

University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

Theses and Dissertations in Animal Science

Animal Science Department

7-26-2018

Identifying Breed Effects for Cow Mature Weight

Madeline J. Zimmermann

University of Nebraska-Lincoln, madelinez@huskers.unl.edu

Follow this and additional works at: <http://digitalcommons.unl.edu/animalscidiss>



Part of the [Agriculture Commons](#), [Beef Science Commons](#), and the [Meat Science Commons](#)

Zimmermann, Madeline J., "Identifying Breed Effects for Cow Mature Weight" (2018). *Theses and Dissertations in Animal Science*. 166.
<http://digitalcommons.unl.edu/animalscidiss/166>

This Article is brought to you for free and open access by the Animal Science Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Theses and Dissertations in Animal Science by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

IDENTIFYING BREED EFFECTS FOR COW MATURE WEIGHT

by

Madeline J. Zimmermann

A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
In Partial Fulfillment of Requirements
For the Degree of Master of Science

Major: Animal Science

Under the Supervision of Professor Ronald M. Lewis

Lincoln, Nebraska

August, 2018

IDENTIFYING BREED EFFECTS FOR COW MATURE WEIGHT

Madeline Jean Zimmermann, M.S.

University of Nebraska, 2018

Advisor: Ronald M. Lewis

Mature weight (**MWT**) in beef cattle has increased over the past 30 yr. In general, larger cows are costlier to maintain than smaller cows, and their profitability depends on their production environment. A wide range of beef production environments exist in the United States. There are also a variety of beef cattle breeds that can be chosen and mated to create a type of cow which will be optimally suited to excel in a given environment. However, there remains a need for tools allowing effective comparison among breeds to facilitate such decision making. Unfortunately, estimated progeny differences (**EPD**) for MWT are not currently available in most breeds. However, understanding growth to maturity and estimating breed effects for MWT can facilitate more informed breeding systems that rely on MWT as a proxy for cow maintenance costs.

First, growth from weaning to maturity was studied using weight data of crossbred cows from the Germplasm Evaluation Program (**GPE**) at the U.S. Meat Animal Research Center in Clay Center, Nebraska. Brody, spline, and quadratic functions were fitted. For the spline and quadratic functions, MWT was estimated at 6 yr of age from fitted parameters. The spline function seemed to fit these data best, but the Brody function was more reliable for estimating MWT. Its estimated values were consistent even when weights taken at younger ages were used to estimate MWT, with few extreme MWT estimates generated.

Second, MWT estimates from the aforementioned functions were analyzed by fitting an animal model including fixed effects of breed fractions and birth year-season contemporary group, and linear covariates of direct and maternal heterosis. Resulting breed covariate solutions were divided by 2 to obtain breed of sire solutions. Breed of sire solutions were adjusted for sire sampling to determine the breed effect for MWT in each of 18 commonly-used beef cattle breeds represented in the GPE population. Since MWT EPD were not available for most breeds, yearling weight EPD was used as a proxy. The breed effects calculated can help seedstock producers identify appropriate breeds that will suit their operation's unique environments and breeding goals.

Key Words: beef cattle, Brody function, growth, mature weight, quadratic function, spline function

DEDICATION

In honor of my grandfather, Karl Zimmermann, a proud Cornhusker (Mechanical Engineering, class of 1950) and Navy veteran.

ACKNOWLEDGEMENTS

I would like to thank Dr. Ron Lewis for sharing his knowledge, support, enthusiasm, and patience with me throughout my graduate studies, and also as an undergraduate at Virginia Tech. It was his teaching which inspired me to pursue quantitative genetics as a career. I am both humbled and grateful for the opportunity to continue my studies under his tutelage and the opportunities that doing so has provided.

I would like to thank my Committee members, Dr. Matt Spangler and Dr. Larry Kuehn, for their engagement in my program. Their input and expertise were invaluable. Additionally, I am extremely grateful for the time they have taken outside of regular committee duties to help and teach me. I am continuously inspired by the depth of their knowledge and efficacy in using it.

I would like to thank the staff at USMARC, especially Dr. Mark Thallman and Dr. Warren Snelling, for allowing me to work with such interesting data and offering valuable contributions along the way. I would also like to thank my colleagues at UNL for their support, advice, and friendship throughout the duration of my program.

I would like to thank my “barn family,” especially Jamie and Eric Carman, for facilitating Bandit’s excellent care so I could focus on my work without worry.

Last but certainly not least, I would like to thank all of my family and friends for cheering me on. I’d especially like to thank my parents for offering their support in innumerable ways, at all hours of the day and night, and Matt Miller for helping me keep things in perspective and reminding me to take care of myself.

TABLE OF CONTENTS

List of Tables	ix
List of Figures	xi
Chapter 1: Literature Review	12
Background	12
Industry Problems	18
Upward Trends in Cow Mature Size	18
Mature Size and Efficiency	19
Mature Size and Cow Retention	23
Comparing EPD from Different Breeds	25
Across-Breed Adjustment Factors	26
Challenges	32
Direct/Maternal Effects	32
Crossbred Population.....	37
Genetic Groups	39
Comprehensively Describing Growth to Maturity	42
Project Objectives	49
Literature Cited	50
Chapter 2: Growth From Weaning to Maturity in Crossbred Beef Cattle.....	59
Abstract	59
Introduction	60

Materials and Methods	61
Animals.....	61
Data.....	63
Statistical Analyses	63
Results	66
Fit of Curves	66
Parameter Estimates	68
Discussion	69
Mature Weight.....	69
Weaning Weight	71
Maturing Constant	72
Knot	72
Conclusions	73
Literature Cited	74
Chapter 3: Breed of Sire Effects for Mature Weight in Crossbred Cattle	89
Abstract	89
Introduction	90
Materials and Methods	92
Animals.....	92
Growth Functions	93
Breed and Heterotic Effects.....	94
Analysis	95
Results	98

Heterosis	98
Genetic Parameters	98
Breed of Sire Effects.....	99
Discussion	100
Heterosis	100
(Co)Variance Ratios	101
Breed of Sire Effects.....	104
Conclusions	105
Acknowledgements	106
Literature Cited	106
Chapter 4: Synthesis	119
Introduction	119
Study 1: Growth from Weaning to Maturity.....	120
Weight Data.....	120
Fitting Growth Curves.....	121
Study 2: Breed of Sire Effect Calculation.....	123
Model Fitting	123
Calculation of Breed of Sire Effects.....	126
Future Applications	127
General Reflections and Suggestions.....	128
Conclusions	130
Literature Cited	131
Complete List of References.....	134

LIST OF TABLES

Table 2.1. Summary of the average quality of the fit of 3 growth functions to individual weight-age data on crossbred cows preceding editing (n = 5,632).....	80
Table 2.2. Measures of skewness and kurtosis of mature weight estimates after editing (n = 4,721) from the Brody, spline, and quadratic functions.....	83
Table 2.3. ANOVA results analyzing significance of model fitted, age at final (oldest) record, and their interaction on mature weight estimate (n = 4,721).....	85
Table 2.4. Pearson (above diagonal) and Spearman (below diagonal) phenotypic correlations between mature weights estimated for crossbred cows (n = 4,721) from Brody, spline, and quadratic functions.....	86
Table 2.5. Average growth parameter values and standard deviations estimated from 3 functions using weight records from crossbred cows (n = 4,721).....	87
Table 2.6. Results of paired t-tests between weights estimated by different functions for crossbred cows (n = 4,721).....	88
Table 3.1. Estimates of direct and maternal heterosis for growth function parameters..	111
Table 3.2. (Co)variances (SE) of direct additive, maternal additive, and residual effects, of Brody parameter functions.....	112
Table 3.3. (Co)variance of direct additive, maternal additive, maternal permanent environment, and residual effects for Spline function growth parameters.....	113
Table 3.4. (Co)variances of direct additive, maternal additive, maternal permanent environment, and residual effects (SE) of parameters from a quadratic function.....	114

Table 3.5. Breed of sire effects expressed as a deviation from Angus, breed of sire solutions, and average EPD of mature weight in 18 different GPE breeds.....	115
Table 3.6. Parameter-specific regression coefficient of cow mature weight estimate (kg) on sire yearling weight EPD (kg).....	117
Table 3.7. Pearson (above diagonal) and Spearman (below diagonal) correlations between breed effects for mature weight estimated by Brody, spline, and quadratic functions.....	118

LIST OF FIGURES

Figure 2.1. Average fits of Brody, spline, and quadratic curves to weight-age data of crossbred cows.....	79
Figure 2.2. Distribution of mature weights estimated for crossbred cows after editing (n = 4,721) from the Brody, spline, and quadratic functions.....	81
Figure 2.3. Quantile-quantile plots of mature weight estimates after editing (n = 4,721) from the Brody, spline, and quadratic functions.....	82
Figure 2.4. Distribution of mature weights estimated for crossbred cows using the Brody, spline, and quadratic functions, separated by age at final (oldest) weight measurement (n = 319 for 3 yr old; n = 672 for 4 yr old; n = 3,730 for 5 yr old).....	84

CHAPTER 1: LITERATURE REVIEW

BACKGROUND

Around the 1970s, the Canadian Department of Agriculture set up quarantine facilities and procedures facilitating the introduction of many European breeds to North America, resulting in an influx of new breeds to Canada and the United States (Gregory et al., 1982; Notter and Cundiff, 1991) New breeds with variable phenotypes were a valuable addition for producers seeking to match genetic resources to varying environments while maximizing output per unit of input. Producers who wished to use only 1 breed now had more options from which to choose a breed best suited to their production environments. Others could select different breeds to systematically mate such that the resulting offspring or genetic pools had a blend of characteristics more favorable to the producer's production environment. Designing a breeding program to optimize cattle's genetic fit to the production environment was viewed as especially useful for production systems maintaining breeding animals; while cattle finishing environments had become more uniform, breeding animals could be subject to a wide range of temperature, precipitation, humidity, and forage quality conditions, creating significant opportunity to tailor genotypes to environments through crossbreeding (Gregory et al., 1982).

In 1969, the United States Meat Animal Research Center (**USMARC**) in Clay Center, Nebraska, implemented the Germ Plasm Evaluation Program (**GPE**) to objectively characterize these new cattle breeds for economically relevant traits (**ERT**) so

that producers could make informed decisions on what biological types would be most useful for their individual production situations (Gregory et al., 1982; USDA-ARS, 1974). In the first breeding cycle (cycle I, 1969-1971), Hereford, Angus, Jersey, South Devon, Limousin, Simmental, and Charolais bulls were bred via artificial insemination (AI) to Angus and Hereford cows. In cycle II (1972-1973), Hereford, Angus, Red Poll, Brown Swiss, Gelbvieh, Maine Anjou, and Chianina bulls were mated to Hereford, Angus, Red Poll, and Brown Swiss cows (USDA-ARS, 1974). In cycle III (1974-1975), Hereford, Angus, Brahman, Sahiwal, Pinzgauer, and Tarentaise bulls were mated to Hereford and Angus cows (USDA-ARS, 1976). In cycle IV (1986-1990), Hereford, Angus, Longhorn, Piedmontese, Charolais, Salers, Galloway, Gelbvieh, Pinzgauer, Nellore, and Shorthorn bulls were used (USDA-ARS, 1990). In cycle V (1992-1994), Hereford, Angus, Tuli, Boran, Belgian Blue, Brahman, and Piedmontese bulls were mated to Hereford, Angus, and MARC III ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Pinzgauer, and $\frac{1}{4}$ Red Poll) cows (USDA-ARS, 1994). In cycle VI (1997-1998), Hereford, Angus, Norwegian Red, Swedish Red and White, Friesian, and Wagyu bulls were mated to Hereford, Angus, and MARC III cows (USDA-ARS, 2001a). In cycle VII (1999-2000), Hereford, Angus, Red Angus, Charolais, Limousin, Simmental, and Gelbvieh bulls were mated to Hereford, Angus, and MARC III cows (USDA-ARS, 2001b). In the final cycle (cycle VIII, 2001-2002), Hereford, Angus, Brangus, Beefmaster, Bonsmarra, and Romosinuano bulls were mated to Angus and MARC III cows (USDA-ARS, 2006). Beginning with the full 2007 calving season, animals have been continuously sampled from the industry. Eighteen sire breeds are represented in the population: Angus, Hereford, Red Angus, Shorthorn, South Devon, Beefmaster, Brahman, Brangus, Santa

Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine-Anjou, Salers, Simmental, and Tarantaise. The population is now maintained such that it reflects industry use: more progeny are produced from breeds with greater registration numbers. Animals are currently evaluated for 8 different traits: birth weight (**BWT**), weaning weight (**WWT**), yearling weight (**YWT**), maternal milk, marbling score, ribeye area, fat thickness, and carcass weight (Kuehn and Thallman, 2016).

Relative to growth traits, breed associations typically record information on BWT, WWT, YWT, and carcass weight and some also record information on mature cow weights (**MWT**). Weights are typically standardized to a common age. The Beef Improvement Federation (**BIF**) and many other associations standardize to 205 d for WWT and 365 d for YWT, although some organizations have developed different adjustment procedures more appropriate to their specific breed (BIF, 2016). However, this practice neglects information collected at intermediate ages which may be of use. For example, there is a management advantage to weaning early during droughts, and animals are often marketed at times besides weaning and yearling ages. Furthermore, collecting weight information is becoming easier with more advanced technology like automated weighing systems. Information on intermediate ages would help characterize each animal's growth (Garrick, 2005), although pragmatically such data may be challenging to collect. As of 2016, BIF guidelines still include only evaluation for BWT, WWT, YWT, and carcass weight (BIF, 2016).

Using breed association data for genetic evaluation tends to limit records to those animals registered with a particular breed association, but crossbred and composite cattle are currently used in both commercial and seedstock operations. Therefore, multi-breed

analyses producing estimated progeny differences (**EPD**) for many breeds on a single genetic base is an area of intense interest. One complication in doing this is combining pedigree and performance data while animals may be registered in multiple breed association databases. If there is no reference to their original association registration numbers, there is a risk that information could be unintentionally duplicated (Garrick, 2005).

Beef cattle evaluation in the 1970s and 1980s also saw rapid advancements with the introduction of best linear unbiased prediction (**BLUP**) theory and rapid methods for assembling the inverse of the pedigree-based numerator relationship matrix (Henderson, 1976). Gradually, more comprehensive EPD, which included more pedigree information, have been developed for use as ERT. According to Golden et al. (2000), ERT directly affect profitability through association with a specific income or expense source. Conversely, indicator traits do not directly affect income or expense but may provide useful information through their correlation with ERT.

Hazel (1943) introduced the concept of a selection index as a more efficient alternative method of selection, as compared to independent culling levels or tandem selection. Basically, a selection index consists of the product of genetic merit and economic merit, summed up for all traits included. In modern selection indexes, ERT should be chosen as the traits of interest, with EPD or EBV typically used as the selection criteria (Pearson, 1982). Among the first ERT for which EPD were developed were growth traits, calving ease, and economically relevant carcass traits. Heifer pregnancy, stayability, and mature cow feed requirements have since followed suit (Garrick, 2005). Additional ERT, for which EPD would be useful, are resistance to various diseases or

parasites, or tolerance for other stressors such as temperature extremes. While some breed organizations report mature height or weight and docility, those that do not could benefit from their inclusion as well, especially if extremes in these traits are problematic.

Economic values may be estimated using a variety of techniques, but they basically relate income and expenses to the animals' traits of interest. Future production levels and prices must be considered since years will pass between implementation of selection goals and realization of the resulting progeny's value (Pearson, 1982). A single, industry-wide set of economic values is acceptable when the index will be applied to a relatively consistent population and production environment with consistent breeding objectives, but it may be less effective when the populations to which the index is applied are variable. Beef cattle production systems are subject to a wide variety of production environments, employ a diverse group of breeds (Notter, 1999), and are run by producers with a variety of marketing needs and risk aversion. Thus, a single, industry-wide set of economic values may not be appropriate for beef cattle (Upton et al., 1988).

Some suggest personalized selection indexes with separate profit equations for unique management scenarios (Bourdon, 1998; Upton et al., 1988). These may be generated by a variety of techniques, including bioeconomic models, non-mechanistic approaches (e.g., profit equations or statistical models), and sire selection by simulation. According to Bourdon (1998), non-mechanistic approaches are often easier to use but can be inferior in accounting for nonlinear biological processes. Bioeconomic models allow for easier model reparameterization, and can simulate the nonlinear biological processes with which non-mechanistic approaches often struggle. However, their development can be challenging, time consuming, and costly. Sire selection by simulation is similar to

bioeconomic modeling. First, physiological breeding value (**PhBV**) is calculated for potential sires. A PhBV is conceptually similar to a conventional EBV, except it indicates additive performance potential under optimal environmental conditions and is not population dependent. Then, the operation and female population are characterized and simulated, including genetic changes and various combinations of sire and dam biological types. The simulation develops an optimal range of PhBV for important traits, which can aid in sire selection. Bourdon (1998) admitted that categorizing real animals into discrete and idealized categories is crude, that some traits may not have an optimal biological type, and that the approach requires tremendous computational effort. However, he also argued that the approach can aid with mating decisions and can better account for genetic change across time than other methods. While calculating individualized selection indexes may be useful, especially in non-uniform industries, all approaches require substantial time, effort, and computation power, which must be practically considered. Individualized indexes are not currently implemented.

A trait which is undergoing selection, whether through use of an index or otherwise, must be heritable (h^2) in order for selection to result in genetic change. Mature weight – and also mature height – is estimated to be moderately to highly heritable. Dib et al. (2009) estimated h^2 of MWT and mature height between 0.4 and 0.7 based on American Angus Association data, although mature height was slightly more heritable and less impacted by permanent environmental effects. When working with repeated records, if permanent environmental impacts are ignored, genetic parameter estimates may be inflated. Since MWT and height are substantially affected by additive genetic effects, selection on MWT and height is expected to yield genetic change. Further, Upton

et al. (1988) suggested MWT as a related trait to cow maintenance cost. The latter is a major factor affecting a herd's costs and returns. Selection for MWT is both genetically feasible and economically meaningful.

INDUSTRY PROBLEMS

Upward Trends in Cow Mature Size

Numerous studies have indicated an increase in MWT and mature hip height since the 1970s (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016). The average weight of cows at slaughter has increased from 475 to 621 kg between 1975 and 2005, which has increased production costs (McMurry, 2008). The USDA-ERS, Commodity and Economic Division (1973) reported the average live weight of Choice steers across 7 markets as 509.8 kg in 1972, and about the same in 1970 and 1971. More recently, the USDA-NASS (2017) reported the average live weight of federally inspected cattle as 621.0 kg. The USDA reports highlight an increase in weight of approximately 111.0 kg from the 1970s to 2017.

Increased MWT has been observed in individual breeds as well as in commercial cattle. Freetly et al. (2011) found an increase of 26 to 98 kg in MWT, and a corresponding increase in hip height, for Angus, Hereford, and Brahman cows born between 1992 and 1994 relative to cows born in the 1970s. While traditionally Brahman cattle were considered heavier than Hereford and Angus cattle, Freetly et al. (2011) suggested that increases in MWT have removed or reranked this difference in modern cows. However, Brahman-sired cows were consistently identified as taller in both 1970s-

born and 1990s-born cows. Hereford-sired cows displayed a greater relative increase in hip height during that time period. An increase in MWT over the past 30 yr is clearly visible within individual breeds.

Mature Size and Efficiency

Logically, larger cows require greater daily dry matter intake (**DMI**), both when dry and when lactating (Walker et al., 2015). Jenkins and Ferrell (1983) estimated that approximately 50% of total feed energy for beef production is used for cow maintenance, and the size and capacity of organs must increase to produce and maintain more body tissue, requiring more energy (DiCostanzo et al., 1990). Accordingly, DMI increases to supply this additional energy at a rate of 1.4 kg/day per 90.7 kg increase in cow weight (NRC, 1996). Despite daily DMI differences, Walker et al. (2015) did not find differences between efficiency (measured as residual feed intake, **RFI**) of heavier and lighter cows. However, this may have reflected the physiological state of the cows evaluated (lactating and non-lactating) and the feeding system used (chopped forage).

An increased demand for nutritional intake associated with heavier weight implies that a production system with a given amount of input would be able to support fewer animals of heavier MWT. Whether this trade-off is profitable depends on whether the increased sale value of the increased weight outweighs the increased cost of feed to maintain the increased weight, which in turn depends on the production system's efficiency (Garrick, 2005). Additionally, the environment and forage provided by each production system creates a distinct relationship between stocking rate (**SR**) and animal performance (Beck et al., 2016).

Beck et al. (2016) tested the effects of SR and mature body size on cow and calf performance, herd efficiency, and system economics. Heavy MWT cows were defined by a weight of approximately 564 kg (SD 27.3) and a hip height of 135 ± 2.5 cm, while light MWT cows were defined by a weight of approximately 459 kg (SD 28.8) with a hip height of 126 ± 2.5 cm. Four SR were tested: 1, 1.5, 2, and 2.5 cow-calf pairs/ha.

Beck et al. (2016) found that heavy-weight cows lost more weight during summer months, an effect which tended to increase ($P = 0.09$) with increased SR. Neither body weight (**BW**) nor SR rate affected pregnancy rates. In May, there was not a difference between BW of calves from heavy MWT versus light MWT cows. When calves were weaned in October, calf BW increased by 19 kg for every 100 kg increase in cow BW. However, the larger cows were less efficient than the smaller cows; each 100 kg increase in cow BW resulted in a 6.7 kg decrease in efficiency (measured as kg calf weaned per 100 kg cow BW). Efficiency and calf BW in both May and October were not affected by SR. Calf BW weaned per ha did increase 217 kg as SR increased by another cow/ha. While heavy and light MWT cows had calves of similar BW in May, the calves from heavy MWT cows had become heavier by weaning in October. However, the heavy cows were less efficient than the lighter cows. Denser SR seemed to increase the kg of calf weaned per ha.

In considering feed requirements, Beck et al. (2016) found that denser SR required more days of hay feeding and more hay fed per cow. Cow BW did not seem to affect these factors. Conversely, hay offered per day as a percentage of metabolic BW was not affected by SR and tended ($P = 0.08$) to increase with increasing BW. However,

neither cow BW nor SR affected the carrying cost per cow or per hectare. Practically, this implies similar costs regardless of whether heavier or lighter MWT cows are used.

Overall, Beck et al. (2016) did not observe the decreased carrying capacity and increased input costs found in other, similar studies they cited. They speculated that the environment in which their research was conducted may have caused this discrepancy to occur. Beck et al. (2016) conducted their research in southwestern Arkansas – a subtropical environment with year-round forage production potential – where pastures were composed of warm-season grasses maintained with ammonium nitrate, herbicide treatments, and an annual seeding. The cows used were mostly of British breeding – specifically Angus – and were treated with a variety of vaccines and parasite treatments. It is possible that different results may have been observed if the experiment was conducted in a different climate, if different grasses and hays were available, possibly of different nutritive values, if forage had been limited, if a different breed composition of cattle was used, or if cattle and/or pasture were treated differently.

Scasta et al. (2015) investigated efficiency of different-sized cows in a different type of environment: high-altitude, semi-arid rangeland near Laramie, Wyoming. Most of the grazing land was populated by native upland plant species producing between 300 and 6,700 kg/ha depending on local rainfall patterns. The pastures used by Scasta et al. (2015) clearly had different species and more variable production environments as compared to those used by Beck et al. (2016). Additionally, Scasta et al. (2015) sought to investigate the effect of drought on WWT independent of cow size; supplemental feed was not provided between June and October regardless of pasture production. There was no mention of pasture treatment or seeding in Scasta et al. (2015). Given the ample space

provided (2,226 ha in the summer pasture and 400 ha in the winter pasture) and lower stocking rate, it is unlikely that the pastures were fertilized or re-seeded.

