

Genetic Heterogeneity of Residual Variance for Production and Functional Traits in
American Angus Cattle

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ABSTRACT

Beef cattle are continuously selected for different traits and the success in improving these traits has been remarkable. However, for certain traits, it is essential not only to improve the average performance, but also to control the variation around the mean. There is evidence that residual variance may be under genetic control, which opens the possibility of selecting for uniformity. In this sense, the objectives of the present dissertation were: 1) to investigate the extent of genetic heterogeneity of residual variance at the pedigree level in birth weight (BW), weaning weight (WW), yearling weight (YW), foot angle (FA), and claw set (CS) in American Angus cattle; 2) to compare the results of different genetic heterogeneity models; 3) to evaluate the effectiveness of Box-Cox transformation in continuous traits; and 4) to address limitations and explore alternative solutions for implementing genetic parameters for residual variance in genetic evaluations. The first study investigated the genetic heterogeneity of residual variances for BW, WW, and YW. Three models were compared: a homoscedastic residual variance model (M1), a double hierarchical generalized linear model (DHGLM, M2), and a genetically structured environmental variance model (MCMC, M3). The results showed significant genetic heterogeneity of residual variances in growth traits, suggesting the possibility of selection for uniformity. The genetic coefficient of variation for residual variance ranged from 0.90 to 0.92 in M2 and 0.31 to 0.38 in M3 for BW, 0.64 in M2 and

0.01 to 0.29 in M3 for WW, and 0.67 to 0.63 in M2 and 0.25 to 0.31 in M3 for YW. Low heritability estimates for residual variance were found, particularly in M2 (0.08 for BW, 0.06 for WW, and 0.09 for YW). The study identified both negative and positive genetic correlations between mean and residual variance, depending on the trait and data transformation. Negative correlations suggest the potential to increase trait means while decreasing residual variance. However, positive correlations indicate that the genetic response to selection for uniformity may be limited unless a selection index is used. Data transformation reduced skewness but did not eliminate genetic heterogeneity of residual variances. The Bayesian approach provided higher estimates of additive genetic variance for residual variance compared to DHGLM. Overall, the findings indicate the potential to reduce variability through selection and lay the groundwork for incorporating uniformity of growth traits into breeding goals. The second study focused on the genetic heterogeneity of residual variance for two foot conformation traits, FA and CS. Using 45,667 phenotypic records collected between 2009 and 2021, three models were compared: a traditional homoscedastic residual variance model (M1), a DHGLM (M2), and a genetically structured environmental variance model (M3). Results showed that heritability estimates for FA and CS means were within expected ranges, although lower in M2. Despite low heritability estimates for residual variance (0.07 for FA and 0.05 for CS in M2), significant genetic coefficients of variation were found, suggesting that selection on trait mean would also influence residual variance. Positive genetic correlations between mean and residual variance in M2 and M3 indicate that selection for uniformity is feasible, but may require additional strategies such as selection indices. The study highlights the potential of FA and CS as indicators for breeding programs aimed at

improving production uniformity in beef cattle. Our findings suggest that selection for uniformity in growth and foot score traits in beef cattle may be limited by low heritability of residual variance and moderate to high positive genetic correlations between mean and residual variance. This was observed for most of the traits studied. To overcome these challenges, further research is needed, particularly to explore genomic information to improve the prediction accuracy of estimated breeding values (EBV) for residual variance. Although studies of uniformity using genomic data are limited, they have shown improved EBV accuracy for residual variance. Additionally, alternative methods for measuring uniformity, such as different uniformity or resilience indicators, should be considered, especially with advances in digital phenotyping. Precision livestock farming technologies that allow for extensive data collection on various production traits should be integrated into the development of new uniformity indicators. This dissertation provides valuable insights into the genetic heterogeneity of residual variance in American Angus cattle and highlights the complexity of selecting for uniformity while improving mean traits. Continued research with larger data sets, genomic information, and further methodological refinement will be critical to advance these findings to improve uniformity and productivity in beef cattle breeding.

Genetic Heterogeneity of Residual Variance for Production and Functional Traits in American Angus Cattle

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GENERAL AUDIENCE ABSTRACT

Uniformity in livestock breeding refers to the goal of reducing variability in certain traits within a livestock population to achieve more consistent and predictable outcomes. This is particularly important for traits that affect productivity, economic efficiency, animal welfare, and product quality. By achieving greater uniformity, producers can optimize management practices, improve marketability, and enhance the overall efficiency of animal production systems. Residual variance refers to the variation in traits that is not explained by known genetic or environmental factors. Recent research suggests that residual variance may be under genetic control, meaning that it is possible to select animals that not only have desirable traits, but also have less variability in those traits. Therefore, this dissertation investigates the genetic control of residual variance that may allow selection for uniformity in traits. The research focused on American Angus cattle and aimed to 1) investigate genetic heterogeneity of residual variance in traits, such as birth weight, weaning weight, yearling weight, foot angle, and claw set; 2) compare different genetic models; 3) evaluate the effectiveness of data transformations; and 4) address limitations in genetic evaluations. The first study examined genetic heterogeneity in growth traits using three models. It revealed significant genetic variability, suggesting the potential for selection for uniformity. The study found both positive and negative genetic correlations between trait means and residual variance, indicating varying

potential for reducing variance while improving trait means. Data transformations reduced skewness but did not eliminate genetic heterogeneity. A Bayesian approach provided higher estimates of genetic variance than other methods. The second study focused on foot conformation traits with over 45,000 records. The study showed that despite low heritability for residual variance, there was significant genetic variation, indicating the possibility of altering residual variance through selection. Positive genetic correlations suggested that additional strategies, such as selection indices, may be needed to achieve uniformity in practice. Overall, the findings highlight the complexity of selecting for uniformity while improving average traits and underscore the need for further research, particularly using genomic data, to improve prediction accuracy. Integrating precision livestock farming technologies could help develop new indicators of uniformity, improving productivity and uniformity in beef cattle breeding.

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Chapter 1: INTRODUCTION

The United States plays a significant role in the global beef market, being one of the largest exporters and importers. According to the United States Department of Agriculture (USDA, 2021), the country is the second-largest beef exporter and the second-largest beef importer in the world. The cattle industry accounts for approximately 18% of agricultural commodity receipts, and beyond its economic importance, the beef cattle industry is highly complex, diverse, and dynamic.

In many ways, the beef industry has evolved significantly over time. Several factors have directly improved productivity indices, such as nutrition, welfare, health management, and genetics. The role of breeding and genetics programs is to increase the frequency of favorable gene combinations for a set of traits related to a given production system, resulting in increased economic efficiency. This efficiency is determined, in part, by the relative emphasis on the traits included as selection objectives (Bourdon, 2014). Selection objectives are a combination of economically important traits, accounting for all traits that influence profits and expenses. After defining the selection objectives, breeding programs choose which traits to use to predict the genetic values of individuals. The traits considered in the selection objectives are the basis for formulating a profit function, from which the economic weights are derived, defined as the additional economic return per unit of improvement in the trait (Smith, 1983; Bourdon, 2014).

Historically, most breeding programs have focused on growth traits, particularly weaning and yearling weights (Middleton and Gibb, 1991; Herring, 2014; Hozáková et al., 2020), but more recently, new phenotypes have been developed for longevity,

structural soundness, reproduction, and sustainability traits (Mateescu, 2020; Pérez-Enciso and Steibel, 2021; Terry et al., 2021). However, factors such as global population growth, increasing consumer demand for specialized beef markets, rising production costs, and varying environmental conditions underscore the critical role of genetics in ensuring uniform products for the market. A practical example is the bonus programs implemented by several slaughterhouses around the world to incentivize farmers to produce carcasses that meet specific standards for slaughter weight and fat deposition. These bonus programs have driven the industry to strive for more uniform animals, primarily through sire selection as males are subject to more intense selection in cattle breeding and produce significantly more offspring than females (Mateescu, 2020).

Uniformity is essential to ensure consistency throughout the production chain and to avoid economic losses. Breeding strategies, such as mating systems (inbreeding, positive assortative mating) and selection, have a significant impact on trait variability within animal populations (Hohenboken, 1985). For example, directional selection has been widely used in industry, resulting in a noticeable change in the mean value of traits over time, such as increased weights. However, improving only the mean of these traits can also increase phenotypic variability. Recent studies in plant and animal species (reviewed in Hill and Mulder, 2010; Iung et al., 2020) have provided evidence for genetic control of residual variance (also known as genetic heterogeneity of residual variance or micro-environmental sensitivity). These studies have shown that different genotypes respond differently to environmental variation, resulting in genetic differences in residual variance.

The overall profitability of beef cattle herds is a function of animal outputs (weights at different stages of life such as birth, weaning, yearling, or after slaughter such as carcass weight) and input costs (labor, culling, land, feed, veterinary costs, etc.). In this sense, genetic studies on genetic heterogeneity of residual variance are a promising tool to investigate the extent of the genetic component influencing the variability of economically important phenotypes and to develop strategies to manage variation and improve uniformity in beef cattle breeding programs. Despite the importance of uniformity as a breeding goal, research on the genetic heterogeneity of residual variance in growth and conformation traits remains scarce in livestock species. The overall objective of this research is to investigate the extent of genetic heterogeneity of residual variance at the pedigree level in growth and functional traits of American Angus cattle and to discuss the applicability of our findings to beef cattle breeding programs for improving uniformity. To accomplish this overarching objective, the following specific objectives were established:

I. Compare the results of different genetic heterogeneity models for birth weight, weaning weight, yearling weight, foot angle, and claw set.

II. Evaluate the effectiveness of data transformation and identify potential scaling effects.

III. Address limitations and explore alternative solutions for implementing genetic parameters for residual variance in genetic evaluations.

BIBLIOGRAPHY

- Bourdon, R. M. 2014. Understanding Animal Breeding. Pearson. Available from: www.pearsoned.co.uk
- Herring, A. D. . 1965-. 2014. Beef cattle production systems. CAB International, Wallingford, Oxfordshire :
- Hill, W. G., and H. A. Mulder. 2010. Genetic analysis of environmental variation. Genet. Res. (Camb). 92:381–395. doi:10.1017/S0016672310000546.
- Hohenboken, W. D. 1985. The Manipulation of Variation in Quantitative Traits: A Review of Possible Genetic Strategies. J. Anim. Sci. 60:101–110. doi:10.2527/JAS1985.601101X.
- Hozáková, K., K. Vavrišínová, P. Neirurerová, and J. Bujko. 2020. Growth of beef cattle as prediction for meat production: A review. Acta Fytotech. Zootech. 23:58–69. doi:10.15414/AFZ.2020.23.02.58-69.
- Iung, L. H. de S., R. Carneiro, H. H. de R. Neves, and H. A. Mulder. 2020. Genetics and genomics of uniformity and resilience in livestock and aquaculture species: A review. J. Anim. Breed. Genet. 137:263–280. doi:10.1111/JBG.12454.
- Mateescu, R. G. 2020. Genetics and breeding of beef cattle. Anim. Agric. Sustain. Challenges Innov. 21–35. doi:10.1016/B978-0-12-817052-6.00002-1.
- Middleton, B. K., and J. B. Gibb. 1991. An overview of beef cattle improvement programs in the United States. J. Anim. Sci. 69:3861–3871. doi:10.2527/1991.6993861X.
- Pérez-Enciso, M., and J. P. Steibel. 2021. Phenomes: the current frontier in animal breeding. Genet. Sel. Evol. 53:1–10. doi:10.1186/S12711-021-00618-1/FIGURES/4.
- Smith, C. 1983. Effects of Changes in Economic Weights on the Efficiency of Index Selection. J. Anim. Sci. 56:1057–1064. doi:10.2527/jas1983.5651057x.
- Terry, S. A., J. A. Basarab, L. L. Guan, and T. A. McAllister. 2021. Strategies to improve the efficiency of beef cattle production. Can. J. Anim. Sci. 101:1–19. doi:10.1139/CJAS-2020-0022/ASSET/IMAGES/LARGE/CJAS-2020-0022F3.JPEG.
- USDA. 2021. 2021 United States Agricultural Export Yearbook. Available from: <https://apps.fas.usda.gov/gats/>.

