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## ESTIMATION OF BREED EFFECTS AND GENETIC PARAMETERS FOR AGE AT SLAUGHTER AND DAYS TO FINISH IN A MULTIBREED BEEF CATTLE POPULATION

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ESTIMATION OF BREED EFFECTS AND GENETIC PARAMETERS FOR AGE AT  
SLAUGHTER AND DAYS TO FINISH IN A MULTIBREED BEEF CATTLE  
POPULATION

by

Lindsay Rae Upperman

A DISSERTATION

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The Graduate College at the University of Nebraska  
In Partial Fulfillment of Requirements  
For the Degree of Doctor of Philosophy

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Under the Supervision of Professor Matthew L. Spangler

Lincoln, Nebraska

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Lindsay Rae Upperman, Ph.D.

University of Nebraska, 2021

Advisor: Matthew L. Spangler

Cattle efficiency during the finishing phase is a crucial factor in determining profit in the beef cattle industry. Economically relevant traits associated with efficient production include age at slaughter (AAS) and days to finish (DtF). Selection to reduce the number of days an animal takes to reach a finish endpoint would ultimately reduce production costs, increase net profits, and result in a more sustainable production system. However, most harvested animals are from commercial herds, necessitating the use of indicator traits from seedstock animals for selection. Potential indicator traits include ultrasound measurements that could be genetically correlated to DtF traits. The objectives of the current work were to i) estimate genetic parameters and breed effects for AAS and DtF and their relationships with routine carcass traits, and ii) estimate genetic correlations between AAS or DtF and ultrasound traits (ultrasound intramuscular fat percentage (UIMF), ultrasound rib fat (URF), and ultrasound ribeye area (UREA)). Performance records and pedigree information were obtained from U.S. Meat Animal Research Center (harvest data) and International Genetic Solutions (seedstock data). Univariate and bivariate animal models were fitted with ASREML (version 4.0) to estimate the genetic parameters. Days to finish and AAS are moderately to highly heritable and generally lowly correlated with routine carcass traits. The phenotypic variability in DtF was low. However, there was greater

variability in AAS, which was due to differences in date of birth of the animals and thus the ages at weaning. Genetic correlations between AAS or DtF with UIMF were negligible. Genetic correlations were negative and low between DtF and UREA and were positive and moderate between AAS and UREA. Genetic correlations were negative and moderate to high between AAS or DtF and URF. Reducing AAS or DtF in commercial cattle is possible through selection in seedstock for ultrasonically measured fat.

DEDICATION

I would like to dedicate this dissertation to my parents, Steve and Jane Upperman.

Thank you for always being there!

## ACKNOWLEDGEMENTS

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## **CHAPTER 1**

### **LITERATURE REVIEW**

#### **Introduction**

Days to finish is a complex trait that has taken on many different definitions. In order to understand the challenge of modeling days to finish, many different factors need to be understood and addressed. The first is how animal growth and development can be mathematically described. The various factors that affect growth and composition as well as how they can change due to selection is also crucial. Furthermore, lessons learned from studies that have investigated different efficiency traits in livestock species and the models that have been utilized to estimate genetic parameters for days to finish are also addressed.

#### **Cattle Industry – Market Values**

Within the United States, approximately 119,000 cattle are slaughtered every day, with approximately 520,000 slaughtered per week, producing over 195 million kg of beef (USDA Livestock, Poultry, & Grain Market News, 2019). Of the cattle slaughtered in 2019, the average live weight was 623 kg with dressing percentages around 63% for both steers and heifers, which resulted in dressed weights of 376 kg. Additionally, the national daily estimated cutout values in 2019 for choice and select grades were \$213.98 and \$207.26 per cwt, respectively, resulting in a choice-select spread of \$6.72 per cwt (USDA Livestock, Poultry, & Grain Market News, 2019). Furthermore, the national steer and heifer grading percent report estimated 10.07% of carcasses graded prime, 73.14% graded choice, 13.98% graded select, and 2.82% graded other in June of 2020 (USDA

Market News, 2020). The main drivers of carcass value are the weight of the carcass, the amount of boneless, closely trimmed retail cuts from the high-value parts of the carcass, including the chuck, rib, loin, and round (yield grade), and the evaluation of factors that affect the palatability of meat such as carcass maturity, firmness, texture, color of lean, and the amount and distribution of marbling within the lean (Hale et al., 2013). Carcasses are discounted from the base carcass price index value for being too heavy or light in weight, as well as for certain combinations of quality and yield grades. In June of 2020, carcass weight discounts ranged -\$30.71 to -\$4.34 per head with 272 to 408-kg carcasses being ideal with no discounts (USDA Market News, 2020). For quality and yield grade combinations, discounts ranged from -\$22.24 to -\$8.98 per head due to being too low in quality grade or too high in yield grade, with all other combinations receiving premiums that ranged from \$0.16 to \$12.80 per head (USDA Market News, 2020). Thus, many factors of an animal's carcass can greatly impact the overall profitability for producers.

### **Growth and Development Curves**

Growth and development are the first biological processes that lead to the changes that will affect an animal's final carcass price. Owens et al. (1993) stated most researchers would describe growth as the production of new cells. Yet, within the livestock industry, growth is typically utilized to define an increase in mass of an individual over a given amount of time (Owens et al., 1993; Speidel, 2011). Brody (1945) described development as the coordination of diverse processes that lead to an adult individual, while growth is the biologic synthesis, or production of new biochemical units (Speidel, 2011). In other words, growth is a part of development, including one or all of

three processes: 1) cell multiplication, 2) cell enlargement, and 3) incorporation of material taken from the environment (Brody, 1945). Focusing on the first two processes which result in an increase in animal mass, hyperplasia (increase in the number of cells) increases mass early in life, while hypertrophy (increase in the size of cells) occurs later in life. Yet, hyperplasia of adipose tissue continues throughout life (Owens et al., 1993). These processes can be further defined through a set of growth and aging equations.

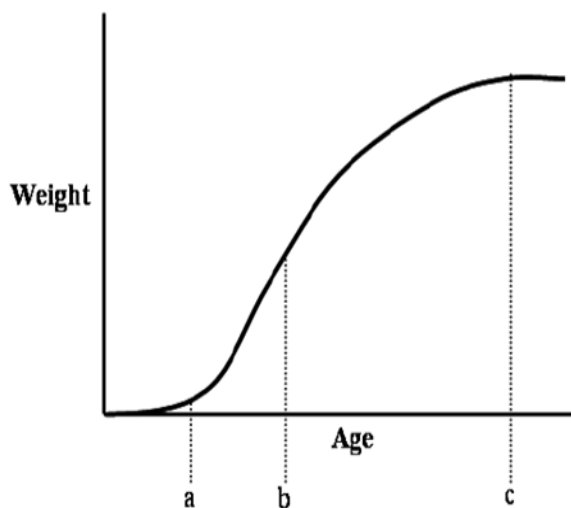
Samuel Brody was one of the first researchers to study the mathematical behavior of growth when he developed his growth and aging equations, which are still utilized today. Brody started by plotting weight versus age to describe the growth of individuals, which resulted in a sigmoidal or s-shaped curve (Brody, 1945). Although the values of parameters for the functions can differ, for instance the starting point, when standardized the shape remains consistent between breeds of the same species or even between species. For example, from weaning to puberty, humans have a longer time interval (approximately 3 to 13 years), but within livestock or laboratory animals this period is shorter or nonexistent. Ultimately, the differences across and within species could be due to differences created when weaning age is determined by production or marketing norms rather than by physiological status. However, when comparisons are made between the growth curves of individuals, especially within a given breed or population, individual curves tend to be very similar in shape to another individual (Brody, 1945).

A growth curve can be segmented into two parts. The first part represents the time before puberty in which an animal increases mass at an increasing rate, also known as the self-accelerating phase (Owens et al., 1993; Speidel, 2011). The second part represents

the time after puberty in which an animal increases mass at a decreasing rate, known as the self-inhibiting phase. Figure 1.1, adapted from Owens et al. (1993) and Speidel (2011), demonstrates the important parts of the growth curve. As shown,

the plotting of weight versus age resulted in the common s-shaped or

sigmoidal curve. The points represent: a) birth, b) the inflection point associated with puberty, and c) maturity. The self-accelerating phase is the portion between points a and b, or from birth to puberty. The inflection point (b) represents the point at which the increase in growth rate ceases but has not yet begun to decrease. It represents when an animal's gain is most rapid and economical, assuming the cost of inputs are less than the value of gain (Brody, 1945). Furthermore, within livestock and laboratory animals, this inflection point generally occurs when the animal has reached 30% of their mature weight, or approximately 6 months of age in cattle. The self-inhibiting phase is the portion between points b and c, or from puberty to maturity (Brody, 1945). During this phase, the animal's body mass is still increasing, but at a decreasing rate. Yet, the reasons



**Figure 1.1.** Generalized growth curve. Adapted from Owens et al. (1993) and Speidel (2011).

for post puberty deceleration are not well understood. From studies on isolated muscle and bone cultures, growth inhibition can be due to; limitation of resources, accumulation of products, or inhibitory factors that restrict cell division (Owens et al., 1993). Lastly, point c on the figure represents the animal's mature weight or stage in life in which additional food resources are not converted into muscle formation, but into fat (both intramuscular and intermuscular) deposition (Owens et al., 1993; Speidel, 2011).

### **Mathematical Representations of Growth Curve**

The growth curve shown above in Figure 1.1 has been depicted through mathematical equations by various researchers. Of these mathematical representations of the growth curve, five non-linear equations have been used to describe growth patterns in beef cattle—Brody, Richards, Von Bertalanffy, Gompertz, and Logistic—with as many as 4 parameters needed to define their shapes (Arango and Van Vleck, 2002). These equations will be presented, as well as, the pros and cons of these equations, based on summarizations by Brown et al. (1976).

The first equation to predict body weight over time was developed by Brody (1945), which is applicable to many species from laboratory to livestock animals. The equation is represented below:

$$W = A(1 - Be^{-kt})$$

where (W) body weight at age (t) is a function of mature weight (A), a time scale parameter (B), and the rate at which a logarithmic function of weight changes per unit of time parameter (k). Within beef cattle studies, the Brody equation has been used

frequently due to it being easily computed, interpreted, and allowing for missing data points (Arango and Van Vleck, 2002).

Several modifications to the Brody model have been made within the literature. Another model that has been frequently utilized is the Richards' function (Richards, 1959). The function is as follows:

$$W = A(1 - Be^{-kt})^M$$

the function is very similar to the Brody equation in which the parameters are described above. However, the Richards' equation has the additional parameter of M. This is a shape parameter, which helps to model the variable inflection point that denotes when the age of puberty occurs. The Richards' function has been reported to fit data better than the Brody equation (DeNise and Brinks, 1985; López de Torre et al., 1992; Arango and Van Vleck, 2002).

The next equation is the Von Bertalanffy equation, which has a slight variation from the Brody function (Brown et al., 1976). The modifications are as follows:

$$W = A(1 - Be^{-kt})^3$$

where the parameters are as described earlier for the Brody function and the form is a Richards' function with M=3. Another note is that this equation has fixed points of inflection relative to mature size (Brown et al., 1976).

Another equation which is based on the Brody model is the Logistic equation. The Logistic equation is represented as:

$$W = A(1 + e^{-kt})^{-M}$$

where the parameters are the same as within the Brody model, except for the removal of B, a time scale parameter, and the inclusion of parameter M from the Richards' equation, which is a shape parameter. This generalized Logistic form permits a variable point of inflection (Nelder, 1962; Brown et al., 1976).

Finally, the last of the highly utilized growth models is the Gompertz model which is described below (Winsor, 1932):

$$W = Ae^{-Be^{-kt}}$$

where (W) is the body weight at age (t) is a function of mature weight (A), a time scale parameter (B), and the rate at which a logarithmic function of weight changes per unit of time parameter (k) as represented in the Brody model. As with the Von Bertalanffy function, this model also has a fixed inflection point, although with respect to mature size (Brown et. al, 1976). The Gompertz model has been reported to show less bias for estimation of 'A' (López de Torre et al., 1992; Arango and Van Vleck, 2002).

**Model Comparisons.** In numerous studies, the advantages and disadvantages of these growth models have been compared, specifically when utilizing beef cattle growth data (Brown et al., 1976; DeNise and Brinks, 1985; López de Torre et al., 1992; Arango and Van Vleck, 2002). When comparing these models, each one gives an estimate of mature weight (A) and rate of maturity (k). Given the k parameter, larger k values indicate early maturing individuals, while a smaller k value indicates late maturing individuals. In regard to inflection point, the point where the growth rate changes from an increasing rate of increase to a decreasing rate of increase, the Brody model is the only model that does not include a point of inflection. However, both the Von Bertalanffy and the Gompertz



functions have a fixed inflection point. Furthermore, the Richards and Logistic equations both permit a variable point of inflection, which is a function of  $M$ , the shape parameter (Richards, 1959; Brown et al., 1976).

Brown et al. (1976) discussed the goodness of fit of these models. First and foremost, one of the issues with each function is that there are dependencies among the parameter values. None of the models described earlier periods of growth as sufficiently as later periods of growth. The Gompertz and Logistic equations overestimated the earlier age weights to a larger degree than the other three models. Furthermore, an important consideration of choosing the appropriate model is how the fit of the curves vary over different time periods. The Gompertz model consistently overestimated weights earlier in age of the animal post-weaning. The Brody model tended to fit data well after 6 months of age; however, prior to 6 months the model either over or underestimated weights for about 50% of the animals, partially due to a non-sigmoidal pattern. The Von Bertalanffy also overestimated weights prior to 6 months of age but fit the data reasonably well for all other ages. Similarly, the Logistic equation overestimated earlier age weights, but underestimated mature weights. Finally, the Richards model, in some circumstances, has been shown to provide a generally unbiased fit at all ages (Brown et al., 1976).

Another study by DeNise and Brinks (1985) focused on the comparison of the Brody and Richards models applied to beef cattle growth data. Although both curves fit the age-weight data and estimated similar mature weights ( $A$ ), the fit of the Brody model depended on the data available. When individuals were missing birth or mature weight observations, the Brody model fit the data poorly when expected to project beyond this

range of information. The Richards model appeared to be less reliant on the range of data provided. Nevertheless, although the Brody model is utilized quite frequently based on the ease of computation and interpretation, with algorithms fitting a four-parameter model just as easily as a three-parameter function, the Richards model may be the best choice (DeNise and Brinks, 1985). López de Torre et al. (1992) also found that the Richards equation better estimated individual growth curves when compared to the Brody model. A summarization of the advantages and disadvantages of the five growth curve models are shown below (Table 1.1).

**Table 1.1.** Advantages and disadvantages of growth curve models<sup>1</sup>.

Model	Advantages	Disadvantages
Brody	Fits observed data Simple Computation	Dependent on input data Over- or underestimated mature weights
Richards	Unbiased fit for all ages Flexible due to additional parameters	Requires higher density of weight records
Von Bertalanffy	Fit data well for all other ages	Overestimated weights prior to 6 months of age
Gompertz	Less bias for mature weight (A) estimation	Overestimated early weights
Logistic	Flexible due to additional parameters	Overestimated early weights Underestimated mature weights

<sup>1</sup>Adapted from Speidel (2011).

