

GENOTYPE BY ENVIRONMENT INTERACTIONS FOR GROWTH
AND STAYABILITY IN US RED ANGUS

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AND STAYABILITY IN RED ANGUS CATTLE

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GENOTYPE BY ENVIRONMENT INTERACTIONS FOR GROWTH
AND STAYABILITY TRAITS IN RED ANGUS

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Abstract

Accuracy of sire selection is limited by how well animals are characterized. Current beef cattle genetic analyses ignore genotype by environment interactions (GxE). The objectives of this study were to evaluate the presence of GxE by comparing reaction norms of Red Angus bulls in the US. The dependent variables were birth weight, weaning weight, gain and stayability. Adjusted weights were provided by the Red Angus Association of America (RAAA). Gain was determined by subtracting adjusted weaning weight from adjusted yearling weight. Environments were defined as nine regions within the continental United States with similar temperature humidity index. The environmental mean was determined and a weighted regression was used to determine the progeny mean. Reaction norms were calculated by regressing the progeny mean on the environmental mean.

The objective of the weight study was to evaluate the genetic parameters for birth weight, weaning weight and gain. The range in reaction norms was the largest for BW and smallest for GN. The correlations of the trait mean to the trait RN was not significant for BW and WW but was for GN (P-value=0.02). The moderately negative ($r=-0.22$) correlation suggests bulls with higher means for GN have more stable production across environments.

The heritabilities of BW and WW RN were 0.40 and 0.39, respectively. Phenotypic and genotypic correlations were 0.19 and 0.54, respectively. These data suggest there is ample heritability for selection.

The objective of the stayability study was to evaluate the genetic parameters using a single-trait animal model for the regional and national datasets. A logit model was used to determine the heritability on the underlying scale. Heritabilities were 0.34, 0.18, 0.19, 0.08, 0.09, 0.28, 0.30, 0.31 and 0.40 for regions C, D, G, L, M, N, P, S and U, respectively and 0.18 for the national dataset. The percentages of females that calved at age four, given that they had calved at age two were 56.7, 39.9, 32.9, 51.1, 56.1, 57.0, 51.4, 47.8 and 58.8 for regions C, D, G, L, M, N, P, S and U, respectively and 55.0% for the national dataset. The Pearson correlation of the progeny mean to the RN was -0.196 (P-value <0.05) and suggest sires with higher means are more stable in their production across environments. The comparisons of regions illustrate the northern regions are more similar to each other compared to the southern regions and the southern regions are not only different from the northern regions but different from each other.

Reaction norms are heritable and there is sufficient variation for effective selection. Further research is warranted in the proper division of environments and the most economical and effective method to employ reaction norms to end-users.

Chapter 1

INTRODUCTION

Beef production requires multi-trait selection to produce low-cost, high-quality beef. The list of traits is potentially long. One study identified 16 “non-trivial” traits important to a beef cattle selection index, stating that calf survival, fertility, residual feed intake and dressing percentage are of primary economic importance (Koots and Gibson, 1998). The importance of reproductive traits has been found in several studies, but selection has been hampered due to lack of data.

Herds that contain females that exhibit longevity need fewer replacements, and have a higher percentage of high-producing mature cows and less involuntary culling. Unfortunately, expression of this trait late in life increases the difficulty of its inclusion into a genetic evaluation. An alternative to measuring longevity is to measure stayability, which is the probability of a cow surviving in a herd to a given age, provided it had the opportunity to do so.

Fertile females must have some level of acceptable adaptation to their environment. However, artificial insemination has made it possible to use bulls across a wide variety of environments. This raises concerns of genotype by environment interactions. If genotype by environment interactions exists, sire selection may be less than optimum, as noted by a low correlation of stayability in different regions. Reaction norms, used in dairy and plant breeding programs, illustrate sensitivity of productivity for a single trait across different environments and may improve sire selection.

There is a limited amount of data on fertility from breed association datasets due to relatively recent collection of reproductive information. The Red Angus Association of America was the first (1995) to require total herd reporting (THR), which is the collection of information on all reproducing females, and the reason for choosing this breed for this study. Breeds that do currently publish stayability EPDs include Red Angus, Simmental, Gelbvieh, Limousin, Saler and Line One Herefords (2012).

The objective of this study was to determine if genotype by environment interactions exists in Red Angus cattle for birth weight, weaning weight, gain and stayability.

Chapter 2

THEORY AND REVIEW OF LITERATURE

Mixed Models

Genetic evaluations have become more sophisticated as computing power has increased. Characterizing a population via its variance components is an important part of genetic evaluations. Variation can be expressed and partitioned as in Table 2.1 and defined in Table 2.2 (Falconer and Mackay, 1996).

Mixed linear model equations (**MME**) have been used for animal evaluations to provide best linear unbiased predictions (**BLUP**). In matrix notation the MME were

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

in which \mathbf{y} was the vector of observations, $\boldsymbol{\beta}$ the vector of fixed effects, \mathbf{u} the vector of random effects, \mathbf{X} and \mathbf{Z} are the incidence (contain 0s and 1s) matrices relating $\boldsymbol{\beta}$ and \mathbf{u} to \mathbf{y} , and \mathbf{e} is the vector of random error effects. Henderson (1984) showed $\hat{\boldsymbol{\beta}}$ was the best linear unbiased estimator (**BLUE**) and $\hat{\mathbf{u}}$ was the best linear unbiased predictor (**BLUP**).

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1}\boldsymbol{\lambda} \end{bmatrix} \begin{bmatrix} \hat{\boldsymbol{\beta}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix}$$

where \mathbf{A}^{-1} was the inverse numerator relationship matrix and $\boldsymbol{\lambda}$ was the residual error variance divided by the additive genetic variance (σ_e^2/σ_a^2).

The distribution of the model has the following assumptions:

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{X}\boldsymbol{\beta} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

$$\text{var} \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{V} & \mathbf{Z}\mathbf{G} & \mathbf{R} \\ \mathbf{G}\mathbf{Z}' & \mathbf{G} & \mathbf{0} \\ \mathbf{R} & \mathbf{0} & \mathbf{R} \end{bmatrix}$$

in which $\mathbf{V} = \text{var}(\mathbf{y}) = \mathbf{ZGZ}' + \mathbf{R} = \mathbf{ZAZ}'\sigma_a^2 + \mathbf{I}\sigma_e^2$ and if \mathbf{Z} is an identity matrix (each animal has an observation), can be written as $\mathbf{A}_{22}\sigma_a^2 + \mathbf{I}\sigma_e^2$

in which \mathbf{A}_{22} is the relationship between all animals with records as noted below:

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1}\lambda \end{bmatrix} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} \\ \mathbf{A}_{21} & \mathbf{A}_{22} \end{bmatrix}$$

in which \mathbf{G} is the genetic variance-covariance matrix and \mathbf{R} is the residual variance-covariance matrix,

$$\mathbf{G} = \text{var}(\mathbf{u}) = \mathbf{A}\sigma_a^2$$

in which \mathbf{A} is the relationship matrix and σ_a^2 is the additive genetic variance and

$$\mathbf{R} = \text{var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$$

in which \mathbf{I} is the identity matrix and σ_e^2 is the residual error variance (Henderson, 1984).

Heritabilities

Heritability is the measure of variation in a population that can be accounted for by genetics. The animal model provides the animal variance and the environmental variance.

Heritability is calculated by the additive variance (σ_a^2) divided by the phenotypic variance (σ_p^2).

Sire models provided the sire variance (σ_s^2), which was multiplied by four to get the additive variance ($\sigma_s^2 * 4 = \sigma_a^2$).

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

Correlations

Phenotypic correlations are calculated with the phenotypic variance and covariance of two traits while the genotypic variance used the additive variance and covariance of two traits (t_1 and t_2). Correlations are calculated by dividing the covariance of the two traits by the square root of the product of the standard deviation of the two traits.

Genetic correlations (r_g) between two traits are estimated from:

$$r_g = \frac{\sigma_{a_1, a_2}}{\sqrt{\sigma_{a_1}^2 \sigma_{a_2}^2}}$$

Phenotypic correlations (r_p) between two traits are estimated from:

$$r_p = \frac{\sigma_{p_1, p_2}}{\sqrt{\sigma_{p_1}^2 \sigma_{p_2}^2}}$$

Univariate models have less computational demands compared to multi-trait models. However, multiple-trait evaluation has two advantages: 1) using information on correlated traits increases the accuracy of the breeding values of the trait of interest and 2) it is the only way to obtain an unbiased estimate for a trait, as it accounts for selection that has already occurred on that group (assuming unbalanced data). For example, calves that are evaluated for yearling weight may be a selected subsample of the group evaluated for weaning weight. Accounting for this selection removes the downward bias of the breeding values.

Genetic analysis of Stayability

Fertility traits may be classified as continuous (scrotal circumference, age to puberty, etc.) or categorical (heifer pregnancy, subsequent rebreeding, stayability, etc.). Categorical traits are inherited in the same way as continuously varying traits (Falconer and Mackay, 1996). The underlying continuous variable is called the “liability”. When the underlying variable is below some threshold, it has one observation and when it is above the threshold, it has another observation. For example, a female may be classified as pregnant or open and assigned a 1 or a 0, respectively. Some traits may have multiple categories, such as number of lambs born, and are assigned a 1, 2, 3, etc. If the litter size is large, such as with mice or pigs, the trait would be considered continuous because there are a large number of classes (Falconer and Mackay, 1996).

Stayability, the analysis of a survival trait (Brigham et al., 2009), has been defined as the probability a cow would remain in the herd until 6 yr of age, given she has calved once. The evaluation was based solely on the success or failure of females to reach age 6. Brigham et al. (2007) explored the possibility of using alternate ages and described the current stayability model (Brigham et al., 2009) included below.

Two methods of transforming binary data are by probit and logit functions (Mrode, 2005). The probit model assumes errors follow the standard normal distribution as opposed to the logit model, where errors are assumed to follow the standard logistic probability distribution. The result is the cumulative density function of the probit is steeper in the middle compared to the standard logistic distribution and more quickly approaches zero on the left and one on the right. When the value is close to 0.5, there is little difference to either model.

The variance components were estimated using ASREML (Gilmour et al., 2002) by fitting residual maximum likelihood linear sire models with the default PROBIT option for categorical data. These were estimated for each stayability benchmark of 3 yrs, 4 yrs, 5 yrs and 6 yrs of age. Dams were required to be at least as old as the defined benchmark to receive a stayability observation for a given endpoint and were required to calve on an annual basis within a 60-d time period of the previous calving. A favorable designation (1) was given to dams that met this criteria and an unfavorable designation (0) was given to dams that did not meet this criteria.

In addition,

$$\mathbf{var} \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} \sigma_a^2 \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \sigma_e^2 \mathbf{I} \end{bmatrix}$$

where \mathbf{A} is Wright's additive numerator relationship matrix, \mathbf{I} is an identity matrix with order equal to the number of observations in \mathbf{Y} . The additive and residual variances are σ_a^2 and σ_e^2 , respectively. The additive genetic variance (σ_a^2) is specific to each stayability age definition for

each set of EPD calculated. Then, in accordance with MAP models, the residual variance (σ_e^2) is forced to be equal to 1.

The aggregate stayability EPD is calculated by weighting each individual observation with the genetic covariance among the age definitions using the equation

$$\mathbf{Y} = [\mathit{diag}[\mathbf{Z}'\mathbf{R}\mathbf{Z}] + \mathbf{G}_0^{-1}]\mathbf{u}$$

where \mathbf{Y} is the vector of stayability observations within a given animal on the underlying scale, $\mathbf{Z}'\mathbf{R}\mathbf{Z}$ is a trait within animal accumulation of diagonal elements from the random portion of the coefficient matrix. Individual animals are represented by a square matrix with order equal to number of traits by number of traits. \mathbf{G}_0 is the variance/covariance matrix for all age definitions and \mathbf{u} is a vector of aggregate breeding values (Brigham et al., 2009).

Genetic Parameters of Growth Traits

Heritabilities were reported by BIF (2010) for several breeds and were moderate for birth weight and somewhat lower for weaning weight and 160-d gain (Table 2.3). Winder et al. (1999) reported heritabilities of Red Angus (Table 2.4) were moderate and higher than reported by BIF (2010).

Gosey (2003) summarized the heritabilities of many production and carcass traits (Table 2.5). In discussing the possible premiums for ideal carcass production, he noted the difficulty in achieving the optimum balance of traits at the ranch level due to the major impact of both reproduction and production traits. The influence of these traits on ranch profitability suggests ranchers should match their cows to their resources and adjust carcass traits only as resources allow.

In general, the heritabilities of performance and carcass traits are moderate to high with the exception of birth weight (maternal), weaning weight (maternal) and yearling weight(maternal) ($h^2 = 0.14, 0.13$ and 0.06 , respectively) and tenderness ($h^2 = 0.13$).

Genetic Parameters of Stayability

The heritabilities for reproductive traits are summarized in Table 2.6 (Gosey, 2003). Generally, heritabilities are low with the exception of scrotal circumference. Cammack et al. (2009) provided a more recent summary (Table 2.7) of heritabilities of reproductive traits, which in general were low, but did include some moderate values ($h^2 > 0.20$).

Rogers et al. (2004) noted the heritability of longevity of composite cows born from 1982 through 1999 in MT was 0.14. In that study, age at first calving and calf birth weight did not influence longevity.

Brigham et al. (2009) estimated the genetic correlations between traditional stayability and stayability to younger ages in Red Angus cattle, attempting to use earlier observations to improve the prediction of stayability EPD to 6 yr (Table 2.8). The genetic correlation of females calving at age 6 and females calving at age 4, given that the female had calved at age 2, was 0.70 and will be used as the basis of the analysis in Chapter 4 to increase the number of records available for analysis. The heritabilities of stayability at various ages were low ($h^2 < 0.12$). Brigham et al. (2007) reported the percentage of Red Angus dams successfully staying in the herd to age 3, 4, 5 and 6 years was 77, 67, 58 and 50%, respectively.

Importance and calculation of GxE

Van Vleck and Cundiff (1998) investigated the genetic relationship between the same trait in males vs. females and concluded that a genetic correlations ≥ 0.85 between the sexes was large enough to ensure that no interactions were present. Robertson (1959) considered

genotype x environment interactions to not be biologically important when genetic correlations were greater than 0.80 between performances in different environments.

Because the expression of genotypes may be different in diverse environments, they may be considered separate but correlated traits. It also brings the question of the appropriate environment to select and develop breeding stock. Should selection be carried out under the same, potentially limited conditions in which the stock will be used, or in an environment more favorable for the expression of the trait? Falconer (1952) states that if only two environments are considered, the interaction may be expressed as a genetic correlation and proposed the following formula:

$$\frac{\text{correlated response}}{\text{direct response}} = \frac{\Delta'G_1}{\Delta G_1} = \frac{h_2}{h_1} r_G$$

in which h_2 and h_1 are the respective square roots of heritability of the traits (the accuracy of phenotypic selection) and r_G is the correlation between the two genotypes (G_1 and G_2). This equation illustrates a need for a high heritability to offset the reduce efficiency through selection of a correlated trait (Falconer, 1952). A full solution of the estimation of three genetic parameters is also required, which includes the two heritabilities and the genetic correlation. In addition, $h_2 r_G$ must be greater than h_1 , which led Falconer to recommend that selection be carried out under the environmental conditions in which the improved breed is destined to live.

Bourdon (2000), as Falconer (1952) showed above, illustrated a method to determine whether selecting for an indicator trait was more effective than selecting directly for the trait of interest. The response to both types of selection are estimated and expressed as a result using the formula (for phenotypic selection)

$$\frac{\Delta BV_{Y|X}}{\Delta BV_Y} = \frac{r_{BV_X, BV_Y} h_X i_X}{h_Y i_Y}$$

in which r = the correlation between the breeding values of trait X and trait Y,

h = the accuracy of selection ($r_{true,index}$), and

i = the intensity of selection

A ratio of less than one would favor direct selection on the trait of interest. If the trait was a threshold trait, the intensities of selection may be dramatically different and have an important effect on the ratio of response (Bourdon, 2000).

Kang (2002) adds that a high GxE variance component will result in a low heritability and progress from selection would be limited. Furthermore, GxE reduces the correlation between phenotypic and genotypic values, thus increasing the difficulty in identifying truly superior genotypes.

Genotype by environmental interactions may be limiting the accuracy of appropriate sire selection and GxE may cause a lower than expected performance in the offspring of sires selected for improved performance. Large genetic correlations of a trait between environments indicate a small GxE effect and vice versa (Falconer and MacKay, 1996).

In beef cattle evaluations, GxE interactions are often ignored by assuming that different environments have the same effect on different genetics but this assumption is not always justified (Falconer and MacKay, 1996). Falconer (1952) defined GxE interaction as the change in relative performance of a characteristic expressed in two or more genotypes when measured in two or more environments. This can be graphically expressed as a change in the magnitude of performance between two genotypes in two different environments or a reranking of those genotypes.

GxE in weight traits

Meyer (1995) analyzed weaning weights using a multiple-trait animal model for Angus cattle in Australia and New Zealand and reported direct genetic and maternal genetic correlations of 0.97 and 0.82, respectfully.

Speidel et al. (2005) estimated heritabilities of weaning weight of calves classified as from a good (n=27,693) or bad (n=14,000) environment. Estimates were the same ($h^2 = 0.20$) and the authors determined the lack of difference may have been to incomplete identification of the calf's environment.

A classical GxE study was performed by the Meat Animal Research Center and the Subtropical Ag Research Station in Brooksville, FL (Olson et al., 1991). Weight and survival data from 2,744 crossbred calves produced from F1 cows were evaluated (Table 2.9). The dams were produced in NE and shortly after weaning, half of the heifers were sent to FL. Heifers raised in NE calved at the age of 2. However, the breeding date in FL was earlier and many heifers had not reached puberty and thus were bred to calve near the age of 3. The pregnancy was 9% higher in NE compared to FL and the pregnancy rates of Zebu crossbred dams were greater than Bos taurus x Bos taurus crossbred dams by 3.8% and this advantage was much higher in FL than NE (5.8% vs. 1.8%, respectively). Bos taurus x Bos taurus cows weaned calves that were ~28 kg lighter in FL while Bos taurus x Bos indicus cows weaned calves that were about the same size in both states.