Chapter 2: LITERATURE REVIEW

Variation in Animal Production

Understanding the factors that determine phenotypes has always been of interest to biologists, geneticists, and plant and animal breeders. Variability is not only essential for evolutionary processes, but also underpins the basis for breeding programs in livestock. In animal production, the lack of homogeneity in the production chain can lead to economic losses.

For example, in pig production, inconsistent birth weight can result in competition for food and increased mortality from birth to weaning (Milligan et al., 2002; Pardo et al., 2013). Similarly, in cattle, low birth weight and high birth weight are both significant concerns for cattle producers (Price and Wiltbank, 1978; Hickson et al., 2006; Mee, 2008). Low birth weight calves are often weaker, have lower survival rates immediately after birth, and are more susceptible to disease and environmental stress. Even if they survive the neonatal period, these calves will have reduced productivity in subsequent periods, whether as beef-producing steers/heifers or as breeding stock. On the other hand, high birth weight calves are a leading cause of dystocia. Dystocia can result in increased labor and veterinary costs and, in severe cases, may require cesarean section or result in death of the calf, dam, or both animals, resulting in increased production costs and potential economic loss due to the potential loss of animals (Price and Wiltbank, 1978).

In terms of final products, the poultry industry seeks uniformity in egg production to ensure efficient processing, grading, and marketing (Wilson, 1991; Wolc et al., 2012). The variation in egg size can affect the grading and packing process (Zeidler, 2002; Abiola et al., 2008). These processes are automated, which means that eggs are sorted primarily by weight. High variability means that the machine must be adjusted

frequently, slowing down the production process. Additionally, packaging lines are optimized for uniform products, and eggs of different sizes can lead to packaging mishaps, such as cracked eggs, which affect producer payments and potential food waste.

Breeding strategies play an important role in influencing trait variability within animal populations. Hohenboken (1985) listed several types of breeding strategies that can reduce phenotypic variability. Mating systems, such as inbreeding, which refers to the mating of closely related individuals over time, increase the proportion of homozygous loci in the population, reducing genetic variability for certain traits and making the population more uniform for those traits (Howard et al., 2017). Similarly, positive assortative mating (mating individuals based on the presence of similar phenotypes or genotypes for a given trait) can reduce variability in target traits, making the population more uniform (Hohenboken, 1985).

In addition to mating systems, selection plays an important role in reducing trait variability. For example, stabilizing (normalizing) selection reduces variability by eliminating or reducing the frequency of extreme phenotypes. Over time, the trait becomes more uniform and its distribution tends to narrow around the mean, preserving the average characteristics of a population by eliminating outliers (Wellmann, 2023). Directional selection favors phenotypic extremes at one end of a distribution over other individuals. Directional selection over successive generations will make the population more homogenous with respect to that trait in the selected direction and can cause a noticeable shift in the mean value of the trait (Hill and Zhang, 2004). Lastly, canalizing selection aims to minimize phenotypic variance despite potential genetic or environmental challenges, meaning that the trait becomes stable and shows little

variability. Such traits are beneficial in production environments where consistency is key and conditions can vary (Sancristobal-Gaudy et al., 1998).

Genetic progress in livestock production systems requires accurate genetic evaluation of animals followed by selection of the "best" individuals as parents of the next generation. Genetic evaluations often use best linear unbiased prediction (BLUP) and mixed model methods. Although substantial genetic progress is achieved with these statistical approaches, the genetic progress achieved is not equal to what is theoretically possible. One possible reason is that the theoretical assumption of homogeneity of residual variance may not always be valid.

Despite the common assumption of homogeneous residual variance in quantitative genetic models, previous studies suggest that not all sources of variance affect phenotypes to the same extent (Clay et al., 1979; Ros et al., 2004; Hill and Mulder, 2010; Iung et al., 2020). This assumption is made primarily for analytical convenience, as models that assume homogeneous variance are simpler and less computationally demanding than more complex models that account for variance heterogeneity in the residual variance.

Economic incentives are a driver for more uniform animal production, encouraging breeders to seek alternatives to maintain uniformity, which can have a significant impact on profitability and operational efficiency. However, selection for uniformity requires the presence of an associated heritable genetic component. Numerous studies in plant and animal species (Hill and Mulder, 2010; Iung et al., 2020) support the idea that residual variance is under genetic control, which can be used to potentially improve uniformity in beef cattle. Unraveling the genetic and genomic basis of residual

variance through quantitative and genomic analysis can lead to improved methods for increasing production uniformity, provide insight into the underlying biology of traits, and potentially provide increased selection response through increased accuracy of estimated breeding values for residual variance.

QUANTITATIVE GENETIC MODELS TO EVALUATE VARIANCE HETEROGENEITY

Traditional quantitative genetic models usually assume that residual variance is constant, i.e., genotypes differ only in mean effect (Falconer and Mackay, 1996).

However, given evidence that residual variance may also be under genetic control, new models and methods have been developed to account for genotypic differences in residual variance.

Two extensions of the classical quantitative genetic model have been proposed. The first model, referred to as the additive model (Hill and Zhang, 2004; Mulder et al., 2007), assumes that the genetic component for variance is modeled as an additive effect on the environmental variance:

$$y = \mu + A_m + \chi\sqrt{\sigma_e^2 + A_v}$$

where μ is the trait mean; A_m is the additive genetic effects for the mean; χ is a standard normal deviate $N(0,1)$ for the environmental effect; σ_e^2 is the population mean residual (environmental) variance; and A_v is the additive genetic effects for the residual variance.

The second model, referred to as the exponential model (Sancristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003; Ros et al., 2004), assumes an exponential distribution for the residual variance as follows:

$$y = \mu + A_m + \chi \exp\left(\frac{1}{2} \ln(\sigma_{E,\exp}^2) + A_{v,\exp}\right)$$

where $\ln(\sigma_{E,\exp}^2)$ is the natural logarithm of the residual variance and $A_{v,\exp}$ is the additive genetic effect for the residual variance.

The use of the log scale to represent variances is useful because as sample sizes increase, the log of these variances tends to follow a normal distribution. This concept led to the development of the most commonly used models for genetic heterogeneity. These models use an estimate of the residual variance as the response variable and are primarily categorized into two main residual maximum likelihood (REML) methods: the two-step approach and the double hierarchical generalized linear model (DHGLM).

Two-Step Approach

The two-step approach was first introduced by Rowe et al. (2006) in their study of broiler body weight. In their study, the residual variance of broiler body weight was examined using the least squares method. First, body weight was fitted to a linear model (referred to as the mean model) that accounted for heterogeneous residual variances across sire families. In the next step (the residual variance model), these residual variance estimates underwent a log-natural transformation and were treated as the phenotype. To account for both genetic and environmental effects on the residual variance for individual records, Mulder et al. (2009) proposed an extended version of this method. In this revised two-step approach, the natural logarithm of the squared estimated residuals ($\ln(\hat{\epsilon}^2)$)

served as the response variable in the second step, rather than using a measure per family.

These estimated residuals were derived from the mean model. The mean and residual variance models used in the two-step method are illustrated as follows:

Step 1 (Mean Model):

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

Step 2 (Residual Variance Model):

$$\ln(\hat{\mathbf{e}}^2) = \mathbf{X}\mathbf{b}_v + \mathbf{Z}\mathbf{a}_v + \mathbf{e}_v$$

where $\mathbf{y}$ is the response variable for the mean model; $\ln(\hat{\mathbf{e}}^2)$ is the response variable for the residual variance model; $\mathbf{X}\mathbf{b}$ is the fixed effects for the mean model; $\mathbf{X}\mathbf{b}_v$ is the fixed effect for the residual variance model; $\mathbf{Z}\mathbf{a}$ and $\mathbf{Z}\mathbf{a}_v$ are the random effects for the mean and residual variance models, respectively; $\mathbf{e}$ is a vector of residual effects for the mean; and $\mathbf{e}_v$ is a vector of residual effects for the residual variance model.

In **Step 1**, either homogeneous or heterogeneous residual variance among families can be assumed, allowing for heterogeneity of the residual variance. To deal with the skewed or non-uniform distribution of the squared residuals, a log transformation is applied to overcome the asymmetry in the distribution. However, Rönnegard et al. (2013) showed that this approach can lead to biased estimates of variance components because it does not account for the uncertainty (or imprecision) of the estimated residuals.

Double Hierarchical Generalized Linear Model (DHGLM)

A more recent method for investigating genetic heterogeneity of residual variance is based on generalized linear models proposed by Lee and Nelder (1996). DHGLM is designed to handle non-normal data by assuming a gamma distribution (a flexible

probability distribution often used to model positively skewed data) for the squared residuals. It is an iterative approach that addresses the non-normality issue by focusing on modeling the squared residuals rather than the raw data. During each iteration, the model fits the gamma distribution to the squared residuals and updates the parameter estimates (Rönnegård et al., 2010). Later, Felleki et al. (2012) extended the DHGLM approach by simultaneously fitting the trait (also referred to as the mean) and residual variance within a bivariate model as follows:

$$\begin{bmatrix} \mathbf{y} \\ \boldsymbol{\psi} \end{bmatrix} = \begin{bmatrix} \mathbf{X} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_v \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{b}_v \end{bmatrix} + \begin{bmatrix} \mathbf{Z} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_v \end{bmatrix} \begin{bmatrix} \mathbf{a} \\ \mathbf{a}_v \end{bmatrix} + \begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix}$$

where $\mathbf{y}$ represents the trait (or mean), $\boldsymbol{\psi}$ is the linearized response variable for the residual variance. $\boldsymbol{\psi}$ is defined as:

$$\psi_i = \log(\hat{\sigma}_{e_i}^2) + ([\hat{e}_i^2 / (1 - h_i)] - \hat{\sigma}_{e_i}^2) / \hat{\sigma}_{e_i}^2$$

where $\hat{\sigma}_{e_i}^2$ is the predicted residual variance for observation i from the previous iteration; $\hat{e}_i^2$ is the squared residual from the mean model estimated for observation i ; h_i is the leverage for observation i that is the i^{th} diagonal element of the hat matrix (Hoaglin and Welsch, 1978); $\mathbf{X}\mathbf{b}$ and $\mathbf{X}_v \mathbf{b}_v$ are fixed effects for the mean and residual variance, respectively; $\mathbf{Z}\mathbf{a}$ is the random effect for the mean; $\mathbf{Z}_v \mathbf{a}_v$ is the random effect for the variance; and $\mathbf{e}$ and $\mathbf{e}_v$ are the random residual effects for the mean and variance, respectively.