Scasta et al. (2015) concluded that smaller cows were more efficient relative to their feed requirements, although this was somewhat conditional on annual precipitation. The study spanned 4 yr: 2011 had average levels of precipitation, 2012 was a severe drought, 2013 was slightly wetter than normal, and 2014 was unusually wet. Lighter cows weaned heavier calves and were significantly more efficient during the unusually wet year. Heavier cows weaned heavier calves but were significantly less efficient during the unusually dry year. The efficiency of light cows was more dramatically impacted by precipitation conditions than heavy cows: the difference in efficiency between the driest and wettest year was 0.18 for the lightest cows and only 0.02 for the heaviest cows. Pregnancy rate was not affected by cow BW. Scasta et al. (2015) speculated that the difference in performance between wet and dry years was partly due to rumen capacities.

Nutt et al. (1980) found that structurally larger cows had larger rumen capacities than structurally smaller cows, but fatter cows had smaller rumen capacities than thinner cows. Structural size was based on measurements of wither height, length, depth at heart girth, and hook width. Differential rumen sizes could possibly act as a physical mechanism for feed intake control. Cows with larger rumen capacities had higher DMI when grazing low quality pasture (e.g., rangeland used by Scasta et al., 2015). No difference in DMI between large- and small-rumen cows was observed when grazing high quality pasture (e.g., pasture used by Beck et al., 2016). Nutt et al. (1980) hypothesized that cows with larger rumens also ate faster. This phenomenon has been observed in sheep by Purser and Moir (1966). It would make sense that, during drought

years, larger cows with larger rumens could quickly consume large amounts of lower-quality forage, thereby securing the nutrients necessary to produce heavier calves as observed by Scasta et al. (2015). However, even though Scasta et al. (2015) reported that smaller cows weaned smaller calves during dry years, the smaller cows were biologically more efficient, i.e., they weaned relatively more pounds of calf per pound of BW and thus per unit of intake. Cow efficiency appears to be related to quality and quantity of feed available, and rumen capacity.

Mature Size and Cow Retention

Besides impacting maintenance costs and production efficiency, links between mature size and cow retention have also been reported. For example, Nugent et al. (1993) found a significant biological type x nutritional environment effect on post-partum interval (**PPI**). Nugent et al. (1993) studied PPI in different biological types of cattle and different daily metabolizable energy (**ME**) intakes. Cows used were multiparous purebred Angus, Braunvieh, Charolais, Gelbvieh, Hereford, Limousin, Pinzgauer, Red Poll, and Simmental. The breeds were classified into the following biological types based on genetic potential for milk production and growth: moderate milk and moderate growth (Angus, Hereford, and Red Poll), moderate milk and high growth (Charolais and Limousin), high milk and moderate growth (Braunvieh and Pinzgauer), and high milk and high growth (Gelbvieh and Simmental). Within breed, cows were randomly assigned non-lactation diets of different energy levels. Energy intakes were increased by the same amount in each dietary treatment during lactation. In all types, PPI was shortened as energy availability increased. High-growth breeds showed the greatest response to

increased energy availability, but they also had the longest PPI. The high-milk, high-growth type cows displayed shorter PPI than the high-growth, moderate-milk type cows. Nugent et al. (1993) concluded that breeds selected for high growth without selection for high milk production may allocate more energy towards maintenance, growth, and lactation than to resuming cyclicity, while breeds selected for both growth and milk production may allocate more energy towards reproduction. The authors did, however, note that breed sampling of biological types may have impacted the results.

Roberts et al. (2015) postulated that the findings of Nugent et al. (1993) may suggest an interaction between genotype and nutritional environment for PPI related to recent genetic trends for increased BW. As previously mentioned, maintaining increased BW requires increased nutritional inputs. Cows producing and reproducing in nutrient-sparse environments may struggle to meet the nutritional requirements to resume estrus due to the increased nutritional demands for maintaining their increased size. Essentially, in environments where nutrition is not plentiful, processes of self-maintenance employ most of the inputted resources, leaving little to be used for postpartum recovery. As a result, heavier BW cows take longer to recover between pregnancies, which is undesirable and inefficient.

This also supports the supposition of Beck et al. (2016) that they did not observe reduced production efficiency associated with heavier BW cows in their experiment, in contrast with numerous other studies, because of the environment in which their research was conducted. With a sub-tropical climate benefiting from year-round forage production in carefully maintained pastures, cows were exposed to more abundant nutrition than cows grazed in areas prone to harsh, barren winters or populated by sparse, weedy forage.

Without nutritional constraints, any differences in nutritional allocation efficiency would not be obvious. Thus, the advantage of a lighter MWT may be apparent in nutrient-sparse environments but not in environments where forage is abundant.

Comparing EPD from Different Breeds

The United States beef cattle industry is unique compared to other industries of animal production in that individual breed associations collect pedigree and performance data on their animals and subsequently report this information (Garrick, 2005). Practically, this entails numerous, independent entities responsible for collecting, evaluating, and disseminating information as opposed to a centralized entity responsible for records as in the poultry, swine, and dairy industries. Records come from different organizations with differing methods of data collection and evaluation, genetic trends, sampling rates, etc., for different breeds. Therefore, the EPD produced from these records are not readily comparable between breeds (Kuehn and Thallman, 2017a).

The lack of comparability between breeds is further complicated by lack of genetic ties and lack of uniform goals. An EPD depends on the population from which an individual has come as well as the individual's additive merit. For example, a large Jersey cow might have a positive WWT EPD within the Jersey breed. However, if that same cow was evaluated by a beef breed organization, it would most likely have a negative EPD since beef breed cows are generally heavier due to selection for growth traits (Bourdon, 1998). Since breed organizations emphasize different traits at different times, the differences between breeds is constantly changing (Kuehn and Thallman, 2016). For example, Notter and Cundiff (1991) noted that, while most of the breeds analyzed

displayed an increase in BWT, WWT, and YWT EPD from 1970 to 1984, Simmental EPD for all 3 traits decreased. This reflected priority in the Simmental breed organization for improving calving ease rather than growth. Overall, Notter and Cundiff (1991) noticed a reduction in BW EPD variance across breeds, indicating that the breeds analyzed were becoming more similar in size at birth, weaning, and as yearlings.

Even when equitable comparisons between EPD of bulls are possible, interactions with other traits that may be impacted by selection for mature size also must be considered (Garrick, 2005). For example, Dib et al. (2009) reported a strong, positive correlation between MWT and mature height, indicating that selection on one would yield a change in the same direction in the other trait. A positive correlation between permanent environmental effect of MWT and permanent environmental effect of mature height was also found.

ACROSS-BREED ADJUSTMENT FACTORS

According to Notter and Cundiff (1991), many breed evaluation experiments were carried out in North America during the 1970s. As previously described, Continental European breeds were being imported, and these experiments provided breeders with valuable information about these breeds' characteristics. However, this information was not updated even though the breeds experienced significant genetic trends, and sire sampling procedures were generally not well described. Thus, the information used to develop breeding plans was out of date and potentially misleading. Notter and Cundiff (1991) addressed this issue by using within-breed EPD to adjust breed comparisons for

sire sampling and genetic trends. Specifically, they focused on EPD for BWT, WWT and YWT. This concept was the forerunner to current, formal across-breed adjustment factors.

Notter and Cundiff (1991) used crossbred calves from cycles I, II, and III from the GPE program. The calves' sires were required to have an EPD available for the trait of interest from a breed active in the national cattle evaluation (NCE) program in 1989. Traits analyzed were BWT, WWT (200 d), YWT (365 d), and 420 d weight. In cases where measurements were obtained on a different day than prescribed, measurements were scaled to the appropriate day using either pre-weaning or post-weaning average daily gain. To make results comparable to previous GPE analyses, Notter and Cundiff (1991) created a model including the fixed effects of dam breed, calf birth year, dam age (2, 3, 4, or ≥ 5 years) and calf sex, sire breed, and covariates of BWT and calf's sire's EPD.

Current sire EPD were obtained from the 1989 NCE for all breeds except Polled Herefords (Notter and Cundiff, 1991). Due to a change in procedures for calculating Polled Hereford EPD, the 1990 NCE sire EPD were used instead for this breed. Mean EPD for all sires in each breed born in 1970 and 1984 also were collected. The 1970-born sires were considered approximately contemporaries of GPE sires, and the 1984-born sires were considered the youngest cohort of sires with enough progeny data to create accurate EPD. Comparison of current GPE sire EPD to 1970-born sire EPD reflected the quality of sire sampling. Little difference between the two would indicate that the sample of current GPE sires accurately reflected all industry sires in their age group. Comparison of current GPE sire EPD to 1984-born sire EPD reflected genetic trends. Regressing

actual calf scores on EPD gauged the ability of EPD to predict a calf's true value for the given traits (Notter and Cundiff, 1991).

Cundiff (1993) expanded the work of Notter and Cundiff (1991) into published across-breed adjustment factors. Others later modified the process to include additional effects. Van Vleck et al. (2007) described a recent application of these concepts. In prior years, across-breed adjustment factors were published only for BWT, WWT, YWT, and milk production, as in Van Vleck and Cundiff (2006). Van Vleck et al. (2007) adjusted breed association EPD for carcass traits: marbling score, fat thickness, ribeye area, and retail percentage. Van Vleck et al. (2007) ultimately calculated the adjustment factor as

$$ADJ(A - X) = [MARC(A) - MARC(X)] - [b_u \overline{EPD}_A - b_x \overline{EPD}_X]$$

where $ADJ(A - X)$ was the adjustment factor to compare some breed, A, to the base breed of X; $MARC(A)$ and $MARC(X)$ were the solutions for sire breeds A and X, respectively, from USMARC progeny; b_u and b_x were the regression coefficients corresponding to the type of measurement used to collect data on the trait (e.g., ultrasound or carcass measurement, accounting for differences in scale), and \overline{EPD}_A and \overline{EPD}_X were the average EPD for sires of breed A and X, respectively, with USMARC progeny, weighted by number of progeny. An explanation of this equation's derivation follows.

First, Van Vleck et al. (2007) adjusted USMARC progeny records for level of heterozygosity. Since the offspring involved in evaluation were F1 crosses, 100% heterosis was expected. However, not all F1 individuals exhibited 100% heterozygosity. Some F1 individuals resulted from similar breeds mating which would be considered to

have no heterozygosity. Alternatively, some individuals were born from mating crossbred dams with sires of a breed also represented in the dam, resulting in some but less than 100% heterozygosity. For example, if a MARC III cow ($\frac{1}{4}$ each Pinzgauer, Red Poll, Hereford, and Angus) was mated to an Angus sire, there would be some loci where Angus-derived alleles from the dam united with the sire's Angus alleles, creating a loss of heterozygosity. Progeny records were adjusted so that they were all equivalent to 100% heterozygosity.

Next, Van Vleck et al. (2007) used the heterosis-adjusted records to estimate sire breed effects and regression coefficients of USMARC progeny measurement on their sires' breed association EPD. Additional calculations included average EPD for each breed for animals born in the chosen base year (2003 in this analysis), average EPD for sires of USMARC progeny, and regression coefficients of USMARC progeny records on their sires' breed association EPD for each breed. Regression coefficients were pooled across breeds and by type of measurement used to generate carcass trait EPD (direct carcass or ultrasound measurement).

Once the appropriate averages and regression coefficients were estimated, Van Vleck et al. (2007) adjusted breed of sire effects to the expectation that the sires chosen had been born in the base year. First, sire breed solutions were adjusted for type of measurement and difference between average breed association EPD in the base year and average EPD of sires from the same breed with USMARC progeny using:

$$MARC(A, adj) = MARC(A) + b_u(\overline{EPD}_{yyA} - \overline{EPD}_A)$$

where $MARC(A, adj)$ was the adjusted breed of sire solution for breed A, $MARC(A)$ was the breed of sire solution from USMARC progeny records, b_u was the regression coefficient used to adjust EPD based on measurement type (ultrasound was used in this example), $\overline{EPD}yyA$ was the average EPD of breed A in the base year (yy), and $\overline{EPD}A$ was the average EPD for breed A sires of USMARC progeny, weighted by number of progeny.

The difference between the EPD of sire m, belonging to breed A, and the average EPD of breed A in the base year, adjusted for measurement type, was then be calculated as

$$MARC(A, m, adj) = MARC(A, adj) + b_u(EPD(A, m) - \overline{EPD}yyA)$$

where $MARC(A, adj)$, b_u , and $\overline{EPD}yyA$ were as previously described, and $EPD(A, m)$ was the breed A EPD of sire m (Van Vleck et al., 2007). Sire m of breed A and sire p of base breed X could then be compared as

$$MARC(A, m, adj) - MARC(X, p, adj)$$

By substitution, this becomes

$$\begin{aligned} & [MARC(A, adj) + b_u(EPD(A, m) - \overline{EPD}yyA)] \\ & - [MARC(X, adj) + b_x(EPD(X, p) - \overline{EPD}yyX)] \end{aligned}$$

where b_x was the appropriate regression coefficient for type of measurement used by breed X. This equation can then be algebraically rearranged (Van Vleck et al., 2007):

$$\begin{aligned} & [MARC(A, adj) - MARC(X, adj)] - [b_u\overline{EPD}yyA - b_x\overline{EPD}yyX] \\ & + [b_uEPD(A, m) - b_xEPD(X, p)] \end{aligned}$$

The first 2 bracketed segments of the above equation are the adjustment factor as they account for the constant factors comparing two breeds. Weight traits, in contrast to these carcass traits, did not require the average base year EPD to be multiplied by a regression coefficient accounting for different methods of collection (Van Vleck et al., 2007).

The process of generating adjustment factors as described by Van Vleck et al. (2007) is similar to using a series of prediction equations. Prediction equations take the common form of $\hat{y}_i = \hat{\mu}_y + b_{y \cdot x}(x_i - \hat{\mu}_x)$ where \hat{y}_i is the predicted value, $\hat{\mu}_y$ is the mean value of the trait for which we are making a prediction, $b_{y \cdot x}$ is the regression coefficient of the trait for which we are predicting on the trait we are using to make the prediction, x_i is the observed value that we are using to make a prediction, and $\hat{\mu}_x$ is the mean of this indicator trait in the animal's population. Further, the regression coefficient is defined as $b_{y \cdot x} = \frac{\hat{\sigma}_{xy}}{\hat{\sigma}_x^2}$, the covariance between indicator trait x and trait-of-interest y divided by the variance of indicator trait x (Van Vleck, 1993).

The process for calculating across-breed adjustment factors has since been updated. Kuehn and Thallman (2017b) calculated the adjustment factor (A_i) as

$$A_i = (M_i - M_x) - (EPD(i)_{YY} - EPD(x)_{YY})$$

where M_i and M_x are the breed of sire effects of breed i and the base breed, x , respectively. The $EPD(i)_{YY}$ and $EPD(x)_{YY}$ are the industry average within-breed EPD for breed i and the base breed, x , respectively. The M_i and M_x are, in turn, calculated as

$$M_i = \frac{USMARC(i)}{b} + (EPD(i)_{YY} - EPD(i)_{USMARC})$$

where M_i and $EPD(i)_{YY}$ are as previously defined. The $USMARC(i)$ is the breed of sire solution for breed i , which is half of the breed solution generated from an animal model accounting for various fixed and random effects as appropriate for the trait. The b is a regression coefficient of progeny performance on sire EPD, and the $EPD(i)_{USMARC}$ is the average EPD of breed i sires with USMARC descendants, weighted by the total relationship to their phenotyped descendants (Kuehn and Thallman, 2017b).

CHALLENGES

Direct/Maternal Effects

In order to study the change in a phenotype such as MWT across generations, both direct and maternal genetic effects must be considered. Direct genetic effects are passed from parent to offspring (Mrode, 2014). A sperm containing a random half of a sire's genetic material and an egg containing a random half of a dam's genetic material unite to form a progeny (Falconer and Mackay, 1996).

Willham (1980) defines maternal effects as an effect contributed to the phenotypic value of an offspring by his dam. These effects are a completely different phenomenon from other, maternally-inherited forms of familial resemblance such as maternal cytoplasmic inheritance or genomic imprinting (Wolf and Wade, 2009). Essentially, maternal effects are the dam's ability to provide an appropriate environment for her offspring.

Maternal effects may also be partitioned, usually into additive, permanent environmental, and random residual effects. The additive maternal effect describes the directly-heritable portion of the dam's ability to provide an appropriate environment for her offspring (Mrode, 2014). The permanent environmental effect captures factors that consistently affect the dam's ability to provide an environment for her offspring but are not directly heritable: the dam's dominance, epistasis, and permanent environmental influences on mothering traits. Residual effects include random environmental influences not accounted for elsewhere. Altogether, a mixed linear model for maternally influenced traits usually includes direct additive effects, maternal additive effects, permanent environmental effects, and residual effects (Mrode, 2014).

Maternally-influenced traits are subject to various complications: maternal additive and direct additive effects tend to be confounded, and there may be a genetic correlation between direct and maternal effects. Maternally-influenced traits also commonly take more time and effort to measure than other traits because they are only expressed in females, once they have reached puberty, mated, given birth, and raised the offspring long enough to measure the offspring's phenotype (Willham, 1980). These factors make it challenging to effectively measure and account for maternal effects in breeding programs, where ideally this type of information can be accumulated on both candidate sires and candidate dams before they reproduce.

Meyer (1992) noted that direct h^2 estimates were substantially inflated when maternal effects were ignored. This was especially true for growth until weaning, as might be expected. Until weaning, the calf is dependent on the dam for sustenance. Thus, it makes sense that the dam's inherent potential to provide a favorable maternal

environment, including a sufficient quantity and quality of milk, significantly affects the calf's growth. Maternal additive effects contribute to the overall additive effects.

If maternal additive effects contribute significantly to phenotypic variation, and are not properly separated from the direct additive variance, then the numerator of the h^2 calculation will be inflated, and so too will be the estimate of direct h^2 . Wolf and Wade (2016) suggested that there may even be situations where a locus that does not functionally affect a given trait – and thus should not appear heritable – appears to be heritable because a maternal effect is present. Willham (1972) stated that, if selection is undertaken on a phenotype for a trait that is affected by both direct and maternal additive effects, the proportion of the selection differential realized is

$$\frac{\sigma_{G_o}^2 + (1.5 \times \sigma_{G_o G_m}) + (0.5 \times \sigma_{G_m}^2)}{\sigma_p^2}$$

where $\sigma_{G_o}^2$ is the direct additive variance, $\sigma_{G_o G_m}$ is the direct-maternal additive covariance, $\sigma_{G_m}^2$ is the maternal additive variance, and σ_p^2 is the phenotypic variance.

This extends direct h^2 to help compensate for the difficulty in separating direct and maternal additive effects.

A common example of a maternally-influenced trait is WWT in beef cattle (Mrode, 2014). The dam passes her offspring half of her genetic potential for growth to weaning, but she also influences the calf's WWT through the quality and quantity of milk she provides, which may or may not foster hearty growth (Wolf and Wade, 2016). The quality and quantity of milk that the dam produces are, in turn, affected by the alleles she carries for milking, dominance and epistasis among the alleles at different loci, and any

environmental factors that may have affected her milking capacity, such as mastitis or frostbite to the udder.

Early work in estimating maternal effects was accomplished by solving linear equations where covariances between types of relatives were calculated separately and equated to their expectations. However, these did not account for how an individual may contribute to multiple covariances, and they did not allow the sampling variances of estimates to be derived. Maximum likelihood calculations are somewhat more appropriate (Meyer 1992).

Meyer (1992) separated direct additive, maternal additive, and maternal permanent environmental effects for genetic growth parameters in Australian beef cattle (Hereford, Angus, and Zebu Cross) fitting an animal model. Records for Hereford cattle came from commercial studs participating in the BREEDPLAN scheme (Nicol et al., 1985). Records for Angus cattle came from an experimental herd at the New South Wales Department of Agriculture and Fisheries' Research Centre. The herd was divided into high-growth rate, low-growth rate, and control lines. The selected period of growth was between birth and 1-yr-old. Parnell et al. (1986) further described the herd. Records for Zebu cross cattle came from C.S.I.R.O.'s National Cattle Breeding Station and included 2 genotypes: Africander cross ($\frac{1}{2}$ Africander, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Shorthorn) and Africander-Brahman ($\frac{1}{2}$ Africander, $\frac{1}{2}$ Brahman). Turner (1982) further described these groups.

Fixed effects considered were sex, single vs twin birth, herd (line)-year-month of weighing, herd-management group subclasses for Herefords, and genotype effect for Zebu crosses. Heterosis was not included in any model. Covariates were fitted for differences in age at weighing (linear) and age of dam (quadratic). The various genetic

and environmental effects were considered as random with the following (co)variance structure:

$$V(\mathbf{a}) = \sigma_A^2 \mathbf{A}$$

$$V(\mathbf{m}) = \sigma_M^2 \mathbf{A}$$

$$V(\mathbf{c}) = \sigma_C^2 \mathbf{I}$$

$$V(\mathbf{e}) = \sigma_E^2 \mathbf{I}$$

$$COV(\mathbf{a}, \mathbf{m}') = \sigma_{AM} \mathbf{A}$$

Direct additive variance was noted as σ_A^2 , maternal additive variance as σ_M^2 , the covariance between these as σ_{AM} , the maternal permanent environmental variance as σ_C^2 , and the error variance as σ_E^2 . Vectors of direct and maternal additive effects, maternal environmental effects, and residual errors were \mathbf{a} , \mathbf{m} , \mathbf{c} , and \mathbf{e} , respectively. The numerator relationship matrix was denoted as \mathbf{A} , and \mathbf{I} was the identity matrix (Meyer, 1992).

Meyer (1992) fitted 6 models varying in complexity, ranging from a simple animal model including only fixed effects and additive effects to a full model including all fixed effects, direct additive effects, maternal additive effects, permanent environmental effects, and a covariance between direct and maternal effects. Models were then analyzed using the log likelihood obtained from the Simplex procedure of DFREML (Meyer, 1991). Finally, sampling errors were calculated for the model with the highest log likelihood in each trait and breed (Meyer, 1992).

Meyer (1992) evaluated these models for final weight as well as BWT, WWT, and YWT. It was expected that maternal influence would be less significant at final

weight as compared to earlier ages, but this was not universally true. A negative correlation between maternal environmental effects of dams and daughters was observed. This would imply that superior mothering ability actually provided an inferior maternal environment, which was an unexpected relationship. Meyer (1992) noted that this outcome may be a result of the simplistic models used, relative to those fitted by Willham (1972).

Negative relationships between heifer growth and her ability to wean a calf have been reported elsewhere. For example, Little and Kay (1979) found that dairy heifers fed a high plane of nutrition to mature quickly had reduced milk yields as compared to conventionally-reared heifers. Johnsson and Morant (1984) found that WWT of dams and their calves had an inverse relationship, although they noted that there was little evidence that the trend extended to WWT heavier than 200 kg, as would be seen in modern production settings. They suggested that mammary development in beef heifers may be increasingly impaired within a certain range of energy intake but that intake beyond this range might not affect milking ability in a measurable way.

Crossbred Populations

Inbreeding occurs when genetically related animals are mated, such as those of the same line or breed. When individuals of shared ancestry mate, the chances of both parents carrying the same allele are increased and, as a result, the chances of the offspring being homozygous at a given locus is also increased. Over time, inbreeding can lead to disproportionately high numbers of homozygous individuals in a population, which generally reduces the population's fitness for loci where dominance occurs. This

phenomenon is called inbreeding depression. If two inbred individuals from different inbred populations with different allele frequencies are mated, their offspring will carry a mixture of alleles, often resulting in a fitter individual. This is called heterosis, and it is the opposite of inbreeding depression (Falconer and Mackay, 1996). Heterosis can be utilized in crossbreeding schemes to maximize the desirable effects of each breed contributing to the mating (Van Vleck, 1993).

As previously implied, heterosis will only be observed if dominance is present. Similar to how maternal effects may skew h^2 and additive variance estimation, dominance at many loci may skew heterosis estimates in crossbred populations. If some loci display positive dominance and others negative, the effects may cancel each other out, causing the appearance of no heterosis even though heterosis may actually occur. Additionally, different lines and offspring from different mating crosses will have different amounts of heterosis (Falconer and Mackay, 1996). Practically, this means that the amount of realized heterosis will vary depending on the populations crossed, how alleles interact with each other, and which alleles from each parent have been inherited among individuals born from identical crosses.

