disease traits, customized weight traits, and even producer-specific indexes (Garrick, 2005). Research in these areas has often focused on problems easy to solve rather than on problems that will benefit genetic improvements (Garrick, 2009). For example, research and evaluation in fertility traits has been limited in the past in the absence of total herd reporting. Females without offspring are generally unfairly discounted due to neglect of owner to record offspring or reproductive failure (Garrick, 2009).

Future research on non-traditional genetic evaluation systems that focus solely on ERT is warranted.

Feed Efficiency

A practical measure of feed efficiency awaits development and is important to both the feedlot segment and the commercial cow/calf producer. In comparison to other meat animal species like poultry or swine, the physiological differences of beef cattle contribute to lesser production efficiency. Feed conversion rate is a major inefficiency in beef cattle. Poultry, for example, have a feed conversion rate of 2:1, meaning that an animal eats 2 kg of feed per 1 kg of bodyweight gain. The beef animal's conversion rate, alternatively, is greater than 6 kg of feed per 1 kg of bodyweight gain (Shike, 2012). Most beef production costs can be attributed to feed costs, so feed efficiency has been recognized as an economically important trait for selection in beef cattle (Koch et al., 1963; Dickerson et al., 1974). Limited data has been collected by the breed associations, in part because of the difficulty and expense of measuring intake under typical production conditions (Middleton and Gibb, 1991). Individual feed intake measurements needed for direct selection on feed efficiency are costly enough to preclude widespread on-farm field data collection, although the expense may be justified for central bull test or research facilities (Snelling et al., 2011). Research to further characterize genetic variation in utilization of feed energy will build the base for effective selection programs to reduce feed energy requirements (Rolfe et al., 2011).

Feed efficiency is a function of both body weight gain and feed consumption. It is defined by Koch et al. (1963) as the gain in body weight resulting from consumption of a given amount of food, or the inverse. Parameter estimates of feed efficiency are moderately heritable, so improving feed efficiency is possible through genetic selection (Koch et al., 1963).

Feed Intake

Feed cost for maintenance is estimated to represent 60 to 65% of total feed requirements for the cowherd, with considerable variation among individuals independent of body size (Montano-Bermudez et al., 1990: Parnell et al., 1994). Consequently, a 10% improvement in feed intake can increase potential profits by 43% (Fox et al., 2001). Phenotype recording for feed intake is essential to capture the maximum amount of variability in feed intake models (Fox et al., 2001). Feed intake must be collected continuously throughout the testing period to be represented as a single number that records average feed intake (Hill, 2012). GrowSafe® Systems, Ltd. (Airdrie, Alberta, Canada), Insentec® Systems (Marknesse, Netherlands), and the Calan® Gate System (American Calan, Northwood, New Hampshire) are all suitable for collecting feed intake data. Advancements in feeding technologies have let to feed intake being readily used as a predictor for feed efficiency. Feed intake systems utilize ear tag identification equipped with radio frequency and electronic scales to create intake records.

Tests at centralized testing stations are expensive and inconvenient. To minimize the cost of testing, tests should be optimized in test length and amount of data collected without compromising accuracy (Archer et al., 1997). Shortening the period of recording individual feed intake may improve selection response for feed efficiency by increasing the number of cattle that can be recorded (Thallman et al., 2018). Studies have shown heritability estimates of feed conversion ratio (FCR) peak at 56-d, with selection efficiency stabilizing at 70-d (Archer et al., 1997). Estimates of heritability for residual feed intake (RFI) were found to maximize at 70-d, with a 70-d test efficiency of selection of 0.99 (Archer et al., 1997). A 70-d test is suitable for assessing growth rate, feed conversion, and RFI without compromising accuracy of measurement (Archer et al., 1997). Recent studies involving variance components, heritability, and correlation

estimates of feed intake in beef cattle suggest a further shortened 35-d test might be sufficient (Archer et al., 1997; Wang et al., 2006). Thallman and others (2018) found a genetic 0.995 between measures of dry matter intake (DMI) for the first 42 days of the test period and DMI at an average of 83 days. Shortening the testing interval would allow for decreased testing costs while also accelerating genetic improvement in feed efficiency (Archer et al., 1999). This would occur by increasing selection intensity because a greater number of animals could be tested in the same amount of time.

A 42-d test is currently recommended by BIF for feed intake records to be included in the NCE (BIF, 2016). Intake data should be collected post-weaning, with weaning data being collected before animals reach 260 d of age (BIF, 2016). Animals starting in feed intake tests should be older than 240 d of age, but younger than 390 d of age upon completion (BIF, 2016). An acclimation period of at least 21 d should be included for animals to adapt to testing facility and test diets (BIF, 2016). Animals should also have start ages within 60 d of each other to be included in the same feed efficiency contemporary group (BIF, 2016). All animals in the same test should be on the same diet, with feed provided ad libitum (BIF, 2016).

Gain

Cost of gain is a valuable ERT (Swiger et al., 1961). Studies have shown 10% greater gains during growing and finishing period improves profit by 18% for group fed cattle (Fox et al., 2001). Measuring rate of gain requires two or more measurements to be taken at different times (Hill, 2012). Time periods between recorded weights must be large enough for the change in weights to be larger than the error of each individual measurement (Hill, 2012). Studies have shown that selection efficiency for average daily gain (ADG) stabilizes, and environmental variance is at a minimum at 70-d (Archer et al., 1997). Heritability estimates are also highest

between 52-d and 70-d for ADG (Archer et al., 1997). No loss of accuracy occurs with weights taken every 2 weeks, but accuracy decreases with weights taken every 5 weeks (Archer et al., 1997). Current BIF guidelines recommend at least a 70-d gain collection to derive phenotypes for feed efficiency (BIF, 2010). The regression equation for on-test ADG is:

$$\mathbf{Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + e}$$

where β_0 is initial body weight, β_1 is the amount of weight gained per d, β_2 is the quadratic term representing the curvature of the growth curve, and e is the error term (BIF, 2010). Rolfe et al. (2011) found ADG to be moderately heritable with an estimate of 0.26. On-test gain evaluations are derived differently than post weaning gains reported in NCE. On-test ADG is not required for evaluation of growth in NCE (Hill, 2012). Producers submit 205-d and 365-d weights and dates for each animal for NCE evaluation, which is used to calculate postweaning gain (Hill, 2012). The difference in data points included in NCE postweaning and ADG on-test gains elicit different degrees of variation in the two phenotypes (Hill, 2012). Performance test gain variation is less than postweaning gain because the number of test days is less than the postweaning time interval (Hill, 2012). Genetic correlation between ADG over the first 42 days on test and postweaning ADG calculated as the difference between yearling and weaning weights was estimated by Thallman et al., (2018) at 0.852. Genetic correlation between ADG averaged at 83 days and postweaning ADG was estimated at 0.822 (Thallman et al., 2018). High correlations indicate progress in selection on gain can be made through selection on postweaning ADG. In related research, MacNeil et al., (2017) evaluated alternative expressions of genetic merit for cow efficiency. The study found ADG from birth to weaning to be heritable at 0.27 and cow weight (CWT) to be heritable at 0.45. Estimates of repeatability for ADG and CWT were 0.42 and 0.67, respectively, indicating both ADG and CWT are repeatable across a

female's lifetime. However, conflicting research by MacNeil et al., (2019) found small genetic correlations between ADG recorded concurrently with feed intake and ADG from related bulls reared on farm. This low correlation could complicate the decoupling of phenotypes for feed intake and growth in an evaluation of feed efficiency.

Tools for Selection

Upon completion of the test period, feed intake and gain records can be compiled to create tools for genetic selection.

Feed conversion ratio is defined as the ratio of amount of feed consumed per the amount of BW gain over a set time period (Archer et al., 1998). Also known as gross efficiency, FCR is a common and easily calculated phenotype (Archer et al., 1998). Feed conversion is generally collected on a set time interval to measure growth and feed intake (Archer et al., 1998). This measure is negatively correlated with mature size, maintenance energy, yearling BW, and postweaning ADG (Koots et al., 1994). While direct selection for FCR increases genetic merit for growth, it also increases mature size and maintenance requirements (Koots et al., 1994b). This leads to an increase in feed consumption, which is antagonistic to overall improvements in system efficiency (Koots et al., 1994).

Residual body weight gain (RG) is derived as the difference predicted and actual BW gain (Koch et al., 1963). Greater RG values are desirable and indicate greater gain with a set amount of feed (Crowley et al., 2010). Calculation of RG is as follows:

$$\mathbf{RG = ADG - (b_1 WT^{0.75} + b_2 FI + b_3(\Delta)Fat + b_4 WT^{0.75} * Fat)}$$

where ADG was calculated as a regression of weight on time, WT is body weight gain, FI is feed intake, and Fat is back fat thickness. Regression coefficients of b_1, b_2, b_3, and b_4

correspond to the components of $WT^{0.75}$, FI, change in Fat, and $WT^{0.75}$*Fat, respectively (Berry and Pryce, 2014). Residual gain places a greater emphasis on the gain component rather than intake, unlike RFI. Parameters like RFI and RG may inhibit producers from reaching maximum profitability by forcing them to emphasize either input or output costs (Crowley et al., 2010).

Residual (net) feed intake was proposed by Koch et al. (1963) as an alternate measure of feed efficiency. It is defined as the difference between actual feed intake and the expected feed requirements for body weight maintenance and some measure of production (Arthur et al., 2001a). Calculation of RFI is as follows:

RFI = Actual Feed Intake – Predicted Feed Intake.

Predicted feed intake is calculated as:

$$\textbf{Predicted Feed Intake} = b_M(BW)^{0.75} + b_P(\textbf{Amount of Production})$$

Where b_M is the amount of feed required per metabolic unit of body size, b_P is the amount of feed required per unit of production, and BW is body weight (Nielsen et al., 2013). Arthur et al. (2001a) found RFI to have a moderate heritability of 0.39 ± 0.03. This is consistent with other estimates in the literature, with most of the values falling in the moderate range (Robinson et al., 1999; Herd and Bishop 2000; Arthur et al., 2001b). A somewhat higher estimate of heritability can be found in Kelly et al., (2011), who found the heritability of residual energy intake (comparable to RFI) to be 0.50 when using live weight and ADG as energy sinks. The same study found the heritability of REI to be 0.36 when using carcass weight and carcass fat as energy sinks. Measures of RFI are phenotypically independent of growth and mature size, which allows for comparison of animals at different stages of production (Archer et al., 1999).

Maintenance energy (ME) is described as the ratio of body weight to feed intake at zero body weight change (Ferrell and Jenkins, 1985). Requirements for ME include essential

metabolic processes, physical activity, and body temperature control (Koong et al., 1982). Maintenance efficiency lacks practicality, as it cannot be measured in growing animals. True measurements of ME require animals to be held at a constant live weight for almost 2 years (Taylor et al., 1981).

Efficiency Trait Correlations

Arthur et al. (2001a) found FCR was genetically (r_g = 0.66) and phenotypically (r_p = 0.53) correlated with RFI. These estimates are somewhat lower than the findings of Fan et al. (1995) who reported a genetic correlation between RFI and FCR of 0.90 and 1.00 for Angus and Hereford bulls respectively, and phenotypic correlations of 0.91 and 0.97 respectively. Koots et al. (1994) who summarized available estimates between feed intake and feed conversion ratio as 0.71 and 0.75 for genetic and phenotypic correlations, respectively. Feed conversion ratio was negatively correlated (r_g = -0.62, r_p = -0.74) with ADG (Arthur et al., 2001a). Average daily gain was found to have a strong genetic correlation with mid-test body weight (0.86) by Rolfe et al. (2011).

Kelly et al., (2011) found correlations between REI and the production traits of carcass weight, dressing difference, and dressing percentage to imply that selection on REI would increase carcass weight, lower the dressing difference and increase dressing percentage.

MacNeil et al., (2013) estimated strong genetic correlations for MBW with ADG, MBW with average daily feed intake (DFI) and ADG with DFI to be 0.79, 0.54, and 0.66, respectively. The study also compared alternative measures of feed efficiency, including RFI, RG, and residual intake and gain (RIG) with the traditional parameters of MBW, ADG, and DFI. Spearman rank correlations between the measures found the various measures of feed efficiency to be highly correlated.

Genomic Enhanced Feed Efficiency

Genetic differences among animals tested for feed efficiency and known relatives can be predicted using BLUP equations, though accuracy of resulting EBV can be limited by available data. (Snelling et al., 2011). Accuracies of parents will increase as progeny records accumulate, but young animals completing the postweaning intake test will have a low-accuracy nonparent EBV (Snelling et al., 2011). Accuracy of the EBV may increase with multiple trait evaluation including traits correlated with intake and efficiency, with further increases in accuracy achieved if DNA markers associated with intake and efficiency can be identified and if information from genotypes is included in genetic evaluations (Snelling et al., 2011). Genomic predictors may lessen the need for phenotypic data to be collected for feed intake genetic evaluations (Rolfe et al., 2011). Genome-wide association studies (GWAS) using the BovineSNP50 BeadChip (50K) assay (Illumina Inc., San Diego, CA) have identified SNP associated with economically important traits in beef and dairy cattle (Cole et al., 2009; Snelling et al., 2010: Bolormaa et al., 2011). The effects of individual and sets of SNPs associated with DMI, metabolic mid-test BW, BW gain, and feed efficiency, expressed as phenotypic and genetic RFI were estimated from body weight and individual feed intake by Snelling et al., in 2011. Effects of 44,163 SNP having minor allele frequencies >0.05 were estimated in this study using a mixed model that included genotype, breed composition, heterosis, age of dam, and slaughter date contemporary groups as fixed effects, and random additive genetic effects with pedigree relationships among animals (Snelling et al., 2011). Variance in the population attributable to sets of SNPs was estimated with models that partitioned the additive genetic effect into a polygenic component attributable to genotypic relationships (Snelling et al., 2011). BovineSNP50 genotypes of the steers were used in GWAS to determine associations between each of the 50K SNP and 140-d BW gain (GN),

DMI, mid-test (d 70) $BW^{.75}$ (MWT), phenotypic residual feed intake (RFI_p) and genetic residual feed intake (RFI_g). The SNP were ranked by significance of association with each trait, and genotypic variances attributable to sets of SNPs were then estimated (Snelling et al., 2011). Trait-specific sets were evaluated only on the associated trait, while sets evaluated on all traits were the full set of 44,163 SNP with minor allele frequencies > 0.05 and the SNP strongly associated ($P < 0.001$) with any trait (Snelling et al., 2011) Ninety SNP were strongly associated ($P < 0.0001$) with at least 1 efficiency or component trait; these accounted for 28 to 46% of the total additive genetic variance of each trait (Snelling et al., 2011). Sets containing 96 SNP having the strongest associations with each trait explained 50 to 97% of additive variance for that trait (Snelling et al., 2011).

Sets of SNP selected by association appear to account for meaningful phenotypic variation, enabling accuracy to be increased by including genotype information in the evaluation of intake and efficiency traits (Snelling et al., 2011). Accuracy gains achieved by including DNA information in an evaluation increase with size of the predictor populations used (VanRaden et al., 2009; Wiggans et al., 2010). In a study by Snelling et al. (2011) expected accuracy of steer breeding values predicted with pedigree and genotypic relationships exceeded the accuracy of their sires predicted without genotypic information. Expected accuracy was increased by including SNP association with phenotypes (Snelling et al., 2011). Expected accuracies of steers with trait-specific sets of 96 to 1,536 SNP were consistently greater than accuracies of sires predicted without genotypes having greater than 10 progeny (Snelling et al., 2011). Accuracies of evaluations incorporating genotypes of SNP strongly associated ($P < 0.001$) with their respective traits increased nonparent accuracies by 2 progeny for both RFI_p and RFI_g and by 4 progeny for GN, MWT, and DMI (Snelling et al., 2011). Snelling et al. (2011) showed that traits

with the smallest estimated heritability, BW gain in their case, benefit most from incorporation of genotypic information, with an increased accuracy equal to roughly 20 tested progeny. This result is consistent with the findings of Van Raden et al. (2009) who found the greatest daughter equivalent benefit for the least heritable trait. Gains in accuracy were not sufficient to encourage that performance testing be replaced by genotyping and genomic evaluations (Snelling et al., 2011). Increases in accuracy by adding genomic information, however, encourage augmenting measures of feedlot intake and BW gain with genotypes to add accuracy to selection of young animals (Snelling et al., 2011).

Feed Efficiency Indexes

Selection index theory can be used to combine multiple traits with their economic values to predict an animal's aggregate breeding value (Henderson, 1963). With correctly weighted traits, an index is a more efficient selection tool than single-trait selection or selection for several traits with independent culling levels (Hazel and Lush, 1943). Index theory using multiple trait NCE EBV models provides a robust measure of selection that allows for selection of both gain and intake traits at once (MacNeil et al., 1997).

Early methodologies to create linear indexes for making improvements on feed efficiency were first explored by Koch et al. (1963). High correlations between growth and feed efficiency in addition to the cost of collecting feed intake led to only growth data included in feed efficiency phenotypes (Koch et al., 1963). More recently, because of increased feed costs and more efficient measuring systems, feed intake phenotypes in selection indices have been more prevalent (MacNeil et al., 2011). Use of an index increases response to selection of feed efficiency, eliciting greater genetic progress (Lin, 1980; Lin & Aggrey, 2013).

Rolfe et al. (2011) evaluated the genetic and economic progress made by selecting on different feed efficiency indexes. Expected responses in DMI and GAIN given selection on measures of RFI were compared with expected responses following selection on single traits of GAIN or DMI. Kennedy et al. (1993) demonstrated that RFI is equivalent to a selection index. The equivalent index for the Rolfe et al. (2011) study was as follows:

$$\mathbf{I_1 = DMI - (0.338)SUMWT^{0.75} - (1.750)GAIN}$$

or the phenotypic index of RFI where $SUMWT^{0.75}$ is the individual animal quadratic regression of BW on days on feed from 0 to 140 days.

Development of a restricted index, based on genotypic regression so no genetic relationship with component output traits existed (Kennedy et al., 1993), yielded the genotypic index of RFI as follows:

$$\mathbf{I_2 = DMI + (0.542)SUMWT^{0.75} + (0.539)GAIN}$$

The first of two economic selection indexes was developed as follows:

$$\mathbf{I_3 = DMI - (0.039)SUMWT^{0.75} - (7.531)GAIN_{140}}$$

Or an economic selection index based on overall breeding value. Indexes were constructed based on a simple economic model and definition of overall net merit breeding value. Relative economic weights used were ($/kg; 2005 to 2009 average for US beef production, http://www.nass.usda. gov/QuickStats/Create_Federal_All.jsp) of −0.134, 2.65, and 2.04 for DMI (corn), body weight at day 0 of the feeding trial (feeder calves), and body weight at day 140 of the feeding trial (slaughter cattle), respectively, and basing the phenotypic data part of the index on only DMI, SUMWT0.75, and GAIN at 140 days (i.e., the same component traits as RFI). The second of two economic selection indexes based on overall breeding value was developed as follows:

$$I_4 = RFI - (12.2)GAIN_{140}$$

Rolfe et al. (2011) found that feed intake and feed costs could be reduced through selection. Body weight and feed intake were found to be positively correlated, so selection that placed positive emphasis on growth in addition to negative emphasis on feed intake would be the most promising to yield economic results (Rolfe et al., 2011). Expected responses per generation for DMI and GAIN (and relative cost of both) were used to evaluation the strengths and weaknesses of selection on each index. An index including GAIN and RFI gave the best economic outcome in this experiment (Rolfe et al., 2011). Macneil et al., (2017) studied the value of six different indexes of cow efficiency, which compared increasing output and decreasing input simultaneously, increasing output and holding input constant, or holding output constant and decreasing input. Indexes that simultaneously increase output and reduce input were recommended as most effective.

Sustained Fertility

Stayability

Sustained cow fertility and long-term production are important contributors to the long-term profitability of the cow herd (Enns et al., 2005). Under typical market conditions, a beef cow must remain in production for many years for revenue created to offset maintenance and development costs (Snelling et al., 1995). For a herd to be profitable, the number of cows remaining in production past the breakeven age must outnumber the cows that were culled before that age (Snelling et al., 1995). Increased reproductive performance impacts sale weights at weaning in two ways. Fewer heifer replacements are required so more female calves are sold at weaning (Garrick, 2006). The cow herd also has a smaller fraction of first calf heifers and a larger fraction of mature cows. This increases average weaning weight as mature cows wean

larger calves than first calf heifers (Garrick, 2006). The combined effect is an increase of 30 lb saleable weaning weight per cow (Garrick, 2006).

Stayability is the probability of surviving to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981). Predictions of genetic merit of stayability may allow selection of animals whose daughters are most likely to remain in production long enough to be profitable (Snelling et al., 1995). Beef cattle stayablity is traditionally defined as the probability a cow will remain in the herd until 6 yr of age given she has calved once (Brigham et al., 2007). In test herds used by Snelling et al., (1995), culling of nonpregnant cows was employed which meant stayability of a dam at a given age could be measured by the potential number of calves produced by that age. Culling of nonpregnant cows also meant stayability was a measurement of continuous fertility to each age (Snelling et al., 1995). Binary observations, with 0 indicating failure and 1 indicating success, were assigned to all dams old enough to have had the required number of calves (Snelling et al., 1995). Observations of failure on culled cows not old enough to have had the required number of cows were excluded (Snelling et al., 1995). Dams with two or more calves at three years of age were assigned a 1, and those with one calf were assigned a 0 (Snelling et al., 1995). Dams that were 2 yr old in the last year of available data had observations considered unknown (Snelling et al., 1995). Similar coding followed for S(5|1), S(8|1), and S(11|1). Animals not recorded as parents were not assigned an observation (Snelling et al., 1995).

In other analysis, dams must have been at least as old as the stayability definition in order to be eligible to receive a stayability observation (Brigham et al., 2007). Dams that calved after the cutoff date for the specific stayability observation received a 1, while dams that did not calve received a 0. Brigham et al., (2007) formed independent data sets for each stayability age, so

animals included in an older stayability definition were not incorporated into younger categories (Brigham et al., 2007). For example, if a female is included in the 5 yr age group, she would not be included in 3 yr, 4 yr, or 6 yr age groups (Brigham et al., 2007).

Analyses from Snelling et al., (1995) included year of birth contemporary group as the only fixed effect, with animal or sire as a random effect. Contemporary grouping based on breeder code of the dam and calf for each separate stayability definition have also been used (Brigham et al., 2007).

Single trait analyses were conducted by Snelling et al., (1995) on S(2|1), S(5|1), S(8|1), and S(11|1). Consideration of more than one stayability trait was not possible because of the binary nature of both phenotypes (Snelling et al., 1195). Brigham et al, (2007) conduced separate stayability analysis for four different age groups, 3 yr, 4 yr, 5 yr, and 6 yr of age.

Heritability estimates of S(2|1) ranged from 0.01 to 0.09 for the two herds used by Snelling et al., (1995). Estimates of heritability for S(5|1) ranged from 0.10 to 0.14. Heritability for S(8|1) was estimated between 0.07 and 0.09 (Snelling et al., 1995). Staybility at 11 had an estimated heritability between 0.06 and 0.19 (Snelling et al., 1995). Stayabilities for 3, 4 , 5, and 6 yr were estimated separately for Gelbvieh, Red Angus, and Simmental cattle and were similar across breeds at 0.16, 0.17, 0.18, and 0.18 respectively, with an obvious upward trend as age definition increased (Brigham et al., 2007). Other estimates of heritability of 3, 4, 5, and 6 yr include 0.39, 0.38, 0.29, and 0.25 in a population of Hereford cows (Martinez et al., 2005).

Genetic and environmental factors influencing stayability may vary with cow age, which will likely alter heritabilities and genetic correlations between stayability at different ages (Brigham et al., 2007). Correlations of EPDs for sires with daughters at different ages can range

from 0.18 to 0.47 (Brigham et al., 2007). This indicates that the merit of a sire for stayability might change depending on the age definition (Brigham et al., 2007).

Analysis using additive genetic groups found the relationship between heifer pregnancy (HP) and S(5|1) to be nonlinear, which indicates that selection for female fertility as a heifer and at S(5/1) would be most effective with different predictions on each trait (Doyle et al., 2000). Research supports a high probability that females in production at 4 yr will remain in production to 6 yr or more, suggesting earlier measures might be indicators of stayability later in life (Brigham et al., 2007). Correlations between 4 and 5 yr or 5 and 6 yr stayabilites have been reported as 0.85 and 0.86, respectively (Martinez et al., 2005).

Longevity

Longevity is a trait of increasing importance to breeders (Essl, 1998). Measurement of longevity is often by date of first calving as the starting point and date of culling as the endpoint (Ducrocq, 1994; Vollema et al., 2000). Increased longevity increases the mean performance of a herd because a greater number of culling decisions are based on production (Sewalem et al., 2003). Increased longevity enables a higher selection intensity, which leads to greater selection response (Sewalem et al., 2003). Two types of longevity were defined by Ducrocq (1987) and Ducrocq et al., (1988). True longevity is as actually observed, or longevity mainly dependent on productivity (Ducrocq, 1994), while functional longevity is the ability to delay involuntary culling because of sterility, lameness, or other diseases (Ducrocq, 1994). Genetic evaluation for longevity is not standardized across countries (Sewalem et al., 2003).

Statistical analysis of longevity is difficult for many reasons: 1) the distribution of survival time is rarely known; 2) for many of the observations, only the lower bound of survival time is known for animals still alive at the end of the study period, an occurrence known as

censoring; 3) independent variables influencing survival time may also vary with time, for example, herd size, disease occurrence, and reproductive performance (Solkner et al., 1999). Survival analysis is an alternative method for assessment of longevity (Sewalem et al., 2003). This method of analysis combines censored and uncensored information, enabling proper use of censored records and accounting for the non-linear nature of longevity data (Sewalem et al., 2003).

A proposed use of statistical methods to properly analyze censored records was developed by Smith (1983). These analyses were based on the concept of hazard rate $\lambda(t)$, defined as the probability of being culled at a time t, given the animal is alive prior to t. The use of a proportional hazard model, also known as a Cox regression, has been advocated in research (Smith, 1983; Smith et al., 1984; Smith et al., 1986). The hazard rate is easier to model as a function of explanatory variables than the survival function, which has an unknown distribution (Ducrocq, 1994). The hazard rate is the product of a baseline hazard function $\lambda 0(t)$ that represents the aging process, and a function of explanatory variables assumed to influence culling rate (Ducrocq, 1994). The effects of explanatory variables can be estimated separately from the baseline hazard function (Ducrocq, 1994). The baseline hazard function can be approximated by a Weibull distribution (Ducrocq, 1994). The Weibull hazard function is defined as

$$\boldsymbol{\lambda 0(t) = \lambda \rho\ (\lambda t)\rho\text{-}1},$$

where $\lambda 0(t)$ represents the baseline hazard function, λ and ρ are positive parameters assumed to influence the culling rate (heard-year and lactation number, for example), and t is time. (Ducrocq, 1994). The Weibull model is a generalization of the exponential model with a constant

hazard rate of $\lambda 0(t) = \lambda$ (Ducrocq, 1994). The Weibull hazard rate increases when ρ is larger than 1, is constant when ρ is equal to 1, and decreases when ρ is less than 1 (Ducrocq, 1994).

The Survival Tool Kit is a set of programs that allows for analysis of survival data (Solkner and Ducrocq, 1999). More specifically, the Survival Tool Kit allows for analysis of data which measure time until a defined event using Cox and Weibull regression models (Solkner and Ducrocq, 1999). The programs are specifically adapted to animal breeders who use large data sets and aim to estimate random effects (Solkner and Ducrocq, 1999). Covariance structure between observations based on genetic relationship can also be included (Solkner and Ducrocq, 1999). The programs allow for analysis of fixed effects on longevity as well as large scale genetic evaluations (Solkner and Ducrocq, 1999).

Routine genetic evaluation of survival analysis has been implemented in several countries, including France (Ducrocq, 1999), Germany (Pasman and Reinhardt, 1999), The Netherlands (Vollema et al., 2000), Italy (Schneider et al., 2000) and Switzerland (Vokasinovic et al., 2001).

In a longevity study on Canadian dairy cattle by Sewalem et al., (2003), length of productive life t was defined as the time from one calving to the next or death or culling. Lifetime record was considered completed (uncensored) if the cow received a termination code, meaning she was either culled or died (Sewalem et al., 2003). Censored animals include those sold, exported, or leased to another herd or cows still in the herd. Cows that transferred herds during their productive life were considered censored (Sewalem et al., 2003). In an alternative model proposed by Roxtrom et al., (2003) the origin point is calving date, with the end point of the culling date or date of next calving, and the record is censored if the cow has a next calving. The trait of interest is the overall risk of failure (Roxtrom et al., 2003).

The hazard function is defined as the probability of a cow being culled and is the product of a baseline hazard function and time-dependent explanatory variables that could possibly influence culling rate (Beaudeau et al., 1995). Hazard analysis completed by Sewalem et al., (2003), defined a longevity model as:

$$\lambda(t) = \lambda 0,s(t) \exp\{x'm(t)\beta+z'mu\}$$

where, $\lambda(t)$ is the hazard of a cow, or her probability of being culled at time t given she is alive just before t; $\lambda_{0,s}(t)=\lambda\rho(\lambda t)^{\rho-1}$ is the Weibull baseline hazard function; β includes time dependent covariates affecting the hazard with $x'_m(t)$ being the corresponding design vectors; and, u is a vector of random variables with associated incidence vector z'_m. Possible covariates adjusted for could include herd-year-season (random), age at first calving, parity, and month of calving (Beaudeau et al., 1995; Vukasinovic et al., 2001). The effect of herd-year-season is used to account for differences in culling policies among herds and over time (Beaudeau et al., 1995). The effect of parity can be treated as a discrete variable with seven classes: 1, 2, 3, 4, 5, 6, and $\geq$ 7 (Beaudeau et a., 1995).

Heritability for functional longevity using hazard analysis were estimated at 0.181, 0.198, and 0.184 for Braunvieh, Simmental, and Holstein cattle, respectively (Vukasinovic et al., 2001). Breeding values were expressed in terms of months of functional productive life (Vukasinovic et al., 2001).

Correlation between EBVs obtained from survival analysis on Canadian dairy cattle and evaluation of direct herd life using all lactations of each cow was 0.72 (Sewalem et al., 2003). When the first three lactation are used in the survival analysis, correlations increased to 0.83 (Sewalem et al., 2003). In dairy cattle, the probability of a cow being culled increased in early

and late stages of lactation in older cows, low producing cows, and in cows with poor reproductive performance (Beaudeau et al., 1995).

Tenderness

Measures of beef quality, composition, and yield are highly heritable traits with high economic importance in value-based marketing (Middleton and Gibb, 1991). Signals from the retail segment are now following the marketing chain all the way back to the seedstock producer, driving a renewed interest in end-product traits (Middleton and Gibb, 1991). Meat tenderness is an important factor leading to consumer satisfaction when eating beef (Casas et al., 2006).

Quantitative Trait Loci Analysis of Tenderness Data

Genetic markers and linkage maps along with the development of statistical methods have provided tools to detect quantitative trait loci (QTL) for economically important traits in cattle (Stone et al., 1999; Casas et al., 2000; Casas et al., 2001). Traits difficult or expensive to measure especially benefit from marker-assisted selection (Casas et al., 2003). Meat quality and carcass composition traits are some that would benefit greatly from the use of genetic marker information (Casas et al., 2003). Initial efforts by Stone et al. (1999) identified presence of loci influencing carcass composition and meat quality traits on chromosomes 1, 2, 3, and 13. Quantitative trait loci detected by Casas et al. (2003) identified the presence of a gene or group of genes influencing meat tenderness in the telomeric region of bovine chromosome 29. Smith et al. (2000).

Effects of Markers on Tenderness Traits

The calpain proteolytic system has been identified as a factor responsible for postmortem meat tenderization (Casas et al., 2006). Two enzymes responsible for this process are the calcium-activated neutral protease μ-calpain (CAPN1), which is encoded by the CAPN1 gene,

and the inhibitor calpastatin (CAST), which is encoded by the CAST gene (Koohmaraie, 1996). The CAPN1 locus produces the protease CAPN1 that breaks down myofibrillar protein postmortem, while the CAST locus produces an inhibitor (CAST) of that protease (Casas et al., 2006).

Studies have determined markers developed at the CAST and CAPN1 genes are suitable for use in identifying animals with genetic potential to produce meat with greater tenderness (Casas et al., 2006). Research conducted at the U.S. Meat Animal Research Center assessed the association of single nucleotide polymorphisms (SNP) at the CAST and CAPN1 genes with meat tenderness and palatability (Casas et al., 2006). A significant SNP discovered at the CAST gene was a transition from guanine to adenine at the 3' region of the gene (Barendse, 2002). A significant marker at the CAPN1 gene was a transition from cytosine to thymine at position 6545 of the BenBank accession AF238054 from the gene (White et al., 2005). The SNP at the CAST gene had a significant ($P < 0.003$) effect on Warner-Bratzler shear force (WBSF; kg) at 14 d postmortem and tenderness score in the GPE7 (Hereford, Angus, Red Angus, Limousin, Charolais, Gelbvieh, and Simmental crossbred animals) and the GPE8 (Hereford, Angus, Brangus, Beefmaster, Bonsmara, and Romosinuano crossbred animals) populations (Casas et al., 2006). Animals possessing the TT genotype at CAST had greater meat tenderness than those with the CC and CT genotypes (Casas et al., 2006). At the CAPN1 gene, the marker was significant ($P < 0.03$) for tenderness in GPE7 and GPE8 (Casas et al., 2006). Animals inheriting CC and CT genotypes on the CAPN1 gene produced more tender meat ($P < 0.05$) than animals with the TT genotype Casas et al., 2006). An interaction between CAST and CAPN1 was detected ($P < 0.05$) for WBSF on GPE8. Animals inheriting the CC genotype at both markers had greater tenderness than other groups (Casas et al., 2006). Animals with the CC genotype for

CAST exhibited tougher meat when they inherited the CT or TT genotypes in CAPN1 (Casas et al., 2006).

QTL Analyses

An example of using QTL analysis to track allele inheritance through generations can be found in Casas et al., (2003). Screening of markers used to genotype animals was done by generating an F-statistic profile at 1-cM intervals for each chromosome by regression of phenotype on the conditional probability of receiving a specific allele. Data was then modeled according to Haley et al. (1994) with effects of sex, year of birth, dam line within year of birth, and days on feed as a covariate. Haley et al. (1994) demonstrated the least squares method as a simple way to extract information contained in multiple linked markers. Use of all markers in a linkage group can increase the power for the detection of QTLs, and remove bias in the estimated positions and effect of a QTL. Least squares analysis can also allow for the inclusion of fixed effects in the model, along with allowing other QTL to be fitted (Haley et al., 1994). Conditional probabilities of inheriting the specific allele were calculated (Casas et al., 2003). Analysis for each chromosome was generated using the GLM procedure from SAS (SAS Inst., Inc., Cary, NC). The experiment-wise threshold value was calculated according to Lander and Kruglyak (1995).

Haplotype Analyses

Whole genome association studies (WGAS) using high-density SNP genotypes are efficient tools to identify genomic regions that explain variation in livestock traits (Onteru et al., 2013). Studies using WGAS can be based on different statistical methods, some of which include frequentist and Bayesian approaches (Onteru et al., 2013). The simplest method for performing WGAS is a linear regression with the association between markers and a trait of interest being

tested one marker at a time (Saatchi et al., 2014). Bayesian selection approaches, alternatively, facilitate simultaneous fitting of all markers in the model and have been used in livestock to improve precision of QTL mapping (Pryce et al., 2010). Among Bayesian methods, BayesB has been shown to map QTL more precisely than other methods, while also accounting for population stratification from resulting from pedigree relationships (Toosi et al., 2010).