In this model, it is assumed that:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{a}_v \end{bmatrix} \sim N(0, \begin{bmatrix} \sigma_a^2 & \sigma_{a,a_v} \\ \sigma_{a,a_v} & \sigma_{a_v}^2 \end{bmatrix} \otimes \mathbf{A})$$

$$\begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix} \sim N(\mathbf{0}, \begin{bmatrix} \mathbf{W}^{-1}\sigma_e^2 & 0 \\ 0 & \mathbf{W}_v^{-1}\sigma_{e_v}^2 \end{bmatrix} \otimes \mathbf{I})$$

where $\mathbf{W} = \text{diag}(\hat{\boldsymbol{\Psi}}^{-1})$ and $\mathbf{W}_v = \text{diag}\left(\frac{1-h}{2}\right)$ consist of the residual variance per observation, since σ_e^2 and $\sigma_{e_v}^2$ are scaling variance that are expected to be equal to 1.

$\boldsymbol{\Psi}$, $\mathbf{W}$, and $\mathbf{W}_v$ are updated in each iteration until the algorithm converges (Felleki et al., 2012).

Genetically Structured Variance Models

An alternative approach to DHGLM is the use of Markov chain Monte Carlo (MCMC) in genetically structured variance models (also referred to as hierarchical Bayesian models) (Sorensen and Waagepetersen, 2003; Ibáñez-Escriche et al., 2008a). The method allows simultaneous estimation of genetic effects at the level of mean and residual variance, but is computationally expensive.

In this model, the sampling distribution of the data $\mathbf{y}$ is assumed to be Gaussian:

$$\mathbf{y} \mid \mathbf{b}, \mathbf{a}, \mathbf{p}, \mathbf{b}^*, \mathbf{a}^*, \mathbf{p}^* \sim N(\boldsymbol{\mu}, \text{diag}(\sigma_i^2)_{i=1}^n)$$

where $\text{diag}(\sigma_i^2)_{i=1}^n$ is the diagonal matrix with diagonal entries σ_i^2

$$\log(\sigma_i^2)_{i=1}^n = \mathbf{X}^* \mathbf{b}^* + \mathbf{Z}^* \mathbf{a}^* + \mathbf{W}^* \mathbf{p}^*$$

and

$$\boldsymbol{\mu} = (\mu_{i=1}^i) = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{p}$$

where $\mathbf{b}$ and $\mathbf{b}^*$ are vectors of systematic effects; $\mathbf{a}$ and $\mathbf{a}^*$ are the additive genetic effects; $\mathbf{p}$ and $\mathbf{p}^*$ are vectors containing other random effects such as permanent environmental effects; $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are known incidence matrices of parameters affecting the mean;

and $\mathbf{X}^*$, $\mathbf{Z}^*$ and $\mathbf{W}^*$ are the incidence matrices of parameters affecting the residual (environmental) variance.

The prior for the systematic effects $\mathbf{b}$ and $\mathbf{b}^*$ is a uniform distribution $\text{Unif}(-\infty, +\infty)$. For the additive genetic effects $\mathbf{a}$ and $\mathbf{a}^*$ the location parameters are assumed to be normally distributed:

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{a}^* \end{pmatrix} | \mathbf{G} \sim N \left(\begin{pmatrix} \mathbf{0} \\ \mathbf{0} \end{pmatrix}, \mathbf{G} \otimes \mathbf{A} \right)$$

$$\mathbf{G} = \begin{bmatrix} \sigma_a^2 & \rho \sigma_a \sigma_{a^*} \\ \rho \sigma_a \sigma_{a^*} & \sigma_{a^*}^2 \end{bmatrix},$$

where $\mathbf{A}$ represents the additive genetic relationship matrix; σ_a^2 and $\sigma_{a^*}^2$ are the additive genetic variance at the level of the trait mean and residual variance, respectively; ρ is a coefficient of genetic correlation; and $\otimes$ is the Kronecker product. The priors for σ_a^2 and $\sigma_{a^*}^2$ are a scaled inverted χ^2 distribution and ρ is a priori uniformly distributed in $(-1, 1)$. Finally, the vectors $\mathbf{p}$ and $\mathbf{p}^*$ are assumed to be independent with the following distributions:

$$\mathbf{p} | \sigma_p^2 \sim N(\mathbf{0}, \mathbf{I}_p \sigma_p^2)$$

$$\mathbf{p}^* | \sigma_{p^*}^2 \sim N(\mathbf{0}, \mathbf{I}_p \sigma_{p^*}^2),$$

where $\mathbf{I}_p$ is the identity matrix with order equal to the number of random effects and σ_p^2 and $\sigma_{p^*}^2$ are the random permanent environmental variances following a scaled inverted χ^2 distribution as in the additive genetic variances.

Controversy and Limitations

The use of appropriate genetic evaluation methods is crucial for improvement, as their results enable the identification of the best animals to serve as parents for future generations. Genetic heterogeneity of residual variance has been studied under the sire model (SM) and the animal model (AM) (Hill and Mulder, 2010; Iung et al., 2020). Briefly, the SM considers the sire as the main random effect, whose variance component accounts for a quarter of the additive genetic effect for the trait. In contrast, the animal model (AM) considers the animal itself, where the variance component is the direct additive genetic effect (Henderson, 1988), and allows simultaneous evaluation of sires and dams. However, bias can arise in SM and AM models. It has been shown that genetic heterogeneity of residual variance studies under AM may result in biased variance component estimates, especially in cross-sectional data without repeated records per individual (Sonesson et al., 2013). The bias occurs when mean and variance models are not properly managed, leading to inaccurate attribution of genetic and environmental variances, which affects the reliability of genetic evaluations. The sire model, on the other hand, includes random genetic variations (Mendelian sampling deviations) in the residual term, allowing the model to account for all genetic differences within a sire family. However, SM can still be biased if significant maternal effects or other genetic variances are not accounted for. This limitation may result in less accurate genetic evaluations compared to AM.

The estimated genetic control of residual variance from the models presented can be used to improve uniformity of production. However, these are not the only approaches to achieve genetic improvement of phenotypic variability, as uniformity can be assessed in a variety of ways. There are three main factors that limit the choice of response

variable for uniformity: the structure of the data, the trait, and the availability of genotypes (mainly required for genomic studies). These limitations arise because statistical analysis for heterogeneity of residual variance requires multiple observations per individual or within-family variance based on offspring groups for each family. When an individual has multiple records of a trait, such as birth weight within litter or milk yield across lactations, the standard deviations and coefficient of variation from these groups can be used to measure uniformity. For example, Khaw et al. (2016) used 6,330 individual weights in 944 pooled records (by family-group) to investigate the genetic variance for uniformity of harvest weight in Nile tilapia (*Oreochromis niloticus*) and Zhang et al. (2016) used within-litter data to estimate heritabilities and genetic and phenotypic correlations of litter uniformity for traits such as total number born, total litter weight at birth, and piglet mortality at birth. The advantage of using these metrics is that they are easy to interpret because they are on the same scale as the trait compared to the response variables used in the statistical models described earlier.

Genetic Parameters for Residual Variance

The genetic control of residual variance can be interpreted and compared using three genetic parameters: heritability of residual variance (h_v^2), evolvability (genetic coefficient of variation, GCV_E), and genetic correlation between mean and residual variance (r_{mv}) as shown in Mulder et al. (2007). The authors showed that h_v^2 is used to determine the accuracy of estimated breeding values (EBV) for residual variance, which is calculated as follows:

$$h_v^2 = \frac{\sigma_{a_v,add}^2}{(2\sigma_p^4 + 3\sigma_{a_v,add}^2)}$$

where $\sigma_{a_{v,add}}^2$ is the additive genetic variance estimated for the residual variance on the additive scale and σ_p^4 is the squared phenotypic variance. $\sigma_{a_{v,add}}^2$ is obtained as:

$$\sigma_{a_{v,add}}^2 = h_{res}^2 2(\sigma_{\hat{e}}^{-2})^2$$

where h_{res}^2 is the heritability of the response variable used in the residual variance model and $\sigma_{\hat{e}}^{-2}$ is the average residual variance in the mean model (Mulder et al., 2007).

The genetic coefficient of variation GCV_E allows the evaluation of the potential response to selection for residual variance, as follows:

$$GCV_E = \frac{\sigma_{a_{v,add}}}{\sigma_{\hat{e}}^{-2}}$$

where $\sigma_{a_{v,add}}$ is the standard deviation of the additive genetic variance for the residual variance on the additive scale. In a review, Hill and Mulder (2010) reported h_v^2 between 0.00 and 0.05 and GCV_E between 0.00 and 0.60. More recently, Lung et al. (2020) reported values close to 0.10 for h_v^2 and 0.79 for GCV_E .

The genetic correlation between mean and residual variance (r_{mv}) is an additional genetic parameter to be considered to guide selection for uniformity. r_{mv} ranges from -1.0 to 1.0, meaning that the negative values are most favorable if the breeding goals are to increase mean and reduce variance, otherwise, mean and residual variance must be included in a selection index to achieve the desired response. The range of r_{mv} estimates in terms of magnitude is influenced by data transformations, such as logarithmic and Box-Cox. They are commonly used to stabilize the variance and make the data more closely follow a normal distribution.

Data Transformation

Data transformations are used to account for scale effects (higher means are associated with higher variances) and to reduce the mean-variance relationship (Box and Cox, 1964). Some examples of a wide range of estimated sign and magnitude of r_{mv} are reported by Yang et al. (2011) using pig and rabbit data. The authors investigated how measurement scale affects results by comparing untransformed data and Box-Cox transformed data using a Bayesian hierarchical model. When the rabbit and pig litter size data were reanalyzed using this transformation, the results differed from the untransformed analysis. In rabbits, the evidence for genetic influence on environmental variance became weaker (r_{mv} for untransformed dataset: -0.73, r_{mv} for transformed data: 0.28), while in pigs, the correlation between additive genetic effects affecting mean and variance changed sign compared to the original data (r_{mv} for untransformed dataset: -0.64, r_{mv} for transformed data: 0.70). Sae-Lim et al. (2015) analyzed body weight in rainbow trout and reported changes in the genetic correlation between mean and residual variance from 0.30 to -0.62 after applying a logarithmic transformation to the data. These results underscore the importance of accounting for potential scale effects when studying genetic heterogeneity of residual variances.

GENETIC AND GENOMIC STUDIES ON VARIANCE HETEROGENEITY OF RESIDUAL VARIANCE IN LIVESTOCK

Livestock have historically been selectively bred for a wide variety of traits, resulting in remarkable success in improving those traits. Recent research has shown that

a portion of the residual variance (σ_e^2) is under genetic control, providing statistical evidence for this phenomenon in several livestock and aquaculture species (Table 1). In this section, we will summarize some genetic studies on variance heterogeneity of residual variance reported in different species.