Jenkins and Ferrell (1994) also took a non-classical approach by containing females and their calves in pens with electronic head gates and changing feed availability, specifically dry matter intake (DMI). One hundred forty-four females of nine breeds (16 hd/breed) were allocated to different pens (four/pen) and four FA levels (58, 76, 93 and 111 g of DM/wt^{.75}). At DMI less than 4,100 kg/yr, Red Poll exhibited the most effective conversion (P<0.05).

Productivity increased for all breeds through 5,000 kg of DMI/yr. When DMI exceeded 5,000 kg of DMI/yr, the conversion of DMI to weaning weight per cow exposed was greater for Gelbvieh, Charolais, Braunvieh, Simmental, Pinzgauer and Limousin compared to Angus, Hereford and Red Poll. At DMI greater than ~6,500 kg/yr, breeds with greater genetic potential for growth and (or) milk (Gelbvieh, Charolais, Braunvieh, Simmental, Pinzgauer and Limousin) were more efficient ($P < 0.05$) compared to Angus, Hereford and Red Poll (Figure 2.1).

Mattos et al., (2000) investigated weaning weight for Herefords in the United States, Canada and Uruguay reported a general absence of genotype x country interactions. The genetic correlation estimates for direct genetic effects were 0.86, 0.90, and 0.88 for United States-Canada, United States-Uruguay and Canada-Uruguay, respectively. The genetic correlation estimates for maternal genetic effects were 0.82, 0.85, and 0.84 for United States-Canada, United States-Uruguay and Canada-Uruguay, respectively. It might be possible no GxE was reported in this study as the effects were averaged over all environments, rather than comparing specific regions (Bertrand et al., 1987).

According to Bertrand et al. (1987), accounting for Limousin sires and dams reduced the magnitude of the GxE by 20 and 38% for birth and weaning weight, respectfully, compared to accounting for sires alone. The interaction variance was 64 and 102% of the sire variance for birth and weaning weight, respectively, even after accounting for the dams. He concludes sires would rerank for progeny performance across contemporary groups within a region.

Bertrand et al. (1987) fit three different sire models to each region's data. The first model was a sire model in which dams and sire x contemporary group effects were not taken into account. The second model was the MPPA-adjusted model, which accounted for dams but not the sire x contemporary group effects. The third model (MPPA-adjusted and interaction term) accounted for both dams and the sire x contemporary group effects, which had the

highest genetic correlations. The genetic correlation is calculated by weighting each region by region correlation by the number of sires, summing across the region by region correlations that contain the region of interest, and dividing the sum by the total number of sires. Important rank changes were found in the South ($r = 0.64$) and Pacific ($r = 0.55$) for birth weight and Cornbelt ($r = 0.65$), South ($r = 0.53$), Lower Plains ($r = 0.54$) and Rocky Mountains ($r = 0.64$) for weaning weight, even after accounting for dams and sire x contemporary group effects. These authors concluded rank changes of sire progeny performance were occurring across contemporary groups and suggested performing separate sire evaluations for some regions, such as the South and Lower Plains for weaning weight (Table 2.10). The regions as defined in this study are below (Figure 2.2).

One potential problem is the use of the same age of dam adjustments (AOD) across all environments. MacNeil and Snelling (1996) suggested inappropriately adjusted weaning weights could be a cause for concern in ranking sires. They reported reranking of maternal BV in Line 1 Herefords due to using AOD adjustments specific for this herd as opposed to using AOD adjustments for the entire Hereford population. They found highly significant AOD constant estimates of 20, 6, 1 and 14 kg for 2, 3, 4, and 11+ year-old females, respectively, illustrating a herd x AOD interaction in the Hereford population. Snelling et al. (1996) acknowledged a priori adjustments do not consider interactions with environment. MacNeil and Snelling (1996) propose a general model for amplified AOD effects under stressful conditions.

Their findings agree with Northcutt et al. (1994) who also observed a diminished range of AOD effects with creep feeding and DeNise et al. (1988) who observed an increasing range of AOD effects for Hereford with increasing environmental severity in a Southwestern range environment.

Cardoso and Templeman (2012) reported imported US Angus sires performed very well in more ideal conditions, but compared poorly to Brazilian Angus in harsher environments.

GxE in fertility traits

Selection for longevity has been difficult due to lack of records and low heritability. One approach is to use correlated traits that can be collected earlier in life. However, Tarres et al. (2006) demonstrated the estimation of these correlations between a nonlinear trait (i.e. longevity) and linear traits is computationally difficult on large datasets.

Morris et al. (1993) reported GxE exists for reproductive and maternal traits in beef cattle. Angus cows were bred to 161 bulls from 11 breeds from 1973 to 1977 in three diverse New Zealand environments. Hereford cows were also used on one of those locations in the same years. A total of 7575 mating records from 2109 cows were analyzed. While Friesian weaned the greatest weight of calf per head in all locations, they were matched or even surpassed by the lighter Jersey crosses in terms of efficiency of calf production, defined as weaning weight per cow exposed and compared on a body weight basis. The European breeds (Blonde d'Aquitaine, Charolais, Chianina, Limousin, Maine Anjou, Simmental and South Devon) performed much better in the more favorable environment than in the harsh environment.

Snelling et al. (1995) estimated heritability using animal model marginal maximum likelihood, sire model marginal maximum likelihood and animal model Method R. Single-trait animal models were used to predict individual genetic merit. He analyzed the females for four measures of stayability. These traits were probabilities of a female having 2 [S(2|1)], 5 [S(5|1)], 8 [S(8|1)] and 11 [S(11|1)] calves, given that she had calved once. These data came from a large Red Angus (Beckton Stock Farm) and a university Angus herd (Colorado State University Beef Improvement Center). The heritability estimates in Beckton were 0.09, 0.11 0.07 and 0.20, respectively, for S(2|1), S(5|1), S(8|1) and S(11|1), respectively (Table 2.11).

Martinez et al. (2005) estimated heritabilities for three measures of stayability. Stayability to a specific age described whether the cow survived to a specific age past the age of two, given that the cow had calved at 2-yrs of age. Stayability to calving described the number of calves born to each cow, given that the cow calved at 2-yrs of age. Stayability at weaning described the number of calves weaned by a cow, given that the cow weaned a calf at 2-yrs of age. Records from 2,019 Hereford cows from a selection experiment with a control line and three lines selected for weaning weight, yearling weight, and an index of yearling weight and muscle score were analyzed with 1) a generalized linear mixed model for a threshold trait and 2) a linear (binomial scale) mixed model. Heritability of the binomial scale was also transformed to an underlying normal scale.

Estimates of heritability to stayability to specific age were low (survived to age five; 0.09 ± 0.08) to moderate (survival to age eight; 0.30 ± 0.14) with the threshold model and ranged from 0.05 ± 0.04 (survival to age five) to 0.15 ± 0.07 (survival to age eight) using a linear (binomial scale) model. Heritability from the linear model was transformed to an underlying normal scale and were low (0.09 for survival to age five) to moderate (0.35 for survival to age eight).

Estimates of heritability of stayability to calving were moderate (ranged from 0.29 ± 0.10 for giving birth to four calves to 0.39 ± 0.11 for giving birth to two calves) with a threshold model, but lower for a linear (binomial scale) model (ranging from 0.18 ± 0.09 for giving birth to six calves to 0.25 ± 0.07 for giving birth to three calves). Estimates of heritability of the underlying scale agreed more closely with the threshold model with a range of 0.30 (giving birth to four calves) to 0.40 (giving birth to two calves).

Estimates of heritability of stayability to weaning were moderate ranging from 0.21 ± 0.14 (weaned five calves given that she had weaned a calf as a 2-yr-old) to 0.47 ± 0.19 (weaned

six calves). Estimates of heritability using the linear model ranged from 0.12 ± 0.08 (weaned five calves) to 0.26 ± 0.12 (weaned six calves). Estimates of heritability transformed to the underlying scale ranged from 0.21 (weaned five calves) to 0.50 (weaned six calves).

Martinez et al. (2005) concludes selection for stayability to calving or weaning is more accurate than selection for stayability to a specific age due to higher estimates of heritability.

Enns et al. (2005) noted the economic value of stayability depends on the average stayability of the herd. In computer simulation, it was shown the value of stayability improvement was 10x greater when stayability was low (20%) compared to the improvement when stayability was high (95%). It was concluded producers would benefit from an interactive web simulation. Since that time, the National Beef Cattle Evaluation Consortium has developed a prototype decision support system (<http://ert.agsci.colostate.edu>).

Reaction Norms

Falconer and MacKay (1996) stated a reaction norm is the environmental sensitivity of a genotype. Reaction norms are determined by the regression of the mean genotype within an environment on the mean of all genotypes in an environment (Falconer and MacKay, 1996). Sensitivity and stability are terms to describe the response of animal (Falconer and MacKay, 1996) and plant varieties (Kang, 2002), respectively, to changes in environments. The average sensitivity of all genotypes is represented by a regression coefficient of one (Falconer and MacKay, 1996) whereas more sensitive genotypes have a coefficient greater than one.

Falconer and MacKay (1996) stated a low genetic correlation means that genotypes react differently to different environments and have regression lines with different slopes. Increased sensitivity appears to increase the environmental variance, V_E , and reduce the heritability.

Sensitivity is increased when synergistic selection is performed (Falconer and Mackay, 1996). Synergistic selection is selection of “good” phenotypes in “good” environments or for “bad” phenotypes in “bad” environments. This is opposed to antagonistic selection of selecting upward for a phenotype in a bad environment or downward selection of phenotype in a good environment.

Animals with a steep or high reaction norm are sensitive to the environment. While performance is excellent in an excellent environment, performance drops quickly when the environment is less than ideal. This has been reported in swine (Knap and Su, 2008)

Table 2.1 Partitioning of variation^a.

Phenotype	Genotype (V_G)			Environment (V_E)
	Additive	Non-additive		
		Dominance	Interactions (V_I)	
V_P	V_A	V_D	$V_{AA} + V_{AD} + V_{DD}$	$V_{Eg} + V_{Es} + V_{GxE}$

$$^aV_P = V_A + V_D + V_{AA} + V_{AD} + V_{DD} + V_{Eg} + V_{Es} + V_{GxE}$$

Variation	Description
V_P	$V_G + V_E$
V_G	$V_A + V_D + V_I$
V_E	$V_{Eg} + V_{Es} + V_{GxE}$
V_A	refers to the deviation from the mean phenotype
V_D	the dominance deviations due to interactions between alternative alleles at a specific locus
V_I	$V_{AA} + V_{AD} + V_{DD}$ refers to the interactions between alleles at different loci
V_{AA}	interactions between two breeding values at different loci
V_{AD}	interactions between the breeding value of one locus and the dominance deviation of the other locus
V_{DD}	interaction between the two dominance deviations at different loci
V_{Eg}	refers to nongenetic sources of variation between individuals that are experienced by multiple individuals in a population (largest component of variation in natural conditions)
V_{Es}	refers to the deviation from the population mean due to the environmental conditions experienced by each individual (statistically known as the error or residual variance)
V_{GxE}	refers to the unique or different responses of genetic lines to general environmental variation

Adapted from Falconer and Mackay, 1996

Table 2.3 Heritabilities and selected genetic correlations used in NCE programs for several US breed associations^a.

Breed	Birth Weight		205-day Weaning Weight			160-day Gain	
	h_A^2	h_M^2	h_A^2	h_M^2	r_{AM}	h_A^2	$r_{AW,AG}$
Angus	.33	.0	.20	.14	.0	.20	.15
Red Angus	.47	.21	.23	.12	.0	.22	.55
Charolais	.42	.14	.23	.27	-.26	.22	.39
Simmental (M)	.45	.0	.33	.15	-.32	.32	.51

^aBIF (2010)

Table 2.4 Phenotypic and genetic parameters for Red Angus^a.

Trait	Wt, kg	SD, kg	h^2	Genetic Correlation		
				WW ^b	GN ^c	YW ^d
Birth Weight	34.1	3.5	0.46	0.56	0.31	0.57
Weaning Weight	231.8	19.4	0.39		0.18	0.78
Post Weaning Gain			0.36			0.75
Yearling Weight	366.6	28.6	0.40			

^aWinder et al., 1990

^bWW = weaning weight

^cGN = post-weaning gain

^dYW = yearling weight

Table 2.5 Heritabilities of beef cattle performance traits

Production Traits	Number of Studies ^a	Weighted Mean, h^{2b}
Birth Weight (Direct)	167	0.31
Birth Weight (Maternal)	34	0.14
Weaning Weight (Direct)	234	0.24
Weaning Weight (Maternal)	38	0.13
Yearling Weight (Direct)	147	0.33
Yearling Weight (Maternal)	6	0.06
Mature Cow Weight	24	0.50
Feed Efficiency	25	0.32
Feed Intake	21	0.34
Relative Growth Rate	12	0.22
Yearling Frame Score	27	0.61
Carcass Traits	Number of Studies ^a	Weighted Mean, h^{2b}
Backfat	26	0.44
Ribeye Area	16	0.42
Slaughter Weight	52	0.41
Carcass Weight	19	0.23
Dressing Percentage	13	0.39
Cutability	12	0.47
Lean:Bone Ratio	4	0.63
Marbling Score	12	0.38
Warner-Bratzler Shear Force	12	0.29
Sensory Panel Tenderness	3	0.13

^aNumber of research studies represented

^bAverage heritability of trait, weighted by number of observations in studies.

Table 2.6 Heritabilities (h^2) of beef cattle reproductive traits^a

Reproduction Traits	Number of Studies ^b	Weighted Mean h^{2c}
Age at First calving	7	0.06
Calving Date	7	0.08
Calving Interval (Cows)	3	0.01
Calving Interval (Heifers)	7	0.06
Calving Ease (Direct)	19	0.10
Calving Ease (Maternal)	11	0.09
Calving Rate	9	0.17
Scrotal Circumference	25	0.48
Heifer Conception Rate (Direct)	9	0.05
Cow conception Rate (Direct)	21	0.17

^aadapted from Gosey, 2003

^bNumber of research studies represented

^cAverage heritability of trait, weighted by number of observations in studies.

Table 2.7 Summary of heritability (h^2) estimates for commonly used reproduction traits in beef cattle^a

Trait	h^2	References
Age at first calving	<0.10	Smith et al., 1989; Martinez-Velazquez et al., 2003
	0.20-0.30	Morris et al., 1992, 2000; Gutierrez et al., 2002
Age at puberty	<0.10	McInerney, 1977
	0.10 to <0.20	Arije and Wiltbank, 1971; Smith et al., 1989; Martinez-Velazquez et al., 2003;
	0.40 to <0.50	Laster et al., 1979; Lunstra, 1982; King et al., 1983; Martin et al., 1992
	≥0.60	Smith et al., 1976; Were and Brinks, 1986; MacNeil et al., 1984
Calving date	<0.10	Buddenberg et al., 1990; MacNeil and Newman, 1994; Morris and Cullen, 1994; Morris et al., 2000
	0.20 to ≤0.30	MacNeil et al., 1984; Buddenberg et al., 1990; Gutierrez et al., 2002
	0.40 to ≤0.50	Cundiff et al., 1986
Calving rate	<0.10	Meyer et al., 1990
	0.10 to ≤0.20	Meyer et al., 1990
Calving success	<0.05	Meyer et al., 1990
	0.05 to ≤0.10	Meyer et al., 1990
Calving to first insemination	<0.10	Donoghue et al., 2004a,b
Days to calving	<0.10	Meyer et al., 1990; Donoghue et al., 2004b
First-service conception rate	<0.10	Minick Bormann et al., 2006
	0.20 to ≤0.30	Dearborn et al., 1973
Heifer pregnancy	<0.20	Evans et al., 1999
	0.20 to ≤0.30	Doyle et al., 2000
Number of calves	<0.10	Meyer et al., 1990; Martinez et al., 2004a
	0.10 to 0.20	Martinez et al., 2004a,b
	0.30 to ≤0.40	Meyer et al., 1990
Pregnancy rate	<0.10	Toelle and Robinson, 1985; Morris and Cullen, 1994; Mathews et al., 1995; Morris et al., 2000
	0.10 to ≤0.20	Evans et al., 1999; Morris et al., 2000; Martinez-Velazquez et al., 2003; Minick Bormann et al., 2006
	0.20 to ≤0.30	Doyle et al., 1996, 2000; Evans et al., 1999; Thallman et al., 1999
Probability of pregnancy	<0.10	Koots et al., 1994
	0.10 to ≤0.20	Evans et al., 1999
	0.20 to ≤0.30	Snelling et al., 1995; Doyle et al., 1996, 2000
	0.50 to ≤0.60	Eler et al., 2002
Scrotal circumference	0.20 to ≤0.40	Latimer et al., 1982; King et al., 1983; Knights et al., 1984
	0.40 to ≤0.50	Neely et al., 1982; Bourdon and Brinks, 1986; Nelsen et al., 1986; Lunstra et al., 1988; Smith et al., 1989; Morris et al., 1992, 2000; Martinez-Velazquez et al., 2003
	0.50 to ≤0.80	Coulter and Foote, 1979; Lunstra, 1982; Evans et al., 1999

^aCammack et al., (2009)

Table 2.8 Estimates of heritability and genetic correlation for each stayability age definition.

Stayability Age Definition	3 yr	4 yr	5 yr	6 yr
3 yr	0.11 (0.0009)	0.84	0.46	0.49
4 yr		0.12 (0.0009)	0.85	0.70
5 yr			0.11 (0.0009)	0.60
6 yr				0.12 (0.01)

Heritabilities and standard error () on the diagonal and genetic correlations above the diagonal.

Table 2.9 Weaning weight of calves raised in NE or FL from F1 dams^a.