Another example of haplotype association analysis (HAA) was performed by Onteru et al. (2013). The study used SNP from 1 Mb genetic windows that explained at least 0.2% of the genetic variance for a trait to construct linkage disequilibrium (LD) blocks. Haplotypes for each LD block were determined using PHASE software, and haplotypes with a frequency greater than 5% in the population were considered for further analyses with phenotypes.

Shear Force Analyses

Examples of how Warner-Bratzler shear force can be modeled in a quantitative analysis can be found in Casas et al. (2006). The study included sire breed, dam breed, sire breed and dam breed interaction, year of birth, slaughter group within year, CAST genotype, CAPN1 genotype, and the CAST and CAPN1 interaction as fixed effects (White et al., 2005). Weaning age was included as a covariate. Other analysis included the fixed effect of contemporary group, which was defined as calves of the same gender, fed in the same pen, and slaughtered on the same date (Casas et al., 2006).

Tenderness has been established as an important factor leading to consumer satisfaction when eating beef (Casas et al., 2006). Genetic markers for both the bovine CAPN1 and CAST genes have been previously associated with meat tenderness in cattle of various breed makeups. Selection for meat tenderness using marker assisted selection can potentially be a valuable tool in improving tenderness in diverse populations of beef cattle. Meat tenderness is critical to

consumer satisfaction and should be included as an economically relevant trait for selection in beef cattle.

Conclusions

The focus of animal breeding research shifted in recent years to ERT versus indicator traits being included in genetic evaluations (Golden et al., 2009). Three main areas of ERT were addressed in the scope of this literature review: feed efficiency, cow longevity, and tenderness.

Most beef production costs can be attributed to feed costs, so feed efficiency has been recognized as an economically important trait for selection in beef cattle (Koch et al., 1963; Dickerson et al., 1974). Research to further characterize genetic variation in utilization of feed energy will build the base for effective selection programs to reduce feed energy requirements (Rolfe et al., 2011).

Sustained cow fertility and long-term production are important contributors to the long-term profitability of the cow herd (Enns et al., 2005). Increased longevity increases the mean performance of a herd because a greater number of culling decisions are based on production (Sewalem et al., 2003). Survival analysis is an alternative method for assessment of longevity (Sewalem et al., 2003). This method of analysis combines censored and uncensored information, enabling proper use of censored records and accounting for the non-linear nature of longevity data (Sewalem et al., 2003). Routine genetic evaluation of survival analysis has been implemented in several countries, including France (Ducrocq, 1999), Germany (Pasman and Reinhardt, 1999), The Netherlands (Vollema et al., 2000), Italy (Schneider et al., 2000) and Switzerland (Vokasinovic et al., 2001).

Measures of beef quality, composition, and yield are highly heritable traits with high economic importance in value-based marketing (Middleton and Gibb, 1991). Meat tenderness is

an important factor leading to consumer satisfaction when eating beef (Casas et al., 2006). Traits difficult or expensive to measure especially benefit from marker-assisted selection (Casas et al., 2003). Meat quality and carcass composition traits are some that would benefit greatly from the use of genetic marker information (Casas et al., 2003).

The success of any beef enterprise is accurate decision making that considers both risk and potential returns (Golden, et al., 2009). The goal of ERT is to enable producers to make informed breeding decisions with accurate information on traits that directly affect their profitability.

References

Archer, J. A., P. F. Arthur, R. M. Herd and E. C. Richardson. 1998. Genetic variation in feed efficiency and its component traits. Proc. 6th World cong. Genet. Appl. Lives. Prod., Armidale, NSW, Australia. 25:81-84.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805-2811.

Arthur, P. F., G. Renand and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. Livest. Prod. Sci. 68:131-139.

Arnold, J. W., J. K. Bertrand and L. L. Benyshek. 1992. Animal model for genetic evaluation of multibreed data. J. Anim. Sci. 70:3322-3332.

Baker, F. H. 1967. History and development of beef and dairy performance programs in the United States. J. Anim. Sci. 26:1261-1263.

Beaudeau F., V. Ducrocq, C. Fourichon, H. Seegers. 1995. Effect of disease on length of productive life of French Holstein dairy cows assessed by survival analysis. J. Dairy Sci. 78:103-117.

Barendse, W. 1999. Assessing lipid metabolism. International patent application PCT/AU98/00882, international patent publication WO 99/23248.

Berry, D. P. and J. E. Pryce. 2014. Feed efficiency in growing and mature animals. Proceedings, 10th World Congress of Genetics Applied to Livestock Production.

Bateson, W. and E. Saunders. 1902. Experimental Studies in the Physiology of Heredity. Rpt. Evolut. Com. Roy. Soc. 1:3.

Benyshek, L. L. 1991. Beef cattle national genetic evaluation programs. Presented at the Beef Seedstock Symp. South Dakota State Univ., Brookings.

Bolormaa, S., B. Hayes, K. Savin, R. Hawken, B. Barendse, P. Arthur, D. Johnston, R. Herd and M. Goddard. 2011. Genome-wide association studies for feedlot and growth traits in cattle. J. Anim. Sci. 10:2572-3079.

Brigham, B. W., S. E. Speidel, R. M. Enns, and D. J. Garrick. 2007. Stayability to alternate ages. Proceedings – American Society of Animal Science Western Section. 58:27.

Casas, E., White, S. N., Wheeler, T. L., Shackelford, S. D., Koohmaraie, M., Riley, D. G., et al. 2006. Effects of calpastatin and l-calpain markers in beef cattle on tenderness traits. J. Anim. Sci. 84:520–525.

Casas, E., S. D. Shackelford, J. W. Keele, M. Koohmaraie, T. P. L. Smith, and R. T. Stone. 2003. Detection of quantitative trait loci for growth and carcass composition in cattle. J. Anim. Sci. 81:2976–2983.

Casas, E., R. T. Stone, J. W. Keele, S. D. Shackelford, S. M. Kappes, and M. Koohmaraie. 2001. A comprehensive search for quantitative loci affecting growth and carcass composition of cattle segregating alternative forms of the myostatin gene. J. Anim. Sci. 79:854–860.

Casas, E., S. D. Shackelford, J. W. Keele, R. T. Stone, S. M. Kappes, and M. Koohmaraie. 2000. Quantitative trait loci affecting growth and carcass composition of cattle segregating alternate forms of myostatin. J. Anim. Sci. 78:560–569.

Cole, J. B., P. M. VanRaden, J. R. O'Connell, C. P. Van Tassell, T. S. Sonstegard, R. D. Schnabel, J. F. Taylor, and G. R. Wiggans. 2009. Distribution and location of genetic effects for dairy traits. J. Dairy Sci. 92:2931-2946.

Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885-894.

Dickerson, G. E., N. Kunzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. J. Anim. Sci. 39:659-673.

Diel, T. D. 1993. "Ideas into Action: 25 Years". Beef Improvement Federation. University Printing Services, Oklahoma State University, Stillwater, OK.

Doyle, S. P., B. L. Golden, R. D. Green and J. S. Brinks. 2000. Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females. J. Anim. Sci. 78:2091-2098.

Ducrocq, V. 1999. Extension of survival analysis models to discrete measures of longevity. Interbull Bull. 21:41–47.

Ducrocq, V., and J. Solkner. 1994. The Survival Kit, a FORTRAN package for the analysis of survival data. Proc. 5th World Congr. Genet. Appl. Livest. Prod. 22:51–52.
Ducrocq, V., R. L. Quaas, E. J. Pollak, and G. Casella. 1988. Length of productive life of dairy cows. 1. Justification of a Weibull mode. J. Dairy Sci. 71:3061–3070.

Ducrocq. V. 1987. An analysis of length of productive life in dairy cattle. Ph.D. Diss. Cornell Univ., Ithaca, NY; Univ. Microfilms Int., Ann Arbor, MI.

Elzo, M. A. and T. R. Famula. 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60:942-952.

Elzo, M. A. and G. E. Bradford. 1985. Multibreed sire evaluation procedures across countries. J. Anim. Sci. 60:953-963.

Essl, A. 1998. Longevity in dairy cattle breeding: a review. Livest. Prod. Sci. 57:79–89.

Evans, J. L., B. L. Golden, R. M. Bourdon and K. L. Long. 1999. Additive genetic relationship between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77:2621-2628.

Ferrell C. L. and T. G. Jenkins. 1985. Cow type and the nutritional environment: nutritional aspects. J. Anim. Sci. 61:725-741.

Fox, D. G., L. O. Tedeschi, and P. J. Guiroy. 2001. Determining feed intake and feed efficiency of individual cattle fed in groups. Proceedings of the 33rd Annual Beef Improvement Federation Annual Research Symposium and Annual Meeting. 80- 98.

Garrick, D. 2005. Trends and developments in genetic evaluation of beef cattle in the United States. Proc. 9th World Angus Forum Tech. Meet., Angus in the Global Market. Am. Angus Assoc., Kansas City, MO.

Garrick, D. 2006. Genetic improvement of beef cattle – assessing the ramifications of genetic change. 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, MG, Brazil.

Garrick, D. J., and B. L. Golden. 2009. Producing and using genetic evaluations in the United States beef industry of today. J. Anim. Sci. 87: E11-E18.

Gianola, D. and J. L. Foulley. Sire evaluation for ordered categorical data with a threshold model. Genet. Sel. Evol. 15:201-224.

Golden, B. L., J. S. Brinks and R. M. Bourdon. 1991. A performance programmed method for computing inbreeding coefficients from large data sets for use in mixed-model analyses. J. Anim. Sci. 87: E11-E18.

Golden, B. L., D. J. Garrick and L. L. Benyshek. 2009. Milestones in beef cattle genetic evaluation. J. Anim. Sci. 97: E3-E10.

Haley, C. S., S. A. Knott, and J.-M. Elsen. 1994. Mapping quantitative trait loci in crosses between outbred lines using least squares. Genetics. 136:1195−1207.

Hazel L. N. and J. L. Lush. 1943. The efficiency of three methods of selection. J. Hered. 33:393-399.

Henderson, C.R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. Biometrics 32, 68-83.

Henderson, C. R. 1975.Best linear unbiased estimation and prediction under a selection model. Biometrics. 31:2 423-447.

Henderson, C. R. 1963. Selection index and expected genetic advance. In: Statistical Genetics and Plant Breeding. Natl. Acad. Sci. Natl. Res. Counc. Publ. 982. pp. 141-163. National Academy of Science, Washington, DC.

Herd, R. M. and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Lives. Prod. Sci. 63:111-119.

Hill, R. A. 2012. Feed efficiency in the beef industry. A John Wiley & Sons, Inc, New Delhi, India.

Hudson, G. F. S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64: 2246-2250.

Kelly, D. N., C. Murphy, R. D. Sleator, M. M. Judge, S. B. Conroy, and D. P. Berry. 2019. Feed efficiency and carcass metrics in growing cattle. J. Anim. Sci. 97:4405-4417.

Koch, R. M., J. B. Gibb, and J. A. Gosey. 1986. Evaluation of beef cattle industry breeding programs: breeders and breed associations. 3rd World Congress on Genetics Applied to Livestock Production. Paper 30.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486-494.

Koch, R. M. and R. T. Clark. 1955. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment J. Anim. Sci. 14:979.

Koger, Marvin and J. H. Knox. 1947. The repeatability of the yearly production of range cows. J. Anim. Sci. 6:461.

Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization process of meat. Meat Sci. 43: S193–S201.

Koong, L. J., C. L. Ferrell, and J. A. Nienaber. 1982. Effects of plane nutrition on organ size and fasting heat production in swine and sheep. Proceedings of 9th Symposium on Energy Metabolism of Farm Animals. EAAP 29:245-248.

Koots, K. R., J. P. Gibson and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:826-853.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825-853.

Kuehn, L. A., Bl. L. Golden, C. R. Comstock, and K. J. Andersen. 1998. Docility EPD for Limousin cattle. J. Dairy Sci. 81:334.

Lander, E., and L. Kruglyak. 1995. Genetic dissection of complex traits: Guidelines for interpreting and reporting linkage results. Nat. Genet. 11:241−247.

Lin, C. Y. and S. E. Aggrey. 2013. Incorporation of economic values into the component traits of a ratio: feed efficiency. Poultry Sci. 92:916-922.

Lin, C. Y. 1980. Relative efficiency of selection methods for improvement of feed efficiency. J. Dairy Sci. 63:491-494.

MacNeil, M. D., M. M. Scholtz, F. J. Jordaan, and A. Maiwashe. 2019. Alternative models for genetic evaluation of feed intake by Afrikaner cattle. S. Afr. J. Anim. Sci. 49: 763-769.

MacNeil, M. D., M. C. Mokolobate, M. M. Scholtz, F. J. Jordaan, and F.W.C Neser. 2017. Alternative approaches to evaluation of cow efficiency. S. Afr. J. Anim. Sci. 47:188-123.

MacNeil, M. D., M. M. Scholtz, and A. Maiwashe. 2013. Estimates of variance components for postweaning feed intake and growth in Bonsmara bulls and evaluation of alternative measures of feed efficiency. S. Afr. J. Anim. Sci. 49:763-769.

MacNeil, M. D., N. Lopez-Villalobos, and S. L. Northcutt. 2011. A prototype national cattle evaluation for feed intake and efficiency of Angus cattle. J. Anim. Sci. 89:3917-3923.

Martinez, G. E., R. M. Koch, L. V. Cundiff, K. E. Gregory, S. D. Kachman, and L. D. Van Vleck. 2005. Genetic parameters for stayability, stayability at calving, and stayability at weaning to specified ages for Hereford cows. J. Anim. Sci. 83:2033-2042.

Meuwissen, T. H. E. and Z. Luo. 1992. Computing inbreeding coefficients in large populations. Genet. Sel. Evol. 24:305-313.

Middleton, B. K. and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861-3871.

Mohler, J. R. 1937. Certification of pedigrees of imported registered livestock. J. Anim. Sci. 1937:309-310.

Montano-Bermudez, M., M. K. Nielsen and G. H. Deutscher. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68:2279-2288.

Mrode, R. A. and R. Thompson. 2005. Linear models for the prediction of animal breeding values. 2nd ed. CABI Publishing, Cambridge, MA.

Nielsen, M. K., M. D. MacNeil, J. C. M. Dekkers, D. H. Crews, Jr., T. A., Rathje, R. M. Enns, and R. L. Weaber. 2013. Review: Lifecycle, total-industry genetic improvement of feed efficiency in beef cattle: blueprint for the Beef Improvement Federation. Prof. Anim. Sci. 29:559-565.

Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny difference: Use of within breed expected progeny difference to adjust breed evaluations for sire sampling and genetic trend. J. Anim. Sci. 69:4763-4766.

Nunez-Dominguez, R., L. D. Van Vleck and L. V. Cundiff. 1993. Breed comparisons for growth traits adjusted for within breed genetic trend using expected progeny differences. J. Anim. Sci. 71:1419-1428.

Onteru, S. K., D. M Gorbach, J. M. Young, D. J. Garrick, J. C. M. Dekkers and M. F. Rothschild. Whole genome association studies of residual feed intake and related traits in the pig. 2013. PLoS ONE. 8 (6): e61756.

Page, B. T., E. Casas, M. P. Heaton, N. G. Cullen, D. L. Hyndman, C. A. Morris, A. M.

Parnell, P. F., R. M. Herd, D. Perry and B. Bootle. 1994. The Trangie experiment—Response to growth rate, size, maternal ability, reproductive performance, carcass composition, feed requirements and herd profitability. Proc. Aust. Soc. Anim. Prod. 20:17-26.

Pasman, E., and F. Reinhardt. 1999. Genetic evaluation for length of productive life of Holstein cattle in Germany. Proc. Int. Workshop on EU Concerted Action Genetic Improvement of Functional Traits in Cattle (GIFT); Longevity.

Pryce, J.E., S. Bolormaa, A. J. Chamberlain, P. J. Bowman, K. Savin, M. E. Goddard, and B. J. Hayes. 2010. A validated genome-wide association study in 2 dairy cattle breeds for milk production and fertility traits using variable length haplotypes. J. Dairy Sci. 93:3331–3345.

Quaas, R. L., and E. J. Pollak. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. J. Anim. Sci. 51:6.

Quaas, R. L. 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. Biometrics. 32:949-953.

Robinson, D. L., V. H. Oddy and C. Smith. 1999. Preliminary genetic parameters for feed intake and efficiency on feedlot cattle. Proc. Assoc. Advancement Anim. Breed. Genet. 13:492-495.

Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H. C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. J. Anim. Sci. 89:3452-3459.

Roxstrom, A., V. Ducrocq, and E. Strandberg. 2003. Survival analysis of longevity in dairy cattle on a lactation basis. Genetics Selection Evolution. 35:305-318.

Saatchi, M., J. E. Beever, J. E. Decker, D. B. Faulkner, H. C. Freetly, S. L. Hansen, H. Yampara-Iquise, K. A. Johnson, S. D. Kachman, M. S. Kerley, J. Kim, D. D. Loy, E. Marques, H. L. Neibergs, E. J. Pollak, R. D. Schnabel, C. M. Seabury, D. W. Shike, W. M. Snelling, M. L. Spangler, R. L. Weaber, D. J. Garrick, J. F. Taylor. 2014. QTLs associated with dry matter intake, metabolic mid-test weight, growth and feed efficiency have little overlap across 4 beef cattle studies. BMC Genomics. 15:1004.

Schneider, M. del P., and F. Miglior. 1999. A proposal for genetic evaluation for functional herd life in Italian Holsteins. Page 11 in Book of Abstracts of the 50th Meeting Eur. Assoc. Anim Prod., Zurich, Switzerland.

Sewalem, A., G. Kistemaker and B. Van Doormal. 2003. Genetic analysis of herd life in Canadian dairy cattle on a lactation basis using the Survival Kit. Interbull Bulletin 31, 73-76.

Shike, Daniel. 2012. Beef Cattle Feed Efficiency. http://www.beefusa.org/CMDocs/BeefUSA/Resources/cc2012-Beef-Feed-Efficiency--Dan-Shike.pdf.

Smith, T. P. L., E. Casas, C. E. Rexroad, III, S. M. Kappes, and J. W. Keele. 2000. Bovine CAPN1 maps to a region of BTA29 containing a quantitative trait locus for meat tenderness. J. Anim. Sci. 78:2589–2594.

Smith. S. P., and F. R. Allaire. 1986. Analysis of failure times measured on dairy cows: theoretical considerations in animal breeding. J. Dairy Sci. 69: 217.

Smith. S. P., and R. L. Quaas. 1984. Productive life span of bull progeny groups: failure time analysis. 1. Dairy Sci. 67:2999.

Smith, S. P. 1983. The extension of failure time analysis to problems of animal breeding. Ph.D. Diss., Cornell Univ., Ithaca. NY; Univ. Microfilms Int. Ann Arbor. MI.

Snelling, W. M., M. F. Allan, J. W. Keele, L. A. Kuehn, R. M. Thallman, G. L. Bennett, C. L. Ferrell, T. G. Jenkins, H. C. Freetly, M. K. Nielsen, and K. M. Rolfe. 2011. Partial-genome

evaluation of postweaning feed intake and efficiency of crossbred beef cattle. J. Anim. Sci. 89:1731-1741.

Snelling, W. M., B. L. Golden and R. M. Bourdon. 1995. Within-herd genetic analyses of stayability of beef females. J. Anim. Sci. 73:993-1001.

Solkner, J., and V. Ducrocq. 1999. The Survival Kit: a tool for analysis of survival data. Interbull Bulletin 21:11.

Stone, R. T., J. W. Keele, S. D. Shackelford, S. M. Kappes, and M. Koohmaraie. 1999. A primary screen of the bovine genome for quantitative trait loci affecting carcass and growth traits. J. Anim. Sci. 77:1379–1384.

Swiger, L. A. and L. N. Hazel. 1961. Optimum length of feeding period in selecting for gain in beef cattle. J. Anim. Sci. 20:189-194.

Swiger, L. A., R. M. Koch, K. E. Gregory, and V. H. Arthaud. 1961. Effect of length of feeding period on accuracy of selection for gain and feed consumption in beef cattle. J. Anim. Sci. 20:802-808.

Taylor, St. C. S., H. G. Turner, and G. B. Young. 1981. Genetic control of equilibrium maintenance efficiency in cattle. Anim. Prod. 33:179-194.

Toosi, A., R. L. Fernando and J. C. M. Dekkers. 2010. Genomic selection in admixed and crossbred populations. J. Anim. Sci. 88:32–46.

Thallman, R. M., L. A. Kuehn, W. M. Snelling, K. J. Retallick, J. M. Bormann, H. C. Freetly, K. E. Hales, G. L. Bennett, R. L. Weaber, D. W. Moser, and M. D. MacNeil. 2018. Reducing the period of data collection for intake and gain to improve response to selection for feed efficiency in beef cattle. J. Anim. Sci. 96:854-866.

VanRaden, P. M., C. P. Van Tassell, G. Wiggans, T. S. Sonstegard, R. D. Schnabel, J. F. Taylor and F. Schenkel. 2009. Invited Review: Reliability of genomic predictions for North American Holstein bulls. J. Dairy Sci. 92:16-24.

Vollema, A. R., S. Van Der Beek, A. G. F. Harbers, and G. De Jong. 2000. Genetic evaluation for longevity of Dutch dairy bulls. J. Dairy Sci. 83:2629–2639.

Vollema, A. R., and A. F. Groen. 1998. A comparison of breeding value predictors for longevity using linear model and survival analysis. J. Dairy Sci. 81:3315–3320.

Vukasinovic, N., J. Moll, and L. Casanova. 2001. Implementation of a routing genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. J. Dairy Sci. 84:2073–2080.

Wang, Z., J. D. Nkrumah, C. Li, J. A. Basarab, L. A. Goonewardene, E. K. Okine, D. H. Crews, Jr., and S. S. Moore. 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the GrowSafe® system. J. Anim. Sci. 84:2289-2298.

Warwick, E.J. 1958. Fifty years of progress in breeding beef cattle. J. Anim. Sci. 17:922-943.

White, S. N., E. Casas, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, D. G. Riley, C. C. Chase Jr., D. D. Johnson, J. W. Keele, and T. P. L. Smith. 2005. A new single nucleotide polymorphism in CAPN1 extends the current tenderness marker test to include cattle of Bos indicus, Bos taurus, and crossbred descent. J. Anim. Sci. 83:2001–2008.

Wiggans, G. R., T. A. Cooper, P. M. VanRaden and M. V. Silva. 2010. Increased reliability of genetic evaluation for dairy cattle in the United States from use of genomic information. Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany.

Willham, R. L. 1979. Evaluation and direction of beef sire evaluation programs. J. Anim. Sci. 49:592-599.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35:1288-1293.

Wright, S. 1922. Coefficients of inbreeding and relationship. American Naturalist. 330-338.

Chapter 2 - Genetic Parameter Estimates for Feed Efficiency in Gelbvieh Influenced Cattle

Introduction

A practical measure of feed efficiency awaits development and is important to both the feedlot segment and the commercial cow/calf producer of the beef industry. In life cycle beef production, feed energy requirements for animal maintenance (not including those required for growth or lactation) account for approximately 70% of feed inputs, resulting in less than 20% of feed energy converted to beef (Williams and Jenkins, 2006). Feed efficiency has been recognized as an economically important trait for selection in beef cattle because most beef production costs can be attributed to feed costs (Koch et al., 1963; Dickerson et al., 1974). Numerous measures of feed intake and efficiency exist for genetic selection. Examples include residual feed intake (RFI), dry matter intake (DMI), residual gain (RG), and predicted dry matter required (PDMR). Despite the plethora of potential traits for selection, limited data has been collected by the breed programs because of the difficulty and expense of measuring intake under typical production conditions (Middleton and Gibb, 1991). Residual feed intake was developed by Koch et al. (1963), and it is defined as the difference between actual and predicted feed intake (Kennedy et al., 1993, Arthur et al., 2001a). An advantage of selecting on RFI for feed efficiency is it accounts for an animal's performance in terms of gain (Berry and Pryce, 2013). Animals can therefore be selected for lower feed intake without sacrificing performance. Selection for RFI is also beneficial as phenotypic independence between RFI and growth rate and body weight are assured by regression to produce predicted intakes (Crews et al., 2005). A disadvantage of direct selection on RFI values is the calculation can be conceptually difficult for producers (Berry and Pryce, 2013). A negative RFI value is favorable, indicating an animal ate less than predicted may

be counter intuitive (Kennedy et al., 1993). Additionally, it has been demonstrated that RFI is not genetically independent of production traits (Kennedy et al., 1993). In an association analysis, Rolf et al., (2012) found that genetic correlations between RFI and DMI resulted in 4.5% of SNPs selected for RFI also being selected for ADG in the analysis of breeding values. Kennedy et al., (1993) suggested using genetic (co)variances to calculate genotypic RFI to ensure genetic independence from production traits. This method of calculation would also more accurately reflect genetic variation between feed intake and production (Archer et al., 1999).

Dry matter intake is the amount of feed an animal ingests, which is easily understood, but has a disadvantage in that it does not account for an animal's performance. An animal's intake depends largely on its body weight, growth rate, and composition, so selection for lower DMI may also lead to selection for cattle with a lower growth rate and a smaller body size (Nielsen, et al., 2013). Residual body weight gain is derived as the difference between predicted and actual BW gain. Greater RG values are desirable and indicate greater gain with a given amount of feed (Koch et al., 1963). Residual gain places a greater emphasis on the gain component rather than intake, unlike RFI. Parameters like RFI and RG may inhibit producers from reaching maximum profitability by forcing them to emphasize either input or output costs (Crowley et al., 2010).

Like other traits that are difficult or expensive to record, genetic gain in feed efficiency could be obtained by selection on genetically correlated indicator traits that are routinely collected (Crews 2005). Specifically, predicted individual feed intake in the form of PDMR can be calculated using group (pen) feed intake, along with performance, diet, growth, and carcass trait estimates (Rolf, 2009). A computerized model known as the Cornell Value Discovery System (CVDS) has been developed to accurately estimate individual animal feed requirements from group feed data and individual performance records (Guiroy et al., 2001). The CVDS uses

weights and carcass or ultrasound data to allocate the total feed intake of the pen to individuals through information on their growth and carcass composition. The model can predict both individual daily intake and gain depending on the type of information included (Tedeschi et al., 2004). High phenotypic and genetic correlations between the CVDS predicted feed intake and observed feed intake (0.662-0.785 and 0.82-0.95, respectively) indicate progress can be made in feed efficiency through selection on predicted feed intake (Williams et al., 2006). In a similar study by Cooper et al., (2010) using pen total feed intake and individual gain was 81% as effective for selection as using individual feed intake and gain to obtain estimated genetic values for feed intake.

Reduction in costs through selection for decreased input traits such as feed intake must be balanced with selection for maintaining or increasing output traits such as gain (Nielsen et al., 2013). An animal's intake depends on its level of gain, age, and size (NRC, 2000). Selection for reduced intake alone can lead to inadvertent selection for smaller cattle (Nielsen et al., 2013). Genetic selection for improved feed efficiency can be obtained through simultaneous selection for all traits that influence production as opposed to single trait selection (Berry and Crowley, 2013). Expressing feed efficiency in a linear form versus a ratio of output and input has better statistical properties and closely mirrors economic measures such as net return (Nielsen et al., 2013). Rolfe et al. (2011) evaluated the genetic and economic progress made by selecting on different feed efficiency indexes. The study found that FI and feed costs could be reduced through selection (Rolfe et al., 2011). Index selection that balances output (growth) and input (feed intake) were found to yield the most favorable economic results (Rolfe et al., 2011). An index including DMI and gain (GAIN) gave the best economic outcome in this experiment (Rolfe et al., 2011).

The objectives of this study were to estimate genetic parameters for DMI, PDMR, RFI, adjusted weaning weight (AWWT), and post weaning gain (PWG) in a multi-breed population of growing beef cattle, in addition to implementing an economic selection index identify genetically favorable animals in the complex of traits associated with feed energy utilization.

Materials and Methods

Animal Care and Use Committee approval was not obtained for this study because the data were accumulated by breeders belonging to the American Gelbvieh Association (AGA) as part of their genetic improvement program. Feed intake and performance data for this analysis included records on animals collected by twelve individual breeders using Growsafe® systems and were later submitted to the AGA. On-test start dates, end dates, feed yard identification, lot (pen) identification, and breeding herd information were also included. Start and end weights, intermediate on-test weights, and on-test gain were reported for some animals. All animals had reported registration numbers, gender, breed fraction, birth date, and weaning date and weight records. Many also had yearling weight and date recorded. Post weaning gain calculated from adjusted yearling and adjusted weaning weights were used as the gain component of this study. Specific phenotypes included from each source varied, as is common in data reported to breed associations. For this reason, some animals had both DMI and RFI, while some only had one measure. Residual feed intake was a product of the Growsafe® system. A primary aim of this study was to use existing field data previously collected by breeders but not yet used in genetic evaluation to develop novel tools for genetic selection. In the current data, body weights and gain were the most frequently reported phenotype, followed by RFI. Distribution of records within ranch can be found in Tables 2-1 through 2-12. No ranch had a record for each animal for each trait. While having the smallest number of animals, ranch D was the most complete in terms of

data with all animals having 4 out of 5 traits reported. Ranch A was the only location to include PDMR in their reported phenotypes. Table 2-13 shows the number of records within each ranch and for the complete data set for each trait. Both within ranch and in the overall data set, AWWT and PWG phenotypes were the most prolific.

Data was edited to exclude duplicate animals and animals without unique identification numbers with the AGA. Animals with weaning dates below 160 days of age and above 250 days of age were also excluded according to AGA weaning reporting guidelines (AGA Gelbvieh Rules, 2018). Animals represented a wide range of Angus or Red Angus and Gelbvieh, which are outlined in table 2-14. Thirty-seven percent of animals having greater than or equal to 88% Gelbvieh.The minimum percent Gelbvieh for animals in the data set was less than 13%, with a maximum of 100% and an average of 58% Gelbvieh. All animals contained at least some Gelbvieh influence. Information was included on 604 steers, 310 females, and 3,586 bulls. The raw data set included 4,500 AWWT records, 3,696 PWG records, 659 PDMR records, 2,927 RFI records and 1,755 DMI records. Counts of record by trait for the combined data set can be found in Table 2-13. Most pairs of traits have greater than 1,000 animals in common, except for DMI and PDMR (0), DMI and RFI (811), PDMR and RFI (0), PDMR and PWG (89), and PDMR and AWWT (650). Pedigree information was obtained on 7,029 animals spanning over 3 generations, including 1,143 sires, 247 paternal grand sires, 4,613 dams, and 749 maternal grand sires. Analysis was also attempted with a 5-generation pedigree to improve relationship ties between herds. Increased pedigree ties did not substantially change results, particularly on correlations between traits, so results from this analysis are not included.

Predicted dry matter required was computed at the feed yard using the CVDS. The CVDS is an iterative growth model used to predict individual feed requirements, carcass composition,

performance, and costs of animals fed in group pens. Several models exist within the CVDS, including models to predict net energy for growth, carcass quality, and yield grades during growth. The models can use as many as 57 variables for prediction, including diet information, length of feeding period, animal information (age, gender, body condition score, etc.) and environmental information (Tedeschi et al., 2004). Specifically, the PDMR of an animal is computed using equations developed by the National Research Council (NRC) that incorporate DMI and average body weight (NRC, 2000). The PDMR is calculated in two portions using energy required for growth and that required for maintenance as inputs. The CVDS model iterates until the mean predicted average daily gain (ADG) matches the observed ADG for each animal (Tedeschi et al., 2004).

Both AWWT and adjusted yearling weight (AYWT) are calculated according to Beef Improvement Federation (BIF) guidelines (BIF, 2010):

AWWT = (Wean Wt. – Birth Wt.)/Weaning Age * 205 + Birth Wt. + Age of dam Adj.

AYWT = (Final Wt. – Wean Wt.)/Days Between Wts.* 160 + AWWT

Post weaning gain was calculated as follows:

PWG = AYWT – AWWT

Mid-test metabolic body weight to the 0.75 (MBW) power was calculated as follows:

$$MBW = ((PWG/2) + \text{on test weight})^{0.75}$$

Contemporary groups were formed for birth, weaning, yearling, and feeding period by standard AGA protocol. Birth contemporary group was formed as a concatenation of breeder, year, and sex. Weaning contemporary group was formed as a concatenation of birth contemporary group, weaning herd, weaning group, and weaning date. Yearling contemporary group was formed as a concatenation of weaning contemporary group, yearling herd, yearling

group, and yearling weight date. Feeding contemporary group was formed as a concatenation of yearling contemporary group, feed yard, feed yard received date, and feed yard out date. Residual feed intake included a total of 440 contemporary groups, PDMR included 6 contemporary groups, PWG had 569 contemporary groups included, AWWT included 609 contemporary groups, and DMI included 377 contemporary groups. Table 15 contains information on the number of contemporary groups for each trait per ranch. An average of 7 animals were included in each contemporary group, with a median number of 41 contemporary groups per ranch. Table 16 contains the average, minimum, and maximum number of animals in a contemporary group per trait. The maximum number of animals in a contemporary group was greatest for AWWT with 344 animals. The mean number of animals per contemporary group was also greatest for AWWT with 50.75 animals.

Data was analyzed using a series of bivariate models to obtain variance and covariance values for initial values for a larger 5 trait animal model with animal and contemporary group as random effects. A single trait model was used for the analysis of MBW to include in the final index value. Weaning contemporary group was used for AWWT, yearling contemporary group was used for PWG, and feeding contemporary group was used for DMI, PDMR, RFI, and MBW. Percent direct heterosis and percent maternal heterosis were fit as covariates in the models, and were calculated as:

% heterosis = 0.5(breed fraction of sire + breed fraction of dam)

Breed composition in the form of percent Gelbvieh was also included as a covariate. Heritabilities were computed as the ratio of additive genetic and phenotypic variance components:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

where σ_a^2 is the additive genetic variance and σ_p^2 is the phenotypic genetic variance.

Genetic and phenotypic correlations between variables were calculated as a function of the covariance of the variables and their standard deviations:

$$r^2 = \frac{\sigma_{xy}}{\sigma_x \sigma_y}$$

where σ_{xy} is the covariance between two traits and σ_x and σ_y are standard deviations of each trait.

The mixed model equation for each of dependent variables can be expressed as:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \end{bmatrix} = \begin{bmatrix} X_1 b_1 \\ X_2 b_2 \\ X_3 b_3 \\ X_4 b_4 \\ X_5 b_5 \end{bmatrix} \begin{bmatrix} Z_1 u_1 \\ Z_2 u_2 \\ Z_3 u_3 \\ Z_4 u_4 \\ Z_5 u_5 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix}$$

where y_i was a vector of observations for DMI, PDMR, RFI, PWG, and AWWT, respectively. X_i was and incidence matrix relating observations to fixed effects, b_i was a vector of fixed effects, Zi was an incidence matrix relating observations to additive genetic effects, u_i was a vector of random additive genetic effects, and e_i was a vector of random residuals. Variances were estimated using ASREML (Ver 3.0, VSN International, LTD., Hemel Hempstead, UK). Matrix **A** is the numerator relationship matrix calculated from pedigree relationships. The variance structure for animal effects was expressed as:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \\ y_5 \end{bmatrix} = \mathbf{A} \begin{bmatrix} \sigma_{a1}2 & & & & \\ \sigma_{a1,a2} & \sigma_{a2}2 & & & \\ \sigma_{a1,a3} & \sigma_{a2,a3} & \sigma_{a3}2 & & \\ \sigma_{a1,a4} & \sigma_{a2,a4} & \sigma_{a3,a4} & \sigma_{a4}2 & \\ \sigma_{a1,a5} & \sigma_{a2,a5} & \sigma_{a3,a5} & \sigma_{a4,a5} & \sigma_{a5}2 \end{bmatrix}$$

The variance structure for the residual effects was expressed as:

$$\begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{bmatrix} = \mathbf{I} \begin{bmatrix} \sigma_{e1}2 & & & & \\ \sigma_{e1,e2} & \sigma_{e2}2 & & & \\ \sigma_{e1,e3} & \sigma_{e2,e3} & \sigma_{e3}2 & & \\ \sigma_{e1,e4} & \sigma_{e2,e4} & \sigma_{e3,e4} & \sigma_{e4}2 & \\ \sigma_{e1,e5} & \sigma_{e2,e5} & \sigma_{e3,e5} & \sigma_{e4,e5} & \sigma_{e5}2 \end{bmatrix}$$

Individual expected progeny differences (EPD) resulting from the analysis were input into a selection index (the third index tested, or I3) outlined by Rolfe et al., (2011), as below:

$$I3 = DMI - (0.039)SUMWT^{0.75} - 7.531(Gain)$$

Where $SUMWT^{0.75}$ is the individual animal quadratic regression of BW on days on feed from 0 to 140 days. For the purposes of this study, the EPD for MBW was used as an alternative to $SUMWT^{0.75}$. The measures of MBW and SUMWT aren't directly comparable, as SUMWT is gain over a 140-day period and MBW is for half of the feeding period. The variation for MBW would be less than the variation for SUMWT since it is over a shortened period.