Although these growth curve models can estimate the weight of an animal at any given age, to improve the beef cattle population the parameters of the growth curve or their relative relationships may need to be changed over time. Some of the reasons for altering the shape of the growth curve were outlined by Fitzhugh Jr. (1976). The first reason mentioned to change the shape of the growth curve was to produce efficient

growth of progeny sent to slaughter, while maintaining smaller and lower maintenance parents. The second and third reasons were to improve efficiency through increased maturation rate or to reduce dystocia by decreasing birth weight of progeny relative to dam size. The final reason to change the shape of the growth curve was to decrease age at puberty to increase fertility or decrease carcass fat at a preferred market weight. One way to alter the shape of the growth curve for the reasons defined above is through selection (Fitzhugh Jr., 1976). However, selection decisions towards altering growth also need to consider the costs or benefits associated with changes to body composition.

### **Cattle Growth and Composition Factors**

The growth curve mainly focused on the change in weight over the life cycle of an animal. Yet, when considering ever-increasing feed costs, the focus of beef cattle production is to balance growth rate and feed intake, thus maximizing the animal's efficiency within the feedlot. However, there are many other biological factors that can impact weight gain as well as the optimum harvest endpoint of an individual. These biological factors include breed, sex, management, and the genetic value of the animal (additive and non-additive). The following sections will discuss how these factors can influence weight or composition of individual animals.

#### **Breed**

Rapid growth rate, due to its economic importance, has been greatly desired to lessen the number of days an animal spends in the feedlot. Berg and Butterfield (1976) stated that the shape of growth curves for different cattle breeds differ, ultimately affecting how quickly an animal grows. These differences in the observed growth rates

during the growing period, including the finishing period, result in animals who differ in size (Berg and Butterfield, 1976). For instance, if an animal spends more time in the self-accelerating phase (Figure 1.1), more weight gain occurs in proportion to the animal's overall body weight than when compared to animals that spend more time in the self-inhibiting phase (Brody, 1945). Thus, animals that spend more time within the self-accelerating phase will appear to have a faster growth rate, which could favor a given breed of cattle.

Growth rate over a given time is often summarized using average daily gain (ADG), or the average daily change in body weight, over that period. One of the studies that evaluated ADG of different breed types was Smith et al. (1976). The steers within this study were produced from Hereford and Angus based dams bred to seven sire breeds. The animals were evaluated after 180 days on feed after weaning and a subsequent backgrounding period. The largest and fastest gaining animals during the pre-weaning stage (200 days) were the Charolais and Simmental sired steers, followed by South Devon, Hereford, Angus, and Limousin-sired steers, while the Jersey-sired steers were the slowest gaining. This breed ranking was the same for 405-day weight as well, meaning Simmental and Charolais sired steers were the heaviest animals, and those animals had a 20% increase in ADG compared to the Jersey-sired steers (Smith et al., 1976). Thus, steers with Continental sires had higher ADG than those steers sired by British or dairy breeds. Another study by Chewning et al. (1990) investigated the ADG of bulls from purebred herds for feedlot performance post-weaning. The bulls with the highest ADG from the first bull test were Charolais based, with Angus bulls being the

slowest gaining. For the second bull test, Charolais, Maine Anjou, and Simmental breeds were the highest, with Brangus and Beefmaster bulls having the lowest ADG (Chewning et al., 1990). Again, the bulls from Continental breeds had higher ADG than those from British or Indicus breeds. Smith and Rahnefeld (1988) had similar findings in which animals with a higher percentage of Continental-based breeds in their pedigree had higher ADG than those animals with more British-based breeds when fed to a constant number of days. Urick et al. (1991) found that ADG to 382 days of age was highest for Simmental-sired steers when compared to Red Poll-, Angus-, and Pinzgauer-sired steers, which were not different in gain. Furthermore, Tarentaise-sired steers were intermediate in ADG, but were not different when compared to all other breeds (Urick et al., 1991). These results showed that some Continental breeds do not always gain more than British breeds, as Tarentaise-sired steers were not significantly different from both the British and Continental-sired steers. Given the breed comparison studies mentioned previously summarized results from the 1970-1990s, caution should be used when making inferences to breed differences among current germplasm given these breeds have been under various degrees of selection for growth and composition traits since the time these studies were conducted.

Other studies regarding differences in ADG between breeds came to different conclusions compared to those discussed above. Wyatt et al. (2002) found that feedlot ADG did not differ among sire or dam breeds. However, this was mostly due to harvesting steers individually at a constant end point of 10mm backfat. However, Block et al. (2001) found that Hereford- and Angus-crossed steers had higher ADG than

Charolais-crossed steers. In another study, medium-framed Hereford steers gained similarly to larger-framed Charolais steers when fed a low-energy diet (McKinnon et al., 1993). In addition to analyzing differences in ADG between cattle breeds, these studies included other factors such as feeding animals to a constant endpoint, as well as variations in diet energy level. These factors may have led to alternate conclusions regarding breed differences for ADG. Yet, the most important factor that could have impacted the change in breed rank for ADG would be genetic trends in the U.S. beef cattle industry over time which will be discussed in subsequent sections.

Evaluating animals that gain more efficiently compared to their contemporaries should also include how much feed intake an animal consumes to meet a particular amount of gain. In regard to feed efficiency, most studies chose a given endpoint to harvest the animals. For the studies with a constant age endpoint, the Continental breeds are more efficient than the British breeds in converting feed into weight gain (Smith et al., 1976; Chewning et al., 1990; Urick et al., 1991). However, when fed to a constant fat endpoint, British breeds were found to be more efficient due to their smaller size, enabling them to reach mature size faster, and begin converting feed into fat quicker than their Continental contemporaries (Smith et al., 1976; Block et al., 2001). For instance, Smith et al. (1976) found that Hereford-, Angus-, Jersey-, and South Devon-sired steers took at least 50 days less to reach 5% fat in the *longissimus* muscle than Limousin-, Charolais-, and Simmental-sired steers. Chewning et al. (1990) also found that in regard to feed:gain Angus bulls had the highest conversion when compared to Simmental, Charolais, and Maine Anjou bulls. This means it took Angus bulls more feed to increase

one unit of gain compared to the Continental breeds. Nonetheless, when making marketing decisions for a group of cattle to reach a specific endpoint, consideration of the breed type and the number of days allotted to reach this endpoint are crucial. Ultimately, British breeds of cattle will need fewer days on feed to reach a given fat endpoint (Block et al., 2001; Wyatt et al., 2002), while Continental breeds of cattle will need less days on feed to reach a given weight endpoint (Smith et al., 1976; Smith and Rahnefeld, 1988; Chewning et al., 1990; Urick et al., 1991).

**Table 1.2. Sire breeds used in the Germplasm Evaluation Program<sup>1</sup>**

Cycle I 70-72	Cycle II 73-74	Cycle III 75-76	Cycle IV 86-90	Cycle V 92-94	Cycle VI 97-98
<b>F1 crosses (Hereford or Angus dams)<sup>2</sup></b>					
Hereford	Hereford	Hereford	Hereford	Hereford	Hereford
Angus	Angus	Angus	Angus	Angus	Angus
Jersey	Red Poll	Brahman	Longhorn	Tuli	Wagyu
S. Devon	Braunvieh	Sahiwal	Salers	Boran	N Red <sup>3</sup>
Limousin	Gelbvieh	Pinzgauer	Galloway	Belgian Blue	S R&W <sup>3</sup>
Simmental	Maine Anjou	Tarentaise	Nellore	Brahman	Friesian
Charolais	Chianina		Shorthorn	Piedmontese	
			Piedmontese		
			Charolais		
			Gelbvieh		
<b>3-way crosses (F1 dams)</b>					
Hereford	Hereford				
Angus	Angus				
Brahman	Brangus				
Devon	Santa Gert.				
Holstein					

<sup>1</sup>Adapted from Cundiff et al. (2001).

<sup>2</sup>In Cycle V and VI, composite MARC III (¼ Angus, ¼ Hereford, ¼ Pinzgauer, and ¼ Red Poll) cows were also included.

<sup>3</sup>N Red = Norwegian Red and S R&W = Swedish Red & White

**Germplasm Evaluation.** In order to reasonably compare breeds and estimate heterotic effects, a designed experiment is required. Given that breeds change overtime due to selection, such an experiment must be long-term in order to provide current estimates of

breed differences to inform breed selection and breeding system designs. The Germplasm Evaluation (GPE) program at the Roman L. Hruska U.S. Meat Animal Research Center was established to investigate heterosis and breed differences for various composite populations. The GPE was originally conducted over a series of cycles to evaluate performance traits of crossbred cattle through a variety of studies. Table 1.2 shows the mating plans for Cycles I through VI. The base cows for this mating plan including Angus (453) and Hereford (217) cows that calved at 4 years of age or older. Starting in 1992, 714 Composite MARC III ( $\frac{1}{4}$  Angus,  $\frac{1}{4}$  Hereford,  $\frac{1}{4}$  Pinzgauer, and  $\frac{1}{4}$  Red Poll) cows were included into the plan that calved at 4 years of age or older. These cows were mated by artificial insemination (AI) for 21 days of the breeding season to produce progeny of the sire breeds listed in Table 1.2 each year (Cundiff et al., 2001).

**Breed Differences.** Large differences among breeds have been found for most bioeconomic traits (Trail and Gregory, 1982; Cundiff et al., 1986). Marshall (1994) found substantial variation for sire breeds for the traits of carcass weight, fat depth, marbling score, ribeye area, and retail product. Charolais, Salers, Hereford Angus cross, Shorthorn, and Maine Anjou were ranked as the largest breeds for carcass weight, with Longhorn and Jersey breeds being the smallest (Marshall, 1994). Gregory et al. (1994) found that Simmental, Charolais, Gelbvieh, and Braunvieh were the heaviest, while Hereford was the lightest along with Red Poll and Angus. For fat depth, Angus, Hereford/Angus cross, Beefmaster, Hereford, and Santa Gertrudis had the most, while Piedmontese, Chianina, Charolais, and Longhorn had the least (Marshall, 1994). Angus had the largest adjusted fat depth followed by Hereford and Red Poll, with Simmental, Charolais, and Gelbvieh



having the least (Gregory et al., 1994). For marbling, Jersey, Red Angus, Angus, Shorthorn, and South Devon ranked the highest, while Chianina, Charolais, Brahman, Limousin, and Sahiwal ranked the lowest (Marshall, 1994). Again, Angus, Red Poll, Hereford and Pinzgauer had the highest marbling scores, while Limousin and Gelbvieh had the lowest (Gregory et al., 1994). The Piedmontese breed easily had the largest ribeye area, followed by Chianina, Charolais, Maine Anjou, and Limousin breeds (Marshall, 1994). Limousin and Braunvieh had the largest ribeye areas while Red Poll, Angus, and Hereford breeds had the smallest ribeye areas (Gregory et al., 1994). Finally, for the most retail product the ranking consisted of Charolais, Piedmontese, Chianina, Holstein, Salers, and Maine Anjou (Marshall, 1994). Breed rankings vary across traits, but for the fat-based traits of marbling or fat thickness British breeds tended to rank higher, while for lean muscle-based traits Continental breeds tended to rank higher than British breeds. However, as stated before, breed differences estimated from the 1990s may greatly differ from present day breed differences given that within-breed selection has occurred.

Albertí et al. (2008) evaluated differences in growth and carcass traits in bulls of European beef breeds. The mean slaughter age of the animals within this study was  $450.6 \pm 39.0$  days; however, Angus, South Devon, Jersey, and Limousin breeds were younger with ages ranging from 398-429 days. The Highland cattle breed was older at approximately 511 days. The heaviest breed at slaughter was Charolais at 634 kg, with Jersey being the lightest. Holstein, Angus, Danish Red, Simmental, Limousin, Highland, Casina, and Pirenaica were intermediate in slaughter weights. Carcass weight differences

showed a greater amount of variation between breeds. Carcass weights ranged from Jersey with 189.7 kg to 386.6 kg for Charolais cattle. The intermediate breeds for carcass weight followed the Charolais breed by Pirenaica, Limousin, Asturiana de los Valles, South Devon, Simmental, Piedmontese, Angus, Holstein, Highland, and Casina. For loin muscle depth the highest-ranking were found with Piedmontese and Asturiana de los Valles with more than 52 cm<sup>2</sup>, then South Devon, Pirenaica, Limousin, Charolais, Simmental, Angus, Holstein, Highland, and lowest for Jersey at 24.9 cm<sup>2</sup>. For fatness score (1-15), the highest-ranking score breeds were Angus, Danish Red, Charolais, Limousin, Holstein, Simmental, Highland, South Devon, Casina, Pirenaica, and Jersey. Piedmontese was the lowest. For fat % from the 6<sup>th</sup> rib dissection, breed rankings were Angus, Highland, Danish Red, Holstein, Charolais, Casina, South Devon, Limousin, Jersey, Simmental, Pirenaica, Asturiana de los Valles, with Piedmontese ranking the lowest (Albertí et al., 2008). These estimates had similar conclusions to the other studies discussed above as dairy and “local” breeds in this study (Jersey, Casina, Highland, Holstein, Danish Red, and Angus) had higher levels of fat, while Piedmontese, Asturiana de los Valles, Charolais, Limousin, and Simmental breeds had larger carcass weights or higher muscle percentages.

**Breed Changes.** Genetic trends of the U.S. beef cattle breeds have been analyzed over time. As breeds put selection emphasis on specific traits towards a more common marketing scheme, differences between breeds may not be as large from year to year (Kuehn and Thallman, 2016). Therefore, in studies that include breed differences, the point of time being referenced is crucial. In general, Van Vleck and Cundiff (2004)

concluded that many breeds were continuing to become more similar to the Angus breed. In 2004, most sire breed weaning weight means were within 4.5 kg of the Angus mean. For yearling weight, Angus-sired calves had heavier yearling weights than 11 breeds, with only two breeds being heavier (Simmental and Charolais breeds; Van Vleck and Cundiff, 2004). In 2016, these results have stayed relatively consistent as the Angus breed had the greatest rate of genetic change for yearling weight with a +1.36 kg increase from 2014 (Kuehn and Thallman, 2016). In regard to carcass traits, breed of sire differences were not included in the study of Van Vleck and Cundiff (2004). In 2016, changes from 2014 breed of sire differences were small for marbling, ribeye area, fat thickness and carcass weight. However, in Limousin, the sire means for marbling increased (+0.06) compared to the average of the other breeds in the GPE program. More importantly, due to improved accuracy of sire carcass EPDs, with the greatest percentage of data being added to performance records on carcass traits, in the GPE program, the breed of sire differences are most likely to change in the future for these traits (Kuehn and Thallman, 2016). Thus, although breed differences are specific to a given time point for both carcass and growth traits, there seems to be greater genetic trends for growth traits in the given studies.