Breed	WW in NE, kg	WW in FL, kg
Hereford x Angus	222	194
Angus x Hereford	230	202
Pinzgauer x Angus	242	213
Pinzgauer x Hereford	245	217
Brahman x Angus	254	251
Brahman x Hereford	254	252
Sahiwal x Angus	238	236
Sahiwal x Hereford	243	238

^aOlson et al., 1991

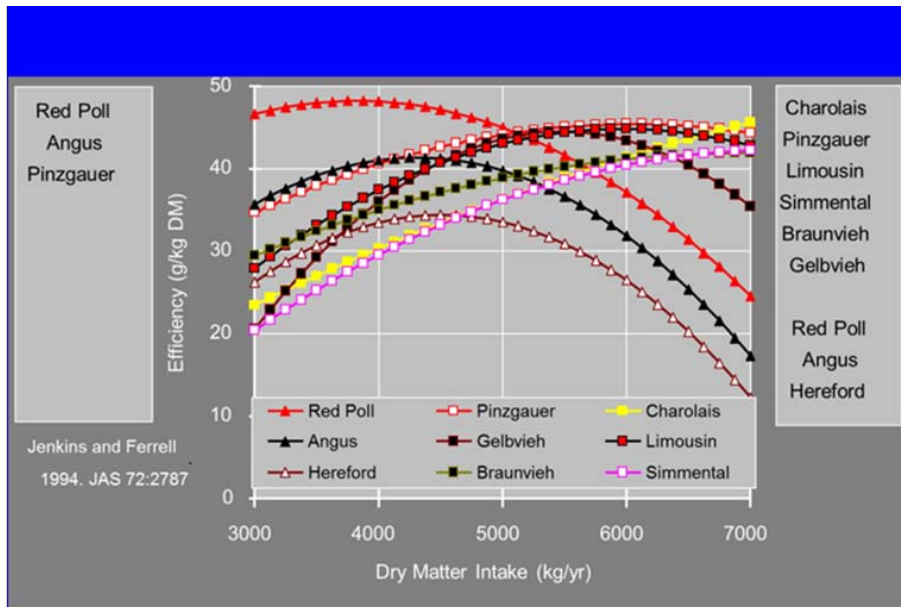


Figure 2.1. Efficiency of various breeds fed different levels of dry matter

Table 2.10 Average Weighted Genetic Correlation estimates of Sire Expected Progeny Differences for Birth Weight and Weaning Weight of Limousin Sires with Progeny in Each of Two Regions of the United States (Figure 2.2).

Region ^A	Genetic correlation MPPA-adjusted and interaction term		Total no. of sires	
	Birth Weight ^B	Weaning Weight	Birth Weight	Weaning Weight
N	.92	.77	793	657
C	.91	.65	1,017	744
S	.64	.53	1,203	787
G	.88	.80	936	580
U	1.00	.81	1,025	816
L	.78	.54	1,264	879
M	.73	.64	938	664
D	.83	.72	882	658
P	.55	.99	484	277
Weighted Mean Estimate	.81	.69	4,271	3,031

^A Each region correlation was calculated by weighting each region by region correlation by the number of sires, summing across the region by region correlations that contain the region of interest and dividing the sum by the total number of sires.

N=Northeast

C=Cornbelt

S=South

G=Gulf Coast

U=Upper Plains

L=Lower Plains

M=Rocky Mountains

D=Desert

P=Pacific

^B Three different sire models were fit to each region's data; these results are the MPPA-adjusted interaction model, which accounted for both dams and the sire x contemporary group effects.

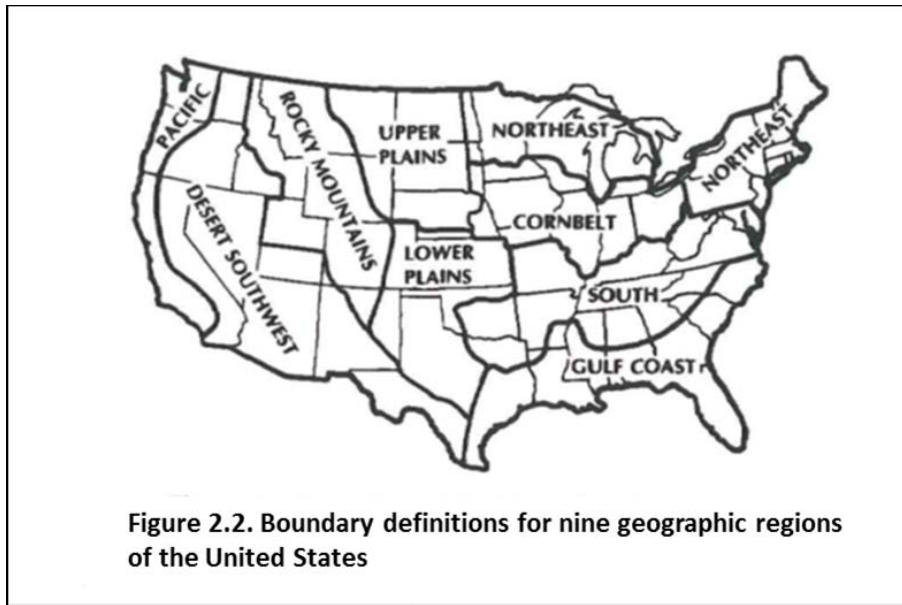


Figure 2.2. Boundary definitions for nine geographic regions of the United States

Table 2.11 Frequency of successful observations for stayability of dams.

Trait	Beckton Stock Farm ^a		Beef Improvement Center ^b	
	n	% Success	n	% Success
S(2 1) ^c	2,130	75	3,105	79
S(5 1)	1,722	39	2,803	38
S(8 1)	1,393	21	2,594	18
S(11 1)	1,081	10	2,276	9

^aRed Angus herd located near Sheridan, WY.

^bColorado State University Angus herd located near Saratoga, WY.

^cS(2|1) the probability of a female having two calves, given she becomes a dam, etc.

Chapter 3

GENETIC PARAMETER ESTIMATES OF GROWTH TRAITS

Introduction

Breed associations have provided Expected Progeny Differences (EPD) to beef producers since the early 1980's and users have made significant change as evident by genetic trends of the major breeds. These genetic evaluations cover a wide geographical area and diverse climates. For many years, there has been recognition of GxE in poultry and swine and these species have addressed these issues in their genetic evaluations. Researchers have also been aware of GxE in beef cattle but this information has not been incorporated into breed association genetic evaluations.

Accurate sire selection is the foundation of genetic improvement, but GxE may present limitations to selecting the best sire for a herd. Breed associations and researchers would need to determine the extent of GxE within a breed and if it is biologically significant. In addition, breed associations would need to address membership education and the added expense in computational time and personnel. Some breeds and traits may not be affected by GxE interactions and thus, would not incur this cost.

The objectives of the present study were to evaluate the presence of genotype by environment interaction for birth weight, weaning weight and gain across nine regions in the US. The single traits were evaluated via weighted regression and the heritabilities of the reaction norms were determined using a single-trait animal model. Using a two-trait animal model, heritabilities and correlations were found within regions and for the entire dataset using BW and WW in model one and WW and GN in model two as dependent variables.

Materials and Methods

Field data from an existing database was used and thus, Animal Care and Use Committee approval was not required.

Nine regions were formed by using the first three digits of US Postal Service Zip Code associated with the mailing address of the herd owner (Leighton et al., 1982 and Bertrand et al., 1987). The boundaries (Figure 2.2) were the same as described by Leighton et al. (1982). The hot, humid areas of Eastern Oklahoma and Northeastern Texas were eliminated from the South due to the minor use of fescue in these areas (Figure 3.1). The map was changed by adding Eastern Oklahoma and Northeastern Texas to the Lower Plains and Northwestern Louisiana to the Gulf (Figure 3.2). Brown et al. (1997) showed GxE for cows grazing endophyte-infected tall fescue compared to cows grazing Bermuda grass, indicating a need to redraw these regions.

These regions are designated

1. Corn (C)
2. Desert (D)
3. Gulf Coast (G)
4. Lower Plains (L)
5. Mountains (M)
6. Northeast (N)
7. Pacific (P)
8. South (S)
9. Upper Plains (U)

The Red Angus dataset (n=1,355,873) was obtained from the Red Angus Association of America (RAAA) at Denton, TX. The PEDIGREE file was created containing the registration

numbers of the animals, sires and dams. If the parent met one of the following conditions, it was considered a foundation sire or dam and its number was changed to zero:

1. the parent's registration number was null
2. the parent's registration number was greater than the animal's registration number
3. the parent's birth date was after the animal's birth date
4. the parent's registration number was less than one
5. the parent's age was less than 365 days at the time of the birth of the animal
6. the sire was not a male or the dam was not a female
7. the sire's registration number was the same as the dam's registration number

The DATA file for the birth weight, weaning weight and gain analyses was created with the following requirements for the calves:

1. All calves had a registration
2. All calves had a recorded sex (B or C)
3. All calves were designated Category A or B
4. All calves were greater than 93.7% Red Angus
5. All calves had a recorded birth date
6. All calves were the result of natural service or artificial insemination
7. All calves were recorded as a single birth
8. All calves had a recorded birth and adjusted weaning weight
9. The birth weight of the calf was greater than 22.7 and less than 50 kg
10. The weaning weight of the calf was greater than 159.1 and less than 409.1 kg
11. If a yearling weight was recorded, it was greater than 159.1 and less than 909.1 kg
12. If a yearling weight was recorded, it was greater than the weaning weight

13. Weaning age was greater than 99 and less than 311 days of age
14. Yearling age was greater than 269 and less than 501 days of age
15. The difference between weaning and yearling date was greater than 59 days
16. Gain was calculated as adjusted yearling weight minus adjusted weaning weight
17. All calves had a recorded owner and breeder number
18. The region of the owner and breeder were the same
19. The region of the owner and breeder was not Hawaii or Alaska
20. The birth year was July 1st to June 30th
21. The dam (class) was considered a (1st calf) heifer if she calved at less than 990 days of age
22. The birth weight contemporary group was defined as
 - a. 93 days in length starting with the first calf born after July 1st
 - b. BW_Mgt_grp (defined by cattle producer)
 - c. Class (born to a 1st calf heifer or cow)
 - d. Birth year
 - e. Sexand contained at least
 - f. five calves
 - g. two sires
 - h. one reference sire
23. The weaning weight contemporary group was defined as:
 - a. Birth weight contemporary group
 - b. Weaning weight management group
 - c. Weaning feed code

d. Weaning weight date

24. The yearling weight contemporary group was defined as:

a. Weaning weight contemporary group

b. Yearling weight management group

c. Yearling weight date

The sires in the DATA file met the following requirements:

1. All sires had a registration number greater than zero

2. All sires appeared in the animal list

3. The reference sires had

a. at least 150 calves

b. at least 50 calves in at least two regions

The dams in the DATA file met the following requirements:

1. All dams had a recorded birth date and a registration number greater than zero

2. All dams appeared in the animal list

3. The age of dam when the calf was born was greater than 449 and less than 7655 days

4. The calving interval was greater than 280 days

The final dataset (n=74,681) contained the animal, sire, dam, region, adjusted BW, adjusted WW and GN. This dataset contained 134 sires whose calves met the constraints. The sires were from 60 breeders and were born from 1965 to 2007. Calves were born from 1972 to 2011.

Mean weights were obtained for each sire for each trait within a region and denoted as SireRegB, SireRegW and SireRegG, respectively. Mean weights were obtained for each trait within each region and denoted as RegAveB, RegAveW and RegAveG, respectively. A new table was (**SIRExREGION** file) formed with each record being a unique sire within a region (n=966).

Variables were sire, region, SireRegAveB, SireRegAveW, SireRegAveG, SireRegCnt (count of calves by the sire within each region), RegAveB, RegAveW, and RegAveG.

The effects of sire, region and region by sire interaction on growth traits (BW, WW and GN) were weighted by SireRegCnt and determined by fitting the following model to data described above in the **SIRExREGION** file:

$$y_{ij} = \mu + \text{sire}_i + \text{RegAveWt}_j + \text{RegAveWt} * \text{sire}_{ij} + e_{ij}$$

in which y_{ij} was the mean weight of the sire's progeny within a region,

μ was the overall mean,

sire_i was the categorical designation for each sire,

RegAveWt_j was the mean weight for the trait within a region (continuous variable),

$\text{RegAveWt} * \text{sire}_{ij}$ was the region*sire interaction and

e_{ij} was the error term.

The regression coefficients were used to estimate a mean weight of progeny for each sire within each region. The following model generated the intercept and slope (reaction norm) across regions:

$$y^*_i = \mu + \text{RegAveWt}_j + e_{ij}$$

in which y^*_i was the estimate of the mean weight of the sire's progeny within a region,

μ was the overall mean,

RegAveWt_j was the mean weight (continuous variable) for the trait within a region,

e_{ij} was the error term.

PROC UNIVARIATE was used to determine the distribution of standard errors of sires and the largest 10% were removed. The remaining 113 sires were used in further analysis of

reaction norm distribution, calculation of reaction norm EPDs and determine variance components of reaction norms.

A **PED** file was created with columns id, sire and dam. The id contained the sires (n=113) from the reaction norm analysis in SAS, their sires, dams, paternal grandsires and maternal grandsires. A three-trait animal model was used in ASReml. Restricted maximum likelihood (REML), developed by Patterson and Thompson (1971), was used to estimate variance parameters.

The acceptable birth weight range was determined by calculating the mean and standard deviation across the US. Calves with birth weights more than three standard deviations from the overall mean were considered outliers and deleted. Weaning weights were confined to 159.1 and 409.1 kg and yearling weights were confined to 159.1 to 909.1 kg (personal communication, American Simmental Association). Although similar WW and YW were acceptable, post-weaning gain was required to be positive.

The count of sires and calves by region are provided in Table 3.1. All regions contained more than 100 sires except D and G. There were 134 sires of 74,681 calves in this dataset. Calves were unevenly distributed across the regions with 62% of the calves produced in regions M and U. Two regions, C and L, had 7,353 and 7,400 calves, respectively, while three regions, N, P and S, had 3,038, 3,707 and 4,883 calves, respectively. Region D had 669 calves represented in this dataset. All calves had BW and WW but only 52.4% had YW with 70.5% of the YW from the two largest regions (U and M). Three regions had fewer than 1,000 records in this dataset while four regions had 1,805 to 4,131.

PROC UNIVARIATE was used to illustrate the distribution of weights (n=74,681 for BW and WW, n=39,104 for GN) in this dataset (Figures 3.3, 3.4 and 3.5) and by region (Figures 3.6, 3.7 and 3.8).

A dataset was created with the sire identification, the intercept, the regression coefficient for RegAveWt, sire and RegAveWt*sire interaction and the standard errors for sire and RegAveWt*sire interactions. The sires with the 10% largest standard errors were eliminated.

Results and Discussion

Overall mean weights and by region are provided in Tables 3.2, 3.3 and 3.4. Overall mean weights were 36.6 ± 4.6 , 267.2 ± 37.9 and 162.0 ± 62.5 for BW, WW and GN, respectively. Birth weights ranged from 33.9 kg to 37.3 kg. Two southern regions, G and S, had the lowest BW, as expected, while the highest BW were in the more northern regions of U and N with BW of 37.0, and 37.3 kg, respectively.

Weaning weights (Table 3.3) ranged from 238.3 to 273.7 with the smallest WW in the southern regions, as expected, and the larger WW in the northern regions. Weaning weight in G, S, D and L were 238.4, 257.3, 261.5 and 262.8 kg, respectively. Weaning weight in N, P, C and M were 273.7, 273.1, 272.3 and 271.7 kg, respectively.

Gain (Table 3.4) ranged from 127.8 to 175.9 kg with the lowest GN in the southern regions and the highest GN in the more northern regions. Gain in G, D, S, M and L were 127.8, 141.6, 150.8, 154.9, 158.7 kg, respectively. Gain in C, U, P and N were 175.9, 171.6, 170.1 and 166.6 kg, respectively. Gain ranged from 1.8 to 496.3 kg. The minimum GN must be a positive number to be considered acceptable for the analysis (personal communication RAAA, 2011).

Reaction Norms

Weighted regressions were produced for the intercept and the RegAveWt term for all animals and for each sire and each RegAveWt*sire interaction. All terms were significant ($P < .05$).

The R^2 were 0.28, 0.30 and 0.34 for BW, WW and GN, respectively. The estimates for the mean in each region (RegAve) were expected to be close to 1.0 and were 1.0, 1.06 and 1.12 for BW, WW and GN, respectively.

Overall intercepts and slopes were determined and intercepts and slopes for each sire for each trait were used to plot the reaction norms for BW, WW and GN, respectively (Figures 3.9, 3.10 and 3.11, respectively). Sires with the 10% largest standard errors were eliminated. Figures 3.12, 3.13 and 3.14 illustrate the RN for BW, WW and GN, respectively for the sires with the 90% smallest standard errors and produced more than $\geq 1,000$ calves in this dataset.

The range in RN was the smallest for BW and greatest for GN (Table 3.5). The mean RN was 0.99, 1.08 and 1.13 for BW, WW and GN, respectively. The figures (Figures 3.15, 3.16 and 3.17) and RN range indicated producers may be identifying sires that have an average slope but little tolerance for outliers for BW. However, the distribution of WW RN indicated producers may have identified sires that perform well across a variety of environments (flatter slopes) but also some sires that perform very well in the environments with high means. The evidence was the RN range and outliers of large RN.

The average reaction norms for the 15 most heavily used sires were 1.0, 1.1 and 1.3 for BW, WW and GN, respectively (Table 3.6). The average reaction norm may indicate producers are identifying sires that are not sensitive to different environments for birth weight (mean BW RN = 1.0) but respond more favorably in growth (mean GN RN = 1.3). However, the minimum RN would suggest producers may not be able to identify sires with these attributes or selections for higher RN are not the goal of every producer.

Correlation of RN to mean weights

The correlations (Table 3.7) of BW mean to BW RN was -0.07 and WW mean to WW RN was 0.17 ($P > 0.05$). The correlation of GN mean to GN RN was -0.22 ($P = 0.02$).

As GN mean increased, GN RN decreased indicating a reduction in sensitivity to different environments. This is in contrast to others who stated higher levels of production results in increased sensitivity to different environments.

The correlations of BW mean to WW and GN means were 0.40 and 0.39, respectively, while the correlation of WW mean to GN mean was 0.28 (Table 3.7). Progeny with higher BW tend to have higher WW and higher GN, as expected. These correlations were significant ($P < 0.05$).

Heritability of Reaction Norms

Variance components for BW and WW RN were determined in ASReml using a two-trait animal model. The **PED** file contained columns for id, sire and dam. The id contained the 113 sires, their sires, dams, paternal grandsires and maternal grandsires. Variance components for the GN RN were outside the parameter space.

The heritabilities of BW and WW RN were 0.40 ± 0.28 and 0.39 ± 0.21 , respectively (Table 3.8). Maricle et al. (2008) found heritability was 0.40 and 0.29 for BW and WW using the same model in Angus cattle. The phenotypic and genotypic correlations were 0.19 ± 0.10 and 0.54 ± 0.40 , respectively. These data indicate heritability for the RN is moderate and producers should be able to select sires with more or less stability as desired. In addition, the relatively high genetic correlation indicates selection can be made prior to collection of WW. These results produced large SE and merit further study of a larger dataset.