Negative values are more favorable for this index. While original index was expressed in $/kg, the current study reported the index in $/lb to be consistent with the units of the AGA selection indices, as below:

$$I = (2.20)\ DMI - (0.086)MBW^{0.75} - 16.603(Gain)$$

The AGA publishes an index for maternal selection ($Cow), which includes components for stayability, reproduction, calving ease, gain, feed efficiency, and carcass value. Stayability is especially emphasized. The AGA also publishes an index for terminal selection (Feeder Profit Index, or FPI), which places emphasis on marbling and carcass weight. Also included in the AGA suite of indexes is their Efficiency Profit Index, or EPI, which puts negative pressure on feed intake while keeping gain at a constant value. Rank comparisons were performed to assess how high-ranking animals on the feed efficiency index compared to AGA published indexes.

Results and Discussion

Descriptive statistics for this data set are presented in Table 2-17. Adjusted weaning weight was the most prolific record with 4,110 observations, while PDMR records were only available on 659 animals.

Estimates for additive genetic, residual, and phenotypic variance are presented in Table 2-18. Estimates of additive genetic variance for RFI were moderate compared to current literature. Genetic variance was greater in the current study than the 0.149 kg^2 found in Arthur et al., (2001b), possibly because of a larger data set in the current study. Rolf (2009) presented a somewhat greater estimate of 0.56 kg^2 for additive genetic variance of RFI in 862 Angus steers. Basarab et al., (2007) found considerable phenotypic variation in RFI across contemporary groups for animals unadjusted (Var_p = 0.85 kg^2) or adjusted for off test backfat thickness (0.77 kg^2). Other estimates of phenotypic variance in the literature for RFI range from 0.44 kg^2 by Basarab et al, (2003) to 0.58 kg^2 reported by Arthur et al., (2001a). Estimates of additive genetic variance for DMI were greater than those found by Thallman et al., (2018) for both 83- and 42-day test periods of 0.51 kg^2 and 0.47 kg^2, respectively. Residual variance in the current study was also higher for DMI than that found by Thallman et al., (2018) for 83- and 42-days test periods of 0.97 kg^2 and 0.82 kg^2, respectively. Rolf (2009) found an estimated additive genetic variance of 0.16 kg^2 for DMI, which is less than the current study with an estimate of 0.99 lb^2. The estimated phenotypic variance of 4.09 kg^2 found by Rolf (2009) for DMI was greater than that found in the current study (4.81 lb^2).

Heritabilities and genetic and phenotypic correlations are provided in Table 2-19. Residual feed intake was found to be moderately heritable at 0.32 ± 0.06. This heritability is greater than the 0.16 ± 0.08 found in the population of British Hereford cattle in Herd and

Bishop (2000). Arthur et al. (2001a) found RFI to have a moderate heritability of 0.39 ± 0.03 in a population of Australian Angus bulls and heifers. Other estimates of heritability in the literature include 0.26 to 0.30 found by Crews et al., (2003), 0.28 by Koch et al., (1963), and 0.39 to 0.43 by Arthur et al., (2001b). Schenkel et al., (2003) found moderate estimates of 0.38 and 0.39 for RFI adjusted for production alone and adjusted for backfat thickness, respectively. This is consistent with other estimates in the literature, with most of the values falling in the moderate range (Robinson et al., 1999; Santana et al., 2014). Rolfe et al. (2011) found a somewhat greater heritability of 0.52 ± 0.12 in a population of mixed breed steers with data collected over a 5-year time span. All steers in the study contained a portion of Hereford or Angus in addition to varying percentages of Simmental, Charolais, Limousin, Gelbvieh, Red Angus, and MARC III composite.

Dry matter intake was estimated to be moderately heritable at 0.39 ± 0.06. This is similar to an estimate of 0.40 by Rolfe et al., (2011). Santana et al., (2014) also found a moderate heritability of 0.40 in their population of Nellore cattle. Thallman et al., (2018) found a somewhat lower heritability for DMI for 42 test periods of 0.34, and a greater heritability for DMI for 83-day test periods of 0.43. A larger heritability of 0.54 ± 0.15 was found in a population of hybrid Angus, Charolais, and Alberta Hybrid animals by Nkrumah et al., (2007). MacNeil et al., (2013) found heritability of the related trait of average daily feed intake (DFI) to be 0.37, roughly comparable to the estimate of 0.39 for DMI in this study. In a study on Afrikaner bulls, MacNeil et al., (2019) found feed intake heritability at 0.30 when random contemporary groups where used. The MacNeil et al., (2019) study further concluded that considering contemporary groups as random consistently increased the accuracy of estimated breeding values.

Predicted dry matter required had an estimated heritability of 0.47 ± 0.15 in the current study. This is much greater than the estimate of 0.04 found by Rolf (2009) in a population of 698 Angus steers and 1,707 Angus bulls. The greater heritability found in the current study could be because of a larger, more diverse population with greater variance in PDMR values. The current study also had greater additive genetic variance (0.99 lb^2 versus 0.16 lb^2 in Rolf (2009)) and less phenotypic variance (2.09 lb^2 versus 4.09 lb^2 in Rolf (2009)). The greater portion of variance explained by the additive genetic component would lead to a greater heritability in the current study. Cooper et al., (2010) found a more similar heritability of 0.42 ± 0.16 for individual feed intake predicted from pen feed intake and gain values from animals is the U.S. Meat Animal Research Center Germ Plasm Evaluation Program. Perry and Fox (1997) found PDMR to account for 48% of the variation in actual DMI with a 3% overprediction bias. Williams et al., (2005) found a similar estimate of the CVDS accounting for 44% of the variation in observed DMI, with a 0.95 genetic correlation between predicted and observed DMI. These prediction equations allow for individual feed allocation from group-feeding environments, enabling selection progress on feed intake through indicator traits.

Post weaning gain was estimated to be moderately heritable at 0.39 ± 0.05. The heritability estimate used by the AGA calculated from the entire data base is a similar 0.38. This is comparable to the estimate in Thallman et al., (2018) of 0.36 ± 0.03 for post weaning average daily gain, defined as the difference between adjusted yearling and weaning weights. Retallick et al., (2017) defined post weaning average daily gain (PWADG) as weaning weight subtracted from yearling weight, divided by the number of days between weights. The study found heritabilities of 0.36 ± 0.05 and 0.42 ± 0.05 for steer and heifer PWADG, respectively. In a

prototype system for conducting a genetic evaluation for feed intake in Angus cattle, MacNeil et al., (2011) published an estimated heritability of 0.31 ± 0.04 for postweaning body weight gain.

Adjusted weaning weight had a heritability estimate of 0.21 ± 0.04. The AGA estimate of heritability for AWWT from the entire database is 0.26. The estimate in this study is lower than the estimate of 0.33 ± 0.03 found by MacNeil et al., (2011). The discrepancy between estimates could be attributed to a much larger data set of 18,169 Angus animals with which to estimate variance components found in the MacNeil et al., (2011) study. Arthur et al., (2001) found a lower estimate of 0.17 ± 0.03 for the direct heritability of the similar trait of 200-d weight in a population of 1,180 young Angus bulls and heifers.

Genetic and phenotypic correlations between traits can be found in Table 2-18. Correlations were estimated for all combinations of traits except for PDMR and RFI, and PDMR and DMI, because no animals had records for each trait in the respective pairs of traits in the current data. Both genetic and phenotypic correlations between DMI and RFI were high at 0.68 ± 0.09 and 0.70 ± 0.02, respectively. A strong positive correlation indicates that favorable (negative) DMI would lead to a more favorable (negative) RFI. The correlations between DMI and RFI were similar to those found by Rolfe et al. (2011) of 0.66 and 0.61 for genetic and phenotypic correlations, respectively. Arthur et al., (2001a) also found strong genetic and phenotypic correlations between DMI and RFI of 0.69 and 0.72, respectively.

Moderate genetic and phenotypic correlations were also found between DMI and PWG (0.53 ± 0.05, 0.50 ± 0.01). Correlations of this nature indicate that animals with greater DMI also tend to have greater PWG, which is expected. This relationship indicates that selection for greater (more favorable) PWG would result in greater (less favorable) DMI values. An increase in DMI associated with selection for growth was also found in Ceacero et al., (2016). Those

results are consistent with the findings of Koch et al., (1963), who found a correlation between feed consumption and gain of 0.64 in a population of Angus, Hereford, and Shorthorn cattle. Correlations between intake and gain are somewhat higher in the literature than those found in the current study.

In this data set, genetic and phenotypic correlations were low between DMI and AWWT at 0.18 ± 0.15 and 0.20 ± 0.02, respectively. Weak correlations indicate selection for animals with lower DMI would result in moderate changes in AWWT. The correlations in the current study are somewhat lower than those in the literature, which find that feed intake and measures of growth and size are well known to be strongly phenotypically and genetically correlated (Crews et al., 2004). Koots et al., (1994) found genetic associations of feed intake and measures of growth rate were positive, with genetic correlation estimates ranging from 0.25 to 0.79.

Weak genetic (0.05 ± 0.01) and phenotypic (0.06 ± 0.00) correlations were found between PDMR and PWG. A low correlation indicates genetic selection on PDMR would have little effect on PWG. A strong genetic correlation of 0.61 ± 0.25 was found between PDMR and AWWT, meaning selection for decreased PDMR would also lead to a decrease in AWWT.

Residual feed intake was lowly correlated genetically and phenotypically with PWG and AWWT in this data set. A well-known feature of RFI shown in the literature is it is phenotypically independent of its component traits of ADG and metabolic body weight (Crews et al., 2004). Phenotypic independence of RFI was verified in several other studies, including Arthur et al., 2001, and Basarab et al., 2003. While RFI may be phenotypically independent of measures of gain, it may not be genetically independent of its component traits. Low genetic correlations in the current study of RFI with PWG and AWWT of 0.18 ± 0.01 and 0.08 ± 0.16,

respectively, echo that concept. Genetic correlations of any magnitude may have implications to long-term selection on RFI with correlated responses in weight and gain (Crews et al., 2004).

A moderate genetic correlation was found between PWG and AWWT, which is expected since weaning weight is a component of PWG. Weak correlations in this data set could be attributed to fewer animals with phenotypes for both traits in a correlation, making it more difficult to obtain reliable estimates.

Index selection is preferable for genetic improvement in feed efficiency traits because of a large unfavorable genetic correlation between DMI and PWG. Single trait selection for one trait would result in a large undesirable effect for the other. The index considered in the current study developed by Rolf et al., (2011) balances gain and dry matter intake, with an emphasis on high gain. Selection based on the index accounts for the large genetic correlation by placing positive emphasis on growth with a negative emphasis on intake. The median index value in this data was -13.62, with a standard deviation of 268.79. Rankings between index values and component traits were compared to assess what animals performed most favorably in the index. Rank correlation between I and DMI was 0.7263. Rank correlations were moderate between I and RFI at 0.4332. Rank correlations between PDMR and I were lower at 0.1769. Rank correlations between I and AWWT and PWG were negative, estimated at -0.3636 and -0.9995. Negative index values are more favorable for this index, so large positive correlations with intake and negative correlations with gain indicate that animals with high gain would perform most favorably on the index, as opposed to animals with lower feed intake. MacNeil et al., (2017) studied the value of six different indexes of cow efficiency, which compared increasing output and decreasing input simultaneously, increasing output and holding input constant, or holding output constant and decreasing input. The study recommended indexes that

simultaneously increase output and reduce input, such as the one developed by Rolf et al., (2011) used in this study.

The rank correlation between I and the AGA $Cow index was 0.0092. The animals with the highest 4 I values ranked in the 20th percentile and below for $Cow, with the number 5 animal for I ranking in the 70th percentile. The weak relationship between the I and $Cow index is expected since feed efficiency traits are not especially emphasized in the $Cow index. However, because feed costs are a large component of cow costs (Koch et al., 1963; Dickerson et al., 1974), greater emphasis on efficiency traits would be practical in any maternal index. The rank correlation between I and the AGA FPI index was 0.3575. Top animals for I performed somewhat more favorably for FPI than for $Cow, with the top 5 I animals ranking in the 30th percentile and better for FPI. This moderate relationship is expected, as both the FPI and I index have a strong growth component. The rank correlation between I and the AGA EPI (feed efficiency) index was 0.2724. The moderate correlation between efficiency indexes was expected, as they both contain measures of feed intake and gain.

Figure 2-1 shows the average EPD value per year for DMI, PDMR, RFI, PWG, and AWWT. Although some upward progress has been made in both PWG and AWWT, no significant change through selection has been made for DMI, PDMR, or RFI. Lack of progress is likely because of limited selection intensity on feed intake because of low number of animals tested, and a lack of selection tools at the time of this study to select for feed efficiency in Gelbvieh cattle. Figure 2-2 shows the average index value per year for $Cow, FPI, EPI, and I. The historical changes in I seen in Figure 2-1 roughly follow changes in AWWT seen in Figure 2-2, suggesting gain is an important component in efficiency. The lack of a similar relationship with DMI suggests that although feed intake is a necessary component of efficiency, in the

market conditions reflected in the index the benefit of a pound of increased gain is more important than the benefit of a pound of decreased intake. A point of interest is the lack of relationship between PWG and I in the trends of figures 2-1 and 2-2. This suggests that while gain is the primary component of I, index selection with intake included is still different than single trait selection on gain alone.

Significant genetic variation in efficiency traits in this study demonstrate that their inclusion in breeding programs is practical. Moderate heritabilities indicate genetic improvement of feed efficiency through selection is possible. Numerous studies, including the current data, have estimated genetic parameters of feed intake and growth traits. More can be learned, however, about how efficiency traits measured in yearling animals in a feedlot correspond to mature animals on pasture. As indicated by Arthur et al., (2001), the expectation when selecting on feed efficiency is that the resultant progeny should be efficient both as steers performing in the feedlot as well as mature cows in the breeding herd. Feed intake measurement is amenable for high energy diets but not for roughage, so measurement of feed intake in the cow herd is not feasible currently (Nielsen et al., 2013). There is some discussion that efficiency as a young, growing animal might be a different trait than efficiency as a mature animal, where efficiency of feed use for maintenance is the key trait (Arthur et al., 2001). Shike, (2012) suggests that roughly 70 percent of feed resources go to the cowherd. Of that, roughly 70 percent of feed is used for maintenance, meaning roughly 50 percent of feed overall is used simply to maintain the cowherd. A study by Arthur et al., (2001b) reported phenotypic and genetic correlations between RFI at 274 d of age and 430 d of age to be 0.43 and 0.75, respectively. While the measurements are relatively close together, the correlations indicate that RFI taken as a weaned calf is a similar trait as RFI taken later in life. Crews et al., (2003) found a genetic correlation of 0.55 ± 0.30

between RFI for 84-day growing and 112-day finishing periods, suggesting a positive genetic association exists between RFI collected on roughage and grain-based diets and different points of maturity. Meyer et al., (2008) found that cows for which RFI had been determined as low as heifers had a 21% numerically lower DMI than cows who had greater RFI values as heifers. A study by Basarab et al., (2007) further quantified the importance of feed efficiency by linking progeny RFI with dam productivity characteristics. Dams that produced low RFI (more efficient) calves were themselves found to be fatter, had fewer twins, and spent less time in feed activity than medium or high RFI (less efficient) RFI cows and calves.

In related research, MacNeil et al., (2017) evaluated alternative expressions of genetic merit for cow efficiency. The study found ADG to be heritable at 0.27 and cow weight (CWT) to be heritable at 0.45. Estimates of repeatability for ADG and CWT were 0.42 and 0.67, respectively, indicating that ADG and CWT are repeatable across a female's lifetime.

Some research also indicates that definitions of feed efficiency such as RFI may not truly reflect production efficiency on the carcass level. Disparities may exist between feed efficiency calculated with live-weight and average daily gain and feed efficiency calculated with carcass weight and carcass fat. Research by Kelly et al., (2019) showed differences ($P < 0.001$) between residual energy intake (REI) calculated with live weight and ADG as the energy sinks and REI calculated with carcass weight and carcass fat as energy sinks. These findings suggest the ability to efficiently convert energy into live-weight gain reflected in traditional efficiency measures such as RFI does not necessarily equate to efficiently converting energy into carcass gain.

Links between efficiency as a growing and mature animal, in addition to links between feed efficiency and dam productivity characteristics, indicate feed intake and gain to be ERT

worth collecting by breed associations. Further studies to discern the best method for selecting on feed efficiency in the cow herd and in mature animals would be beneficial.

The number of animals available for genetic evaluation of feed intake is limited, largely because the collection of individual intake and gain data is expensive and time consuming. Recent studies have shown that shortening the required test period could reduce costs and subsequently result in testing a larger number of animals without impacting the quality of data. Culbertson et al., (2015) found that average daily DMI (ADMI) values from a 42-day test and RFI values from a 56-day test adequately predict ADMI and RFI compared to a 70-day test. Similarly, a study by Thallman et al., (2018) found a high genetic correlation (0.995) between DMI for the first 42 days of the test period and DMI for the mean of 83 days for the entire test period. Additionally, the study found PWADG highly correlated with ADG at 42 and 83 days (0.852 and 0.822, respectively). Retallick et al., (2018) also found high correlations between steer and heifer PWG and on-test ADG. This suggests PWG from weaning to yearling can be combined with intake and gain records from a shortened test period to accurately evaluate feed efficiency. The current study used PWG as the gain component of the efficiency index tested, meaning the intake component could be from a shortened and less expensive testing period. Shortening the recording period for individual feed intake has the potential to improve selection response for feed efficiency by increasing the number of animals that can be recorded in fixed capacity facilities (Thallman et al., 2018).

Conclusions

Feed efficiency parameters were estimated to be moderately heritable in this data set of Gelbvieh influenced cattle, indicating producers can make genetic improvement through

selection for the traits. In addition, correlations among certain feed efficiency traits indicate selection for one trait should result in a correlated response in others. Index selection is preferable for genetic improvement in feed efficiency traits because of a large unfavorable genetic correlation between FI and growth. Single trait selection for one trait would result in a large undesirable effect for the other. Selection based on an index accounts for the large genetic correlations by placing positive emphasis on growth with a negative emphasis on intake. Continued collection of feed efficiency phenotypes is essential to identifying animals that are profitable in feed energy utilization. Increased feed efficiency in Gelbvieh influenced animals could lead to increased profits in identifying animals that will either grow at a faster rate with constant levels of feed intake or have a lower feed intake with constant levels of gain. Animals with a combination of higher gain and lower intake relative to gain can be identified with a selection index that places downward pressure on intake while selecting for increased gain, such as the I3 index in Rolfe, et al., (2011). Increased profitability of animals in the feed yard could lead to greater market share of Gelbvieh influenced animals in the terminal beef market.

Table 2-1. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch A.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	62				
PDMR	0	659			
RFI	54	0	136		
PWG	59	89	135	230	
AWWT	62	659	136	230	854

Table 2-2. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch B.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	120				
PDMR	0	0			
RFI	62	0	62		
PWG	119	0	62	119	
AWWT	120	0	62	119	120

Table 2-3. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch C.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	852				
PDMR	0	0			
RFI	90	0	747		
PWG	780	0	659	1391	
AWWT	852	0	747	1391	1509

Table 2-4. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch D.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	23				
PDMR	0	0			
RFI	23	0	23		
PWG	23	0	23	23	
AWWT	23	0	23	23	23

Table 2-5. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch E.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	0				
PDMR	0	0			
RFI	0	0	68		
PWG	0	0	51	51	
AWWT	0	0	68	51	68

Table 2-6. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch F.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	199				
PDMR	0	0			
RFI	199	0	893		
PWG	166	0	809	809	
AWWT	199	0	893	809	893

Table 2-7. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch G.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	117				
PDMR	0	0			
RFI	117	0	157		
PWG	98	0	123	123	
AWWT	117	0	157	123	157

Table 2-8. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch H.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	26				
PDMR	0	0			
RFI	0	0	0		
PWG	26	0	0	47	
AWWT	26	0	0	47	56

Table 2-9. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch I.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	37				
PDMR	0	0			
RFI	0	0	0		
PWG	36	0	0	36	
AWWT	37	0	0	36	37

Table 2-10. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch J.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	0				
PDMR	0	0			
RFI	0	0	78		
PWG	0	0	78	78	
AWWT	0	0	78	78	78

Table 2-11. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch K.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	319				
PDMR	0	0			
RFI	319	0	420		
PWG	317	0	408	315	
AWWT	319	0	420	415	420

Table 2-12. Number of records for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) for each trait and each pair of traits (below the diagonal) for ranch L.

	Trait				
Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	0				
PDMR	0	0			
RFI	0	0	155		
PWG	0	0	137	137	
AWWT	0	0	155	137	155

Table 2-13. Number of raw records (before editing) for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) by ranch for each trait.

		Trait				
Ranch	Total	DMI	PDMR	RFI	PWG	AWWT
A	854	62	659	136	230	854
B	120	120	0	62	119	120
C	1,509	852	0	747	1,391	1,509
D	23	23	0	23	23	23
E	68	0	0	68	51	68
F	893	199	0	893	809	893
G	157	117	0	157	123	157
H	56	26	0	0	47	56
I	37	37	0	0	36	37
J	266	0	0	266	265	266
K	420	319	0	420	415	420
L	155	0	0	155	137	155
Total	4,500	1,755	659	2,927	3,696	4,500

Table 2-14. Number and percent of animals per breed fraction group[1] of percentage Gelbvieh for the final (edited) data set.

Breed fraction	Number of animals	Percent of total
<13	25	1
13	63	1
25	244	5
38	267	6
50	1,668	37
63	244	5
75	355	8
88	98	2
94	1,991	27
100	345	8

[1]American Gelbvieh Association assigned breed group, where the actual breed percentage of the animal is rounded to fit within the nearest group.

Table 2-15. Number of contemporary groups for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) by ranch.

Ranch	DMI	PDMR	RFI	PWG	AWWT
A	23	6	79	253	344
B	6	0	6	6	6
C	122	0	129	101	71
D	5	0	5	5	6
E	6	0	6	4	2
F	68	0	68	62	54
G	35	0	35	35	33
H	11	0	11	11	11
I	6	0	6	6	7
J	55	0	55	49	45
K	25	0	25	22	20
L	15	0	15	15	10
Total	377	6	440	569	609

Table 2-16. Number of contemporary groups (N), mean number of animals in contemporary group (Mean), minimum number of animals in contemporary group (Min), maximum number of animals in contemporary group (Max) for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) (diagonal) in the final data set.

Trait	N	Mean	Min	Max
DMI	377	25.08	4	68
PDMR	6	2.00	6	6
RFI	440	36.66	5	129
PWG	569	47.42	4	253
AWWT	609	50.75	2	344

Table 2-17. Descriptive statistics for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT).

Trait	N	Mean (lbs)	SD	Min	Max
DMI	1,755	23.29	4.71	10.14	51.18
PDMR	659	21.02	2.40	9.05	31.25
RFI	2,927	-0.16	1.60	-12.07	5.73
PWG	3,696	474.80	102.60	116.00	766.00
AWWT	4,110	635.30	82.92	332.00	922.00

[1]Combined data represents the final data set after removing duplicate records, single animal contemporary groups, and animals with no feed intake phenotypes recorded.

Table 2-18. Estimates for additive genetic (σa^2), phenotypic (σp^2), and residual (σe^2) variances for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) in lbs^2.

Trait	σ_a^2	σ_p^2	σ_e^2
DMI	1.89	4.81	2.93
PDMR	0.99	2.09	1.10
RFI	0.38	1.16	0.78
PWG	1,409.00	3,576.80	2,168.00
AWWT	635.10	3,019.10	2,384.00

Table 2-19. Estimates of heritabilities (diagonal), genetic correlations (above diagonal), phenotypic correlations (below diagonal), with SE in parentheses and number of records below for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT).

Trait	DMI	PDMR	RFI	PWG	AWWT
DMI	0.39 (0.06)	NE[1]	0.68 (0.09)	0.53 (0.05)	0.18 (0.15)
	1676		811	1544	1676
PDMR	NE[1]	0.47 (0.15)	NE[1]	0.05 (0.01)	0.61 (0.25)
		659		89	650
RFI	0.70 (0.02)	NE[1]	0.32 (0.06)	0.18 (0.11)	0.08 (0.16)
	811		2358	2280	2534
PWG	0.50 (0.01)	0.06 (0.00)	0.11 (0.02)	0.39 (0.05)	0.28 (0.13)
	1544	89	2280	3224	3224
AWWT	0.20 (0.02)	0.23 (0.05)	-0.04 (0.02)	0.05 (0.02)	0.21 (0.04)
	1676	650	2534	3224	4110

[1]NE=Non-estimable because no animals have both traits recorded

Figure 2-1. Average EPD value per year for Dry Matter Intake (DMI), Predicted Dry Matter Required (PDMR), Residual Feed Intake (RFI), Post Weaning Gain (PWG), and Adjusted Weaning Weight (AWWT) in lbs.

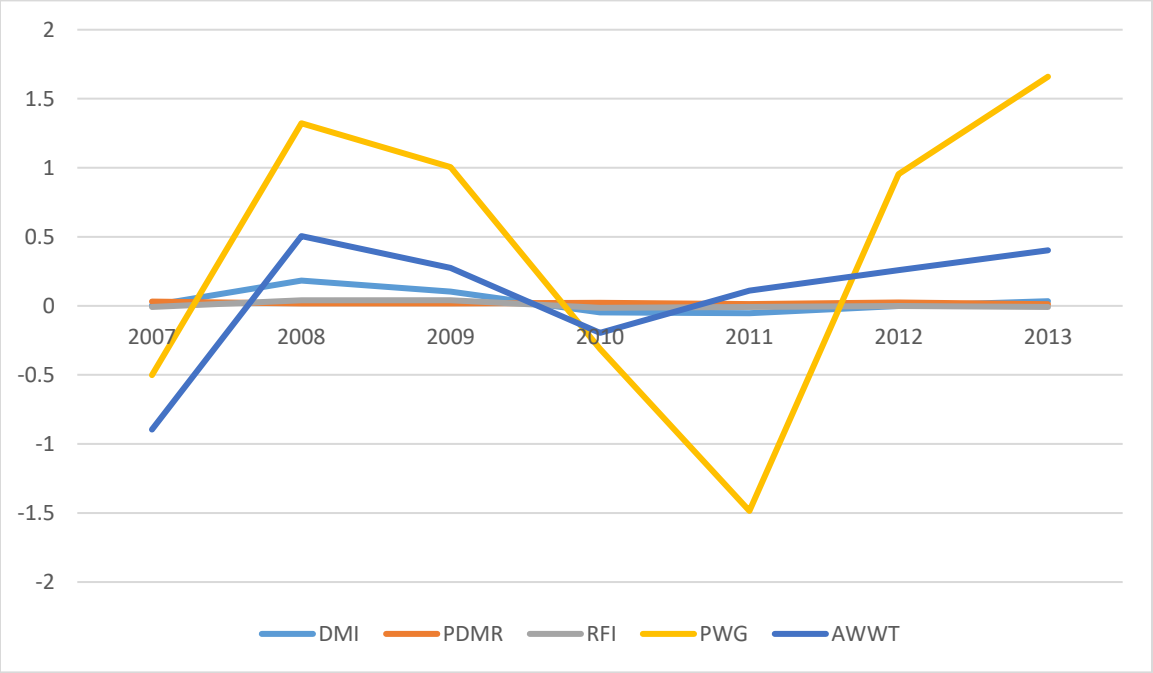
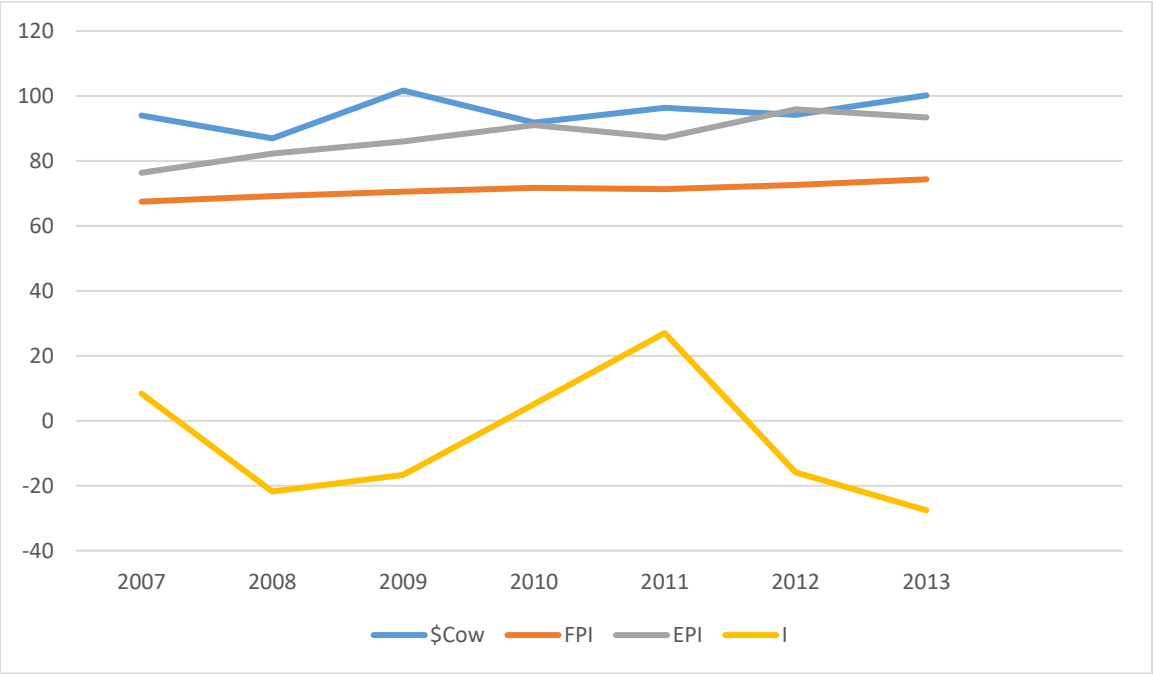


Figure 2-2. Average index value per year for $Cow, Feeder Profit Index (FPI), Efficiency Profit Index (EPI), and I.



References

Archer, J. A., P. F. Arthur, R. M. Herd and E. C. Richardson. 1998. Genetic variation in feed efficiency and its component traits. Proc. 6th World cong. Genet. Appl. Lives. Prod., Armidale, NSW, Australia. 25:81-84.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805-2811.

Arthur, P.F., Renand, G. and Krauss, D. 2001b. Genetic and phenotypic relationships among different measures of growth and efficiency in young Charolais bulls. Livest. Prod. Sci. 68: 131-139.

Basarab, J. A., M. G. Colazo, D. J. Ambrose, S. Novak, D. McCartney, and V. S. Baron. 2011. Residual feed intake adjusted for backfat thickness and feed frequency is independent of fertility in beef heifers. Can. J. Anim. Sci. 91:573–584.

Berry, D. P. and J. J. Crowley. 2013. Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. J. Anim. Sci. 91: 1594-1613.

Berry, D. P. and J. E. Pryce. 2013. Feed efficiency in growing and mature animals. Proc. 10th World Congr. Genet. Appl. to Livest. Prod., Vancouver, Canada.

Cooper, A. J., C. L. Ferrell, L. V. Cundiff, and L. D. Van Vleck. 2010. Prediction of genetic values for feed intake from individual body weight gain and total feed intake of the pen. J. Anim. Sci. 88: 1967-2391.

Crews, D.H., Jr., N. H. Shannon, B. M. A. Genswein, R. E. Crews., C. M. Johnson, and B. A. Kendrick. 2003. Genetic parameters for net feed efficiency of beef cattle measured during postweaning growing versus finishing periods. Proc. West. Sec. Am. Soc. Anim. Sci. 54: 125-128.

Crews D.H., Jr. 2005. Genetics of efficient feed utilization and national cattle evaluation: A review. Genetics and Molecular Research. 4:152-165.

Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885-894.

Culbertson, M. M., S. E. Speidel, R. K. Peel, R. R. Cockrum, M. G. Thomas, and R. M. Enns. 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. J. Anim. Sci. 93:2482–2487.

Dickerson, G. E., N. Kunzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. J. Anim. Sci. 39:659-673.

Guiroy P.J., D. G. Fox, Tedeschi L.O., Baker M.J. & Cravey M.D. (2001) Predicting individual feed requirements of cattle fed in groups. J. Anim. Sci. 79:1983-1995.

Kelly, D. N., C. Murphy, R. D. Sleator, M. M. Judge, S. B. Conroy, and D. P. Berry. 2019. Feed efficiency and carcass metrics in growing cattle. J. Anim. Sci. 97:4405-4417.

Kennedy, B. W., J. H. J. van der Werf and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci. 71:3239-3250.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486-494.

Koots, K. R., J. P. Gibson and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:826-853.

MacNeil, M. D., M. M. Scholtz, F. J. Jordaan, and A. Maiwashe. 2019. Alternative models for genetic evaluation of feed intake by Afrikaner cattle. S. Afr. J. Anim. Sci. 49: 763-769.

MacNeil, M. D., M. C. Mokolobate, M. M. Scholtz, F. J. Jordaan, and F.W.C Neser. 2017. Alternative approaches to evaluation of cow efficiency. S. Afr. J. Anim. Sci. 47:188-123.

MacNeil, M. D., M. M. Scholtz, and A. Maiwashe. 2013. Estimates of variance components for postweaning feed intake and growth in Bonsmara bulls and evaluation of alternative measures of feed efficiency. S. Afr. J. Anim. Sci. 49:763-769.

MacNeil, M. D., N. Lopez-Villalobos, and S. L. Northcutt. 2011. A prototype national cattle evaluation for feed intake and efficiency of Angus cattle. J. Anim. Sci. 89:3917-3923.

Middleton, B. K. and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861-3871.

Nielsen, M.K., M.D. MacNeil, J.C.M Dekkers, D.H. Crews Jr., T. A. Rathje, R.M. Enns, and R.L. Weaber. 2013. Review: Lifecycle, total industry genetic improvement of feed efficiency in beef cattle: Blueprint for the Beef Improvement Federation. Prof. Anim. Sci. 29: 559-565.

Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews Jr., and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measure of efficiency with growth and carcass merit of beef cattle. J. Anim. Sci. 85:2711–2720.

NRC (2000) Nutrient Requirements of Beef Cattle. National Academy Press.

Perry T.C. and D. G. Fox. 1997. Predicting carcass composition and individual feed requirement in live cattle widely varying in body size. J. Anim. Sci. 75: 300-307.