**Crossbreeding.** In addition to selection, crossbreeding is another method of creating genetic improvement within livestock systems (Cundiff, 1970). Crossbreeding allows for the utilization of heterosis and combining desired characteristics in commercial cattle that may not be present in purebred parents (Cundiff, 1970). The benefits of crossbreeding cattle have been well documented, showing improvements in fertility, maternal ability,

and growth rate through heterosis (Cundiff, 1970; Fitzhugh et al., 1975; Gray et al., 1978). Cundiff (1970) found that within crossbreds, especially crossbred cows, pregnancy rates could be increased by 20-25% within British breeds. Furthermore, crossbreeding between Zebu and British breeds resulted in higher degrees of heterosis than between Continental and British breeds (Cundiff, 1970; Williams et al., 2013), as well as for Zebu and Continental crossed breeds. Furthermore, individual heterosis was found to be larger for British-by-British crossbreds than British-by-Continental crossbreds (Williams et al., 2013). This could be due to present British breeds being closer to Continental breeds from gains made through selection, or that current Continental breeds are the result of grading up from British breeds (Williams et al., 2013). In regard to carcass traits, British by Zebu crosses had the heaviest carcass weights, largest ribeye areas and most fat thickness (Williams et al., 2013), with British-by-British crosses having the lightest carcass weights and smallest ribeye areas, and British-by-Continental crosses having the least fat thickness. For marbling score, Continental-by-Zebu had the highest marbling scores, while Continental-by-Continental crosses had the lowest (Williams et al., 2013). Nonetheless, commercial producers who would like to take advantage of the benefits of crossbreeding are met with a challenge when comparing bulls across breeds to be utilized in the next breeding season, as not all current genetic evaluations compare bulls from different breeds (Williams et al., 2013). This is another benefit of the GPE program as it enables the calculation of across-breed EPD adjustment factors for producers wanting to compare breeds for sire selection.

## **Sex**

Other than breed type, sex can also greatly impact the growth and composition of an animal's carcass. In all species, intact males tend to have more lean mass, which is attributed to the hormone testosterone within the body (Bredella, 2017). On the other hand, females tend to have more body fat than males due to the absence of testosterone (Bredella, 2017). Tanner et al. (1970) reported that bulls, steers, and heifers had ADG of 1.33, 1.16, and 0.94 kg, respectively. Carcass cutability was 2.3 to 2.7% higher for bulls than steers and heifers which were not significantly different (Tanner et al., 1970; Mandell et al., 1997). Furthermore, bulls have increased rate of gain, feed efficiency, and yield of retail cuts when compared to steers and heifers (Hedrick, 1968; Hedrick et al., 1969; Mandell et al., 1997; Bureš and Bartoň, 2012). However, steers and heifers are advantageous in marbling scores and carcass quality (Hedrick et al., 1969). Overall, bulls tend to gain faster, have larger carcass weights, and convert feed into more lean muscle mass. Steers fall in the middle of the sexes for gain, while still having increased marbling scores when compared to bulls. Finally, heifers gain the slowest of the sexes, but will have increased backfat and marbling scores when compared to bulls.

## **Management**

Decisions made by cattle producers or feedlot owners on the management of their cattle can greatly influence growth or carcass composition of an animal. There are several management decisions that can alter the growth curve of an animal. For instance, hormone implants and nutrition changes are the two biggest factors that could modify the chosen endpoint to market a given animal.

Hormone implants can fall into two basic categories, estrogenic or androgenic compounds. Estrogenic compounds imitate the naturally occurring hormone estrogen, which are found in compounds estradiol benzoate, estradiol 17-beta, and zeranol (Reuter et al., 2005). Androgenic compounds imitate the naturally occurring hormone testosterone and is found in testosterone propionate or trenbolone acetate (TBA) implants. Another compound utilized in implants is synthetic progesterone, yet its effect on animals is less effective than the other two types of compounds. The implants are typically made of a powder that is compacted into a pellet form. This pellet is then placed under the skin on the back of an animal's ear. The implant is designed to slowly release the compound into the animal's bloodstream over time (Reuter et al., 2005). The main reason to utilize a hormonal implant in cattle production is to improve growth rates by 10-30%, and feed efficiency by 5-15% (Galbraith, 1982; Duckett et al., 1996; Preston, 1999; Montgomery et al., 2001; Nichols et al., 2002; Ribeiro et al., 2020). Furthermore, carcass traits such as ribeye area and hot carcass weight were improved with the addition of an implant (Duckett et al., 1996; Preston, 1999; Roeber et al., 2000). However, in regard to carcass quality, marbling scores and tenderness decreased with the addition of hormone implants (Roeber et al., 2000; Hunter et al., 2001; Boles et al., 2009). Importantly, the amount of time and how aggressive the implant treatment protocol utilized is can affect the resulting marbling scores, as less time or lower dose implants can result in little to no difference in performance (Apple et al., 1991; Hunter et al., 2001; Montgomery et al., 2001). Overall, hormonal implants tend to increase lean muscle gain and depending on the treatment can reduce fat deposition.

Feedlot ration composition can be categorized by concentrate level, crude protein concentration, and fat supplementation, including the differences in source of crude protein (Owens and Gardner, 2000). As concentrate level increased within the diet, dressing percentage, ribeye area, and marbling score increased at a decreasing rate (McKinnon et al., 1993; Owens and Gardner, 2000; Block et al., 2001). Higher crude protein levels provided larger dressing percentages and marbling scores (Owens and Gardner, 2000; Pethick et al., 2004). Fat supplement additions can increase dressing percentages, marbling score, and ribeye area (Owens and Gardner, 2000; Pethick et al., 2004). In regard to the different use of protein sources, soybean meal has been found to increase ribeye area, (Loerch and Berger, 1981); however, no significant differences were detected when averaged across multiple studies for soybean meal, specifically (Owens and Gardner, 2000). The additions of various supplements or amounts of grain tend to increase energy levels within the diet, which increase the amount of muscle or fat gained by the animal. However, due to the effects of other factors such as breed or sex, generalizing these results is challenging.

### **Genetics**

**Additive.** Multiple studies have concluded that most genetic variation is due to additive variance when using traditional pedigree information for various livestock species (Falconer and Mackay, 1996; Lynch and Walsh, 1988; Hill et al., 2008). Furthermore, no difference was found in the accuracy of prediction across traits when models including only additive effects were compared to models that included additive and dominance effects (Bolormaa et al., 2015). In many studies, the heritabilities of growth and carcass

traits have been estimated. Koots et al. (1994) reported average heritabilities for post-weaning gain, market weight, and backfat thickness as 0.31, 0.41, and 0.44, respectively. Gregory et al. (1995) estimated heritabilities for purebred and composite cattle for various growth and carcass traits, which included fitting breed groups as fixed effects. For purebred cattle, reported estimates were 0.33, 0.26, 0.20, 0.20, 0.45, and 0.17 for post-weaning ADG, slaughter weight, carcass weight, adjusted 12<sup>th</sup> rib fat, marbling score, and ribeye area, respectively. For composite cattle, the authors reported estimates of 0.48, 0.37, 0.34, 0.39, 0.55, 0.35 for post-weaning ADG, slaughter weight, carcass weight, adjusted 12<sup>th</sup> rib fat, marbling score, and ribeye area, respectively. Overall, there was no consistent tendency for heritability estimates to be higher for composites than the purebred animals, even though higher heritability estimates would be expected without accounting for heterosis as a fixed effect in the model (Gregory et al., 1995). Koch et al. (1982) reported heritability estimates of 0.57, 0.58, 0.41, 0.56, 0.40 for feedlot gain, retail product, fat thickness, ribeye area, marbling score, respectively.

**Non-additive.** Although most estimates of dominance and epistatic variances have been reported as negligible, several studies have found small, but significant non-additive variance estimates (Bolormaa et al., 2015). Starting with pedigree-based studies, Montaldo and Kinghorn (2003) utilized a multiple-trait animal model that included fixed effects of direct breed, maternal additive genetic, and direct dominance effects. Direct dominance effects were positive for weights including birth, 200-day, and 600-day weight, except for 400-day weight. However, the author's cautioned drawing conclusions on additive and dominance effects, and values of (co)variances among breeds, especially



from populations with non-designed crosses (Rodríguez-Almeida et al., 1997; Montaldo and Kinghorn, 2003). Abdel-Aziz et al. (2003) analyzed growth traits with a univariate animal model that included fixed effects of sex, contemporary group, individual heterosis, maternal heterosis, breed, and age of dam. They found individual and maternal heterosis estimates for ADG were significant ( $P < 0.01$ ). Similarly, Dillard et al. (1980) studied growth traits with a univariate animal model including contemporary group, age of dam, direct and maternal breed, and direct and maternal heterosis fixed effects. They reported that maternal heterosis was significant ( $P < 0.01$ ) for ADG; however, the effects were not large (0.02 kg). Furthermore, these effects only accounted for 1% of the phenotypic variation (Dillard et al., 1980). For genome-wide association studies on growth and carcass traits, Bolormaa et al. (2015) utilized the model below:

$$y = \mathbf{1}_n\mu + \mathbf{Xb} + \text{het}\beta + \mathbf{g} + \mathbf{d} + \mathbf{e},$$

in which  $\mathbf{y}$  is the vector of phenotypic values,  $\mathbf{1}_n$  a vector of 1's,  $\mu$  is the overall mean,  $\mathbf{X}$  is a design matrix relating observations to fixed effects of contemporary group, sex, and breed,  $\mathbf{b}$  is a vector of fixed effects,  $\text{het}$  is a vector containing the average heterozygosity over all single nucleotide polymorphisms (SNP) for each animal,  $\beta$  is the regression of each trait on heterozygosity,  $\mathbf{g}$  is a vector of genomic breeding values distributed as  $N \sim (0, \mathbf{G}\sigma_g^2)$ , where  $\sigma_g^2$  is additive genetic variance explained by SNPs and  $\mathbf{G}$  is the genomic relationship matrix,  $\mathbf{d}$  is a vector of dominance deviations distributed as  $N \sim (0, \mathbf{D}\sigma_d^2)$ , where  $\sigma_d^2$  is dominance variance explained by the SNP and  $\mathbf{D}$  is the dominance relationship matrix, and  $\mathbf{e}$  is the vector of random residual effects. A significant dominance variance ( $P < 0.05$ ) was detected for intramuscular fat (%), carcass

retail beef yield (%), live weight at post-weaning, and live weight at feedlot exit, although the estimates had large standard errors and the variance explained by SNPs varied widely between traits. Furthermore, no difference in accuracy of predictions across nine traits was found when comparing a model with only additive effects fitted and a model with both additive and dominance effects fitted (Bolormaa et al., 2015). For epistatic effects, post-weaning weight had 153 significant interactions ( $P < 10^{-5}$ ) between the lead SNP (BTA14\_25), which explained the most additive variation, and other SNPs. The highest number of epistatic interactions between the lead SNP and other SNPs was found with post-weaning weight, feedlot weight, intramuscular fat, rib fat, and residual feed intake (Bolormaa et al., 2015). Although significant non-additive effects were found in multiple studies, further evaluation is needed to determine the importance of non-additive effects for growth traits, as well as the importance of including non-additive genetic effects in genetic evaluations.

### **Genetic Evaluations for Efficiency**

Reducing the number of days for an animal to reach a desired endpoint is not a new idea. Lindholm and Stonaker (1957) evaluated the phenotype for reducing the number of days it takes to reach a finish endpoint for cattle in the feedlot. A phenotypic correlation of -0.46 was estimated between the number of days taken to reach a given quality grade and net income per cwt (Lindholm and Stonaker, 1957). Further research has been conducted across species for days to finish and the studies including cattle will be discussed hereafter.

Beef cattle researchers termed “Economically Relevant Traits” as those traits that directly increase profit or reduce costs, which include traits such as days to slaughter weight, days to fat thickness, and days to finish (Golden et al., 2000). Regarding these traits, some studies have been conducted to evaluate their potential to respond to selection. McWhir and Wilton (1987) found that days to market finish when adjusted to a constant 7 mm backfat was highly heritable (0.80) and when adjusted to a constant market weight heritability increased ( $h^2=0.90$ ). However, the study reported large standard errors for these estimates. The large standard errors were determined to be from pooling of within breed estimates, removal of environmental variation from station tests, or random sampling error (McWhir and Wilton, 1987), which would impair the reliability of these estimates. Johnston et al. (1992) reported a heritability estimate of 0.24 for number of days to a constant backfat of 8.9 mm. In this study, genetic correlations were also estimated between carcass traits and number of days to finish. Genetic correlations between number of days to finish and adjusted marbling score, adjusted ribeye area, and adjusted carcass weight were 0.24, 0.32, and 0.29, respectively. Estimates of genetic correlations between number of days to finish and birth weight, weaning weight, yearling weight, and average daily gain were -0.09, -0.39, -0.52, and -0.38, respectively (Johnston et al., 1992). Speidel et al. (2016) evaluated three different traits of days to weight, days to ultrasound back fat, and days to ultrasound ribeye area. Heritability estimates for days to weight ranged from 0.54 to 0.72, with endpoints at 293 and 863 kg. For days to ultrasound ribeye area the heritability estimates ranged from 0.34 to 0.51, corresponding to ultrasound ribeye areas of 125 and 35 cm<sup>2</sup>. For days to ultrasound backfat heritability

estimates ranged from 0.37 to 0.55, corresponding to ultrasound backfat endpoints of 30 and 1.53 mm, respectively (Speidel et al., 2016).

The swine industry has been more focused on reducing the number of days to finish weight. The first within-herd evaluations for days to 105 kg and days to backfat depth were reported in 1986, and the first across-herd evaluations in 1990 (Stewart et al., 1991). Harris and Newman (1994) discussed indexes used by the swine industry. The performance of a single animal from weaning at 6.8 kg to 105 kg at market was called the post-weaning function. The sow-herd function represented the time from conception to weaning for one female but included the post-weaning function of each offspring in the litter. Additional indexes were developed depending on how a breed was utilized within a commercial crossbreeding program. A terminal sire index was the numerical representation of how the post-weaning function deviated from a mean of 100. Similarly, the maternal line index was the numerical representation of how the sow-herd function deviated from a mean of 100. Finally, the general-purpose index was an average of the maternal line and terminal sire indexes, usually employed for rotational crossbreeding systems. Finally, an indirect EPD for feed per kg of gain was predicted through genetic variances and covariances from backfat and days to 105 kg. Incorporation of a function for days to 105 kg or days from weaning to market was utilized in the formation of each of these swine indexes.

Genetic parameter estimates for days to finish traits for various swine breeds are summarized below. Kennedy et al. (1985) found that for days to 90 kg for Yorkshire, Landrace, Duroc, and Hampshire swine breeds the heritability estimates were 0.36, 0.40,

0.27, and 0.46, respectively. Furthermore, genetic correlations between backfat and days to 90 kg ranged from -0.43 to -0.07 for all breeds (Kennedy et al., 1985). Keele et al. (1988) reported heritability estimates for days to 100 kg of  $0.25 \pm 0.01$ ,  $0.22 \pm 0.04$ , and  $0.11 \pm 0.05$  for Duroc, Yorkshire, Hampshire breeds, respectively, and  $0.22 \pm 0.01$  pooled across these breeds. In the National Swine Improvement Federation guidelines, it was concluded that for days to 104.4 kg the heritability estimate is 0.35 (Keele et al., 1988). Kaplon et al. (1991) stated that for Duroc the heritability estimate for days to 113 kg was 0.69. Overall, the heritability estimates for days to a given weight ranged from 0.11 to 0.69. For both species, there seems to be sufficient genetic variation to select for a reduction in the number of days to a given endpoint.