The distributions of the EPDs are illustrated in Figures 3.19 and 3.20. The descriptive statistics (Table 3.9) indicate a wider range and larger SD for WW RN compared to BW RN. While it is not clear if it is intentional, producers may be selecting for less variation at birth.

Cluster Analysis

Cluster analysis was explored but regions were not combined for these analyses. Others have used clusters to create the diverse groups such that genotypes (or environments) are homogeneous within groups but heterogeneous among groups (Lin and Lin, 1994, Ceron-Munoz et al., 2004; Cardoso and Tempelman, 2012). As few as three clusters (using eight descriptive herd variables) were effective to combine records from two countries (Ceron-Munoz et al., 2004). Groups were assigned by genetic correlations.

Region means were used to perform two-trait (BW and WW) and three-trait (BW, WW and GN) cluster analyses (PROC CLUSTER, SAS 9.2). In the two-trait analysis, three clusters (Table 3.10) were identified; 1) a single hot, humid region (G), 2) a region stretching from the southwest to the Fescue Belt and north from Texas through the Upper Plains (D, L, S and U) and 3) a more northern cluster (P, C, M, and N) covering the Northeast, Upper Midwest corn belt, the Rocky Mountains and the Pacific coast (Figure 3.20). The shorter vertical and horizontal bars indicated these regions tended to be more similar in the two-trait cluster compared to the three-trait cluster shown in Figure 3.21. There was some overlap of the second and third cluster for BW but not WW (Table 3.11).

In the three-trait analysis, three clusters (Table 3.12) were again identified; 1) a single hot, humid region (G), 2) a cluster that included the lower latitude regions (D, L, and S) but also the Rocky Mountains (M) and 3) a cluster of upper latitude regions (C, N, P and U).

Region G was unique from the other regions with the lowest BW, WW and GN (33.8, 234.5 and 124.6 kg, respectively). Regions D, L, S and M had BW, WW and GN ranges from 35.1 to 36.9 kg, 256.9 to 270.0 kg, and 139.3 to 158.5 kg, respectively. Regions C, N, P and U had BW, WW and GN ranges from 35.9 to 37.4 kg, 265.3 to 272.9 kg and 165.3 to 176.3 kg, respectively.

There was some overlap of the second and third cluster for BW and WW, but not GN (Table 3.13).

The regions were the same in these cluster analysis (Figure 3.21) except regions M and U, in which GN was different (153.6 vs. 172.8 kg, respectively). Several reasons for this might include greater and/or cheaper feed resources in U compared to M or producers are rewarded monetarily for greater GN and/or yearling weights by buyers in U compared to M. Future analysis should consider clustering WW and GN only, which would mimic the two-trait analysis by breed associations for post-weaning performance.

Growth EPDs

A three-trait sire model was used in ASReml to analyze the individual records (n=74,681), which included the individual adjusted weights (BW, WW and GN) and contemporary groups (BWcg, WWcg and GNcg). Covariances, variances and genetic correlations were obtained (Table 3.14).

The genetic correlations were calculated as the covariance divided by the product of the square root of the variances for each trait. The genetic correlations were 0.36, 0.20 and 0.08 for BW to WW, BW to GN and WW to GN, respectively. These results indicate selection for BW was also selection for genes that increase WW and to a lesser extent GN. However, selection for WW would have little effect on GN.

Heritabilities

A comparison of heritabilities among regions was made by using a single- or two-trait animal model. The single-trait animal model heritabilities were shown in Tables 3.15, 3.16 and 3.17 for BW, WW and GN, respectively. The estimates for BW h^2 were slightly lower compared to BIF (2010) and Winder et al. (1990) who reported 0.47 and 0.46, respectively, and slightly higher compared to Maricle et al. (2008), who reported BW h^2 of 0.40 in Angus. The BW h^2

range was 0.0 (G) to 0.46 (U) with a national estimate of 0.43. The dramatic drop in h^2 was unexpected in regions G and L (0.0 and 0.17, respectively). In comparison, a two-trait animal model with BW and WW as dependent variables showed a similar wide range in h^2 (Table 3.18). Heritability was 0.0, 0.0, and 0.02 for regions G, L and M, respectively. Other estimates were greater than 0.2.

Heritability ranged from 0.05 (G) to 0.41 (D) with a national estimate of 0.38 for WW using the single-trait animal model (Table 3.16). The estimate for WW was similar to Winder et al. (1990), but much higher than BIF (2010), Maricle (2008) and Speidel et al. (2005) ($h^2 = 0.39$, 0.23, 0.29 and 0.20, respectively). Using the two-trait animal model (Table 3.18), h^2 estimates were slightly lower (reductions of 0.01 to 0.02) for regions G, L, P, S and U. It was noticeably lower for region M (0.27 vs. 0.11, respectively).

Heritabilities for GN were generally lower (Table 3.17) than reported by Winder et al. (1990), BIF (2010) and Maricle (2008), who reported h^2 of 0.36, 0.22 and 0.26, respectively. They range from 0.0 (D) to 0.29 (G) in the single-trait animal model. The two-trait animal model (Table 3.19) provided similar h^2 estimates to the single-trait animal model. However, there were dramatic differences in the genetic correlation of WW to GN within each region compared to the national estimate ($r_g = 0.33$). Genetic correlations ranged from -0.69 (N) and -0.55 (G) up to 0.69 (C) and 1.0 (P). Convergence did not occur in region D.

Correlations of Growth Traits within regions

Phenotypic correlations were moderate for BW and WW ($r_p=0.35$) and much lower for WW and GN ($r_p=0.10$) (Tables 3.18 and 3.19, respectively). This trend held within all regions. Genetic correlations were moderate ($r_g=0.29$) for BW and WW but slightly higher for WW and GN ($r_g=0.33$) (Tables 3.18 and 3.19, respectively). The genetic correlations of BW to WW were

generally positive within each region and agreed with the national estimate. Correlations in Regions G, L and M, were not estimable.

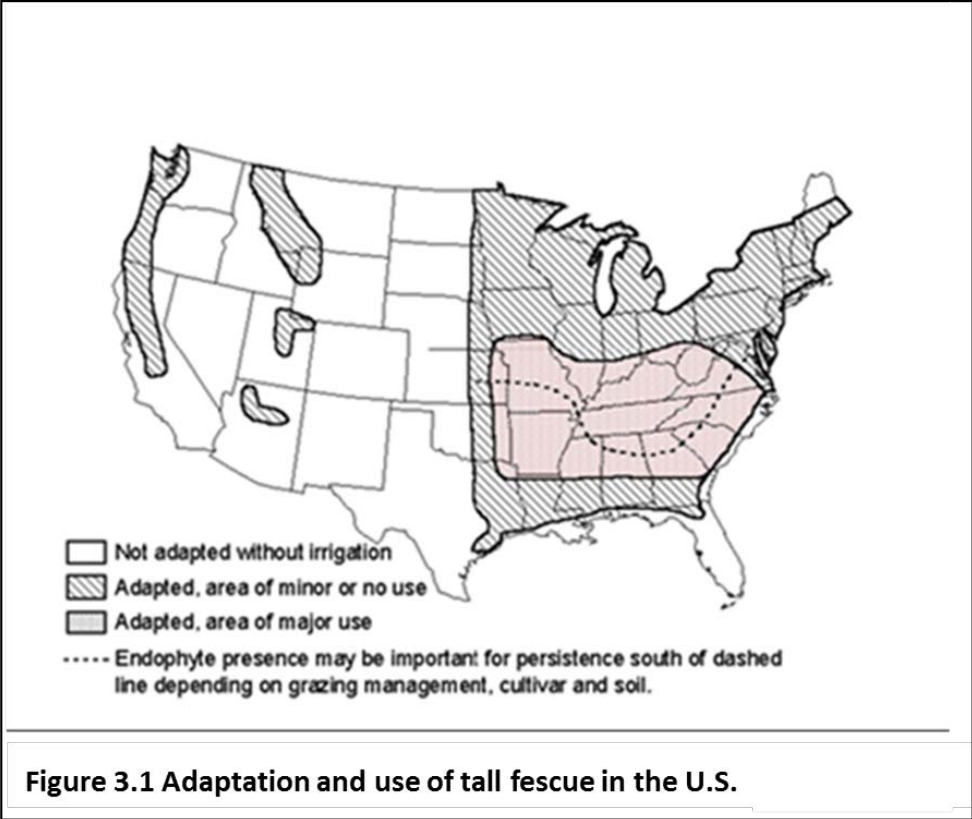


Figure 3.1 Adaptation and use of tall fescue in the U.S.

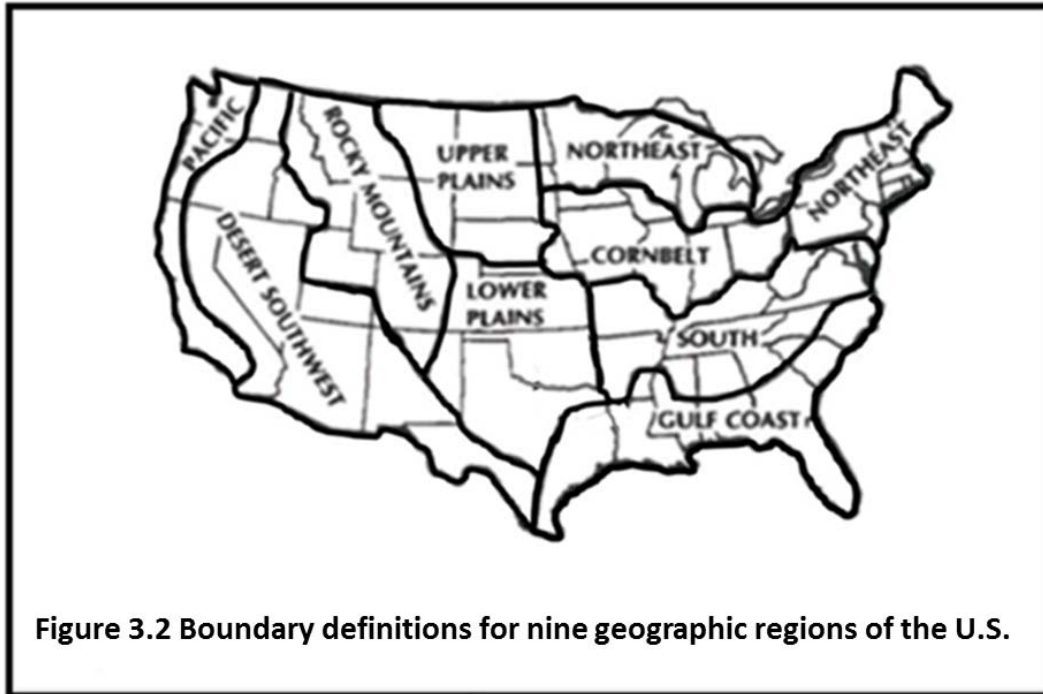


Figure 3.2 Boundary definitions for nine geographic regions of the U.S.

Table 3.1 Count of qualifying sires and their calves by region.

Region	Sires, count	Calves, Count	
		BW and WW	GN
C	120	7353	1991
D	62	669	314
G	82	1305	317
L	113	7400	4131
M	131	25778	15222
N	109	3038	723
P	102	3707	1805
S	115	4883	2250
U	132	20548	12351
Total	134	74681	39104