Retallick, K. M., D. B. Faulkner, S. L. Rodrigues-Zas, J. D. Nkrumah, and D. W. Shike. 2013. The effect of breed and individual heterosis on the feed efficiency, performance, and carcass characteristics of feedlot steers. J. Anim. Sci. 91:5161-5166.

Retallick, K. J., J. M. Bormann, R. L. Weaber, M. D. MacNeil, H. L. Bradford, H. C. Freetly, K. E. Hales, D. W. Moser, W. M. Snelling, R. M. Thallman. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. J. Anim. Sci. 95:1444–1450.

Rolf, M. M., J. F. Taylor, R. D. Schnabel, S. D. McKay, M. C. McClure, S. L. Northcutt, M. S. Kerley, and R. L. Weaber. 2012. Genome-wide association analysis for feed efficiency in Angus cattle. Anim Genetics. 43:367-374.

Rolf, M. M. 2009. Implementation of high-density SNP data for genetic evaluation and QTL discovery in beef cattle. Master's Thesis. University of Missouri-Columbia.

Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H. C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. J. Anim. Sci. 89:3452-3459.

Santana, M. H. A., G. A. Oiveria, Jr., R. C. Gomes, S. L. Silva, P. R. Leme, T. R. Stella, E. C. Mattos, P. Rossi Jr, F. S. Baldi, J. P. Eler, J. B. S. Ferraz. Genetic parameter estimates for feed efficiency and dry matter intake and their association with growth and carcass traits in Nellore cattle. 2014. Livestock Science. 167:80-85.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth and body composition traits of young beef bulls. Can. J. Anim. Sci. 84: 177-184.

Shike, Daniel. 2012. Beef Cattle Feed Efficiency. http://www.beefusa.org/CMDocs/BeefUSA/Resources/cc2012-Beef-Feed-Efficiency--Dan-Shike.pdf

Tedeschi L.O., D. G. Fox, and P. J. Guiroy. 2004. A decision support system to improve individual cattle management. 1. A mechanistic, dynamic model for animal growth. Agricultural Systems. 79:171-204.

Williams, C. B., and T. G. Jenkins. 2006. Impact of selection for feed efficiency on beef life cycle performance. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Minas Gerais, Brazil, 13-18 August 2006.

Williams, C. B., G. L. Bennett, T. G. Jenkins, L. V. Cundiff, and C.L. Ferrell. 2005. Using simulation models to predict feed intake: Phenotypic and genetic relationships between observed and predicted values. J. Anim. Sci. 83(Suppl. 1):13. (Abstr.)

Chapter 3 - Genetic Parameter Estimates for Sustained Productivity in Gelbvieh Influenced Cattle

Introduction

A beef cow must typically remain in production for many years for revenue created to offset maintenance and development costs (Snelling et al., 1995). Based on $50 to $100 annual net return per cow and $100 to $200 difference between heifer development costs and cow salvage value, 2 to 8 calves are required to break even (Dalsted and Gutierrez, 1989). Cows remaining in production past the breakeven age must outnumber cows that were culled before that age for a herd to be profitable (Snelling et al., 1995). Increased productivity impacts sale weights at weaning in two ways. Fewer heifer replacements are required each year, so more female calves are sold at weaning (Garrick, 2006). Average weaning weight will subsequently increase because of the greater number of older cows in production, as mature cows wean larger calves than first calf heifers (Garrick, 2006).

Genetic selection for sustained productivity in terms of successful reproduction has traditionally been achieved through an expected progeny difference (EPD) for the probability of surviving to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981), often called stayability. Specifically, stayability is the probability a cow will remain in production until 6 years old given she calved as a 2-year old (Brigham et al., 2007). Predictions of genetic merit of sustained production allow selection of sires whose daughters are more likely to remain in production long enough to be profitable (Snelling et al., 1995).

Statistical analysis of sustained reproductive success can become challenging because of partial records on females and the length of time an animal must be in the herd before it receives an accurate prediction for the trait (MacNeil, 2011). Traditionally, a female must reach the age of

6 before receiving a stayability observation. At that age, the sire of that female will be at least 8 years old, meaning very low prediction accuracy for sires less than 8 years old (Brigham et al., 2007). The discrepancy between accurate prediction of stayability and the need for young replacements has been a point of consistent criticism (Hudson and Van Vleck, 1981).

The existence of partial records, or censored records, is the main issue associated with the calculation of direct measures of productivity. Some animals are still alive at the end of a study, or have incomplete calving data, so only the lower bound of their true productive life is known (Ducrocq, 1994). Considering those records complete or removing them from the data set would produce biased results (Ducrocq, 1994). An alternate form of assessing productive life can be obtained by using survival analysis to account for time-dependent variables and censored records (Ducrocq and Solkner, 1994, 1998). A proposed use of statistical methods to properly analyze censored records was developed by Smith (1983). The analysis of censored records by Smith involves the use of hazard rate $\lambda(t)$, with the objective of estimating an animal's probability of being culled at time t. The hazard function is the product of a baseline hazard function and time-dependent explanatory variables that could possibly influence culling rate (Beaudeau et al., 1995). This method of analysis combines censored and uncensored information, enabling proper use of censored records and accounting for the non-linear nature of longevity data (Sewalem et al., 2003).

The objectives of this study were to calculate an estimated breeding value (EBV) for each sire for relative risk of failing to calve consecutively within 425 days from 1 to 9 parities. The EBV for relative risk could then be used as genetic selection tool for sires whose daughters are more likely to reproduce in the herd within 425 days from 1 to 9 parities.

Materials and Methods

Animal Care and Use Committee approval was not obtained for this study because the data were accumulated by breeders belonging to the American Gelbvieh Association (AGA) as part of their genetic improvement program. The AGA implemented total herd reporting in 2001 to more accurately report the reproductive success of females in the cowherd. Data for this analysis were birth dates and disposal codes reported by breeders to the AGA. Every animal in the AGA database has an associated code. Animals without a recorded disposal date and reason code receive a code of "Active". Dam birthdate was used as a baseline, while calf birthdate was used to indicate productive life of the dam in number of calves per dam. A detailed diagram of data editing can be found in Figure 3-1. A total of 269,037 females were recorded from 2001 to 2015 which coincides with the AGA implementing total herd reporting. Of the females recorded during that time frame, 61,982 recorded their first calf at 2 years of age. Females where breeder did not equal the owner at the time of the data extract were excluded, leaving a total of 40,105 females in the analysis. Females that were sold but not transferred were used in the analysis until the time of their first missed calf. Single animal contemporary groups and donor females were removed, for a final total of 38,549 females in the analysis. Contemporary group was defined as animal breeder and birth year. A total of 9,788 contemporary groups were included in the analysis with a median number of 4 females per group.

Censored records are those where the value of an observation is only partially known (Kachman, 1999). An example of censoring in this data set can be found in Table 3-1. For the purposes of this analysis, a female was considered to have a complete record (uncensored, code "0") if she failed to calve within 425 days of the previous calving, with no reported disposal code. A female was also considered uncensored, or considered to have a complete record, if she

was greater than 11 years and 60 days old at the time of data extraction without a calving interval greater than 425 days in her lifetime. An uncensored female received a zero for censor code and a phenotype of the sum of the number of consecutive calves she mothered within 425 days of the previous calving (sum of calf consecutive count) like the uncensored female record in Table 3-1. At the time of the data extract, no female in the AGA database was reported as culled specifically for reproductive failure. To impose absolute culling for failing to produce a calf each year, females were required to have a live calf recorded within 425 days of the previous calving date. A female was considered to have an incomplete record (censored, code 1) if she had a defined non-reproductive disposal code, indicating she was culled from the herd for a reason other than reproduction. Females still active and producing in the herd but younger than 11 years 60 days of age at the time of data extract were also considered censored, since the upper bound of their productive life was still unknown. Females with incomplete records (censored) received a phenotype of sum of consecutive calf count and a censoring code of one, like the censored female in Table 3-1.

Statistical analysis for this study were performed using The Survival Kit 6.12 (Meszaros et al., 2013). The Survival Tool Kit is a set of programs that allows for analysis of survival data (Solkner and Ducrocq, 1999). More specifically, the Survival Tool Kit allows for analysis of data which measure time until a defined event using Cox and Weibull regression models (Solkner and Ducrocq, 1999). The programs are specifically adapted to animal breeders who use large data sets and aim to estimate random effects, or animals in the context of this study (Solkner and Ducrocq, 1999). Covariance structure between observations based on genetic relationship was also included (Solkner and Ducrocq, 1999). The programs allow for analysis of fixed effects

such as contemporary group on survival, enabling large scale genetic evaluations (Solkner and Ducrocq, 1999).

Productive life has been modeled in a variety of ways using the Survival Toolkit. For instance, length of productive life as an estimate of survival was modeled by Sewalem et al., (2003) in Canadian dairy cattle. Length of productive life (t) in the Sewalm et al., (2003) study was defined as the time from one calving to the next or death or culling. Lifetime record was considered completed (uncensored) if the cow received a termination code, meaning she was either culled or died (Sewalem et al., 2003). Censored animals included those sold, exported, or leased to another herd, or cows still producing in the herd at the time of the study. Cows that transferred herds during their productive life were considered censored (Sewalem et al., 2003). In an alternative model proposed by Roxtrom et al., (2003) the origin point was calving date, with the end point of the culling date or date of next calving. The record was considered censored if the cow had a next calving. The trait of interest was the overall risk of failure (Roxtrom et al., 2003).

For the purposes of this analysis, the origin point was birth year of the female, with the end point of failure to calve within 425 days, culling date, or date of next calving. The hazard function, or time to failure, was defined as the probability of a cow being culled for failing to calve within 425 days of the previous calving. Time to failure was a function of a baseline hazard function and time-dependent explanatory variables that influence culling rate (Beaudeau et al., 1995), in this case number of consecutive calves. An integer representing the sum of number of consecutive calves a female had in her lifetime was used as the phenotype of each female. In this data set, cow birth year was considered the start value, with the sum of the number of calves from the female's birth year to cull date used as the time-dependent explanatory variable.

The Survival Tool Kit allows for analysis of survival data using covariance structure between observations based on pedigree, producing sire solutions analogous to estimated breeding values (EBVs). The genetic prediction of interest is the Risk Ratio (RR), which is the random effect solution for sire. Risk ratio is defined as the ratio of the comparison category's probability of failure (here, the uncensored animals) to the reference category's probability of failure (here, censored animals). A risk ratio greater than one indicates increased risk. In the current data set, a sire with more fertile daughters would have a RR less than 1, while sires with fewer fertile daughters would have a RR greater than 1. A greater RR would indicate a fewer number of days to failure, along with a decreased chance of being successful through the next calving period (MacNeil et al., 2011). A sire with a RR of 0.90 would be expected to produce 10% more daughters that calve consecutively in 425-day intervals or less for 9 calves than sires with daughters in the reference, or censored category. Nine calves is the number of calves a female can have if she successfully calves within 425 days from 2 to 11 years of age, which is the definition of a successful complete record in the uncensored group. Contemporary group was considered a fixed, time dependent variable, reflecting females exposed for breeding in the same herd-year.

Sustained fertility is a complex trait. Some effects are time independent, meaning they are constant over time, such as the animal effect. Many events that can lead to involuntary culling, however, do not have the same probability of occurrence during the life of the cow. For example, some fertility problems are more likely to occur later in life (Ducrocq and Solkner, 1998). It is therefore useful to model those events, such as contemporary group in this case, as time dependent. The dependency in time-dependent covariates is modelled through "piecewise" uniform hazard functions with jumps at times corresponding either to calendar dates or linked to

the individual itself (starting and stopping calving, for example) (Ducrocq et al., 2014). The concept of hazard rate λ(t), is defined as the probability of being culled at a time t, given the animal is alive prior to t (Smith, 1983). The hazard rate is easier to model as a function of explanatory variables than the survival function, which has an unknown distribution (Ducrocq, 1994). The hazard rate is the product of a baseline hazard function $\lambda_0(t)$ that represents the aging process, and a function of explanatory variables assumed to influence culling rate (Ducrocq, 1994). The effects of explanatory variables can be estimated separately from the baseline hazard function (Ducrocq, 1994). The baseline hazard function can be approximated by a Weibull distribution (Ducrocq, 1994). The Weibull hazard function is defined as

$$\lambda_{ijk}(t) = 1- \exp\{-\exp[C_i(t) + u_j + \xi_k]\},$$

where λ(t) represents the hazard function, or probability of reproducing for a cow at parity (t) within contemporary group (i), with sire (j), and parity (k); $C_i(t)$ represents contemporary group effects; and u_j represents the random sire effect assumed to be normally distributed, with mean 0 and variance $A\sigma_u^2$, where A is the additive relationship matrix between animals or sires and σ_u^2 is the animal or sire variance; $\xi_k = \log(-\log\alpha_k)$, and

$$\alpha_k = \exp\left[\int_{\tau_{k-1}}^{\tau_k} \lambda_0(\omega)d\omega\right],$$

where λ_0 is the baseline hazard function, ω is the conditional probability of success in parity τ_k (Macneil and Vukasinovic, 2011). The Weibull model is a generalization of the exponential model with a constant hazard rate of $\lambda_0(t) = \lambda$ (Ducrocq, 1994).

Time independent variables are modelled as a function of the proportional hazard function explained by Ducrocq (1994). Pedigree information was obtained on 43,854 sires over 3 generations, including 2,669 paternal grand-sires, and 2,668 paternal great-grand sires.

A model using sire as the random variable provided solutions in the analysis in the form of Risk Ratios. Results from this model used pedigree and phenotype information to provide a genetic evaluation that is equivalent to breeding values for the sustained productivity trait. Effective heritability was calculated as:

$$h^2_{eff} = 4\sigma^2_s/(\sigma^2_s+1)$$

where σ^2_s is the additive variance of the sire which calculates heritability on the original scale not dependent on Weibull parameters (Yazdi et al., 2002).

Results and Discussion

Distribution of females by parity for censored animals (those with a defined, non-reproductive disposal code or females active and still producing in the herd at data extract) can be found in Figure 3-2. Number of females by birth year for censored animals can be found in Figure 3-3. A description of how many females leave the herd with each disposal code per age can be found in Table 3-2. Difference in number of females at different parities reflects the relative culling rate between parities. The largest culling rate for censored females happened between parities 1 and 2, with only 50% of females who calved at parity 1 calving again at parity 2. The large culling rate for censored animals between parities 1 and 2 indicate females are highly likely to fall out of the herd between their first and second calves. The main disposal code for females at the 2nd parity (besides "Other" and "Old Code") was cows being moved to commercial herds. Selection tools for rebreeding after the 1st parity would enable selection for what is clearly an economically relevant trait. Parity 9 had the lowest culling rate, with 82% of females calving at parity 8 calving again at parity 9. Initially, it may seem that a female at parity 8 has a greater chance of staying in the herd than a female at parity 1. While the culling rate is less between parity 8 and 9 than parity 1 and 2, animals that stay in the herd until parity 9 have a

greater chance of success because females likely to be culled have already been disposed of by advanced parities. This is a principal of conditional probability and hazard functions, where the probability of success later is conditional on success at a previous date.

Distribution of females by parity for uncensored animals (females with no disposal code that fail to calve within 425 days of previous calving, or females 11 years 60 days old at data extract) can be found in Figure 3-4. Number of females by birth year for uncensored females can be found in Figure 3-5. As a comparison, number of females by birth year in the full (unedited) data can be found in Figure 3-6. The largest culling rate for uncensored females was between parities 1 and 2, with only 42% of females who calved at parity 1 calving again at parity 2. Like censored animals, the large culling rate between parities 1 and 2 for uncensored females indicate females are highly likely to fall out of the herd between their first and second calves. While a culling rate of 42% between the first and second calves is quite high, it could be that atrophy for females is higher in seedstock data than we would expect to see in commercial data. Uncensored females were least likely to leave the herd between their 8^{th} and 9^{th} parities, with the number of females in parity 9 being greater than those in parity 8.

Similar culling rates between 1^{st} and 2^{nd} parities for both censored and uncensored animals indicate females are equally likely to fall out of the herd after their first parity, whether for non-reproductive reasons or for failing to calve within 425 days of their first parity. Low culling rates for both censored and uncensored females between parities 8 and 9 indicate females likely to fall out of the herd for either non-reproductive reasons or for failing to calve within 425 days of their first parity have already done so by advanced parities. An animal being censored or uncensored did not make a substantial difference in culling rate between parities in this data set.

Summary information on censored and uncensored animals in this data set can be found in Table 3-3. Of the 38,549 females included in the analysis, 12,764 records were considered uncensored, meaning their record was considered complete. A total of 25,785 females were considered censored or considered to have an incomplete record. The phenotype of interest is expressed as the number of consecutive calves born within 425 days of the previous calving. The average consecutive calf count of uncensored females was 2.19 calves, with a minimum failure time of 1 calf and a maximum failure time of 9 calves. Uncensored females are those that continued to produce until 11 years 60 days of age at the time of data extraction, or those that failed to reproduce a calf within 425 days of the previous calf with no associated disposal code. An average failure time of 2.19 calves means that uncensored females fail to calve between their 2nd and 3rd calves. The average failure time of censored females was 2.39 calves, with a minimum failure time of 1 calf and a maximum failure time of 9 calves. An average failure time of 2.39 calves mean the largest percentage of censored females are culled for non-reproductive reasons between 2 and 3 calves.

The average RR in the current dataset was 0.99. The minimum value was 0.96, with a maximum value of 1. All sires in the current data set having RR values less than 1 indicate a large percentage of sires are likely to pass genes to daughters that increase the probability they of calving in 425 days or less. The small range between minimum and maximum values in the population suggest a lack of variation that could be a challenge in making selection progress based on RR values.

Estimated additive sire variance for RR was 0.01. Effective heritability was estimated at 0.04. A similar estimate of 0.05 was provided by MacNeil et. al., (2011). Estimates in related traits range from 0.02 to 0.20 in both beef (Snelling et al., 1995; Donoghue et al., 2004; Rogers

et al., 2004) and dairy (Ducrocq et al., 1988b; Vollema and Groen 1998). Variance estimates of risk of failure and progress through selection using a sire model have been outlined in MacNeil et al., (2011) and Ducrocq and Solkner (1994, 1998). Low heritability of survival traits indicates a strong influence of environment affecting the length of an animal's productive life in a herd. While the current data set does not yield a substantial amount of heritability, this study may not have enough data to accurately estimate sire genetic variance. If a genetic variance component exists, it might also be confounded with contemporary group because no variation exists within the contemporary group.

Genetic selection for productive life in the Gelbvieh population is currently limited to the Stayability EPD. Genetic trend for AGA animals in both Stayability and Sustained Productivity can be found in Figure 3-7. From the time the AGA began whole herd reporting in 2001, a small but positive increase in Stayability has been achieved. In contrast, no changes have been made in Sustained Productivity since 2001. The correlation between AGA Stayability EPD and Sustained Productivity was low at 0.14. Assuming Sustained Productivity puts more emphasis on culling for reproductive failure than traditional Stayability, it appears that selecting for increased Staybility does not improve the rate of calving within 425 days of the previous calving as measured in Sustained Productivity. A lack of association of this nature indicates that traditional Stayability reflects culling for traits other than reproduction. If the breeding objective is to select solely for improved reproductive performance, only females who successfully record a calf every year should be included as a success in Stayability calculations.

Practically, producers have culled for many things in the past that may have been economically relevant but not related to successful calving. Examples of this kind of voluntary culling may include frame size, docility, or even color. A selection tool specifically targeted for

sustained reproductive success could be helpful in selection for improved calving rate in Gelbvieh influenced cattle. As a breeder, a tool such as sustained productivity could be selected for in conjunction with other traits economically relevant to a successful operation, such as rate of gain and calving ease. Multiple trait selection in this manner would allow for continued selection on traits vital to the financial success of an operation, while also ensuring animals with those traits remain in the herd long past their financial break-even point. Ideally, selection for multiple traits would be done through an economic selection index, which would allow for more consistent selection progress across all component traits (Hazel and Lush, 1943).

Data quality for sustained productivity could be improved by more information given on the reproductive status of an animal and subsequent culling decisions. For example, breeders submitting pregnancy testing results or specifically recording when a female was culled for a missing pregnancy would be especially relevant. In registered herds, information on females that succeed in calving every year but perhaps register calves in different associations depending on the breed of sire should be reported to each registry as opposed to reporting a missing calf. A low heritability will make it difficult to make selection progress in productive life based on RR alone. Like all lowly heritable traits, potential exists for improvement in rate of genetic change using genomic technologies to account for a greater amount of additive variance in a trait.

Length of productive life of a cow has traditionally been analyzed as the difference between age at first calving to culling or death (Forabosco et al., 2002; Szabo and Dakay, 2009). True length of productive life in a beef cow herd can be affected by both voluntary and involuntary culling (MacNeil et al., 2011). Improving reproductive potential to increase profitability of an operation can be accomplished by addressing culling of open cows as the primary cause of voluntary culling (Arthur et al., 1992; McDermott et al., 1992).

The current analysis intended to use censoring based on reproductive and disposal data to reflect the voluntary culling of females with poor performance as dams. This goal proved difficult, as the most frequent disposal codes in the AGA database ("other" and "old code") do not indicate the reproductive success of a females. Due to the lack of specific reproductive disposal codes, data in the current study was edited to reflect a management system that required a cow to calve yearly, starting at 2 years of age, with absolute culling of cows not meeting that requirement. A whole-herd reporting system that required the explicit reporting of reproductive status of each cow for each breeding season could greatly improve AGA reproductive data for future evaluations. Information on the success or failure of each insemination, perhaps at pregnancy check, could also improve this evaluation in the future. An alternative approach to longevity analysis using success at pregnancy check could be a successful approach that doesn't rely on disposal code data. Real time recording of calving/pregnancy information closer to the time of the event, as opposed to during a mass whole-herd enrollment period, might encourage breeders to submit data that more accurately reflects the results of their calving season.

Conclusions

Sustained cow fertility and production are important contributors to the long-term profitability of the cow herd (Enns et al., 2005). Genetic and environmental factors influencing productivity may vary with cow age, which will likely alter the relationship between productivity at different ages (Brigham et al., 2007). Research supports a high probability that females in production at 4 years will remain in production to 6 years or more, suggesting earlier measures might be indicators of productivity later in life (Brigham et al., 2007).

Analysis indicated that animals in our data set that failed to calve within 425 days of previous calving, or those who were still producing in the herd at 11 years 60 days of age

(uncensored) exited the herd at an average of 2.19 years. Animals with a defined non-reproductive disposal code, or those still active in the herd at less than 11 years 60 days of age (censored) exited the herd at an average of 2.39 years. Younger parities had a greater culling rate that decreased at later parities. This indicates failure occurs at a higher rate at younger ages. It should be noted that while it appears younger parities have a greater risk of failure, animals most likely to be culled for reproductive failure have already left the herd by later parities. As a result, culling rate is lower in advanced parities.

Sustained reproductive success and length of productive life as indicators of cow fertility are of great economic importance to the beef industry. The current study is a prototype genetic evaluation that will allow the AGA to select for sires that have daughters with improved length of productive life. Continued use of total herd reporting by the AGA will help to improve the analysis of reproductive success over time. Data reporting in the form of birth dates of all calves and exposure data for both AI and natural service would help further improve the analysis. Most importantly, accurate reporting of disposal dates and reasons would help further refine the analysis by separating reasons of involuntary and voluntary culling.

Table 3-1 Example of Censored and Uncensored records, based on calf count [1].

		Age											
Type		**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Disposal code**	**Censor code**	**Sum of CC**
Censored	**Calf Count (CC)**	1	1	0	0	0	0	0	0	0	Active	1	2
Censored	**Calf Count (CC)**	1	1	1	1	1	1	0	0	0	Cow culled – poor feet	1	6
Uncensored	**Calf Count (CC)**	1	1	1	1	1	1	1	1	1	Active	0	9
Uncensored	**Calf Count (CC)**	1	1	0	1	1	0	0	0	0	Active	0	2

[1] For analysis, animals successfully calving past age 11 years 60 days were considered uncensored

Table 3-2. Number of females per disposal code for each age in censored (code 1) animals.

	Age							
Disposal Code[1]	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Active	3,091	1,913	1,346	832	577	389	266	104
Genetic conditions	4	1	--	--	1	--	--	1
Freemartin	1	1	--	1	--	--	--	--
Poor feet	3	1	2	1	--	--	1	--
Temperament	2	--	1	1	--	--	1	--
Herd reduction	151	78	44	40	27	26	8	15
Dystocia	143	34	11	6	2	--	--	--
Health	287	117	74	40	31	20	11	6
Injury	227	82	65	34	23	16	8	7
Old age	200	80	78	60	49	56	43	62
Other	1,458	684	349	267	151	89	31	26
Prolapse	93	15	13	4	2	--	--	
Moved commercial	493	248	156	84	59	27	14	13
Old code	4,904	2,338	1,215	669	458	254	58	14
On hold	10	3	--	--	1	1	--	--

[1] Disposal codes relating to preweaning performance for females that had at least 1 calf were removed from this table but were included in the data for analysis.

Table 3-3. Number of animals in censored and uncensored groups, with their associated mean, minimum and maximum age of failure.

Type	N	Mean	Min	Max
Uncensored	12,764	2.19	1	9
Censored	25,785	2.39	1	9

Figure 3-1. Data editing for females born from 2001-2015 for the American Gelbvieh Association used in the sustained productivity analysis.

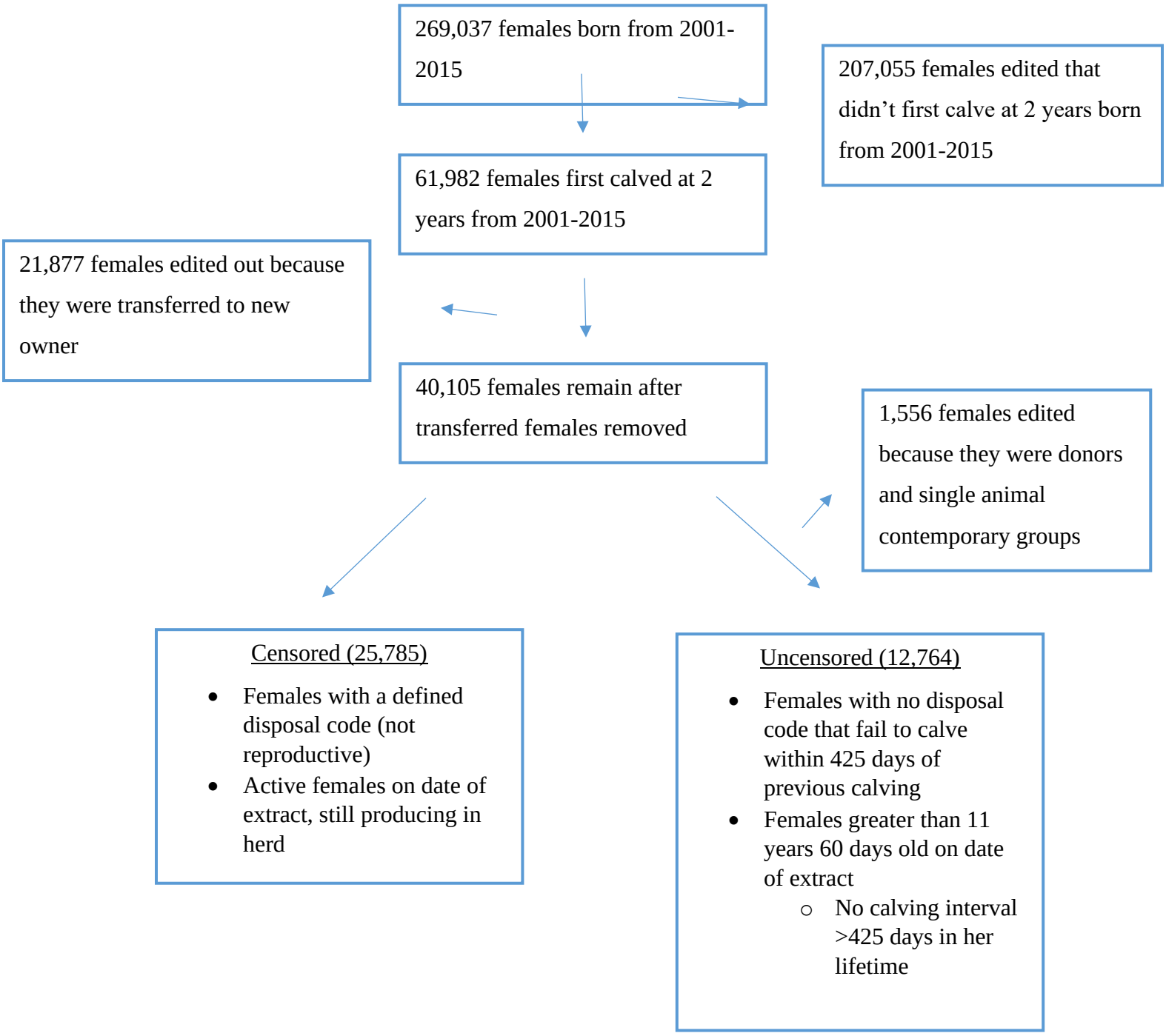


Figure 3-2. Number of females by parity in censored (code 1) animals.

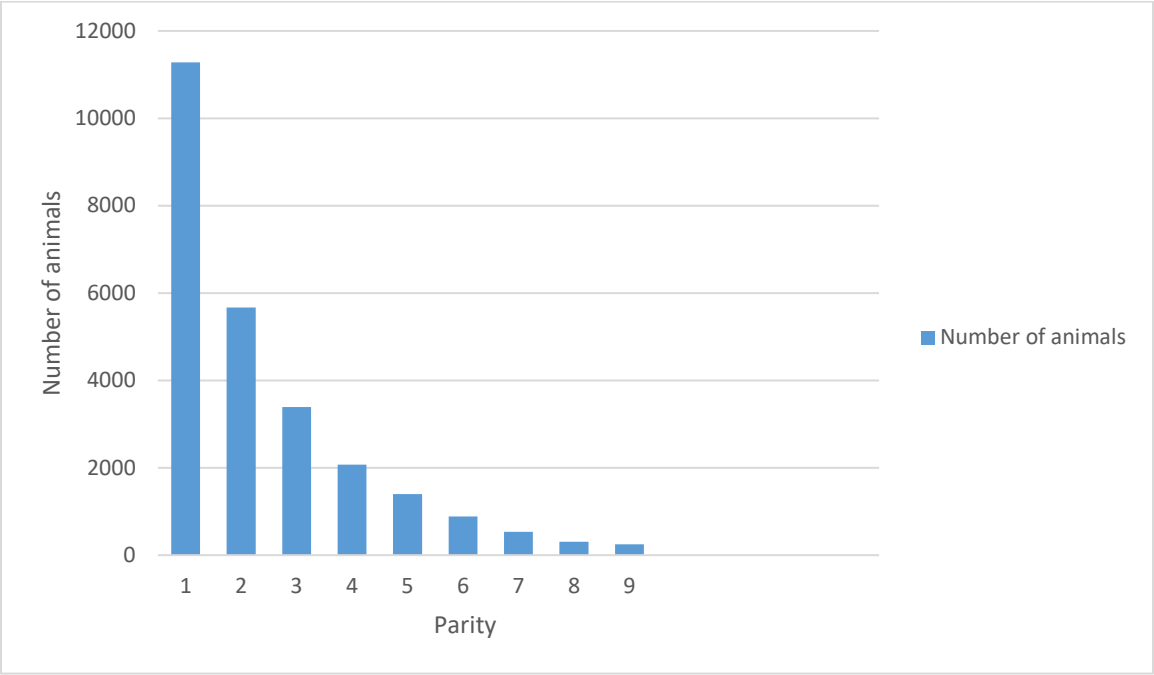


Figure 3-3. Number of females by birth year in the edited data for censored (code 1) animals.

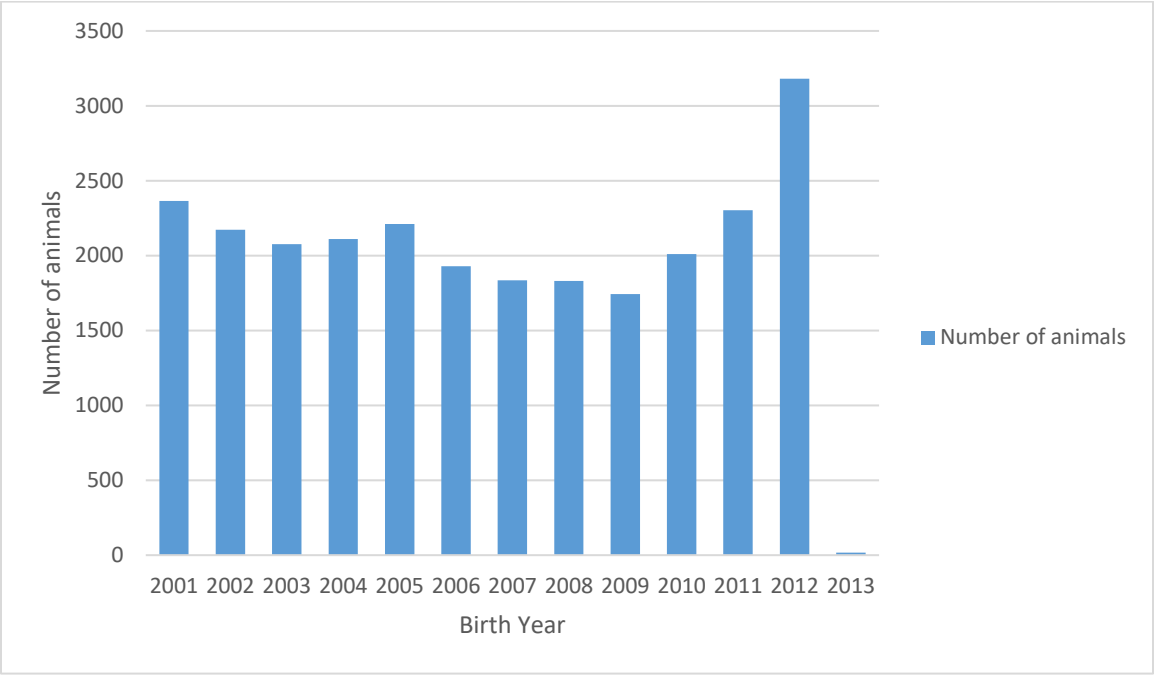


Figure 3-4. Number of females by parity in uncensored (code 0) animals.

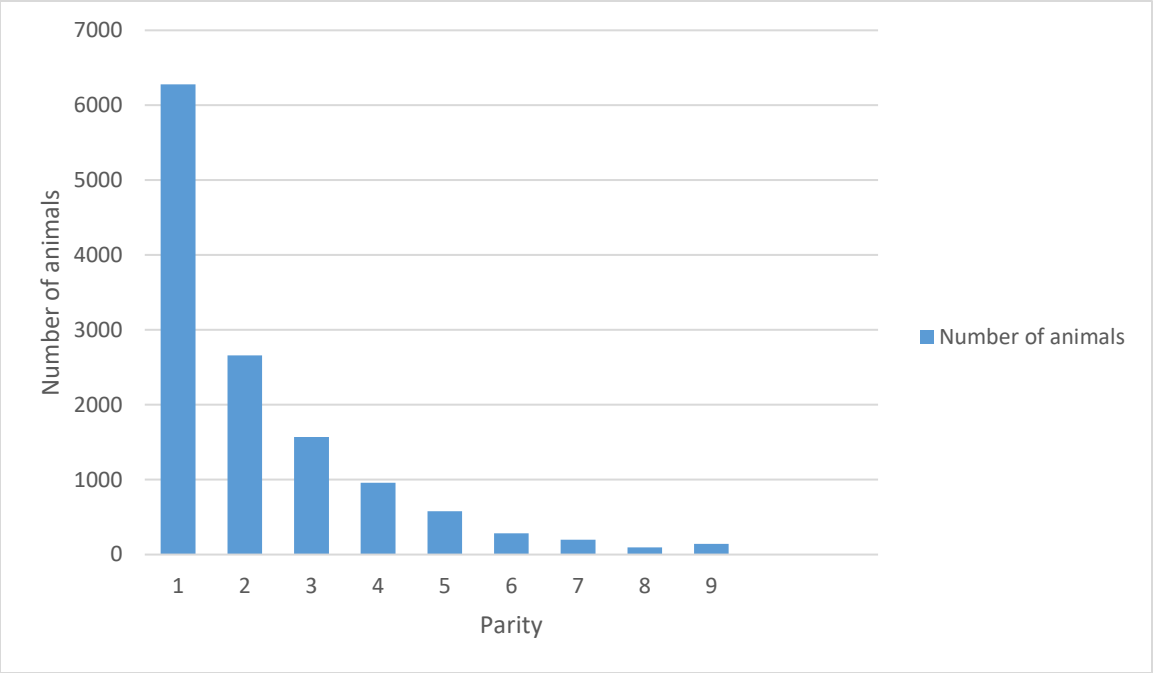


Figure 3-5. Number of females by birth year in the edited data for uncensored (code 0) animals.