## **Genetic Evaluations of Beef Cattle Data**

### **Models Utilized**

Within the beef cattle industry, a given trait can be measured once to several endpoints for the purpose of genetic evaluation. Days to finish observations have been represented in multiple ways through past research studies. McWhir and Wilton (1987) and Johnston et al. (1992) had a single observation of the number of days an animal took to reach a finish endpoint. Days to a single endpoint was evaluated by a univariate model, but a multivariate model was utilized to estimate genetic correlations between days to finish and carcass traits. However, Speidel et al. (2016) had approximately five weight or age observations per animal to analyze for days to a given endpoint enabling a random regression model. Furthermore, data summarization can provide an idea of how the data are distributed, which may lead to the use of survival analysis models if the data are not-

normally distributed. Discussion of the benefits and restrictions for each of the models will be addressed individually, along with considerations of the distribution of the data. The first group of models discussed will be those that utilize normally distributed data.

### **Normally Distributed Data**

**Univariate models.** In 1973, Henderson developed the statistical approach now widely used to predict additive genetic merit in livestock (Benyshek et al., 1988; Golden et al., 2009). The mixed model procedures, which provided BLUP (Best Linear Unbiased Predictions) of breeding values soon became a crucial component of national beef sire evaluations (Henderson, 1975). In matrix notation, the animal model is represented as:

$$y = Xb + Zu + e,$$

where  $y$  is a vector of observations,  $X$  is an incidence matrix relating fixed effects in vector  $b$  to observations in  $y$ ,  $Z$  is an incidence matrix relating random effects in vector  $u$  to observations in  $y$ , and  $e$  is a vector of random residuals. The model specifications are:

$$E(y) = Xb, \quad E(u) = 0, \quad E(e) = 0$$

and:

$$V(u) = A\sigma_u^2, \quad V(e) = I\sigma_e^2$$

where  $A$  is Wright's numerator relationship matrix for animals in  $u$ , and  $I$  is an identity matrix with order equal to the number of observations. The mixed model equations or the linear system to be solved for the continuously observed traits is represented below:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\frac{\sigma_e^2}{\sigma_u^2} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

From 1973 to 1984, the univariate animal model was utilized within National Cattle Evaluations (NCE) (Benyshek et al., 1988). However, a problem during this time was the performance limitations of computers. These evaluations were run on mainframe computers that were housed at universities or at companies with time-sharing service. Thus, due to being shared resources, the availability of computing resources was restricted. Furthermore, at that time, computers were extremely expensive, slow, and had limited memory and storage capacity. A breakthrough was achieved with methodologies for deriving the elements of the inverse of A without computing A itself (Henderson, 1975; Quaas, 1976). The simultaneous advancements in both computer performance and developments in computational methods drove the evolution from univariate models to multivariate models within cattle evaluations (Benyshek et al., 1988; Golden et al., 2009).

**Multivariate models.** Henderson and Quaas (1976) introduced multivariate genetic evaluation, which predicts genetic values for multiple traits through the incorporation of genetic and residual covariance among the traits (Mrode, 2005). Furthermore, this model can be extended to analyze different measurements on an individual animal if the measurements are treated as separate and are genetically correlated. For instance, birth weight and weaning weight are analyzed using a multivariate model as separate measurements but genetically correlated traits, even though both observations are from a single animal (Speidel, 2011). The multivariate model in matrix form is shown below as described by Mrode (2005):

$$y_i = X_i b_i + Z_i u_i + e_i,$$

Where  $y_i$  is a matrix of observations for the  $i^{\text{th}}$  trait,  $b_i$  is a vector of fixed effects for the  $i^{\text{th}}$  trait,  $u_i$  and  $e_i$  are vectors of random animal genetic and residual effects for the  $i^{\text{th}}$  trait, respectively.  $X_i$  and  $Z_i$  are incidence matrices relating the observations in  $y$  to the fixed effects in  $b$  and random animal genetic effects in  $u$ .

This model can then be represented as:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Random effects in the model are assumed to have means of zero and genetic variances equal to:

$$\text{var} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \sigma_{g_1}^2 & \sigma_{g_1, g_2} \\ \sigma_{g_2, g_1} & \sigma_{g_2}^2 \end{bmatrix} \otimes A$$

and residual variances equal to:

$$\text{var} \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I\sigma_{e_1}^2 & I\sigma_{e_1, e_2} \\ I\sigma_{e_2, e_1} & I\sigma_{e_2}^2 \end{bmatrix}$$

where  $\sigma_{g_1}^2, \sigma_{g_2}^2$  are the additive genetic variances for  $y_1$  and  $y_2$  and  $\sigma_{g_1, g_2}, \sigma_{g_2, g_1}$  are the additive genetic covariances between  $y_1$  and  $y_2$ , respectively. Additionally,  $\sigma_{e_1}^2, \sigma_{e_2}^2$  are the residual variances for  $y_1$  and  $y_2$  and  $\sigma_{e_1, e_2}, \sigma_{e_2, e_1}$  are the residual covariances between  $y_1$  and  $y_2$ , respectively. Furthermore,  $A$  is Wright's numerator relationship matrix, and  $I$  is an identity matrix. Henderson and Quass (1976) were the first to implement the multivariate BLUP model shown above to analyze a three-trait beef cattle model, including birth weight, weaning weight, and post-weaning gain.



One issue with the multivariate model is the potential for high correlations between successive measurements. For example, within beef cattle evaluations, weaning weight and yearling weight have genetic and phenotypic correlations between the two traits of 0.78 and 0.72, respectively (Koots, 1994). As weaning weight is a part of yearling weight, post-weaning gain is instead utilized for yearling weight predictions. These high correlations can result in two main issues for the analysis. First, the two traits within the model predict the same information and therefore including both traits is not necessary. Second, the power of various tests of significance could be affected due to the high correlation between the traits (Foster et al., 2006).

**Random Regression.** Random regression has been utilized to analyze longitudinal data, or data collected over multiple time points. During the 1980's random regression, also known as random coefficients models, were introduced (Henderson, 1982; Jennrich and Schluchter, 1986). Yet, these models were not utilized on livestock data until the 1990's with the analysis of milk production records for dairy cattle by Ptak and Schaeffer (1993). This study grouped dairy cows into similar herd, year, and season by a general shape or curve for mean lactation records. However, these groupings did not represent a true random regression model as it did not account for the differences between individual animals. Soon after, Schaeffer and Dekkers (1994) were able to account for the curves of the lactation records within similar herd, year, and season, as well as the deviation of each individual animal's lactation curve from the overall mean shape. Additionally, they were able to account for changes in correlation structure of repeated records on individuals over time (Schaeffer and Dekkers, 1994). Meyer (2004) has shown that being

able to account for changes in the correlation structure can increase prediction accuracy of the random regression model by 5.9% when compared to a multivariate model.

The random regression model can be represented in matrix form as shown by Mrode (2005):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Qu} + \mathbf{Zpe} + \mathbf{e},$$

where  $\mathbf{y}$  is a vector of repeated test day yields,  $\mathbf{X}$  is an incidence matrix relating observations in  $\mathbf{y}$  to fixed effects and fixed regression coefficients,  $\mathbf{b}$  is a vector of solutions for fixed effects and fixed regressions,  $\mathbf{Q}$  is an incidence matrix of covariates relating observations in  $\mathbf{y}$  to random additive genetic regression coefficients,  $\mathbf{u}$  is a vector of random additive direct genetic effects,  $\mathbf{Z}$  is an incidence matrix of covariates relating observations in  $\mathbf{y}$  to  $\mathbf{pe}$  for each animal,  $\mathbf{e}$  is a vector of random residuals, including temporary environmental effects for each observation. The variances for this model are:

$$\text{var} \begin{bmatrix} \mathbf{u} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G} & 0 & 0 \\ 0 & \mathbf{I} \otimes \mathbf{P} & 0 \\ 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where  $\mathbf{A}$  is Wright's numerator relationship matrix,  $\mathbf{G}$  is the (co)variance matrix of the additive genetic random regression coefficients,  $\mathbf{I}$  is an identity matrix,  $\mathbf{P}$  is the (co)variance matrix of the permanent environmental random regression coefficients, and  $\sigma_e^2$  is the variance of random residuals.

Additionally, as some measurements are taken between multiple years, the random residual variance has been allowed to vary. The residual variance structure was modified from  $\mathbf{I}\sigma_e^2$  as described above to:

$$\text{var}[\mathbf{e}] = \text{diag}\{\sigma_{e_k}^2\},$$

where  $k$  is equal to the total number of differing residual variances (Jamrozik et al., 1997). An additional method utilized to model heterogeneous residual variances is for the variance to follow a continuous function (Rekaya et al., 2000). Furthermore, if homogeneous residual variances do not hold across all phases of production, a change in the model should be made to account for the changes in residual variance between production phases (Olori et al., 1999). The assumption of homogeneous residual variances biases the estimates of residual variances which results in over- or under-estimation of heritability values for the given trait being analyzed (Olori et al., 1999). Although, in regard to permanent environmental variances, the assumption of homogeneous residual variances has no effect (López-Romero et al., 2003).

### **Non-Normally Distributed**

**Survival Analysis.** Survival analysis is a way of analyzing traits that consist of the length of time between two events. As days to finish is the number of days between feedlot entry and harvest (two events), survival analysis can be utilized to model this trait (Márquez et al., 2013). This model is used to study the length of time until a part fails or the length of time an individual survives (Ducroqc, 1994; Beaudeau et al., 1995). Yet, another way of utilizing this model is when analyzing the length of time until a success (Kachman, 1999). The survival function is the probability that animal  $i$  survives to at least until time  $t$ , given its risk function, which can be represented as:

$$S(t; \eta_i) = \Pr(T_i \geq t) = 1 - F(t; \eta_i) = \int_t^{\infty} f(w; \eta_i) dw$$

where  $T_i$  is the time to failure,  $F(t; \eta_i)$  is the cumulative distribution for  $T_i$ , and  $f(w; \eta_i)$  is the density function for  $T_i$ . As described in Kachman (1999), the challenge was to then

develop a reasonable model for the survival function. A hazard function was one approach utilized. The hazard function measures the risk of failure of an individual at time  $t$ , and is denoted below:

$$\lambda(t; \eta_i) = \lim_{\Delta t \rightarrow 0} \frac{\Pr(T_i < t + \Delta t | T_i > t)}{\Delta t} = \frac{f(t; \eta_i)}{S(t; \eta_i)}$$

The hazard function can also be looked at over short periods of time ( $\Delta t$ ), or at a constant time (endpoint) over a given time. This function can be modeled several ways with the Cox (Cox, 1972) and Weibull (Kachman, 1999; Kalbfleish and Prentice, 2002) models being the most common (Márquez et al., 2013). The Weibull model allows for the flexibility to model increasing or decreasing hazards but assumes that the hazard function has a Weibull distribution (Kachman, 1999; Márquez et al., 2013). However, the Cox model makes no distributional assumption on the hazard function (Márquez et al., 2013). Thus, to determine the appropriate model to utilize for the hazard function, the fit of the models to the data should be investigated.

### **Utilizing crossbred data in genetic evaluations**

A multibreed evaluation that includes all purebred and crossbred individuals within a single analysis would benefit commercial producers (Arnold et al., 1992). This would allow for all progeny of an individual to be utilized within the evaluation, resulting in greater accuracies and less bias associated with breeding value estimates (Klei et al., 1996). The first multibreed model for weight traits was conducted in 1997 by the American Simmental (ASA) and Canadian Simmental Associations (CSA), which was implemented by Cornell University (Pollak and Quaas, 1998). Soon after, the same collaboration worked on carcass traits that included ultrasound measurements.

Meanwhile the University of Georgia developed a multibreed evaluation for weight traits (Pollak and Quaas, 1998). Arnold et al. (1992) suggested the importance of correctly identifying the amount of a given breed within an individual, as their estimates will be a function of their breed makeup. However, breed associations do not always keep track of exact breed fractions, as they are often designated to a certain group by a given set of rules. Thus, two animals could be considered purebreds although there could be different amounts of other breeds within their pedigree, resulting in differing heterosis effects. Therefore, the correct breed fractions for each animal within a multibreed evaluation is crucial for accurate breeding value estimates (Arnold et al., 1992; Pollak and Quaas, 1998). Another challenge with a multibreed evaluation is accounting for direct and maternal breed and heterosis effects (Williams et al., 2013). Although these effects can be estimated through breed association data or literature studies (Williams et al., 2013), there would need to be genetic connectedness between animals within the evaluation through similar breeds or sires (Kennedy and Trus, 1993). A strength of the GPE program is that it has a mating plan with the animals utilized recorded from the start of the evaluation program, resulting in accurate information on breed fractions and genetic connectedness between the management groups. This design allows for reliable assessments of breed and heterosis effects for genetic evaluations.

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**CHAPTER 2**

**GENETIC PARAMETER ESTIMATES FOR AGE AT SLAUGHTER AND DAYS  
TO FINISH IN A MULTIBREED POPULATION**

**ABSTRACT**

Efficiency during the finishing phase is an important trait complex in the beef cattle industry. Selection to improve traits that impact feedlot efficiency such as number of days on feed would lead to decreased production costs, increased net profit, and ultimately aid in improving sustainability. The objective of this study was to estimate genetic parameters for various definitions of days to finish (DtF), the number of days from weaning to slaughter and age at slaughter (AAS), the number of days from birth to slaughter, as well as the given carcass traits. Records were from 7,747 steers and heifers from the Germplasm Evaluation (GPE) project at the U.S. Meat Animal Research Center (USMARC). Age at weaning (AAW), DtF, AAS, and carcass/growth traits including adjusted fat thickness (AFT), final weight (FW), hot carcass weight (HCW), marbling score (MARB), and ribeye area (REA) were analyzed using univariate and bivariate animal models. Age at slaughter and DtF were adjusted to different carcass trait endpoints to depict differences in potential marketing systems. Fixed effects fitted for AAS, DtF, and carcass traits included contemporary group (concatenation of birth year, birth season, sex, and treatment group), and linear covariates of breed proportions, direct heterosis, and the carcass trait that represented a market endpoint (i.e., AFT, FW, HCW, MARB, or REA), which the others were rotated through when one carcass trait was a

response variable. Fixed effects for AAW, treated as a trait of the dam, included contemporary group (birth year and season), and linear covariates of breed proportions, direct heterosis, and age in days. For bivariate models, the same linear covariate of a given carcass trait was fitted for both models (i.e., same assumed market endpoint). Univariate heritability estimates for AAS, AAW, DtF, AFT, FW, HCW, MARB, and REA ranged from 0.52-0.59, 0.04, 0.33-0.39, 0.45-0.52, 0.34-0.55, 0.34-0.55, 0.54-0.55, and 0.50-0.56, respectively. Including MARB or AFT as the linear covariate led to the highest and lowest, respectively, heritability estimates for AAS and DtF. Depending on the endpoint, genetic correlations between AAS and AFT, FW, HCW, MARB, and REA ranged from 0.16 to 0.32, -0.08 to 0.33, 0.19 to 0.36, 0.14 to 0.20, and -0.06 to 0.13, respectively. Genetic correlations between DtF and AFT, MARB, and REA were negligible. Genetic correlations between DtF and FW and HCW ranged from -0.10 to 0.29 and -0.37 to -0.17, respectively. Genetic correlations between AAW and DtF ranged from -0.64 to -0.73. Standard errors were less than 0.12 for all estimates. Phenotypic variability in DtF was low, and increased variability in AAS was due to differences in date of birth and thus AAW, which varied among calves due differences in weaning dates at the various management units. Overall, DtF and AAS were moderately to highly heritable and generally lowly correlated with routine carcass traits, while AAW was lowly heritable with moderate to high, negative correlations to DtF. Despite the encouraging heritability estimates obtained for AAS and DtF, the low degree of variation for DtF and the increased variation in AAS due to variation in date of birth, potentially hinders genetic progress.