Dominance interactions present a unique challenge for analyzing a highly crossbred population like USMARC GPE cattle; 18 different breeds are represented in the mating population, and some breeds are already composites of other breeds (Kuehn and Thallman, 2016), creating numerous opportunities for unique line crosses with unique heterosis and dominance properties.

Both maternal and direct effects may exhibit heterosis. A simple model to calculate estimates of crossbred progeny for direct and maternal effects is

$$\overline{AB} = DIR \left[\frac{AA}{2} + \frac{BB}{2} + H(AB) \right] + MAT[BB]$$

where \overline{AB} is the expected performance of progeny resulting from a 2-way cross of purebred breed A sires and purebred breed B dams, DIR indicates direct effects, MAT indicates maternal effects, $\frac{AA}{2}$ and $\frac{BB}{2}$ represent the additive contributions (breeding value) of the breed A and breed B parents, respectively, $H(AB)$ is the extra effect of heterosis gained from the cross, and $MAT[BB]$ is the average maternal genetic effect for the dam's breed (Van Vleck, 1993). Maternal heterosis estimates can be obtained in much the same way (Van Vleck, 1993):

$$MAT[(CD)] = MAT \left[\frac{CC}{2} + \frac{DD}{2} \right]$$

As more breeds are added to the model, calculations become increasingly complicated as each breed's effects must be weighted by the proportion of genes they contribute (Van Vleck, 1993).

Genetic Groups

Use of AI has allowed frozen semen to be transported and used farther than would be possible with natural mating. As a result, any given AI sire may have multiple groups of offspring in geographically dispersed locations. Due to sampling effects and differences in the genetic merit of mates, average EPD among progeny groups may vary. Genetic grouping accounts for these differences, which are not accounted for by genetic relationship. By accounting for the underlying structure created by different populations

of the sire's offspring, differences between these populations can be overcome when evaluating the sire (Famula et al., 1983; Westell et al., 1988).

Genetic groups may be accounted for by modifying a mixed linear model. Mrode (2014) defined the mixed linear model as

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

where \mathbf{y} was a vector of observations, \mathbf{X} was an incidence matrix for fixed effects, \mathbf{b} was an unknown vector of fixed effects, \mathbf{Z} was an incidence matrix for random effects (e.g., transmitting abilities or EPD; measures of genetic merit), \mathbf{a} was a vector of random animal effects, and \mathbf{e} was the random error. If only sires were being evaluated for their genetic merit, then the model became a sire model. In this case, the matrix \mathbf{Z} related only sires to records and the vector \mathbf{a} became a vector of random effects for sires only (Mrode, 2014).

To employ genetic grouping representing populations of sires, Famula et al. (1983) reparametrized the mixed model equation such that $\mathbf{a} = \mathbf{u} = \mathbf{Q}\mathbf{g} + \mathbf{s}$ where \mathbf{Q} was an incidence matrix classifying sires into groups, \mathbf{g} was a vector of mean breeding values for the groups, and \mathbf{s} was a sire's deviation from his group's mean EBV. Since \mathbf{s} was randomly distributed, its expected value was zero, but a sire's deviation from his group's mean can be accounted for by adding a term $\mathbf{Z}\mathbf{s}$. The definitions of \mathbf{Z} and \mathbf{s} were unchanged. Put together, an equivalent form of the mixed linear model which accounts for sire groups is formed (Famula et al., 1983):

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{Q}\mathbf{g} + \mathbf{Z}\mathbf{s} + \mathbf{e}.$$

However, the mixed linear model including sire groups is not without its flaws. Famula et al. (1983) noted that \mathbf{Qg} defined in this way can rarely be estimated, implying that there is not always a single, unique solution for $\mathbf{Q}\hat{\mathbf{g}}$. This is not desirable considering that a mixed linear model is designed to estimate unique breeding values for individual sires. The Northeast Artificial Insemination Sire Comparison (**NEAISC**), a genetic evaluation used in the New England and New York state dairy industry (Bolgiano et al., 1979), has overcome this challenge by using a procedure similar to estimating the difference of each group relative to one other group. If \mathbf{g} is estimated as the difference between group effects, \mathbf{Qg} can yield a unique solution (Famula et al., 1983).

Westell et al. (1988) employed a similar but more computationally feasible model to account for genetic groups. They assigned “phantom parents” where parentage was unknown. These phantom parents were grouped based on likely similarity in genetic background. Descendants of phantom parents were assigned a fraction of the phantom parents’ genetic group effects depending on their genetic distance. The modified mixed linear model was

$$\mathbf{y} = \mathbf{Xh} + \mathbf{Za} + \mathbf{ZQ}_1\mathbf{g} + \mathbf{e}$$

where \mathbf{X} was an incidence matrix relating records to fixed effects, \mathbf{h} was a vector of fixed effects, \mathbf{Z} was an incidence matrix relating records to genetic values of identified (non-phantom) animals, \mathbf{Q}_1 was a coefficient matrix relating identified animals to group effects, \mathbf{g} was a vector of the phantom parents’ group effects, and \mathbf{e} was the random residual (Westell et al., 1988). Through additional transformation and simplification, the

relationship submatrices in the coefficient matrix could be easily constructed (Westell et al., 1988).

A complication of using genetic groups is the ambiguity of genetic group definitions. A group may be defined as individuals born in the same year, individuals born in the same geographic area, or individuals sharing some other common factor. Due to the wide range of possible strategies, the properties distinguishing one group from another can easily become subjective. If the distinction between genetic groups is not made judiciously, the underlying population structure may not be appropriately described, thus resulting in poor evaluation (Famula et al., 1983).

Comprehensively Describing Growth to Maturity

An animal can be considered a collection of chemical reactions that transform a food input into heat, work, live weight, and products such as offspring or milk. If growing animals are freely fed, food input will transform into a well-defined trajectory (Parks, 1982). If an animal is fed a limited diet or is subjected to nutritionally poor feed, then it will not achieve its full potential for mature size and thus these growth functions will not accurately describe the animal's growth. Therefore, use of a growth function requires that animals are not limited at any time for which the function is fitted (Lewis et al., 2006). It is important to emphasize that "ad libitum" feeding indicates that an animal is allowed to eat whatever it was offered. It does not imply that the diet offered was nutritionally adequate. Each species – and possibly even each breed within a species – responds differently to a given feed consumed, so it is possible that a nutritionally poor diet fed ad libitum is growth limiting (Parks, 1982). The Spillman function has been

suggested to model the relationship between cumulative feed intake and growth under limiting conditions, although Lewis et al. (2006) found significant issues with applying the function. Residuals were not normally distributed when fitting the relationship between live weight and cumulative feed intake, measured under variously limiting nutritional treatments in male sheep.

Parks (1982) defined growth simply as a change of size, live weight, or biomass with time or some other variable. Traditionally, growth is considered a sigmoidal process approaching an asymptote at MWT, commonly denoted A . However, Freetly et al. (2011) noted that, if data are missing between birth and inflection point, a simpler model excluding the inflection point may be more appropriate. Brody (1964) notes that the inflection point of a growth curve is the time where rate of growth has reached its maximum and has not yet begun to decrease. Physiologically, this roughly corresponds to puberty.

Mathematically, a growth curve must be asymptotic to A at some advanced point in time (t) and have some point at age t' and weight W' in which the growth rate changes from increasing to decreasing. The growth rate decreases until MWT is achieved (Parks, 1982), usually around 5 to 6 years of age in cattle (Taylor, 1965). The time around the maximum rate of change is commonly referred to as the “growth spurt” (Parks, 1982).

Many growth functions have been proposed in literature, which tend to be similar in form except they highlight different growth processes. For example, Von Bertalanffy's (1938) function considers growth as a function of anabolic and catabolic rates, Weiss and Kavanau's (1957) function considers biomass produced and destroyed, while Parks

(1965) proposed a model based on an inductance-resistance-capacitance circuit which is designed to incorporate energetic input into the growth function. Richards (1959) described a flexible function which could be parameterized into common growth functions (Gompertz, logistic, and Brody functions) based on the shape of the data.

The Gompertz function is similar to a logistic function in that it is S-shaped and has 3 parameters: an upper asymptote, a time origin, and a time unit or rate constant. A fourth parameter can be added to modify the lower asymptote so that it is not zero. Due to the functions' similarities, they are expected to fit similarly and properties of the logistic generally apply to the Gompertz. However, unlike the logistic function, the inflection point of the Gompertz function is not equidistant between upper and lower asymptotes (Winsor, 1932).

For quite a while after its introduction in 1825, the Gompertz curve was primarily of interest to actuaries (Winsor, 1932). Wright (1926) suggested the Gompertz to describe biological growth. Following suit, some studies in the 1930s began applying the Gompertz function to describe growth of a variety of animals, reporting good fit. For example, Weymouth et al. (1931) fit the Gompertz to razor clam shell growth, finding probable errors less than 0.14 cm. Shell lengths calculated from the fit of the Gompertz curve differed from observed values by only about 0.5% on average. The authors did, however, use 2 sets of parameters: one to describe the early half of the data and one to describe the latter half; the later trends differed from the earlier trends. Winsor (1932) expected the function to suit growth data if the first inflection point occurred at around 35 to 40% of the upper asymptote. Growth rate and maximum growth rate can also be estimated from the Gompertz function (Winsor, 1932).

Applying the Gompertz curve to growth, the function may be parametrized such that constants are A (MWT), B (rate of maturation), t (time since birth), and W (BW). Problematically, parameters A and B are highly correlated. As a result, estimates tend to display noticeable skewedness. An alternate parameter Z , the product of A and B , circumvents the issue and may also be used to calculate the maximum daily growth rate, Z/e , where e is the base of the natural logarithm (Lewis et al., 2006).

Alternatively, Brody (1964) described a simple, nonlinear function of growth to its asymptote at maturity. Taylor (1965) analyzed Brody's function, expanding it to generalized regression equations which justify the relationship between MWT and maturation time. Taylor (1965) noted that Brody's curve was applicable to growth beyond approximately 30% of MWT, which roughly corresponds to growth from the end of puberty onwards. Like the logistic function and the Gompertz curve, Brody's function uses 3 parameters: a "live-weight scaling parameter," "an age scaling parameter," and a parameter setting the time origin (Taylor, 1965). The function is basically expressed as

$$W = A[1 - e^{-k(t-t^*)}]$$

where W represents weight at some age t , while t^* represents the curve's time origin.

The A is the asymptote of mature age, and k is an index representing an exponential constant if considering growth rate or a maturation index if considering an animal's

approach to its MWT. This index is applied in the term $\tau = \frac{1}{k} = k^{-1}$, which is the

maturing interval. This is used to standardize an animal's physiological age: $t^n =$

$\frac{1}{\tau}(t - t^*) = k(t - t^*)$, where t^n is the time scale. The maturing interval and time origin

parameters are error-prone and negatively correlated. The derivative of W with respect to t gives the growth rate (Taylor, 1965).

An animal is considered fully mature at 98% of its asymptotic MWT. The degree of maturity is expressed as the proportion of its MWT ($p = \frac{W}{A}$) while the proportion of MWT attained at a given age, t_p , is $t^* - \tau \ln(1 - p)$. Generally, an animal's predicted age at some proportion of MWT greater than 0.3, assuming a common age of origin of 3.5 days after conception, is $100 \times A^{0.27} \left[\frac{1}{2} \ln(1 - p) \right]$. Taylor (1965) also noted that Brody (1964) attributed most differences in intra-species growth constants to differing environments, most notably food supply.

Taylor (1965) found the “most satisfactory” coefficient for the regression of $\log \tau$ on $\log A$ (log of maturing interval on log of MWT) for nonhuman animals to be 0.27 ± 0.04 , creating an overall regression equation of $\log \tau = 0.27 \log A + 2.0$. Between species variation was highly significant, implying that growth curve parameters vary significantly between species. Taylor (1965) noted that the basic regression equation can be rearranged into various other non-logarithmic functions, all revolving around the quantity $A^{0.27}$. Thus, $A^{0.27}$ is a key value to describe growth patterns over time using Brody's curve. The time origin parameter t^* is proportional to approximately $A^{0.27}$. For example, the expected maturing interval of a mammal is $100 \times A^{0.27}$ and the expected value of the time origin is approximately $50 \times A^{0.27}$.

While Brody (1964) considered a standardized physical age, $k(t - t^*)$, Taylor (1965) proposed that the logarithm of metabolic age was more useful to compare ages of different animals. Metabolic age combines concepts of physiological age and metabolic

turnover time and is based only on MWT, which is easier to estimate and more accurate than using Brody's maturing index (k). It also conveniently uses fewer parameters. Metabolic weight (θ) is measured by dividing age from conception ($t - t_0$) multiplied by a constant (γ) and divided by $A^{0.27}$:

$$\theta = \gamma(t - t_0)A^{-0.27}$$

As with physiological age, the expected metabolic age of a mammal at some degree of maturity greater than $p = 0.30$ can be predicted by $100\gamma \left[\frac{1}{2} - \ln(1 - p) \right]$.

Parks (1982) provided some criticisms of Brody's curve. First, most accepted growth functions imply growth is continuous and has higher order continuous rates of change, which would allow calculation of the age of onset of the growth spurt. Brody's curve implies different rates of change on either side of the inflexion point. After the inflexion point, the animal's growth is suddenly constrained by its MWT. As a result, the function dW/dt is discontinuous at t' – which Brody (1964) assigned to the age at onset of puberty rather than the growth spurt – and thus the function cannot be further differentiated.

Freetly et al. (2011) used the Brody curve to evaluate growth curves of females sired by 6 different breeds – Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli – to determine if differences existed between mature size and relative rates of maturation among the breeds. The sire breeds selected each had some unique properties that may affect their growth. Brahman, Boran, and Tuli cattle are all heat-tolerant breeds. The Brahman and Boran are both *Bos indicus* breeds while Tuli, Hereford, Angus, and Belgian Blue are *Bos taurus* breeds. A breed-specific, minimum BW and age must be

achieved before heifers express puberty, and it is known that *Bos indicus* cattle (i.e., Brahman and Boran) must achieve a greater proportion of mature size before puberty will occur (Freetly et al., 2011).

Cows used for the study were bred from sires of the 6 breeds previously listed and dams of either Angus, Hereford, or MARC III ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Red Poll and $\frac{1}{4}$ Pinzgauer) breeds, resulting in 516 cows for evaluation. Heifers fed restricted diets were not included in the analysis since the family of growth curves that Freetly et al. (2011) wished to use required the assumption that growth substrate – in this case feed – was not limiting. These cows were weighed at birth, 9 additional times between weaning and heifer breeding, and then twice per year until they reached 5 yr of age. Hip heights were collected at 27 wk of age (weaning), 1 yr of age, and at each additional BW measurement. Puberty was marked at the first incidence of behavioral estrus, which was observed in 488 of the 516 cows (Freetly et al., 2011).

Due to lack of data between birth and the inflection point, Freetly et al. (2011) found a better fit of the Brody function when BWT were excluded. Mature skeletal size was reached before MWT. *Bos indicus* breeds reached mature height at a greater percentage of MWT than *Bos taurus* breeds, suggesting that *Bos indicus* breeds reach puberty at older age (Freetly et al. 2011). While the 1990-born animals were larger than cows evaluated in the 1970s, the 1990-born cows achieved a similar proportion of MWT at puberty, suggesting that proportion of MWT at puberty was fairly well conserved. However, as selection for increased size continues, the minimum target BW at puberty will also change. The minimum target BW at puberty should therefore be considered a function of MWT rather than an absolute value (Freetly et al., 2011).

Parks (1982) claimed that a polynomial function may be appropriate for some data if the proper order is used. However, polynomials quickly become nonsensical toward the boundaries or extremes of data, so they cannot be used for extrapolation. Additionally, while a polynomial might mathematically fit a given data set, it does not consider biological properties of the system from which data were collected.

Alternatively, a spline function may be used to model data. A spline is a piecewise function consisting of polynomial segments joined at some number of interior knots. The name is derived from a flexible tool used to create a smooth curve between fixed points. (Racine, 2014). In its most basic form, the spline consists of 2 linear functions joined at a single knot and is often called a “broken stick” model. It can be expanded to higher-order polynomials with many knots, although these tend to create rough or “wiggly” curves (Meyer, 2005).

A variety of functions are available to model growth, including Brody, Gompertz, polynomial, and spline functions. Each function offers a different perspective on how an animal grows, but lack of nutritional constraints is a prerequisite to appropriate fitting of most functions.

PROJECT OBJECTIVES

Using data from the USMARC GPE, the following 2 objectives will be accomplished:

- 1) Investigate growth from weaning to maturity of various breeds of beef cattle used in the United States using Brody, spline, and quadratic regression. Describing

growth is a critical step towards developing tools to evaluate MWT in genetic prediction and to allow equitable comparisons across breeds when producers are deciding which breed to use in their operations.

- 2) Calculate variance components and breed of sire effects for MWT. These measures can then be used to develop pragmatic across-breed adjustment factors.

LITERATURE CITED

- Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. *J. Anim. Sci.* 94:1689-1702. doi:10.2527/jas2015-0049
- Beef Improvement Federation. 2016. Guidelines for uniform beef improvement programs, 9th edition. https://beefimprovement.org/wp-content/uploads/2013/07/BIFGuidelinesFinal_updated0916.pdf (Accessed 10 December 2017.)
- Bolgiano, D. C., L. D. Van Vleck, and R. W. Everett. 1979. Fluctuations in sire evaluations. *J. Dairy Sci.* 62:760-767.
- Bourdon, R. M. 1998. Shortcomings of current genetic evaluation systems. *J. Anim. Sci.* 76:2308-2323.
- Brody, S. 1945. Bioenergetics and growth. First published: Reinhold Publishing Corp., New York. (Reprinted: Hafner Press, New York, 1964.)

- Cundiff, L. V. 1993. Breed comparisons adjusted to a 1991 basis using current EPD's. In: Proc. Beef Improv. Fed. Research Symp., Asheville, NC. p. 114-123.
- Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Estimates of genetic parameters for weight and height of angus cows using a repeatability model. Proc. West. Sec. Amer. Soc. Anim. Sci. 60:40-41.
- DiCostanzo, A., J. C. Meiske, S. D. Plegge, T. M. Peters, and R. D. Goodrich. 1990. Within-herd variation in energy utilization for maintenance and gain in beef cows. J. Anim. Sci. 68:2156-2165. doi:10.2527/1990.6872156x
- Falconer, D. S. and T. F. C. Mackay. 1996. Introduction to Quantitative Genetics. 5th ed. Longman Group Ltd. Essex, England.
- Famula, T. R., E. J. Pollak, and L. D. Van Vleck. 1983. Genetic groups in dairy sire evaluation under a selection model. J. Dairy Sci. 66:927-934. doi:10.3168/jds.S00220302(83)81879-7
- Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. J. Anim. Sci. 89:2373-2379. doi:10.2527/jas.2011-3847.
- Garrick, D. J. 2005. Trends and developments in genetic evaluation of beef cattle in the United States. In: Proc. 9th World Angus Forum Tech. Meet., Angus in the Global Market. Am. Angus Assoc., Kansas City, MO. p. 24-31.
- Golden, B. L., D. J. Garrick, S. Newman, and R. M. Enns. 2000. Economically relevant traits: A framework for the next generation of EPDs. In: Proc. of the Beef Improv. Federation Ann. Meet. & Symp., Wichita, KS. p. 2-13.

- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1982. Characterization of breeds representing diverse biological types: Preweaning traits. In: Beef Research Program Prog. Rep. No. 1. Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE. p. 7-8.
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics*. 28(6):476-490.
- Henderson, C. R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics*. 32:69-83. doi:10.2307/2529339.
- Jenkins, T. G. and C. L. Ferrel. 1983. Nutrient requirements to maintain weight of mature, nonlactating, nonpregnant cows of four diverse breed types. *J. Anim. Sci.* 54:761-770. doi:10.2527/jas1983.564761x
- Johnsson, I. D. and S. V. Morant. 1984. Evidence of a negative relationship between heifer growth and first calf weaning weight in commercial beef herds. *Aust. J. Exp. Agric. Anim. Husb.* 24:10-14.
- Kuehn, L. A. and R. M. Thallman. 2016. Across-Breed EPD tables for the year 2016 adjusted to breed differences for birth year of 2014. In: Beef Improv. Federation Ann. Meet. & Symp., Manhattan, Kansas. p. 127-154.
- Kuehn, L. A. and R. M. Thallman. 2017a. 2016 Across-breed EPD table. <https://beefimprovement.org/wp-content/uploads/2017/03/2016-Across-Breed-EPD-Table.pdf> (Accessed 24 March 2017.)

- Kuehn, L. A. and R. M. Thallman. 2017b. Across-breed EPD tables for the year 2017 adjusted to breed differences for birth year of 2015. *Proc. Beef Improv. Federation Ann. Meet. & Symp.*, Athens, Georgia. p. 112-144.
- Lewis, R. M., G. C. Emmans, and G. Simm. 2006. Describing effects of genetic selection, nutrition, and their interplay in prime lambs using growth and efficiency functions. *Aust. J. Ag. Res.* 57:707-719. doi:10.1071/AR05196
- Little, W. and R. M. Kay. 1979. The effects of rapid rearing and early calving on the subsequent performance of dairy heifers. *Anim. Prod.* 29:131-142.
- McMurry, B. 2008. Just how big are our beef cows these days? *Feedstuffs.* 80(51):16–17.
- Meyer, K. 1991. DFREML – A set of programs to estimate variance components by restricted maximum likelihood using a derivative-free algorithm. User notes, version 2.0. Mimeo. Animal Genetics and Breeding Unit, University of New England, Armidale.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179-204. doi:10.1016/0301-6226(92)90017-X
- Meyer, K. 2005. Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genet. Sel. Evol.* 37:473-500. doi:10.1051/gse:2005012
- Mrode, R. A. 2014. *Linear models for the prediction of animal breeding values.* 3rd ed. CABI. Boston, MA.
- Nicol, D. C., H. U. Graser, B. Tier, and K. Hammond. 1985. BREEDPLAN – A within-herd evaluation system for the National Beef Recording Scheme. In: *Proc. 5th Conf. Aust. Assoc. Anim. Breed. Genet.*, Sydney, Australia. p. 151-153.

- Notter, D. R. 1999. The importance of genetic diversity in livestock populations of the future. *J. Anim. Sci.* 77:61-69.
- Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny differences: Use of within-breed expected progeny differences to adjust breed evaluations for sire sampling and genetic trend. *J. Anim. Sci.* 69:4763-4776. doi: 10.2527/1991.69124763x
- NRC. 1996. Nutrient requirements for beef cattle. 7th ed. Natl. Acad. Press, Washington, DC.
- Nugent III, R. A., T. G. Jenkins, A. J. Roberts, and J. Klindt. 1993. Relationship of post-partum interval in mature beef nutritional environment, biological type and serum concentrations. *Anim. Prod.* 56:193-200.
- Nutt, B. G., J. W. Holloway, and W. T. Butts, Jr. 1980. Relationship of rumen capacity of mature Angus cows to body measurements, animal performance and forage consumption on pasture. *J. Anim.Sci.* 51:1168-1176. doi: 10.2527/jas1980.5151168x
- Parks, J. R. 1965. Prediction and entropy of half-tone pictures. *Behav. Sci.* 10:436-445. doi: 10.1002/bs.3830100407
- Parks, J. R. 1982. A theory of feeding and growth of animals. Springer-Verlag Berlin Heidelberg New York.
- Parnell, P. F., R. Barlow, and B. Tier. 1986. Realised responses to divergent selection for yearling growth rate in Angus cattle. In Proc. 3rd World Congr. Genet. Appl. Livest. Prod., Lincoln, NE. p. 330-334.