Table 1. Number of studies (N) on variance heterogeneity of residual variance in livestock and aquaculture species.

Species	N
Sheep	4
Chicken	4
Pig	11
Fish	8
Dairy Cattle	5
Beef Cattle	3
Total	35

Sheep

Sheep farming is observed worldwide, and its widespread adoption is linked to the species' ability to adapt to different environments. It is estimated that small ruminants account for 56% of the world's domestic ruminant population, with approximately 1.1 billion sheep and 0.9 billion goats, for a total of 2.0 billion animals (FAO, 2013). Typically, these animals are small and highly efficient in terms of survival and adaptation across multiple ecosystems, unlike other ruminants whose performance may be compromised under less favorable environmental conditions (Zygoyiannis, 2006). A summary of genetic parameters for sheep is presented in Table 2.

SanCristobal-Gaudy et al. (2001) used data from the National Recording Scheme in France to evaluate whether Lacaune sheep can be selected for litter size, focusing on twin births, since a single lamb and more than three lambs are economically undesirable. The authors used data from Lacaune ewe lambs born over the course of 11 years,

resulting from the use of 157 different sires in 57 flocks. These flocks participated in a selection program initiated in 1975 within the Lacaune population to improve prolificacy through a sire progeny test. In the experimental design, each ram had an average of 25 daughters distributed among five different flocks. Furthermore, each flock had ewe lambs sired by approximately eight different rams, providing an adequate sample size for estimating genetic values. Variance components were estimated in an infinitesimal model that included genes controlling the mean level (homoscedastic threshold model) as well as its environmental variability (heteroscedastic model). The authors reported heritability estimates for the mean (h_u^2) of 0.34, heritability of residual variance (h_v^2) of 0.048, genetic coefficient of variation of residual variance (GCV_E) of 0.51, and genetic correlation between mean and residual variance (r_{mv}) of 0.19. The authors reported that the sheep population studied was selected to increase mean litter size. The high heterogeneity in this study may be due to two factors. First, the authors stated that the population studied had previously been selected to increase litter size. Secondly, the high heterogeneity may also be due to the presence of many genes controlling the residual variance for litter size, thereby increasing environmental sensitivity. Polygenic traits, such as those related to reproduction, are known to be influenced by a combination of genetic and environmental factors and typically have low heritability estimates (Amorim et al., 2018).

Similarly, Cottle et al. (2016) studied twinning rates in Belclare ewes, where the percentages of pedigreed lambing ewes with singles, twins, and triplets were 30, 54, and 14%, respectively. The authors reported that the rates of singles, twins, and triplets were constant over 15 years, and the variance in the number of lambs born increased with the

mean of singles, twins, and triplets. Using a DHGLM model including ewe age, birth flock, sire, permanent environmental effects of the ewe, and contemporary group, the authors found a strong r_{mv} (0.88 ± 0.07) between sire effects for residual and number of lambs born. This study is consistent with the results of SanCristobal-Gaudy et al. (2001) and confirms the general observation that increased average litter size is associated with increased variability for the trait.

Lastly, Sae-Lim et al. (2018) investigated the extent of direct and maternal genetic variances for birth weight uniformity in Norwegian white sheep. The authors evaluated 136,922 birth weight records of lambs born between 2000 and 2017 and their corresponding sire-maternal grand sire pedigree. Using a DHGLM model, the authors reported a maternal heritability for birth weight uniformity of 0.08, a GCV_E of 0.58, and a moderate r_{mv} (0.39). Birth weight is one of the most important traits in animal production, where high or low birth weight is undesirable because it can lead to stillbirth, dystocia, or reduced animal vigor (especially in species with potential for increased litter size). Economically, uniform birth weight is desirable for livestock species. From a welfare perspective, uniform birth weight can help reduce animal stress due to birth complications, reduced competition for food and contact with humans. The reported heritability estimates indicate that uniformity in birth weight is heritable. Additionally, the genetic correlation between mean birth weight and residual variance indicates that selection for more uniform birth weights could potentially lead to a reduction in average birth weight.

Table 2. Summary of genetic parameters for genetic heterogeneity of residual variance in sheep.

Species	Traits	Method	h_v^2	GCV_E	r_{mv}	Reference
Sheep	Litter size	REML	0.048	0.51	0.19	SanCristobal-Gaudy et al. (2001)
	Litter size	REML	0.10	0.50	0.88 (0.07)	Cottle et al. (2016)
	Birth weight	REML	0.08	0.58	0.39	Sae-Lim et al. (2018)
	Daily Feed Intake	REML	0.08 to 0.14	-	-	Garcia-Baccino et al. (2021)

h_v^2 : heritability of residual variance. GCV_E : genetic coefficient of variation of residual variance. r_{mv} : genetic correlation between mean and residual variance, **REML**: restricted estimate maximum likelihood; standard errors, if available, are given in parentheses.

- Not reported in the study.

Poultry

Uniformity in poultry production is a crucial indicator of quality and efficiency.

When chicken batches are uniform in size and weight, it has a positive impact on several aspects of the production chain. In processing, broiler chickens of similar weight facilitate automation because lines can be adjusted for chickens of similar size, increasing efficiency, and reducing the need for human intervention. In terms of growth and feed conversion, uniform chickens generally indicate a healthy flock with good access to feed and water, which improves feed conversion rate, optimizes growth, and reduces competition for feed. Finally, chicken uniformity is also related to animal welfare, as it means chickens have equal access to feed and space, and animal management can be simplified, from feed distribution to programmed vaccinations or other veterinary interventions.

Rowe et al. (2006) investigated the extent of genetic heterogeneity in the environmental variance of broiler chicken data. The dataset consisted of 99,535 35-day body weight records of broiler chickens raised in a controlled environment. The authors estimated residual variance within dam families using ASREML software, and residual variance was calculated separately for male and female offspring. In their study, the

standard deviation between sires within variance was 15–18% of the mean using untransformed data, and after log-transformation, the variance was still over 10%, showing evidence of heterogeneity. The GCV_E reported in this study ranged from 0.30 to 0.32, the r_{mv} was low and negative (-0.17 to -0.11), and the heritability estimates of residual variance ranged from 0.029 to 0.030.

Later, Wolc et al. (2009) studied the genetic variability in the residual variation of body weight and conformation scores in broiler chickens. The authors used performance records of 52,349 female and 49,001 male birds using REML and Bayesian. In the REML analysis, each sex was analyzed separately for each trait using an iterative mean-variance REML procedure in which estimation of effects on means is followed by estimation of effects on variances (two step approach). The Bayesian approach consisted of a model with structured residual variance (hierarchical Bayesian model). Only the results of the REML approach are presented here because the authors reported good agreement between the REML and Bayesian approaches. For body weight, h_v^2 was 0.04 ± 0.01 for females and 0.03 ± 0.01 for males. The genetic coefficient of variation of residual variance ranged from 0.37 ± 0.03 for females to 0.32 ± 0.03 for males. Lastly, the genetic correlation between mean and residual variance was -0.27 for females and -0.23 for males. When evaluating conformation scores (scale from 1 to 5, where 1 is poor conformation and 5 is excellent conformation), the authors reported h_v^2 ranging from 0.03 ± 0.01 for females and 0.02 ± 0.004 for males. GCV_E ranged from 0.31 ± 0.03 for females and 0.25 ± 0.03 for males and r_{mv} was 0.33 for females and 0.40 for males. These results are in agreement with the evidence for a substantial genetic component in broiler body weight variation in Rowe et al. (2006), however, the authors emphasized the need

for large family sizes to obtain accurate estimates of breeding values at the level of variance.

Mulder et al. (2009) estimated the genetic variance in the residual variance of body weight in broiler chickens using a two-step approach, first estimating the variance components for the trait mean and then using the log-transformed squared estimated residuals as the response variable in the residual variance model. The authors reported h_v^2 of 0.03 ± 0.003 and 0.05 ± 0.004 , GCV_E of 0.35 and 0.57, and negative r_{mv} of -0.41 and -0.45 for females and males, respectively.

More recently, Mulder et al. (2016) quantified the genetic variance in the environmental variance of eggshell color in purebred and crossbred laying hens. Their data set included 167,651 and 79,345 eggshell color records from purebred and crossbred laying hens, respectively. A DHGLM model was used to estimate the genetic variance of mean eggshell color and its residual variance. In their study, the authors reported h_v^2 ranging from 0.01 ± 0.001 to 0.01 ± 0.003 , a moderate GCV_E ranging from ~ 0.26 to ~ 0.28 , and the genetic correlation between mean and residual variance varied from -0.057 to 0.43 for purebred and crossbred laying hens, respectively. Their low heritability estimates indicate that large amounts of data are needed to obtain accurate breeding values for residual variances. Table 3 presents a summary of studies on genetic heterogeneity of residual variance/uniformity in poultry.

Table 3. Summary of genetic parameters for genetic heterogeneity of residual variance/uniformity in poultry.

Species	Traits	Method	h_v^2	GCV_E	r_{mv}	Reference
Poultry	Body weight	REML	0.02 to 0.03	0.30 to 0.32	-0.17 to -0.11	Rowe et al. (2006)
	Body Weight ¹	REML	0.03 (0.05) to 0.03 (6.00×10^{-3})	0.32 (0.03) to 0.37 (0.03)	-0.27 to -0.23	Wolc et al. (2009)
	Conformation Score ¹	REML	0.02 (4.00×10^{-3}) to 0.03 (5.00×10^{-3})	0.25 (0.02) to 0.31 (0.02)	0.33 to 0.40	Wolc et al. (2009)
	Body weight ¹	REML	0.04 (5.00×10^{-3}) to 0.04 (4.00×10^{-3})	0.49 to 0.57	-0.45 (0.04) to -0.41 (0.03)	Mulder et al. (2009)
	Eggshell color	REML	0.01 (1.00×10^{-3}) to 0.01 (3.00×10^{-3})	0.26 (0.03) to 0.28 (0.01)	-0.05 (0.08) to 0.43 (0.10)	Mulder et al. (2016)
	Hatching Weight ¹	REML	2.00×10^{-3} (1.00×10^{-3}) to 5.00×10^{-3} (2.00×10^{-3})	0.31 to 0.42	0.13 (0.12) to 0.88 (0.04)	Silva et al. (2021)
	Body Weight ¹	REML	3.00×10^{-4} (0.01) to 0.02 (0.01)	0.09 to 0.25	-0.75 (0.06) to 0.59 (0.11)	Silva et al. (2021)

h_v^2 : heritability of residual variance. GCV_E : genetic coefficient of variation of residual variance. r_{mv} : genetic correlation between mean and residual variance, **REML**: restricted estimate maximum likelihood; when available, standard errors are given in parentheses.

¹Estimates separated by sex. First male, second female.

- Not reported in the study.