**Key Words:** age at slaughter, beef cattle, days to finish, genetic parameters

## **INTRODUCTION**

Feedlot efficiency has been a main concern relative to environmental sustainability of the beef cattle industry (Opio et al., 2013). The number of days to finish and feed intake are economically relevant traits that ultimately affect production costs (Golden et al., 2000); improving these two traits would lead to increased economic returns to the production system (Archer et al., 1999) and decreased environmental footprint. Lindholm and Stonaker (1957) reported a moderate phenotypic correlation of -0.46 between the number of days to a given quality grade and the net income per cwt. Considerable effort and expense have been spent on collecting individual animal feed intake on immature seedstock animals as a means of producing Expected Progeny Differences (EPDs) for dry matter intake as indicators of feed consumption in commercial growing animals (Rolfe et al., 2011; Welch et al., 2012).

Currently in the U.S., dry matter intake EPDs represent the only predictions of genetic merit for costs associated with finishing cattle. However, the amount of feed consumed only represents a portion of the variable costs of finishing cattle, with other costs including yardage, morbidity, and mortality (Koch et al., 1963; Anderson et al., 2005). The number of days cattle spend in a feedlot to reach a desired endpoint (e.g., weight, fatness, quality grade) is a function of the amount of feed they consume, rate of growth, and rate of tissue deposition (Owens et al., 1995). Reducing the amount of time on feed needed to reach a desired endpoint would be economically advantageous (MacNeil et al.,

1991). However, the choice of the finish endpoint, such as weight, back fat, marbling, or ribeye area, depends on the biological type of cattle being marketed and the marketing systems available to the owners (Bullock and Logan, 1972; Amer et al., 1994; Williams and Bennett, 1995). Unfortunately, the number of published studies relative to days to finish are limited. Speidel et al. (2016) utilized random regression models for the prediction of the number of days to reach a given finish end point within an Angus- and Charolais-based dataset. The authors reported moderate to high heritability estimates for days to reach 513 kg, days to ultrasound ribeye area, and ultrasound back fat, which ranged from 0.54 to 0.74, 0.35 to 0.51, and 0.37 to 0.55, respectively. In another study, Berry et al. (2017) analyzed the deviation in age at slaughter adjusted to a predefined carcass weight and subcutaneous fat cover; heritability estimates ranged from 0.23 to 0.26. Based on these earlier studies, there clearly is potential for selection to reduce the number of days an animal spends in the feedlot. The objective of this study was to estimate genetic parameters for age at slaughter (AAS), age at weaning (AAW), days to finish (DtF), and their relationships with growth and carcass traits including adjusted fat thickness (AFT), adjusted based on the fat covering over the outside of the carcass, final live weight (FW), hot carcass weight (HCW), marbling score (MARB), and ribeye area (REA) in a multibreed beef cattle population.

## **MATERIALS AND METHODS**

### **Animals**

Data were recorded from steers and heifers (n=7,747) from 4,109 dams from the U.S. Meat Animal Research Center (USMARC) Germplasm Evaluation (GPE) project near Clay Center, Nebraska, during the years 2007 to 2017. The pedigree included 85,872 animals. Within each year, spring and fall calving seasons were observed. Multiple weaning dates within a year-season combination occurred due to different management units (pole sheds) at USMARC weaning calves on separate days. Calves from a single pole shed were then allocated to multiple feedlot pens with calves from other pole sheds, so as not to confound feedlot pen and pole shed. After weaning, calves were placed into a feedlot where they received a starter ration from 6 to 19 weeks and were then transitioned to a finishing ration for the duration of time until harvest. A feedlot pen was managed as one pen with all animals in a pen harvested at the same time. During the time on feed, some cattle were allocated to experimental studies. These experimental studies included treatments such as implants, beta agonists, and probiotics. As these treatments can alter the amount of feed converted to lean muscle mass, experimental treatment was considered as part of the contemporary group definition. Harvest was determined by visual inspection of group averages for weight and fat endpoints for a given pen. All animal procedures followed USMARC standard operating procedure and cattle were treated according to Federation of Animal Science Societies guidelines (FASS, 2010). The breeds evaluated were part of the continuous GPE project, which periodically samples artificial insemination (AI) sires of the 18 most influential breeds in the U.S.

with genetic evaluation programs (Angus, Beefmaster, Brahman, Brangus, Braunvieh, Charolais, ChiAngus, Gelbvieh, Hereford, Limousin, Maine Anjou, Red Angus, Salers, Santa Gertrudis, Shorthorn, Simmental, South Devon, and Tarentaise) that conduct national cattle evaluations (Snelling et al., 2019). Continuous GPE included a fall calving season, whereas the early iterations of the GPE program only had spring calving seasons. In each breeding season, the females were designated into two groups; the first group received a single service AI mating followed by natural service, while the other group were bred using natural service for the full season. Cows were exposed to F<sub>1</sub> and purebred bulls developed in GPE, and occasionally some Angus calving ease bulls from the USMARC selection program (Bennett, 2008) as heifers. Matings were designated by breed composition groups (F<sub>1</sub>, 50% to <75%; backcross, 75% to <87.5%; and purebred, ≥87.5% of any single breed) and birth year x season (Snelling et al., 2019).

### **Traits**

Before harvest, a final live weight (FW) was recorded. At harvest, hot carcass weight (HCW), ribeye area (REA), fat thickness (AFT), which was adjusted based on the distribution of fat elsewhere on the carcass, and marbling score (MARB), where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup>, were collected. Age at weaning (AAW) was defined as the number of days from birth until weaning. However, given replacement heifers were retained and were often born earlier in the calving season, deviations of animal age from the average age of animals weaned on the same date were used as phenotypes for AAW. Days to finish (DtF) was calculated as the number of days from weaning until harvest.



The age at slaughter (AAS) is the sum of AAW and DtF and was calculated as the number of days from birth until harvest.

### Statistical Analysis

Variance components and fixed effects were estimated using ASReml version 4.0 (Gilmour et al., 2015).

*Univariate Animal Models.* The univariate animal models used to analyze AAS, DtF, and carcass traits is shown below:

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

where  $\mathbf{y}$  is a vector of phenotypic records,  $\mathbf{X}$  is a design matrix relating the observations to the fixed effects in  $\mathbf{b}$ ,  $\mathbf{Z}$  is an incidence matrix relating observations to random additive genetic effects in  $\mathbf{u}$ , and  $\mathbf{e}$  is a vector of random residuals. The random additive genetic effects and residuals were assumed to be distributed  $\sim N(0, \mathbf{A}\sigma_a^2)$  and  $\sim N(0, \mathbf{I}\sigma_e^2)$ , respectively where  $\mathbf{A}$  was the numerator relationship matrix, and  $\mathbf{I}$  was an identity matrix. Fixed effects included contemporary group (concatenation of birth year, birth season, sex, and treatment group), and linear covariates of direct heterosis, breed proportions, and the chosen endpoint (i.e., AFT, FW, HCW, MARB, REA, or AAS. For the univariate animal models used to analyze the carcass traits, the fixed effects described above were utilized with the linear covariates of the chosen endpoint rotating among the remaining carcass traits.

The univariate animal model to analyze AAW is shown below:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{W}\mathbf{p}\mathbf{e} + \mathbf{e},$$

where  $\mathbf{y}$  is a vector of phenotypic records,  $\mathbf{X}$  is a design matrix relating the observations to the fixed effects in  $\mathbf{b}$ ,  $\mathbf{Z}$  is an incidence matrix relating observations to random additive genetic effects in  $\mathbf{u}$ ,  $\mathbf{W}$  is an incidence matrix relating observations to permanent environmental effects in  $\mathbf{pe}$ , and  $\mathbf{e}$  is a vector of random residuals. The random additive genetic effects, permanent environmental effects, and residuals were assumed to be distributed  $\sim N(0, \mathbf{A}\sigma_a^2)$ ,  $\sim N(0, \mathbf{I}\sigma_{pe}^2)$ , and  $\sim N(0, \mathbf{I}\sigma_e^2)$ , respectively. Age at weaning was treated as a trait of the cow and the model included fixed effects of contemporary group (concatenation of calf's birth year and birth season), as well as linear covariates of direct heterosis, breed proportions, and cow age in days.

*Bivariate Animal Models.* The bivariate animal models used to analyze AAS or DtF with carcass traits is shown below:

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

where  $\mathbf{y}_i$  is a vector containing records on the  $i^{\text{th}}$  trait,  $\mathbf{X}_i$  is a design matrix relating the observations to the fixed effects in  $\mathbf{b}_i$ ,  $\mathbf{Z}_i$  is an incidence matrix relating observations to random additive genetic effects in  $\mathbf{u}_i$ , and  $\mathbf{e}_i$  is a vector of random residuals. The genetic effects were assumed to be distributed multivariate normal with mean 0 and (co)variance  $\mathbf{\Phi} \otimes \mathbf{A}$ , where  $\otimes$  is the Kronecker product,  $\mathbf{\Phi}$  is the additive genetic (co)variance matrix, and  $\mathbf{A}$  is the numerator relationship matrix. The residuals were assumed to be distributed multivariate normal with mean 0 and variance  $\mathbf{R} \otimes \mathbf{I}$ , where  $\mathbf{R}$  was the residual (co)variance matrix and  $\mathbf{I}$  was an identity matrix. For a given bivariate analyses, both traits were adjusted to the same carcass endpoint.

The relationship between AAW and DtF was also investigated with the bivariate model defined below:

$$\mathbf{y}_i = \mathbf{X}_i \mathbf{b}_i + \mathbf{Z}_i \mathbf{u}_i + \mathbf{W} \mathbf{pe} + \mathbf{e}_i,$$

where  $\mathbf{y}_i$  is a vector containing records on the  $i^{\text{th}}$  trait,  $\mathbf{X}_i$  is a design matrix relating the observations to the fixed effects in  $\mathbf{b}_i$ ,  $\mathbf{Z}_i$  is an incidence matrix relating observations to random additive genetic effects in  $\mathbf{u}_i$ ,  $\mathbf{W}$  is an incidence matrix relating observations to permanent environmental effects in  $\mathbf{pe}$  for AAW, and  $\mathbf{e}_i$  is a vector of random residuals. The residual effects between AAW and DtF were assumed uncorrelated. Models for AAW and DtF included the same fixed effects as described in the univariate animal models.

## RESULTS & DISCUSSION

Summary statistics of the growth and carcass traits are reported in **Table 2.1**.

### Heritability estimates

Univariate heritability estimates for AAS and DtF ranged from 0.52-0.59 and 0.33-0.39, respectively (**Table 2.2**). Heritability estimates for DtF were lower than estimates for AAS. A covariate of AFT led to the lowest heritability estimates for both AAS and DtF (**Table 2.2**). Berry et al. (2017) reported lower heritability estimates for AAS ranging from 0.23 to 0.26. Berry et al. (2017) modelled age at slaughter fitting fixed effects of contemporary group, sex, carcass weight, and carcass fat. Residuals from this model were then used as response variables in an animal model to estimate genetic parameters. In either case, the lower heritability estimates reported by Berry et al. (2017) could be a

function of the population used and the fact that the authors simultaneously adjusted records for both carcass weight and fat cover. Relative to DtF, Speidel et al. (2016) reported heritability estimates for days to reach 513 kg, days to ultrasound ribeye area, and ultrasound back fat which ranged from 0.54 to 0.74, 0.35 to 0.51, and 0.37 to 0.55, respectively, using random regression models applied to data from Angus and Charolais based animals. The fact that these estimates were obtained with random regression models over a larger time period could account for the differences observed, as animals may be within different points of their growth curve, resulting in different heritability estimates. McWhir and Wilton (1987) reported heritability estimates for days to 7 mm subcutaneous back fat depth of 0.65 for a data set with various breeds of cattle, while Johnston et al. (1992) reported an estimate of heritability of 0.24 for days to 8.9 mm back fat in a Charolais population. Previous estimates of heritability are within the same ranges reported herein except for the estimate of DtF adjusted to a HCW endpoint, which was lower than the reported range from Speidel et al. (2016).

The heritability estimate for AAW was 0.04 (**Table 2.2**) which falls within the range of estimates reported by other studies. Snelling et al. (2019) reported heritability estimates for calf weaning age by parity from random regressions models which ranged from 0.03 for 2-year-old dams to 0.50 for 12-year-old dams. Much of the data used herein was also used by Snelling et al. (2019) and most cows were between ages 2 and 5. The age at weaning of the calf is affected by calf date of birth and date of weaning. The birth date of the calf is dependent on when a cow conceives and gestation length. Days to calving is the interval of time from exposure to calving for the cow (Johnston and Bunter, 1996).

Other studies reported heritability estimates for days to calving from 0.06 to 0.11 (Donoghue et al., 2004; Minick-Bormann and Wilson, 2010). Heritability estimates for AFT, FW, HCW, MARB, and REA can be found in **Table 2.3** and were within the ranges reported by Koots et al. (1994). One note is that when a weight trait was a response variable and had a weight trait fitted as a covariate, the additive genetic variation and residual variation decreased, as well as the heritability. The variation that was left over would have been association with non-carcass weight gain.

### **Genetic correlation estimates**

Genetic correlations between AAS and carcass traits are reported in **Table 2.4**. Genetic correlation estimates between AAS and AFT or MARB ranged from 0.16 to 0.32 and 0.14 to 0.20, respectively, depending on the chosen endpoint for AAS. These correlations suggest that the younger an animal is at harvest, the less back fat or marbling the animal will have. In the growth curve, fat deposition occurs last when compared to bone or muscle, in agreement with these estimates (Berg and Butterfield, 1976). Genetic correlations between AAS and REA ranged from -0.06 to 0.18, with the carcass weight variable as the covariates being close to zero, suggesting REA is independent of AAS. For AAS and FW or HCW, genetic correlations ranged from -0.08 to 0.33 and 0.19 to 0.36, respectively.