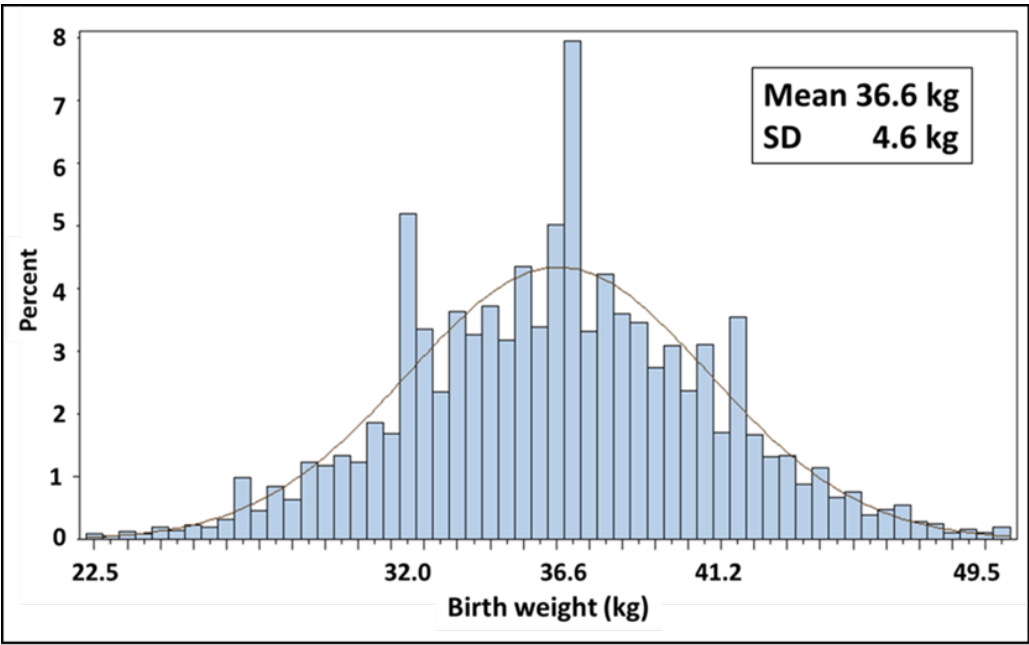


Figure 3.3 Observed and theoretical distribution of birth weight

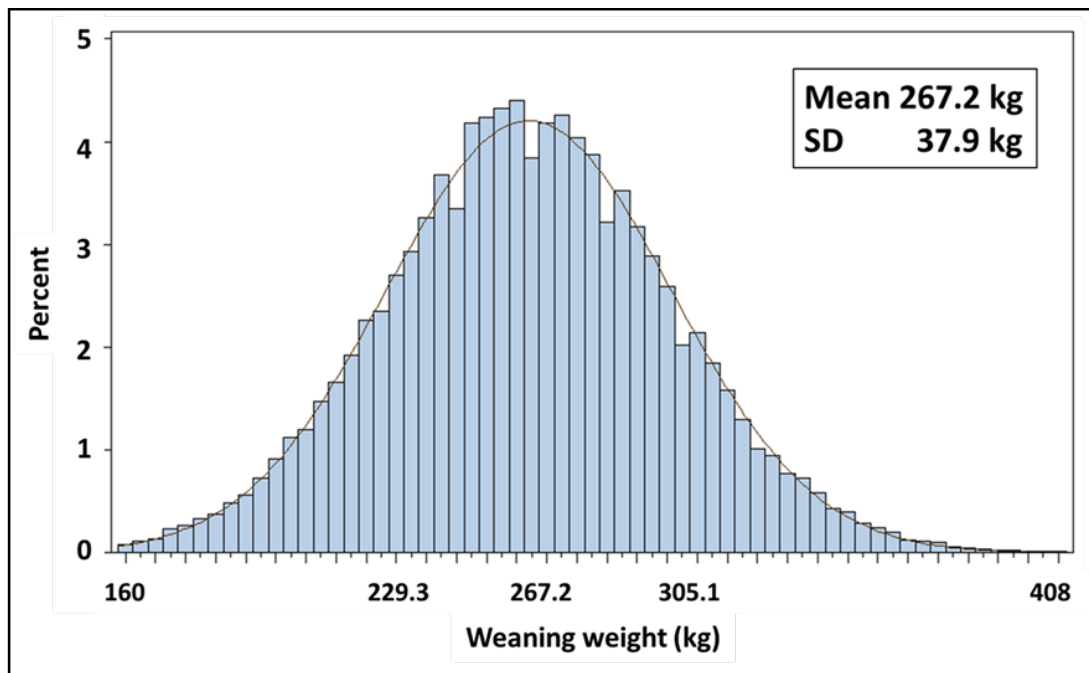


Figure 3.4 Observed and theoretical distribution of weaning weight

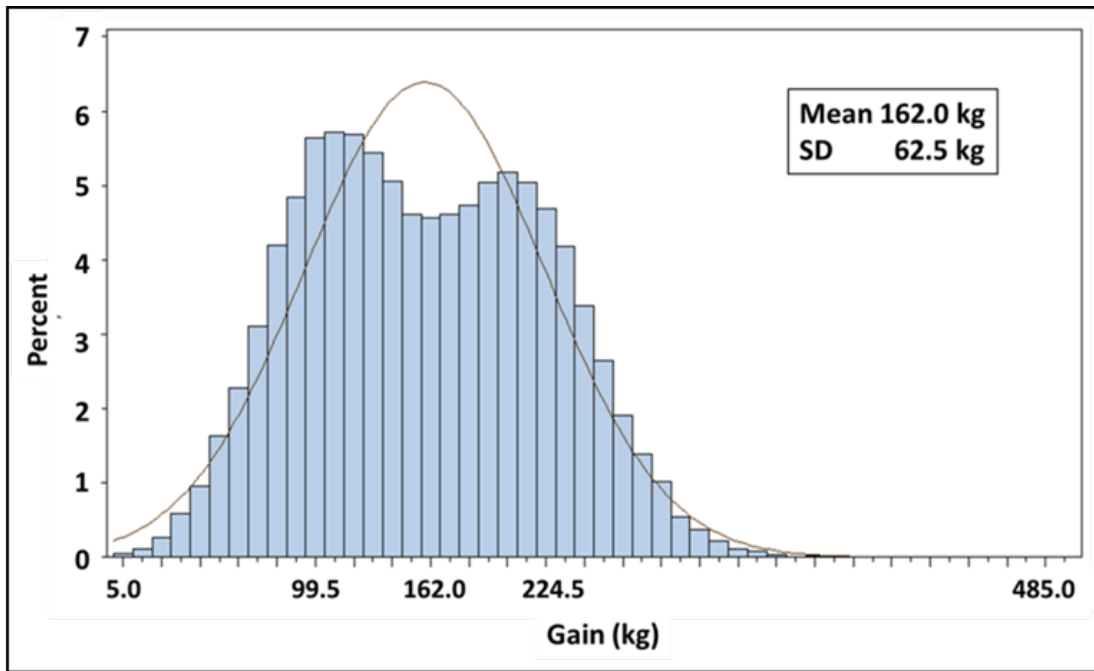


Figure 3.5 Observed and theoretical distribution of gain

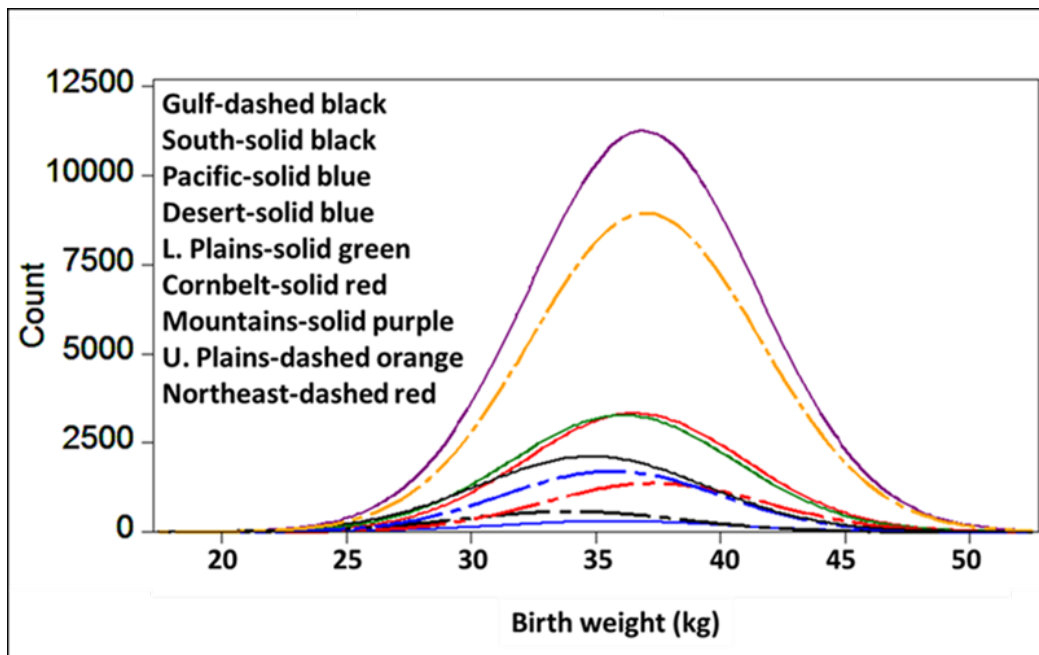


Figure 3.6 Distribution of birth weight by region

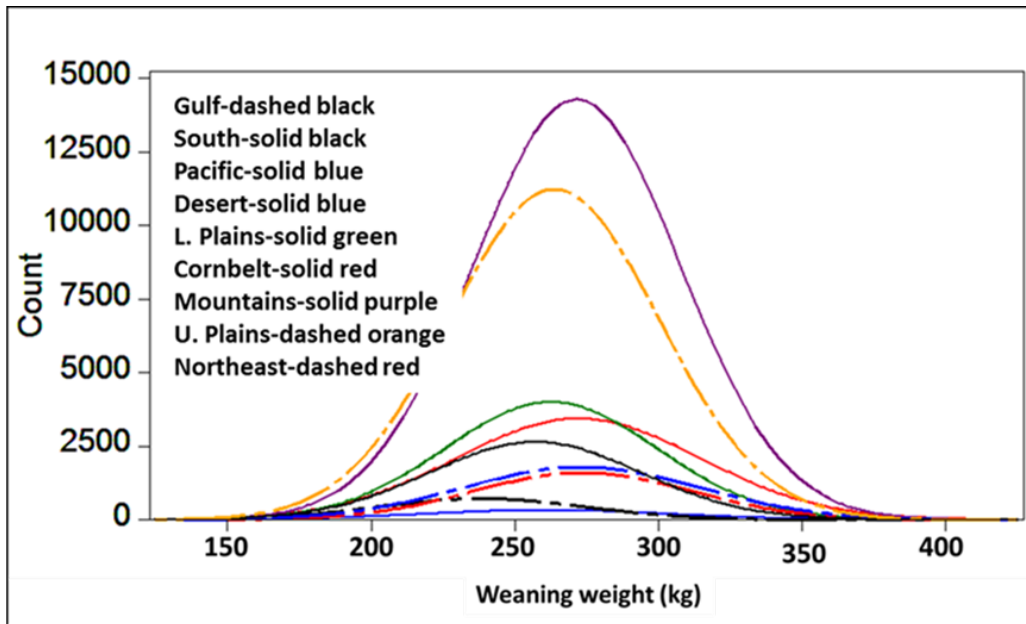


Figure 3.7 Distribution of weaning weight by region

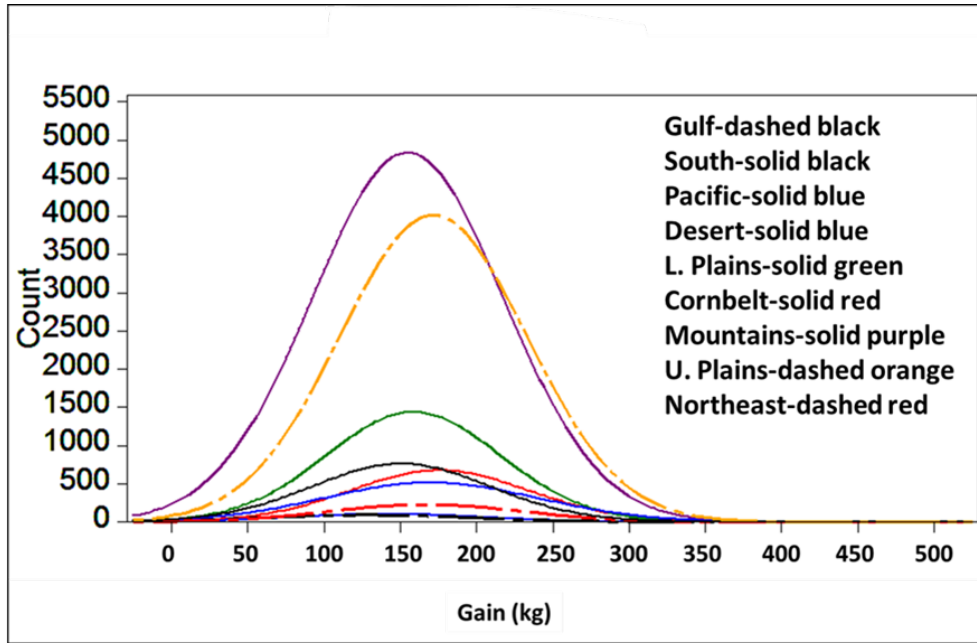


Figure 3.8 Distribution of gain by region

Table 3.2 Descriptive statistics for birth weight by region

Region	N	Mean, kg	SD, kg	Min, kg	Max, kg
C	7353	36.6	4.1	22.7	50.0
D	669	35.8	4.5	23.1	50.0
G	1305	33.9	4.5	22.7	50.0
L	7400	36.1	4.5	22.7	50.0
M	25778	36.9	4.6	22.7	50.0
N	3038	37.3	4.4	23.6	50.0
P	3707	35.6	4.3	22.7	50.0
S	4883	34.8	4.6	22.7	50.0
U	20548	37.0	4.6	22.7	50.0
USA	74681	36.6	4.6	22.7	50.0

Table 3.3 Descriptive statistics for weaning weight by region

Region	N	Mean, kg	SD, kg	Min, kg	Max, kg
C	7353	272.3	42.7	159.0	408.6
D	669	261.5	41.4	162.2	391.8
G	1305	238.4	36.2	159.0	391.8
L	7400	262.8	37.0	160.9	407.7
M	25778	271.7	36.0	159.0	409.0
N	3038	273.7	37.9	160.4	409.0
P	3707	273.1	41.4	160.0	408.6
S	4883	257.3	37.0	160.9	391.8
U	20548	263.8	36.5	159.0	408.1
USA	74681	267.2	37.9	159.0	496.3

Table 3.4 Descriptive statistics for gain by region

Region	N	Mean, kg	SD, kg	Min, kg	Max, kg
C	1991	175.9	59.01	14.50	343.60
D	314	141.6	61.48	7.20	300.90
G	317	127.8	69.30	2.70	315.00
L	4131	158.7	57.26	3.10	401.80
M	15222	154.9	62.79	6.30	366.30
N	723	166.6	63.18	12.2	370.00
P	1805	170.1	70.12	3.10	389.00
S	2250	150.8	59.10	1.80	333.60
U	12351	171.6	61.36	1.80	496.30
USA	39104	162.0	62.5	1.80	496.30