Pigs

In the pig production industry, traits such as litter size, litter birth weight, litter mortality, teat count, individual birth weight, backfat thickness, and slaughter weight play an important role in developing and improving production and economic profits. Genetic uniformity in pig production is a key aspect of maximizing profitability. Breeders often have specific goals for the above traits, and producers strive to meet these goals by delivering a uniform group of animals.

Genetic variation at the level of residual variance opens up the possibility of modifying it by selection. In addition to the benefits of homogeneity in the processing of animal products, this will also allow a consequent reduction in costs. In the pig industry, homogeneity of pig carcass weight significantly reduces meat processing costs (Hennessy, 2005), as most commercial slaughterhouses impose price penalties for carcasses above or below a pre-determined optimum weight. For litter-related traits,

reproductive traits, such as litter size, birth weight, and mortality, are critical to production and profit. For example, litter size has historically been a marker of sow productivity, but larger litters often result in higher piglet mortality. Studies show that birth weight uniformity within a litter correlates with survival rates (Southwood and Kennedy, 1991; Blasco et al., 1998; Damgaard et al., 2003; Campos et al., 2012; Camargo et al., 2020). Additionally, calving interval is a key reproductive measure that includes lactation and gestation length. Both piglet uniformity and farrowing interval have low heritability (Wittenburg et al., 2008; Neto et al., 2009; Banville et al., 2015; Zhang et al., 2016; Sell-Kubiak, 2021; Zaalberg et al., 2023), making genetic improvement challenging. Understanding the factors that influence these traits is essential for improving breeding programs. Table 4 presents a summary of genetic parameters for residual variance reported in pig studies.

Ibáñez-Escriche et al. (2008) examined the heterogeneity of the environmental variance affecting the slaughter weight of pigs at 175 days. In the study, the authors used a hierarchical Bayesian model assuming the presence of additive genetic effects affecting the mean and environmental variance. The authors reported the presence of genetic variation at the level of mean and variance, with a h_v^2 of 0.01 for slaughter weight, a genetic coefficient of variation of residual variance of 0.34, and a small negative r_{mv} of -0.07. In addition to analyzing the heterogeneity of the environmental variance, the authors showed that the additive genetic effects on the mean and those on the environmental variance have an important influence on the future economic performance of selected individuals by predicting the economic income of different sires. They selected two sires with almost identical posterior means of breeding values affecting the

mean (Sire A: 2.01 kg; Sire B: 2.10 kg), but different posterior means of breeding values affecting the environmental variance (Sire A: 0.48 kg²; Sire B: 20.50 kg²). When the economic income of 500 offspring was considered, the sire with lower breeding values affecting the environmental variance (B) produced a higher income, with a mean difference of €2 per pig, or €1000 in total, corresponding to a 2.2% higher income.

Breeding efforts over the past decade have successfully increased litter sizes in pigs. However, the number of teats must also be increased to meet the needs of the piglets. Sow nursing behavior is complex and requires that each piglet has access to a dedicated functional teat (Van Nieuwamerongen et al., 2014). Felleki and Lundeheim (2015) used a DHGLM model to estimate the heritability of teat counts (0.35) but found low h_v^2 (0.06-0.07), moderate GCV_E ranging from 0.48 to 0.51, and high r_{mv} ranging from 0.76 ± 0.03 to 0.79 ± 0.03 . In breeding programs, heritability and genetic correlations are tools to determine whether a trait can be controlled or modified by selection. In this study, the authors found a high r_{mv} , which translates into an expected increase in variance as the mean increases. However, due to the low heritability of residual variance, selection for reduced residual variance may have a limited effect.

Sell-Kubiak et al. (2015b) investigated within-litter variation in piglet birth weight using genomic or pedigree relationship matrices and used a DHGLM model to compare the accuracy of EBV for this trait. They used 2 dam lines, including Landrace and Large White. The Landrace data consisted of 748 sows with 1,938 litters and 29,430 piglets. The Large White data consisted of 989 sows with 3,320 litters and 51,818 piglets. The genomic relationship matrix was constructed with 46,466 (Landrace) and 44,826 (Large White) single nucleotide polymorphisms, and the pedigree relationship matrix

included 5 generations of pedigree. Similar genetic parameters for mean and residual variance were estimated using either pedigree-based or genomic relationship matrices. Their results showed an increase in the accuracy of EBV for mean and residual variance of body weight when genomic information was considered, although the difference was not significant, probably due to the small size of the reference population used for genomic prediction.

Table 4. Summary of genetic parameters for genetic heterogeneity of residual variance/uniformity in pigs.

Species	Traits	Method	h_v^2	GCV_E	r_{mv}	Reference
Pigs	pH muscle	REML	0.03	0.40	0.79	SanCristobal-Gaudy et al. (1998)
	Litter size	MCMC	0.02	0.31	-0.62	Sorensen and Waagepetersen (2003)
	Slaughter weight	MCMC	0.01	0.34	-0.07 (0.26;0.12)	Ibáñez-Escriche et al. (2008)
	Litter size ²	MCMC	-	-	-0.64 (0.82;-0.45)	Yang et al. (2011)
	Litter size	MCMC	-	-	0.70 (0.44;0.98)	Yang et al. (2011)
	Birth weight	REML	8.00×10^{-3} to 0.01	0.08 to 0.10	0.23 (0.41) to 0.62 (0.12)	Sell-Kubiak et al. (2015)
	Birth weight	REML	1.10×10^{-2} to 1.50×10^{-2}	0.10 to 0.12	0.53 (0.08) to 0.59 (0.06)	Sell-Kubiak et al. (2015b)
	Litter size	REML	6.00×10^{-3} (1.00×10^{-3}) to 0.01 (6.00×10^{-3})	0.08 (0.004)	0.49 (0.04) to 0.68 (0.04)	Sell-Kubiak et al. (2015c)
	Teat count	REML	0.06 to 0.07	0.48 to 0.51	0.76 (0.03) to 0.79 (0.025)	Felleki and Lundeheim (2015)
	Teat count ²	REML	0.04	0.40 to 0.41	0.50 (0.05) to 0.54 (0.04)	Felleki and Lundeheim (2015)
	Growth Traits	REML	6.00×10^{-3} (1.00×10^{-3}) to 8.00×10^{-3} (1.00×10^{-3})	0.24 (0.01) to 0.27 (0.01)	0.12 to 0.21	Gorssen et al. (2018)
	Total Number Born	REML	0.12 to 0.19	-	-	Sell-Kubiak et al. (2019)

h_v^2 : heritability of residual variance. GCV_E : genetic coefficient of variation of residual variance. r_{mv} : genetic correlation between mean and residual variance, **REML**: restricted estimate maximum likelihood; if available, standard errors are shown in parentheses. **MCMC**: Markov chain Monte Carlo; if available, standard errors or posteriors are shown in parentheses.

¹Estimates separated by sex. First male, second female.

²Transformed dataset.

- Not reported in the study.

Fish

Over the past 50 years, global production of fish and seafood has quadrupled worldwide. In addition to the fact that the global population has more than doubled during this time, the average person now eats nearly twice as much seafood as they did half a century ago (Koehn et al., 2017). Aquaculture, the farming of fish and seafood, has emerged as a solution to reduce reliance on wild fish. This practice is analogous to livestock farming as opposed to hunting wild animals, although it is a relatively recent development for seafood, having become significant only in the past 50 years.

Commercial fish production is mostly characterized by animals raised in tanks or ponds, which allows for control of the production environment, including water temperature, water quality, salinity, and oxygen levels (Cole et al., 2009; Koehn et al., 2017). Genetic variation in micro-environmental sensitivity could increase the potential for selection for reduced sensitivity and consequently reduced trait variation among animals within a single production environment such as fish. Potential benefits of uniformity in growth include reduced competition for food, reduced cannibalistic behavior, and increased survival rate (Gilmour et al., 2005; Janhunen et al., 2012; Marjanovic et al., 2018). Most studies on uniformity in fish production focus on body weight and size. A summary of the genetic parameters for the fish studies is presented in Table 5.

Sae-Lim et al. (2015) investigated the genetic (co)variance of rainbow trout (*Oncorhynchus mykiss*) body weight and its uniformity across production environments using a DHGLM approach. The authors analyzed data from two different environments, including genetic nucleus and production, and found h^2_V values of 0.01 and 0.01, a genetic coefficient of variation of residual variances of 0.19 and 0.21, and moderate to high genetic correlations between means and residual variances of 0.30 and 0.79 for genetic

nucleus and production environments, respectively. Although the heritability estimates for uniformity of body weight were low, the corresponding coefficients of genetic variation in this study reached 19 and 21%, indicating a potential for response to selection. Additionally, the authors considered the genotype by environment interaction on uniformity that was present for both environments and recommended conducting sib-testing, where sibs are tested in the actual production environment, to enhance uniformity across environments. This approach aims to better understand how genetic and environmental factors influence trait uniformity and to improve the uniformity of traits in different environmental conditions.

Later, Sae-Lim et al. (2017) estimated breeding values for growth uniformity in Atlantic salmon (*Salmo salar*) using single-step genomic (ssGBLUP)-based DHGLM and compared the predictive ability of EBV for body weight uniformity when implementing either the **A** or **H** matrix in genetic evaluation. The ssGBLUP augments the numerator relationship (**A**) matrix by the genomic relationship (**G**) matrix (Misztal et al., 2009). This combined numerator and genomic relationship matrix is known as the **H** matrix (Legarra et al., 2009). In their study, the authors found h_v^2 values ranging from 0.036 ± 0.02 to 0.04 ± 0.02 , a genetic coefficient of variation of residual variance ranging from 0.48 to 0.52, and a high genetic correlation between mean and residual variance estimates of 0.95. In addition, the authors reported that the use of the **H** matrix increased the correlation between predicted EBV and adjusted phenotypes, which is a measure of predictive ability for both body weight and its uniformity (41.1 to 78.1%), suggesting an increase in response to selection for uniformity.

Table 5. Summary of genetic parameters for genetic heterogeneity of residual variance/uniformity in fish.

Species	Traits	Method	h_v^2	GCV_E	r_{mv}	Reference
Fish	Body weight	REML	0.02 (6.00×10^{-3})	0.37	-0.16 (0.03)	Janhunen et al. (2012)
	Body weight	REML	-	-	0.42	Sonesson et al. (2013)
	Body weight ²	REML	-	-	-0.17 to 0.14	Sonesson et al. (2013)
	Body weight	REML	0.01 to 0.01	0.19 to 0.21	0.30 (0.15) to 0.79 (0.13)	Sae-Lim et al. (2015)
	Body weight ²	REML	0.01 to 0.02	0.17 to 0.29	-0.62 (0.21) to -0.83	Sae-Lim et al. (2015)
	Body weight and size	REML	-	0.39 to 0.58	0.11 (0.16) to 0.60 (0.09)	Marjanovic et al. (2016)
	Harvest weight	REML	0.21 (0.06)	0.17	0.09 (0.18)	Khaw et al. (2016)
	Body weight	REML	0.03 (0.01) to 0.03 (0.02)	0.48 (0.11) to 0.52 (0.11)	0.95	Sae-Lim et al. (2017)
	Body weight ²	REML	0.01 (0.01) to 0.01 (0.01)	0.29 (0.10) to 0.29 (0.09)	-0.09 to 0.02	Sae-Lim et al. (2017)

h_v^2 : heritability of residual variance. GCV_E : genetic coefficient of variation of residual variance. r_{mv} : genetic correlation between mean and residual variance, **REML**: restricted estimate maximum likelihood; if available, standard errors are shown in parentheses. **MCMC**: Markov chain Monte Carlo; if available, standard errors or posteriors are shown in parentheses.