Genetic correlations between DtF and carcass traits are found in **Table 2.5**. Genetic correlations between DtF and AFT, MARB, and REA were near zero. However, genetic correlations of DtF with FW and HCW ranged from -0.10 to 0.29 and -0.37 to -0.17, respectively. The only positive genetic correlation was between DtF and FW with a HCW

covariate (0.29). This estimate implies a positive relationship between the non-carcass weight gain and increased days on feed. However, the -0.37 genetic correlation between DtF and HCW with a FW covariate implies increased carcass weight, while a decrease in days on feed. Genetic correlation estimates between AAS or DtF and carcass traits have not been previously reported for beef cattle. In swine Kennedy et al. (1985) reported genetic correlation estimates between back fat and days to 90 kg ranging from -0.43 to -0.05 for various breeds. Bryner et al. (1992) estimated genetic correlations between back fat and average daily gain of approximately zero for Yorkshire boars.

Genetic correlations between AAW and DtF adjusted to given endpoint are found in **Table 2.6**. Depending on the chosen endpoint for DtF, the genetic correlations between AAW and DtF ranged from -0.73 to -0.64. These high, negative genetic correlations suggest that older animals at weaning require fewer days to reach a finish endpoint. Given AAW and DtF are components of AAS, reducing the length of time spent in one phase (i.e., pre-weaning) would increase the length of time spent in the second phase (i.e., finishing). Genetic correlation estimates between AAW and DtF have not been previously reported for beef cattle.

In general, phenotypic variability was low for DtF, with respect to AAS, ranging from 19.24 to 21.96 days<sup>2</sup>, with a CV of 0.04-0.05 compared to 0.12-0.11 for AAS depending on the carcass trait covariate that was fitted (Table 2.1). Animals entered the feedlot and were harvested at based on an average weight or fat whilst maintaining an industry acceptable average number of days on feed, reducing the total amount of phenotypic variation observed. Given that weaning date varied across management units at the

USMARC within a year-season, within contemporary group variation for DtF is at least partially attributable to differences in weaning date. Increased phenotypic variation in AAS was observed, ranging from 179 to 192 days<sup>2</sup>, depending on the carcass trait covariate that was fitted. As AAS is comprised of the two components of AAW and DtF, the increased variation results from AAW, or the differences in date of birth of the calf. The relatively low variation observed in DtF, and its origin, make this trait complex problematic for inclusion in routine genetic evaluations. Data for routine genetic evaluations would likely come from limited cull seedstock animals and predominately from commercial animals where sire was known (i.e., sire testing programs or part of breed organization marketing programs). In the case of data from commercial entities, the sources of variation contributing to DtF and AAS in field data could not be deconstructed to appropriately account for differences in date of birth or weaning. Given AAS in a calf-fed system is comprised of AAW and DtF, it is possible that selection to reduce AAS, absent simultaneous consideration of AAW, could indirectly reduce AAW leading to sub-fertile females (Johnston and Bunter, 1996; Minick-Bormann and Wilson, 2010). Collectively, these issues may prohibit the inclusion of either DtF or AAS in genetic evaluations.

Due to the low variability observed in this dataset, breed effect estimates for AAS and DtF were less than the standard errors and thus were not reported. Estimates (SE) of direct heterosis for DtF and AAS ranged from -0.60 to -0.95 (0.19) day and -6.62 to -8.37 (0.56) day, respectively, suggesting that crossbred animals will require fewer days to reach a desired finish endpoint.

## **Implications**

The heritability estimates obtained from the current study for AAS and DtF suggest that selection could be utilized to reduce the age at slaughter or the number of days on feed to reach a desired endpoint. However, the general lack of variation for days to finish and that variation that exists for both DtF and AAS includes components related to weaning age and date make the utility of DtF and AAS in routine genetic evaluations questionable. It is evident that in calf-fed systems the age at which an animal is harvested is dictated by the age at which they were weaned and the number of days they were in the feedlot. The two traits appear to be favorably correlated (negative correlation), but selection for reduced age at slaughter without consideration of the components could lead to an indirect and undesirable decrease in the age at weaning.

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## TABLES

**Table 2.1.** Summary statistics for growth and carcass traits

Trait <sup>1</sup>	Mean (SD)		CV
	Steers	Heifers	Steers/Heifers
AAS	451 (18.4)	433 (20.4)	0.04/0.05
AAW	164 (18.9)	151 (17.0)	0.12/0.11
AFT	1.33 (0.48)	1.25 (0.44)	0.36/0.35
DtF	287 (11.0)	281 (15.2)	0.04/0.05
FW	626 (60.8)	548 (51.4)	0.10/0.09
HCW	395 (39.9)	348 (33.8)	0.10/0.10
MARB	506 (77.0)	501 (66.5)	0.15/0.13
REA	87.9 (10.2)	88.4 (9.58)	0.12/0.11

<sup>1</sup>AAS = age at slaughter, the number of days from birth until harvest (days), AAW = age at weaning, the number of days from birth until weaning (days), AFT = adjusted fat thickness (cm), DtF = days to finish, the number of days from weaning until harvest (days), FW = final live weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

**Table 2.2.** Genetic parameter estimates<sup>1</sup> (SE) for univariate models for age at slaughter (AAS<sup>2</sup>), age at weaning (AAW<sup>3</sup>), and days to finish (DtF<sup>4</sup>)

Response Trait	Covariate <sup>4</sup>				
		$h^2$	$\sigma_a^2$	$\sigma_e^2$	$\sigma_{pe}^2$
AAS	AFT	0.52 (0.04)	95.0 (7.45)	86.1 (6.05)	-
	FW	0.57 (0.04)	103 (7.52)	78.6 (5.99)	-
	HCW	0.56 (0.04)	100 (7.39)	78.3 (5.90)	-
	MARB	0.59 (0.04)	110 (7.89)	77.6 (6.24)	-
	REA	0.59 (0.04)	112 (8.04)	78.4 (6.35)	-
	None	0.59 (0.04)	113 (8.10)	78.2 (6.39)	-
DtF	AFT	0.33 (0.03)	6.41 (0.58)	12.83 (0.53)	-
	FW	0.38 (0.03)	8.29 (0.70)	13.65 (0.61)	-
	HCW	0.38 (0.03)	8.37 (0.70)	13.59 (0.61)	-
	MARB	0.39 (0.03)	8.40 (0.70)	13.40 (0.61)	-
	REA	0.38 (0.03)	8.31 (0.70)	13.63 (0.61)	-
	None	0.38 (0.03)	8.34 (0.70)	13.61 (0.60)	-
AAW	None	0.04 (0.01)	7.39 (2.76)	184.8 (3.83)	4.73 (3.53)

<sup>1</sup> $h^2$  = heritability,  $\sigma_a^2$  = additive genetic variance,  $\sigma_e^2$  = residual variance.

<sup>2</sup>AAS = age at slaughter, the number of days from birth until harvest (days).

<sup>3</sup>AAW = age at weaning, the number of days from birth until weaning (days).

<sup>4</sup>DtF = days to finish, the number of days from weaning until harvest (days).

<sup>5</sup>AFT = adjusted fat thickness (cm), FW = final live weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup>(USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

**Table 2.3.** Genetic parameter estimates<sup>1</sup> (SE) for univariate models for carcass traits<sup>2</sup>

Response Trait	Covariate			
		$h^2$	$\sigma_a^2$	$\sigma_e^2$
AFT	Age	0.48 (0.04)	0.08 (0.01)	0.08 (0.005)
	FW	0.52 (0.04)	0.07 (0.01)	0.07 (0.005)
	HCW	0.52 (0.04)	0.07 (0.01)	0.07 (0.005)
	MARB	0.49 (0.04)	0.07 (0.01)	0.08 (0.005)
	REA	0.45 (0.04)	0.07 (0.01)	0.08 (0.005)
	None	0.50 (0.04)	0.08 (0.01)	0.08 (0.005)
FW	AFT	0.55 (0.04)	1341 (101)	1087 (81.5)
	Age	0.51 (0.04)	1313 (104)	1287 (84.8)
	HCW	0.34 (0.03)	88.8 (9.18)	176 (8.15)
	MARB	0.53 (0.04)	1432 (110)	1277 (88.8)
	REA	0.53 (0.04)	1267 (96.9)	1112 (78.2)
	None	0.53 (0.04)	1453 (112)	1293 (85.3)
HCW	AFT	0.55 (0.04)	588 (44.3)	473 (35.6)
	Age	0.50 (0.04)	578 (45.9)	578 (37.6)
	FW	0.34 (0.03)	40.2 (4.15)	79.5 (3.68)
	MARB	0.53 (0.04)	641 (49.1)	575 (39.8)
	REA	0.53 (0.04)	537 (41.1)	482 (33.3)
	None	0.53 (0.04)	655 (50.2)	584 (40.6)
MARB	AFT	0.55 (0.03)	2092 (153)	1747 (123)
	Age	0.54 (0.03)	2211 (161)	1904 (130)
	FW	0.54 (0.03)	2249 (163)	1898 (131)
	HCW	0.54 (0.03)	2236 (162)	1891 (130)
	REA	0.54 (0.03)	2253 (165)	1942 (133)
	None	0.54 (0.03)	2281 (165)	1927 (133)
REA	AFT	0.50 (0.04)	36.0 (2.95)	36.0 (2.42)
	Age	0.55 (0.04)	42.9 (3.19)	34.5 (2.55)
	FW	0.56 (0.04)	37.7 (2.79)	29.6 (2.23)
	HCW	0.55 (0.04)	35.4 (2.63)	28.5 (2.11)
	MARB	0.55 (0.04)	42.8 (3.20)	34.7 (2.57)
	None	0.56 (0.04)	43.3 (3.21)	34.5 (2.57)

<sup>1</sup> $h^2$ =heritability,  $\sigma_a^2$ = additive genetic variance,  $\sigma_e^2$ = residual variance.

<sup>2</sup>AFT = adjusted fat thickness (cm), FW = final live weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>)

**Table 2.4.** Genetic parameter estimates<sup>1</sup> (SE) for multivariate models for age at slaughter (AAS<sup>2</sup>) and carcass traits<sup>3</sup>

Response Trait		Covariate				
1	2		$r_g$	$r_r$	$h_1^2$	$h_2^2$
AAS	AFT	None	0.27 (0.05)	0.07 (0.05)	0.59 (0.04)	0.50 (0.04)
		FW	0.18 (0.05)	0.02 (0.05)	0.57 (0.04)	0.52 (0.04)
		HCW	0.16 (0.05)	0.00 (0.05)	0.56 (0.04)	0.52 (0.04)
		MARB	0.21 (0.05)	0.05 (0.05)	0.59 (0.04)	0.49 (0.04)
		REA	0.32 (0.05)	0.07 (0.05)	0.59 (0.04)	0.46 (0.04)
AAS	FW	None	0.33 (0.05)	0.11 (0.05)	0.59 (0.04)	0.53 (0.04)
		AFT	0.25 (0.05)	0.09 (0.05)	0.53 (0.04)	0.55 (0.04)
		HCW	-0.08 (0.06)	-0.03 (0.04)	0.56 (0.04)	0.34 (0.03)
		MARB	0.31 (0.05)	0.10 (0.05)	0.59 (0.04)	0.53 (0.04)
		REA	0.31 (0.05)	0.11 (0.05)	0.59 (0.04)	0.53 (0.04)
AAS	HCW	None	0.36 (0.05)	0.13 (0.05)	0.59 (0.04)	0.53 (0.04)
		AFT	0.28 (0.05)	0.12 (0.05)	0.53 (0.04)	0.55 (0.04)
		FW	0.19 (0.06)	0.09 (0.04)	0.57 (0.04)	0.34 (0.03)
		MARB	0.34 (0.05)	0.12 (0.05)	0.59 (0.04)	0.53 (0.04)
		REA	0.35 (0.05)	0.13 (0.05)	0.59 (0.04)	0.53 (0.04)
AAS	MARB	None	0.18 (0.05)	0.10 (0.05)	0.59 (0.04)	0.55 (0.03)
		AFT	0.15 (0.05)	0.08 (0.05)	0.52 (0.04)	0.55 (0.03)
		FW	0.15 (0.05)	0.09 (0.05)	0.57 (0.04)	0.55 (0.03)
		HCW	0.14 (0.05)	0.09 (0.05)	0.56 (0.04)	0.55 (0.03)
		REA	0.20 (0.05)	0.10 (0.05)	0.59 (0.04)	0.54 (0.03)
AAS	REA	None	0.10 (0.05)	0.04 (0.06)	0.59 (0.04)	0.56 (0.04)
		AFT	0.18 (0.06)	0.04 (0.05)	0.52 (0.04)	0.50 (0.04)
		FW	-0.02 (0.05)	-0.01 (0.05)	0.57 (0.04)	0.56 (0.04)
		HCW	-0.06 (0.05)	-0.02 (0.05)	0.56 (0.04)	0.56 (0.04)
		MARB	0.13 (0.05)	0.02 (0.05)	0.59 (0.04)	0.55 (0.04)

<sup>1</sup> $r_g$  = additive genetic correlation,  $r_r$  = residual genetic correlation,  $h_1^2$  = heritability of trait 1,  $h_2^2$  = heritability of trait 2.

<sup>2</sup>AAS = age at slaughter (days), the number of days from birth until harvest.

<sup>3</sup>AFT = adjusted fat thickness (cm), FW = final weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).



**Table 2.5.** Genetic parameter estimates<sup>1</sup> (SE) for multivariate models for days on feed (DtF<sup>2</sup>) and carcass traits<sup>3</sup>

Response Trait		Covariate				
1	2		$r_g$	$r_r$	$h_1^2$	$h_2^2$
DtF	AFT	None	-0.05 (0.06)	0.10 (0.04)	0.38 (0.03)	0.50 (0.04)
		FW	0.01 (0.06)	0.08 (0.04)	0.38 (0.03)	0.52 (0.04)
		HCW	0.04 (0.06)	0.03 (0.04)	0.38 (0.03)	0.52 (0.04)
		MARB	-0.05 (0.06)	0.06 (0.04)	0.39 (0.03)	0.49 (0.04)
		REA	-0.06 (0.06)	0.11 (0.04)	0.38 (0.03)	0.45 (0.04)
DtF	FW	None	-0.18 (0.06)	0.09 (0.04)	0.38 (0.03)	0.53 (0.04)
		AFT	-0.10 (0.06)	0.02 (0.04)	0.34 (0.03)	0.55 (0.04)
		HCW	0.29 (0.07)	-0.25 (0.03)	0.38 (0.03)	0.33 (0.03)
		MARB	-0.18 (0.06)	0.07 (0.04)	0.39 (0.03)	0.53 (0.04)
		REA	-0.16 (0.06)	0.09 (0.04)	0.38 (0.03)	0.53 (0.04)
DtF	HCW	None	-0.26 (0.06)	0.19 (0.04)	0.39 (0.03)	0.53 (0.04)
		AFT	-0.17 (0.06)	0.13 (0.04)	0.34 (0.03)	0.55 (0.04)
		FW	-0.37 (0.07)	0.29 (0.03)	0.37 (0.03)	0.33 (0.03)
		MARB	-0.26 (0.05)	0.17 (0.04)	0.39 (0.03)	0.53 (0.04)
		REA	-0.24 (0.06)	0.20 (0.04)	0.38 (0.03)	0.53 (0.04)
DtF	MARB	None	0.01 (0.06)	0.15 (0.04)	0.38 (0.03)	0.55 (0.03)
		AFT	0.02 (0.06)	0.11 (0.04)	0.33 (0.03)	0.55 (0.03)
		FW	0.03 (0.06)	0.14 (0.04)	0.38 (0.03)	0.55 (0.03)
		HCW	0.05 (0.05)	0.13 (0.04)	0.38 (0.03)	0.55 (0.03)
		REA	0.01 (0.06)	0.16 (0.04)	0.38 (0.03)	0.54 (0.03)
DtF	REA	None	-0.10 (0.06)	0.04 (0.04)	0.38 (0.03)	0.56 (0.04)
		AFT	-0.02 (0.06)	0.04 (0.04)	0.33 (0.03)	0.50 (0.04)
		FW	-0.03 (0.06)	0.00 (0.04)	0.38 (0.03)	0.56 (0.04)
		HCW	0.01 (0.06)	-0.05 (0.04)	0.38 (0.03)	0.56 (0.04)
		MARB	-0.09 (0.06)	0.04 (0.04)	0.39 (0.03)	0.55 (0.04)

<sup>1</sup>  $r_g$  = additive genetic correlation,  $r_r$  = residual genetic correlation,  $h_1^2$  = heritability of trait 1,  $h_2^2$  = heritability of trait 2.