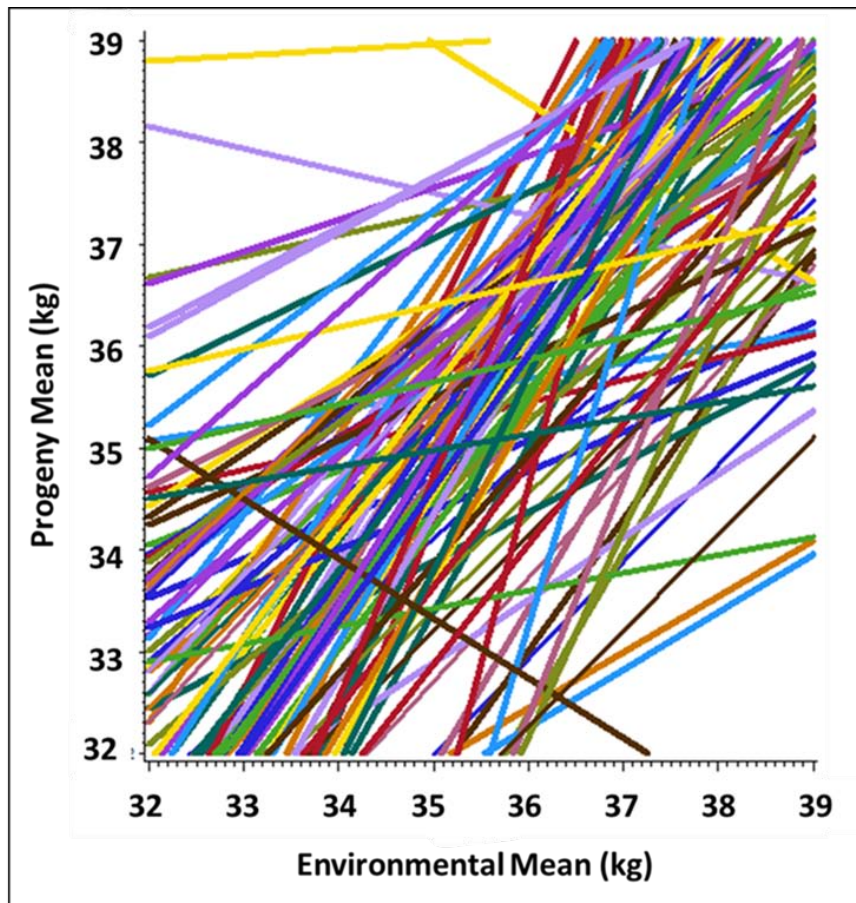


Figure 3.9 Birth weight reaction norms

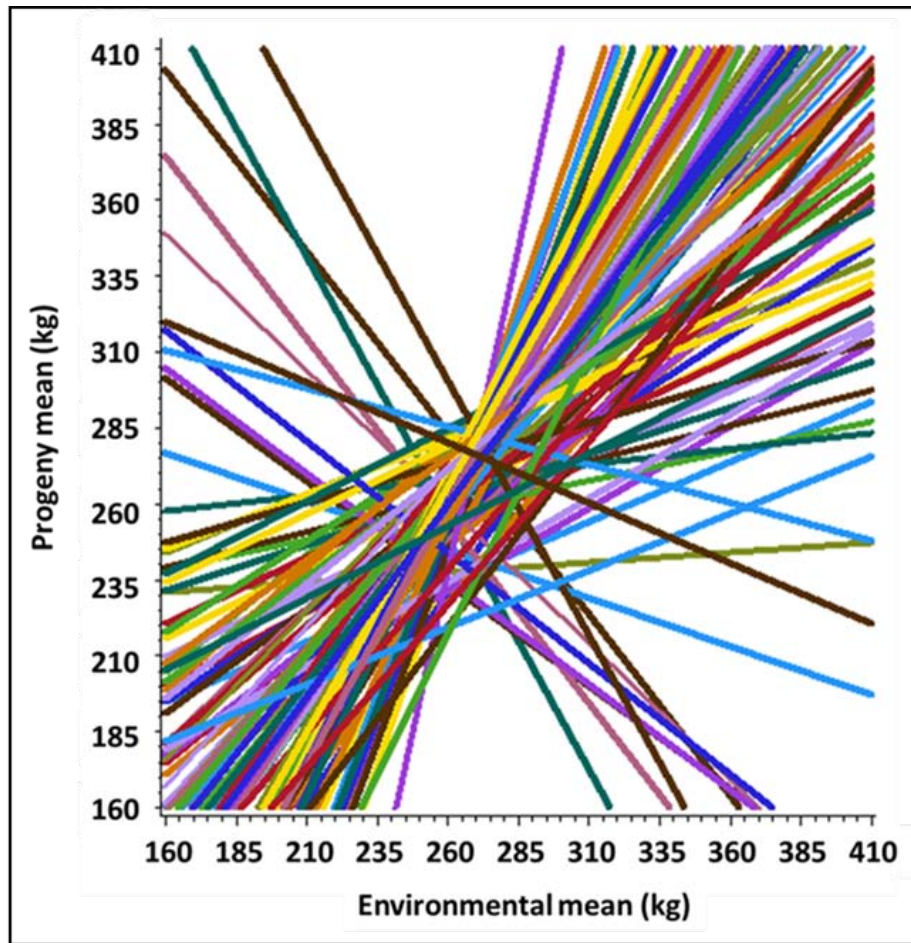


Figure 3.10 Weaning weight reaction norms

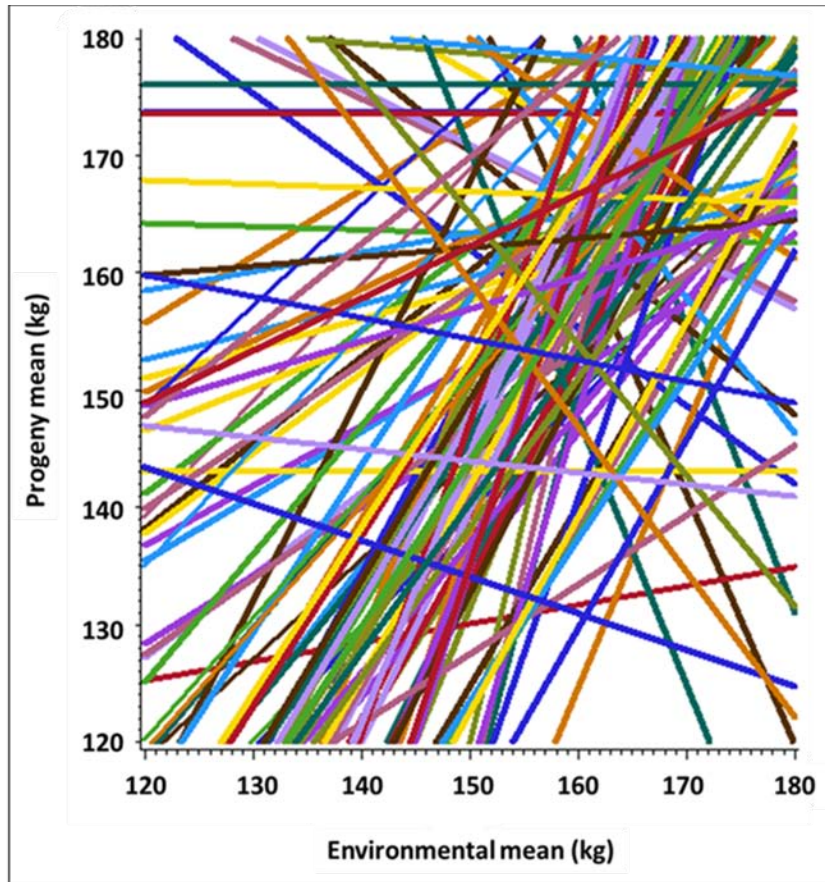


Figure 3.11 Gain reaction norms

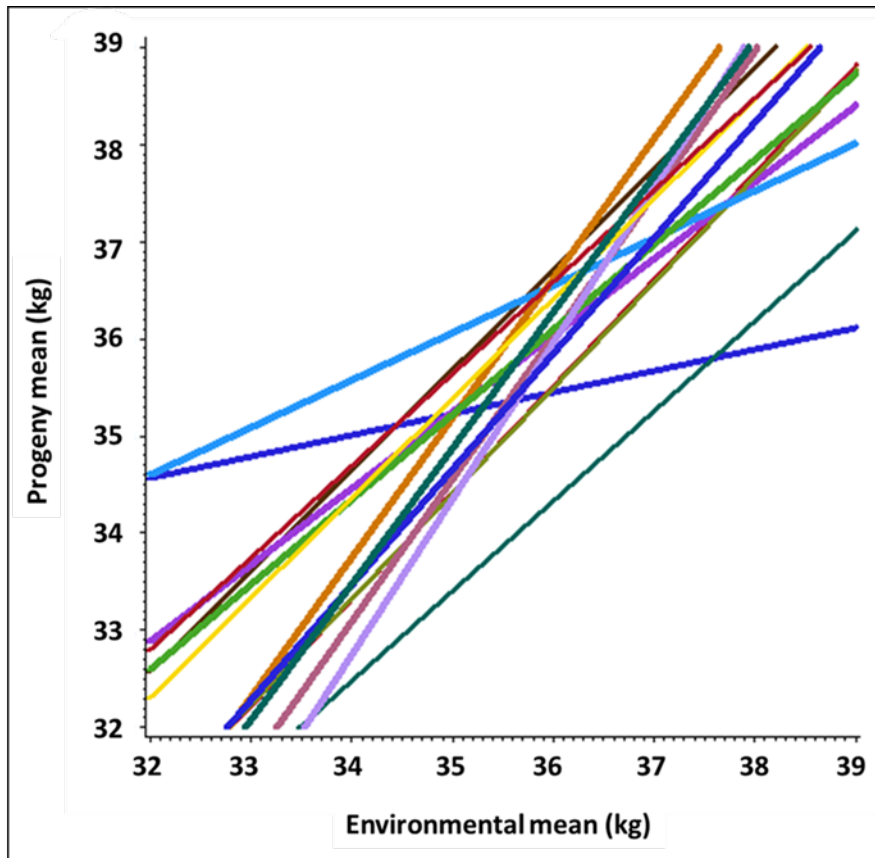


Figure 3.12 Birth weight reaction norms of the most heavily used bulls

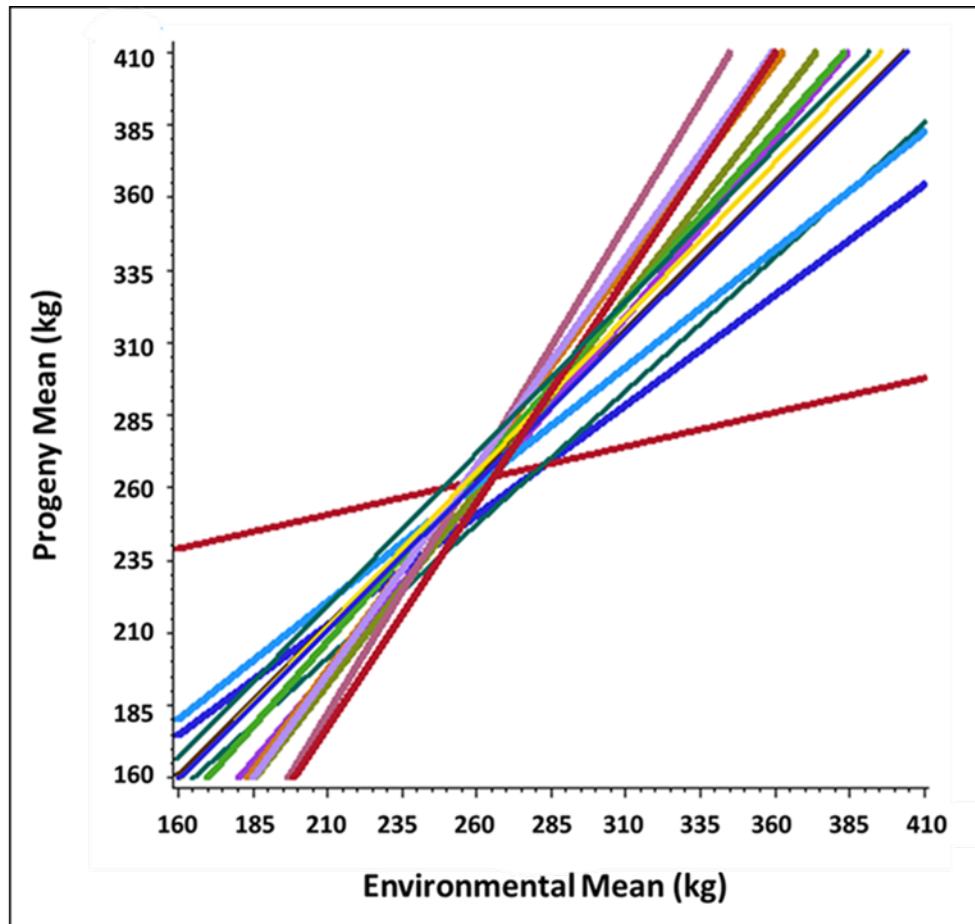


Figure 3.13 Weaning weight reaction norms of the most heavily used bulls

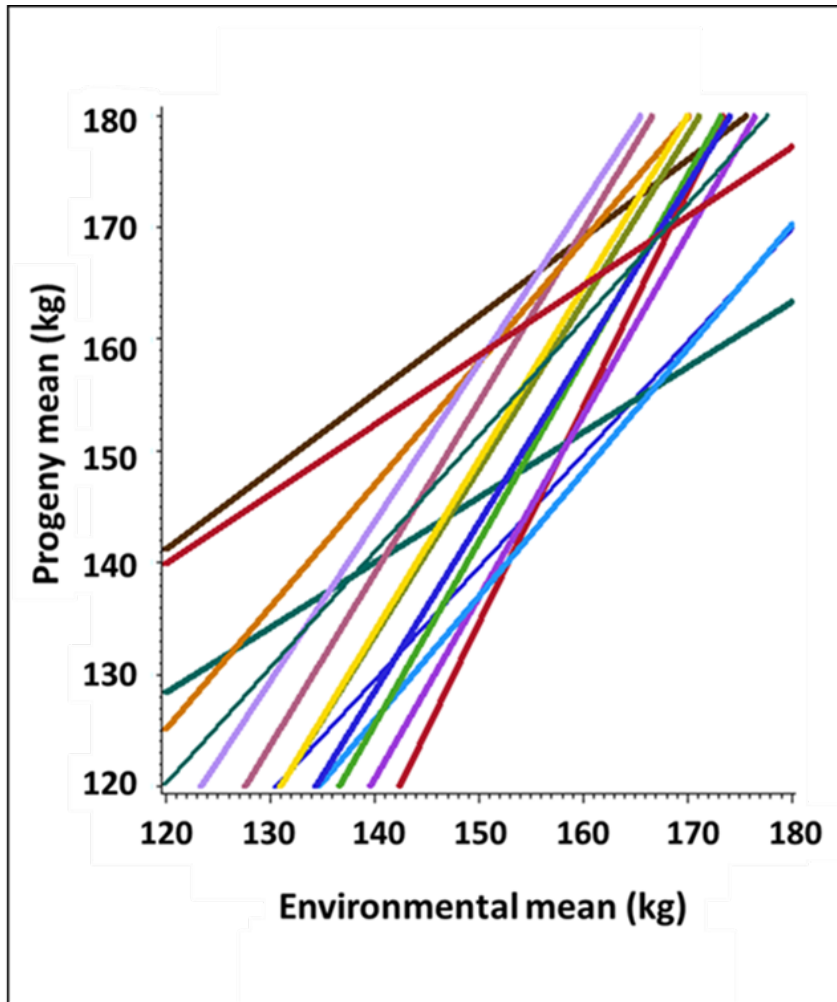


Figure 3.14 Gain reaction norms of the most heavily used bulls

Table 3.5 Percentile rank of reaction norms for birth weight, weaning weight, and gain

Percentile rank	BW	WW	GN
100	3.51	4.44	4.96
99	3.07	4.27	4.06
95	2.23	2.58	3.00
90	1.82	2.10	2.37
75	1.41	1.57	1.71
50	0.99	1.08	1.13
25	0.60	0.49	0.32
10	0.22	-0.28	-0.65
5	-0.01	-0.85	-1.20
1	-0.59	-1.68	-2.28
0	-1.06	-2.24	-2.45

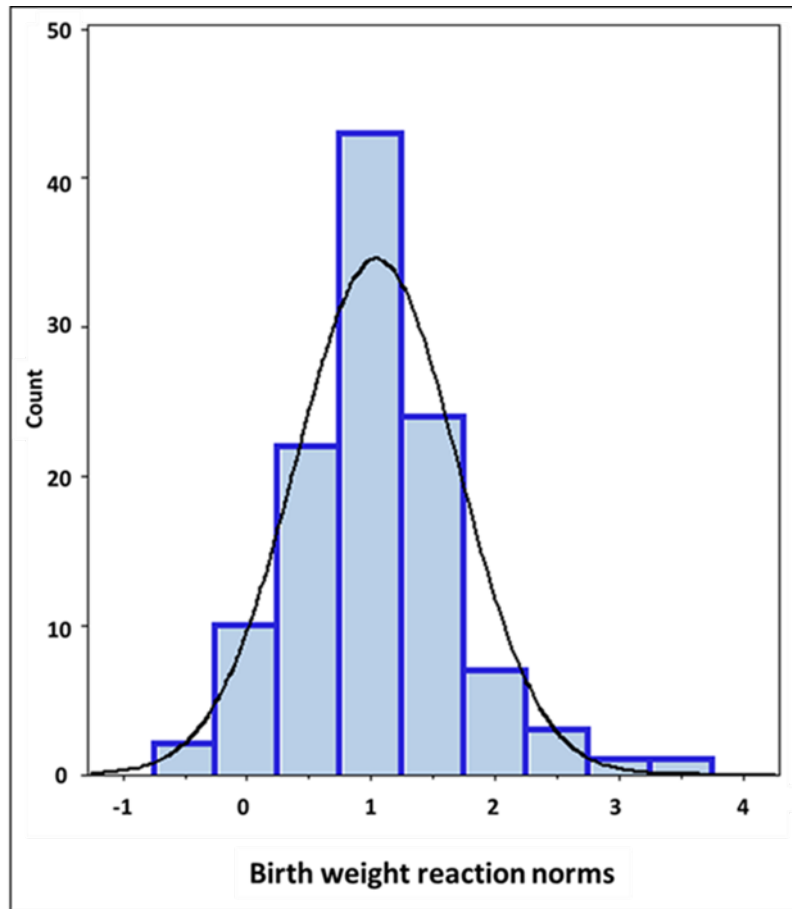


Figure 3.15 Observed and theoretical distribution of birth weight reaction norms

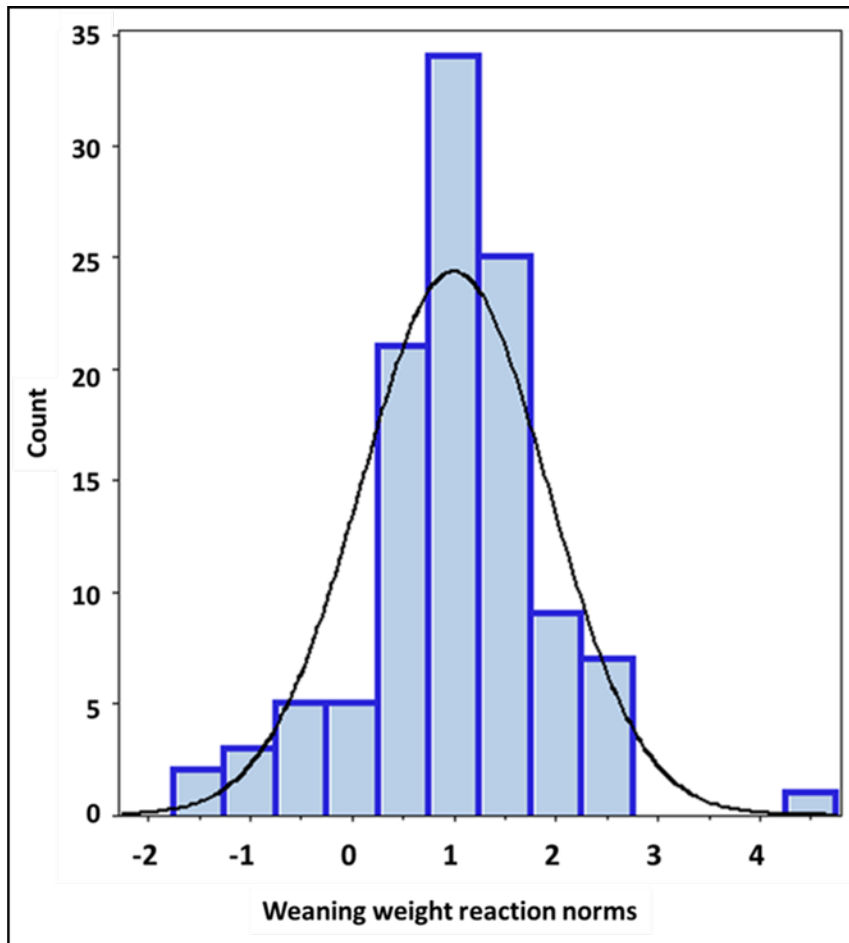


Figure 3.16 Observed and theoretical distribution of weaning weight reaction norms

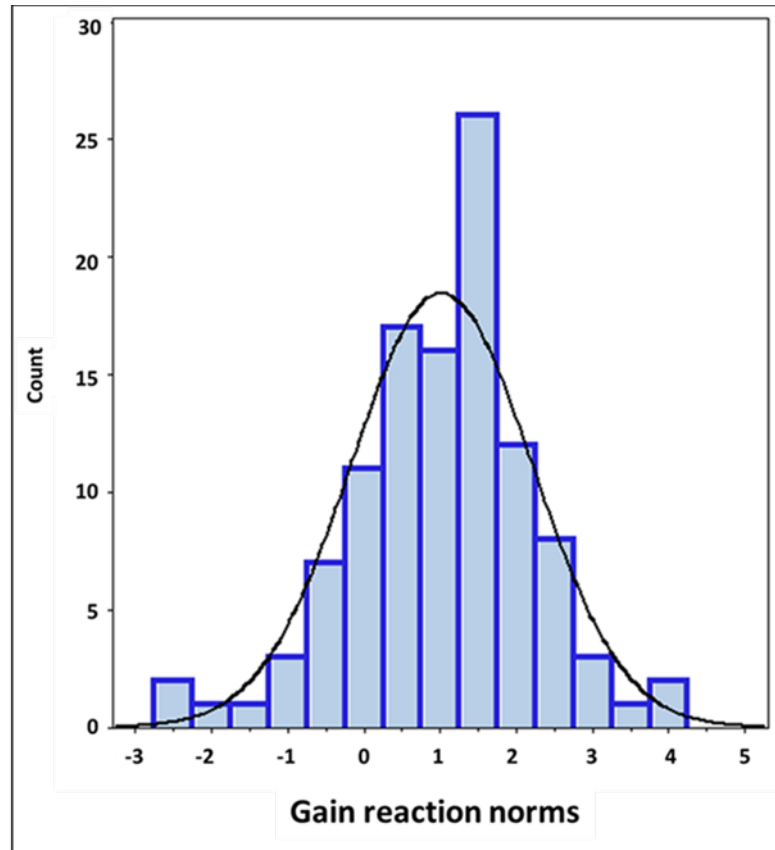


Figure 3.17 Observed and theoretical distribution of gain reaction norms

Table 3.6 Descriptive statistics of the reaction norms for weight traits for the 15 most heavily used bulls.

Variable	N	Mean	Std Dev	Min	Max
BW RN	15	1.0	0.4	0.2	1.6
BW Mean (kg)	15	35.9	0.6	34.3	36.7
WW RN	15	1.1	0.4	0.2	1.7
WW Mean (kg)	15	265.7	7.1	250.7	275.8
GN RN	15	1.3	0.4	0.6	1.9
GN Mean (kg)	15	157.6	8.3	145.3	171.4

Sires with smallest SE (90%) for the sire and RegAveWt*sire regression coefficients for BW, WW and GN and one of the 15 most heavily used bulls.

Table 3.7 Rank correlation coefficients and P-values for the reaction norms and mean of weight traits.

	BW RN	BW Mean	WW RN	WW Mean	GN RN	GN Mean
BW RN	1	-0.07	0.18	0.16	0.04	0.13
		0.45	0.06	0.10	0.66	0.17
BW Mean		1	0.13	0.40	-0.21	0.39
			0.17	<.0001	0.03	<.0001
WW RN			1	0.17	0.06	-0.04
				0.08	0.53	0.68
WW Mean				1	0.10	0.28
					0.32	0.00
GN RN					1	-0.22
						0.02
GN Mean						1

Table 3.8 Variance components for birth weight and weaning weight reaction norms

Heritabilities and Correlations	Est	SE
h_B^2	0.40	0.28
h_W^2	0.39	0.21
r_P	0.19	0.10
r_G	0.54	0.40

Table 3.9 Descriptive statistics of birth weight and weaning weight reaction norm EPDs

RN	N	Mean	Std Dev	Min	Max
BW	442	0.00	0.09	-0.35	0.39
WW	442	0.00	0.12	-0.70	0.40

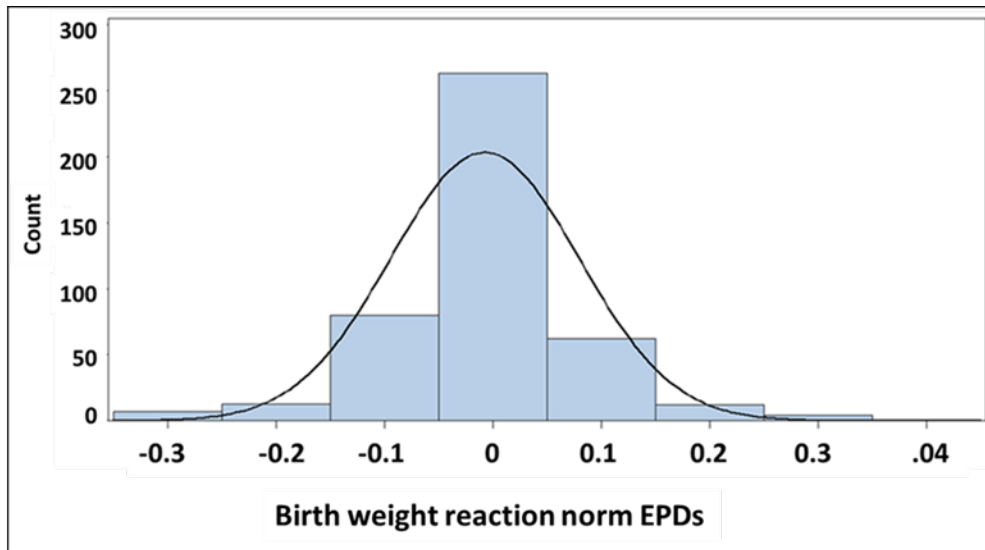


Figure 3.18 Observed and theoretical distribution of birth weight reaction norm EPDs

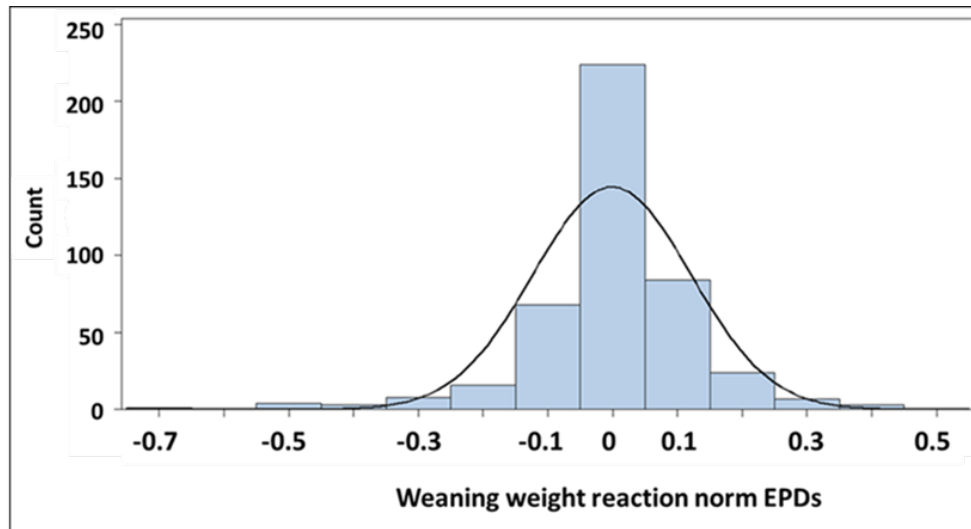


Figure 3.19 Observed and theoretical distribution of weaning weight reaction norm EPDs

Table 3.10 Result of two-trait cluster analysis.