- Pearson, R. E. 1982. Economic aspects of the choice of a breeding objective. In Proc. 2nd World Congr. Genet. Appl. Livest. Prod., Madrid, Spain. p. 50-59.
- Purser, D. B. and R. J. Moir. 1966. Rumen volume as a factor involved in individual sheep differences. *J. Anim. Sci.* 25:509-515. doi: 10.2527/jax1966.252509x
- Racine, J. S. 2014. A primer on regression splines. https://cran.r-project.org/web/packages/crs/vignettes/spline_primer.pdf. (Accessed 1 August 2017.)
- Richards, F. J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10(29):290-300.
- Roberts, A. J., M. K. Petersen, and R. N. Funston. 2015. BEEF SPECIES SYMPOSIUM: Can we build the cowherd by increasing longevity of females? *J. Anim. Sci.* 93:4235-4243. doi:10.2527/jas.2014-8811
- Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. *J. Anim. Sci.* 93:5829-5839. doi:10.2527/jas2015-9172
- Taylor, St. C. S. 1965. A relation between mature weight and time taken to mature in mammals. *Anim. Sci.* 7(2):203-220. doi:10.1017/S0003356100025629
- Turner, H. G. 1982. Genetic variation of rectal temperature in cows and its relationship to fertility. *Anim. Prod.* 35(3):401-412. doi: 10.1017/S0003356100001094
- Upton, W. H., A. T. G. McArthur, and R. J. Farquharson. 1988. Economic values applied to breeding objectives: A decentralized approach for BREEDPLAN. Proc. 7th Conf. AAABG, Armidale, Australia: 95-104.

USDA-ARS. 1974. Progress report: Germ plasm evaluation program report no. 1.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE01.pdf> (Accessed 9 November 2016.)

USDA-ARS. 1976. Germ plasm evaluation program report no. 4.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE04.pdf> (Accessed 9 November 2017.)

USDA-ARS. 1990. Germ plasm evaluation program report no. 12.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE12.pdf> (Accessed 9 November 2017.)

USDA-ARS. 1994. Germ plasm evaluation program report no. 13.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE13.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2001a. Germ plasm evaluation program report no. 20.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE20.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2001b. Germ plasm evaluation program report no. 21.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE21.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2006. Germ plasm evaluation program report no. 23.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE23.pdf> (Accessed 9 November 2017.)

- USDA-ERS, Commodity Economic Division. 1973. Livestock and meat situation.
<http://usda.mannlib.cornell.edu/usda/ers/LMS//1970s/1973/LMS-08-17-1973.pdf>
(Accessed 24 March 2017.)
- USDA-NASS. March 2017. Livestock slaughter. <http://usda.mannlib.cornell.edu/usda/nass/LiveSlau//2010s/2017/LiveSlau-03-23-2017.pdf> (Accessed 24 March 2017.)
- Van Vleck, L. D. 1993. Selection index and introduction to mixed model methods. CRC Press, Inc., Boca Raton, FL.
- Van Vleck, L. D. and L. V. Cundiff. 2006. Across-breed EPD tables for the year 2006 adjusted to breed differences for birth year of 2004. In: Proc. 38th Beef Improv. Fed. Ann. Meet., Choctaw, MS. http://www.bifconference.com/bif2006/pdfs/Cundiff_Van_Vleck.pdf (Accessed 24 March 2017.)
- Van Vleck, L. D., L. V. Cundiff, T. L. Wheeler, S. D. Shackelford, and M. Koohmaraie. 2007. Across-breed adjustment factors for expected progeny differences for carcass traits. *J. Anim. Sci.* 85:1369-1376. doi: 10.2527/jas.2006-658
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.* 10:181-213.
- Walker, R. S., R. M. Martin, G. T. Gentry, and L. R. Gentry. 2015. Impact of cow size on dry matter intake, residual feed intake, metabolic response, and cow performance. *J. Anim. Sci.* 93:672-684. doi:10.2527/jas2014-7702
- Weiss, P. and J. L. Kavanau. 1957. Model of growth and growth control. *J. Gen. Physiol.* 41:41- 47. doi: 10.1085/jgp.41.1.1
- Westell, R. A., R. L. Quaas, and L. D. Van Vleck. 1988. Genetic groups in an animal model. *J. Dairy Sci.* 71:1310-1318.

- Weymouth, F. W., H. C. McMillin, and W. H. Rich. 1931. Latitude and relative growth in the razor clam, *Siliqua patula*. *J. Exp. Biol.* 8:228-249.
- Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 55(6):1288-1293.
- Willham, R. L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7:405-418.
- Winsor, C. P. 1932. The Gompertz curve as a growth curve. In: *Proc. Natl. Acad. Sci.* 18:1-8.
- Wolf, J. B. and M. J. Wade. 2009. What are maternal effects (and what are they not)? *Philos. Trans. R. Soc. Lond., B., Biol. Sci.* 364:1107-1115.
doi:10.1098/rstb.2008.0238
- Wolf, J. B. and M. J. Wade. 2016. Evolutionary genetics of maternal effects. *Evolution.* 70(4):827-839. doi:10.1111/evo.12905
- Wright, S. 1926. Reviews: *The Biology of Population Growth*, by R. Pearl; *The Natural Increase of Mankind*, by J. S. Sweeney. *J. Am. Stat. Assoc.* 21:493-497.

CHAPTER 2: GROWTH FROM WEANING TO MATURITY IN CROSSBRED BEEF CATTLE

ABSTRACT

Cow mature weight (**MWT**) has increased in the past 30 yr. Larger cows cost more to maintain, but their efficiency – and thus profitability – depends on the production environment. Incorporating MWT effectively into selection and mating decisions requires understanding of growth to maturity. The objective of this study was to describe growth to maturity in crossbred beef cattle using Brody, spline, and quadratic functions. The Brody function was fitted with parameters MWT and maturing constant. The spline was fitted as piecewise linear where the 2 linear functions join at a knot. Key parameters were b_0 (intercept and estimate of weaning weight, **WWT**), knot position, and SMWT (MWT estimated at 6 yr old using fitted parameters). For the quadratic model, the main parameters considered were β_0 (intercept and estimate of WWT) and QMWT (MWT estimated at 6 yr old using fitted parameters). Data were scaled for fitting such that WWT, defined at 180 d, was the y-intercept, with the average weight at 180 d (214.3 kg) subtracted from all weights. Weights were expressed by adding back 214.3 kg after analysis. Parameter estimates reflected data on 4,721 crossbred cows from cycle VII and continuous sampling phases of the Germplasm Evaluation Program (**GPE**) at the U.S. Meat Animal Research Center (**USMARC**). Average estimates for WWT from the spline and quadratic function (SD) were 229.8 kg (32.0 kg) and 273.1 kg (38.9 kg), respectively. The average maturing constant (SD) was 0.0022 d⁻¹ (0.0008 d⁻¹). The average MWT

estimates from the Brody, spline, and quadratic functions (SD) were 664.4 kg (69.2 kg), 705.2 kg (77.0 kg), and 601.0 kg (110.5 kg), respectively. The spline function had the highest average R^2 value when fit to individual cows' data, but the Brody function produced more consistent MWT estimates, regardless of the time frame of data available and produced the fewest extreme MWT. Of the 3 functions fitted, the Brody was best suited for estimating MWT at a later age in crossbred beef cattle.

Key words: beef cattle, Brody function, growth, mature weight, quadratic function, spline function

INTRODUCTION

There has been a well-documented increase in mature cow weight (**MWT**) and hip height since the 1970s (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016) due to an increase in desirability of cattle with heavier WWT and greater average daily gain (Jenkins and Ferrell, 2006). Although few breeds report estimated progeny differences (**EPD**) for MWT (Kuehn and Thallman, 2016a), there is a positive genetic correlation between weaning weight (**WWT**) and yearling weight (**YWT**) and MWT (Brinks et al., 1964; Smith et al., 1976). Thus, genetic trends for increased WWT and YWT since 1972 (Kuehn and Thallman, 2016b) has resulted in increased cow MWT over the past 30 yr.

Larger cows can be costly to maintain. Cow maintenance occupies about half of an operation's feed requirements (Ferrell and Jenkins, 1984). Larger cows, requiring more energy than smaller cows (DiCostanzo et al., 1990), are thus expected to increase an operation's gross feed requirements. The relationship between cow size and calf

WWT appears to be affected by environmental circumstances. For example, Scasta et al. (2015) reported that, in a semi-arid rangeland environment, lighter cows weaned heavier calves in the wettest year but lighter calves in the driest year. Production efficiency relative to intake requirements of all weights varied with different levels of annual precipitation. Effectively selecting and breeding cows of profitable size for a given environment when they are fully grown requires an understanding of growth to maturity.

Growth data may be modeled by a variety of functions, including Brody, spline, and quadratic; these models may facilitate understanding how different biological types grow to maturity. The Brody function is a growth model which is asymptotic at MWT (Brody, 1945). The spline, in its most basic form, consists of 2 linear functions joined at a knot (Meyer, 2005). The quadratic curve is a type of polynomial consisting of a single curve (Parks, 1982). The purpose of this study was to describe growth from weaning to maturity in crossbred beef cattle using 3 different models – Brody, spline, and quadratic – and to compare the robustness of the MWT estimates generated from these functions. These are first steps towards estimating breed differences for MWT.

MATERIALS AND METHODS

Animals

Data used were from the Germplasm Evaluation (**GPE**) program conducted at the Roman L. Hruska U.S. Meat Animal Research Center (**USMARC**) in Clay Center, Nebraska. Animals were raised in accordance with the Guide for the Care and Use of

Agricultural Animals in Agricultural Research and Teaching (FASS, 2010), and their care was approved by the USMARC Animal Care and Use Committees.

A crossbred population has been developed and maintained at USMARC through 8 cycles of mating and, since 2007, from continuous sampling of industry bulls. Data for this project specifically were from 2,234 cycle VII GPE cows and from 3,048 continuous sampling GPE cows, which reached a maximum age of 14 yr. Cycle VII was described by Cushman et al. (2007). Sires from the 7 most common U.S. breeds – Angus, Hereford, Red Angus, Charolais, Gelbvieh, Limousin, and Simmental – were mated via artificial insemination (AI) to Angus, Hereford, and MARC III (¼ each Angus, Hereford, Pinzgauer, and Red Poll) dams. Half of bulls used from each breed type were top 50 proven sires, while the other half were young, unproven sires but considered excellent prospects (Wheeler et al., 2005; Cushman et al., 2007). Continuous sampling began with the 2007 calving; bulls from 5 to 7 breeds have been mated to Angus, Hereford, and MARC III cows. Use of Angus and Hereford bulls provided a benchmark for comparison. All cows were exposed annually. Cows which failed to breed twice in a row, or developed substantial impairments to productivity, were culled. Cycle VII cows used for this project were born in spring calving seasons between 1999 and 2008. Continuous sampling cows were born in spring and fall calving seasons between 2007 and 2014. The following breed types were represented: Angus, Hereford, Red Angus, Shorthorn, Beefmaster, Brahman, Brangus, Santa Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine Anjou, Salers, Simmental, Tarentaise, Devon, Bonsmarra, Romosinuano, MARC II (¼ each Simmental, Hereford, Angus, and Gelbvieh), and MARC III.

Data

Animals lacking weights beyond 3 yr of age or missing pedigree information were removed from the data. Some cows were used in other projects requiring a restricted diet. For these cows, records were truncated at the beginning of the feed restriction. Additionally, records were truncated at any gaps between subsequent records greater than 2 yr and at 6 yr of age. Birth weight records were not modeled as no weights were available to fit growth trajectories between birth and weaning.

Statistical Analyses

Before any models were fitted, the data were scaled. Age data were scaled by subtracting 180 d as an early boundary of the age WWT was recorded. Weight data were scaled by subtracting 214.3 kg, the average weight at 180 days. After parameter estimates were obtained, weight estimates were re-expressed by adding back 214.3 kg.

The Brody function fitted was $W_t = A[1 - e^{-k(t-t^*)}]$, where W_t was weight at a certain age (the scaled weight data), A was the mature (asymptotic) weight, k was the maturation constant, t was the observed age, and t^* was the time origin of the curve (Taylor, 1965). The deviation $t - t^*$ coincided with the scaled age. The model was fitted using the nls function (nonlinear least squares) in R (R Core Team, 2017). Starting values for A for each animal were obtained as the average of the animal's last 6 weight records. Starting values for k for each animal were calculated by algebraically solving the Brody function for k . Estimates of A and k were estimated for each animal individually.

The spline function fitted was a piecewise linear function with 1 interior knot. The segmented package in R (Muggeo, 2008) was used with the start value for the interior knot set at 750 d of age for all cows. Output included estimates of slopes and intercepts from both sides of the knot for each animal. The intercept before the knot was used as an estimate of WWT. Estimates of the slope and intercept after the knot were used to predict MWT at 6 yr of age. A paired t-test was conducted to determine if the slope after the knot was significantly less than the slope before the knot, and thus, if growth slows significantly after the knot occurs.

The quadratic function fitted was $W_t = \beta_0 + (\beta_1 \times t) + (\beta_2 \times t^2)$, where W_t was the animal's weight, t was the animal's age, β_0 was the intercept, β_1 was the linear coefficient, and β_2 was the quadratic coefficient. The lm function (linear models) in R (R Core Team, 2017) was used for the analyses. As with the spline function, coefficient estimates were used to predict MWT at 6 yr of age, and the intercept was taken as an estimate of WWT.

Data on cows with MWT estimates considered extreme from any function fitted were removed. Such outliers were defined as values more than 2.2 interquartile range units from the mean (Ott, 1993), which coincided with approximately 3 SD. Additionally, all parameters from cows on which any model failed to converge were removed. In total 4,721 cows remained with 102,177 age and weight records. Parameter values obtained for the individual cows were averaged to obtain means and standard deviations.

The final weight estimates underwent further analysis. Distributions of the MWT from all 3 functions were checked for normality using histograms, quantile-quantile plots,

and skewness and kurtosis parameters computed using the e1071 package in R (Meyer et al., 2017). Differences of MWT estimates between functions were investigated using paired t-tests. Additionally, the potential interaction between the function used to estimate MWT and the maximum age attained was investigated. Cows were grouped based on age at final record: 3 yr olds reached 1095 to 1459 d of age, 4 yr olds reached 1460 to 1824 d of age, and 5 yr olds reached 1825 to 2189 d of age. Resulting groups were orthogonal such that, for example, the 5 yr old group contained only cows which were recorded into their 5th yr and none of the cows with records terminating in their 3rd or 4th yr. An ANOVA was used to fit the model

$$Y_{ijk} = \mu + F_i + R_j + FR_{ij} + e_{ijk}$$

where Y_{ijk} was the MWT estimate for animal k , μ was the overall mean, F_i was the function used to generate the MWT estimate ($i = 1, 2, \text{ or } 3$, for Brody, spline, or quadratic, respectively), R_j was age, expressed in years, at the final record of the cow providing the MWT estimate ($j = 1, 2, \text{ or } 3$, for 3, 4, or 5 yr age categories, respectively), and FR_{ij} was the interaction between the function and cow age, and e_{ijk} was the random residual. The same analysis was run for WWT estimates using WWT as the response variable. Finally, Pearson and Spearman correlations between MWT estimates from each of the 3 functions were calculated.

RESULTS

Fit of Curves

Figure 2.1 shows the 3 functions plotted to age-weight data of all crossbred cows. The Brody function was asymptotic to MWT. The spline, in the form presently used, was piecewise linear with 2 segments joined at a single knot. The quadratic was a concave-down curve. The apex was expected to occur around 6 yr of age. However, in some cases, depending on the extent of the data, it occurred earlier with weights predicted to decrease thereafter. This is reflected in the average fit shown in Figure 2.1; the apex of the curve occurred at 1864.5 d of age (about 5.1 yr of age), after which the function decreased.

The fit of each curve is summarized in Table 2.1. On average, the spline function had the greatest R^2 and smallest root mean squared error; it also, however, generated about 7 times as many extreme MWT estimates as the Brody function. An estimate was considered extreme if it was farther than 2.2 interquartile range units from the mean estimate. The Brody function generated the fewest extreme MWT estimates with, on average, goodness-of-fit intermediate to the spline and quadratic functions. The quadratic function had the least suitable fit. It generated the greatest number of extreme MWT estimates: over 16 times as many as with the Brody function. Overall, the Brody function produced fewest extreme MWT estimates while the spline function fitted the shape of these combined data best.

After removing extreme values, MWT estimates were normally distributed overall. However, the distribution of MWT estimates from the quadratic function were left skewed, as shown in Figure 2.2. The normal quantile-quantile plots for MWT of the 3

functions (Figure 2.3) and skewness and kurtosis statistics (Table 2.2) also reflected this skewness. The Brody function quantiles follow the reference line closely and had the least deviation in both skewness and kurtosis. The spline function was similar with some deviation in the uppermost quantiles. It had stronger measures of skewness and kurtosis, indicating a greater deviation from normality. The quadratic function quantiles followed the reference line near the median but showed clear deviation at data extremes. The deviation in the lowermost quantiles, corresponding to lower MWT, was most pronounced. Accordingly, the quadratic function had the strongest measures of skewness and kurtosis, with the skewness negative.

The distribution of MWT estimates for cows with weight records collected up until 3 yr, 4 yr, and 5 yr of age were compared (Figure 2.4). Estimates of MWT for cows with weight data collected over shorter timeframes – 3 and 4 yr – were lighter when obtained with the quadratic function. The opposite was true with the spline function: cows with records ending as 3-yr-olds were estimated to have heavier MWT than those with records extending to later ages. Estimates from records ending in the 4th and 5th yr were similar in magnitude. The MWT estimated with the Brody function were the most consistent across all 3 age groups. As shown in Table 2.3, there was a clear interaction between the functional form used to obtain MWT and the extent of data available for its estimation ($P < 0.001$).

Pearson and Spearman correlations between MWT estimates from each function are presented in Table 2.4. Cows were most consistent in ranking for MWT obtained with the Brody and quadratic functions, and there was also a strong correlation between Brody

and spline functions. Rankings of MWT based on the spline and quadratic functions were quite different.

Parameter Estimates

Average parameter values from all 3 functions are summarized in Table 2.5. The MWT estimates ranged from 243.7 to 947.5 kg with an overall average across all functions of 656.9 kg (SD 97.4 kg). The average spline MWT was heaviest and the average quadratic MWT was lightest. The average Brody function MWT was intermediate and near the overall average. Mature weights were significantly different between each of the 3 functions ($P < 0.001$; Table 2.6). The WWT estimates ranged from 101.3 kg to 409.2 kg, with an overall average across both spline and quadratic functions of 251.4 kg (SD 41.7 kg). Converse to MWT estimates, spline WWT estimates were, on average, lighter than quadratic WWT estimates. No WWT estimates were obtained from the Brody function. Like MWT, WWT were also significantly different between the 2 functions used to estimate them ($P < 0.001$; Table 2.6).

On average, the location of the spline knot, the point where the piecewise functions join, was at 602 d of age, or about 1.6 yr. The slope of the linear segment before the knot was significantly greater than that after the knot ($P < 0.001$). For 90% of the cows, the 95% confidence interval for the slope of the linear segment after the knot did not include – and was greater than – zero. The average maturing constant was 0.0022 d^{-1} .

DISCUSSION

Mature Weight

Mature weights estimated from the Brody and spline functions tended to be heavier than previously reported values. While the average MWT from the quadratic function was lightest of the 3 functions fitted, it is similar to previously reported estimates. Kaps et al. (1999) reported an average MWT of Angus cows of 600.8 kg (SD 75.3 kg). This agrees with our average quadratic MWT of 601.0 kg (SD 110.5 kg). However, Kaps et al. (1999) obtained that estimate from the Brody function, and our Brody function estimate of MWT was about 60 kg heavier. DeNise and Brinks (1985) published even lighter Brody-derived MWT estimates in inbred and linecrossed Hereford- and Red Angus-sired cows: 509.7 ± 4.5 kg overall, and 522.3 ± 5.6 kg for linecross cows. Our heavier estimates may be indicative of genetic trends toward heavier weights, which have been documented in other studies (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016) and in publications of EPD trends in WWT and YWT (Kuehn and Thallman, 2016b) in beef cattle.

The MWT estimated with the spline function were heavier than those obtained with the Brody and quadratic functions. This increase in weight was because the spline function lacks an asymptote: values increase or decrease indefinitely after the knot if the slope for the final segment is not zero (Figure 2.1). In this study, that slope was positive for 90% of cows, resulting in heavier estimates of weight at 6 yr. This was more pronounced in cows with weight records extending only through 3 yr of age: their MWT estimates were heavier than their older counterparts (Figure 2.4). There was little

difference, on average, between MWT estimates of cows with weight records extending into their 4th as compared to 5th yr of age; weight records through at least 4 yr of age seem necessary to obtain reasonably accurate MWT estimates from the fit of the spline function. The spline function also generated more extreme MWT estimates than the Brody function. While the spline function fit these data reasonably well, its predictive utility appears to be suboptimal.

Estimates of MWT from the quadratic function were lighter than with the Brody and spline functions, likely due to its parabolic shape. An increasing, concave-down quadratic function must eventually decrease, with weights predicted after the apex necessarily reduced. A lower tail in the distribution of MWT obtained with the quadratic function was therefore not surprising (Figures 2.2 and 2.3; Table 2.2). Cows with weight records only extending until younger ages had substantially lighter estimates of MWT (6 yr old) than those for cows with weight records extending until older ages; inferring MWT where data were only available at younger ages was clearly unreliable with the polynomial model. While on average MWT obtained with the spline stabilized once cows were 4 yr old, the quadratic MWT estimates were noticeably different for each age group. The MWT were also more variable (larger SD; Table 2.5). The tendency for polynomials to fit poorly with sparse or extreme data, and to extrapolate poorly, is well known (e.g., Parks, 1982). Among the 3 functions studied, the quadratic was least suitable for modeling growth or for estimating MWT at a later age.

The Brody function behaved best among the functions fitted. Estimates of MWT were largely insensitive to the timeframe of weight data available: they were reasonable and consistent regardless of whether cow's weight records extended until 3, 4, or 5 yr of

age (Figure 2.4). The shape of the curve also conformed to notions of growth through maturity (Parks, 1982). Since it is asymptotic, it was expected that the Brody function would fit the data better than the spline function; that, however, was not the case in these analyses. It is possible that by truncating the data at 6 yr, some cows had not yet reached their MWT. Since the fit of the Brody function presumes an asymptote is reached, the quality of the fit may have been hampered. Although the quality of the fit of the Brody function to these data was intermediate to that of the spline and quadratic functions, it generated fewer extreme and generally more stable estimates of MWT. On whole, it provided the best description of growth from weaning to maturity.

Weaning Weight

The WWT were defined as the weight at 180 d of age. The quadratic function yielded heavier WWT estimates than the spline function, on average. The shape of the spline function appeared to better fit the data around weaning age than the quadratic curve, likely because growth is relatively linear around weaning.

The average WWT estimated from the spline function was 229.8 kg (SD 32.0 kg) and from the quadratic function was 273.1 kg (SD 38.9 kg). Kaps et al. (1999) reported similar mean WWT of 230.9 kg (SD 32.3 kg) for Angus females and 260.3 kg (SD 41.4 kg) for Angus males. Given the positive genetic correlation between WWT and MWT (Brinks et al., 1964; Smith et al., 1976), documented trends toward heavier weights in cattle (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016), and estimated larger MWT in this study, it is somewhat surprising that the estimated WWT were not heavier than those published in the 1980s and 1990s. This result, however, likely reflects differences

in how WWT were defined. Kaps et al. (1999) considered a 205-d WWT pre-adjusted for age of dam. Thus, estimates published by Kaps et al. (1999) reflected weights on older calves. Furthermore, the estimates obtained in the current analyses were heavier than those published decades prior. Smith et al. (1976) reported mean WWT (200 d) estimates between 181 kg and 206 kg in straight bred and reciprocal cross Hereford, Angus, and Shorthorn cows.

Maturing Constant

The maturing constant in the Brody function defines the overall shape of the function and the rate at which its asymptote is approached. The average value of 0.0022 d^{-1} (SD 0.0008 d^{-1}) was similar to those published previously. Kaps et al. (2000) reported maturing constants of 0.062 mo^{-1} (SD 0.012 mo^{-1}); converting to days yields 0.0021 d^{-1} . DeNise and Brinks (1985) reported an overall maturing constant of $0.00181 \text{ d}^{-1} \pm 0.00002 \text{ d}^{-1}$ across the categories of cattle they evaluated. In linecross cows specifically, the value was $0.00185 \text{ d}^{-1} \pm 0.00003 \text{ d}^{-1}$.