<sup>2</sup> DtF = days on feed (days), the number of days from feedlot entry until harvest.

<sup>3</sup> AFT = adjusted fat thickness (cm), FW = final weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>)

**Table 2.6.** Genetic parameter estimates<sup>1</sup> (SE) for multivariate models for age at weaning (AAW<sup>2</sup>) and days to finish (DtF<sup>3</sup>)

Response Trait		Covariate				
1	2	for 2 <sup>4</sup>	$r_g$	$r$	$h_1^2$	$h_2^2$
AAW	DtF	None	-0.69 (0.11)	0.07 (0.01)	0.06 (0.01)	0.39 (0.03)
		AFT	-0.64 (0.12)	0.07 (0.01)	0.05 (0.01)	0.38 (0.03)
		FW	-0.68 (0.11)	0.07 (0.01)	0.05 (0.01)	0.39 (0.03)
		HCW	-0.70 (0.11)	0.07 (0.01)	0.06 (0.01)	0.39 (0.03)
		MARB	-0.73 (0.11)	0.07 (0.01)	0.06 (0.01)	0.40 (0.03)
		REA	-0.69 (0.11)	0.07 (0.01)	0.06 (0.01)	0.39 (0.03)

<sup>1</sup> $r_g$  = additive genetic correlation,  $r$  = repeatability for trait 1,  $h_1^2$  = heritability of trait 1,  $h_2^2$  = heritability of trait 2.

<sup>2</sup>AAW = age at weaning (days), the number of days from birth until weaning.

<sup>3</sup>DtF = days to finish (days), the number of days from weaning until harvest.

<sup>4</sup>AFT = adjusted fat thickness (cm), FW = final weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

**CHAPTER 3**

**GENETIC CORRELATION ESTIMATES BETWEEN ULTRASOUND TRAITS  
IN SIRES AND AGE AT SLAUGHTER AND DAYS TO FINISH IN  
COMMERCIAL PROGENY**

**ABSTRACT**

Ultrasound traits measured on seedstock animals have been utilized as indicator traits that are genetically correlated to economically relevant carcass traits in commercial relatives. In beef cattle genetic evaluations, there is a reduced availability of carcass data and as ultrasound measurements are relatively inexpensive to collect, the use of ultrasound measurements combined with carcass records can help to increase the accuracy of carcass trait evaluations. One economically relevant trait important to feedlot profitability is the number of days on feed to reach a desired endpoint. The availability of indicator traits for the number of days on feed in seedstock operations would be beneficial to making more timely and accurate selection decisions towards improving efficiency in the finishing phase. The objective of this study was to estimate genetic parameters between age at slaughter (AAS) or days to finish (DtF) and ultrasound traits including ultrasound intramuscular fat percentage (UIMF), ultrasound rib fat (URF), and ultrasound ribeye area (UREA). Data from steers and heifers (n=7,747) from the Germplasm Evaluation (GPE) project at the U.S. Meat Animal Research Center (USMARC) were collected including AAS, DtF and growth/carcass traits of adjusted fat thickness (AFT), final live weight (FW), hot carcass weight (HCW), marbling (MARB), and ribeye area (REA).

Ultrasound measurements from bulls and heifers (n= 6,631) with same sires as the crossbred progeny from USMARC were provided by International Genetic Solutions (IGS) for traits UIMF, URF, and UREA. AAS and DtF were adjusted to different carcass endpoints to reflect different potential marketing systems. Bivariate animal models including AAS and ultrasound traits, or DtF and ultrasound traits, were fitted including fixed effects of contemporary group (concatenation of birth year, birth season, sex, and treatment group), and linear covariates of breed proportion, direct heterosis, and for both AAS and DtF a carcass endpoint trait. Fixed effects for the ultrasound traits included contemporary group (ultrasound scan group which included sex), and linear covariates of breed proportion, direct heterosis, and age. Heritability estimates for UIMF, URF, and UREA were 0.42, 0.38, and 0.45, respectively. Genetic correlations between AAS or DtF and UIMF were negligible. Genetic correlations were low between DtF and UREA, ranging from -0.13 to -0.19, and were moderate between AAS and UREA, ranging from 0.25 to 0.42. Genetic correlations were moderate to high between AAS or DtF and URF, ranging from -0.52 to -0.68 and -0.54 to -0.59, respectively. Reduced AAS or DtF in commercial progeny therefore appears possible through selection in seedstock cattle based on ultrasonically measured rib fat.

**Key Words:** beef cattle, age at slaughter, days to finish, genetic parameters, carcass ultrasound

## INTRODUCTION

Carcass trait prediction using ultrasound technology has been utilized for over fifty years (Stouffer et al., 1959), and has been incorporated in beef cattle genetic evaluations (Bertrand et al., 2001). Even more importantly, records on growth and ultrasound traits are abundantly available to estimate variance components for incorporation into genetic selection programs; however, there is much less data available for carcass traits (Su et al., 2017). Therefore, most beef cattle breed associations utilize ultrasound traits along with carcass measurements in multi-trait models to increase accuracy of the evaluations as opposed to using just carcass data alone (Crews and Kemp, 2002; MacNeil and Northcutt, 2008). Live-animal ultrasound measurements on seedstock cattle have been shown to be accurate predictors of their respective carcass traits in harvested progeny (Perkins et al., 1992; Moser et al., 1998; Reverter et al., 2000; Hassen et al., 2001; Bergen et al., 2006a, Bergen et al., 2006b). However, most of these studies have focused on the carcass traits collected at harvest and not traits associated with feedlot efficiency. Santana et al. (2012) estimated genetic correlations between ultrasound carcass traits and residual feed intake (RFI) and feed conversion ratio (FCR). The genetic correlation estimate between RFI and rump fat thickness was 0.34, while the estimates between FCR and ultrasound ribeye area and backfat thickness were -0.43 and -0.31, respectively. The number of days an animal spends on feed has also been proposed as an economically relevant trait that could be used to improve efficiency but would not require directly capturing individual animal feed intake (Golden et al., 2000). Increased economic return to the production system could be achieved through selection to reduce the number of

days to a harvest specific endpoint (Archer et al., 1999). However, given days to harvest would only be recorded on terminal progeny, live-animal indicators that could be measured on seedstock animals could improve the rate of genetic gain for this trait complex. The objective of this study was to estimate genetic correlations between age at slaughter (AAS) or days to finish (DtF) recorded on commercial cattle and carcass ultrasound records including ultrasound intramuscular fat percentage (UIMF), ultrasound rib fat (URF), and ultrasound ribeye area (UREA) from seedstock relatives.

## **MATERIALS & METHODS**

For carcass data, all animal procedures followed USMARC standard operating procedure and cattle were treated according to Federation of Animal Science Societies guidelines (FASS, 2010). For ultrasound data, Animal Care and Use committee approval was not obtained given the data were extracted from existing industry databases, specifically the American Simmental Association and the American Gelbvieh Association.

### **Carcass Data**

All carcass data including AAS, DtF, adjusted fat thickness (AFT), adjusted based on the fat covering the outside of the carcass, final live weight (FW), hot carcass weight (HCW), marbling (MARB), and ribeye area (REA) ( $n = 7,747$ ) were obtained from the Continuous Germplasm Evaluation (GPE) project at the U.S. Meat Animal Research Center (USMARC) in Clay Center, Nebraska from 2007 to 2017. The breeds evaluated were part of the continuous GPE project, which periodically samples artificial insemination (AI) sires of the 18 most influential breeds in the U.S. with genetic

evaluation programs (Angus, Beefmaster, Brahman, Brangus, Braunvieh, Charolais, ChiAngus, Gelbvieh, Hereford, Limousin, Maine Anjou, Red Angus, Salers, Santa Gertrudis, Shorthorn, Simmental, South Devon, and Tarentaise) that conduct national cattle evaluations (Snelling et al., 2019). Continuous GPE included both spring and fall calving seasons each year. In each breeding season, the females were designated into two groups; the first group received a single service AI mating followed by natural service, while the other group were bred using natural service for the full season. Cows were exposed to F<sub>1</sub> and purebred bulls developed in GPE, and occasionally some Angus calving ease bulls from the USMARC selection program (Bennett, 2008) as heifers. Matings were designated by breed composition groups (F<sub>1</sub>, 50% to <75%; backcross, 75% to <87.5%; and purebred, ≥87.5% of any single breed) and birth year x season (Snelling et al., 2019). The pedigree included 85,872 animals.

Steers and heifers at a given management unit (pole shed) were weaned on the same date and were placed into the feedlot and co-mingled in pens with animals from other pole sheds. The animals were put on a starter ration that lasted 6 to 19 weeks before they were transitioned to a finishing ration until harvest. The animals placed into a pen at weaning stayed in the same pen until harvest. During finishing, some cattle were subjected to various experimental studies including treatments such as implants, beta agonists, and probiotics. Given these treatments can modify the amount of feed converted to lean muscle mass, treatment was considered as part of the contemporary group definition. Visual determination of group averages for predicted weight and fat endpoints for a given pen determined the time of harvest, with all animals in a pen harvested on the same date.

Final live weight was recorded before harvest. At harvest, fat thickness (adjusted based on the distribution of fat elsewhere on the carcass) (AFT), HCW, REA, and MARB (score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup>; USDA (1997)) were collected. The AAS is calculated as the number of days from birth until harvest and DtF is the number of days from weaning until harvest.

### **Ultrasound Data**

Ultrasound records (n=37,591) from bulls and heifers were obtained from International Genetic Solutions (IGS), along with pedigree information (n=63,134). Further description of the data can be found in Su et al. (2017). These data represented the progeny of Gelbvieh and Simmental sires (n=97) that had offspring in the USMARC dataset with AAS and DtF records (n=324). Ultrasound measurements included UIMF, URF, and UREA traits. After removing contemporary groups that had less than 20 animals included, the remaining dataset had 6,731 animals.

### **Statistical Analysis**

Variance components and fixed effects were estimated using ASReml version 4.0 (Gilmour et al., 2015). Bivariate models included either AAS or DtF and each ultrasound trait (UIMF, URF, and UREA). The bivariate model utilized is shown below:

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



where  $\mathbf{y}_i$  is a vector containing records on the  $i^{\text{th}}$  trait,  $\mathbf{X}_i$  is a design matrix relating the observations to the fixed effects in  $\mathbf{b}_i$ ,  $\mathbf{Z}_i$  is an incidence matrix relating observations to random additive genetic values in  $\mathbf{u}_i$ , and  $\mathbf{e}_i$  is a vector of random residuals. The random animal effects were assumed to have null means and (co)variances:

$$\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{u_1}^2 & \mathbf{A}\sigma_{u_1u_2} \\ \mathbf{A}\sigma_{u_2u_1} & \mathbf{A}\sigma_{u_2}^2 \end{bmatrix},$$

where  $\mathbf{A}$  is the Wright's numerator relationship matrix and  $\sigma_{u_i}^2$  is the additive direct genetic variance for  $i^{\text{th}}$  trait and  $\sigma_{u_1u_2}$  is the additive direct genetic covariance between the  $i^{\text{th}}$  traits. The random residual effects were assumed to have variances:

$$\begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_{e_1}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_{e_2}^2 \end{bmatrix},$$

where  $\mathbf{I}$  is an identity matrix and  $\sigma_{e_i}^2$  is the residual error variance for the  $i^{\text{th}}$  trait. No animal had both harvest data (AAS and DtF) and ultrasound data; therefore, residual covariances were null. For AAS and DtF, fixed effects included contemporary group (concatenation of birth year, birth season, sex, and treatment group), and linear covariates of breed proportion, direct heterosis, and a carcass trait for a given market endpoint (AFT, FW, HCW, MARB, REA). For the ultrasound traits (UIMF, URF, and UREA), fixed effects included contemporary group (scan group which included sex), and linear covariates of scan age, direct heterosis, and breed proportion.

## RESULTS AND DISCUSSION

Summary statistics for the growth, carcass, and ultrasound traits are shown in **Table 3.1**.

### Heritability estimates

Univariate heritability estimates were 0.42, 0.40, and 0.47 for UIMF, URF, and UREA, respectively (**Table 3.2**). Su et al. (2017) reported heritability estimates of 0.42, 0.37, and 0.44 for UIMF, URF, and UREA, respectively, from records taken from the American Simmental Association. Crews and Kemp (2001) obtained heritability estimates for ultrasound longissimus muscle area of 0.52 (0.47) and ultrasound fat depth of 0.35 (0.49) in composite bulls (heifers) at 14 months of age. Crews et al. (2003) observed heritability estimates of 0.47 (0.52) for ultrasound intramuscular fat percentage, 0.53 (0.69) for ultrasound fat thickness, and 0.37 (0.51) for ultrasound longissimus muscle area for Simmental bulls (heifers).

From the bivariate analyses, the heritability estimates for AAS ranged from 0.52 to 0.59 (**Table 3.3**) and for DtF ranged from 0.33 to 0.38 (**Table 3.4**), respectively, depending on the chosen endpoint.

### Genetic correlation estimates

Genetic correlation estimates (SE) between AAS and UIMF ranged from -0.11 to 0.10 (0.24 to 0.26), depending on the chosen endpoint for AAS (**Table 3.3**). For AAS and URF, the estimates ranged from -0.68 to -0.52 (0.19 to 0.21). The largest genetic correlation estimate was -0.68 between AAS and URF when the covariate AFT was used. This suggests with a fat-constant endpoint, greater genetic progress can be made in decreasing AAS if URF would be included within the genetic evaluation with positive

selection pressure. Although this was the largest genetic correlation, all estimates between AAS and URF were moderate regardless of the endpoint assumed for AAS. This is a possible artifact of harvest being, in part, determined by visual inspection of average weight or visual fatness of the pens of cattle. For AAS and UREA, the genetic correlations (SE) ranged from 0.21 to 0.43 (0.20 to 0.21), depending on the chosen endpoint for AAS (**Table 3.3**). Interestingly, the largest estimate of 0.43 between AAS and UREA was when no endpoint covariate for AAS was fitted. This was similar to the estimates when AFT (0.41) and MARB (0.37) covariates were fitted. This suggests that increasing UREA has the potential to increase AAS, specifically when non-weight endpoints are utilized.