Cluster	Region	BW	WW	GN
1	G	33.8	234.5	124.6
2	S	35.1	256.9	151.2
2	L	36.2	262.4	158.5
2	D	35.8	260.4	139.3
2	U	37.2	265.3	172.8
3	M	36.9	270.0	153.6
3	C	36.7	269.7	176.3
3	P	35.9	271.6	170.4
3	N	37.4	272.9	165.3

Table 3.11 Two-trait cluster analysis

Cluster	BW, kg		WW, kg		GN, kg	
	Range	Mean	Range	Mean	Range	Mean
1	33.8	33.8	234.5	234.5	124.6	124.6
2	35.8 to 37.2	36.1	256.9 to 265.3	261.3	139.3 to 172.8	165.5
3	35.9 to 37.4	36.7	269.7 to 272.9	271.1	153.6 to 176.3	166.4

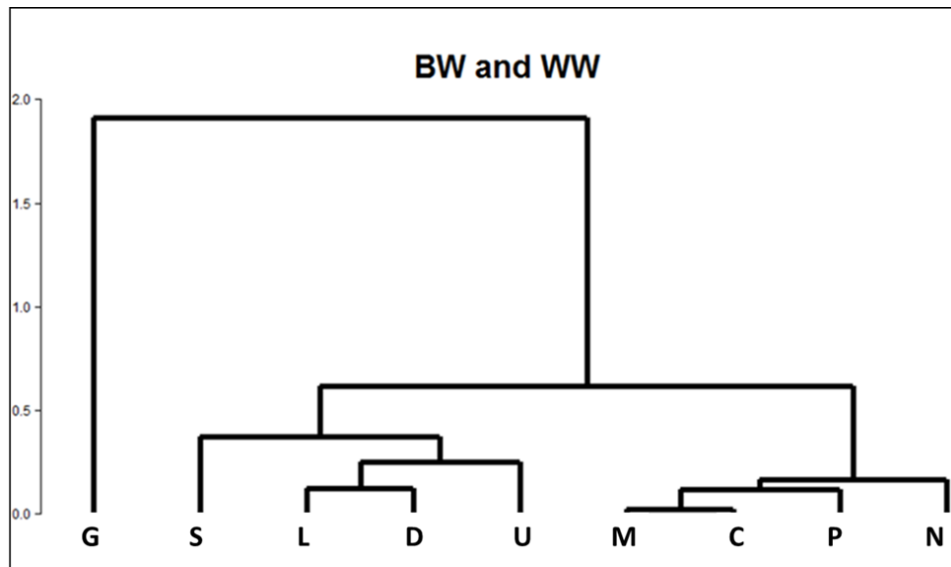


Figure 3.20 Two-trait cluster analysis of birth weight and weaning weight

Table 3.12 Results of three-trait cluster analysis.

Cluster	Region	BW	WW	GN
1	G	33.8	234.5	124.6
2	S	35.1	256.9	151.2
2	L	36.2	262.4	158.5
2	M	36.9	270.0	153.6
2	D	35.8	260.4	139.3
3	P	35.9	271.6	170.4
3	N	37.4	272.9	165.3
3	C	36.7	269.7	176.3
3	U	37.2	265.3	172.8

Table 3.13 Three--trait cluster analysis

Cluster	BW, kg		WW, kg		GN, kg	
	Range	Mean	Range	Mean	Range	Mean
1	33.8	33.8	234.5	234.5	124.6	124.6
2	35.1 to 36.9	36.0	256.9 to 270.0	262.4	139.3 to 158.5	150.7
3	35.9 to 37.4	36.8	265.3 to 272.9	269.9	165.3 to 176.3	171.2

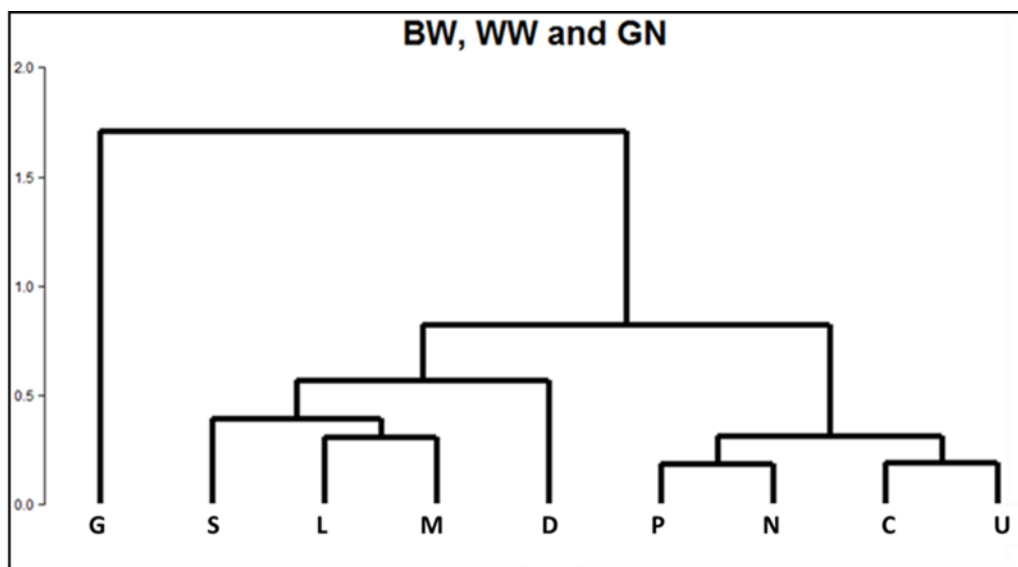


Figure 3.21 Three-trait analysis of birth weight, weaning weight and gain

Table 3.14 (Co)variance and genetic correlation using a three-trait sire model.

BW	14.5 ± 0.1	0.36 ± 0.004	0.20 ± 0.005
WW	32.1 ± 0.3	561.6 ± 3.3	0.08 ± 0.006
GN	18.3 ± 0.5	42.0 ± 3.3	550.5 ± 4.4

Covariances are below, variances on and genetic correlation above the diagonal.

Table 3.15 Variance components of birth weight by region using a single-trait animal model.

Region	Phenotypic		Additive		h ²	
	Var.	SE	Var.	SE	Est.	SE
C	14.1	0.3	3.4	0.8	0.24	0.06
D	13.6	1.1	4.1	3.0	0.30	0.21
G	13.5	0.6	0.1	0.8	0.00	0.06
L	14.4	0.3	2.5	0.7	0.17	0.05
M	16.5	0.3	6.1	0.8	0.37	0.04
N	14.9	0.6	4.2	1.5	0.28	0.09
P	13.9	0.5	4.2	1.4	0.30	0.09
S	15.6	0.5	5.1	1.5	0.33	0.09
U	17.1	0.3	7.9	1.0	0.46	0.05
USA	16.4	0.19	7.1	0.6	0.43	0.03

Table 3.16 Variance components of weaning weight by region using a single-trait animal model.

Region	Phenotypic		Additive		h ²	
	Var.	SE	Var.	SE	Est.	SE
C	669.8	14.2	80.1	28.0	0.12	0.04
D	535.4	43.5	217.8	123.4	0.41	0.21
G	465.7	22.3	25.4	36.3	0.05	0.08
L	562.7	11.2	41.9	19.3	0.07	0.03
M	578.2	8.7	155.8	24.3	0.27	0.04
N	599.3	19.5	61.1	34.3	0.10	0.06
P	691.6	26.6	253.1	76.9	0.37	0.10
S	634.0	18.4	131.4	46.7	0.21	0.07
U	601.3	10.7	222.2	31.3	0.37	0.05
USA	623.1	6.9	234.2	20.6	0.38	0.03

Table 3.17 Variance components of gain by region using a single-trait animal model.

Region	Phenotypic		Additive		h ²	
	Var.	SE	Var.	SE	Est.	SE
C	592.5	24.8	109.6	59.7	0.18	0.10
D	453.4	43.5	1.3	72.5	0.00	0.16
G	876.7	92.5	253.5	252.0	0.29	0.27
L	520.4	13.4	39.1	19.6	0.08	0.04
M	501.6	8.1	95.7	19.2	0.19	0.04
N	587.8	40.1	76.0	96.1	0.13	0.16
P	755.3	33.0	114.3	72.6	0.15	0.09
S	654.7	24.5	79.9	47.6	0.12	0.07
U	629.4	10.6	112.1	24.2	0.18	0.04
USA	575.1	6.0	99.1	14.6	0.17	0.02

Table 3.18 Variance components of birth weight and weaning weight analyzed in a two-trait animal model.

	C	D	G	L	M	N	P	S	U	USA
Pheno var.										
σ^2_{BW}	14.1	13.6	13.5	14.1	24.9	14.9	13.9	15.6	17.0	16.4
$\sigma^2_{BW, SE}$	0.3	1.1	0.6	0.3	0.1	0.6	0.5	0.5	0.3	0.2
$\sigma_{B,W}$	30.0	35.5	22.3	31.9	32.2	36.0	36.4	33.4	32.3	35.4
$\sigma_{B,W, SE}$	1.6	5.3	2.7	1.2	*	2.5	2.8	2.3	1.4	0.8
σ^2_{WW}	670.2	536.4	463.6	561.6	548.9	599.9	691.0	638.4	600.5	623.5
$\sigma^2_{WW, SE}$	14.2	43.7	21.8	10.4	*	19.6	26.5	18.9	10.6	6.9
Additive var.										
σ^2_{BW}	3.5	3.8	-0.2	0.0	0.5	4.0	4.1	5.1	7.8	7.1
$\sigma^2_{BW, SE}$	0.8	2.9	0.6	0.1	*	1.4	1.4	1.5	1.0	0.6
$\sigma_{B,W}$	4.0	18.5	-2.4	-2.5	-6.8	5.9	12.5	12.4	5.4	11.7
$\sigma_{B,W, SE}$	3.4	15.0	3.4	*	*	5.5	7.8	6.4	4.0	2.6
σ^2_{WW}	80.1	222.0	12.9	14.4	60.4	62.8	251.5	145.1	218.9	234.2
$\sigma^2_{WW, SE}$	28.0	124.3	31.1	*	*	34.9	76.5	48.7	30.8	20.5
Heritability										
h^2_{BW}	0.25	0.28	0.00	0.002	0.02	0.27	0.30	0.33	0.46	0.43
$h^2_{BW, SE}$	0.06	0.20	0.00	0.004	0.0001	0.09	0.09	0.09	0.05	0.03
h^2_{WW}	0.12	0.41	0.03	0.026	0.11	0.10	0.36	0.23	0.36	0.38
$h^2_{WW, SE}$	0.04	0.21	0.07	0.001	*	0.06	0.10	0.07	0.05	0.03
Correlation										
r_p	0.31	0.42	0.28	0.36	0.28	0.38	0.37	0.33	0.31	0.35
r_p, SE	0.01	0.05	0.03	0.01	0.0004	0.02	0.02	0.02	0.01	0.00
r_g	0.24	0.63	*	*	*	0.37	0.39	0.46	0.13	0.29
r_g, SE	0.20	0.32	*	*	*	0.27	0.20	0.18	0.10	0.05

*not estimable

Table 3.19 Variance components of weaning weight and gain analyzed in a two-trait animal model.

	C	D	G	L	M	N	P	S	U	USA
Pheno var.										
σ^2_w	673.4	535.9	465.7	563.5	577.0	599.0	685.4	633.3	598.0	621.0
$\sigma^2_{w, SE}$	14.6	43.6	22.2	11.4	8.5	19.4	25.2	18.4	10.4	6.7
$\sigma_{w,G}$	102.1	-22.2	81.6	50.2	51.6	39.9	66.0	-7.3	76.1	59.9
$\sigma_{w,G, SE}$	18.7	34.7	46.2	10.2	6.6	29.7	24.4	18.1	8.3	5.1
σ^2_{GN}	605.3	452.9	883.6	521.6	502.6	589.1	760.4	655.3	632.2	575.5
$\sigma^2_{GN, SE}$	26.6	43.3	94.3	13.5	8.1	40.9	32.8	24.6	10.6	5.9
Additive var.										
σ^2_w	96.4	220.3	25.2	45.6	151.5	59.4	227.3	129.7	210.0	226.9
$\sigma^2_{w, SE}$	30.7	123.7	35.9	20.3	23.8	33.4	70.6	46.3	29.9	20.2
$\sigma_{w,G}$	85.0	-51.7	-45.1	14.6	32.5	-46.8	173.0	28.1	69.7	49.3
$\sigma_{w,G, SE}$	35.7	71.9	79.3	15.1	15.8	40.4	57.6	35.4	20.3	13.2
σ^2_G	159.5	-4.1	271.1	42.4	96.3	77.7	127.8	81.8	117.1	97.2
$\sigma^2_{G, SE}$	68.2	68.1	259.9	20.7	19.1	93.8	67.4	48.0	24.0	14.0
Heritability										
h^2_{ww}	0.14	0.41	0.05	0.08	0.26	0.10	0.33	0.20	0.35	0.37
$h^2_{ww, SE}$	0.04	0.21	0.08	0.04	0.04	0.05	0.09	0.07	0.05	0.03
h^2_{GN}	0.26	-0.01	0.31	0.08	0.19	0.13	0.17	0.12	0.19	0.17
$h^2_{GN, SE}$	0.11	0.15	0.28	0.04	0.04	0.16	0.09	0.07	0.04	0.02
Correlation										
r_p	0.16	-0.05	0.13	0.09	0.10	0.07	0.09	-0.01	0.12	0.10
$r_{p, SE}$	0.03	0.07	0.07	0.02	0.01	0.05	0.03	0.03	0.01	0.01
r_g	0.69	*	-0.55	0.33	0.27	-0.69	1.02	0.27	0.44	0.33
$r_{g, SE}$	0.19	*	0.99	0.31	0.12	0.61	0.19	0.33	0.11	0.08

*not estimable

Chapter 4

Stayability

Introduction

Reproductive fitness is important to a beef cattle enterprise. Females are expected to calve at the age of two, then breed back and remain productive for many years. They are exposed to a wide variety of climatic conditions within and across years. Fitness traits tend to be low in heritability and may be more likely to be affected by GxE compared to traits high in heritability. It may benefit producers if the reproductive genetic analysis was regional to identify animals more adaptive to local conditions.

Heritability estimates tend to be low and selection for these traits would result in limited genetic improvement. In addition, some traits, such as heifer pregnancy and stayability are recorded as binary data instead of continuous data. The analysis of “0” and “1” is often done using a probit model.

The objective of the present study was to evaluate the genetic parameters for stayability using a single-trait animal model using the entire Red Angus dataset and subsets of each region.

Materials and Methods

Field data from an existing database were used and thus Animal Care and Use Committee approval was not required.

Stayability has been defined as the probability of having a calf at some age after six, given that the female had a calf at age two. To increase the number of records, in this analysis stayability was defined as the probability of having a calf at age four, given that the female had a calf at age two. In addition, this younger age requirement could potentially reduce the concern

that culling for non-reproductive reasons had occurred (Brigham et al., 2007). The females used for this analysis met the following requirements;

1. The females were born between 1/1/1993 and 6/30/2004
2. Their calves were born in the appropriate age range (Table 4.1)
3. Calves were born in the same season of birth as the dam
4. Dams could not skip to another season
5. The owner and the breeder were in the same region
6. The calving interval was greater than 280 and less than 425 days (14 months)
7. The calves were born when the dam was greater than 670 (22 months) and less than 1520 days (4.16 years) of age
8. All sires were known, were 365 days of age at the time of conception and had qualifying daughters in more than one region.

Contemporary groups were defined as females born in the same herd in the same season of the same year (HYS). Each HYS had at least five females with at least two sires represented and in which those sires had daughters in at least one other region.

In this dataset, 365,133 calves were born to 115,408 females. After applying the requirements above, only 22,735 females were eligible for the analysis when using the traditional definition (6 yrs of age).

Bingham et al. (2009) showed the correlation of calving at different ages to improve accuracy of sire selection at younger ages. Anecdotally, most of the reproductive failure occurred when the females were two or three years of age (trying to conceive for the second and third calf). Therefore, this analysis used females old enough to have three calves instead of five calves, which increased the number of females over 27% to 28,985 females.

Two methods of transforming binary data are a probit and logit functions (Mrode, 2005). The probit model assumes errors follow the standard normal distribution as opposed to the logit model, where errors are assumed to follow the standard logistic probability distribution. The result is the cumulative density function of the probit is steeper in the middle compared to the standard logistic distribution and more quickly approaches zero on the left and one on the right. Convergence failed when the EPD analysis was conducted using the probit threshold model. A logit model replaced the probit model.

Variance components were estimated by fitting residual maximum likelihood linear animal models with the logit option for categorical data. Animal models were preferred over sire models due to more reliable solutions (Snelling et al., 1995). These were estimated for the stayability benchmark of 4 yrs of age. Dams were required to be at least as old as the defined benchmark to receive a stayability observation for a given endpoint and were required to have calved on an annual basis within a 60-d time period of the previous calving. A favorable designation (1) was given to dams that met these criteria (SUCCESS) and an unfavorable designation (0) was given to dams that did not meet these criteria (FAILURE). A chi-square test (PROC FREQ) was used to determine if the proportions of SUCCESSES were different between regions. A logit model (PROC GENMOD) was used to compare the proportions of SUCCESSES by region.

Stayability was analyzed as a univariate on the underlying scale using the model

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

in which \mathbf{y} was the vector of transformed observations on the underlying scale, \mathbf{X} was a known design matrix relating fixed effects to those individuals in vector \mathbf{y} . The only fixed effect included was the stayability contemporary group contained in vector $\boldsymbol{\beta}$. \mathbf{Z} was the design matrix

relating the random additive genetic effects in \mathbf{u} to the individuals in vector \mathbf{y} , and \mathbf{e} was a vector of random residual errors.