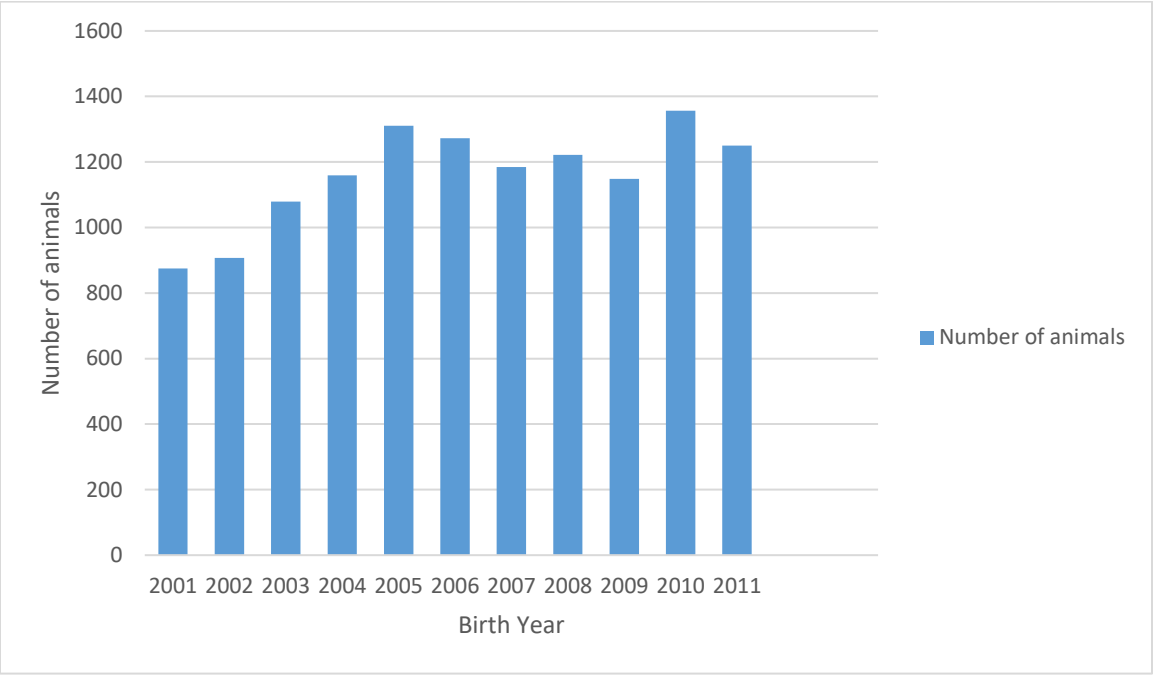


Figure 3-6. Number of females by birth year in the full (unedited) data.

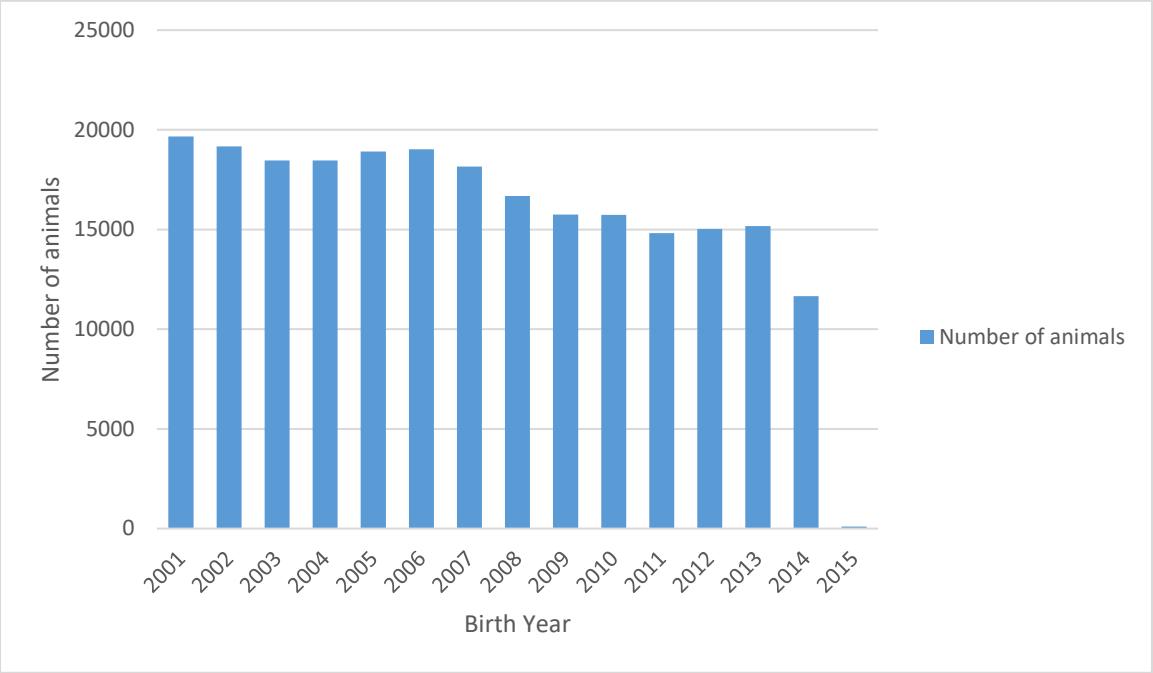
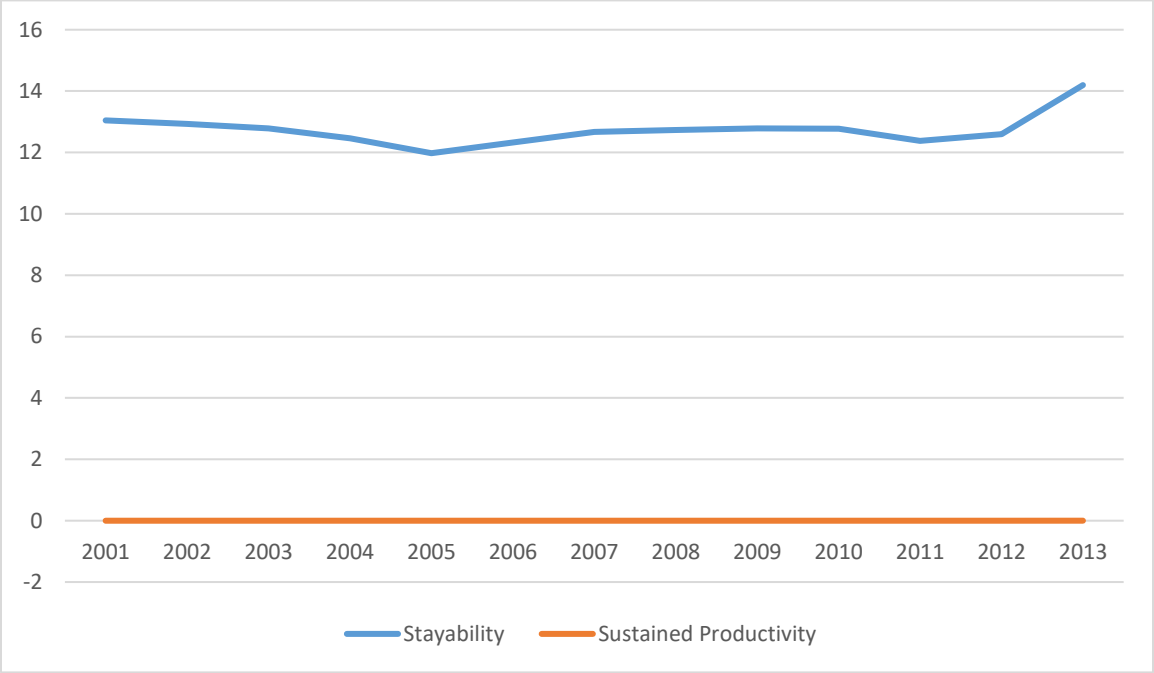


Figure 3-7. Genetic trend of American Gelbvieh Association (AGA) Stayability Expected Progeny Difference (EPD) versus Sustained Productivity Risk Ratio (RR).



References

Beaudeau F., V. Ducrocq, C. Fourichon, H. Seegers. 1995. Effect of disease on length of productive life of French Holstein dairy cows assessed by survival analysis. J. Dairy Sci. 78:103-117.

Brigham, B. W., S. E. Speidel, R. M. Enns, and D. J. Garrick. 2007. Stayability to alternate ages. Proceedings – American Society of Animal Science Western Section. 58:27.

Dalsted, N. L., and P. H. Gutierrez. 1989. How long do you keep her? BEEF Spring:15.

Ducrocq, V., R. L. Quaas, E. J. Pollak, and G. Casella. 1988. Length of productive life of dairy cows. I. Justification of a Weibull model. J. Dairy Sci. 71:3061.

Ducrocq. V. 1987. An analysis of length of productive life in dairy cattle. Ph.D. Diss. Cornell Univ., Ithaca,NY; Univ. Microfilms Int., Ann Arbor, MI.

Ducrocq, V., and J. Solkner. 1998. The Survival Kit V3.0, a package for large analyses of survival data. Proc. 6th World Congr. Genet. Appl. Livest. Prod. 27:447–448.

Ducrocq, V., Solkner, J. and G. Meszaros. 2014. The Survival Kit v6.12 User's Manual.

Enns, R. M., D. J. Garrick, and B. W. Brigham. 2005. Variability in economic value is dependent upon herd average stayability. J. Anim. Sci. 83 (Suppl 2):112-115.

Hazel L. N. and J. L. Lush. 1943. The efficiency of three methods of selection. J. Hered. 33:393-399.

Hudson, G.F.S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64:2246.

Macneil, M. D. and N. Vukasinovic. 2011. A prototype national cattle evaluation for sustained reproductive success in Hereford cattle. J. Anim. Sci. 89:1712-1718.

Meszaros,G., Solkner,J., Ducrocq,V. 2013. The Survival Kit: Software to analyze survival data including possibly correlated random effects. Computer Methods and Programs in Biomedicine, 110(3): 503-510.

Roxstrom, A., V. Ducrocq, and E. Strandberg. 2003. Survival analysis of longevity in dairy cattle on a lactation basis. Genetics Selection Evolution. 35:305-318.

Sewalem, A., G. J. Kistemaker, and B. J. Van Doormaal. 2003. Genetic analysis of herd life in Canadian dairy cattle on a lactation basis using the survival kit. Pages 73–76 in Interbull Bull. No. 31, Uppsala, Sweden.

Snelling, W. M., B. L. Golden, and R. M. Bourdon. 1995. Within-herd genetic analyses of stayability of beef females. J. Anim. Sci. 73:993-1001.

Solkner, J., and V. Ducrocq. 1999. The Survival Kit: a tool for analysis of survival data. Interbull Bulletin 21:11.

Vukasinovic, N., J. Moll, and L. Casanova. 2001. Implementation of a routine genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. J. Dairy Sci. 84: 2073-2080.

Chapter 4 - Genetic and Phenotypic Relationships between Measures of Tenderness in Beef Cattle

Introduction

Meat tenderness is an important factor influencing consumer satisfaction when eating beef (Casas et al., 2006). Several methods have been developed to measure tenderness for beef carcasses at processing. Warner-Bratzler shear force (WBSF) is highly repeatable when the measurement is obtained correctly (Wheeler et al., 1994, 1996, 1997). Slice shear force (SSF) was developed by Shackelford et al. (1999a) as a simplified method for measuring tenderness and has shown increased repeatability (.89) compared with the repeatability estimates (.53 to .86) of WBSF (Wheeler et al., 1996, 1997). Methods for obtaining samples are similar for both WBSF and SSF. For the collection of SSF, the ribeye roll containing the longissimus thoracis is removed from each carcass at 48 hours postmortem, aged at 2 °C for 14 days postmortem, and frozen at -30 °C. Each frozen ribeye roll is then sliced into steaks. Steaks are thawed until an internal temperature of 5 °C is reached and then rapidly cooked to an internal temperature of 70 °C using a belt grill (TBG-60 Magigrill, MagiKitch'n Inc., Quakertown, PA). A single 1-cm-diameter, 5-cm-long longissimus sample is removed parallel to the muscle fiber and sheared across the fibers. A flat blade with a thickness of 1.016 mm and a half-round bevel on the shearing edge is used (Shackelford et al., 1999a, 1999b). Sample preparation for WBSF is a similar process to SSF, except for six 1.27-cm-diameter cores removed from each steak for shear force determination (Shackelford et al., 1999a, 199b). Over the past three decades, near infrared reflectance (NIR) and visible spectroscopy have proven to be efficient tools to estimate tenderness of meat and meat products (Prieto, et al., 2009; Shackelford et al., 2012).

Genetic markers and linkage maps have provided tools to detect QTL of economically important traits in cattle (Stone et al., 1999; Casas et al., 2005; MacNeil and Grosz, 2002). Quantitative traits, including meat tenderness, can be improved through marker assisted selection (McClure et al., 2012). This is especially effective for traits that are difficult or expensive to measure (Casas et al., 2006). The calpain proteolytic system has been identified as a factor responsible for postmortem meat tenderization (Casas et al., 2006). Two enzymes largely responsible for postmortem meat tenderization are the protease μ-calpain (encoded by the *CAPN1* gene), and its inhibitor, calpastatin (encoded by the *CAST* gene) (Koohmaraie, 1996). Numerous studies have revealed an association of markers in CAST and CAPN1 with meat tenderness in beef cattle, (Barendse, 2002; Page et al., 2002, 2004, White et al., 2005). Research by McClure et al. (2012) found moderate correlations between GBLUP predictions of allele substitution effects computed in across and within breed analysis, suggesting that selection using estimates of genetic merit from prediction equations for genomic selection in multi-breed populations is possible.

The objectives of this study were to quantify the genetic and phenotypic relationships between various methods of tenderness evaluation for fresh and frozen samples, quantitatively estimate breed effects of tenderness, and to assess the interaction of breed with CAST and μ-CAPN1 markers.

Materials and Methods

Data Structure

Data for 7,282 animals for various measures of tenderness were provided by the U.S. Meat Animal Research Center (USMARC), Clay Center, Nebraska, as outlined in Table 4-1.

Data used in this analysis included SSF predicted by visible spectroscopy (LED), visible/near-infrared hyperspectral imaging (VISNIR) predicted SSF, fresh and frozen SSF aged to approximately 14 days (SSF14), frozen SSF aged to approximately 3 and 4 days combined (SSF3), and frozen WBSF aged to approximately 14 days and 3 and 4 days combined (WBS14 and WBS3). Units for measures of tenderness are in newtons (N), which is the International System of Units derived unit of force. One newton is the force needed to accelerate one kilogram of mass at the rate of one meter per second squared. Animal care and use procedures were approved by IACUC at USMARC in accordance with FASS (2010) guidelines. Cattle were fed on a concentrated diet for a minimum of 180 days. Slaughter age was calculated as slaughter date minus birth date. Slaughter contemporary group was defined as the concatenation of gender and slaughter date. The breed fraction of each animal was defined as the percent of each breed an animal possessed based on pedigree information. A five-generation pedigree containing 42,250 animals was used including founder animals representing 29 breeds including eighteen purebred groups (Angus, Hereford, Red Angus, Shorthorn, South Devon, Beefmaster, Brangus, Brahman, Santa Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine-Anjou, Salers, Simmental, and Tarentaise). Additionally, 11 different breeds including commercial Angus, Hereford, Simmental, Charolais, Brahman, Santa Gertrudis, Red Angus x Simmental composite, Bonsmarra, Romosinuano, and MARC II and MARC III composite populations were included in the model but are not reported in the results.

Tenderness Measurements

Slice Shear Force

Optimal protocols for collection of slice shear force (SSF) as an objective method of assessing beef tenderness can be found in detail in Shackelford et al., (1999a, 1999b). In

summary, at 48 hours postmortem, the ribeye roll containing the longissimus thoracis is removed from each carcass, vacuum-packaged, aged at 2 °C for 14 days postmortem, and frozen at -30 °C. Each frozen ribeye roll is sliced to yield 2.54 cm thick steaks. Following initial fresh or frozen storage, steaks are thawed until an internal temperature of 5 °C is reached and then rapidly cooked to an internal temperature of 70 °C using a belt grill (TBG-60 Magigrill, MagiKitch'n Inc., Quakertown, PA). A single 1-cm-thick, 5-cm-long longissimus sample is removed parallel to the longitudinal orientation of muscle fiber and sheared across the fibers. A flat blade with a thickness of 1.016 mm and a half-round bevel on the shearing edge is used (Shackelford et al., 1999a, 1999b).

Warner-Bratzler Shear Force

Protocols for obtaining WBSF for beef longissimus can be found in detail in Wheeler et al., (1994, 1996, 1997). The longissimus lumborum (LL) between the 13th rib and the 4th lumbar vertebra is removed from the left side of the carcass at 48 h postmortem, vacuum packaged, and stored at 2°C. Cuts are frozen at 7 d postmortem at -30°C. Six 1.27-cm-diameter cores are removed from each steak while frozen for shear force determination. Samples are removed parallel to the muscle fiber as in SSF, however, a V shaped blade with a 1.016 mm thickness is used to obtain WBSF measurements. Steaks are thawed at 3°C for 24 h before cooking to an internal temperature of 70 °C using a belt grill (TBG-60 Magigrill, MagiKitch'n Inc., Quakertown, PA).

Visible spectroscopy (LED) predicted SSF

Visible spectroscopy collection procedures can be found outlined in Shackelford et al., (2005). At 24 h postmortem, carcasses are ribbed between the 12th and 13th ribs and spectroscopy is conducted on the fresh *longissimus dorsi* cross-section shortly following collection. Like

traditional tenderness phenotypes, a lower number indicates a lower shear force (more tender) value.

Visible/near-infrared hyperspectral imaging (VISNIR) predicted SSF

The procedure for visible/near infrared hyperspectral imaging prediction of tenderness is outlined in Naganathan, et al., (2008). Hyperspectral imaging systems consist of both a digital camera and a spectrograph and can acquire images with high spatial and spectral resolution content. Tenderness is predicted on 14-day aged beef from hyperspectral images of fresh ribeye steaks acquired at 14-day post-mortem. Steaks from the *longissimus dorsi* muscle are collected between the 12th and 13th ribs and aged in vacuum packages. Steaks are removed from vacuum packages and allowed to oxygenate for 30 min before imaging. When compared to SSF as a tenderness reference in a leave-one-out cross validation procedure, VISNIR predicted tender, intermediate, and tough tenderness categories with 96.4% accuracy.

Statistical Analysis

Statistical analysis for this study was computed using ASReml 3.0 (VSN International; Hemel Hempstead, UK). Univariate models for LED, VISNIR, SSF14, SSF3, WBS14 and WBS3 were constructed to estimate starting values for bivariate or multi-variate models. Convergence was an issue in higher order models greater than 3 traits. The mixed model equations were implemented for 3 trait models as follows:

$$\begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \end{bmatrix} = \begin{bmatrix} X_1\beta_1 \\ X_2\beta_2 \\ X_3\beta_3 \end{bmatrix} + \begin{bmatrix} Z_1u_1 \\ Z_2u_2 \\ Z_3u_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where Y_i was a vector of observations for each trait. X_i was the incidence matrix relating observations to fixed effects. Z_i was an incidence matrix relating observations to additive genetic

effects, u_i was a vector of random additive genetic effects, and e_i was a vector of random residuals.

Slaughter age and expected heterozygosity were fit as covariates. Breed composition was fit as a covariate for each breed. Decimal values within breed composition were fit for each breed for each animal. Breed composition was expressed as a decimal value for each of the 11 breed groups. For example, an animal that was 75 percent Angus and 25 percent Gelbvieh was expressed as 0.75 in the Angus column and 0.25 in the Gelbvieh column. This method is equivalent to the Westell genetic grouping procedure, where the function of genetic groups is specific for each animal. Group coefficients account for genetic selection that cannot be defined by known genetic relationships (Westell et al., 1988). Slaughter contemporary group was fit as a fixed effect, and animal was a random effect.

Marker Analysis

Animals from the U.S. MARC Cycle 7 population with tenderness phenotypes were genotyped at low density (LD). Low density genotypes were then imputed to Illumina 770,000 SNP BovineHD (high density) BeadChip and GeneSeek GGP-F250 densities. Haplotypes were generated in findhap.f90 (Ver 4, Van Raden, et al., 2014). Haplotypes were determined for founder animals of known breed composition. The haplotypes were then traced through each generation to determine the breed of origin (BOO) of each haplotype (and thus each allele) for each animal. For each allele, 0, 1, or 2 copies of Illumina allele B were possible. The number of copies for each CAPN1 or CAST marker was defined as 0, 1, or 2 copies of Illumina allele B.

Statistical analysis for including marker data was computed using ASReml 3.0 (VSN International; Hemel Hempstead, UK). Data was analyzed using a multiple trait animal model with phenotypic or estimated SF value as the dependent variable. Fixed effects were the same as

those used in variance component estimation, but with an added covariate of number of copies of Illumina allele B for each of the 87 markers. Interaction between BOO and marker was also fit as a covariate. Slaughter contemporary group was fit as a fixed effect, with animal as a random effect. Significance values for marker effects were adjusted for multiple hypothesis testing bias by multiplying by the number of markers tested (Bonferroni multiple testing adjustment).

Results and Discussion

Variance Components

Summary statistics for tenderness measures can be found in Table 4-1. The number of records for each measure ranged from 896 to 3152. Parameter estimates for additive, phenotypic, and residual variance can be found in Table 4-2. Estimates of variance components for SSF and WBSF specific to Gelbvieh influenced animals have not been previously reported in the literature. Moderate to high additive variance estimates for both SSF and WBSF indicate a significant amount of variation in tenderness is genetic. Significant genetic variation in tenderness is important to AGA breeders, because it indicates progress can be made in postmortem tenderness through selection. Moderate phenotypic variances indicate that at least part of the trait is influenced by the environment, likely the amount of time an animal is in the feed yard or type of finishing ration.

Breed Effects

Significance values and effect estimates obtained using conditional Wald F statistics for covariate effects can be found in Table 4-3. Parameter estimates and significance values from Wald F testing indicate the effect of the included covariates on LED, VISNIR, SSF14, SSF3, WBS3 and WBS14. Slaughter age was significant at $p < 0.05$ for LED, VISNIR, SSF14 and WBSF14. This significance indicates slaughter age has an effect of post-mortem beef tenderness

measured by those traits. Tenderness estimated by VISNIR was highly affected by slaughter age, with one day of age decreasing tenderness value by 10.39 ± 0.02. Heterosis was significant at $p < 0.05$ for LED and VISNIR (1.57 and 1.66, respectively), indicating that heterosis has a beneficial effect on meat tenderness measured by the two traits. Gregory et al., (1994) previously found retained heterosis to have a beneficial effect on both WBSF (0.44 kg) and sensory panel tenderness score (-0.24) in the MARC III composite population. Breed was significant at $p < 0.05$ for LED, VISNIR, SSF14, SSF3, and WBS14. Our findings show that breed differences significantly influence post-mortem meat tenderness in beef cattle. Gregory et al., (1994) also analyzed effects of breed groups for various carcass traits, including WBSF and tenderness score. Populations were MARC I, MARC II, and MARC III composite populations which represent various purebred breed groups with both *Bos Tarus* and *Bos Indicus* influence. Differences among breed groups were found to be a significant effect for all traits included in the study (Gregory et al., 1994).

Specific breed effects estimated as relative to purebred Angus (set at zero), can be found in Table 4-4. For LED, the largest breed difference relative to Angus was from South Devon with an estimate of 91.30 ± 3.12, indicating a lower post-mortem meat tenderness relative to Angus. Breed differences in meat tenderness between Australian cattle breeds, including Angus and South Devon, was analyzed in a study by Pitchford et al., (2002). Unlike the current study, the Australian study was unable to detect significant breed differences in meat tenderness. The largest breed difference relative to Angus for VIS was Tarentaise, with an estimate of -35.40 ± 1.18. For SSF14, the largest breed difference relative to Angus was also from South Devon with an estimate of -101.89 ± 4.44. A negative estimate would indicate a more tender measurement of SSF14 for South Devon than Angus, which is opposite of the breed differences for South Devon

found for LED and VISNIR. In a similar study, Koch et al., (1976) found means WBSF values for Jersey and South Devon crosses were significantly lower than other breed groups tested, which included Angus. For SSF3, the largest breed difference relative to Angus was found in Tarentaise at -134.06 ± 10.18, which would indicate greater tenderness for Slice Shear Force aged to 3 and 4 days as a breed relative to Angus. Similar studies in the literature involving Tarentaise have only noted that meat from Taurine cattle (including Angus and Tarentaise) is more tender than that of Bos Indicus breeds (Lage et al., 2012; Pereria et al., 2015). Salers had the largest breed difference relative to Angus for WBSF14 of 15.00 ± 1.64, indicating a more tough estimate of meat tenderness for Salers cattle relative to Angus. For WBSF3, the largest breed difference relative to Angus was Charolais at 6.86 ± 0.21, indicating a more tough estimate of meat tenderness for Charolais. Some estimates of breed differences have large standard errors, likely because of the limited numbers of animals representing specific breed crosses.

Heritabilities

Heritabilities (on diagonal), genetic correlations (above the diagonal), and phenotypic correlations (below the diagonal) can be found in Table 4-5. The traits SSF14 and SSF3 were moderately heritable (>0.20 and <0.40). Previous estimates of variance components and heritability of SSF do not exist in the literature.

The traits of LED, VISNIR, WBS14 and WBS3 were all found to be moderate to highly heritable (>0.40). The estimates of WBSF heritability found in this work (WBS14, 0.76; WBS3, 0.53) fell at the high end of the range found in the literature (0.26, Splan et al., 1998; 0.06-0.40, Robinson et al., 2001; 0.13, Fernandes et al., 2002; 0.06-0.14, Riley et al., 2003). The heritability estimate of 0.59 for VISNIR reported in this study was much higher than the estimate of 0.10 reported by Cecchinato et al., (2011) on 1,230 Piedmontese bulls. A much larger data set with

VISNIR samples in the current study accounting for a larger amount of variation could account for the greater heritability found in the current study. High heritability of estimated and measured tenderness values indicate that progress can be made in post-mortem meat tenderness through selection for these traits.

Phenotypic correlations

Slice shear force 3 and WBS3 were the highest phenotypically correlated values (0.84 ± 0.01). As SSF3 tenderness values increase, WBS3 tenderness values would increase. Phenotypic correlations between the estimated tenderness phenotypes of LED and SSF phenotypes were mixed, with SSF14 being 0.24 ± 0.02 and SSF3 being -0.27 ± 0.34. Only 4 animals had both SSF3 and LED in common, which limits the validity of the negative correlation. Estimates of phenotypic correlations between VISNIR and SSF were negative. Correlations between VISNIR and WBS were mixed, with WBS14 being 0.10 ± 0.05 and WBS3 being -0.03 ± 0.05. Phenotypic correlations between SSF and WBS measures were all above 0.39, indicating a strong phenotypic relationship between the different methods of tenderness collection.

Genetic correlations

Slice shear force 3 and WBS3 had the greatest genetic correlation of 0.93 (0.03). As SSF3 tenderness additive genetic values increase in the data, WBS3 additive genetic values would also be expected to increase. Genetic correlations between estimated tenderness values (LED and VIS) and measured tenderness values (SSF and WBSF) ranged from low (0.02) to moderate (0.36) for LED and from low (0.02) to moderate (0.48) for VIS. Number of observations for each pair of traits can be found in Table 4-5. Low correlations between measured and estimated tenderness in this data set could be because of the small numbers of animals with phenotypes for both traits. Number of animals with both an estimated SF value

(LED or VIS) and SSF value ranged from 4 to 3107, but were much lower between estimated SF and WBSF, which ranged from 0 to 484. Moderate genetic correlations between estimated and measured tenderness values in this data set indicate that LED and VIS could be used as an indicator of post-mortem meat tenderness. Improvement in traits that are lowly heritable or difficult to collect phenotypes on through correlated response to selection on indicator traits has been successfully used in other carcass traits apart from tenderness. Devitt et al., (2001) found that strong, positive genetic correlations between bull ultrasound and steer carcass measurements suggest genetic improvements for steer carcass traits can be achieved using yearling bull ultrasound measurements for selection criteria. In the current data, significant genetic progress could be made in SSF14 by selecting on the indicator trait of LED, for example. Assuming the top 5% of bulls are selected and the average generation interval is 5 years, a selection response of 7 N in tenderness phenotype per breeding cycle could be made in SSF14 by selecting on LED, assuming a genetic correlation of 0.36. The low to moderate correlations between estimated and measured tenderness in the current study, however, might prevent the rapid uptake of estimated tenderness as a proxy for the measured values. The use of estimated meat tenderness values could save both time and money, replacing the need for sample collection from expensive cuts of meat.

Warner-Bratzler shear force values at different days of post-mortem aging were found to be highly genetically correlated at 0.81 ± 0.05. Genetic correlations between SSF and WBSF values ranged from moderate (0.39) to high (0.93) depending on aging. Previous values of genetic correlations between SSF and WBSF cannot be found in the literature, though both are found to be highly repeatable phenotypic measures of assessing beef tenderness (Shackleford et

al., 1999a,b). Moderate to high phenotypic and genetic correlations between SSF and WBSF shear force indicate that either value could be used as an acceptable measure of tenderness.

Marker Analysis

Marker name, map position, and chromosome number for CAPN1 and CAST can be found in Tables 4-6 through 4-8. Results for markers are presented for marker within gene, within trait. Marker effect estimates, standard errors, conditional F-values, significance values, and Bonferroni adjusted significance values for the LED phenotype can be found in Tables 4-9 and 4-10. Eight markers on the CAPN1 gene and 42 markers on the CAST gene were significant for LED at the adjusted $p < 0.05$ level. Marker 2 had the largest estimate for CAPN1 of -4.69 ± 0.41. Marker 89 had the largest estimate for CAST of -4.33 ± 0.41. Marker effect estimates, standard errors, significance values, and Bonferroni adjusted significance values for the VISNIR phenotype can be found in Table 4-11 through 4-13. Eight markers on the CAPN1 gene and 55 markers on the CAST gene were significant at the adjusted $p <0.05$ level for the VISNIR phenotype. Marker 12 had the largest positive estimate for CAPN1 of 1.45 ± 0.29. Marker 101 had the largest estimate for CAST of 2.50 ± 0.86. For the SSF14 trait, 10 out of 23 markers (Tables 4-14 through 4-16) were significant at the adjusted $p < 0.05$ level for the CAPN1 gene. Marker 190 had the largest effect at -27.07 ± 0.30. Sixty-seven out of 80 markers were significant for the CAST gene with marker 134 having the largest effect at -118.27 ± 0.85. Marker effect estimates for SSF3 can be found in Tables 4-17 through 4-19. Ten markers were significant for the CAPN1 gene, with marker 2 having the largest effect at -45.99 ± 0.41. Sixty-seven markers were significant for the CAST gene, with marker 138 having the largest effect at -58.35 ± 0.27. The WBSF14 trait had 10 out of 23 markers significant (Tables 4-20 through 4-21) for the CAPNI gene, with marker one having the largest effect at -5.69 ± 0.28. Twenty-three out

of 80 markers were significant for the CAST gene, with marker 138 having the largest effect at -4.41 ± 0.21. Two markers for CAPN1 and 26 markers for CAST were significant (Tables 4-22 through 4-23) at the adjusted $p < 0.05$ level for the WBSF3 trait. Marker 2 had the largest estimate for CAPN1 of -8.14 ± 0.39. Marker 156 had the largest estimate for CAST of-23.24 ± 0.26.

Markers previously found to influence tenderness in the CAPN1 gene have been found by White et al., (2005). The study found a transition from cytosine to thymine at position 6545 of the GenBank accession AF248054. Page et al., (2002) identified SNP affecting meat tenderness by sequencing 22 exons and 19 of 21 introns on BTA29 in two sires. Exons 14 and 9 were found to contain SNP predicted to alter the protein sequence. Resource populations were then genotyped for the two SNP. Analysis of genotypes and shear force values found marker 316 map location (44069063) to affect functional variation for tenderness. The allele encoding isoleucine at position 530 (map location 48753080) and glycine at position 316 were both associated with increased shear force values relative to the allele encoding valine at position 530 and alanine at position 316. Barendese (2002) and Casas et al., (2006) previously found a SNP at the 3' untranslated region of the CAST to be associated with WBSF. The marker is a transition from guanine to adenine. Animals that inherited the TT genotype at CAST had more tender meat than animals inheriting the CC genotype.

The values of markers discovered to be significantly related to tenderness measures has the potential to increase change due to selection for the trait. Traditionally, tenderness phenotypes have been difficult to obtain because data on an animal are collected after harvest (White et al., 2005). The use of marker assisted selection to identify variation in meat tenderness can provide selection tools to facilitate genetic improvement (Page et al., 2004). Genetic testing

and subsequent animal selection can also be done at any point in an animal's life. The resulting genetic progress can lead to greater customer satisfaction through product on the market with greater tenderness, contributing to a better eating experience. A simulation study performed by Weaber and Lusk (2010) determined genetic improvements through genome-enabled selection strategies for multiple traits resulted in an estimated $7.6 billion in economic benefits.

Interaction Analysis

Marker x breed interaction effects and associated standard errors for traits that had unadjusted significance values < 0.05 can be found starting in Table 4-24. While there were several marker/breed interaction combinations that had significance values < 0.05, when adjusted for multiple testing bias no combinations were significant. Similar studies that tested interaction between breed and markers influencing tenderness in the CAPN1 gene can be found in White et al., (2005). The White et al., (2005) study examined three specific SNP in CAPN1 for association with tenderness in a large American Brahman population. Marker 4751 (map location 44087629) in the current study was found to be a marker for functional variation affecting tenderness in both Germ Plasm Evaluation Cycle 7 (GPE7) and Cycle 8 (GPE8) populations, which include cattle of both *Bos taurus* and *Bos indicus* influence. The significant association with marker 4751 and both GPE7 and GPE8 populations, which are large multi-sire populations of crossbred decent, indicate marker 4751 can be useful in cattle of all subspecies backgrounds. Page et al., (2004) tested the association between markers at position 316 and 530 and WBSF in a commercial sample of Simmental x Angus crossbred calves and in the GPE7 population. Both markers showed an association with shear force in the commercial sample and GPE7, indicating the markers could be useful for selection in commercial crossbred populations. Casas et al., (2006) studied the association of SNP at the CAST and CAPN1 genes with

tenderness in 3 populations with diverse genetic backgrounds. Populations included GPE7 and GPE8, in addition to a population of purebred Brahman. The study found a SNP at the 3' untranslated region of the CAST gene previously reported by Barendese (2002) to be associated with WBSF and tenderness score in GPE7 and GPE8 populations. The same study also found associations between tenderness score and the marker previously reported by White et al. (2005) at the CAPN1 gene in both GPE7 and GPE8 populations.