Knot

The knot was the point – in this case, age – at which the spline's piecewise functions joined. On average, the knot was placed at 602 d of age, or at approximately 1.6 yr. It was hypothesized that the knot might reflect a breakpoint, after which growth ceased. That would coincide with a slope not differing from zero, indicating cows had reached MWT. However, such was not the case. While the slope after the knot was less than before the knot, it was positive for most cows. This suggests that cows continued to

grow past 1.6 yr. Freetly et al. (2011) found that cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli sires achieved puberty between 48.5 ± 0.7 and 58.2 ± 0.6 wk old (approximately 339.5 to 407.4 d, or near 1 yr old). By that age, these cows had achieved most but not all of their mature height, and just over half of their MWT. Kaps et al. (2000) reported that cows were only 68% mature (SD 7%) even at 550 d old (about 1.5 yr). The age associated with the knot clearly did not coincide with cows reaching their mature size.

Conclusions

Brody, spline, and quadratic functions were fit to weight data from 4,721 crossbred GPE cows. Estimates of MWT were heavier than those published in the 1980s and 1990s, possibly reflecting genetic trends for increasing live weights in cattle.

The spline function seemed to fit these data well but appeared to overestimate MWT. Cows that reached only 3 yr were estimated to be heavier at 6 yr than those that reached 4 or 5 yr, suggesting that the spline function may not be appropriate for estimating MWT from weight records on younger cows.

The quadratic function fit poorest, and tended to underestimate MWT. This was a consequence of fitting a polynomial function that reaches an apex and then decreases. Even after editing extreme MWT, the distribution of MWT obtained with the quadratic function were skewed towards lighter weights. Cows that reached 3 or 4 yr were estimated to be lighter at maturity than cows that reached 5 yr. Similar to the spline, the quadratic function was unsuitable for estimating MWT from earlier weight records.

The Brody function generally estimated MWT intermediate to the spline and quadratic functions. Additionally, it generated consistent MWT regardless of the timeframe weights were collected: average MWT were similar in cows that reached 3 yr and those that reached 5 yr. Of the 3 functions analyzed, the Brody function appeared to be most appropriate for modeling growth and for estimating weight at maturity (6 yr of age) in these crossbred cows. The mean MWT estimated from this function was 664.4 kg (SD 69.2 kg).

Future analyses of these data will incorporate pedigree relationships among cows to estimate direct and maternal additive variances, individual breed effects, and direct and maternal heterotic effects for MWT.

LITERATURE CITED

- Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. *J. Anim. Sci.* 94:1689-1702. doi:10.2527/jas2015-0049
- Beef Improvement Federation. 2016. Guidelines for uniform beef improvement programs, 9th edition. https://beefimprovement.org/wp-content/uploads/2013/07/BIFGuidelinesFinal_updated0916.pdf (Accessed 10 December 2017.)
- Brinks, J. S., R. T. Clark, N. M. Kieffer, J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. *J. Anim. Sci.* 23(3):711-716. doi:10.2527/jas1964.233711x

- Brody, S. 1945. Bioenergetics and growth; With special reference to the efficiency complex in domestic animals. Reinhold, Oxford, England.
- Cushman, R. A., M. F. Allan, R. M. Thallman, and L. V. Cudiff. 2007. Characterization of biological types of cattle (Cycle VII): influence of postpartum interval and estrous cycle length on fertility. *J. Anim. Sci.* 85:2156-2162.
- DeNise, R. S. K. and J. S. Brinks, 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. *J. Anim. Sci.* 61(6):1431-1440.
- DiCostanzo, A., J. C. Meiske, S. D. Plegge, T. M. Peters, and R. D. Goodrich. 1990. Within-herd variation in energy utilization for maintenance and gain in beef cows. *J. Anim. Sci.* 68:2156-2165. doi:10.2527/1990.6872156x
- Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Estimates of genetic parameters for weight and height of angus cows using a repeatability model. *Proc. West. Sec. Amer. Soc. Anim. Sci.* 60:40-41.
- Ferrell, C. L. and T. G. Jenkins. 1984. Energy utilization by mature, nonpregnant, nonlactating cows of different types. *J. Anim. Sci.* 58(1):234-243. doi:10.2527/jas1984.581234x
- Federation of Animal Science Societies. 2010. Guide for the Care and Use of Agricultural Animals in Research and Teaching. 3rd ed. Champagne, IL.
- Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. *J. Anim. Sci.* 89:2373-2379. doi:10.2527/jas.2011-3847.

- Jenkins, T. G. and C. L. Ferrell. 2006. Matching beef genetics with production environment. Proc. Beef Improv. Federation Ann. Meet. & Symp., Chocktaw, Mississippi. p. 41-46.
- Kaps, M., W. O. Herring, and W. R. Lamberson, 1999. Genetic and environmental parameters for mature weight in Angus cattle. *J. Anim. Sci.* 77:569-574.
- Kaps, M., W. O. Herring, and W. R. Lamberson. 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationship with weaning weight in Angus cattle. *J. Anim. Sci.* 78:1436-1442.
- Kuehn, L. A. and Thallman, R. M. 2016a. Mean EPDs reported by different breeds. Proc. Beef Improv. Federation Ann. Meet. & Symp., Manhattan, Kansas. p. 122-126.
- Kuehn, L. A. and R. M. Thallman. 2016b. Across-Breed EPD tables for the year 2016 adjusted to breed differences for birth year of 2014. Proc. Beef Improv. Federation Ann. Meet. & Symp., Manhattan, Kansas. p. 127-154.
- Meyer, D., E. Dimitriadou, K. Hornik, A. Weingessel, and F. Leisch. 2017. e1071: Misc functions of the department of statistics, probability theory group (formerly: E1071), TU Wien. <https://CRAN.R-project.org/package=e1071>. (Accessed 28 June 2018.)
- Meyer, K. 2005. Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genet. Sel. Evol.* 37:473-500. doi:10.1051/gse:2005012
- Muggeo, V. M. R. 2008. Segmented: An R package to fit regression models with broken-line relationships. *R News*, 8/1. 20-25. <https://cran.r-project.org/doc/Rnews/> (Accessed 17 October 2017.)

- Ott, R. L. 1993. An introduction to statistical methods and data analysis. 4th ed.
Duxbury Press, Belmont, California.
- Parks, J. R. 1982. A theory of feeding and growth of animals. Springer-Verlag Berlin
Heidelberg New York.
- R Core Team, 2017. R: A language and environment for statistical computing. R
Foundation for Statistical Computing, Vienna, Austria. [https://www.R-
project.org/](https://www.R-project.org/). (Accessed 17 October 2017.)
- Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and
efficiency relative to cow size in semiarid rangeland. *J. Anim. Sci.* 93:5829-5839.
[doi:10.2527/jas2015-9172](https://doi.org/10.2527/jas2015-9172)
- Smith, G. M., H. A. Fitzhugh, Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory.
1976. A genetic analysis of maturing patterns in straightbred and crossbred
Hereford, Angus and Shorthorn cattle. *J. Anim. Sci.* 43(2):389-395.
- Taylor, St. C. S. 1965. A relation between mature weight and time taken to mature in
mammals. *Anim. Sci.* 7(2):203-220. [doi:10.1017/S0003356100025629](https://doi.org/10.1017/S0003356100025629)
- USDA-ERS, Commodity Economic Division. 1973. Livestock and meat situation.
<http://usda.mannlib.cornell.edu/usda/ers/LMS//1970s/1973/LMS-08-17-1973.pdf>
(Accessed 24 March 2017.)
- USDA-NASS. March 2017. Livestock slaughter. [http://usda.mannlib.cornell.edu/
usda/nass/LiveSlau//2010s/2017/LiveSlau-03-23-2017.pdf](http://usda.mannlib.cornell.edu/usda/nass/LiveSlau//2010s/2017/LiveSlau-03-23-2017.pdf) (Accessed 24 March
2017.)

Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2005.

Characterization of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability traits. *J. Anim. Sci.* 83:196-207.

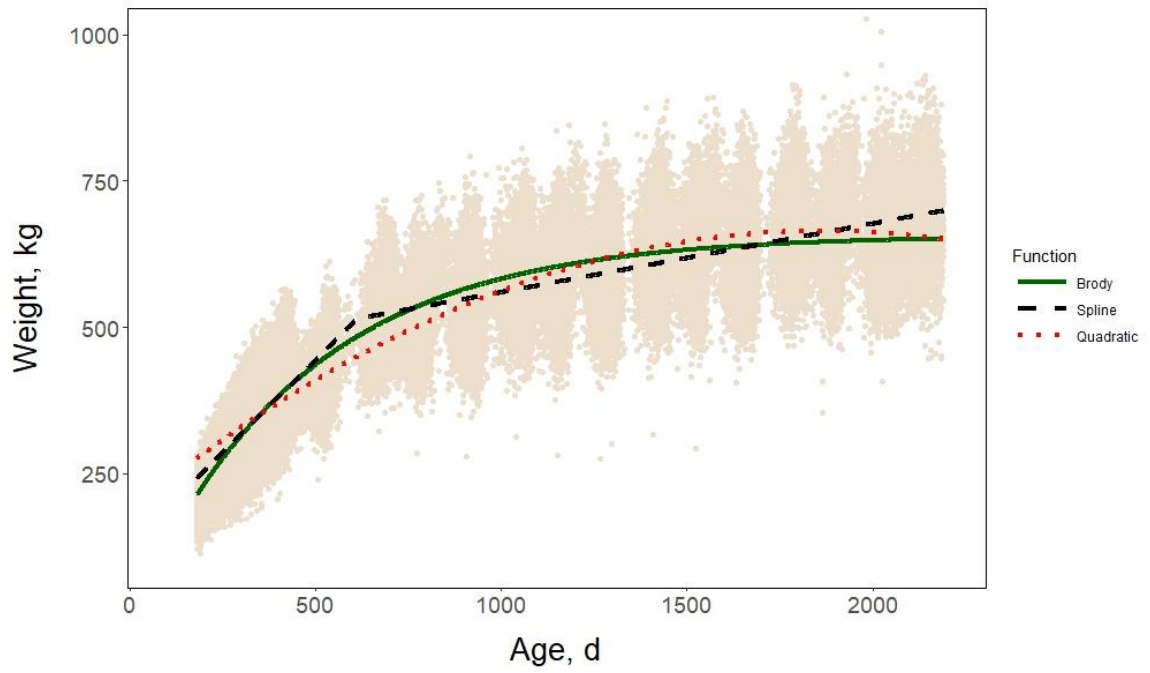


Figure 2.1. Average fits of Brody, spline, and quadratic curves to weight-age data of crossbred cows.

Table 2.1. Summary of the average quality of the fit of 3 growth functions to individual weight-age data on crossbred cows preceding editing (n = 5,632).

Function	Extreme Mature Weight Estimates ¹				R-square ²		RMSE ³	
	Threshold High (kg)	Threshold Low (kg)	% High	% Low	Mean	SD	Mean	SD
Brody	879.4	445.2	0.33	0.04	0.952	0.027	70.10	18.52
Spline	947.8	473.4	2.08	0.54	0.965	0.021	61.49	16.90
Quadratic	892.1	242.8	0.21	5.94	0.942	0.032	75.44	18.52

¹ Extreme was defined as exceeding 2.2 interquartile range units from the mean. Thus, for example, Brody mature weight estimates greater than 879.4 kg were considered extreme.

Percent high and low are the percent of MWT estimates falling outside of these thresholds.

² R-square values presented are the average R^2 of individual fits of individual fits for all cows for a given function.

³ RMSE is the Root Mean Square Error. RMSE values presented are average RMSE of individual fits for all cows in a given function.

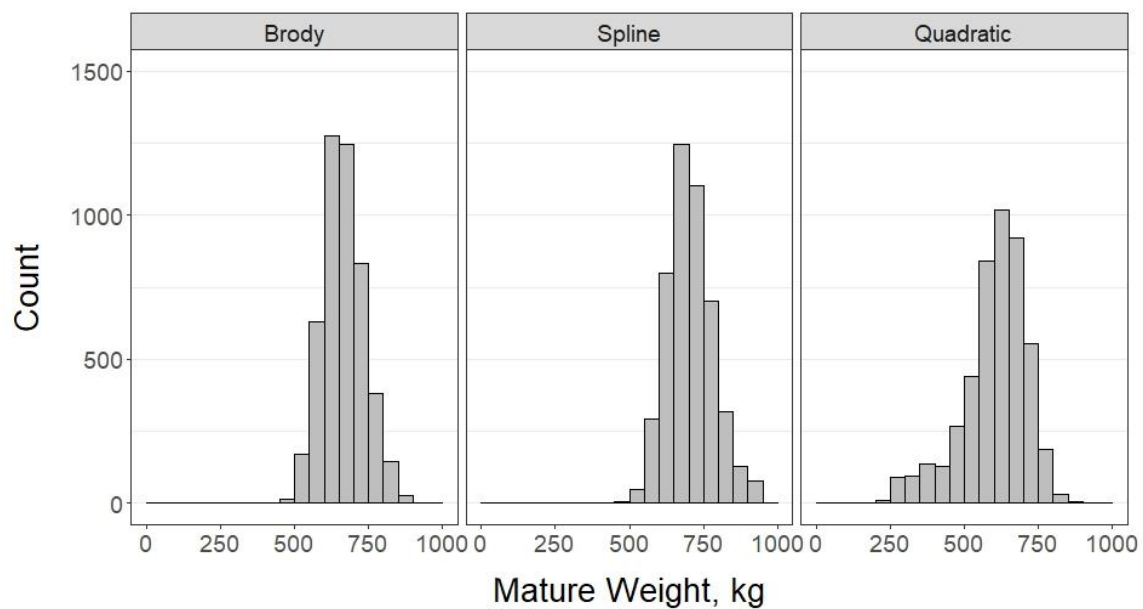


Figure 2.2. Distribution of mature weights estimated for crossbred cows after editing ($n = 4,721$) from the Brody, spline, and quadratic functions.

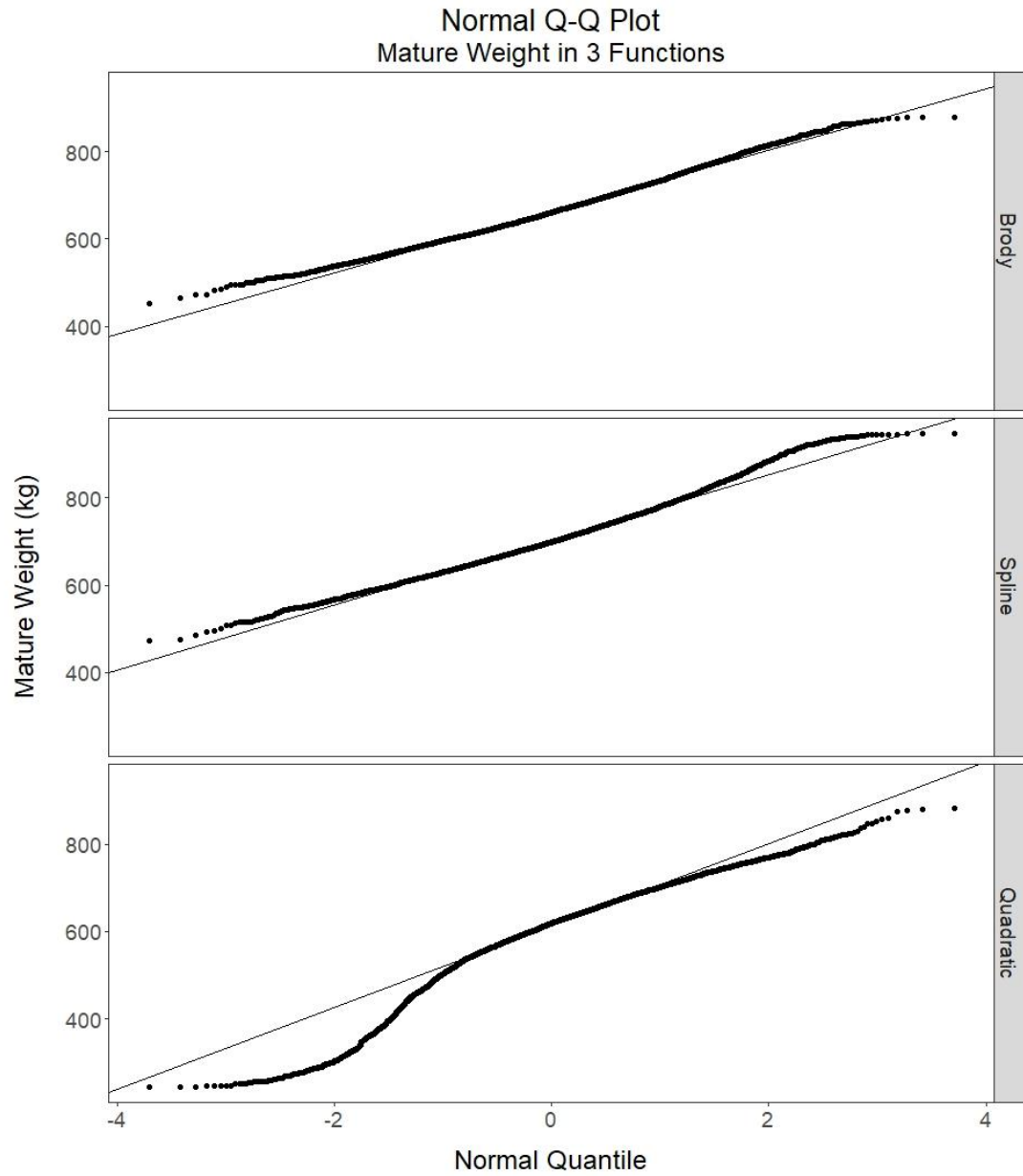


Figure 2.3. Quantile-quantile plots of mature weight estimates after editing ($n = 4,721$) from the Brody, spline, and quadratic functions.

Table 2.2. Measures of skewness and kurtosis of mature weight estimates after editing (n = 4,721) from the Brody, spline, and quadratic functions.

Function	Skewness	Kurtosis
Brody	0.28	-0.12
Spline	0.41	0.21
Quadratic	-0.91	0.85

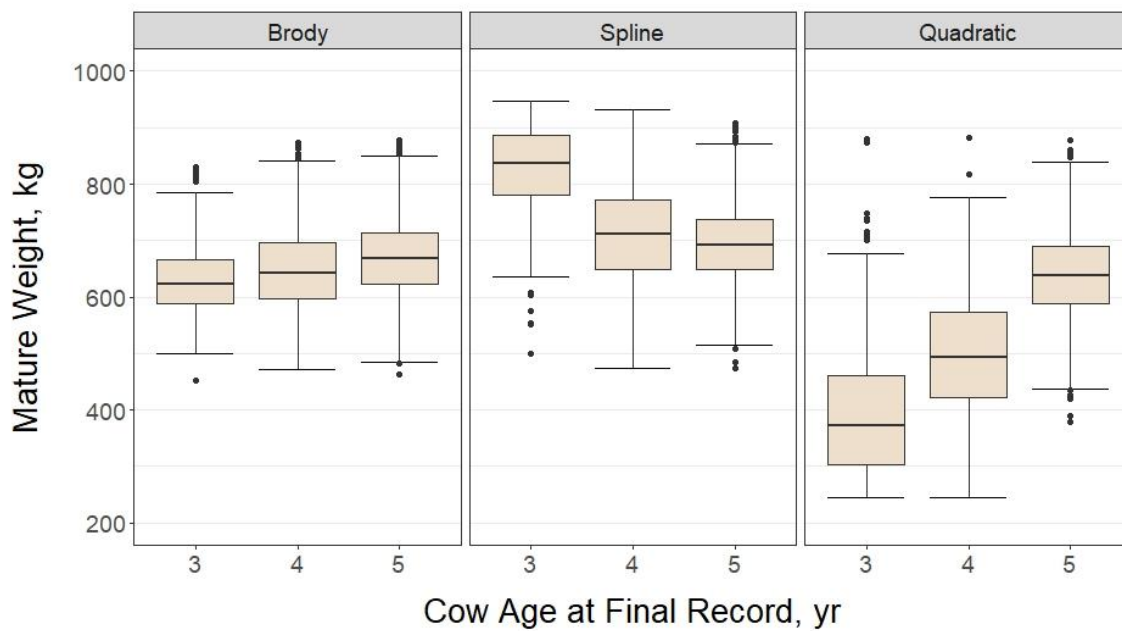


Figure 2.4. Distribution of mature weights estimated for crossbred cows using the Brody, spline, and quadratic functions, separated by age at final (oldest) weight measurement (n = 319 for 3 yr old; n = 672 for 4 yr old; n = 3,730 for 5 yr old).

Table 2.3. ANOVA results analyzing significance of model fitted, age at final (oldest) record, and their interaction on mature weight estimate (n = 4,721).

Term ¹	DF ²	Sum of Squares	Mean Squares	F value	P ³
Function	2	26021240	13010620	2385.59	< 0.001
Age	2	5252115	2626058	481.51	< 0.001
Interaction	4	25790133	6447533	1182.2	< 0.001
Residuals	14154	77193580	5454		

¹ Function was the was the function used to generate the mature weight estimate (Brody, spline, or quadratic), Age was the cow's age at final (oldest) record (3, 4, or 5 yr), with Interaction the interaction of those 2 effects.

² DF = Degrees of Freedom

³ Significance at $\alpha = 0.05$.

Table 2.4. Pearson (above diagonal) and Spearman (below diagonal) phenotypic correlations between mature weights estimated for crossbred cows (n = 4,721) from Brody, spline, and quadratic functions.

Function	Brody	Spline	Quadratic
Brody		0.61	0.63
Spline	0.66		0.28
Quadratic	0.73	0.48	

Table 2.5. Average growth parameter values and standard deviations estimated from 3 functions using weight records from crossbred cows (n = 4,721).

Parameter	Brody		Spline		Quadratic	
	Mean	SD	Mean	SD	Mean	SD
Weaning Weight, kg	---	---	229.8	32.0	273.1	38.9
Knot, d	---	---	602	188	---	---
Maturing Constant, d ⁻¹	0.0022	0.0008	---	---	---	---
Mature Weight, kg	664.4	69.2	705.2	77.0	601.0	110.5

Table 2.6. Results of paired t-tests between weights estimated by different functions for crossbred cows (n = 4,721).

Weight Estimate	Difference Taken	T Value	P Value ¹
Mature Weight	Brody – Spline	-43.19	< 0.001
	Brody – Quadratic	51.00	< 0.001
	Spline – Quadratic	61.71	< 0.001
Weaning Weight	Spline – Quadratic	-104.58	< 0.001

¹ Significance at $\alpha = 0.05$.

CHAPTER 3: BREED OF SIRE EFFECTS FOR MATURE WEIGHT IN CROSSBRED CATTLE

ABSTRACT

Mature cow weight (**MWT**) is heritable and affects the costs and efficiency of a breeding operation. Cow efficiency is also influenced by the environment, with the relationship between the size and profitability of a cow varying depending on production setting. There is a need to provide producers with tools for incorporating MWT into their breeding programs. The goal of this study was to estimate breed of sire effects for MWT using estimates from Brody, spline, and quadratic functions. Functions were previously fitted using 102,177 weight records from 4,721 crossbred cows from the U.S. Meat Animal Research Center Germplasm Evaluation Program. Variance components were estimated for several of the parameters values obtained from the functions fitted including weaning weight (**WWT**), MWT and maturing constant (**k**). Multivariate animal models were fitted that included the fixed effect of birth year-season contemporary group, covariates of breed fractions and direct and maternal heterosis, and random effects of direct additive and residual. Additionally, for WWT a maternal additive and permanent environmental effect was fitted, and for k a maternal additive effect. Due to the lack of published MWT estimated progeny differences (**EPD**), breed effects were calculated using breed of sire solutions adjusted for the difference between breed average yearling weight (**YWT**) EPD and the weighted average breed-specific YWT EPD of bulls with progeny with MWT. A regression coefficient of progeny MWT on sire YWT EPD was

calculated using the previously-defined animal model, with the addition of sire YWT EPD as a covariate. Direct heterosis ranged from 11.8 to 22.2 kg for all weight traits, and was 0.00011 d^{-1} for k. Maternal heterosis was between -1.7 and -19.8 kg for weight traits, and was 0.00018 d^{-1} for k. Heritability (SE) for Brody, spline, and quadratic MWT were 0.55 (0.03), 0.49 (0.03), and 0.22 (0.03), respectively. Direct heritability (SE) for WWT from spline and quadratic functions were 0.29 (0.03) and 0.30 (0.03), respectively. The genetic correlation between WWT and MWT was 0.56 (0.06) in the spline function and 0.47 (0.09) in the quadratic. Breed of sire effects, expressed as a deviation from Angus, for MWT ranged from approximately -80.0 to 0.0 kg. Angus, Charolais, and Brahman had consistently heavier breed of sire effects. Braunvieh, Tarentaise, and Gelbvieh had consistently lighter breed of sire effects. Breed of sire effects for Limousin, Brangus, Chianina, and Simmental were consistently intermediate. Breed of sire effects for MWT can be useful in breeding programs where selection for MWT is considered.