¹Estimates separated by sex. First male, second female.

²Transformed dataset.

- Not reported in the study.

Dairy Cattle

The heterogeneity of variance in genetic evaluations in cattle has been widely documented for many years (Hill et al., 1983; Brotherstone and Hill, 1986; Boldman and Freeman, 1990; Neves et al., 2011; Neves et al., 2012; Rönnegard et al., 2013; Iung et al., 2017; Iung et al., 2020; Júnior et al., 2023). Studies have shown that sire and residual variances tend to increase as the production level of the herd increases (Hill et al., 1983; Boldman and Freeman, 1990). It is also important to study the heterogeneity of variance in cattle to quantify the considerable variation in performance of some sires that exists within their daughter group, while the offspring of other sires show relatively little variation (Van Vleck, 1968; Clay et al., 1979). Table 6 presents a summary of genetic parameters for residual variance in dairy and beef cattle.

Rönnegard et al. (2013) used a DHGLM model to estimate genetic parameters and breeding values for micro-environmental sensitivity for milk yield and somatic cell score in a dairy cattle data set with more than 1.6 million records. The authors found a genetic standard deviation for residual variance of 0.21 for somatic cell score and 0.22 for milk yield. These results indicate moderate genetic variance for residual variance and imply that a standard deviation change in micro-environmental sensitivity breeding values for any of these traits would change the residual variance by 20% (GCV_E). In other words, a 1 standard deviation decrease in microenvironmental sensitivity breeding values for milk yield would also decrease the residual variance for that trait by ~20%. Additionally, the authors reported h_v^2 values of 0.01, and moderate to high sample correlation between the EBV and breeding values for micro-environmental sensitivity estimates ranging from 0.38 to 0.60. Unlike other studies presented in this review, this study showed the estimation of genetic parameters using a large dataset, which is an important factor for this analysis but not always possible due to computational requirements and data availability.

Mulder et al. (2013) investigated the genetic architecture of mean and environmental variance of somatic cell score in dairy cows and quantified the accuracy of genome-wide breeding values. The authors used residual variance per individual from DHGLM as a response variable to identify genomic regions associated with residual variance of somatic cell score in Holstein heifers. The authors reported 43 SNP that were significantly associated with either the mean (22) or the environmental variance (21) of somatic cell score.

Beef Cattle

Studies on uniformity in beef cattle remain scarce. Neves et al. (2012) used a two-step approach to study the genetic heterogeneity of residual variance in birth-to-weaning weight gain and long-yearling weight in Nellore cattle. The dataset included records from 382 herds reared in Brazil and Paraguay. The authors found h_v^2 values ranging from 0.00 to 0.058, a GCV_E ranging from 0 to 0.787, and a negative to positive genetic correlation between mean and residual variance estimates ranging from -0.01 to 0.36. Their results suggest that genetic and environmental factors influence the residual variance of weight gain from birth to weaning and long-yearling and that uniformity of these traits could be improved by selecting for lower residual variance when considering a large amount of information to predict genetic merit for this criterion. The authors also applied a Monte Carlo simulation, a technique that can be used to assess risk in quantitative analysis and decision making. This simulation uses repeated random sampling to simulate a wide range of possible outcomes in a process or system that has random variables, helping to predict the probability of different scenarios (Harrison, 2010). The simulation evaluated the reliability of variance component estimation and the accuracy of EBV for residual variation. The results suggested that using the two-step approach would lead to biased estimates of variance components, a recurring problem reported in the literature related to this method.

Also, in Nellore cattle, Iung et al. (2017) investigated the genetic heterogeneity of residual variance for yearling weight and compared the results of the two-step approach and DHGLM. The comparison was based on genetic parameters, accuracy of EBV for residual variance and cross-validation to evaluate the predictive performance of both approaches. Their dataset included a total of 194,628 yearling weight records from 625

sires. Their results supported the hypothesis of genetic heterogeneity of residual variance of yearling weight in Nellore cattle, as shown in Neves et al. (2012). The genetic coefficient of variation of residual variance ranged from 0.10 to 0.12 for the two-step approach and 0.17 for DHGLM. At the same time, the authors reported low estimates of genetic variance associated with positive genetic correlations between mean and residual variance, 0.20 for the two-step approach, and 0.76 for DHGLM. These results suggest that these estimates of variance and correlation would limit the genetic response to selection for production uniformity while increasing yearling performance. Additionally, the heritability estimates for residual variance ranged from 0.002 ± 0.001 (two-step approach) to 0.001 ± 0.002 (DHGLM), suggesting that larger sire families are needed to obtain accurate estimates of genetic merit for residual variance, as indicated by the low h_v^2 estimates.

Table 6. Summary of genetic parameters for genetic heterogeneity of residual variance/uniformity in cattle.

Species	Traits	Method	h_v^2	GCV_E	r_{mv}	Reference
Dairy Cattle	Milk yield and somatic cell score	REML	0.005	0.20	0.38 to 0.60	Rönnegard et al. (2013)
	Milk yield, somatic cell score and fatty acids	REML	1.00×10^{-3} to 4.00×10^{-3}	0.12 to 0.17	0.22 (0.13;0.30) to 0.47 (0.40;0.54)	Vandenplas et al. (2013)
	Calving to first service ²	REML	5.00×10^{-3}	0.12	0.69 (0.09)	Ghiasi and Felleki (2016)
	Milk Yield and Composition	REML	-	-	0.597 to 0.660	Ehsaninia et al. (2019)
	Milk Yield	REML	0.01 (9.00×10^{-3}) to 0.04 (6.00×10^{-3})	0.21 to 0.26	-	Ehsaninia et al. (2020)
	Fat Yield	REML	0.01 (0.01) to 0.02 (9.00×10^{-3})	0.19 to 0.24	-	Ehsaninia et al. (2020)
	Protein Yield	REML	0.01 (0.01)	0.17 to 0.21	-	Ehsaninia et al. (2020)
Beef Cattle	Beef production traits	REML	4.00×10^{-3} (2.00×10^{-3}) to 0.09 (6.00×10^{-3})	0.12 to 0.70	-0.21 to 0.42	Neves et al. (2011)
	Beef growth traits ¹	REML	0 to 0.05	0 to 0.78	-0.01 to 0.36	Neves et al. (2012)
	Yearling Weight ¹	REML	0.002 (5.00×10^{-3}) to 0.01 (0.02)	0.03 to 0.20 (0.02)	-0.04 (0.04) to 0.89 (0.05)	Iung et al. (2017)

h_v^2 : heritability of residual variance. GCV_E : genetic coefficient of variation of residual variance. r_{mv} : genetic correlation between mean and residual variance, **REML**: restricted estimate maximum likelihood; if available, standard errors are shown in brackets.. **MCMC**: Markov chain Monte Carlo; if available, standard errors or posteriors are shown in parentheses.

¹Estimates separated by sex. First male, second female.

²Transformed dataset.

- Not reported in the study.

BEEF CATTLE INDUSTRY IN THE US

Beef production in the United States (US) is characterized by a wide variety of environmental conditions, different climates, and management systems (Drouillard, 2018). The beef cattle industry is a major component of the agricultural sector and plays an important role in the domestic and global economy (Greenwood, 2021; Martinez et al., 2021). In general, the production cycle involves several stages of production, each of which is an integral part of the supply chain that brings beef from the pasture to the plate.

The industry is broadly divided into three sectors: cow-calf, stocker, and finishing operations (Herring, 2014). Cow-calf operations are the first stage of the beef production system, where producers maintain a breeding herd of cows that raise calves yearly. These operations focus on producing healthy, weaned calves. Cows graze on pasture and calves are usually weaned at six to ten months of age. After weaning, calves may enter a stocker operation where they are raised on pasture with or without supplemental feed. This phase allows them to gain weight before entering a feedlot. The main goal of this phase is to increase the weight of the calves by feeding them forage-based diets (e.g., hay, silage, and pasture grass). Finally, the feedlot phase includes the final growth and fattening phase. In general, the majority of cattle are fed a high-energy diet (rich in grains such as corn and soybeans) to prepare them for slaughter, although grass-fed finished cattle are becoming increasingly popular in the country (Hayek et al., 2018). Approximately 70-80% of all beef cattle are raised in these intensive feedlots at some point in the production cycle. The feedlot system allows for efficient management and feeding of large numbers of animals, resulting in rapid weight gain and a more consistent product for the beef market (Herring, 2014; Maxwell et al., 2014).

Growth Traits

Selection criteria for beef cattle are based on easily measured growth traits, such as weight at specific ages or weight gain. For several decades, growth traits, such as age adjusted weight, have been incorporated into beef cattle breeding programs to improve herd production performance (Herring, 2014). Traits, such as birth weight, weaning weight, and yearling weight, are easily measurable, and their heritability estimates range from moderate to high. Weaning and yearling weights should be adjusted for dam and

animal age, as dam age is known to affect calf weight. Calves will not be the same age at weaning (205 days) or year old when weaning and yearling weights are measured, so an adjustment for these traits is necessary. The following equations are used to obtain adjusted phenotypes for weaning and yearling weight (Bormann, 2010):

$$WW_{adj} = \frac{\text{Weaning Weight} - \text{Birth Weight}}{\text{Age at Weaning in Days}} \times 205 + \text{Birth Weight}$$

and

$$YW_{adj} = \frac{\text{Yearling Weight} - \text{Weaning Weight}}{\text{Number of days between weights}} \times 160 + WW_{adj}$$

where WW_{adj} and YW_{adj} are the weaning weight adjusted to 205 days of age and the yearling weight adjusted to 365 days of age, respectively.

In beef cattle production systems, understanding the factors that determine growth and development of body tissues is fundamental to tailoring breeding programs, nutritional management, environmental conditions, and determining slaughter age. Collecting weight at different stages of life is essential to understanding animal growth. Animal growth is a complex biological phenomenon involving interactions between hormonal, nutritional, genetic, and metabolic factors (Gerrard and Grant, 2006). One way to assess animal growth is through growth curves, which allow the monitoring of animal development at all life stages, the evaluation of biologically important parameters, such as animal size and weight and sexual maturity, and the determination of appropriate management techniques to identify more efficient animals (Owens et al., 1993).

Historically, beef cattle breeding programs have focused on growth and weight gain traits, mainly because selection for faster growth is justified by slaughtering heavier animals at a given age, resulting in a heavier final carcass weight. More recently, the focus of beef cattle breeding programs has begun to include other morphological traits, such as key breeding goals in addition to growth traits (Alvarenga et al., 2023).