Our findings indicate that breed does not have a significant effect on markers that influence tenderness in beef cattle. Implications of this result mean genomic enhanced EPDs for tenderness can be calculated without fitting an effect for BOO and marker interaction. While our findings failed to detect significant marker by breed interactions, that does not conclusively indicate that non-zero interactions do not exist. Power of test, variation in sampled population, or random chance could have prevented the detection of significant results in this data set. Other implications of the lack of a marker by breed interaction include the possibility that markers found to be significantly associated with tenderness may be used for selection in populations with a wide variety of genetic backgrounds, including commercial crossbred animals.

Conclusions

Tenderness has been established as an important factor leading to consumer satisfaction when eating beef (Casas et al., 2006). Genetic markers for both the bovine CAPN1 and CAST genes have been previously associated with meat tenderness in cattle of various breed makeups. The aim of the current study was to further characterize relationships between the various measures of meat tenderness, as well as further quantify the specific effect of breed and breed by marker interaction for those predictors of tenderness. Predicted measures of meat tenderness (LED and VISNIR) were estimated to be highly heritable at 0.78 and 0.59, respectively. High

heritability in predicted measures of tenderness indicate they may be useful as correlated traits for selection. Breed was found to be a significant effect at $p < 0.05$ for LED, VISNIR, SSF14, SSF3, and WBS14. Individual breed effects relative to Angus suggest variation between breeds when selecting for meat tenderness. Non-zero breed effects would be important to include in multi-breed genetic evaluations of tenderness to ensure accurate predictions of genetic merit. Multiple markers on both CAPN1 and CAST were found to be associated with each trait, indicating marker assisted selection could be employed as a selection tool for post-mortem tenderness. Our data did not indicate a significant interaction between breed and marker, which suggests markers significantly associated with tenderness phenotypes traits may possibly be used for animals from a wide variety of breed groups. Results from this study provide an opportunity to use marker data from USMARC to estimate genomic enhanced tenderness for Gelbvieh influenced cattle because there is a lack of significant interaction between breed and marker. Selection for meat tenderness using marker assisted selection can potentially be a valuable tool in improving tenderness in diverse populations of beef cattle. Meat tenderness is critical to consumer satisfaction and should be included as an economically relevant trait for selection in beef cattle.

Table 4-1. Count, mean, standard deviation (SD), minimum value and maximum value for shear force phenotypes.

Trait[1]	N	Mean	SD	Min	Max
LED, N[a]	1,954	0.42	0.99	-58.35	37.86
VISNIR, N	3,152	-0.98	0.98	-39.42	46.49
SSF14, N	896	-0.59	0.99	-17.85	115.23
SSF3, N	900	0.00	0.97	-18.73	44.62
WBS14, N	1,428	-3.82	0.78	-22.07	62.47
WBS3, N	900	0.19	0.97	-22.96	46.29

[1]LED=LED predicted slice shear force, VISNIR=visible/near-infrared hyperspectral imaging predicted SSF, SSF14=fresh and frozen SSF aged to approximately 14 days, SSF3=frozen SSF aged to approximately and 3-4 days, WBS14=frozen WBSF aged to approximately 14 days, WBS3=frozen WBSF aged to approximately 3-4 days.

[a] Deviation in shear force, one newton is the force needed to accelerate one kilogram of mass at the rate of one meter per second squared.

Table 4-2. Estimates for additive genetic (σ_a^2), phenotypic (σ_p^2), and residual (σ_e^2) variances for tenderness data.

Trait[1]	σ_a^2	σ_p^2	σ_e^2
LED, N[a]	60.59	77.90	69.25
	(0.12)	(0.04)	(0.11)
VISNIR, N	50.97	86.56	35.59
	(0.07)	(0.03)	(0.06)
SSF14, N	44.76	116.23	71.47
	(0.10)	(0.04)	(0.03)
SSF3, N	33.66	95.22	61.55
	(0.08)	(0.05)	(0.07)
WBS14, N	76.94	90.41	12.50
	(0.09)	(0.04)	(0.09)
WBS3, N	39.43	95.22	54.82
	(0.08)	(0.05)	(0.07)

[1]LED=LED predicted slice shear force, VISNIR=visible/near-infrared hyperspectral imaging predicted SSF, SSF14=fresh and frozen SSF aged to approximately 14 days, SSF3=frozen SSF aged to approximately and 3-4 days, WBS14=frozen WBS aged to approximately 14 days, WBS3=frozen WBS aged to approximately 3-4 days.

[a] Deviation in shear force, one newton is the force needed to accelerate one kilogram of mass at the rate of one meter per second squared.

Table 4-3. Covariate effect solutions for slaughter age, heterosis, and breed with associated significance values related to tenderness measures.

Covariate	Trait					
	LED	VISNIR	SSF14	SSF3	WBS14	WBS3
Slaughter age	5.79	10.39	0.01	-0.09	34.72	0.09
	(0.00)	(0.02)	(<0.00)	(0.28)	(0.00)	(0.72)
Heterosis	1.57	1.66	-0.23	1.96	2.84	0.49
	(0.01)	(0.00)	(0.09)	(0.09)	(0.08)	(0.79)
Breed	(<0.00)	(<0.00)	(<0.00)	(0.01)	(0.01)	(0.00)

[1]LED=LED predicted slice shear force, VISNIR=visible/near-infrared hyperspectral imaging predicted SSF, SSF14=frozen SSF aged to approximately 14 days, SSF3=frozen SSF aged to approximately and 3-4 days, WBS14=frozen WBSF aged to approximately 14 days, WBS3=frozen WBSF aged to approximately 3-4 days.

Table 4-4. Breed Effects for Shear Force Phenotypes with Associated Standard Error (SE).

	Effect[1] (SE)					
Breed[2]	LED, N[a]	VISNIR, N	SSF14, N	SSF3, N	WBS14, N	WBS3, N
AN	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
HH	10.19 (0.49)	12.06 (0.48)	2.16 (0.78)	23.73 (1.26)	1.27 (0.15)	5.29 (0.23)
AR	-28.05 (0.71)	-1.47 (0.57)	-6.77 (0.84)	-14.91 (1.24)	-0.39 (0.16)	-5.09 (0.23)
SS	10.89 (0.90)	3.04 (0.82)	-13.24 (1.53)	--	--	--
DS	91.30 (3.12)	23.54 (2.48)	-101.89 (4.44)	--	-0.29 (2.24)	2.45 (1.48)
BM	19.32 (0.55)	23.34 (0.71)	18.24 (1.33)	26.77 (1.96)	3.82 (0.29)	4.71 (0.36)
BR	18.73 (0.60)	11.87 (0.68)	13.53 (1.35)	31.48 (2.08)	2.75 (0.30)	4.02 (0.39)
BN	20.79 (0.59)	2.66 (2.12)	-4.02 (1.31)	15.20 (2.16)	0.19 (0.32)	1.57 (0.42)
SG	-0.59 (0.91)	-4.61 (0.83)	-27.07 (1.58)	--	-1.27 (0.87)	-1.37 (0.93)
BU	27.46 (0.71)	4.32 (0.72)	5.19 (1.41)	--	0.39 (1.09)	1.86 (0.51)
CH	24.71 (0.44)	21.97 (0.46)	20.79 (0.74)	44.92 (1.17)	2.94 (0.15)	6.86 (0.21)
GV	22.75 (0.54)	25.49 (0.53)	13.24 (0.84)	32.17 (1.27)	4.22 (0.16)	6.08 (0.22)
LM	27.55 (0.52)	22.27 (0.52)	-12.06 (0.82)	-4.22 (1.21)	-1.27 (0.16)	1.17 (0.22)
MA	22.77 (0.53)	12.35 (0.60)	6.28 (1.06)	18.44 (1.59)	3.24 (0.23)	4.02 (0.29)
SA	17.84 (0.81)	-0.69 (0.82)	1.37 (1.58)	-30.59 (10.08)	15.00 (1.64)	3.53 (0.76)
SM	22.46 (0.55)	13.34 (0.48)	15.10 (0.77)	36.38 (1.20)	3.24 (0.16)	6.47 (0.22)
TA	0.78 (0.92)	-35.40 (1.18)	-63.55 (3.89)	-134.06 (10.18)	-0.49 (0.68)	0.09 (0.44)

[1] LED=LED predicted slice shear force, VISNIR=visible/near-infrared hyperspectral imaging predicted SSF, SSF14=fresh and frozen SSF aged to approximately 14 days, SSF3=frozen SSF aged to approximately and 3-4 days, WBS14=frozen WBSF aged to approximately 14 days, WBS3=frozen WBSF aged to approximately 3-4 days.

[a] Deviation in shear force, one newton is the force needed to accelerate one kilogram of mass at the rate of one meter per second squared. [2] AN=Angus, HH=Hereford, AR=Red Angus,

SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-5. Estimates of heritabilities (diagonal), genetic correlations (above diagonal), phenotypic correlations (below diagonal), with SE in parentheses and number of records for each pair of traits.

Trait[1]	LED	VISNIR	SSF14	SSF3	WBS14	WBS3
LED	0.78	0.53	0.36	0.02	--[2]	--
	(0.12)	(0.10)	(0.08)	(0.17)	0	4
		2794	1650	4		
VISNIR	0.51	0.59	0.02	0.05	0.48	0.10
	(0.03)	(0.07)	(0.08)	(0.17)	(0.11)	(0.16)
	2794		3107	484	435	484
SSF14	0.24	-0.08	0.39	--	0.39	0.79
	(0.02)	(0.05)	(--)	976	(0.24)	(0.09)
	1650	435			1190	927
SSF3	-0.27	-0.13	--	0.34	0.82	0.93
	(0.34)	(0.05)	976	(0.07)	(0.05)	(0.03)
	4	484			927	1190
WBS14	--	0.10	0.64	0.72	0.76	0.81
	0	(0.05)	(0.02)	(0.02)	(0.06)	(0.05)
		435	1190	927		927
WBS3	--	-0.03	0.66	0.84	0.71	0.53
	4	(0.05)	(0.02)	(0.01)	(0.02)	(0.06)
		484	927	1190	927	

[1]LED=LED predicted slice shear force, VISNIR=visible/near-infrared hyperspectral imaging predicted SSF, SSF14=fresh and frozen SSF aged to approximately 14 days, SSF3=frozen SSF aged to approximately and 3-4 days, WBS14=frozen WBSF aged to approximately 14 days, WBS3=frozen WBSF aged to approximately 3-4 days.

[2] No samples in common for this specific combination of traits.

Table 4-6. Name, Coordinates and Chromosome numbers for μ-calpain and calpastatin).

Name	Position	Chromosome
5	98448831	7
BovineHD0700028727	98449505	7
BovineHD0700028728	98450117	7
BovineHD0700028729	98454085	7
BovineHD0700028730	98457153	7
BovineHD0700028731	98463330	7
BovineHD0700028732	98466806	7
BovineHD0700028733	98467371	7
BovineHD0700028734	98467934	7
BovineHD0700028735	98471546	7
BovineHD0700028736	98473634	7
BovineHD0700028737	98474995	7
BovineHD0700028738	98476556	7
BovineHD0700028739	98480585	7
BovineHD0700028740	98481274	7
BovineHD4100006349	98482074	7
BovineHD0700028741	98484691	7
7-98485273-T-C-rs137601357	98485273	7
BovineHD0700028742	98488255	7
BovineHD0700028743	98492079	7
BovineHD0700028744	98492868	7
ARS-BFGL-NGS-43901	98498047	7
BovineHD0700028746	98498729	7
BovineHD0700028747	98499702	7
BovineHD0700028748	98502599	7
BovineHD0700028749	98506739	7
BovineHD0700028750	98507574	7
BovineHD0700028751	98508282	7
BovineHD0700028752	98508931	7
BovineHD0700028753	98510114	7
BovineHD0700028754	98511880	7
BovineHD0700028755	98512675	7
BovineHD0700028756	98513190	7
BovineHD0700028757	98520428	7
BovineHD0700028758	98524220	7
BovineHD0700028759	98526859	7
BovineHD0700028760	98531321	7
BovineHD0700028761	98531781	7
BovineHD0700028762	98532654	7
7-98533663-C-T-rs433558933	98533663	7

Table 4-7. Name, Coordinates and Chromosome numbers for μ-calpain and calpastatin) continued...

Name	Position	Chromosome
ARS-USMARC-670	98534197	7
BovineHD0700028763	98534736	7
7-98535683-A-G-rs210072660	98535683	7
7-98535716-G-A-rs384020496	98535716	7
BovineHD0700028764	98537976	7
BovineHD0700028765	98540675	7
7-98541482-T-C	98541482	7
BovineHD0700028766	98541844	7
7-98542988-T-C-rs207596630	98542988	7
7-98544377-A-T	98544377	7
7-98544384-G-A	98544384	7
7-98544903-A-C	98544903	7
BovineHD0700028767	98545774	7
BovineHD0700028768	98547086	7
BovineHD0700028769	98551183	7
BovineHD0700028770	98551927	7
7-98552538-C-A-rs384484749	98552538	7
BovineHD0700028771	98552632	7
BovineHD0700028772	98553659	7
BovineHD0700028773	98554459	7
BovineHD0700028774	98557529	7
BovineHD0700028775	98560223	7
7-98560787-A-G-rs110712559	98560787	7
BovineHD0700028776	98562742	7
BovineHD0700028777	98563418	7
7-98563500-A-C	98563500	7
7-98565035-A-C	98565035	7
7-98565084-A-C-rs434203856	98565084	7
ARS-USMARC-116	98566391	7
7-98566736-G-C-rs110914810	98566736	7
7-98566778-T-G	98566778	7
BovineHD0700028778	98570487	7
BovineHD0700028779	98571597	7
7-98573255-A-G-rs437031693	98573255	7
BovineHD0700028780	98574139	7

Table 4-8. Name, Coordinates and Chromosome numbers for μ-calpain and calpastatin) continued…

Name	Position	Chromosome
BovineHD0700028781	98574903	7
BovineHD0700028782	98575799	7
BovineHD0700028783	98576940	7
7-98578261-A-C	98578261	7
BovineHD0700028784	98578836	7
BovineHD4100006350	98579574	7
7-98581038-A-G-rs110927869	98581038	7
29-44064848-A-C-rs469489763	44064848	29
BovineHD2900013183	44067207	29
29-44067217-T-G	44067217	29
BovineHD2900013184	44067968	29
29-44068197-A-C-rs448108280	44068197	29
CAPN1_1	44069063	29
29-44069114-A-G	44069114	29
BovineHD2900013185	44070926	29
BovineHD2900013186	44076213	29
BovineHD2900013187	44081056	29
29-44085525-A-insA	44085525	29
29-44085642-G-A-rs17871051	44085642	29
UA-IFASA-1370	44085769	29
CAPN1_2	44087629	29
29-44087931-A-G	44087931	29
BovineHD2900013188	44088897	29
29-44089184-A-G-rs483248035	44089184	29
29-44089872-A-C	44089872	29
29-44089934-G-A-rs382933099	44089934	29
BovineHD2900013189	44093671	29
29-44094383-A-C-rs211221854	44094383	29
29-44097612-G-A-rs136612179	44097612	29
BovineHD2900013190	44097970	29
29-44100024-C-T-rs133478041	44100024	29

Table 4-9. Marker effects for slice shear force predicted by visible spectroscopy (LED) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44064848	1	-1.67	0.59	7.76	0.000001	0.0001
CAPN1	44067207	2	-4.69	0.41	85.43	0.000001	0.0001
CAPN1	44067217	3	0.00	0.00	28.52	0.000001	0.0001
CAPN1	44081056	10	0.99	0.38	6.70	0.000001	0.0001
CAPN1	44085642	12	2.35	0.42	31.49	0.000001	0.0001
CAPN1	44087629	190	-4.33	0.47	85.31	0.000001	0.0001
CAPN1	44097970	198	1.19	0.39	9.34	0.000001	0.0001
CAPN1	44100024	199	0.97	0.44	4.80	0.000001	0.0001
CAST	[2]	88	1.55	0.39	15.67	0.000001	0.0001
CAST	98448831	89	-4.33	0.41	112.55	0.000001	0.0001
CAST	98454085	92	2.33	0.42	32.52	0.000001	0.0001
CAST	98463330	94	-4.25	0.40	111.65	0.000001	0.0001
CAST	98467934	97	2.28	0.41	31.36	0.000001	0.0001
CAST	98473634	99	-4.15	0.41	102.65	0.000001	0.0001
CAST	98474995	100	-0.76	0.52	2.15	0.000001	0.0001
CAST	98480585	102	2.35	0.42	30.89	0.000001	0.0001
CAST	98482074	104	-4.23	0.41	108.15	0.000001	0.0001
CAST	98484691	105	-0.67	0.52	1.63	0.000008	0.01
CAST	98488255	107	2.29	0.41	30.57	0.000001	0.0001
CAST	98492868	109	-4.29	0.41	111.32	0.000001	0.0001
CAST	98499702	112	2.23	0.41	29.57	0.000001	0.0001
CAST	98502599	113	-4.11	0.39	111.10	0.000001	0.0001
CAST	98506739	114	-4.11	0.39	111.10	0.000001	0.0001
CAST	98507574	115	-0.84	0.51	2.77	0.000001	0.0001
CAST	98508931	117	1.77	0.39	21.01	0.000001	0.0001
CAST	98510114	118	1.78	0.39	20.02	0.000001	0.0001

Table 4-10. Marker effects for slice shear force predicted by visible spectroscopy (LED) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98512675	120	-4.19	0.39	114.62	0.000001	0.0001
CAST	98513190	121	-0.79	0.51	2.39	0.000001	0.0001
CAST	98524220	123	1.76	0.38	21.01	0.000001	0.0001
CAST	98526859	124	1.69	0.39	18.30	0.000001	0.0001
CAST	98531781	126	-4.19	0.39	114.62	0.000001	0.0001
CAST	98532654	127	-0.79	0.51	2.39	0.000001	0.0001
CAST	98535716	132	-4.02	0.39	100.84	0.000001	0.0001
CAST	98537976	133	-0.93	0.51	3.28	0.000001	0.0001
CAST	98541844	135	1.76	0.40	19.32	0.000001	0.0001
CAST	98544377	136	1.79	0.40	19.79	0.000001	0.0001
CAST	98544903	138	-4.03	0.40	99.73	0.000001	0.0001
CAST	98545774	139	-0.97	0.51	3.56	0.000001	0.0001
CAST	98551183	141	1.58	0.41	14.96	0.000001	0.0001
CAST	98551927	142	1.84	0.41	20.47	0.000001	0.0001
CAST	98552632	144	-4.14	0.39	108.95	0.000001	0.0001
CAST	98553659	145	-0.83	0.52	2.61	0.000001	0.0001
CAST	98557529	147	1.79	0.39	20.45	0.000001	0.0001
CAST	98560223	148	1.79	0.39	20.37	0.000001	0.0001
CAST	98560787	149	1.59	0.39	16.47	0.000001	0.0001
CAST	98562742	150	-3.78	0.44	73.94	0.000001	0.0001
CAST	98566778	156	-4.21	0.39	114.49	0.000001	0.0001
CAST	98570487	157	-0.81	0.52	2.39	0.000001	0.0001
CAST	98573255	159	1.73	0.39	20.13	0.000001	0.0001
CAST	98574139	160	1.77	0.39	19.81	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin [2]Position unclear from the map file

Table 4-11. Marker effects for visible/near infrared hyperspectral imaging (VISNIR) predicted slice shear force with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44064848	1	1.42	0.38	4.33	0.000001	0.0001
CAPN1	44067207	2	-1.27	0.34	14.13	0.000001	0.0001
CAPN1	44067217	3	0.00	0.00	17.41	0.000001	0.0001
CAPN1	44085525	11	0.52	0.29	2.99	0.000001	0.0001
CAPN1	44085642	12	1.45	0.29	23.52	0.000001	0.0001
CAPN1	44085769	189	0.50	0.27	3.39	0.000001	0.0001
CAPN1	44087629	190	-1.45	0.32	21.12	0.000001	0.0001
CAPN1	44100024	199	0.95	0.30	9.79	0.000001	0.0001
CAST	[2]	88	2.08	0.21	95.84	0.000001	0.0001
CAST	98448831	89	-1.52	0.23	45.19	0.000001	0.0001
CAST	98450117	91	1.38	0.77	3.24	0.000001	0.0001
CAST	98454085	92	-0.85	0.36	5.60	0.000001	0.0001
CAST	98457153	93	2.27	0.19	133.23	0.000001	0.0001
CAST	98463330	94	-1.76	0.22	65.95	0.000001	0.0001
CAST	98467371	96	1.73	0.77	5.11	0.000001	0.0001
CAST	98467934	97	-0.61	0.34	3.21	0.000001	0.0001
CAST	98471546	98	2.46	0.21	135.29	0.000001	0.0001
CAST	98473634	99	-1.94	0.23	68.86	0.000008	0.0001
CAST	98476556	101	2.50	0.86	8.55	0.000001	0.0001
CAST	98480585	102	-0.67	0.36	3.46	0.000001	0.0001
CAST	98481274	103	2.04	0.21	95.57	0.000001	0.0001
CAST	98482074	104	-1.60	0.23	48.70	0.000001	0.0001
CAST	98485273	106	2.17	0.81	7.23	0.000001	0.0001
CAST	98488255	107	-0.51	0.35	2.13	0.000001	0.0001
CAST	98492079	108	2.05	0.20	100.88	0.000001	0.0001
CAST	98492868	109	-1.49	0.22	43.70	0.000001	0.0001

Table 4-12. Marker effects for visible/near infrared hyperspectral imaging (VISNIR) predicted slice shear force with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98498729	111	1.69	0.81	4.42	0.000001	0.0001
CAST	98499702	112	-0.65	0.35	3.46	0.000001	0.0001
CAST	98502599	113	-2.00	0.21	91.69	0.000001	0.0001
CAST	98506739	114	-2.00	0.21	91.69	0.000001	0.0001
CAST	98508282	116	1.09	0.77	2.01	0.000001	0.0001
CAST	98508931	117	-0.94	0.32	8.49	0.000001	0.0001
CAST	98510114	118	1.09	0.25	18.83	0.000001	0.0001
CAST	98511880	119	1.71	0.19	85.39	0.000001	0.0001
CAST	98512675	120	-1.64	0.21	62.55	0.000001	0.0001
CAST	98520428	122	1.23	0.77	2.53	0.000001	0.0001
CAST	98524220	123	-0.66	0.32	4.32	0.000001	0.0001
CAST	98526859	124	1.14	0.25	20.85	0.000001	0.0001
CAST	98531321	125	1.71	0.19	85.39	0.000001	0.0001
CAST	98531781	126	-1.64	0.21	62.55	0.000001	0.0001
CAST	98532654	127	-0.33	0.26	1.56	0.0003	0.034
CAST	98533663	128	1.23	0.77	2.53	0.000001	0.0001
CAST	98535683	131	1.40	0.20	47.66	0.000001	0.0001
CAST	98535716	132	-1.38	0.23	35.93	0.000001	0.0001
CAST	98537976	133	-0.94	0.26	12.67	0.000001	0.0001
CAST	98540675	134	1.95	0.74	6.97	0.000001	0.0001
CAST	98541844	135	-0.82	0.36	5.26	0.000001	0.0001
CAST	98544377	136	0.93	0.26	12.64	0.000001	0.0001
CAST	98544384	137	1.58	0.21	57.12	0.000001	0.0001
CAST	98544903	138	-1.66	0.23	50.17	0.000001	0.0001
CAST	98545774	139	-0.65	0.27	5.74	0.000001	0.0001

Table 4-13. Marker effects for visible/near infrared hyperspectral imaging (VISNIR) predicted slice shear force with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98547086	140	1.48	0.81	3.36	0.000001	0.0001
CAST	98551183	141	-1.45	0.37	15.36	0.000001	0.0001
CAST	98551927	142	1.31	0.27	22.93	0.000001	0.0001
CAST	98552538	143	1.40	0.20	51.09	0.000001	0.0001
CAST	98552632	144	-1.37	0.22	39.44	0.000001	0.0001
CAST	98554459	146	1.43	0.79	3.28	0.000001	0.0001
CAST	98557529	147	-1.20	0.34	12.39	0.000001	0.0001
CAST	98560223	148	1.26	0.25	24.81	0.000001	0.0001
CAST	98566736	155	2.21	0.19	136.8	0.000001	0.0001
CAST	98566778	156	-2.26	0.21	114.16	0.000001	0.0001
CAST	98573255	159	-0.56	0.32	3.09	0.000001	0.0001
CAST	98574139	160	1.37	0.25	28.77	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin [2]Position unclear from the map file

Table 4-14. Marker effects for fresh and frozen slice shear force aged to approximately 14 days (SSF14) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44064848	1	25.11	0.36	11.61	0.000001	0.0001
CAPN1	44067207	2	-24.22	0.33	57.63	0.000001	0.0001
CAPN1	44067217	3	0.00	0.00	60.89	0.000001	0.0001
CAPN1	44081056	10	15.79	0.25	42.82	0.000001	0.0001
CAPN1	44085525	11	13.44	0.28	23.69	0.000001	0.0001
CAPN1	44085642	12	-23.14	0.29	64.81	0.000001	0.0001
CAPN1	44085769	189	12.85	0.26	24.88	0.000001	0.0001
CAPN1	44087629	190	-27.07	0.30	84.85	0.000001	0.0001
CAPN1	44097970	198	12.16	0.25	24.71	0.000001	0.0001
CAPN1	44100024	199	8.92	0.29	10.00	0.000001	0.0001
CAST	[2]	88	18.24	0.24	59.32	0.000001	0.0001
CAST	98448831	89	-11.87	0.26	22.52	0.000001	0.0001
CAST	98450117	91	-113.66	0.88	12.12	0.000001	0.0001
CAST	98454085	92	26.18	0.42	171.34	0.000001	0.0001
CAST	98457153	93	11.28	0.23	40.22	0.000001	0.0001
CAST	98463330	94	-10.20	0.25	17.10	0.000001	0.0001
CAST	98466806	95	-11.18	0.33	12.19	0.000001	0.0001
CAST	98467371	96	-113.37	0.88	172.43	0.000001	0.0001
CAST	98467934	97	22.56	0.40	32.99	0.000001	0.0001
CAST	98471546	98	20.59	0.24	77.26	0.000001	0.0001
CAST	98473634	99	-15.40	0.26	36.06	0.000001	0.0001
CAST	98474995	100	-19.71	0.33	37.89	0.000001	0.0001
CAST	98476556	101	-78.36	0.96	68.68	0.000001	0.0001
CAST	98480585	102	21.67	0.42	27.70	0.000001	0.0001
CAST	98481274	103	17.65	0.24	57.90	0.000001	0.0001
CAST	98482074	104	-13.53	0.26	28.65	0.000001	0.0001

Table 4-15. Marker effects for fresh and frozen slice shear force aged to approximately 14 days (SSF14) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98484691	105	-14.61	0.33	153.27	0.000001	0.0001
CAST	98488255	107	20.79	0.41	26.46	0.000001	0.0001
CAST	98492079	108	14.51	0.23	29.63	0.000001	0.0001
CAST	98492868	109	-14.12	0.25	32.10	0.000001	0.0001
CAST	98498047	110	-8.43	0.34	6.47	0.000001	0.0001
CAST	98498729	111	-115.04	0.92	162.3	0.000001	0.0001
CAST	98499702	112	19.52	0.41	24.01	0.000001	0.0001
CAST	98502599	113	-17.16	0.24	51.43	0.000001	0.0001
CAST	98506739	114	-17.16	0.24	51.43	0.000001	0.0001
CAST	98507574	115	-27.36	0.31	81.80	0.000001	0.0001
CAST	98508282	116	-98.36	0.88	129.49	0.000001	0.0001
CAST	98508931	117	0.00	0.00	1.75	0.000007	0.0007
CAST	98510114	118	49.43	0.31	269.79	0.000001	0.0001
CAST	98511880	119	5.69	0.22	7.07	0.000001	0.0001
CAST	98512675	120	-19.22	0.24	64.67	0.000001	0.0001
CAST	98513190	121	-23.05	0.31	56.74	0.000001	0.0001
CAST	98520428	122	6.37	0.38	160.07	0.000001	0.0001
CAST	98524220	123	6.37	0.38	2.92	0.000001	0.0001
CAST	98526859	124	48.64	0.31	261.82	0.000001	0.0001
CAST	98531321	125	5.69	0.22	7.07	0.000001	0.0001
CAST	98531781	126	-19.22	0.24	64.67	0.000001	0.0001
CAST	98532654	127	-23.05	0.31	56.74	0.000001	0.0001
CAST	98533663	128	-110.03	0.89	160.07	0.000001	0.0001
CAST	98535683	131	8.92	0.23	15.64	0.000001	0.0001
CAST	98535716	132	-17.65	0.26	48.91	0.000001	0.0001
CAST	98537976	133	-24.81	0.31	64.91	0.000001	0.0001

Table 4-16. Marker effects for fresh and frozen slice shear force aged to approximately 14 days (SSF14) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98540675	134	-118.27	0.85	200.22	0.000001	0.0001
CAST	98541844	135	6.86	0.41	2.93	0.000001	0.0001
CAST	98544377	136	47.17	0.31	235.78	0.000001	0.0001
CAST	98544384	137	16.57	0.24	51.56	0.000001	0.0001
CAST	98544903	138	-26.48	0.26	107.43	0.000001	0.0001
CAST	98545774	139	-25.89	0.32	67.51	0.000001	0.0001
CAST	98547086	140	-104.64	0.90	139.00	0.000001	0.0001
CAST	98551183	141	11.57	0.43	7.67	0.000001	0.0001
CAST	98551927	142	44.03	0.33	187.79	0.000001	0.0001
CAST	98552538	143	10.89	0.23	23.94	0.000001	0.0001
CAST	98552632	144	-25.30	0.25	105.99	0.000001	0.0001
CAST	98553659	145	-26.48	0.32	71.64	0.000001	0.0001
CAST	98554459	146	14.02	0.79	13.19	0.000001	0.0001
CAST	98560223	148	47.47	0.31	246.43	0.000001	0.0001
CAST	98560787	149	22.36	0.24	88.16	0.000001	0.0001
CAST	98562742	150	-12.85	0.26	25.46	0.000001	0.0001
CAST	98563418	151	0.00		99.15	0.000001	0.0001
CAST	98563500	152	-94.05	0.96	140.02	0.000001	0.0001
CAST	98566736	155	3.92	0.22	3.29	0.000001	0.0001
CAST	98566778	156	-18.04	0.25	56.03	0.000001	0.0001
CAST	98570487	157	-25.11	0.32	63.20	0.000001	0.0001
CAST	98571597	158	-91.11	0.98	89.35	0.000001	0.0001
CAST	98574139	160	52.47	0.31	293.21	0.000001	0.0001
CAST	98575799	162	-10.59	0.27	16.37	0.000001	0.0001
CAST	98576940	163	-16.38	0.35	22.59	0.000001	0.0001
CAST	98578261	164	-91.11	0.95	96.59	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin [2]Position unclear from the map file

Table 4-17. Marker effects for frozen slice shear force aged to approximately 3 days (SSF3) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44064848	1	5.20	0.39	11.61	0.000001	0.0001
CAPN1	44067207	2	-45.99	0.41	57.63	0.000001	0.0001
CAPN1	44067217	3	0.00		49.22	0.000001	0.0001
CAPN1	44081056	10	37.56	0.33	42.82	0.000001	0.0001
CAPN1	44085525	11	1.86	0.33	23.69	0.000001	0.0001
CAPN1	44085642	12	-39.13	0.33	64.81	0.000001	0.0001
CAPN1	44085769	189	18.93	0.34	24.88	0.000001	0.0001
CAPN1	44087629	190	-43.84	0.36	84.85	0.000001	0.0001
CAPN1	44097970	198	29.72	0.34	24.71	0.000001	0.0001
CAPN1	44100024	199	-7.26	0.34	10.00	0.000001	0.0001
CAST	[2]	88	33.54	0.25	59.32	0.000001	0.0001
CAST	98448831	89	-36.58	0.26	22.52	0.000001	0.0001
CAST	98450117	91	0.00	0.00	12.12	0.000001	0.0001
CAST	98454085	92	0.00	0.00	171.34	0.000001	0.0001
CAST	98457153	93	29.91	0.24	40.22	0.000001	0.0001
CAST	98463330	94	-36.19	0.25	17.10	0.000001	0.0001
CAST	98466806	95	0.00	0.00	12.19	0.000001	0.0001
CAST	98467371	96	0.00	0.00	172.43	0.000001	0.0001
CAST	98467934	97	0.00	0.00	32.99	0.000001	0.0001
CAST	98471546	98	53.55	0.26	77.26	0.000001	0.0001
CAST	98473634	99	-57.67	0.26	36.06	0.000001	0.0001
CAST	98474995	100	0.00	0.00	37.89	0.000001	0.0001
CAST	98476556	101	0.00	0.00	68.68	0.000001	0.0001
CAST	98480585	102	0.00	0.00	27.70	0.000001	0.0001
CAST	98481274	103	29.81	0.26	57.90	0.000001	0.0001
CAST	98482074	104	-45.60	0.26	28.65	0.000001	0.0001

Table 4-18. Marker effects for frozen slice shear force aged to approximately 3 days (SSF3) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98484691	105	0.00	0.00	153.27	0.000001	0.0001
CAST	98488255	107	0.00	0.00	26.46	0.000001	0.0001
CAST	98492079	108	36.58	0.25	29.63	0.000001	0.0001
CAST	98492868	109	-44.62	0.25	32.10	0.000001	0.0001
CAST	98498047	110	0.00	0.00	6.47	0.000001	0.0001
CAST	98498729	111	0.00	0.00	162.3	0.000001	0.0001
CAST	98499702	112	0.00	0.00	24.01	0.000001	0.0001
CAST	98502599	113	-47.96	0.24	51.43	0.000001	0.0001
CAST	98506739	114	-47.96	0.24	51.43	0.000001	0.0001
CAST	98507574	115	0.00	0.00	81.80	0.000001	0.0001
CAST	98508282	116	0.00	0.00	129.49	0.000001	0.0001
CAST	98508931	117	0.00	0.00	1.75	0.000007	0.0007
CAST	98510114	118	0.00	0.00	269.79	0.000001	0.0001
CAST	98511880	119	31.97	0.23	7.07	0.000001	0.0001
CAST	98512675	120	-40.11	0.24	64.67	0.000001	0.0001
CAST	98513190	121	0.00	0.00	56.74	0.000001	0.0001
CAST	98520428	122	0.00	0.00	160.07	0.000001	0.0001
CAST	98524220	123	0.00	0.00	2.92	0.000001	0.0001
CAST	98526859	124	0.00	0.00	261.82	0.000001	0.0001
CAST	98531321	125	31.97	0.23	7.07	0.000001	0.0001
CAST	98531781	126	-40.11	0.24	64.67	0.000001	0.0001
CAST	98532654	127	0.00	0.00	56.74	0.000001	0.0001
CAST	98533663	128	0.00	0.00	160.07	0.000001	0.0001
CAST	98535683	131	27.36	0.26	15.64	0.000001	0.0001
CAST	98535716	132	-35.99	0.27	48.91	0.000001	0.0001
CAST	98537976	133	0.00	0.00	64.91	0.000001	0.0001

Table 4-19. Marker effects for frozen slice shear force aged to approximately 3 days (SSF3) with associated standard error (SE), significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98540675	134	0.00	0.00	200.22	0.000001	0.0001
CAST	98541844	135	0.00	0.00	2.93	0.000001	0.0001
CAST	98544377	136	0.00	0.00	235.78	0.000001	0.0001
CAST	98544384	137	49.92	0.26	51.56	0.000001	0.0001
CAST	98544903	138	-58.35	0.27	107.43	0.000001	0.0001
CAST	98545774	139	0.00	0.00	67.51	0.000001	0.0001
CAST	98547086	140	0.00	0.00	139.00	0.000001	0.0001
CAST	98551183	141	0.00	0.00	7.67	0.000001	0.0001
CAST	98551927	142	0.00	0.00	187.79	0.000001	0.0001
CAST	98552538	143	32.76	0.25	23.94	0.000001	0.0001
CAST	98552632	144	-42.56	0.25	105.99	0.000001	0.0001
CAST	98553659	145	0.00	0.00	71.64	0.000001	0.0001
CAST	98554459	146	0.00	0.00	13.19	0.000001	0.0001
CAST	98560223	148	0.00	0.00	246.43	0.000001	0.0001
CAST	98560787	149	46.88	0.25	88.16	0.000001	0.0001
CAST	98562742	150	-46.49	0.25	25.46	0.000001	0.0001
CAST	98563418	151	0.00	0.00	99.15	0.000001	0.0001
CAST	98563500	152	0.00	0.00	140.02	0.000001	0.0001
CAST	98563500	155	42.17	0.24	3.29	0.000001	0.0001
CAST	98566736	156	-50.02	0.24	56.03	0.000001	0.0001
CAST	98566778	157	0.00	0.00	63.20	0.000001	0.0001
CAST	98570487	158	0.00	0.00	89.35	0.000001	0.0001
CAST	98574139	160	0.00	0.00	293.21	0.000001	0.0001
CAST	98574903	161	35.50	0.28	171.22	0.000001	0.0001
CAST	98575799	162	0.00	0.27	329.05	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin [2]Position unclear from the map file

Table 4-20. Marker effects for Warner-Bratzler shear force aged to 14 days (WBSF14) with associated standard error (SE) significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44064848	1	-5.69	0.28	4.30	0.000001	0.0001
CAPN1	44067207	2	-5.10	0.26	4.09	0.000001	0.0001
CAPN1	44067217	3	0.00		4.52	0.000001	0.0001
CAPN1	44081056	10	5.10	0.25	4.26	0.000001	0.0001
CAPN1	44085525	11	1.86	0.25	0.62	0.000001	0.0001
CAPN1	44085642	12	-3.43	0.26	1.83	0.000001	0.0001
CAPN1	44085769	189	-1.47	0.25	0.35	0.000001	0.0001
CAPN1	44087629	190	-4.41	0.26	3.04	0.000001	0.0001
CAPN1	44097970	198	4.51	0.25	3.36	0.000001	0.0001
CAPN1	44100024	199	2.26	0.25	0.86	0.000001	0.0001
CAST	98448831	89	-1.27	0.20	2.93	0.000001	0.0001
CAST	98457153	93	-3.24	0.20	2.74	0.000001	0.0001
CAST	98463330	94	-2.65	0.20	1.80	0.000002	0.0002
CAST	98473634	99	-3.24	0.21	2.45	0.000001	0.0001
CAST	98482074	104	-3.14	0.20	2.36	0.000001	0.0001
CAST	98492079	108	-2.55	0.20	1.59	0.0002	0.0185
CAST	98492868	109	-3.24	0.21	2.57	0.000001	0.0001
CAST	98502599	113	-2.94	0.20	2.29	0.000001	0.0001
CAST	98506739	114	-2.94	0.20	2.29	0.000001	0.0001
CAST	98511880	119	-3.04	0.19	2.54	0.000001	0.0001
CAST	98512675	120	-3.04	0.20	2.37	0.000001	0.0001
CAST	98531321	125	-3.14	0.19	2.54	0.000001	0.0001
CAST	98531781	126	-3.04	0.20	2.37	0.000001	0.0001
CAST	98535683	131	-2.84	0.21	2.06	0.000001	0.0001
CAST	98535716	132	-3.43	0.21	2.81	0.000001	0.0001
CAST	98544903	138	-4.41	0.21	4.62	0.000001	0.0001

Table 4-21. Marker effects for Warner-Bratzler shear force aged to 14 days (WBSF14) with associated standard error (SE) significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98552632	144	-3.92	0.21	3.87	0.000001	0.0001
CAST	98560787	149	-1.27	0.20	0.40	0.000001	0.0001
CAST	98562742	150	-0.88	0.20	0.20	0.000001	0.0001
CAST	98563500	155	-3.24	0.20	2.78	0.000001	0.0001
CAST	98566736	156	-2.84	0.20	2.06	0.000001	0.0001
CAST	98574903	161	-0.98	0.22	0.21	0.000001	0.0001
CAST	98575799	162	0.00	0.20	0.04	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin

Table 4-22. Marker effects for Warner-Bratzler shear force aged to approximately 3 days (WBSF3) with associated standard error (SE) significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05.