Key words: beef cattle, breed of sire effect, genetic parameters, mature weight

INTRODUCTION

Cow mature weight (**MWT**) has increased considerably over the past 30 yr (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016). Between 1975 and 2005 the average weight of cows at slaughter increased from 475 to 621 kg, and production costs also have increased (McMurry, 2008). Selection pressure for faster growth and heavier slaughter weight has contributed to this increase in MWT (Jenkins and Ferrell, 2006). Larger cows require greater daily intake than smaller cows (Walker et al., 2015), but whether larger

cows are more, less, or equally as efficient as smaller cows is equivocal. Studies conducted in different climactic areas have drawn different conclusions (Scasta et al., 2015; Walker et al., 2015; Beck et al., 2016), suggesting that efficiency is influenced by environment. A variety of biological types of cows are available to suit the diverse environments and management conditions found in beef operations in the United States (Arango and Van Vleck, 2002). The challenge is identifying the best choice.

Crossbreeding is a valuable tool for matching cow to environment. Mating unlike breeds with complementary strengths can create a combination of traits which make the progeny optimally suited for their production environment. Additionally, when unlike alleles combine, the resulting progeny may display heterosis: a superiority of the crossbred progeny over the average of the parental breeds (Weaber, 2010).

Currently, published Expected Progeny Difference (**EPD**) are not readily comparable across breeds. United States beef breed organizations and their genetic evaluation service providers are responsible for collecting data on, calculating, and publishing EPD for their own animals, so published information for each breed generally represents a unique population. As a consequence, EPD are generally not directly comparable across breeds, although there are currently multi-breed evaluations underway. This limitation can create challenges for breeders wishing to utilize bulls from multiple breeds in an informed crossbreeding program towards a common goal. The U.S. Meat Animal Research Center (**USMARC**) in Clay Center, Nebraska, publishes across-breed adjustment factors for 18 breeds on various traits using crossbred animals from its Germplasm Evaluation (**GPE**) program; doing so allows producers to compare EPD from animals of different breeds. However, MWT is not currently among traits analyzed.

Mature weight EPD are also not commonly published by U.S. breed organizations at this time.

Breed of sire effects for MWT can provide additional information to aid in informed breed utilization. They can also be used to calculate across-breed adjustment factors should MWT EPD become more widely available. The objective of this study was to estimate breed of sire and heterotic effects for MWT in 18 beef breeds using data from GPE cattle.

MATERIALS AND METHODS

Animals

Animals were raised in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (FASS, 2010), and their care was approved by the USMARC Animal Care and Use Committees.

Cows used were from the USMARC GPE program as described by Zimmermann et al. (2018). Briefly, the cows were from cycle VII and continuous sampling phases, born between 1999 and 2014 and that reached a maximum of 14 yr of age. The breed-types represented were: Angus, Hereford, Red Angus, Shorthorn, Beefmaster, Brahman, Brangus, Santa Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine Anjou, Salers, Simmental, Tarentaise, Devon, Bonsmarra, Romosinuano, MARC II (¼ each Simmental, Hereford, Angus, and Gelbvieh), and MARC III (¼ each Angus, Hereford, Pinzgauer, and Red Poll). Sires from 7 most common U.S. breeds were mated via artificial insemination (**AI**) to mostly Angus, Hereford, and MARC III dams.

A total of 4,721 cows with 102,177 weight records contributed to analysis after editing. Editing included removing cows with weight records not extending past 3 yr of age or with missing pedigree data. Additionally, weight records were removed after 6 yr of age, after a gap between subsequent records greater than 2 yr, and after the start of a feed restriction diet (Zimmerman et al., 2018).

Growth Functions

Growth from weaning to maturity was described for each animal by fitting 3 functional forms to the data on individual cows considering the relationship between their weight and age. Before fitting the functions, age data were scaled by subtracting 180 d and weight data were scaled by subtracting 214.3 kg. These were an early boundary of age at which weaning weights (**WWT**) were collected and the average body weight at this age, respectively. First, a Brody function was used that consisted of 2 parameters: **A** (MWT) and **k** (maturing constant). Second, a spline was fitted as a piecewise linear function. Its parameters included slopes and intercepts before and after a knot where the functions joined. The age, expressed in days of age, at which the knot occurred also was estimated. Weight at 6 yr of age, considered as at maturity, were obtained from the fitted parameter values. Last, a quadratic polynomial containing an intercept, and linear and quadratic terms, was fitted. The solutions for these coefficients were used to estimate weight at 6 yr, or maturity. Further details on the fitting of these functions is described in Zimmermann et al. (2018).

Three sets of key parameter values were analyzed in the present study. From the Brody function, these were A (**AMWT**) and k . From the spline function, these parameters were the intercept of the first piecewise function (Sb_0), knot, and MWT estimated at 6 yr of age based on parameter values (**SMWT**). The Sb_0 estimated WWT. The knot reflected when cows' growth slowed. From the quadratic function, these parameters were the intercept (Qb_0) and MWT estimated at 6 yr of age based on parameter values (**QMWT**). The Qb_0 also estimated WWT. Each of the growth prediction summary statistics from individual animal models were used as response variables in subsequent analyses.

Breed and Heterotic Effects

The covariates for heterosis direct and maternal were allocated as the regression on expected heterozygosity fraction. Expected heterozygosity fraction was calculated as 1 minus the sum of products of the same breeds from the sire and dam. For heterosis calculation, AI sires and commercial cows of the same breed were considered the same breed, Red Angus was assumed the same as Angus, and composite breeds were considered according to their nominal breed composition. Composite breeds consisted of MARC II ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Simmental, and $\frac{1}{4}$ Gelbvieh), MARC III ($\frac{1}{4}$ Angus, $\frac{1}{4}$ Hereford, $\frac{1}{4}$ Red Poll, and $\frac{1}{4}$ Pinzgauer), Brangus ($\frac{3}{8}$ Brahman and $\frac{5}{8}$ Angus), Santa Gertrudis ($\frac{3}{8}$ Brahman and $\frac{5}{8}$ Shorthorn), Beefmaster ($\frac{1}{2}$ Brahman, $\frac{1}{4}$ Angus, and $\frac{1}{4}$ Shorthorn), Chiangus ($\frac{1}{2}$ Chianina and $\frac{1}{2}$ Angus), and $\frac{1}{2}$ Red Angus $\frac{1}{2}$ Simmental cross cows. If the individual's dam was unknown, its maternal heterosis was calculated as the expected heterozygosity of the dam's breed in general. For example, if a cow had a dam

whose identity was not recorded, but the dam was known to be Brangus, then the dam's expected heterozygosity would be $1 - \left[\left(\frac{5}{8} \right) \left(\frac{5}{8} \right) + \left(\frac{3}{8} \right) \left(\frac{3}{8} \right) \right] = 0.47$, where the 5/8 and 3/8 corresponds with proportion of Angus and Brahman in its breeding, respectively.

Breed fractions were determined based on pedigree information. Founder animals, sires or dams with known breed but unknown parentage, were assigned to their respective breeds and used to assign breed fractions throughout the pedigree; each animal was assigned half of its sire breed and half of its dam breed. For breed fraction calculation, all breeds, including composites, were considered separate genetic groups. Breed fractions assigned for each individual were fit as covariates for the estimation of breed effects.

Analysis

Model selection and (co)variance components. ASReml version 4 (Gilmour et al., 2015) was used to estimate variance components for parameter values obtained from the Brody, spline and quadratic functions, and breed solutions for MWT, fitting an animal model. The models analyzed for all growth function parameters included the fixed effect of birth year-season contemporary group, covariates of breed fractions, direct heterosis, and maternal heterosis, and random effects of direct additive and residual.

For each parameter, the addition of random effects of maternal additive (with and without covariance to direct additive) and uncorrelated maternal permanent environment were tested for significance. Testing was done by adding each effect marginally and performing a log-likelihood ratio test between the incrementally simpler and more complex model. With the test, -2 times the difference in log likelihoods was compared to a

χ^2 value with 1 df and α of 0.05. Additionally, variance component estimates and ratios were compared between models to ensure partitioning was reasonable.

The final model selected for MWT and knot only included the direct additive and residual as random terms. The same model was also selected for linear and quadratic coefficients of the quadratic function, but analysis of those parameters are not presented since they are not biologically easy to interpret. The best-fit model for k included a maternal additive effect, while that for WWT included both maternal additive and permanent environmental effects. Based on the log-likelihood ratio test, the direct-maternal additive covariance defined significant variation in WWT. However, it resulted in unusually large, negative correlations (-0.83 in the spline function and -0.65 in the quadratic function) and large increases in the estimates of the direct and maternal additive variances. The direct heritability roughly doubled and the maternal heritability increased to roughly 6 times its previous value upon addition of the direct-maternal additive covariance in both spline and quadratic functions. As suggested by Lewis and Beatson (2009), this likely reflected the data structure. Only WWT on cows were considered, with limited depth of weight information along maternal ancestral pathways. Therefore, the direct-maternal additive covariance for WWT was excluded from the final model fitted.

The final statistical models selected were analyzed by function (Brody, spline, quadratic), including all parameters obtained within the function, fitting a multivariate model (ASReml version 4; Gilmour et al., 2015). Additive and residual covariances among the parameter values were included.

Breed of Sire Effect Solutions. Breed of sire effects were calculated in a similar manner to Kuehn and Thallman (2017). However, EPD for MWT were not available in many breeds. As a result, breed effects for MWT were calculated from MWT breed of sire solutions estimated from USMARC data, adjusted for sire sampling using YWT as a proxy. Yearling weight was chosen as a point of adjustment because it was commonly reported and was closer to maturity than other weight traits. The equation used was

$$M_i = USMARC(i) + b[EPD(i)_{average} - EPD(i)_{USMARC}]$$

where M_i was the breed of sire effect for breed i , $USMARC(i)$ was the breed of sire solution for breed i (half of the breed solution), b was the regression coefficient relating progeny performance – estimated MWT from each of the 3 functions – to sire YWT EPD, $EPD(i)_{average}$ was the mean industry-published YWT EPD for bulls of breed i , and $EPD(i)_{USMARC}$ was the mean YWT EPD of bulls sampled at USMARC with progeny in the analysis, weighted by sires' total relationship to phenotyped descendants.

Values of b were obtained by its addition to the animal model already described for MWT. Yearling weight EPD were assigned based on their sire. Offspring of sires with EPD received their respective sire's full EPD, and subsequent generations of offspring received the EPD diluted by a factor of $\frac{1}{2}$ for each generation of separation.

For all analyses, commercial breed groups were included as well as AI breed groups. Only AI breed group solutions are reported given the fact that AI breed groups are more reflective of industry trends.

RESULTS

Heterosis

Table 3.1 shows the estimated direct and maternal heterosis for selected growth function parameters. Direct heterosis estimates were positive and between 14.9 and 22.2 kg for MWT and about 12 kg for WWT. Maternal heterosis estimates for weight traits were negative and more variable: for MWT they ranged from -1.7 to -19.8 kg, and for WWT were -2.9 (Qb_0) and -6.2 (Sb_0) kg. Both direct and maternal heterosis for k were positive (0.00011 and 0.00018 d^{-1} , respectively).

Genetic Parameters

Table 3.2 shows (co)variances among the direct, maternal, and residual effects of the Brody function parameters, AMWT and k . The AMWT was highly heritable (0.55 ± 0.03) while k was moderately heritable (0.25 ± 0.03). There was a negative additive correlation between AMWT and both direct (-0.16 ± 0.08) and maternal (-0.24 ± 0.09) effects of k .

Table 3.3 shows (co)variance components, among the spline parameters Sb_0 (WWT), knot, and SMWT. Their direct heritabilities were 0.29 ± 0.03 , 0.23 ± 0.03 , and 0.49 ± 0.03 , respectively. The correlation between the direct additive effect for SMWT and the maternal additive effect for Sb_0 was negative and moderate in size (-0.19 ± 0.18), but all other correlations were positive. A high positive direct additive correlation existed between WWT and MWT (0.56 ± 0.06), implying that a cow larger at weaning also will

be larger at maturity. The maternal heritability of Sb_0 was negligible (0.03 ± 0.03), and the proportion of phenotypic variance due to maternal permanent environment in Sb_0 was small (0.10 ± 0.03). There appears to be a positive additive correlation between knot and all other parameters (0.19 ± 0.08 with SMWT; 0.42 ± 0.09 and 0.30 ± 0.21 with direct and maternal additive effects for Sb_0 , respectively).

Table 3.4 shows the (co)variances of quadratic function parameters Qb_0 (WWT) and QMWT. Only Qb_0 and QMWT parameters are reported as the variance components of linear and quadratic coefficients have no clear biological interpretation. The direct heritability of Qb_0 and QMWT were 0.30 ± 0.03 and 0.22 ± 0.03 , respectively. The direct additive correlation between Qb_0 and QMWT (0.47 ± 0.09) was similar to that for the spline function. For Qb_0 the heritability estimate for maternal effect (0.06 ± 0.03) was small. The ratio of maternal permanent environment to phenotypic variance (0.01 ± 0.03), and the correlation between the maternal additive effect of Qb_0 and the direct additive effect of QMWT (-0.01 ± 0.16), were negligible.

Breed of Sire Effects

Breed of sire effects for MWT are provided in Table 3.5, reported as deviations from Angus. Breed YWT EPD, which were used to calculate adjusted breed of sire effects, are also given. The estimates of the regression coefficients of cow MWT on sire YWT EPD are shown in Table 3.6. Angus had the heaviest breed of sire effect while Braunvieh had the lightest breed of sire effect, 57 to 80 kg lighter than Angus. Charolais

and Brahman also consistently ranked among the heaviest in MWT, while Tarentaise, Gelbvieh, and Shorthorn were consistently among the lightest in MWT.

Pearson and Spearman correlations among breed of sire effect solutions for MWT are presented in Table 3.7. Correlations between breed of sire solutions were highest when MWT were obtained using the Brody and spline functions, and lowest when those estimates were obtained with the quadratic and spline functions.

DISCUSSION

Breed effects for MWT obtained from the fit of 3 functions – Brody, spline and quadratic polynomial – were calculated for 18 breeds using data from the USMARC admixed GPE herd. In addition, direct and maternal heterotic effects, and (co)variances, heritabilities and correlations for and between parameters of each function, were estimated.

Heterosis

Direct heterosis for MWT in the 3 functions ranged from 14.9 to 22.2 kg, which were at the lower end of estimates reported by Gregory et al. (1966) among Hereford, Angus, and Shorthorn cross heifers (22 to 24 kg). Few studies report effects of maternal heterosis past weaning. Olson et al. (1978) found that offspring from crossbred cows were heavier than offspring from straightbred cows at 200 d of age, implying a positive maternal heterotic effect on WWT. Such is contrary to the results of the current study, where maternal heterosis for WWT was small but consistently negative. However, Olson

et al. (1978) also reported that maternal heterosis reduced post-weaning ADG, with a general reduction in maternal heterotic effects in weights at more advanced ages. While maternal heterosis may be negative, given the weight of cows at maturity, its impact appears to be small. The negative heterosis could have been related to the structure of the data, as it was limited to females.

From analyses of other subsets of USMARC data, solutions for maternal effects differed from those obtained in the current study, suggesting structural differences among data sets. Van Vleck and Cundiff (2004) reported WWT direct heterosis that was about half of present estimates (6.7 kg), and WWT maternal heterosis that was greater and opposite in sign (10.4 kg). Their analysis was performed as part of the EPD adjustments to a birth year of 2002, which is within the range of birth years represented in the current data.

Both direct and maternal heterosis values for k were positive, indicating that heterosis, both in the individual and in the dam, are expected to increase the rate at which a cow approaches MWT. Gregory et al. (1966) and Smith et al. (1976) postulated that heterosis hastens maturation. Results obtained in the present study support that concept.

(Co)variance Ratios

Estimates of MWT heritability were near 0.50 for Brody and spline functions, but 0.22 for the quadratic function. The former two estimates agree well with published literature values, which were generally between 0.40 and 0.60 (DeNise and Brinks, 1985; Bullock et al., 1993; Kaps et al., 2000). Heritability for live weight at 445 d of age in the

same overall population (GPE cycle VII) was also reported near 0.50 (0.48 ± 0.15 ; Wheeler et al., 2005). Heritability near 0.30 was reported in some Zebu-type populations (Abreu Silva et al., 2018; Meyer, 1992) and in a Hereford population (Meyer, 1992). However, in the present case, the unusually low heritability of MWT obtained from quadratic function likely reflected its poorer fit to the weight-age data on individual cows. Polynomial curves are known to behave erratically at data boundaries and extremes (Parks, 1982; deBoor, 2001; Meyer, 2005). This phenomenon was observed when fitting the quadratic curve to these data (Zimmermann et al., 2018).

Weaning weight direct heritability was about 0.30 in both spline and quadratic functions. Published values of WWT heritability are variable, ranging from near 0.20 (Meyer, 1992; Bullock et al., 1993; Abreu Silva et al., 2018) to greater than 0.40 (DeNise and Brinks, 1985; Bullock et al., 1993; Kaps et al., 2000). The values obtained in the current study fall within this range. The heritability of 200 d weight in an older cohort of USMARC cattle was similar: 0.34 ± 0.09 , 0.33 ± 0.10 , and 0.31 ± 0.17 in all breed groups, purebreds, and composites, respectively (Gregory et al., 1995). For WWT at 205 d, Schiermiester et al. (2015) estimated a heritability of 0.22 ± 0.03 . These literature values agree with the present estimates. It is important to note that, while 205 d is the standard age for collection of WWT, weight at 180 d of age was considered as WWT for this study.

Maternal heritability of WWT was small for both spline (0.03) and quadratic (0.06) functions. Abreu Silva et al. (2018) also reported small maternal heritability for this trait. Some others have reported larger maternal heritabilities (Meyer, 1992; Kaps et al., 2000), but Meyer (1993) notes that maternal effects vary in importance between

breeds. Rather than due to breed composition, our smaller values more likely related to structure of these data, as it represents a small subset of a larger population. In another subset of GPE cycle VII cattle, Schiermiester et al. (2015) reported greater maternal heritability of WWT (0.17 ± 0.05).

The direct-maternal additive covariance was not fitted in the current study. However, using WWT collected on GPE cycle VII and later calves, Schiermiester et al. (2015) was able to fit the direct-maternal additive covariance along with direct and maternal additive and permanent environmental effects. They obtained reasonable estimates of the direct-maternal additive correlation (-0.33). Although our data also consisted of cycle VII and later cattle, our attempts to fit this covariance resulted in large, negative correlations and erratic variance components.

Maternal permanent environment effect for WWT, expressed as a proportion of total phenotypic variation, differed somewhat between the spline (0.10) and quadratic (0.01) functions, but were consistent with literature estimates overall. Meyer (1992) reported an effect of 0.035 in an Angus population and 0.138 in a Zebu-cross population, although reflected a broad range of weaning ages (120 to 300 d). Schiermiester et al. (2015) reported an estimate of 0.24 ± 0.03 and 0.23 ± 0.03 from 2 different models analyzing data on similar GPE cattle. Like maternal heritability, maternal permanent environment effect seems to be variable depending on breed-type and environmental circumstances.

Strong, positive correlations between WWT and MWT existed in these data (0.56 in the spline function and 0.47 in the quadratic function). Similarly large, and even larger,

positive correlations are commonly reported (Brinks et al., 1964; Bullock et al., 1993; Kaps et al., 2000; Abreu Silva et al., 2018).

The position of the knot in the fit of the spline function was moderately heritable (0.23 ± 0.03), with moderate to strong positive correlations with both direct (0.42 ± 0.09) and maternal (0.30 ± 0.21) additive effects of WWT, but a bit lower with MWT (0.19 ± 0.08). It was hypothesized that the knot may coincide with the age at which a cow's growth had significantly slowed, perhaps reflecting its approach to sexual maturity. On average, the values of knot obtained for individual cows occurred after the age of puberty reported by Freetly et al. (2011). To our knowledge, the heritability of knot location has not previously been reported.

Breed of Sire Effects

Angus had the heaviest breed of sire effect for MWT based on AMWT, SMWT, and QMWT. Deviations from Angus ranged from -4.9 kg to -57.2 kg based on AMWT, from -19.7 kg to -80.0 kg based on SMWT, and from -10.3 kg to -59.1 kg based on QMWT. There was a very strong, positive correlation between breed of sire effects derived from the Brody and spline functions, indicating that MWT obtained from them ranked similarly in the different breeds. The lowest correlation was between the spline and quadratic functions.

Given the lack of published MWT EPD, breed of sire effects were calculated using YWT EPD and the breed of sire solution. The regression of offspring MWT on sire YWT EPD contribution was necessary to perform this calculation. The coefficient was between 1.1 and 1.9 kg/kg for the 3 functions used to estimate MWT. This was

unexpectedly low. If the regression coefficient was 1, this suggests that, for every kg increase in YWT EPD, MWT will also increase by the same amount. A coefficient substantially larger than 1 was expected.

Angus, Charolais, and Brahman cattle had consistently large breed of sire effects while Braunvieh, Tarentaise, and Gelbvieh cattle had consistently small breed of sire effects. Individuals belonging to the former 3 breeds would thus be expected to reach a heavier MWT, while individuals belonging to the latter 3 breeds would be expected to reach a lighter MWT. Limousin, Brangus, Chianina, and Simmental had intermediary breed of sire effects, suggesting that they might be appropriate breed choices if an intermediate MWT was desired.

Conclusions

The incorporation of breed of sire effects for MWT in decision-making in pure and crossbreeding breeding programs undoubtedly will depend on individual goals of producers. Beef cattle in the United States are managed across vastly different environments; the optimal size for a mature breeding cow in a beef operation will vary based on the operation's unique environment, management style, breeding objective, present WWT averages, and resource availability. No universal recommendations can be offered regarding the favorability of using breeds with larger to smaller MWT. However, whether an operation's goal is to increase, maintain, or decrease MWT, the information presented can improve the efficacy of breed selection.

ACKNOWLEDGEMENTS

The authors wish to thank the technical staff at the Roman L. Hruskra U.S. Meat Animal Research Center (Clay Center, NE, USA) for their support of the experimental program.

LITERATURE CITED

- Abreu Silva, B. C., J. P. Eler, M. L. Santana Jr., E. C. Mattos, I. R. Menezes, J. B. S. Ferraz. 2018. Genetic association between mature weight and early growth and heifer pregnancy traits in Nellore cattle. *Livest. Sci.* 211:61-65.
doi:10.1016/j.livsci.2018.03.003
- Arango, J. A. and L. D. Van Vleck. 2002. Size of beef cows: Early ideas, new developments. *Genet. Mol. Res.* 1:51-63.
- Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. *J. Anim. Sci.* 94:1689-1702. doi:10.2527/jas2015-0049
- Beef Improvement Federation. 2016. Guidelines for uniform beef improvement programs, 9th edition. https://beefimprovement.org/wp-content/uploads/2013/07/BIFGuidelinesFinal_updated0916.pdf (Accessed 10 December 2017.)
- Brinks, J. S., R. T. Clark, N. M. Kieffer, J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. *J. Anim. Sci.* 23(3):711-716. doi:10.2527/jas1964.2337x

- Bullock, K. D., J. K. Bertrand, and L. L. Benyshek. Genetic and environmental parameters for mature weight and other growth measured in Polled Hereford cattle. *J. Anim. Sci.* 71:1737-1741.
- de Boor, C. 2001. A practical guide to splines. 2nd ed. Springer-Verlag, New York.
- DeNise, R. S. K. & J. S. Brinks, 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. *J. Anim. Sci.* 61(6):1431-1440.
- Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Estimates of genetic parameters for weight and height of angus cows using a repeatability model. *Proc. West. Sec. Amer. Soc. Anim. Sci.* 60:40-41.
- Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. *J. Anim. Sci.* 89:2373-2379. doi:10.2527/jas.2011-3847.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2015. ASReml user guide Release 4.1 Structural Specification. VSN International Ltd., Hemel Hempstead, HP1 1ES, UK.
- Gregory, K. E., L. A. Swiger, R. M. Koch, L. J. Sumpton, J. E. Ingalls, W. W. Rowdan, and J. A. Rothlisberger. 1966. Heterosis effects on growth rate of beef heifers. *J. Anim. Sci.* 25(2):290-298. doi:10.2527/jas1966.252290x
- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. *J. Anim. Sci.* 73:1920-1926.