Foot Score Traits

In a country where animals are raised in a variety of production systems over extensive pasturelands with significant climatic variability, good hoof structure is crucial. Animals with very straight legs can have difficulties in the breeding process, while animals with curved legs tend to have joint problems. Animals that do not move well do not eat properly, lose body condition, and consequently suffer a decline in productive and reproductive performance (Boggs, Merkel, and Doumit, 1998). One way to minimize foot and leg disorders is to conduct genetic evaluations and use them as selection criteria. The American Angus Association has developed the most widely used and recognized foot scoring system for beef cattle in the U.S. The scoring system consists of two nine-point scales, with a score of five considered optimal. It requires that animals be scored prior to any hoof trimming and at approximately one year of age (Retallick, 2019), as age affects foot and leg characteristics due to increased body weight and prolonged use (Van Dorp et al., 2004). Figure 1 shows foot score sketches and the scoring system developed by the American Angus Association.

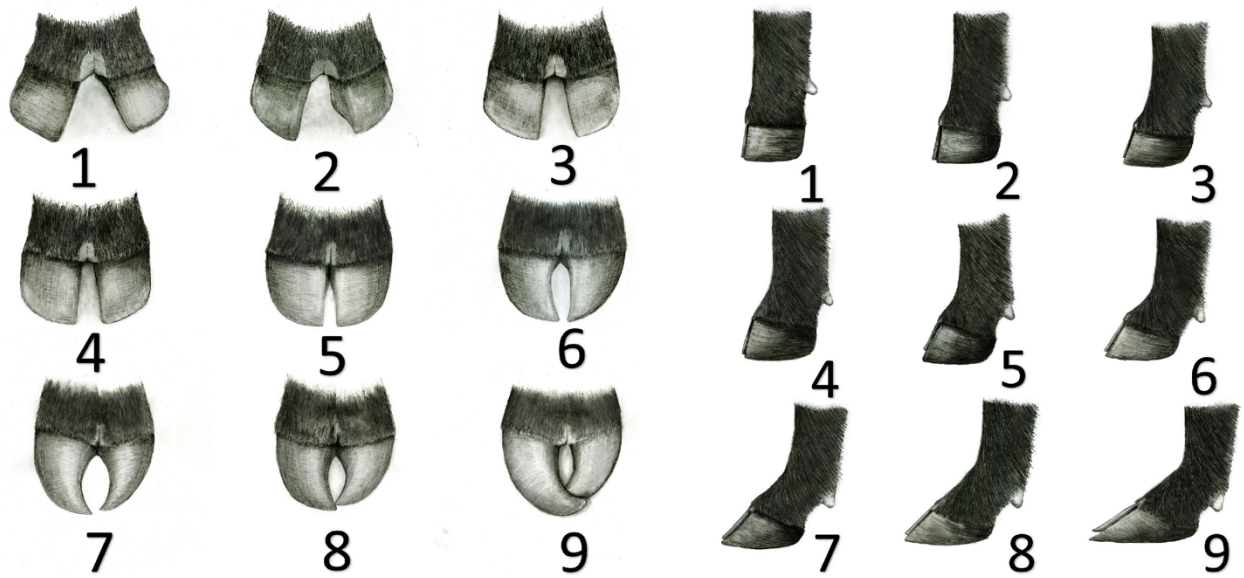


Figure 1. Foot scoring system developed by the American Angus Association. Left panels represent claw scores and right panels represent foot angles (image courtesy of the American Angus Association).

Foot angle is the first criterion in foot scoring, with a score of one reflecting extremely straight pasterns and very short toes, which are considered as unsound. Conversely, a score of nine indicates a notably shallow heel, long toes, and extremely weak pasterns, which are also considered unsound. An optimal score of five indicates a pastern joint at a 45-degree angle, appropriate toe length, and a deep heel, which are considered sound. The second criterion, claw set, uses a scoring system where a score of one indicates weak, diverging toes (unsound). A score of nine indicates scissor claws, curled and crossing toes, which are also unsound. An ideal claw set score of five indicates symmetrical, evenly spaced claws (considered sound) (Retallick, 2019).

BIBLIOGRAPHY

- Abiola, S. S., O. O. Meshioye, B. O. Oyerinde, and M. A. Bamgbose. 2008. Effect of egg size on hatchability of broiler chicks. *Arch. Zootec.* 57:83–86.
- Alvarenga, A. B., K. J. Retallick, A. Garcia, S. P. Miller, A. Byrne, H. R. Oliveira, and L. F. Brito. 2023. Across-country genetic and genomic analyses of foot score traits in American and Australian Angus cattle. *Genet. Sel. Evol.* 55. doi:10.1186/S12711-023-00850-X.
- Amorim, S. T., S. Kluska, M. P. Berton, M. V. A. de Lemos, E. Peripolli, N. B. Stafuzza, J. F. Martin, M. S. Álvarez, B. V. Gaviña, M. A. Toro, G. Banchemo, P. S. Oliveira, L. Grigoletto, J. P. Eler, F. Baldi, and J. B. S. Ferraz. 2018. Genomic study for maternal related traits in Santa Inês sheep breed. *Livest. Sci.* 217:76–84. doi:10.1016/j.livsci.2018.09.011.
- Banville, M., J. Riquet, D. Bahun, M. Sourdioux, and L. Canario. 2015. Genetic parameters for litter size, piglet growth and sow's early growth and body composition in the Chinese–European line Tai Zumu. *J. Anim. Breed. Genet.* 132:328–337. doi:10.1111/JBG.12122.
- Blasco, A., D. Sorensen, and J. P. Bidanel. 1998. Bayesian inference of genetic parameters and selection response for litter size components in pigs. *Genetics.* 149:301. doi:10.1093/GENETICS/149.1.301.
- Boggs, Donald L., Merkel, Robert A., Doumit, Matthew E., Bruns, Kelly. 2006. *Livestock & Carcasses an Integrated Approach to Evaluation, Grading, and Selection* (sixth). USA: Kendall/Hunt Publishing Company.
- Boldman, K. G., and A. E. Freeman. 1990. Adjustment for Heterogeneity of Variances by Herd Production Level in Dairy Cow and Sire Evaluation. *J. Dairy Sci.* 73:503–512. doi:10.3168/JDS.S0022-0302(90)78698-5.
- Bormann, J.M., 2010. Data Collection and Interpretation. *Beef Sire Selection Manual*. Pages 21-23. http://www.nbcec.org/producers/sire_selection/chapter7.pdf. 06 June 2024.
- Box, G. E. P., and ; D R Cox. 1964. An Analysis of Transformations. *J. R. Stat. Soc. Ser. B.* 26:211–252.
- Brotherstone, S., and W. G. Hill. 1986. Heterogeneity of variance amongst herds for milk production. *Anim. Sci.* 42:297–303. doi:10.1017/S0003356100018067.
- Camargo, E. G., D. B. D. Marques, E. A. P. de Figueiredo, F. F. e. Silva, and P. S. Lopes. 2020. Genetic study of litter size and litter uniformity in Landrace pigs. *Rev. Bras. Zootec.* 49:e20180295. doi:10.37496/RBZ4920180295.

- Campos, P. H. R. F., B. A. N. Silva, J. L. Donzele, R. F. M. Oliveira, and E. F. Knol. 2012. Effects of sow nutrition during gestation on within-litter birth weight variation: a review. *animal*. 6:797–806. doi:10.1017/S1751731111002242.
- Clay, J. S., W. E. Vinson, and J. M. White. 1979. Heterogeneity of Daughter Variances of Sires for Milk Yield. *J. Dairy Sci.* 62:985–989. doi:10.3168/JDS.S0022-0302(79)83359-7.
- Cole, D. W., R. Cole, S. J. Gaydos, J. Gray, G. Hyland, M. L. Jacques, N. Powell-Dunford, C. Sawhney, and W. W. Au. 2009. Aquaculture: Environmental, toxicological, and health issues. *Int. J. Hyg. Environ. Health.* 212:369–377. doi:10.1016/J.IJHEH.2008.08.003.
- Cottle, D. J., A. R. Gilmour, T. Pabiou, P. R. Amer, and A. G. Fahey. 2016. Genetic selection for increased mean and reduced variance of twinning rate in Belclare ewes. *J. Anim. Breed. Genet.* 133:126–137. doi:10.1111/JBG.12173.
- Damgaard, L. H., L. Rydhmer, P. Løvendahl, and K. Grandinson. 2003. Genetic parameters for within-litter variation in piglet birth weight and change in within-litter variation during suckling. *J. Anim. Sci.* 81:604–610. doi:10.2527/2003.813604X.
- Van Dorp, T. E., P. Boettcher, and L. R. Schaeffer. 2004. Genetics of locomotion. *Livest. Prod. Sci.* 90:247–253. doi:10.1016/J.LIVPRODSCI.2004.06.003.
- Drouillard, J. S. 2018. Current situation and future trends for beef production in the United States of America — A review. *Asian-Australasian J. Anim. Sci.* 31:1007. doi:10.5713/AJAS.18.0428.
- Ehsaninia, J., N. Ghavi Hossein-Zadeh, and A. A. Shadparvar. 2019. Estimation of genetic variation for macro- and micro-environmental sensitivities of milk yield and composition in Holstein cows using double hierarchical generalized linear models. *J. Dairy Res.* 86:145–153. doi:10.1017/S0022029919000293.
- Ehsaninia, J., N. G. Hossein-Zadeh, A. A. Shadparvar, J. Ehsaninia, N. G. Hossein-Zadeh, and A. A. Shadparvar. 2020. Estimation of genetic parameters for micro-environmental sensitivities of production traits in Holstein cows using two-step method. *Anim. Prod. Sci.* 60:752–757. doi:10.1071/AN18687.
- Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Pearson.
- FAO. 2013. Statistical Yearbook of the Food And Agricultural Organization for Feeding the world. In: *FAO Statistical Yearbook 2013*. p. 123–158.
- Felleki, M., D. Lee, Y. Lee, A. R. Gilmour, and L. Rönnegård. 2012. Estimation of breeding values for mean and dispersion, their variance and correlation using double

hierarchical generalized linear models. *Genet. Res. (Camb)*. 94:307–317.
doi:10.1017/S0016672312000766

Felleki, M., and N. Lundeheim. 2015. Genetic heteroscedasticity of teat count in pigs. *J. Anim. Breed. Genet.* 132:392–398. doi:10.1111/JBG.12134

Garcia-Baccino, C. A., C. Marie-Etancelin, F. Tortereau, D. Marcon, J. L. Weisbecker, and A. Legarra. 2021. Detection of unrecorded environmental challenges in high-frequency recorded traits, and genetic determinism of resilience to challenge, with an application on feed intake in lambs. *Genet. Sel. Evol.* 53:1–14. doi:10.1186/S12711-020-00595-X/FIGURES/6.

Gerrard, D. E., and A. L. Grant. 2006. *Principles of animal growth and development*, Kendall/Hunt Publishing.

Ghiasi, H., and M. Felleki. 2016. Joint estimation of (co) variance components and breeding values for mean and dispersion of days from calving to first service in Holstein cow. *Anim. Prod. Sci.* 57:760–766. doi:10.1071/AN15643.

Gilmour, K. M., J. D. DiBattista, and J. B. Thomas. 2005. Physiological Causes and Consequences of Social Status in Salmonid Fish. *Integr. Comp. Biol.* 45:263–273. doi:10.1093/ICB/45.2.263.