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAPN1	44067207	2	-8.14	0.39	4.46	0.000001	0.0001
CAPN1	44087629	190	-7.65	0.39	3.94	0.000001	0.0001
CAST	98448831	89	-15.69	0.28	3.67	0.000001	0.0001
CAST	98449505	90	0.00	0.00	33.37	0.000001	0.0001
CAST	98457153	93	-6.08	0.26	5.60	0.000001	0.0001
CAST	98463330	94	-17.95	0.27	46.17	0.000001	0.0001
CAST	98471546	98	-7.16	0.28	6.88	0.000001	0.0001
CAST	98473634	99	-32.07	0.28	132.27	0.000001	0.0001
CAST	98481274	103	-5.39	0.28	3.97	0.000001	0.0001
CAST	98482074	104	-22.26	0.28	65.08	0.000001	0.0001
CAST	98492079	108	-4.12	0.27	2.37	0.000001	0.0001
CAST	98492868	109	-20.40	0.28	56.55	0.000001	0.0001
CAST	98502599	113	-19.91	0.26	59.84	0.000001	0.0001
CAST	98506739	114	-19.91	0.26	59.84	0.000001	0.0001
CAST	98511880	119	-7.85	0.25	9.97	0.000001	0.0001
CAST	98512675	120	-16.77	0.26	43.20	0.000001	0.0001
CAST	98531321	125	-7.85	0.25	9.97	0.000001	0.0001
CAST	98531781	126	-16.77	0.26	43.20	0.000001	0.0001
CAST	98535683	131	-7.16	0.28	6.91	0.000001	0.0001
CAST	98535716	132	-11.28	0.28	16.38	0.000001	0.0001
CAST	98544903	138	-18.04	0.29	41.46	0.000001	0.0001
CAST	98552538	143	-8.14	0.27	9.69	0.000001	0.0001
CAST	98552632	144	-16.18	0.27	37.05	0.000001	0.0001
CAST	98560787	149	0.78	0.28	0.09	0.000001	0.0001
CAST	98562742	150	-16.08	0.28	33.18	0.000001	0.0001
CAST	98566736	155	-3.53	0.26	1.92	0.000001	0.0001

Table 4-23. Marker effects for Warner-Bratzler shear force aged to approximately 3 days (WBSF3) with associated standard error (SE) significance value (Pval), and Bonferroni adjusted significance value (BPval) for multiple testing for BPval < 0.05 continued…

Gene[1]	Position	Marker	Estimate	SE	F-con	Pval	BPval
CAST	98566778	156	-23.24	0.26	80.55	0.000001	0.0001
CAST	98574903	161	8.53	0.31	8.10	0.000001	0.0001
CAST	98575799	162	-15.89	0.30	30.09	0.000001	0.0001

[1]CAPN1 = μ-calpain, CAST = calpastatin

Table 4-24. μ-calpain marker x breed interaction effects for slice shear force predicted by visible spectroscopy (LED, N[a]) with associated standard error (SE).

	Marker number (SE)
Breed[1]	189
Hereford	-1.47 (0.12)
Red Angus	1.37 (0.12)
Shorthorn	-0.69 (0.15)
South Devon	8.73 (1.06)
Beefmaster	-2.65 (0.16)
Brahman	-5.10 (0.20)
Brangus	0.59 (0.13)
Santa Gertrudis	-1.08 (0.16)
Braunvieh	2.55 (0.19)
Charolais	2.16 (0.12)
ChiAngus	-0.88 (0.18)
Gelbvieh	-0.29 (0.12)
Limousin	-1.67 (0.12)
Maine - Anjou	0.98 (0.15)
Salers	-1.57 (0.15)
Simmental	0.49 (0.12)
Tarentaise	-18.14 (2.15)
perHH	2.35 (0.23)
perAN	2.16 (0.26)
perSM	-0.49 (0.16)
perCH	0.78 (0.24)
Angus	0.00 (0.00)

[1]perAN=Commercial Angus, perHH=Commercial Hereford, perSM=Commercial Simmental, perCH=Commercial Charolais

[a] Deviation in shear force, one newton is the force needed to accelerate one kilogram of mass at the rate of one meter per second squared.

Table 4-25. Calpastatin marker x breed interaction effects for slice shear force predicted by visible spectroscopy (LED) with associated standard error (SE).

	Marker number (SE)										
Breed[1]	92	95	97	104	106	107	146	150	161	162	163
HH	0.09 (0.16)	0.09 (0.16)	0.08 (0.16)	0.11 (0.17)	-0.00 (0.21)	0.09 (0.16)	0.16 (0.22)	0.32 (0.19)	-0.30 (0.16)	0.17 (0.16)	0.13 (0.16)
AR	-0.09 (0.39)	-0.09 (0.39)	-0.48 (0.39)	-0.04 (0.39)	0.23 (0.39)	-0.02 (0.39)	-0.05 (0.43)	0.52 (0.38)	0.07 (0.41)	-0.05 (0.39)	-0.06 (0.39)
SS	--	--	--	--	--	--	--	--	--	--	--
DS	0.94 (0.60)	0.94 (0.60)	0.91 (0.60)	0.35 (0.93)	1.47 (0.99)	0.41 (0.93)	1.15 (0.98)	1.22 (0.94)	0.24 (0.49)	0.71 (0.71)	0.37 (0.93)
BR	0.90 (0.28)	0.90 (0.28)	0.89 (0.28)	0.57 (0.24)	0.47 (0.27)	0.88 (0.28)	0.26 (0.27)	0.37 (0.27)	0.03 (0.26)	0.51 (0.26)	0.77 (0.28)
BN	0.37 (0.48)	0.37 (0.48)	0.69 (0.53)	1.38 (0.79)	-0.44 (0.65)	0.35 (0.48)	0.14 (0.66)	-0.16 (0.67)	-0.20 (0.63)	0.33 (0.49)	0.41 (0.53)
SG	-0.09 (0.32)	-0.09 (0.32)	-0.09 (0.32)	-0.21 (0.35)	-0.38 (0.39)	-0.06 (0.34)	-0.46 (0.39)	-0.04 (0.33)	0.07 (0.29)	-0.18 (0.35)	-0.11 (0.35)
BU	0.18 (0.51)	0.18 (0.51)	0.16 (0.51)	0.09 (0.51)	0.59 (0.53)	0.19 (0.51)	0.78 (0.59)	0.65 (0.55)	0.14 (0.45)	-0.29 (0.53)	-0.10 (0.57)
CH	-0.06 (0.18)	-0.06 (0.18)	-0.06 (0.18)	0.06 (0.18)	-0.10 (0.19)	0.07 (0.18)	-0.08 (0.19)	0.11 (0.18)	0.00 (0.19)	-0.01 (0.18)	0.03 (0.18)
ChiAngus	-0.38 (0.37)	-0.38 (0.37)	-0.38 (0.37)	-0.21 (0.36)	-0.55 (0.39)	-0.15 (0.37)	-0.66 (0.40)	-1.01 (0.38)	0.36 (0.35)	-0.29 (0.37)	-0.12 (0.38)
GV	-0.03 (0.14)	-0.03 (0.14)	-0.01 (0.14)	-0.14 (0.14)	-0.26 (0.15)	-0.04 (0.14)	-0.32 (0.15)	-0.20 (0.14)	0.04 (0.15)	-0.09 (0.14)	-0.09 (0.15)
LM	0.37 (0.15)	0.37 (0.15)	0.34 (0.15)	0.33 (0.16)	0.27 (0.20)	0.36 (0.16)	0.19 (0.21)	0.12 (0.20)	-0.36 (0.15)	0.37 (0.15)	0.33 (0.15)
MA	0.43 (0.49)	0.43 (0.49)	0.56 (0.49)	0.22 (0.47)	0.10 (0.53)	0.49 (0.49)	-0.01 (0.53)	0.19 (0.49)	-0.22 (0.53)	0.43 (0.16)	0.47 (0.49)

SA	-0.79 (0.44)	-0.79 (0.44)	-0.80 (0.44)	-1.12 (0.45)	-1.38 (0.47)	-0.79 (0.45)	-1.46 (0.47)	-1.30 (0.47)	0.94 (0.40)	-1.16 (0.45)	-0.84 (0.45)
Simmental	0.38 (0.18)	0.38 (0.18)	0.37 (0.17)	0.49 (0.16)	0.36 (0.17)	0.42 (0.17)	0.27 (0.17)	0.28 (0.17)	-0.08 (0.18)	0.42 (0.16)	0.48 (0.17)
TA	--	--	--	--	--	--	--	--	--	--	--
perHH	0.24 (0.28)	0.24 (0.28)	0.24 (0.28)	0.20 (0.28)	0.17 (0.29)	0.22 (0.28)	0.14 (0.29)	0.36 (0.31)	-0.21 (0.39)	0.17 (0.28)	0.18 (0.28)
perAN	-0.17 (0.20)	-0.17 (0.20)	-0.16 (0.20)	-0.11 (0.23)	-0.81 (0.46)	-0.11 (0.19)	-0.61 (0.42)	-0.42 (0.27)	-0.59 (0.16)	0.03 (0.23)	-0.12 (0.19)
perSM	0.17 (0.15)	0.17 (0.15)	0.18 (0.15)	0.21 (0.17)	0.12 (0.17)	0.18 (0.15)	0.02 (0.19)	-0.34 (0.18)	0.09 (0.17)	0.18 (0.14)	0.20 (0.15)
perCH	0.33 (0.15)	0.33 (0.15)	0.32 (0.15)	0.28 (0.15)	0.17 (0.16)	0.29 (0.14)	0.06 (0.17)	0.28 (0.17)	0.05 (0.16)	0.29 (0.15)	0.27 (0.15)
MARCIII	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	-0.09 (0.18)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
AN	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)

[1]AN=Angus, HH=Hereford, AR=Red Angus, SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-26. μ-calpain marker x breed interaction effects for visible/near infrared hyperspectral imaging (VISNIR) with associated standard error (SE).

Breed	189	191	195	197	198	199
Hereford	0.19	-0.09	-0.07	-0.06	0.08	-0.29
	(0.10)	(0.10)	(0.11)	(0.11)	(0.10)	(0.13)
Red Angus	0.11	-0.26	-0.15	-0.13	0.10	-0.01
	(0.12)	(0.10)	(0.10)	(0.10)	(0.10)	(0.14)
Shorthorn	0.12	-0.12	0.01	0.00	0.01	-0.12
	(0.25)	(0.11)	(0.13)	(0.13)	(0.13)	(0.18)
South Devon	0.08	-0.20	0.00	-0.01	0.29	-0.05
	(0.14)	(0.27)	(0.36)	(0.36)	(0.27)	(0.43)
Beefmaster	-0.13	-0.23	-0.02	-0.01	0.04	0.01
	(0.18)	(0.14)	(0.14)	(0.14)	(0.15)	(0.15)
Brahman	-0.03	0.11	0.13	0.13	-0.00	-0.03
	(0.12)	(0.14)	(0.16)	(0.16)	(0.14)	(0.16)
Brangus	0.29	0.04	-0.17	-0.15	0.07	-0.22
	(0.14)	(0.13)	(0.13)	(0.12)	(0.12)	(0.15)
Santa Gertrudis	-0.08	-0.14	-0.04	-0.07	0.42	-0.09
	(0.15)	(0.14)	(0.15)	(0.10)	(0.14)	(0.16)
Braunvieh	0.08	0.14	0.14	0.14	0.08	-0.12
	(0.10)	(0.15)	(0.16)	(0.16)	(0.15)	(0.19)
Charolais	0.07	-0.14	-0.08	-0.07	0.09	-0.13
	(0.14)	(0.10)	(0.10)	(0.10)	(0.10)	(0.13)
ChiAngus	-0.02	-0.17	0.02	0.04	0.06	0.13
	(0.10)	(0.13)	(0.13)	(0.13)	(0.14)	(0.16)
Gelbvieh	0.04	-0.13	-0.07	0.02	-0.05	0.01
	(0.11)	(0.09)	(0.11)	(0.10)	(0.11)	(0.15)
Limousin	0.08	-0.18	-0.12	-0.13	-0.01	-0.09
	(0.13)	(0.09)	(0.10)	(0.10)	(0.11)	(0.12)
Maine-Anjou	0.15	-0.10	0.12	0.06	0.04	0.01
	(0.14)	(0.13)	(0.15)	(0.14)	(0.14)	(0.19)
Salers	-0.21	-0.01	0.12	0.13	0.12	0.01
	(0.10)	(0.13)	(0.14)	(0.14)	(0.14)	(0.18)
Simmental	0.32	0.09	-0.24	-0.27	-0.14	-0.24
	(0.32)	(0.10)	(0.10)	(0.10)	(0.10)	(0.15)
Tarentaise	-0.17	-0.56	-0.75	-0.64	0.05	0.47
	(0.23)	(0.34)	(0.37)	(0.48)	(0.31)	(0.45)
Angus	0.00	0.00	0.00	0.00	0.00	0.00
	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)

Table 4-27. Calpastatin marker x breed interaction effects for visible/near infrared hyperspectral imaging (VISNIR) with associated standard error (SE) below.

Breed[1]	88	90	91	94	96	100	104	109	110	112	113	114	18	119	120	123	126	129	130
HH	-0.42	-0.26	-0.43	-0.22	-0.10	-0.13	0.21	-0.43	-0.13	-0.28	-0.41	-0.41	-0.26	0.11	0.21	-0.29	0.18	0.15	-0.29
	0.15	0.14	0.14	0.13	0.15	0.14	0.13	0.14	0.14	0.15	0.14	0.14	0.14	0.13	0.13	0.14	0.13	0.12	0.14
AR	-0.32	-0.42	-0.29	-0.21	-0.19	-0.22	0.45	-0.33	-0.22	-0.41	-0.45	-0.45	-0.23	0.27	0.47	-0.43	0.30	0.38	-0.34
	0.11	0.14	0.11	0.14	0.13	0.13	0.12	0.11	0.13	0.12	0.11	0.11	0.14	0.12	0.12	0.14	0.12	0.12	0.11
SS	-0.19	-0.32	-0.13	0.37	0.23	-0.04	0.71	-0.24	-0.04	-0.13	-0.16	-0.16	0.53	0.39	0.75	-0.15	0.74	0.88	0.16
	0.41	0.49	0.39	0.39	0.39	0.46	0.41	0.41	0.46	0.39	0.44	0.44	0.55	0.43	0.45	0.39	0.41	0.39	0.39
DS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BM	-0.83	-0.59	-0.85	1.85	0.43	1.96	0.00	1.91	1.96	0.57	0.79	0.79	1.67	0.83	0.77	0.78	0.00	0.69	0.87
	0.54	0.79	0.54	0.86	0.51	0.85	0.00	0.86	0.85	0.51	0.60	0.60	0.86	1.03	1.04	0.61	0.00	1.02	0.61
BR	0.34	0.49	0.49	0.52	0.82	0.69	0.19	0.22	0.69	0.69	0.35	0.35	0.47	0.38	0.23	0.69	0.37	0.38	0.67
	0.30	0.24	0.29	0.24	0.25	0.25	0.24	0.26	0.25	0.25	0.24	0.24	0.29	0.24	0.24	0.26	0.24	0.23	0.25
AN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[1]AN=Angus, HH=Hereford, AR=Red Angus, SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-28. Calpastatin marker x breed interaction effects for visible/near infrared hyperspectral imaging VISNIR with associated standard error SE continued…

Breed[1]	88	90	91	94	96	100	104	109	110	112	113	114	18	119	120	123	126	129	130
BN	-0.79	1.66	-0.79	-0.97	1.46	1.19	1.42	-0.81	1.19	0.01	-1.12	-1.12	-1.03	0.83	0.44	0.91	1.43	0.72	-0.18
	0.64	1.71	0.62	0.63	1.38	1.32	0.70	0.62	1.32	0.50	0.67	0.67	0.65	0.56	0.64	0.68	0.58	0.55	0.59
SG	0.32	0.39	0.34	0.49	0.63	0.54	-0.04	0.31	0.54	0.79	0.43	0.43	0.74	0.46	-0.16	0.39	0.26	0.02	0.37
	0.28	0.33	0.29	0.29	0.34	0.32	0.34	0.29	0.32	0.30	0.30	0.30	0.33	0.35	0.38	0.35	0.35	0.34	0.30
BU	0.64	0.07	0.28	1.23	0.36	0.54	-0.38	0.39	0.54	0.10	0.21	0.21	0.59	-0.68	-0.11	0.33	-0.57	-0.64	0.25
	0.45	0.51	0.43	0.47	0.36	0.36	0.39	0.36	0.36	0.35	0.35	0.35	0.59	0.44	0.42	0.36	0.40	0.39	0.36
CH	-0.00	0.10	-0.01	0.06	0.18	0.14	0.06	0.04	0.14	0.13	0.05	0.05	0.04	-0.02	0.04	-0.03	0.03	0.07	0.10
	0.14	0.15	0.14	0.14	0.14	0.14	0.13	0.14	0.14	0.13	0.13	0.13	0.15	0.13	0.13	0.14	0.13	0.13	0.13
ChiAn	0.31	0.52	0.28	0.27	0.59	0.78	-0.05	0.18	0.78	0.31	0.11	0.11	0.35	-0.20	-0.04	0.48	-0.24	-0.29	0.34
gus	0.34	0.40	0.33	0.46	0.39	0.38	0.33	0.33	0.38	0.35	0.35	0.35	0.46	0.34	0.13	0.39	0.33	0.34	0.35
GV	-0.01	-0.04	-0.12	-0.03	0.23	0.16	0.62	-0.06	0.16	0.10	0.04	0.04	-0.09	0.26	-0.01	-0.00	0.12	0.15	0.07
	0.13	0.13	0.13	0.12	0.13	0.13	0.12	0.13	0.13	0.12	0.12	0.12	0.14	0.12	0.12	0.13	0.12	0.11	0.12
AN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[1]AN=Angus, HH=Hereford, AR=Red Angus, SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-29. Calpastatin marker x breed interaction effects for visible/near infrared hyperspectral imaging VISNIR with associated standard error SE continued…

Breed[1]	88	90	91	94	96	100	104	109	110	112	113	114	18	119	120	123	126	129	130
LM	-0.19	-0.22	-0.22	-0.11	-0.11	-0.03	0.13	-0.21	-0.03	-0.25	-0.14	-0.14	-0.14	-0.01	0.04	-0.29	0.09	0.18	-0.13
	0.11	0.15	0.12	0.12	0.14	0.13	0.11	0.11	0.13	0.12	0.11	0.11	0.13	0.12	0.12	0.14	0.11	0.13	0.11
MA	-0.27	-0.43	-0.24	0.52	-0.18	-0.17	0.84	-0.26	-0.17	-0.11	-0.42	-0.42	0.48	-0.11	0.83	-0.39	0.74	0.73	-0.32
	0.46	0.48	0.46	0.62	0.48	0.48	0.48	0.46	0.48	0.47	0.48	0.48	0.62	0.51	0.48	0.48	0.49	0.49	0.48
SA	0.03	0.28	0.09	-0.65	0.57	0.45	-0.04	0.05	0.45	-0.27	0.11	0.11	-0.51	0.47	-0.03	0.58	0.09	0.17	0.35
	0.37	0.38	0.36	0.54	0.38	0.35	0.36	0.38	0.35	0.12	0.38	0.38	0.52	0.44	0.36	0.38	0.40	0.38	0.36
SM	-0.31	-0.16	-0.28	-0.21	-0.01	-0.09	0.15	-0.34	-0.09	0.00	-0.32	-0.32	-0.38	0.27	0.17	-0.21	0.00	0.12	-0.13
	0.12	0.13	0.13	0.12	0.12	0.12	0.12	0.11	0.12	0.00	0.11	0.11	0.14	0.12	0.11	0.12	0.11	0.11	0.11
TA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[1]AN=Angus, HH=Hereford, AR=Red Angus, SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-30. Calpastatin marker x breed interaction effects for visible/near infrared hyperspectral imaging VISNIR with associated standard error SE continued…

Breed[1]	132	134	135	139	141	143	144	145	147	150	153	154	155	157	158	160	161
HH	-0.15	-0.40	-0.42	0.12	-0.26	-0.25	-0.39	-0.39	-0.22	-0.07	-0.29	-0.26	-0.24	-0.19	-0.23	-0.39	-0.39
	0.16	0.13	0.15	0.13	0.14	0.17	0.14	0.14	0.15	0.13	0.19	0.27	0.14	0.14	0.14	0.14	0.14
AR	-0.19	-0.41	-0.30	0.27	0.03	0.16	-0.30	-0.29	-0.19	0.21	0.05	0.23	-0.27	-0.27	-0.33	-0.29	-0.36
	0.24	0.11	0.11	0.13	0.14	0.16	0.11	0.11	0.20	0.13	0.14	0.27	0.14	0.13	0.11	0.11	0.11
SS	0.23	0.46	-0.19	0.97	-0.32	0.09	-0.48	-0.48	0.15	0.82	0.62	-0.44	0.47	0.01	-0.18	-0.02	-0.24
	0.48	0.39	0.41	0.41	0.44	0.52	0.43	0.43	0.48	0.39	0.45	0.55	0.62	0.39	0.40	0.39	0.42
DS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BM	1.75	1.89	0.73	0.93	0.78	0.72	0.77	0.28	0.71	0.82	0.84	0.35	1.77	0.74	0.78	0.74	0.76
	0.86	0.85	0.61	1.04	0.61	0.61	0.61	0.61	0.60	1.04	0.77	1.02	0.86	0.59	0.60	0.60	0.60
BR	1.29	0.35	0.46	0.28	0.37	0.47	0.35	0.35	0.57	-0.07	0.02	0.03	0.48	0.88	0.48	0.57	0.35
	0.35	0.24	0.27	0.23	0.24	0.25	0.26	0.26	0.24	0.24	0.29	0.27	0.26	0.24	0.27	0.25	0.23
BN	1.23	-0.26	-0.79	-0.11	-2.09	-1.04	-0.78	-0.77	1.77	-1.03	0.11	0.21	1.15	1/59	-0.77	-0.69	-0.65
	1.31	0.58	0.63	0.69	1.73	0.94	0.62	0.62	1.57	0.74	0.51	0.98	1.32	0.85	0.62	0.62	0.62
SG	0.69	0.24	0.31	0.06	0.57	0.45	0.34	0.34	0.96	0.78	0.02	-0.15	0.56	0.55	0.27	0.11	0.12
	0.28	0.28	0.29	0.38	0.30	0.43	0.28	0.28	0.34	0.32	0.35	0.59	0.44	0.32	0.28	0.29	0.29
BU	0.16	0.63	0.66	-0.66	0.84	0.75	0.73	0.74	0.64	-0.06	0.67	-0.24	0.28	0.85	0.97	0.94	0.37
	0.53	0.35	0.37	0.39	0.44	0.58	0.36	0.36	0.45	0.45	0.42	0.51	0.38	0.26	0.36	0.36	0.36
CH	0.05	0.03	0.00	0.09	-0.08	0.05	0.01	0.01	0.02	-0.01	0.32	-0.18	0.21	0.16	-0.07	-0.05	-0.10
	0.15	0.13	0.14	0.14	0.13	0.15	0.13	0.13	0.15	0.14	0.13	0.17	0.17	0.13	0.13	0.13	0.13
ChiAngus	0.57	0.22	0.31	-0.36	0.29	0.28	0.29	0.29	0.55	0.17	0.87	-0.06	0.38	0.64	0.36	0.35	0.19
	0.76	0.35	0.34	0.36	0.39	0.39	0.33	0.33	0.76	0.34	0.42	0.69	0.38	0.36	0.33	0.33	0.33
GV	0.21	-0.14	-0.08	0.14	0.07	-0.05	-0.06	-0.06	0.19	-0.09	0.23	-0.39	0.01	0.19	-0.16	-0.03	-0.11
	0.14	0.12	0.13	0.12	0.12	0.15	0.13	0.13	0.13	0.12	0.13	0.14	0.14	0.12	0.13	0.13	0.12
LM	-0.22	-0.16	-0.21	0.14	-0.33	-0.42	-0..11	-0.11	-0.12	-0.02	-0.16	-0.34	-0.17	-0.20	-0.19	-0.21	-0.22
	0.17	0.11	0.11	0.14	0.14	0.19	0.11	0.11	0.15	0.15	0.12	0.19	0.17	0.13	0.11	0.11	0.12
MA	-0.34	0.59	-0.27	0.72	-0.12	0.65	-0.19	-0.19	-0.36	0.95	-0.38	3.73	0.98	-0.18	-0.19	-0.21	-0.17
	0.49	0.59	0.46	0.52	0.43	0.50	0.46	0.46	0.49	0.48	0.52	0.98	0.68	0.47	0.46	0.46	0.46
SA	0.00	-0.11	0.04	-0.09	-0.03	-0.02	0.09	0.10	0.22	-0.45	0.87	-0.38	0.16	0.17	0.11	0.04	0.19
	0.00	0.33	0.37	0.38	0.38	0.69	0.36	0.36	0.43	0.39	0.45	0.49	0.42	0.36	0.36	0.37	0.37
SM	0.33	-0.36	-0.35	-0.11	-0.12	-0.29	-0.32	-0.33	-0.21	-0.04	-0.04	-0.12	-0.18	-0.20	-0.39	-0.39	-0.39
	0.44	0.12	0.12	0.12	0.12	0.14	0.12	0.12	0.14	0.12	0.12	0.19	0.14	0.12	0.12	0.12	0.12
TA	-0.11	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.14	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

AN	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[1]AN=Angus, HH=Hereford, AR=Red Angus, SS=Shorthorn, DS=South Devon, BM=Beefmaster, BR=Brahman, BN=Brangus, SG=Santa Gertrudis, BU=Braunvieh, CH=Charolais, GV=Gelbvieh, LM=Limousin, MA=Maine-Anjou, SA=Salers, SM=Simmental, TA=Tarentaise

Table 4-31. Calpastatin marker x breed interaction effects for visible/near infrared hyperspectral imaging VISNIR with associated standard error SE continued…

	Marker number (SE)		
Breed[1]	162	165	166
Hereford	0.14	-0.42	-0.16
	0.13	0.15	0.14
Red Angus	0.31	-0.30	-0.27
	0.11	0.11	0.14
Shorthorn	0.68	-0.18	0.04
	0.40	0.41	0.39
South	0.00	0.00	0.00
Devon	0.00	0.00	0.00
Beefmaster	0.48	0.73	0.83
	1.02	0.61	0.59
Brahman	0.29	0.42	0.67
	0.24	0.28	0.26
Brangus	0.57	-0.75	1.26
	0.51	0.64	1.34
Santa	0.16	0.32	0.62
Gertrudis	0.34	0.29	0.29
Braunvieh	-0.84	0.86	0.93
	0.37	0.37	0.36
Charolais	0.13	-0.03	0.17
	0.13	0.13	0.14
ChiAngus	-0.23	0.31	0.73
	0.33	0.34	0.39
Gelbvieh	0.11	-0.02	0.13
	0.11	0.13	0.12
Limousin	0.06	-0.22	-0.02
	0.11	0.11	0.13
Maine-	0.69	-0.19	-0.06
Anjou	0.48	0.46	0.48
Salers	-0.14	0.03	0.50
	0.38	0.37	0.38
Simmental	0.13	-0.25	-0.22
	0.11	0.12	0.12
Tarentaise	0.00	0.00	0.00
	0.00	0.00	0.00
Angus	0.00	0.00	0.00
	0.00	0.00	0.00

Table 4-32. µ-calpain Marker x Breed Interaction Effects for frozen slice shear force aged to day 14 (SSF14) with associated standard error (SE) below.

	Marker number (SE)
Breed[1]	198
Hereford	0.26 0.23
Red Angus	0.30 0.20
Shorthorn	0.00 0.00
South Devon	0.00 0.00
Beefmaster	0.00
Brahman	0.00 0.00
Brangus	0.00
Santa Gertrudis	0.00
Braunvieh	0.00
Charolais	0.74 0.20
ChiAngus	0.00
Gelbvieh	-0.18 0.23
Limousin	0.41 0.21
Main - Anjou	0.00
Salers	0.00
Simmental	0.29 0.19
Tarentaise	0.00
perHH	0.00
perAN	0.00
perSM	0.00
perCH	0.00
Angus	0.00

References

Barendse,W. J. 2002. DNA markers for meat tenderness. International patent application PCT/AU02/00122. International patent publication WO 02/064820 A1.

Casas, E., S. N. White, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, D. G. Riley, C. C. Chase, D. D. Johnson, and T. P. L. Smith. 2006. Effects of calpastatin and μ-markers in beef cattle on tenderness traits. J. Anim. Sci. 84: 520-525.

Casas, E., S. N. White, D. G. Riley, T. P. L. Smith, R. A. Brenneman, T. A. Olson, D. D. Johnson, S. W. Coleman, G. L. Bennett, and C. C. Chase, Jr. 2005. Assessment of single nucleotide polymorphisms in genes residing on chromosomes 14 and 29 for association with carcass composition traits in *Bos indicus* cattle. J. Anim. Sci. 83:13–19.

Cecchinato, A., M. De Marchi, M. Penasa, A. Albera, and G. Bittante. 2011. Near-infrared reflectance spectroscopy predictions as indicator traits in breeding programs for enhanced beef quality. J. Anim. Sci. 89:2687-2695.

Chambaz, A., M. Richard, L. Scheeder, M. Kreuzer, and P. A. Dufey. 2003. Meat quality of Angus, Simmental, Charolais and Limousin steers compared at the same intramuscular fat content. Meat Sci. 63:491-500.

Devitt, C. J., and Wilton, J. W. 2001. Genetic correlation estimates between ultrasound measurements on yearling bulls and carcass measurements on finished steers. J. Anim. Sci. 79:2790-2797.

Fernandes, T. L., J. W. Wilton, I. B. Mandell, and C.J.B. Devitt. 2002. Genetic parameter estimates for meat quality traits in beef cattle managed under a constant finishing program. 7th World Congress on Genetics Applied to Livestock Production. August 19-23, Montpellier, France.

Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. J. Anim. Sci. 72:1174-1183.

Koch, R. M., M. E. Dikeman, D. M. Allen, M. May, J. D. Crouse, and D. R. Campion. 1976. Characterization of biological types of cattle III. Carcass composition, quality and palatability. J. Anim. Sci. 43:48-61.

Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization process of meat. Meat Sci. 43:S193–S201.

Lage, J.F., P. V. R. Paulino, S. C. Valadares Filho, E. J. O. Souza, M. S. Duarte, P. D. B. Benedeti. 2012. Influence of genetic type and level of concentrate in the finishing diet on carcass and meat quality traits in beef heifers. Meat Sci. 90:770–74.

MacNeil, M. D. and M. D. Grosz. 2002. Genome-wide scans for QTL affecting carcass traits in Hereford x composite double backcross populations. J. Anim. Sci. 80:2316-2324.

McClure, M. C., H. R. Ramey, M. M. Rolf, S. D. McKay, J. E. Decker, R. H. Chapple, J. W. Kim, T. M. Taxis, R. L. Weaber, R. D. Schnabel, and J. F. Taylor. 2012. Genome-wide association analysis for quantitative trait loci influencing Warner–Bratzler shear force in five taurine cattle breeds. Anim Genetics. 43:662-673.