- Jenkins, T. G. and C. L. Ferrell. 2006. Matching beef genetics with production environment. Proc. Beef Improv. Federation Ann. Meet. & Symp., Chocktaw, Mississippi. p. 41-46.
- Kaps, M., W. O. Herring, and W. R. Lambertson. 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationship with weaning weight in Angus cattle. J. Anim. Sci. 78:1436-1442.
- Kuehn, L. A. and R. M. Thallman. 2017. Across-breed EPD tables for the year 2017 adjusted to breed differences for birth year of 2015. Proc. Beef Improv. Federation Ann. Meet. & Symp., Athens, Georgia. p. 112-144.
- Lewis, R. M., and P. R. Beatson. 1999. Choosing maternal-effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. Livest. Prod. Sci. 58:137-150.
- McMurry, B. 2008. Just how big are our beef cows these days? Feedstuffs. 80(51):16-17.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31:179-204. doi:10.1016/0301-6226(92)90017-X
- Meyer, K. 1993. Covariance matrices for growth traits of Australian Polled Hereford cattle. Anim. Prod. 57:37-45.
- Meyer, K. 2005. Estimates of genetic covariance functions for growth of Angus cattle. J. Anim. Breed. Genet. 122:73-85.
- Olson, L. W., L. V. Cundiff, and K. E. Gregory. 1978. Maternal heterosis effects on postweaning growth and carcass traits in beef cattle. J. Anim. Sci. 46(6):1552-1562. doi:10.2527/jas1978.4661552x

- Parks, J. R. 1982. A theory of feeding and growth of animals. Springer-Verlag Berlin Heidelberg New York.
- Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. *J. Anim. Sci.* 93:5829-5839. doi:10.2527/jas2015-9172
- Schiermiester, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. *J. Anim. Sci.* 93:46-52. doi:10.2527/jas2014-8493.
- Smith, G. M., H. A. Fitzhugh Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976. Heterosis for maturing patterns in Hereford, Angus, and Shorthorn cattle. *J. Anim. Sci.* 43(2):380-388.
- Van Vleck, L. D. and L. V. Cundiff. 2004. Across-breed EPD tables for the year 2004 adjusted to breed differences for birth year of 2002. In: Proc. 36th Beef Improv. Federation Ann. Meet. & Symp., Sioux Falls, South Dakota. http://www.bifconference.com/bif2004/BIFsymposium_pdfs/vleckcundiff.pdf (Accessed 25 July 2018)
- Walker, R. S., R. M. Martin, G. T. Gentry, and L. R. Gentry. 2015. Impact of cow size on dry matter intake, residual feed intake, metabolic response, and cow performance. *J. Anim. Sci.* 93:672-684. doi:10.2527/jas2014-7702
- Weaber, B. 2010. Crossbreeding for commercial beef production. In: M. K. Nielsen, editor, National Beef Cattle Evaluation Consortium beef sire selection manual. 2nd ed. p. 50-57.

Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2005.

Characterization of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability traits. *J. Anim. Sci.* 83:196-207.

Zimmermann, M. J., L. A. Kuehn, M. L. Spangler, R. M. Thallman, W. M. Snelling, and

R. M. Lewis. 2018. Growth from weaning to maturity in beef cattle breeds.

Submitted.

Table 3.1. Estimates of direct and maternal heterosis for growth function parameters.

Function	Parameter ¹	Units	Direct Heterosis		Maternal Heterosis	
			Estimate	SE	Estimate	SE
Brody	AMWT	kg	14.9	2.8	-14.6	2.9
	k	d ⁻¹	0.00011	0.000029	0.00018	0.000031
	Sb ₀	kg	12.4	1.4	-6.2	1.4
Spline	Knot	d	3	7	-48	8
	SMWT	kg	22.2	3.1	-1.7	3.2
Quadratic	Qb ₀	kg	11.8	1.6	-2.9	1.6
	QMWT	kg	19.0	4.1	-19.8	4.3

¹ AMWT, SMWT, and QMWT are estimates of mature weight, the latter two obtained from solving for the model coefficients at 6 years of age; k is the maturing constant; Sb₀ and Qb₀ are weaning weight estimates; knot is the age at which the break in the spline function occurs.

Table 3.2. (Co)variances (SE) of direct additive, maternal additive, and residual effects, of Brody parameter functions.

Parameter ¹	AMWT _d , kg	k _d , day ⁻¹	k _m , day ⁻¹	AMWT _r , kg	k _r , day ⁻¹
AMWT _d , kg	1988.5 (138.9)	-0.0021 (0.0012)	-0.0021 (0.0008)		
k _d , day ⁻¹		8.7 x10 ⁻⁸ (1.2 x10 ⁻⁸)			
k _m , day ⁻¹			3.9 x10 ⁻⁸ (8.0 x10 ⁻⁹)		
AMWT _r , kg				1613.1 (101.5)	-0.0086 (0.0008)
k _r , day ⁻¹					2.3 x10 ⁻⁷ (1.1 x10 ⁻⁸)

¹ AMWT is mature weight; k is the maturing constant; subscript d indicates direct additive effect, m indicates maternal additive effect, and r indicates residual. Covariance between direct and maternal additive effect of k was not fitted.

Table 3.3. (Co)variance of direct additive, maternal additive, maternal permanent environment, and residual effects for Spline function growth parameters.

Param. ¹	Sb _{0d} , kg	knot _d , day	SMWT _d , kg	Sb _{0m} , kg	Sb _{0MPE} , kg	Sb _{0r} , kg	knot _r , day	SMWT _r , kg
Sb _{0d} , kg	211.8 (24.8)	450.2 (113.1)	379.6 (51.7)					
knot _d , day		5372.7 (807.9)	644.7 (257.9)	107.9 (73.9)				
SMWT _d , kg			2148.2 (164.6)	-43.9 (34.6)				
Sb _{0m} , kg				24.8 (19.7)				
Sb _{0MPE} , kg					72.0 (20.5)			
Sb _{0r} , kg						421.4 (22.8)	850.1 (97.3)	161.8 (39.0)
knot _r , day							18494.7 (774.8)	-2486.4 (226.4)
SMWT _r , kg								2248.3 (127.0)

¹ Sb₀ is the intercept; an estimate of weaning weight; SMWT is mature weight estimated at 6 yr of age using fitted coefficients for the piecewise linear function after the knot; knot is the age at which the break in the spline function occurs; subscript d indicates direct additive effect, m indicates maternal additive effect, MPE indicates maternal permanent environment, and r indicates residual. Covariance between direct and maternal additive effect of Sb₀ was not fitted.

Table 3.4. (Co)variances of direct additive, maternal additive, maternal permanent environment, and residual effects (SE) of parameters from a quadratic function.

Parameter ¹	Qb _{0d} , kg	QMWT _d , kg	Qb _{0m} , kg	Qb _{0MPE} , kg	Qb _{0r} , kg	QMWT _r , kg
Qb _{0d} , kg	297.0 (36.0)	325.9 (75.6)				
QMWT _d , kg		1646.8 (236.6)	-2.4 (47.5)			
Qb _{0m} , kg			61.0 (28.9)			
Qb _{0MPE} , kg				10.9 (27.9)		
Qb _{0r} , kg					636.0 (33.6)	852.1 (64.7)
QMWT _r , kg						5717.4 (230.0)

¹ Qb₀ is the intercept; an estimate of weaning weight; QMWT is mature weight estimated at 6 years of age using fitted quadratic coefficients; subscript d indicates direct additive effect, m indicates maternal additive effect, MPE indicates maternal permanent environment, and r indicates residual. Covariance between direct and maternal additive effect of Qb₀ was not fitted.

Table 3.5. Breed of sire effects expressed as a deviation from Angus, breed of sire solutions, and average EPD of mature weight in 18 different GPE breeds.

Breed	USMARC Breed of Sire Solution, kg (1) ¹			Industry Average YWT EPD, kg (2)	USMARC Average YWT EPD, kg (3)	Breed of Sire Effect, kg (4) ²		
	A MWT	S MWT	Q MWT			A MWT	S MWT	Q MWT
Solution								
Angus	0.0	0.0	0.0	39.9	28.7	0.0	0.0	0.0
Red Angus	-8.3	-20.6	-9.7	39.7	33.7	-14.0	-26.3	-19.7
Beef-master	-11.2	-28.9	-11.9	18.6	17.9	-22.7	-40.3	-32.0
Brangus	-10.4	-27.4	-5.0	22.3	17.5	-17.4	-34.4	-17.4
Brahman	2.6	-10.4	6.0	12.2	10.2	-7.5	-20.4	-11.7
Braunvieh	-47.9	-70.7	-42.7	30.8	28.2	-57.2	-80.0	-59.1
Chiangus	-5.3	-20.9	-9.9	27.5	27.8	-17.8	-33.3	-31.8
Charolais	3.2	-11.7	-1.0	22.3	18.4	-4.9	-19.7	-15.0
Gelbvieh	-24.8	-44.1	-24.9	43.1	37.4	-30.8	-50.1	-35.5
Hereford	2.7	-14.1	-14.0	36.2	32.7	-5.8	-22.6	-28.8
Limousin	-12.0	-29.1	-10.1	38.5	33.6	-19.0	-36.0	-22.3
Maine Anjou	4.7	-19.6	1.7	26.3	25.2	-6.4	-30.6	-17.7
Salers	-0.6	-21.5	3.6	37.8	34.6	-9.4	-30.2	-11.8
South Devon	-3.7	-27.5	13.6	37.6	38.9	-17.4	-41.1	-10.3
Santa Gertrudis	4.1	-11.5	0.9	2.8	4.4	-9.9	-25.4	-23.6
Shorthorn	-13.8	-28.5	-6.0	27.2	30.4	-29.7	-44.3	-33.7
Simm-ental	-7.5	-19.7	-6.2	41.3	41.3	-19.8	-31.9	-27.6
Tarentaise	-24.9	-49.4	-22.5	12.2	12.4	-37.4	-61.8	-44.4
Error								
Min. ³	57.3	63.0	79.8	NA	0.44	NA	NA	NA
Max. ³	63.5	69.9	88.7	NA	0.93	NA	NA	NA

¹ AMWT is asymptotic mature weight from the Brody function; SMWT and QMWT are mature weight estimated at 6 yr from the fitted spline and quadratic function coefficients, respectively. Solutions are expressed as a deviation from Angus.

² $(4) = (1) + b [(2) - (3)]$, where b is the coefficient given in Table 3.6. Calculations for each parameter used a different coefficient. Effects are expressed as a deviation from Angus.

³ Error for (1) is standard error, kg; Error for (2) and (3) is accuracy.

Table 3.6. Parameter-specific regression coefficient of cow mature weight estimate (kg) on sire yearling weight EPD (kg).

Function	Parameter Name	Coefficient, kg/kg	SE
Brody	AMWT	1.099	0.105
Spline	SMWT	1.087	0.129
Quadratic	QMWT	1.920	0.185

Table 3.7. Pearson (above diagonal) and Spearman (below diagonal) correlations between breed effects for mature weight estimated by Brody, spline, and quadratic functions.

Function	Brody	Spline	Quadratic
Brody		0.96	0.88
Spline	0.93		0.86
Quadratic	0.78	0.69	

CHAPTER 4: SYNTHESIS

INTRODUCTION

Selection pressure has been placed on cattle for increased size at market age (Jenkins and Ferrell, 2006). As a result, the mature weight (**MWT**) of slaughter animals has increased substantially in the past 30 yr (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016). There are now concerns that cattle are becoming too large, perhaps negatively affecting their production efficiencies. The concern is especially relevant for breeding operations, which continue maintaining cattle for years beyond typical market ages and weights. Larger cows have greater energy requirements (Walker et al., 2015) – and therefore cost more to maintain – and must produce marketable calves for multiple years before the income they have generated has outweighed the cost of input they require. Mature cow efficiency seems to vary in different environments (Beck et al., 2016; Scasta et al., 2015; Walker et al., 2015). Depending on the resources available to the operation, larger cows may or may not be able to return a profit. Crossbreeding – the mating of unlike biological types – is a valuable tool to design cows that are well suited for a given environment (Weaber, 2010). By understanding growth to maturity in various breeds, breed differences can be more effectively utilized to produce cattle that will be appropriate for an operation's resources. This understanding is especially useful in beef cattle because MWT is measured late in life: it takes 5 to 6 yr for cattle to reach MWT (Taylor, 1965). To control MWT, selection decisions must be made years before the trait is observable.

Two studies were conducted to further the understanding of growth in beef cattle and facilitate more informed breed utilization in beef breeding programs wishing to control MWT. Growth patterns to maturity in 18 beef cattle breeds were studied, and then breed effects for MWT in the same breeds were estimated.

STUDY 1: GROWTH FROM WEANING TO MATURITY

Weight Data

Data was previously collected as part of the Germplasm Evaluation Program (GPE) at the United States Meat Animal Research Center (USMARC). While growth typically follows a sigmoidal pattern (Parks, 1982), these data did not allow fitting of the typical sigmoidal growth curve because there were no data between birth and weaning. Thus, birth weight records were removed, leaving only records from weaning onwards. The shape of the remaining weights appeared as an increasing concave-down curve.

Judicious data editing is important to ensure results are not biased by extraneous factors but that important variation is not removed. Considering biological implications, the distribution of the data, and any assumptions required by the planned analyses can help define what editing criteria are acceptable. In these data, the ages at the first weights after birth, supposedly weaning weights (WWT), were checked to ensure that they adhered to standard definition of WWT. In the United States beef industry, 205 d of age is considered standard for WWT (BIF, 2016). Accepting weights taken at ages too much earlier as WWT could cause bias. A cutoff of 180 d was determined appropriate, and any weights recorded at younger ages were removed. Similarly, cows with records not

extending past 3 years of age were removed since the intent was to predict weight at a later age and records until at least 3 yr of age were required to predict MWT with acceptable accuracy. Conversely, weights showed a decrease at advanced ages, likely due to unrelated factors. Records were truncated at 6 yr so that decreasing weights would not cause a downward bias in MWT estimates.

Most growth curves assume that the animals' growth has not been limited (Parks, 1982). It was known that some animals were placed on feed restriction diets, which violates this assumption. Records for affected cows were thus truncated at the start of the feed restriction. Removing records that could bias analyses is required for accurate model fitting, but removing too much data can omit important variation.

Fitting Growth Curves

After data editing, growth models could be fitted. The Brody function was chosen out of a variety of growth-specific models available because it is appropriate for fitting weights from about 30% of MWT onwards, beyond the inflection point of the typical growth curve. It is asymptotic, where the asymptote corresponds with MWT (Taylor, 1965). These properties matched the data available. A linear spline ("broken stick") model was chosen as the second model. It was a piecewise function where two linear segments were joined at a knot (Meyer, 2005). We hypothesized that the knot would fall near puberty, when animals were approaching maturity and typically slowed in growth. If the slope after the knot was near zero, then the knot would reflect the point at which the animal effectively stopped growing and had reached MWT. At that point, waiting longer to observe MWT would not be useful. If maturity can be assessed at earlier ages,

selection decisions incorporating MWT can be made earlier saving cost associated with keeping and breeding unproven cows later in life and increasing the rate of genetic change. The most desirable direction for genetic change is not uniform. This issue will be discussed later. However, the slopes after the knot were generally greater than zero. A quadratic polynomial was the final model chosen because our data had only a concave-down pattern, as does a quadratic polynomial.

Polynomials are easy to fit but are known to behave erratically at data extremes or when data are sparse. This was found to be a problem even though records on cows retained for 3 or fewer years were removed. Lack of data at older ages in some cows manifested as curves fitted well past their apexes, resulting in unreasonably light or even negative MWT estimates. Comparison of the distribution of MWT estimates for cows with records ending in their 3rd, 4th, and 5th yr of age validated that MWT estimates were heavier for the oldest as compared to youngest age category. The apex of the quadratic curve occurred before 6 yr of age, where the data was truncated. Truncating data at a slightly younger age, occurring closer to the apex, may have improved fit. Fit may also have improved with the use of random regression (Meyer, 2000).

Mature weight estimated from the spline function tended to be heavier than those based on the Brody and quadratic functions due to its lack of asymptote. Cattle do not increase in weight indefinitely although, as defined in the current analyses, this functional form will allow them to do so. The spline was also more challenging to fit. Various R (R Core Team, 2017) packages were tried before one was found that fit as we intended and gave understandable output.

The Brody function was best for estimating MWT. By allowing weights to increase to an asymptote, it more closely matched typical growth across a cow's lifespan (Parks, 1982) as compared to the quadratic and the spline. The quadratic will eventually decrease if extrapolated far enough, and the spline can only increase according to the knot and slope. Interestingly, the spline function had the highest mean R^2 value. It is possible that truncating data at 6 yr removed some of the plateau at maturity such that a continuously-increasing function provided better fit. Nevertheless, the Brody function more consistently estimated reasonable MWT from earlier weight records.

STUDY 2: BREED OF SIRE EFFECT CALCULATION

Model Fitting

Before calculating breed of sire effects, additional editing was employed in which cows were omitted if their MWT estimate from any function exceeded 2.2 interquartile range units from the population mean. This measure of spread is approximately bounding the mean by 3 standard deviations but is less sensitive to outliers. The Empirical Rule for a normal distribution is that approximately 65% and 95% of measurements lie within 1 SD and 2 SD of the mean, respectively. With non-parametric procedures, the SD can be approximated by dividing the difference between the observations recorded at the specified boundaries by the corresponding number of SD units they define (Ott, 1993). Extending this, the interquartile range spans from the 25th to the 75th percentile, capturing the center half of the data. These percentiles are 0.6745 SD below and above the mean, respectively, so the interquartile range spans 1.349 SD. Thus, dividing the interquartile

range by 1.349 approximates 1 SD. Since this approximation of SD considers only the center half of the data, the influence of any extreme data points is mitigated.

There were some extreme outliers present in these data which were removed: 19 from the Brody function, 135 from the spline function, and 317 from the quadratic function. Some cows had extreme MWT estimates in more than one function, but an extreme MWT in any was cause for exclusion.

Following editing, the remaining estimates of the parameter values were considered as the measures of the traits of interest. Through a process of model selection, potential sources of fixed and random variation in these traits were investigated. The most basic model fitted included fixed effects of each breed and birth year-season contemporary group, covariates of direct and maternal heterosis, and random effect of animal. During model testing, additional random effects (maternal additive, direct-maternal additive covariance, and maternal permanent environment) were added sequentially, and variance components were compared to the next-simplest model. Variance components, variance ratios, log likelihood values, AIC values, and BIC values were collected and compared to determine if the additional random term was significant. If not, the simpler model in the comparison was chosen for that parameter.

An additional effect was deemed significant if the comparison of log likelihood values – the likelihood ratio test – was greater than the threshold χ^2 value at 1 df and α of 0.05. Additionally, the partitioning of variance components had to be logical. It is expected that additional effects in the model will improve fit, but if the partitioning of variation becomes too complex for the data, then the variance components will change

erratically. Comparing variance components between models can identify from where the variation of additional terms is being pulled, and comparing variance ratios can identify if any drastic, relative changes have occurred.

For all parameters, the covariance between direct and maternal additive effects seemed to be too much for the depth of our data. In fitting simpler models, direct heritability was either constant or changed by less than 0.04. When fitting the covariance, direct heritability changed by 0.10 or more, even doubling in some cases. For the fit of one parameter, an error message was generated by ASReml (Gilmour et al., 2015) indicating that the (co)variance matrix was not positive definite. For another parameter, heritability did not change drastically, but an illogical direct-maternal correlation estimate was obtained: -33.92 where correlations should be bound between -1 and 1. In other cases, the direct-maternal correlation estimate was within bounds but also large and negative, exceeding -0.50.

Total heritability can help interpret the consequences of seemingly strong relationships between direct and maternal effects. Instead of using only direct additive variance as the numerator, proportions of direct and maternal additive variance and their covariance are used (Willham, 1972). Applying this concept to the parameters with large, negative correlations yielded heritability estimates that were similar to what was calculated under simpler models. Erratic heritabilities, erratic variance components, and large, negative correlations were indicative that the fit of a direct-maternal additive covariance was suspect in these data.

Finally, 3 multivariate models were run, one for each function, including all parameters from the function. This allowed estimation of the covariances between

parameters of a function, which allowed further understanding of how the parameters of each function were related. The parameter values from the multivariate models were expected to be – and were similar to – those obtained from the fit of univariate models.

Calculation of Breed of Sire Effects

Ordinarily, breed of sire effects are calculated using breed of sire solutions for the trait of interest adjusted for USMARC versus industry management conditions in two steps: first dividing a regression coefficient of progeny performance on sire EPD of the same trait and, second, adjusting for genetic trends by adding the difference between USMARC bull EPD and base industry EPD (Kuehn and Thallman, 2017). However, MWT EPD are not currently available for most breeds. As a result, the calculation process had to be modified. Yearling weight (YWT) EPD were used in the adjustment instead of MWT EPD. This was done because YWT has a high correlation with MWT, is more advanced in maturity than birth or weaning weights, and is widely reported.

The regression of offspring's MWT estimate on its sire's EPD contribution was necessary to apply the differences between industry and USMARC YWT EPD to MWT. If the regression coefficient is 1, then the phenotype is expected to increase 1 unit for each unit change in EPD. In previous analyses, the EPD was for the phenotyped trait and therefore a regression coefficient of 1 was expected. However, in this case, the phenotype was MWT and the EPD was for YWT. Given the correlation between YWT and MWT, the coefficient was expected to be around 2 or 3. However, the coefficient was near 1 in all functions.

Why these regression coefficients were so close to 1 is not yet fully understood. An early thought was that it had something to do with how we scaled data in the beginning of the project. However, the scaling was done simply by subtracting a constant to all data. Changing all data by an additive constant would not change any variances, and the variances are what make up the regression coefficient. Multiplying or dividing by a constant would change variances, and therefore regression coefficients, but that is not warranted in this case.

Future Applications

Ordinarily, across breed adjustment factors would then be calculated using breed of sire effects, but this is not currently practical given the lack of MWT EPD to adjust. Similarly, actual MWT EPD should be used when developing adjustment factors rather than YWT EPD, which will only be possible when MWT EPD are actually available. The breed of sire effects provide information about which breeds tend to be larger or smaller, but the bull-specific comparisons that are enabled by across-breed adjustment factors is lacking.

Part of the reason MWT EPD are unavailable is that MWT are not reported as commonly as other traits. On one hand, it is understandable because not all cows will survive within the herd to maturity, whether because of culling, sale, or natural death. Collecting weights at maturity also entails additional labor. Not every operation will invest the resources. Nevertheless, MWT is a topic of concern and some effort must be taken to measure it properly if it is to be addressed properly. Some incentive will likely need to be introduced to increase the reporting rate among producers.

Unlike currently-reported traits, no common goal exists for MWT. Since the target MWT depends on the production environment, this information cannot be accompanied by a single recommendation for use, and individual operations will need to decide what target weight will best suit their production environment. Effective use may therefore require some decision support, especially considering potentially-unfavorable correlations between MWT and other traits such as weaning weight. The best way to balance these sorts of antagonistic relationships is through an index (Hazel, 1943). Index development can be complex, requiring thorough economic and system analysis. Additionally, with varying production systems and environments, an ideal index under one situation may not be ideal under another (Bourdon, 1998). However, creating customized indexes for each operation would require unreasonable effort. Approaches for incorporating MWT in breeding decisions necessitates a separate and more complex analysis for the most effective application.