In addition,

$$\mathit{var}\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} \sigma_a^2 \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \sigma_e^2 \mathbf{I} \end{bmatrix}$$

in which \mathbf{A} was Wright's additive numerator relationship matrix, \mathbf{I} was an identity matrix with order equal to the number of observations in \mathbf{Y} . The additive and residual variances were σ_a^2 and σ_e^2 , respectively. The residual variances (σ_e^2) were forced to be equal to 1.

Results and Discussion

Females in the hotter, more Southern regions had reduced stayability compared to the more Northern regions (Table 4.2). Less than 40% of females were still in production in regions D and G at the age of four (had 3 calves) and greater than 55% of the females were still in production in regions C, M, N and U. These frequencies were similar compared to Snelling et al. (1995), who found frequencies of 75 and 39%, respectively, for a Red Angus herd and 79 and 38%, respectively, for a black Angus herd, for females who had 2 and 5 calves, respectively, given she had calved once. Similarly, Martinez et al. (2005) found 53% of Herefords had weaned three calves, given that she had weaned one calf.

The distribution of observations is shown in Figure 4.1. Regions M and U have the majority of the observations (60.5%). Comparisons of region SUCCESS (Table 4.3) showed all regions to be different (P-value <0.05) except C to M, C to N, C to U, L to P, M to N, and N to U. These regions, except L, are located in the northern half of the USA and may offer some guidance for clustering regions for further analysis. The northern regions (C, M, N and U) appear to be more similar to each other whereas G, D, and S are not only different from the northern regions, but different from each other. Regions L and P appear to be intermediate and may

form a unique cluster. Interestingly, the northern regions appear to be similar from the Northeast to the Mountains, but that does not appear to be true for southern regions. Females in regions G, D, L and S may be exposed to environmental extremes which warrant further study. Extremes in humidity and forages between the southern regions may be important to explaining differences in SUCCESS. Regions D and G in particular, and S and L to a lesser extent, are plagued by a small number of observations, which may limit the ability to fully explain these differences.

The heritability of SUCCESS on the underlying scale for the national dataset was 0.23 (Table 4.4). Within region h^2 ranged from lows of 0.08 and 0.09 in regions L and M, respectively, to highs of 0.34 and 0.40 in regions U and C, respectively. Overall, h^2 were greater in this analysis compared to Snelling et al. (1995) and Doyle et al. (2000), but similar to those by Van Melis et al. (2007) and Martinez et al. (2005). These were higher compared to those of Snelling et al. (1995) who calculated a within herd stayability using a single-trait animal model. Those estimates were 0.09, 0.10, 0.07 and 0.20 for stayability on the underlying scale defined as having 2, 5, 8 and 11 calves, respectively, given the females had calved at the age of 2 in a Red Angus herd.

The Pearson correlation (Table 4.5) of the mean of SUCCESS to the reaction norm for each sire was -0.196 (p -value<0.05) and suggest daughters of higher genetic merit sires may be less sensitive to environmental challenges. The distribution of SUCCESS reaction norms ranged from -16 to 19 (Figure 4.2) and is similar to the distribution of SUCCESS reaction norms of the most heavily used bulls, which ranged from -14 to 19 (Figure 4.3). The distribution of SUCCESS EPDs ranged from -7 to 9 (Figure 4.4). The distribution of reaction norms and EPDs were calculated from 303 sires and the range is larger than expected. These results were produced from a very unbalanced dataset, in which most of the female records were produced in two

regions (M and U). Given the economic importance of stayability, a more in-depth study is justified.

Table 4.1. Age at calving and calf requirements.

Age of dam, yrs	Age at calving, days		
	Min	Max	Required calves
2	670	790	1
3	1035	1155	2
4	1400	1520	3
5	1765	1885	4
6	2130	2250	5

Table 4.2. Count of stayability to age four by region

Region	Success	N	Percent
C	0	1432	43.3
C	1	1872	56.7
D	0	239	60.1
D	1	159	39.9
G	0	235	67.1
G	1	115	32.9
L	0	1228	48.9
L	1	1282	51.1
M	0	4638	43.9
M	1	5929	56.1
N	0	611	43.0
N	1	810	57.0
P	0	651	48.6
P	1	690	51.4
S	0	1104	52.2
S	1	1010	47.8
U	0	2897	41.5
U	1	4083	58.5
Total	0	13035	45.0
Total	1	15950	55.0

Failure=0

Success=1

P-value <0.0001

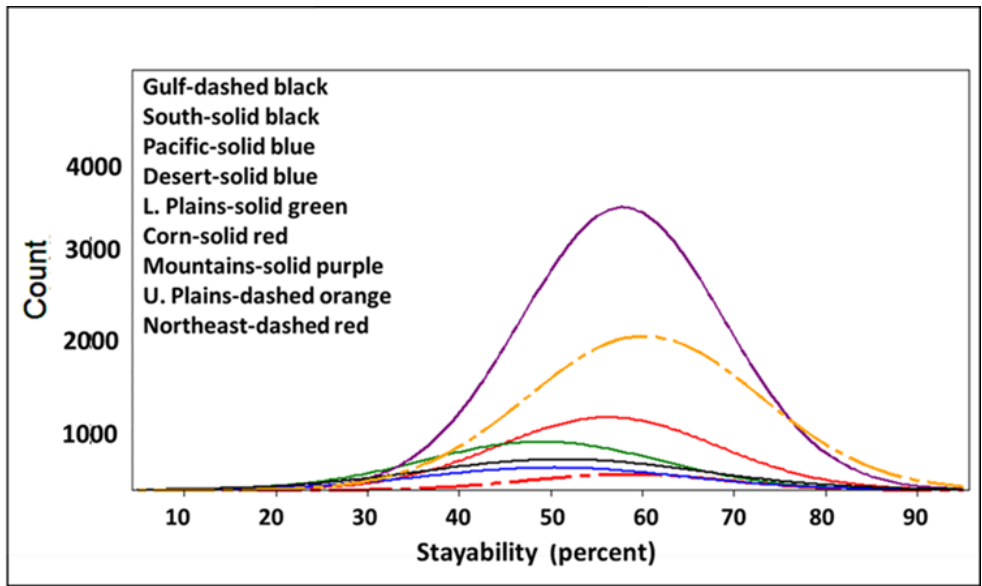


Figure 4.1. Distribution of stayability by region

Table 4.3 Comparison of SUCCESS differences by region.

Region		Est	SE	P-value	Upper	Lower
C	D	0.68	0.11	<.0001	0.46	0.89
C	G	0.98	0.12	<.0001	0.75	1.22
C	L	0.22	0.05	<.0001	0.12	0.33
C	M	0.02	0.04	0.5781	-0.06	0.10
C	N	-0.01	0.06	0.827	-0.14	0.11
C	P	0.21	0.06	0.0012	0.08	0.34
C	S	0.36	0.06	<.0001	0.25	0.47
C	U	-0.08	0.04	0.0781	-0.16	0.01
D	G	0.31	0.15	0.0448	0.01	0.61
D	L	-0.45	0.11	<.0001	-0.67	-0.24
D	M	-0.65	0.10	<.0001	-0.86	-0.45
D	N	-0.69	0.12	<.0001	-0.92	-0.46
D	P	-0.47	0.12	<.0001	-0.69	-0.24
D	S	-0.32	0.11	0.0042	-0.54	-0.10
D	U	-0.75	0.11	<.0001	-0.96	-0.54
G	L	-0.76	0.12	<.0001	-0.99	-0.52
G	M	-0.96	0.12	<.0001	-1.19	-0.73
G	N	-1.00	0.13	<.0001	-1.24	-0.75
G	P	-0.77	0.13	<.0001	-1.02	-0.53
G	S	-0.63	0.12	<.0001	-0.86	-0.39
G	U	-1.06	0.12	<.0001	-1.29	-0.83
L	M	-0.20	0.04	<.0001	-0.29	-0.12
L	N	-0.24	0.07	0.0004	-0.37	-0.11
L	P	-0.02	0.07	0.8229	-0.15	0.12
L	S	0.13	0.06	0.0254	0.02	0.25
L	U	-0.30	0.05	<.0001	-0.39	-0.21
M	N	-0.04	0.06	0.5239	-0.15	0.08
M	P	0.19	0.06	0.0012	0.07	0.30
M	S	0.33	0.05	<.0001	0.24	0.43
M	U	-0.10	0.03	0.0018	-0.16	-0.04
N	P	0.22	0.08	0.0035	0.07	0.37
N	S	0.37	0.07	<.0001	0.24	0.51
N	U	-0.06	0.06	0.2981	-0.18	0.05
P	S	0.15	0.07	0.0352	0.01	0.28
P	U	-0.29	0.06	<.0001	-0.40	-0.17
S	U	-0.43	0.05	<.0001	-0.53	-0.33

Table 4.4. Heritability of Success by region.

Region	Additive		Phen Var	h ²
	Variance	SE		
C	1.66	0.37	5.0	0.34
D	0.71	0.11	4.0	0.18
G	0.77	0.09	4.1	0.19
L	0.28	0.28	3.6	0.08
M	0.33	0.33	3.6	0.09
N	1.26	0.24	4.5	0.28
P	1.43	0.64	4.7	0.30
S	1.50	0.23	4.8	0.31
U	2.22	1.04	5.5	0.40
USA	0.96	0.07	4.3	0.23

Table 4.5. Pearson correlation of progeny mean to the reaction norm

Variable	N	Mean	StdDev	Minimum	Maximum
Progeny mean	303	0.52	0.16	0.00	1.00
Reaction norm	303	0.76	4.49	-15.51	19.10

r = -0.196

p-value = <0.05

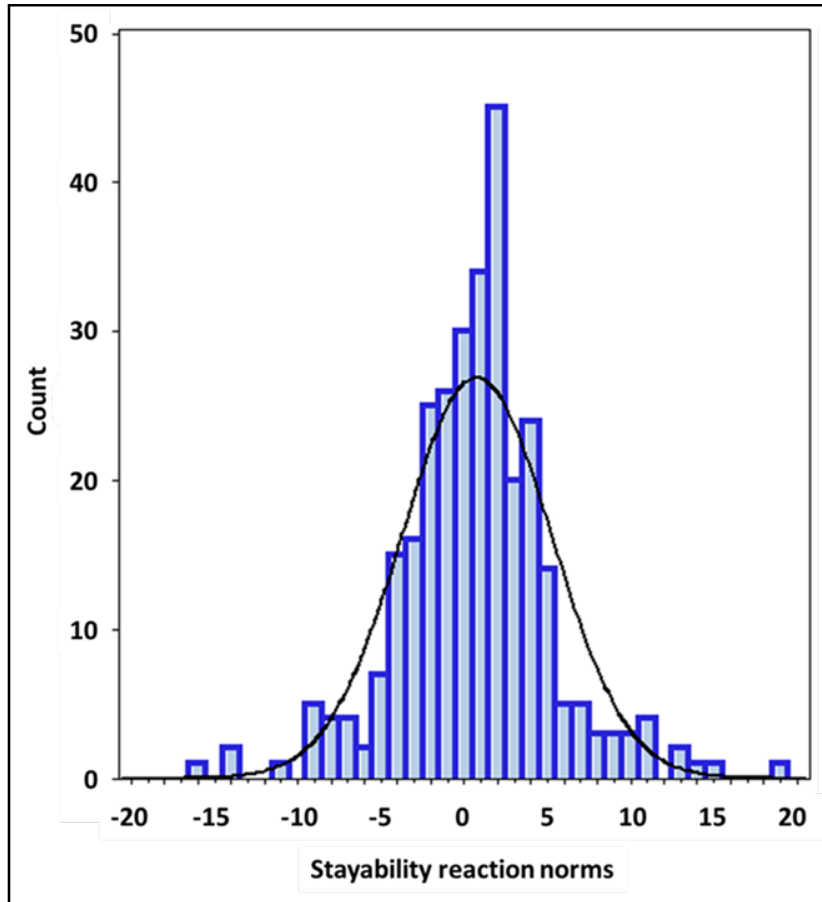


Figure 4.2. Observed and theoretical distribution of stayability reaction norms

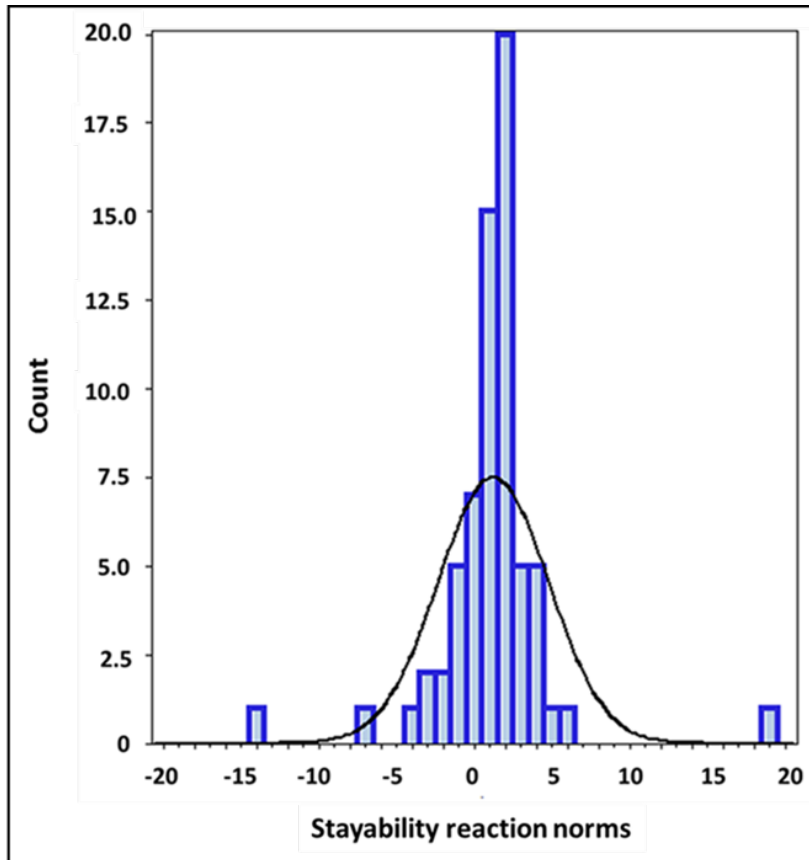


Figure 4.3. Observed and theoretical distribution of stayability reaction norms of most heavily used bulls

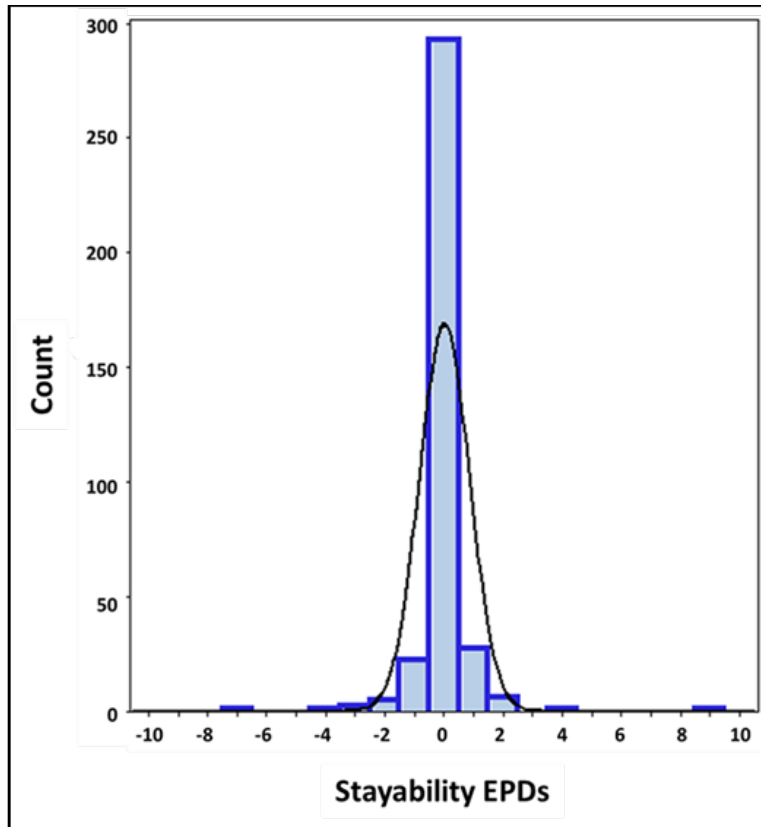


Figure 4.4. Observed and theoretical distribution of stayability EPDs

Chapter 5

IMPLICATIONS

There are several ways to address GxE, which include computing the EPD for the trait, then providing an adjustment factor for specific regions to be applied by producers in those regions. A second method is to compute EPDs as required by region and a third method is to provide reaction norm EPDs. Reaction norm EPDs are highly heritable in this study as well as previous studies. Advantages are that every bull could have a reaction norm EPD for every trait without changing the current EPD analysis provided by the breed associations. Producers in harsher environments may be able to select bulls that are more stable and whose progeny are much more productive. Producers in the “best” environments could take advantage of bulls that produce better than their EPDs for that trait suggests. Disadvantages include the education of producers, the proper division of environments and providing more information that may not be needed by the majority of producers. The issue of proper division of environments is important and has not been fully resolved.

The most heavily used bulls in the Red Angus breed (Table 5.1) illustrate the opportunity for producers to select sires that provide more stability (flatter reaction norm) for harsher environments and sires that may excel in better, more climatically stable environments (steeper reaction norm). Each of these bulls produced $\geq 1,000$ calves and, except for bull 14, ≥ 300 daughters in this dataset. Three of these bulls are carriers of a known genetic defect which may influence stability EPDs and thus stayability reaction norms. This is not necessarily a problem as producers may avoid these bulls entirely or mate them to unrelated females.

Breed associations may want to pursue genetic evaluations in the form of reaction norms and education of producers to exploit this information.

Table 5.1 Reaction norms of selected sires

Sire	Reaction Norms			
	BW	WW	GN	STAY
1	0.2	0.8	1.0	3.3
2	1.1	0.2	1.9	1.6
3	0.9	0.9	0.6	1.8
4	1.0	1.0	0.7	0.2
5	0.8	1.2	1.6	0.9
6	1.1	1.3	1.5	1.1
7	0.5	0.8	1.1	1.0
8	1.5	1.7	1.5	2.3
9	1.4	1.4	1.1	1.2
10	0.9	1.2	1.6	1.6
11	1.6	1.4	1.4	1.1
12	1.0	1.1	1.5	2.0
13	1.2	1.0	1.5	0.8
14	0.9	1.6	0.6	NA
15	1.4	1.0	1.0	2.0

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