Middleton, B. K. and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861-3871.

Naganathan, G. K., L. M. Grimes, J. Subbiah, C. R. Calkins, A. Samal, and G. E. Meyer. 2008. Visible/near-infrared hyperspectral imaging for beef tenderness prediction. Computers and Electronics in Agriculture 64: 225-233.

Page, B. T., E. Casas, M. P. Heaton, N. G. Cullen, D. L. Hyndman, C. A. Morris, A. M. Crawford, T. L. Wheeler, M. Koohmaraie, J. W. Keele, and T. P. L. Smith. 2002. Evaluation of single nucleotide polymorphisms in *CAPN1* for association with meat tenderness in cattle. J. Anim. Sci. 80:3077–3085.

Page, B. T., E. Casas, R. L. Quaas, R. M. Thallman, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, S. N. White, G. L. Bennett, J. W. Keele, M. E. Dikeman, and T. P. L. Smith. 2004. Association of markers in the bovine *CAPN1* gene with meat tenderness in large crossbred populations that sample influential industry sires. J. Anim. Sci. 82:3474–3481.

Pereira, A.S.C., F. Baldi, R. D. Sainz, B. L. Utembergue, H. L. J. Chiaia, and C. U. Magnabosco. 2015. Growth performance, and carcass and meat quality traits in progeny of Poll Nellore, Angus and Brahman sires under tropical conditions. Anim Prod Sci. 55:1295–02.

Pitchford, W. S., Z. A. Kruk, E. M. Stephens, P. A. Speck and M. P. B. Deland. 2002. Are there meat quality differences between cattle breeds in southern Australia? Anim. Prod. Aust. 24:177-180.

Prieto, N., R. Roehe, P. Lavín, G. Batten, and S. Andrés. 2009. Application of near infrared reflectance spectroscopy to predict meat and meat products quality: A review. Meat Science. 83:175–186.

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

Robinson, D. L., D. M. Ferguson, V. H. Oddy, D. Perry, and J. M. Thompson. 2001. Genetic and environmental influences on beef tenderness. Aust. J. Exp. Agric. 41:997–1004.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 2012. Technical note: validation of a model for online classification of US Select beef carcasses for longissimus tenderness using visible and near-infrared reflectance spectroscopy. J Anim. Sci. 90:973-977.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 2005. On-line classification of US select beef carcasses for longissimus tenderness using visible and near-infrared reflectance spectroscopy. J. Meat. Sci. 69:409-415.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1999a. Tenderness classification of beef. II: Design and analysis of a system to measure beef longissimus shear force under commercial processing conditions. J. Anim. Sci. 77:1474–1481.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1999b. Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. J. Anim. Sci. 77:2693-2699.

Splan, R. K., L. V. Cundiff, and L. D. Van Vleck. 1998. Genetic parameters for sex-specific traits in beef cattle. J. Anim. Sci. 76:2272–2278.

Stone, R. T., J. W. Keele, S. D. Shackelford, S. M. Kappes, and M. Koohmaraie. 1999. A primary screen of the bovine genome for quantitative trait loci affecting carcass and growth traits. J. Anim. Sci. 77:1379−1384.

VanRaden, P. 2014. findhap.f90. http://aipl.arsusda.gov/software/findhap.

Weaber, R. L., and J. L. Lusk. 2010. The economic value of improvements in beef tenderness by genetic marker selection. American J of Agricultural Economics. 92:1456-1471.

Westell, R. A., R. L. Quaas, and D. L. Van Vleck. 1988. Genetic Groups in an Animal Model. Faculty Papers and Publications in Animal Science. 309. http://digitalcommons.unl.edu/animalscifacpub/309

Wheeler, T. L., S. D. Shackelford, and M. Koohmaraie. 1997. Standardizing collection and interpretation of Warner-Bratzler shear force and sensory tenderness data. Proc. Recip. Meat Conf. 50:68-77.

Wheeler, T.L., S. D. Shackelford, M. Koohmaraie. 1996. Sampling, cooking, and coring effects on Warner-Bratzler shear force values in beef. J. Anim. Sci. 74:1553-1562.

Wheeler, T.L., M. Koohmaraie, M., L. V. Cundiff and M. E. Dikeman. 1994. Effects of cooking and shearing methodology on variation in Warner-Bratzler shear force values in beef. J. Anim. Sci. 72:2325-2330.

White, S. N., E. Casas, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, D. G. Riley, C. C. Chase, Jr., D. D. Johnson, J. W. Keele, and T. P. L. Smith. 2005. A new SNP in CAPN1 is associated with tenderness in cattle of Bos indicus, Bos taurus, and cross bred descent. J. Anim. Sci. 83:2001-2008.

Aggregate List of References

Archer, J. A., P. F. Arthur, R. M. Herd and E. C. Richardson. 1998. Genetic variation in feed efficiency and its component traits. Proc. 6th World cong. Genet. Appl. Lives. Prod., Armidale, NSW, Australia. 25:81-84.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. J. Anim. Sci. 79:2805-2811.

Arthur, P. F., G. Renand and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. Livest. Prod. Sci. 68:131-139.

Arnold, J. W., J. K. Bertrand and L. L. Benyshek. 1992. Animal model for genetic evaluation of multibreed data. J. Anim. Sci. 70:3322-3332.

Baker, F. H. 1967. History and development of beef and dairy performance programs in the United States. J. Anim. Sci. 26:1261-1263.

Bateson, W. and E. Saunders. 1902. Experimental Studies in the Physiology of Heredity. Rpt. Evolut. Com. Roy. Soc. 1:3.

Beaudeau F., V. Ducrocq, C. Fourichon, H. Seegers. 1995. Effect of disease on length of productive life of French Holstein dairy cows assessed by survival analysis. J. Dairy Sci. 78:103-117.

Barendse,W. J. 2002. DNA markers for meat tenderness. International patent application PCT/AU02/00122. International patent publication WO 02/064820 A1.

Barendse, W. 1999. Assessing lipid metabolism. International patent application PCT/AU98/00882, international patent publication WO 99/23248.

Basarab, J. A., M. G. Colazo, D. J. Ambrose, S. Novak, D. McCartney, and V. S. Baron. 2011. Residual feed intake adjusted for backfat thickness and feed frequency is independent of fertility in beef heifers. Can. J. Anim. Sci. 91:573–584.

Berry, D. P. and J. E. Pryce. 2014. Feed efficiency in growing and mature animals. Proceedings, 10th World Congress of Genetics Applied to Livestock Production.

Berry, D. P. and J. J. Crowley. 2013. Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. J. Anim. Sci. 91: 1594-1613.

Benyshek, L. L. 1991. Beef cattle national genetic evaluation programs. Presented at the Beef Seedstock Symp. South Dakota State Univ., Brookings.

Bolormaa, S., B. Hayes, K. Savin, R. Hawken, B. Barendse, P. Arthur, D. Johnston, R. Herd and M. Goddard. 2011. Genome-wide association studies for feedlot and growth traits in cattle. J. Anim. Sci. 10:2572-3079.

Brigham, B. W., S. E. Speidel, R. M. Enns, and D. J. Garrick. 2007. Stayability to alternate ages. Proceedings – American Society of Animal Science Western Section. 58:27.

Casas, E., White, S. N., Wheeler, T. L., Shackelford, S. D., Koohmaraie, M., Riley, D. G., et al. 2006. Effects of calpastatin and l-calpain markers in beef cattle on tenderness traits. J. Anim. Sci. 84:520–525.

Casas, E., S. N. White, D. G. Riley, T. P. L. Smith, R. A. Brenneman, T. A. Olson, D. D. Johnson, S. W. Coleman, G. L. Bennett, and C. C. Chase, Jr. 2005. Assessment of single nucleotide polymorphisms in genes residing on chromosomes 14 and 29 for association with carcass composition traits in *Bos indicus* cattle. J. Anim. Sci. 83:13–19.

Casas, E., S. D. Shackelford, J. W. Keele, M. Koohmaraie, T. P. L. Smith, and R. T. Stone. 2003. Detection of quantitative trait loci for growth and carcass composition in cattle. J. Anim. Sci. 81:2976–2983.

Casas, E., R. T. Stone, J. W. Keele, S. D. Shackelford, S. M. Kappes, and M. Koohmaraie. 2001. A comprehensive search for quantitative loci affecting growth and carcass composition of cattle segregating alternative forms of the myostatin gene. J. Anim. Sci. 79:854–860.

Casas, E., S. D. Shackelford, J. W. Keele, R. T. Stone, S. M. Kappes, and M. Koohmaraie. 2000. Quantitative trait loci affecting growth and carcass composition of cattle segregating alternate forms of myostatin. J. Anim. Sci. 78:560–569.

Cecchinato, A., M. De Marchi, M. Penasa, A. Albera, and G. Bittante. 2011. Near-infrared reflectance spectroscopy predictions as indicator traits in breeding programs for enhanced beef quality. J. Anim. Sci. 89:2687-2695.

Chambaz, A., M. Richard, L. Scheeder, M. Kreuzer, and P. A. Dufey. 2003. Meat quality of Angus, Simmental, Charolais and Limousin steers compared at the same intramuscular fat content. Meat Sci. 63:491-500.

Cole, J. B., P. M. VanRaden, J. R. O'Connell, C. P. Van Tassell, T. S. Sonstegard, R. D. Schnabel, J. F. Taylor, and G. R. Wiggans. 2009. Distribution and location of genetic effects for dairy traits. J. Dairy Sci. 92:2931-2946.

Cooper, A. J., C. L. Ferrell, L. V. Cundiff, and L. D. Van Vleck. 2010. Prediction of genetic values for feed intake from individual body weight gain and total feed intake of the pen. J. Anim. Sci. 88: 1967-2391.

Crews D.H., Jr. 2005. Genetics of efficient feed utilization and national cattle evaluation: A review. Genetics and Molecular Research. 4:152-165.

Crews, D.H., Jr., N. H. Shannon, B. M. A. Genswein, R. E. Crews., C. M. Johnson, and B. A. Kendrick. 2003. Genetic parameters for net feed efficiency of beef cattle measured during postweaning growing versus finishing periods. Proc. West. Sec. Am. Soc. Anim. Sci. 54: 125-128.

Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews, Jr., R. D. Evans, and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. J. Anim. Sci. 88:885-894.

Culbertson, M. M., S. E. Speidel, R. K. Peel, R. R. Cockrum, M. G. Thomas, and R. M. Enns. 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. J. Anim. Sci. 93:2482–2487.

Dalsted, N. L., and P. H. Gutierrez. 1989. How long do you keep her? BEEF Spring:15.

Devitt, C. J., and Wilton, J. W. 2001. Genetic correlation estimates between ultrasound measurements on yearling bulls and carcass measurements on finished steers. J. Anim. Sci. 79:2790-2797.

Dickerson, G. E., N. Kunzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. J. Anim. Sci. 39:659-673.

Diel, T. D. 1993. "Ideas into Action: 25 Years". Beef Improvement Federation. University Printing Services, Oklahoma State University, Stillwater, OK.

Doyle, S. P., B. L. Golden, R. D. Green and J. S. Brinks. 2000. Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females. J. Anim. Sci. 78:2091-2098.

Ducrocq, V., Solkner, J. and G. Meszaros. 2014. The Survival Kit v6.12 User's Manual.

Ducrocq, V. 1999. Extension of survival analysis models to discrete measures of longevity. Interbull Bull. 21:41–47.

Ducrocq, V., and J. Solkner. 1998. The Survival Kit V3.0, a package for large analyses of survival data. Proc. 6th World Congr. Genet. Appl. Livest. Prod. 27:447–448.

Ducrocq, V., and J. Solkner. 1994. The Survival Kit, a FORTRAN package for the analysis of survival data. Proc. 5th World Congr. Genet. Appl. Livest. Prod. 22:51–52.

Ducrocq, V., R. L. Quaas, E. J. Pollak, and G. Casella. 1988. Length of productive life of dairy cows. 1. Justification of a Weibull mode. J. Dairy Sci. 71:3061–3070.

Ducrocq. V. 1987. An analysis of length of productive life in dairy cattle. Ph.D. Diss. Cornell Univ., Ithaca, NY; Univ. Microfilms Int., Ann Arbor, MI.

Elzo, M. A. and T. R. Famula. 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60:942-952.

Elzo, M. A. and G. E. Bradford. 1985. Multibreed sire evaluation procedures across countries. J. Anim. Sci. 60:953-963.

Enns, R. M., D. J. Garrick, and B. W. Brigham. 2005. Variability in economic value is dependent upon herd average stayability. J. Anim. Sci. 83 Suppl 2:112-115.

Essl, A. 1998. Longevity in dairy cattle breeding: a review. Livest. Prod. Sci. 57:79–89.

Evans, J. L., B. L. Golden, R. M. Bourdon and K. L. Long. 1999. Additive genetic relationship between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77:2621-2628.

Fernandes, T. L., J. W. Wilton, I. B. Mandell, and C.J.B. Devitt. 2002. Genetic parameter estimates for meat quality traits in beef cattle managed under a constant finishing program. 7th World Congress on Genetics Applied to Livestock Production. August 19-23, Montpellier, France.

Ferrell C. L. and T. G. Jenkins. 1985. Cow type and the nutritional environment: nutritional aspects. J. Anim. Sci. 61:725-741.

Fox, D. G., L. O. Tedeschi, and P. J. Guiroy. 2001. Determining feed intake and feed efficiency of individual cattle fed in groups. Proceedings of the 33rd Annual Beef Improvement Federation Annual Research Symposium and Annual Meeting. 80- 98.

Garrick, D. 2005. Trends and developments in genetic evaluation of beef cattle in the United States. Proc. 9th World Angus Forum Tech. Meet., Angus in the Global Market. Am. Angus Assoc., Kansas City, MO.

Garrick, D. 2006. Genetic improvement of beef cattle – assessing the ramifications of genetic change. 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, MG, Brazil.

Garrick, D. J., and B. L. Golden. 2009. Producing and using genetic evaluations in the United States beef industry of today. J. Anim. Sci. 87:E11-E18.

Gianola, D. and J. L. Foulley. 1983. Sire evaluation for ordered categorical data with a threshold model. Genet. Sel. Evol. 15:201-224.

Golden, B. L., J. S. Brinks and R. M. Bourdon. 1991. A performance programmed method for computing inbreeding coefficients from large data sets for use in mixed-model analyses. J. Anim. Sci. 87:E11-E18.

Golden, B. L., D. J. Garrick and L. L. Benyshek. 2009. Milestones in beef cattle genetic evaluation. J. Anim. Sci. 97:E3-E10.

Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. J. Anim. Sci. 72:1174-1183.

Guiroy P.J., D. G. Fox, Tedeschi L.O., Baker M.J. & Cravey M.D. 2001. Predicting individual feed requirements of cattle fed in groups. J. Anim. Sci. 79:1983-1995.

Haley, C. S., S. A. Knott, and J.-M. Elsen. 1994. Mapping quantitative trait loci in crosses between outbred lines using least squares. Genetics. 136:1195−1207.

Hazel L. N. and J. L. Lush. 1943. The efficiency of three methods of selection. Journ. Hered. 33:393-399.

Henderson, C.R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. Biometrics 32, 68-83.

Henderson, C. R. 1975.Best linear unbiased estimation and prediction under a selection model. Biometrics. 31:2 423-447.

Henderson, C. R. 1963. Selection index and expected genetic advance. In: Statistical Genetics and Plant Breeding. Natnl. Acad. Sci. Natnl. Res. Counc. Publ. 982. pp. 141-163. National Academy of Science, Washington, DC.

Herd, R. M. and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. Lives. Prod. Sci. 63:111-119.

Hill, R. A. 2012. Feed efficiency in the beef industry. A John Wiley & Sons, Inc, New Delhi, India.

Hudson, G. F. S., and L. D. Van Vleck. 1981. Relationship between production and stayability in Holstein cattle. J. Dairy Sci. 64: 2246-2250.

Kelly, D. N., C. Murphy, R. D. Sleator, M. M. Judge, S. B. Conroy, and D. P. Berry. 2019. Feed efficiency and carcass metrics in growing cattle. J. Anim. Sci. 97:4405-4417.

Kennedy, B. W., J. H. J. van der Werf and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. J. Anim. Sci. 71:3239-3250.

Koch, R. M., J. B. Gibb, and J. A. Gosey. 1986. Evaluation of beef cattle industry breeding programs: breeders and breed associations. 3rd World Congress on Genetics Applied to Livestock Production. Paper 30.

Koch, R. M., M. E. Dikeman, D. M. Allen, M. May, J. D. Crouse, and D. R. Campion. 1976. Characterization of biological types of cattle III. Carcass composition, quality and palatability. J. Anim. Sci. 43:48-61.

Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486-494.

Koch, R. M. and R. T. Clark. 1955. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment J. Anim. Sci. 14:979.

Koger, Marvin and J. H. Knox. 1947. The repeatability of the yearly production of range cows. J. Anim. Sci. 6:461.

Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization process of meat. Meat Sci. 43:S193–S201.

Koong, L. J., C. L. Ferrell, and J. A. Nienaber. 1982. Effects of plane nutrition on organ size and fasting heat production in swine and sheep. Proceedings of 9th Symposium on Energy Metabolism of Farm Animals. EAAP 29:245-248.

Koots, K. R., J. P. Gibson and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:826-853.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825-853.

Kuehn, L. A., Bl. L. Golden, C. R. Comstock, and K. J. Andersen. 1998. Docility EPD for Limousin cattle. J. Dairy Sci. 81:334.

Lage, J.F., P. V. R. Paulino, S. C. Valadares Filho, E. J. O. Souza, M. S. Duarte, P. D. B. Benedeti. 2012. Influence of genetic type and level of concentrate in the finishing diet on carcass and meat quality traits in beef heifers. Meat Sci. 90:770–74.

Lander, E., and L. Kruglyak. 1995. Genetic dissection of complex traits: Guidelines for interpreting and reporting linkage results. Nat. Genet. 11:241−247.

Lin, C. Y. and S. E. Aggrey. 2013. Incorporation of economic values into the component traits of a ratio: feed efficiency. Poultry Sci. 92:916-922.

Lin, C. Y. 1980. Relative efficiency of selection methods for improvement of feed efficiency. J. Dairy Sci. 63:491-494.

MacNeil, M. D., M. M. Scholtz, F. J. Jordaan, and A. Maiwashe. 2019. Alternative models for genetic evaluation of feed intake by Afrikaner cattle. S. Afr. J. Anim. Sci. 49: 763-769.

MacNeil, M. D., M. C. Mokolobate, M. M. Scholtz, F. J. Jordaan, and F.W.C Neser. 2017. Alternative approaches to evaluation of cow efficiency. S. Afr. J. Anim. Sci. 47:188-123.

MacNeil, M. D., M. M. Scholtz, and A. Maiwashe. 2013. Estimates of variance components for postweaning feed intake and growth in Bonsmara bulls and evaluation of alternative measures of feed efficiency. S. Afr. J. Anim. Sci. 49:763-769.

MacNeil, M. D., N. Lopez-Villalobos, and S. L. Northcutt. 2011. A prototype national cattle evaluation for feed intake and efficiency of Angus cattle. J. Anim. Sci. 89:3917-3923.

MacNeil, M. D. and M. D. Grosz. 2002. Genome-wide scans for QTL affecting carcass traits in Hereford x composite double backcross populations. J. Anim. Sci. 80:2316-2324.

Martinez, G. E., R. M. Koch, L. V. Cundiff, K. E. Gregory, S. D. Kachman, and L. D. Van Vleck. 2005. Genetic parameters for stayability, stayability at calving, and stayability at weaning to specified ages for Hereford cows. J. Anim. Sci. 83:2033-2042.

McClure, M. C., H. R. Ramey, M. M. Rolf, S. D. McKay, J. E. Decker, R. H. Chapple, J. W. Kim, T. M. Taxis, R. L. Weaber, R. D. Schnabel, and J. F. Taylor. 2012. Genome-wide association analysis for quantitative trait loci influencing Warner–Bratzler shear force in five taurine cattle breeds. Anim Genetics. 43:662-673.

Meszaros,G., Solkner,J., Ducrocq,V. 2013. The Survival Kit: Software to analyze survival data including possibly correlated random effects. Computer Methods and Programs in Biomedicine, 1103: 503-510.

Meuwissen, T. H. E. and Z. Luo. 1992. Computing inbreeding coefficients in large populations. Genet. Sel. Evol. 24:305-313.

Middleton, B. K. and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861-3871.

Mohler, J. R. 1937. Certification of pedigrees of imported registered livestock. J. Anim. Sci. 1937:309-310.

Montano-Bermudez, M., M. K. Nielsen and G. H. Deutscher. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. J. Anim. Sci. 68:2279-2288.

Mrode, R. A. and R. Thompson. 2005. Linear models for the prediction of animal breeding values. 2nd ed. CABI Publishing, Cambridge, MA.

Naganathan, G. K., L. M. Grimes, J. Subbiah, C. R. Calkins, A. Samal, and G. E. Meyer. 2008. Visible/near-infrared hyperspectral imaging for beef tenderness prediction. Computers and Electronics in Agriculture 64: 225-233.

Nielsen, M. K., M. D. MacNeil, J. C. M. Dekkers, D. H. Crews, Jr., T. A., Rathje, R. M. Enns, and R. L. Weaber. 2013. Review: Lifecycle, total-industry genetic improvement of feed efficiency in beef cattle: blueprint for the Beef Improvement Federation. Prof. Anim. Sci. 29:559-565.

Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews Jr., and S. S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measure of efficiency with growth and carcass merit of beef cattle. J. Anim. Sci. 85:2711–2720.

Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny difference: Use of within breed expected progeny difference to adjust breed evaluations for sire sampling and genetic trend. J. Anim. Sci. 69:4763-4766.

NRC 2000 Nutrient Requirements of Beef Cattle. National Academy Press.

Nunez-Dominguez, R., L. D. Van Vleck and L. V. Cundiff. 1993. Breed comparisons for growth traits adjusted for within breed genetic trend using expected progeny differences. J. Anim. Sci. 71:1419-1428.

Onteru, S. K., D. M Gorbach, J. M. Young, D. J. Garrick, J. C. M. Dekkers and M. F. Rothschild. 2013. Whole genome association studies of residual feed intake and related traits in the pig. PLoS ONE. 8 6: e61756.

Page, B. T., E. Casas, M. P. Heaton, N. G. Cullen, D. L. Hyndman, C. A. Morris, A. M. Crawford, T. L. Wheeler, M. Koohmaraie, J. W. Keele, and T. P. L. Smith. 2002. Evaluation of single nucleotide polymorphisms in CAPN1 for association with meat tenderness in cattle. J. Anim. Sci. 80:3077–3085.

Page, B. T., E. Casas, R. L. Quaas, R. M. Thallman, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, S. N. White, G. L. Bennett, J. W. Keele, M. E. Dikeman, and T. P. L. Smith. 2004. Association of markers in the bovine CAPN1 gene with meat tenderness in large crossbred populations that sample influential industry sires. J. Anim. Sci. 82:3474–3481.

Parnell, P. F., R. M. Herd, D. Perry and B. Bootle. 1994. The Trangie experiment—Response to growth rate, size, maternal ability, reproductive performance, carcass composition, feed requirements and herd profitability. Proc. Aust. Soc. Anim. Prod. 20:17-26.

Pasman, E., and F. Reinhardt. 1999. Genetic evaluation for length of productive life of Holstein cattle in Germany. Proc. Int. Workshop on EU Concerted Action Genetic Improvement of Functional Traits in Cattle GIFT; Longevity.

Pereira, A.S.C., F. Baldi, R. D. Sainz, B. L. Utembergue, H. L. J. Chiaia, and C. U. Magnabosco. 2015. Growth performance, and carcass and meat quality traits in progeny of Poll Nellore, Angus and Brahman sires under tropical conditions. Anim Prod Sci. 55:1295–02.

Perry T.C. and D. G. Fox. 1997. Predicting carcass composition and individual feed requirement in live cattle widely varying in body size. J. Anim. Sci. 75: 300-307.

Pitchford, W. S., Z. A. Kruk, E. M. Stephens, P. A. Speck and M. P. B. Deland. 2002. Are there meat quality differences between cattle breeds in southern Australia? Anim. Prod. Aust. 24:177-180.

Prieto, N., R. Roehe, P. Lavín, G. Batten, and S. Andrés. 2009. Application of near infrared reflectance spectroscopy to predict meat and meat products quality: A review. Meat Science. 83:175–186.

Pryce, J.E., S. Bolormaa, A. J. Chamberlain, P. J. Bowman, K. Savin, M. E. Goddard, and B. J. Hayes. 2010. A validated genome-wide association study in 2 dairy cattle breeds for milk production and fertility traits using variable length haplotypes. J. Dairy Sci. 93:3331–3345.

Quaas, R. L., and E. J. Pollak. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. J. Anim. Sci. 51:6.

Quaas, R. L. 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. Biometrics. 32:949-953.

Retallick, K. M., D. B. Faulkner, S. L. Rodrigues-Zas, J. D. Nkrumah, and D. W. Shike. 2013. The effect of breed and individual heterosis on the feed efficiency, performance, and carcass characteristics of feedlot steers. J. Anim. Sci. 91:5161-5166.

Retallick, K. J., J. M. Bormann, R. L. Weaber, M. D. MacNeil, H. L. Bradford, H. C. Freetly, K. E. Hales, D. W. Moser, W. M. Snelling, R. M. Thallman. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. J. Anim. Sci. 95:1444–1450.

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

Robinson D.L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livestock Production Science. 90:255–70.

Robinson, D. L., D. M. Ferguson, V. H. Oddy, D. Perry, and J. M. Thompson. 2001. Genetic and environmental influences on beef tenderness. Aust. J. Exp. Agric. 41:997–1004.

Robinson, D. L., V. H. Oddy and C. Smith. 1999. Preliminary genetic parameters for feed intake and efficiency on feedlot cattle. Proc. Assoc. Advancement Anim. Breed. Genet. 13:492-495.

Rolf, M. M. 2009. Implementation of high-density SNP data for genetic evaluation and QTL discovery in beef cattle. Master's Thesis. University of Missouri-Columbia.

Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H. C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. J. Anim. Sci. 89:3452-3459.

Roxstrom, A., V. Ducrocq, and E. Strandberg. 2003. Survival analysis of longevity in dairy cattle on a lactation basis. Genetics Selection Evolution. 35:305-318.

Saatchi, M., J. E. Beever, J. E. Decker, D. B. Faulkner, H. C. Freetly, S. L. Hansen, H. Yampara-Iquise, K. A. Johnson, S. D. Kachman, M. S. Kerley, J. Kim, D. D. Loy, E. Marques, H. L. Neibergs, E. J. Pollak, R. D. Schnabel, C. M. Seabury, D. W. Shike, W. M. Snelling, M. L. Spangler, R. L. Weaber, D. J. Garrick, J. F. Taylor. 2014. QTLs associated with dry matter intake, metabolic mid-test weight, growth and feed efficiency have little overlap across 4 beef cattle studies. BMC Genomics. 15:1004.

Santana, M. H. A., G. A. Oiveria, Jr., R. C. Gomes, S. L. Silva, P. R. Leme, T. R. Stella, E. C. Mattos, P. Rossi Jr, F. S. Baldi, J. P. Eler, J. B. S. Ferraz. Genetic parameter estimates for feed

efficiency and dry matter intake and their association with growth and carcass traits in Nellore cattle. 2014. Livestock Science. 167:80-85.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth and body composition traits of young beef bulls. Can. J. Anim. Sci. 84: 177-184.

Schneider, M. del P., and F. Miglior. 1999. A proposal for genetic evaluation for functional herd life in Italian Holsteins. Page 11 in Book of Abstracts of the 50th Meeting Eur. Assoc. Anim Prod., Zurich, Switzerland.

Sewalem, A., G. Kistemaker and B. Van Doormal. 2003. Genetic analysis of herd life in Canadian dairy cattle on a lactation basis using the Survival Kit. Interbull Bulletin 31, 73-76.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 2012. Technical note: validation of a model for online classification of US Select beef carcasses for longissimus tenderness using visible and near-infrared reflectance spectroscopy. J Anim. Sci. 90:973-977.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 2005. On-line classification of US select beef carcasses for longissimus tenderness using visible and near-infrared reflectance spectroscopy. J. Meat. Sci. 69:409-415.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1999a. Tenderness classification of beef. II: Design and analysis of a system to measure beef longissimus shear force under commercial processing conditions. J. Anim. Sci. 77:1474–1481.

Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1999b. Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. J. Anim. Sci. 77:2693-2699.

Shike, Daniel. 2012. Beef Cattle Feed Efficiency. http://www.beefusa.org/CMDocs/BeefUSA/Resources/cc2012-Beef-Feed-Efficiency--Dan-Shike.pdf.

Smith, T. P. L., E. Casas, C. E. Rexroad, III, S. M. Kappes, and J. W. Keele. 2000. Bovine CAPN1 maps to a region of BTA29 containing a quantitative trait locus for meat tenderness. J. Anim. Sci. 78:2589–2594.

Smith. S. P., and F. R. Allaire. 1986. Analysis of failure times measured on dairy cows: theoretical considerations in animal breeding. J. Dairy Sci. 69: 217.

Smith. S. P., and R. L. Quaas. 1984. Productive life span of bull progeny groups: failure time analysis. 1. Dairy Sci. 67:2999.

Smith, S. P. 1983. The extension of failure time analysis to problems of animal breeding. Ph.D. Diss., Cornell Univ., Ithaca. NY; Univ. Microfilms Int.. Ann Arbor. MI.

Snelling, W. M., M. F. Allan, J. W. Keele, L. A. Kuehn, R. M. Thallman, G. L. Bennett, C. L. Ferrell, T. G. Jenkins, H. C. Freetly, M. K. Nielsen, and K. M. Rolfe. 2011. Partial-genome evaluation of postweaning feed intake and efficiency of crossbred beef cattle. J. Anim. Sci. 89:1731-1741.

Snelling, W. M., B. L. Golden and R. M. Bourdon. 1995. Within-herd genetic analyses of stayability of beef females. J. Anim. Sci. 73:993-1001.

Solkner, J., and V. Ducrocq. 1999. The Survival Kit: a tool for analysis of survival data. Interbull Bulletin 21:11.

Splan, R. K., L. V. Cundiff, and L. D. Van Vleck. 1998. Genetic parameters for sex-specific traits in beef cattle. J. Anim. Sci. 76:2272–2278.

Stone, R. T., J. W. Keele, S. D. Shackelford, S. M. Kappes, and M. Koohmaraie. 1999. A primary screen of the bovine genome for quantitative trait loci affecting carcass and growth traits. J. Anim. Sci. 77:1379–1384.

Swiger, L. A. and L. N. Hazel. 1961. Optimum length of feeding period in selecting for gain in beef cattle. J. Anim. Sci. 20:189-194.

Swiger, L. A., R. M. Koch, K. E. Gregory, and V. H. Arthaud. 1961. Effect of length of feeding period on accuracy of selection for gain and feed consumption in beef cattle. J. Anim. Sci. 20:802-808.

Taylor, St. C. S., H. G. Turner, and G. B. Young. 1981. Genetic control of equilibrium maintenance efficiency in cattle. Anim. Prod. 33:179-194.

Tedeschi L.O., D. G. Fox, and P. J. Guiroy. 2004. A decision support system to improve individual cattle management. 1. A mechanistic, dynamic model for animal growth. Agricultural Systems. 79:171-204.

Toosi, A., R. L. Fernando and J. C. M. Dekkers. 2010. Genomic selection in admixed and crossbred populations. J. Anim. Sci. 88:32–46.

VanRaden, P. 2014. findhap.f90. http://aipl.arsusda.gov/software/findhap.

VanRaden, P. M., C. P. Van Tassell, G. Wiggans, T. S. Sonstegard, R. D. Schnabel, J. F. Taylor and F. Schenkel. 2009. Invited Review: Reliability of genomic predictions for North American Holstein bulls. J. Dairy Sci. 92:16-24.

Vollema, A. R., S. Van Der Beek, A. G. F. Harbers, and G. De Jong. 2000. Genetic evaluation for longevity of Dutch dairy bulls. J. Dairy Sci. 83:2629–2639.

Vollema, A. R., and A. F. Groen. 1998. A comparison of breeding value predictors for longevity using linear model and survival analysis. J. Dairy Sci. 81:3315–3320.

Vukasinovic, N., J. Moll, and L. Casanova. 2001. Implementation of a routing genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. J. Dairy Sci. 84:2073–2080.

Wang, Z., J. D. Nkrumah, C. Li, J. A. Basarab, L. A. Goonewardene, E. K. Okine, D. H. Crews, Jr., and S. S. Moore. 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the GrowSafe® system. J. Anim. Sci. 84:2289-2298.

Warwick, E.J. 1958. Fifty years of progress in breeding beef cattle. J. Anim. Sci. 17:922-943.
Wheeler, T. L., S. D. Shackelford, and M. Koohmaraie. 1997. Standardizing collection and interpretation of Warner-Bratzler shear force and sensory tenderness data. Proc. Recip. Meat Conf. 50:68-77.

Weaber, R. L., and J. L. Lusk. 2010. The economic value of improvements in beef tenderness by genetic marker selection. American J of Agricultural Economics. 92:1456-1471.

Westell, R. A., R. L. Quaas, and D. L. Van Vleck. 1988. Genetic Groups in an Animal Model. Faculty Papers and Publications in Animal Science. 309.
http://digitalcommons.unl.edu/animalscifacpub/309

Wheeler, T. L., S. D. Shackelford, and M. Koohmaraie. 1997. Standardizing collection and interpretation of Warner-Bratzler shear force and sensory tenderness data. Proc. Recip. Meat Conf. 50:68-77.

Wheeler, T.L., S. D. Shackelford, M. Koohmaraie. 1996. Sampling, cooking, and coring effects on Warner-Bratzler shear force values in beef. J. Anim. Sci. 74:1553-1562.

Wheeler, T.L., M. Koohmaraie, M., L. V. Cundiff and M. E. Dikeman. 1994. Effects of cooking and shearing methodology on variation in Warner-Bratzler shear force values in beef. J. Anim. Sci. 72:2325-2330.

White, S. N., E. Casas, T. L. Wheeler, S. D. Shackelford, M. Koohmaraie, D. G. Riley, C. C. Chase Jr., D. D. Johnson, J. W. Keele, and T. P. L. Smith. 2005. A new single nucleotide polymorphism in CAPN1 extends the current tenderness marker test to include cattle of Bos indicus, Bos taurus, and crossbred descent. J. Anim. Sci. 83:2001–2008.

Wiggans, G. R., T. A. Cooper, P. M. VanRaden and M. V. Silva. 2010. Increased reliability of genetic evaluation for dairy cattle in the United States from use of genomic information. Proc. 9th World Congr. Genet. Appl. Livest. Prod., Leipzig, Germany.

Willham, R. L. 1979. Evaluation and direction of beef sire evaluation programs. J. Anim. Sci. 49:592-599.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35:1288-1293.

Williams, C. B., and T. G. Jenkins. 2006. Impact of selection for feed efficiency on beef life cycle performance. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Minas Gerais, Brazil, 13-18 August, 2006.

Williams, C. B., G. L. Bennett, T. G. Jenkins, L. V. Cundiff, and C.L. Ferrell. 2005. Using simulation models to predict feed intake: Phenotypic and genetic relationships between observed and predicted values. J. Anim. Sci. 83Suppl. 1:13. Abstr.

Wright, S. 1922. Coefficients of inbreeding and relationship. American Naturalist. 330-338.

Yokoo, M. J., R. B. Lobo, F. R. C. Araujo, L. A. F. Bezerra, R. D. Sainz, and L. G. Albuquerque. 2010. Genetic associations between carcass traits measured by real-time ultrasound and scrotal circumference and growth traits in Nelore cattle. J. Anim. Sci. 88:52–8.