GENERAL REFLECTIONS AND SUGGESTIONS

During this work, I had a general idea of where the project was headed but, in retrospect, I could have been more proactive about understanding the complete process I would embark on before making a schedule and beginning work. I often found myself faced with many unexpected challenges and approaching deadlines, even when allocating some extra time for unforeseen challenges. Some unexpected challenges could have been avoided by actively seeking to understand the process I would be undertaking more completely before starting. In the future, when I am responsible for scheduling projects

and analysis, I will ensure that I know as much detail as possible about what work will need to be completed and/or what information will need to be collected, and I will allow additional extra time when possible.

While it was convenient that all data already existed so that work could focus on analysis rather than data collections, there were some challenges associated with this arrangement. In one instance, data had to be recollected from the database – and therefore cleaning had to be redone – because there was an error in how necessary information had merged. Later, records were truncated, in some cases causing entire cows to be removed, because records were missing. When assembling subsets of data from large databases, care must be taken to ensure the required information was, in fact, appropriately queried.

Finally, some consideration should be taken towards how physiological state affects weight. Two cows of the same weight will have different biological types and growth if one is emaciated and the other is obese. Similarly, cows that all weigh the same will have different tissue compositions if they are open, pregnant, or lactating. In an open cow, the weight more clearly reflects the cow's growth potential. In a pregnant or lactating cow, the fetus and associated tissues or milk produced, respectively, will add to the cow's own MWT. Throughout this project, some ways for incorporating these considerations were discussed but never came to fruition. Body condition score could possibly be added to the model as a covariate or correlated trait. Then some regression coefficient would be obtained to help account for the change in MWT for every increase in condition score. Alternatively, if added as a fixed effect, each body condition score will have some associated deviation from the mean. With regard to pregnancy status, weights could be collected at common states of gestation. Specifically, using weights

collected during palpation was discussed. A palpation weight was measured shortly after breeding, when the cow was being checked to confirm that the pregnancy had taken. In this scenario, the fetus will have minimal mass and the cow will not be lactating, minimizing the extra weight associated with reproductive function. Additionally, since the cow would already be confined, weight collection at this point would not entail much extra labor. Accounting for body condition score and gestational stage would reduce the fluctuation of MWT measurements associated with unrelated causes.

CONCLUSIONS

Cattle with different body sizes have metabolic requirements, and genetic trends have increased the size of cattle recently. The efficiency of a cow depends on how her metabolic requirements match the environment in which she is kept. Crossbreeding is a valuable tool to match cow to environment, but effective crossbreeding requires an accurate comparison of stock available to cross. Breed of sire effects aid in breed selection by providing information on what breeds are generally larger or smaller at maturity. If MWT EPD were more widely reported and published, then across-breed adjustment factors could also be offered, adding to the accuracy of comparison. More informed breed utilization enabled by breed of sire effects, and ideally across-breed adjustment factors in the future, will provide valuable tools for producers to design a more efficient cow for their unique production environment.

LITERATURE CITED

- Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. *J. Anim. Sci.* 94:1689-1702. doi:10.2527/jas2015-0049
- Beef Improvement Federation. 2016. Guidelines for uniform beef improvement programs, 9th edition. https://beefimprovement.org/wp-content/uploads/2013/07/BIFGuidelinesFinal_updated0916.pdf (Accessed 10 December 2017.)
- Bourdon, R. M. 1998. Shortcomings of current genetic evaluation systems. *J. Anim. Sci.* 76:2308-2323.
- Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Estimates of genetic parameters for weight and height of angus cows using a repeatability model. *Proc. West. Sec. Amer. Soc. Anim. Sci.* 60:40-41.
- Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. *J. Anim. Sci.* 89:2373-2379. doi:10.2527/jas.2011-3847.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2015. ASReml user guide Release 4.1 Structural Specification. VSN International Ltd., Hemel Hempstead, HP1 1ES, UK.
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics.* 28(6):476-490.

- Jenkins, T. G. and C. L. Ferrell. 2006. Matching beef genetics with production environment. Proc. Beef Improv. Federation Ann. Meet. & Symp., Chocktaw, Mississippi. p. 41-46.
- Kuehn, L. A. and R. M. Thallman. 2017. Across-breed EPD tables for the year 2017 adjusted to breed differences for birth year of 2015. Proc. Beef Improv. Federation Ann. Meet. & Symp., Athens, Georgia. p. 112-144.
- Meyer, K. 2000. Random regressions to model the phenotypic variation in monthly weights of Australian beef cows. Livest. Prod. Sci. 65:19-38.
- Meyer, K. 2005. Random regression analyses using B-splines to model growth of Australian Angus cattle. Genet. Sel. Evol. 37:473-500. doi:10.1051/gse:2005012
- Parks, J. R. 1982. A theory of feeding and growth of animals. Springer-Verlag Berlin Heidelberg New York.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. (Accessed 17 October 2017.)
- Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. J. Anim. Sci. 93:5829-5839. doi:10.2527/jas2015-9172
- Taylor, St. C. S. 1965. A relation between mature weight and time taken to mature in mammals. Anim. Sci. 7(2):203-220. doi:10.1017/S0003356100025629
- Walker, R. S., R. M. Martin, G. T. Gentry, and L. R. Gentry. 2015. Impact of cow size on dry matter intake, residual feed intake, metabolic response, and cow performance. J. Anim. Sci. 93:672-684. doi:10.2527/jas2014-7702

- Weaber, B. 2010. Crossbreeding for commercial beef production. In: M. K. Nielsen, editor, National Beef Cattle Evaluation Consortium beef sire selection manual. 2nd ed. p. 50-57.
- Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35(6):1288-1293.

COMPLETE LIST OF REFERENCES

- Abreu Silva, B. C., J. P. Eler, M. L. Santana Jr., E. C. Mattos, I. R. Menezes, J. B. S. Ferraz. 2018. Genetic association between mature weight and early growth and heifer pregnancy traits in Nelore cattle. *Livest. Sci.* 211:61-65.
doi:10.1016/j.livsci.2018.03.003
- Arango, J. A. and L. D. Van Vleck. 2002. Size of beef cows: Early ideas, new developments. *Genet. Mol. Res.* 1:51-63.
- Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. *J. Anim. Sci.* 94:1689-1702. doi:10.2527/jas2015-0049
- Beef Improvement Federation. 2016. Guidelines for uniform beef improvement programs, 9th edition. https://beefimprovement.org/wp-content/uploads/2013/07/BIFGuidelinesFinal_updated0916.pdf (Accessed 10 December 2017.)
- Bolgiano, D. C., L. D. Van Vleck, and R. W. Everett. 1979. Fluctuations in sire evaluations. *J. Dairy Sci.* 62:760-767.
- Bourdon, R. M. 1998. Shortcomings of current genetic evaluation systems. *J. Anim. Sci.* 76:2308-2323.
- Brinks, J. S., R. T. Clark, N. M. Kieffer, J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. *J. Anim. Sci.* 23(3):711-716. doi:10.2527/jas1964.2337x

- Brody, S. 1945. Bioenergetics and growth; With special reference to the efficiency complex in domestic animals. Reinhold, Oxford, England.
- Bullock, K. D., J. K. Bertrand, and L. L. Benyshek. Genetic and environmental parameters for mature weight and other growth measured in Polled Hereford cattle. *J. Anim. Sci.* 71:1737-1741.
- Cundiff, L. V. 1993. Breed comparisons adjusted to a 1991 basis using current EPD's. In: *Proc. Beef Improv. Fed. Research Symp.*, Asheville, NC. p. 114-123.
- Cushman, R. A., M. F. Allan, R. M. Thallman, and L. V. Cudiff. 2007. Characterization of biological types of cattle (Cycle VII): influence of postpartum interval and estrous cycle length on fertility. *J. Anim. Sci.* 85:2156-2162.
- de Boor, C. 2001. A practical guide to splines. 2nd ed. Springer-Verlag, New York.
- DeNise, R. S. K. & J. S. Brinks, 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. *J. Anim. Sci.* 61(6):1431-1440.
- DiCostanzo, A., J. C. Meiske, S. D. Plegge, T. M. Peters, and R. D. Goodrich. 1990. Within-herd variation in energy utilization for maintenance and gain in beef cows. *J. Anim. Sci.* 68:2156-2165. doi:10.2527/1990.6872156x
- Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Estimates of genetic parameters for weight and height of angus cows using a repeatability model. *Proc. West. Sec. Amer. Soc. Anim. Sci.* 60:40-41.
- Falconer, D. S. and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. 5th ed. Longman Group Ltd. Essex, England.

- Famula, T. R., E. J. Pollak, and L. D. Van Vleck. 1983. Genetic groups in dairy sire evaluation under a selection model. *J. Dairy Sci.* 66:927-934.
doi:10.3168/jds.S00220302(83)81879-7
- Federation of Animal Science Societies. 2010. *Guide for the Care and Use of Agricultural Animals in Research and Teaching*. 3rd ed. Champagne, IL.
- Ferrell, C. L. and T. G. Jenkins. 1984. Energy utilization by mature, nonpregnant, nonlactating cows of different types. *J. Anim. Sci.* 58(1):234-243.
doi:10.2527/jas1984.581234x
- Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. *J. Anim. Sci.* 89:2373-2379.
doi:10.2527/jas.2011-3847.
- Garrick, D. J. 2005. Trends and developments in genetic evaluation of beef cattle in the United States. In: *Proc. 9th World Angus Forum Tech. Meet., Angus in the Global Market*. Am. Angus Assoc., Kansas City, MO. p. 24-31.
- Gilmour, A. R., B. J. Gogel, B. R. Cullis, and R. Thompson. 2015. *ASReml user guide Release 4.1 Structural Specification*. VSN International Ltd., Hemel Hempstead, HP1 1ES, UK.
- Golden, B. L., D. J. Garrick, S. Newman, and R. M. Enns. 2000. Economically relevant traits: A framework for the next generation of EPDs. In: *Proc. of the Beef Improv. Federation Ann. Meet. & Symp.*, Witchita, KS. p. 2-13.

- Gregory, K. E., L. A. Swiger, R. M. Koch, L. J. Sumpton, J. E. Ingalls, W. W. Rowdan, and J. A. Rothlisberger. 1966. Heterosis effects on growth rate of beef heifers. *J. Anim. Sci.* 25(2):290-298. doi:10.2527/jas1966.252290x
- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1982. Characterization of breeds representing diverse biological types: Preweaning traits. In: *Beef Research Program Prog. Rep. No. 1*. Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE. p. 7-8.
- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. *J. Anim. Sci.* 73:1920-1926.
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics.* 28(6):476-490.
- Henderson, C. R. 1976. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics.* 32:69-83. doi:10.2307/2529339.
- Jenkins, T. G. and C. L. Ferrel. 1983. Nutrient requirements to maintain weight of mature, nonlactating, nonpregnant cows of four diverse breed types. *J. Anim. Sci.* 54:761-770. doi:10.2527/jas1983.564761x
- Jenkins, T. G. and C. L. Ferrell. 2006. Matching beef genetics with production environment. *Proc. Beef Improv. Federation Ann. Meet. & Symp., Chocktaw, Mississippi.* p. 41-46.

- Johnsson, I. D. and S. V. Morant. 1984. Evidence of a negative relationship between heifer growth and first calf weaning weight in commercial beef herds. *Aust. J. Exp. Agric. Anim. Husb.* 24:10-14.
- Kaps, M., W. O. Herring, and W. R. Lambertson, 1999. Genetic and environmental parameters for mature weight in Angus cattle. *J. Anim. Sci.* 77:569-574.
- Kaps, M., W. O. Herring, and W. R. Lambertson. 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationship with weaning weight in Angus cattle. *J. Anim. Sci.* 78:1436-1442.
- Kuehn, L. A. and Thallman, R. M. 2016a. Mean EPDs reported by different breeds. *Proc. Beef Improv. Federation Ann. Meet. & Symp.*, Manhattan, Kansas. p. 122-126.
- Kuehn, L. A. and R. M. Thallman. 2016b. Across-Breed EPD tables for the year 2016 adjusted to breed differences for birth year of 2014. *Proc. Beef Improv. Federation Ann. Meet. & Symp.*, Manhattan, Kansas. p. 127-154.
- Kuehn, L. A. and R. M. Thallman. 2017a. 2016 Across-breed EPD table. <https://beefimprovement.org/wp-content/uploads/2017/03/2016-Across-Breed-EPD-Table.pdf> (Accessed 24 March 2017.)
- Kuehn, L. A. and R. M. Thallman. 2017b. Across-breed EPD tables for the year 2017 adjusted to breed differences for birth year of 2015. *Proc. Beef Improv. Federation Ann. Meet. & Symp.*, Athens, Georgia. p. 112-144.
- Lewis, R. M. and P. R. Beatson. 1999. Choosing maternal-effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. *Livest. Prod. Sci.* 58:137-150.

- Lewis, R. M., G. C. Emmans, and G. Simm. 2006. Describing effects of genetic selection, nutrition, and their interplay in prime lambs using growth and efficiency functions. *Aust. J. Ag. Res.* 57:707-719. doi:10.1071/AR05196
- Little, W. and R. M. Kay. 1979. The effects of rapid rearing and early calving on the subsequent performance of dairy heifers. *Anim. Prod.* 29:131-142.
- McMurry, B. 2008. Just how big are our beef cows these days? *Feedstuffs.* 80(51):16–17.
- Meyer, K. 1991. DFREML – A set of programs to estimate variance components by restricted maximum likelihood using a derivative-free algorithm. User notes, version 2.0. Mimeo. Animal Genetics and Breeding Unit, University of New England, Armidale.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179-204. doi:10.1016/0301-6226(92)90017-X
- Meyer, K. 1993. Covariance matrices for growth traits of Australian Polled Hereford cattle. *Anim. Prod.* 57:37-45.
- Meyer, K. 2000. Random regressions to model the phenotypic variation in monthly weights of Australian beef cows. *Livest. Prod. Sci.* 65:19-38.
- Meyer, K. 2005a. Estimates of genetic covariance functions for growth of Angus cattle. *J. Anim. Breed. Genet.* 122:73-85.
- Meyer, K. 2005b. Random regression analyses using B-splines to model growth of Australian Angus cattle. *Genet. Sel. Evol.* 37:473-500. doi:10.1051/gse:2005012
- Mrode, R. A. 2014. Linear models for the prediction of animal breeding values. 3rd ed. CABI. Boston, MA.

- Muggeo, V. M. R. 2008. Segmented: An R package to fit regression models with broken-line relationships. *R News*, 8/1. 20-25. <https://cran.r-project.org/doc/Rnews/> (Accessed 17 October 2017.)
- Nicol, D. C., H. U. Graser, B. Tier, and K. Hammond. 1985. BREEDPLAN – A within-herd evaluation system for the National Beef Recording Scheme. In: *Proc. 5th Conf. Aust. Assoc. Anim. Breed. Genet.*, Sydney, Australia. p. 151-153.
- Notter, D. R., and L. V. Cundiff. 1991. Across-breed expected progeny differences: Use of within-breed expected progeny differences to adjust breed evaluations for sire sampling and genetic trend. *J. Anim. Sci.* 69:4763-4776. doi: 10.2527/1991.69124763x
- Notter, D. R. 1999. The importance of genetic diversity in livestock populations of the future. *J. Anim. Sci.* 77:61-69.
- NRC. 1996. Nutrient requirements for beef cattle. 7th ed. Natl. Acad. Press, Washington, DC.
- Nugent III, R. A., T. G. Jenkins, A. J. Roberts, and J. Klindt. 1993. Relationship of post-partum interval in mature beef nutritional environment, biological type and serum concentrations. *Anim. Prod.* 56:193-200.
- Nutt, B. G., J. W. Holloway, and W. T. Butts, Jr. 1980. Relationship of rumen capacity of mature Angus cows to body measurements, animal performance and forage consumption on pasture. *J. Anim.Sci.* 51:1168-1176. doi: 10.2527/jas1980.5151168x

- Olson, L. W., L. V. Cundiff, and K. E. Gregory. 1978. Maternal heterosis effects on postweaning growth and carcass traits in beef cattle. *J. Anim. Sci.* 46(6):1552-1562. doi:10.2527/jas1978.4661552x
- Ott, R. L. 1993. *An introduction to statistical methods and data analysis*. 4th ed. Duxbury Press, Belmont, California.
- Parks, J. R. 1965. Prediction and entropy of half-tone pictures. *Behav. Sci.* 10:436-445. doi: 10.1002/bs.3830100407
- Parks, J. R. 1982. *A theory of feeding and growth of animals*. Springer-Verlag Berlin Heidelberg New York.
- Parnell, P. F., R. Barlow, and B. Tier. 1986. Realised responses to divergent selection for yearling growth rate in Angus cattle. In *Proc. 3rd World Congr. Genet. Appl. Livest. Prod.*, Lincoln, NE. p. 330-334.
- Pearson, R. E. 1982. Economic aspects of the choice of a breeding objective. In *Proc. 2nd World Congr. Genet. Appl. Livest. Prod.*, Madrid, Spain. p. 50-59.
- Purser, D. B. and R. J. Moir. 1966. Rumen volume as a factor involved in individual sheep differences. *J. Anim. Sci.* 25:509-515. doi: 10.2527/jax1966.252509x
- R Core Team, 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. (Accessed 17 October 2017.)
- Racine, J. S. 2014. *A primer on regression splines*. https://cran.r-project.org/web/packages/crs/vignettes/spline_primer.pdf. (Accessed 1 August 2017.)
- Richards, F. J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10(29):290-300.

- Roberts, A. J., M. K. Petersen, and R. N. Funston. 2015. BEEF SPECIES SYMPOSIUM: Can we build the cowherd by increasing longevity of females? *J. Anim. Sci.* 93:4235-4243. doi:10.2527/jas.2014-8811
- Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. *J. Anim. Sci.* 93:5829-5839. doi:10.2527/jas2015-9172
- Schiermiester, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. *J. Anim. Sci.* 93:46-52. doi:10.2527/jas2014-8493.
- Smith, G. M., H. A. Fitzhugh Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976a. Heterosis for maturing patterns in Hereford, Angus, and Shorthorn cattle. *J. Anim. Sci.* 43(2):380-388.
- Smith, G. M., H. A. Fitzhugh, Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976b. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Shorthorn cattle. *J. Anim. Sci.* 43(2):389-395.
- Taylor, St. C. S. 1965. A relation between mature weight and time taken to mature in mammals. *Anim. Sci.* 7(2):203-220. doi:10.1017/S0003356100025629
- Turner, H. G. 1982. Genetic variation of rectal temperature in cows and its relationship to fertility. *Anim. Prod.* 35(3):401-412. doi: 10.1017/S0003356100001094
- Upton, W. H., A. T. G. McArthur, and R. J. Farquharson. 1988. Economic values applied to breeding objectives: A decentralized approach for BREEDPLAN. Proc. 7th Conf. AAABG, Armidale, Australia: 95-104.

USDA-ARS. 1974. Progress report: Germ plasm evaluation program report no. 1.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE01.pdf> (Accessed 9 November 2016.)

USDA-ARS. 1976. Germ plasm evaluation program report no. 4.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE04.pdf> (Accessed 9 November 2017.)

USDA-ARS. 1990. Germ plasm evaluation program report no. 12.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE12.pdf> (Accessed 9 November 2017.)

USDA-ARS. 1994. Germ plasm evaluation program report no. 13.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE13.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2001a. Germ plasm evaluation program report no. 20.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE20.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2001b. Germ plasm evaluation program report no. 21.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE21.pdf> (Accessed 9 November 2017.)

USDA-ARS. 2006. Germ plasm evaluation program report no. 23.

<https://www.ars.usda.gov/ARSUserFiles/30400000/GPE/GPE23.pdf> (Accessed 9 November 2017.)

USDA-ERS, Commodity Economic Division. 1973. Livestock and meat situation.

<http://usda.mannlib.cornell.edu/usda/ers/LMS//1970s/1973/LMS-08-17-1973.pdf>

(Accessed 24 March 2017.)

USDA-NASS. March 2017. Livestock slaughter. <http://usda.mannlib.cornell.edu/usda/nass/LiveSlau//2010s/2017/LiveSlau-03-23-2017.pdf> (Accessed 24 March 2017.)

<http://usda.mannlib.cornell.edu/usda/nass/LiveSlau//2010s/2017/LiveSlau-03-23-2017.pdf> (Accessed 24 March 2017.)

Van Vleck, L. D. 1993. Selection index and introduction to mixed model methods. CRC

Press, Inc., Boca Raton, FL.

Van Vleck, L. D. and L. V. Cundiff. 2004. Across-breed EPD tables for the year 2004

adjusted to breed differences for birth year of 2002. In: Proc. 36th Beef Improv.

Federation Ann. Meet. & Symp., Sioux Falls, South Dakota.

http://www.bifconference.com/bif2004/BIFsymposium_pdfs/vleckcundiff.pdf

(Accessed 25 July 2018)

Van Vleck, L. D. and L. V. Cundiff. 2006. Across-breed EPD tables for the year 2006

adjusted to breed differences for birth year of 2004. In: Proc. 38th Beef Improv.

Fed. Ann. Meet., Choctaw, MS. [http://www.bifconference.com/bif2006/pdfs/](http://www.bifconference.com/bif2006/pdfs/Cundiff_Van_Vleck.pdf)

[Cundiff_Van_Vleck.pdf](http://www.bifconference.com/bif2006/pdfs/Cundiff_Van_Vleck.pdf) (Accessed 24 March 2017.)

Van Vleck, L. D., L. V. Cundiff, T. L. Wheeler, S. D. Shackelford, and M. Koohmaraie.

2007. Across-breed adjustment factors for expected progeny differences for

carcass traits. *J. Anim. Sci.* 85:1369-1376. doi: 10.2527/jas.2006-658

Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth

laws. II). *Hum. Biol.* 10:181-213.

- Walker, R. S., R. M. Martin, G. T. Gentry, and L. R. Gentry. 2015. Impact of cow size on dry matter intake, residual feed intake, metabolic response, and cow performance. *J. Anim. Sci.* 93:672-684. doi:10.2527/jas2014-7702
- Weaber, B. 2010. Crossbreeding for commercial beef production. In: M. K. Nielsen, editor, National Beef Cattle Evaluation Consortium beef sire selection manual. 2nd ed. p. 50-57.
- Weiss, P. and J. L. Kavanau. 1957. Model of growth and growth control. *J. Gen. Physiol.* 41:41- 47. doi: 10.1085/jgp.41.1.1
- Westell, R. A., R. L. Quaas, and L. D. Van Vleck. 1988. Genetic groups in an animal model. *J. Dairy Sci.* 71:1310-1318.
- Weymouth, F. W., H. C. McMillin, and W. H. Rich. 1931. Latitude and relative growth in the razor clam, *Siliqua patula*. *J. Exp. Biol.* 8:228-249.
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2005. Characterization of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability traits. *J. Anim. Sci.* 83:196-207.
- Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35(6):1288-1293.
- Willham, R. L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7:405-418.
- Winsor, C. P. 1932. The Gompertz curve as a growth curve. In: *Proc. Natl. Acad. Sci.* 18:1-8.

Wolf, J. B. and M. J. Wade. 2009. What are maternal effects (and what are they not)?

Philos. Trans. R. Soc. Lond., B., Biol. Sci. 364:1107-1115.

doi:10.1098/rstb.2008.0238

Wolf, J. B. and M. J. Wade. 2016. Evolutionary genetics of maternal effects. *Evolution*.

70(4):827-839. doi:10.1111/evo.12905

Wright, S. 1926. Reviews: *The Biology of Population Growth*, by R. Pearl; *The Natural*

Increase of Mankind, by J. S. Sweeney. *J. Am. Stat. Assoc.* 21:493-497.

Zimmermann, M. J., L. A. Kuehn, M. L. Spangler, R. M. Thallman, W. M. Snelling, and

R. M. Lewis. 2018. Growth from weaning to maturity in beef cattle breeds.

Submitted.