Genetic correlation estimates (SE) between DtF and UIMF ranged from -0.14 to -0.01 (0.26 to 0.27), between DtF and URF ranged from -0.59 to -0.54 (0.23), and between DtF and UREA ranged from -0.19 to -0.12 (0.25), depending on the chosen endpoint for DtF (**Table 3.4**). The moderate negative genetic correlation estimates between DtF and URF suggest that regardless of the assumed endpoint for DtF, decreasing URF in seedstock animals could lead to decreased days on feed in commercial offspring.

Most studies that have evaluated age at slaughter and days to finish traits focused on estimating heritabilities and not genetic correlations with carcass traits (Berry et al., 2017; Speidel et al., 2016). Furthermore, multiple studies have reported genetic correlation estimates between ultrasound traits on yearling bulls and the carcass traits associated with their harvested progeny (e.g., Perkins et al., 1992; Moser et al., 1998; Reverter et al., 2000; Hassen et al., 2001; Bergen et al., 2006a, Bergen et al., 2006b), but only a few have

reported genetic correlations between ultrasound or carcass traits and feed efficiency traits such as residual feed intake and feed conversion ratio (Hoque et al., 2005; Santana et al., 2012). Santana et al. (2012) reported genetic correlation estimates between FCR and ultrasound ribeye area or backfat thickness of -0.43 and -0.31, respectively. Furthermore, Hoque et al. (2005) found genetic correlations between FCR in Waygu bulls and carcass traits such as ribeye area, backfat thickness, and marbling score of their progeny as 0.99, -0.81, and -0.95, respectively. Additionally, genetic correlations between RFI and ribeye area, backfat thickness, and marbling score were 0.83, -0.74, and -0.41, respectively. Nkrumah et al. (2007) obtained genetic correlation estimates of feed efficiency traits and ultrasound traits for composite steers that differed from those reported by Hoque et al. (2005). They looked at a partial efficiency of growth (the energetic efficiency for ADG above maintenance), which was calculated as the ratio of ADG to the difference between average daily dry matter intake and expected dry matter intake for maintenance. The genetic correlation estimates between ultrasound back fat and residual feed intake, feed to gain ratio, partial efficiency of growth, and dry matter intake were -0.04, -0.29, 0.02, and 0.29, respectively. Genetic correlation estimates between ultrasound marbling score and those feed efficiency traits were 0.44, 0.08, -0.56, and 0.53, respectively, and for ultrasound longissimus muscle area the correlations were -0.65, 0.54, -0.76, and 0.44, respectively. The standard errors for these estimates ranged from 0.16 to 0.23. Given age at slaughter implicitly considers the amount of feed intake required to achieve a given weight gain, these traits would be more closely related to the feed to gain ratio rather than traits that only consider feed intake or partial efficiency. The

genetic correlation estimates between ultrasound traits and feed to gain ratio were similar to estimates in the current study both in direction and magnitude for AAS. Contrastingly, for days to finish and ultrasound traits, especially for UREA and UIMF, the genetic correlations estimated herein differed in direction. Mao et al. (2013) reported genetic correlations between feed efficiency traits and ultrasound traits for Angus or Charolais steers. For Angus steers, the genetic correlation estimates between ultrasound longissimus muscle area and residual feed intake, midpoint metabolic body weight, dry matter intake, average daily gain, and feed conversion ratio were 0.31, 0.89, 0.64, 0.53, and 0.06, respectively. The Charolais steers estimates were 0.30, 0.37, 0.34, 0.13, and 0.11 for the same traits, consecutively. Genetic correlation estimates between ultrasound back fat and residual feed intake, midpoint metabolic body weight, dry matter intake, average daily gain, and feed conversion ratio for Angus steers were 0.17, 0.23, 0.26, 0.21, and -0.02, respectively; in Charolais steers, the corresponding estimates were 0.33, 0.04, 0.29, 0.06, and 0.30, consecutively. The standard errors for these estimates ranged from 0.18 to 0.40, which was attributed to the small sample size in this study, which ranged from 71 to 100 animals depending on the year or breed on which the data were collected. The genetic correlation estimates reported in the current study differed in magnitude, and in some cases direction, from those involving FCR presented in Mao et al. (2013). The largest estimates tended to be those including midpoint metabolic body weight, specifically those from Angus steers. Mao et al. (2013) concluded that the small sample size, uniform management, and feedlot test environments could have led to increased estimates of genetic correlations.

## CONCLUSIONS

Moderate genetic correlation estimates between AAS or DtF and ultrasound traits suggest that selection to reduce a commercial animal's age at slaughter or days on feed is feasible with the addition of seedstock ultrasound traits into a genetic evaluation. Of the ultrasound traits investigated, the inclusion of URF would be the most likely to improve the accuracy of an evaluation for AAS or DtF in seedstock animals. However, progress could be limited if genetic variation for either the goal trait (preferably AAS) or the indicator trait (URF) is limited.

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## TABLES

**Table 3.1.** Summary statistics for harvest and ultrasound traits

Harvest Traits <sup>1</sup>	Counts	Mean (SD)	
		Steers <sup>3</sup>	Heifers <sup>3</sup>
AAS	7747	451 (18.4)	433 (20.4)
AAW	7747	164 (18.9)	151 (17.0)
AFT	7747	1.33 (0.48)	1.25 (0.44)
DtF	7747	287 (11.0)	281 (15.2)
FW	7747	626 (60.8)	548 (51.4)
HCW	7747	395 (39.9)	348 (33.8)
MARB	7747	506 (77.0)	501 (66.5)
REA	7747	87.9 (10.2)	88.4 (9.58)
Ultrasound Traits <sup>2</sup>		Bulls <sup>4</sup>	Heifers <sup>4</sup>
UIMF	6731	2.84 (0.77)	3.44 (0.98)
URF	6731	0.50 (0.19)	0.46 (0.19)
UREA	6731	86.9 (10.2)	68.7 (11.8)

<sup>1</sup>AAS = age at slaughter, the number of days from birth until harvest (days), AAW = age at weaning, the number of days from birth until weaning (days), AFT = adjusted fat thickness (cm), DtF = days to finish, the number of days from weaning until harvest (days), FW = final live weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

<sup>2</sup>UIMF = ultrasound intramuscular fat percentage (%), URF = ultrasound rib fat (cm), UREA = ultrasound ribeye area (cm<sup>2</sup>).

<sup>3</sup>Data obtained from the US Meat Animal Research Center from harvested animals.

<sup>4</sup>Data obtained from International Genetic Solutions from seedstock animals.

**Table 3.2.** Genetic parameter estimates<sup>1</sup> (SE) for univariate models for ultrasound intramuscular fat percentage (%) (UIMF), ultrasound rib fat (cm) (URF), and ultrasound ribeye area (cm<sup>2</sup>) (UREA)

Response			
Trait	Heritability	$\sigma_a^2$	$\sigma_e^2$
UIMF	0.42 (0.06)	0.17 (0.02)	0.23 (0.02)
URF	0.40 (0.05)	0.007 (0.001)	0.01 (0.001)
UREA	0.47 (0.05)	28.1 (3.69)	31.9 (2.72)

<sup>1</sup> $\sigma_a^2$ = additive genetic variance,  $\sigma_e^2$ = residual variance.

**Table 3.3.** Genetic parameter estimates<sup>1</sup> (SE) for multivariate models for ultrasound intramuscular fat (%) (UIMF), ultrasound rib fat (cm) (URF), ultrasound ribeye area (cm<sup>2</sup>) (UREA) and age at slaughter (days) (AAS)

Response Trait		Covariate <sup>2</sup>			
1	2		$r_g$	$h_1^2$	$h_2^2$
UIMF	AAS	None	0.08 (0.25)	0.42 (0.06)	0.54 (0.04)
		AFT	0.01 (0.26)	0.42 (0.06)	0.52 (0.04)
		FW	0.10 (0.24)	0.42 (0.06)	0.57 (0.04)
		HCW	0.06 (0.24)	0.42 (0.06)	0.56 (0.04)
		MARB	-0.11 (0.25)	0.42 (0.06)	0.58 (0.04)
		REA	0.07 (0.25)	0.42 (0.06)	0.59 (0.04)
URF	AAS	None	-0.57 (0.21)	0.41 (0.05)	0.54 (0.04)
		AFT	-0.68 (0.19)	0.41 (0.05)	0.52 (0.04)
		FW	-0.58 (0.20)	0.40 (0.05)	0.57 (0.04)
		HCW	-0.55 (0.20)	0.40 (0.05)	0.56 (0.04)
		MARB	-0.54 (0.20)	0.41 (0.05)	0.59 (0.04)
		REA	-0.52 (0.21)	0.41 (0.05)	0.59 (0.04)
UREA	AAS	None	0.43 (0.20)	0.47 (0.05)	0.54 (0.04)
		AFT	0.41 (0.20)	0.47 (0.05)	0.53 (0.04)
		FW	0.24 (0.21)	0.47 (0.05)	0.57 (0.04)
		HCW	0.21 (0.21)	0.47 (0.05)	0.56 (0.04)
		MARB	0.37 (0.20)	0.47 (0.05)	0.59 (0.04)
		REA	0.31 (0.21)	0.47 (0.05)	0.59 (0.04)

<sup>1</sup> $r_g$  = genetic correlation,  $h_1^2$  = heritability of trait 1,  $h_2^2$  = heritability of trait 2.

<sup>2</sup>AFT = adjusted fat thickness (cm), FW = final weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

**Table 3.4.** Genetic parameter estimates<sup>1</sup> (SE) for multivariate models for ultrasound intramuscular fat (%) (UIMF), ultrasound rib fat (cm) (URF), ultrasound ribeye area (cm<sup>2</sup>) (UREA) and days to finish (days) (DtF)

Response Trait		Covariate <sup>2</sup>			
1	2		$r_g$	$h_1^2$	$h_2^2$
UIMF	DtF	None	-0.09 (0.26)	0.42 (0.05)	0.33 (0.03)
		AFT	-0.12 (0.26)	0.42 (0.06)	0.33 (0.03)
		FW	-0.01 (0.27)	0.42 (0.05)	0.38 (0.03)
		HCW	-0.04 (0.27)	0.42 (0.06)	0.38 (0.03)
		MARB	-0.14 (0.27)	0.42 (0.06)	0.38 (0.03)
		REA	-0.06 (0.27)	0.42 (0.06)	0.38 (0.03)
URF	DtF	None	-0.54 (0.23)	0.39 (0.05)	0.33 (0.03)
		AFT	-0.56 (0.23)	0.39 (0.05)	0.33 (0.03)
		FW	-0.58 (0.23)	0.40 (0.05)	0.38 (0.03)
		HCW	-0.58 (0.23)	0.40 (0.05)	0.38 (0.03)
		MARB	-0.56 (0.23)	0.40 (0.05)	0.38 (0.03)
		REA	-0.59 (0.23)	0.40 (0.05)	0.38 (0.03)
UREA	DtF	None	-0.14 (0.25)	0.47 (0.05)	0.38 (0.03)
		AFT	-0.19 (0.25)	0.47 (0.05)	0.33 (0.03)
		FW	-0.13 (0.25)	0.47 (0.05)	0.38 (0.03)
		HCW	-0.14 (0.25)	0.47 (0.05)	0.38 (0.03)
		MARB	-0.13 (0.25)	0.47 (0.05)	0.38 (0.03)
		REA	-0.12 (0.25)	0.47 (0.05)	0.38 (0.03)

<sup>1</sup> $r_g$  = genetic correlation,  $h_1^2$  = heritability of trait 1,  $h_2^2$  = heritability of trait 2.

<sup>2</sup>AFT = adjusted fat thickness (cm), FW = final weight (kg), HCW = hot carcass weight (kg), MARB = score where 400 = Slight<sup>00</sup> and 500 = Small<sup>00</sup> (USDA, 1997), REA = ribeye area (cm<sup>2</sup>).

## CHAPTER 4

### SYNTHESIS

#### CONCLUDING REMARKS

The goal of increased efficiency in the production system for the beef cattle industry has gained momentum in the past two decades. Particularly in the feedlot sector, a drive for efficiency has risen both due to a desire to decrease costs and increase outputs as well as concerns regarding environmental sustainability. Yet, even with the large efforts to identify efficient animals, a dry matter intake EPD was the only genetic evaluation trait available to predict genetic merit for costs related to finishing cattle. However, feed intake is only one of the components that affect production costs. For instance, animals who spend less time in the feed yard will utilize less resources, including less labor, less yardage, and less morbidity or mortality. Due to the elevated costs to collect feed intake data as well as the various definitions that represent this trait, the question of which traits selection pressure should be applied to became challenging. Fortunately, another definition for feedlot efficiency, days to finish, can be described as a function of the amount of feed consumed, growth rate, and most importantly the rate of tissue deposition. As this trait is calculated as the difference between harvest date and weaning date, there is no need to collect expensive feed intake data. Days to finish was identified in other studies with the potential for selection to reduce the number of days an animal spends on feed. Therefore, the purpose of this dissertation was to estimate genetic parameters for days to finish with carcass trait covariates towards a specific finish target as well as other

traits such as age at slaughter and age at weaning, and to consider their relationships with growth and harvest traits. Animals that would have days to finish or age at slaughter traits are predominately within the commercial sector, where record keeping is not always a top priority. Thus, to make genetic progress in future generations, a need to identify indicator traits that could be utilized for selection to reduce days to finish or age at slaughter in genetic evaluations at the seedstock level were essential. A second objective of this dissertation was to estimate genetic correlations between days to finish and age at slaughter traits from commercial progeny with a common sire to ultrasound traits collected from seedstock progeny.

A key conclusion was that selection could be utilized to reduce the age at slaughter and the number of days on feed. However, the extent of variation in days to finish was less than in other efficiency traits considered, with most of the variation resulting from different weaning dates. As days to finish was a portion of the time for age at slaughter, the lack of variation is consistent across both traits, making the utilization of these traits in genetic evaluations questionable. Furthermore, a reduction in the age at slaughter could have an undesirable impact on the age at weaning component, if not considered together. Based on the genetic correlation estimates, selection decisions based on seedstock ultrasound traits could be used to reduce a commercial animal's age at slaughter or days to finish. Although ultrasound rib fat would provide improved accuracy in the evaluations, the genetic progress could be limited when low variation exists for days to finish or even one of the ultrasound traits. Ultimately, although age at slaughter and days to finish could be used for selection, the lack of variation within the dataset limits the



utility of using these traits towards reducing production costs and increasing environmental sustainability within the beef cattle industry.