Gorssen, W., N. Buys, and S. Janssens. 2018. Genetic parameters for uniformity of fattening pigs' growth traits. In: *Proceedings of the World Congress on Genetics Applied to Livestock Production*.

Greenwood, P. L. 2021. Review: An overview of beef production from pasture and feedlot globally, as demand for beef and the need for sustainable practices increase. *Animal*. 15:100295. doi:10.1016/J.ANIMAL.2021.100295.

Harrison, R. L. 2010. Introduction To Monte Carlo Simulation. *AIP Conf. Proc.* 1204:17. doi:10.1063/1.3295638.

Hayek, M. N., R. D. Garrett, M. E. Skidmore, K. M. Sims, and L. L. Rausch. 2018. Nationwide shift to grass-fed beef requires larger cattle population. *Environ. Res. Lett.* 13:084005. doi:10.1088/1748-9326/AAD401.

Henderson, C. R. 1988. Theoretical Basis and Computational Methods for a Number of Different Animal Models. *J. Dairy Sci.* 71:1–16. doi:10.1016/S0022-0302(88)79974-9.

Hennessy, D. A. 2005. Slaughterhouse rules: animal uniformity and regulating for food safety in meat packing. *Am J Agric Econ.* 87:600–609. doi:10.1111/j.1467-8276.2005.00750.x.

Herring, A. D. . 1965-. 2014. *Beef cattle production systems*. CAB International,

Wallingford, Oxfordshire :

Hickson, R. E., S. T. Morris, P. R. Kenyon, and N. Lopez-Villalobos. 2006. Dystocia in beef heifers: A review of genetic and nutritional influences. *N. Z. Vet. J.* 54:256–264. doi:10.1080/00480169.2006.36708.

Hill, W. G., M. R. Edwards, M. K. A. Ahmed, and R. Thompson. 1983. Heritability of milk yield and composition at different levels and variability of production. *Anim. Sci.* 36:59–68. doi:10.1017/S0003356100039933.

Hill, W. G., and H. A. Mulder. 2010. Genetic analysis of environmental variation. *Genet. Res. (Camb).* 92:381–395. doi:10.1017/S0016672310000546.

Hill, W. G., and X. S. Zhang. 2004. Effects on phenotypic variability of directional selection arising through genetic differences in residual variability. *Genet. Res. (Camb).* 83:121–132. doi:10.1017/S0016672304006640.

Hoaglin, D. C., and R. E. Welsch. 1978. The hat matrix in regression and anova. *Am. Stat.* 32:17–22. doi:10.1080/00031305.1978.10479237.

Hohenboken, W. D. 1985. The Manipulation of Variation in Quantitative Traits: A Review of Possible Genetic Strategies. *J. Anim. Sci.* 60:101–110. doi:10.2527/JAS1985.601101X.

Howard, J. T., J. E. Pryce, C. Baes, and C. Maltecca. 2017. Invited review: Inbreeding in the genomics era: Inbreeding, inbreeding depression, and management of genomic variability. *J. Dairy Sci.* 100:6009–6024. doi:10.3168/JDS.2017-12787.

Ibáñez-Escriche, N., L. Varona, D. Sorensen, and J. L. Noguera. 2008. A study of heterogeneity of environmental variance for slaughter weight in pigs. *Animal.* 2:19–26. doi:10.1017/S1751731107001000.

Iung, L. H. de S., R. Carvalheiro, H. H. de R. Neves, and H. A. Mulder. 2020. Genetics and genomics of uniformity and resilience in livestock and aquaculture species: A review. *J. Anim. Breed. Genet.* 137:263–280. doi:10.1111/JBG.12454.

Iung, L. H. S., H. H. R. Neves, H. A. Mulder, and R. Carvalheiro. 2017. Genetic control of residual variance of yearling weight in Nellore beef cattle. *J. Anim. Sci.* 95:1425–1433. doi:10.2527/JAS.2016.1326.

Janhunen, M., A. Kause, H. Vehviläinen, and O. Jarvisalo. 2012. Genetics of Microenvironmental Sensitivity of Body Weight in Rainbow Trout (*Oncorhynchus mykiss*) Selected for Improved Growth. *PLoS One.* 7:e38766. doi:10.1371/JOURNAL.PONE.0038766.

- Júnior, R. N. C. C., L. da Silva Fernandes, J. C. do Carmo Panetto, M. V. G. B. da Silva, C. V. de Araújo, A. G. M. Silva, J. R. F. Marques, W. C. da Silva, S. I. de Araújo, S. R. S. de Castro, L. K. X. Silva, S. V. Castro, and J. de Brito Lourenço Júnior. 2023. Heterogeneity of variance and genetic parameters for milk production in cattle, using Bayesian inference. *PLoS One*. 18. doi:10.1371/JOURNAL.PONE.0288257.
- Khaw, H. L., R. W. Ponzoni, H. Y. Yee, M. A. bin Aziz, H. A. Mulder, J. Marjanovic, and P. Bijma. 2016. Genetic variance for uniformity of harvest weight in Nile tilapia (*Oreochromis niloticus*). *Aquaculture*. 451:113–120. doi:10.1016/J.AQUACULTURE.2015.09.003.
- Koehn, J. Z., E. H. Allison, N. Franz, and E. S. Wieggers. 2017. How Can the Oceans Help Feed 9 Billion People? *Conserv. Anthr. Ocean Interdiscip. Sci. Support Nat. People*. 65–88. doi:10.1016/B978-0-12-805375-1.00004-0.
- Lee, Y., and J. A. Nelder. 1996. Hierarchical Generalized Linear Models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 58:619–656. doi:10.1111/J.2517-6161.1996.TB02105.X.
- Legarra, A., I. Aguilar, and I. Misztal. 2009. A relationship matrix including full pedigree
- Marjanovic, J., H. A. Mulder, H. L. Khaw, and P. Bijma. 2016. Genetic parameters for uniformity of harvest weight and body size traits in the GIFT strain of Nile tilapia. *Genet. Sel. Evol.* 48:1–10. doi:10.1186/S12711-016-0218-9/TABLES/4.
- Marjanovic, J., H. A. Mulder, L. Rönnegård, and P. Bijma. 2018. Modelling the co-evolution of indirect genetic effects and inherited variability. *Hered.* 2018 1216. 121:631–647. doi:10.1038/s41437-018-0068-z.
- Martinez, C. C., J. G. Maples, and J. Benavidez. 2021. Beef Cattle Markets and COVID-19. *Appl. Econ. Perspect. Policy*. 43:304–314. doi:10.1002/AEPP.13080.
- Maxwell, C. L., C. R. Krehbiel, B. K. Wilson, B. T. Johnson, B. C. Bernhard, C. F. O'Neill, D. L. Vanoverbeke, G. G. Mafi, D. L. Step, and C. J. Richards. 2014. Effects of beef production system on animal performance and carcass characteristics. *J. Anim. Sci.* 92:5727–5738. doi:10.2527/JAS.2014-7639.
- Mee, J. F. 2008. Prevalence and risk factors for dystocia in dairy cattle: A review. *Vet. J.* 176:93–101. doi:10.1016/J.TVJL.2007.12.032.
- Milligan, B. N., D. Fraser, and D. L. Kramer. 2002. Within-litter birth weight variation in the domestic pig and its relation to pre-weaning survival, weight gain, and variation in weaning weights. *Livest. Prod. Sci.* 76:181–191. doi:10.1016/S0301-6226(02)00012-X.
- Misztal, I., A. Legarra, and I. Aguilar. 2009. Computing procedures for genetic evaluation including phenotypic, full pedigree, and genomic information. *J. Dairy Sci.* 92:4648–4655. doi:10.3168/jds.2009-2064.

- Mulder, H. A., P. Bijma, and W. G. Hill. 2007. Prediction of Breeding Values and Selection Responses With Genetic Heterogeneity of Environmental Variance. *Genetics*. 175:1895. doi:10.1534/GENETICS.106.063743.
- Mulder, H. A., R. E. Crump, M. P. L. Calus, and R. F. Veerkamp. 2013. Unraveling the genetic architecture of environmental variance of somatic cell score using high-density single nucleotide polymorphism and cow data from experimental farms. *J. Dairy Sci.* 96:7306–7317. doi:10.3168/JDS.2013-6818.
- Mulder, H. A., W. G. Hill, A. Vereijken, and R. F. Veerkamp. 2009. Estimation of genetic variation in residual variance in female and male broiler chickens. *Animal*. 3:1673–1680. doi:10.1017/S1751731109990668.
- Mulder, H. A., J. Visscher, and J. Fablet. 2016. Estimating the purebred-crossbred genetic correlation for uniformity of eggshell color in laying hens. *Genet. Sel. Evol.* 48:1–13. doi:10.1186/S12711-016-0212-2/TABLES/6.
- Neto, A. C., J. F. Lui, J. L. R. Sarmiento, M. N. Ribeiro, J. M. C. Monteiro, C. Fonseca, and H. Tonhati. 2009. Estimation models of variance components for farrowing interval in swine. *Brazilian Arch. Biol. Technol.* 52:69–76. doi:10.1590/S1516-89132009000100009.
- Neves, H. H. R., R. Carneiro, and S. A. Queiroz. 2012. Genetic and environmental heterogeneity of residual variance of weight traits in Nellore beef cattle. *Genet. Sel. Evol.* 44:1–12. doi:10.1186/1297-9686-44-19/TABLES/5.
- Neves, H. H. R., R. Carneiro, V. M. Roso, and S. A. Queiroz. 2011. Genetic variability of residual variance of production traits in Nellore beef cattle. *Livest. Sci.* 142:164–169. doi:10.1016/J.LIVSCI.2011.07.010.
- Van Nieuwamerongen, S. E., J. E. Bolhuis, C. M. C. Van Der Peet-Schwering, and N. M. Soede. 2014. A review of sow and piglet behaviour and performance in group housing systems for lactating sows. *Animal*. 8:448–460. doi:10.1017/S1751731113002280.
- Owens, F. N., P. Dubeski, and C. F. Hanson. 1993. Factors that alter the growth and development of ruminants. *J. Anim. Sci.* 71:3138–3150. doi:10.2527/1993.71113138X.
- Pardo, C. E., M. Kreuzer, and G. Bee. 2013. Effect of average litter weight in pigs on growth performance, carcass characteristics and meat quality of the offspring as depending on birth weight. *animal*. 7:1884–1892. doi:10.1017/S1751731113001419.
- Price, T. D., and J. N. Wiltbank. 1978. Dystocia in cattle a review and implications. *Theriogenology*. 9:195–219. doi:10.1016/0093-691X(78)90030-4.

- Retallick K. New foot structure EPDs: claw set and foot angle. 2019. <https://www.angus.org/media/news/fullarticle?aiid=1030<itle=new-foot-structure-epds-claw-set-and-foot-angle>. Accessed June 2024.
- Rönnegård, L., M. Felleki, F. Fikse, H. A. Mulder, and E. Strandberg. 2010. Genetic heterogeneity of residual variance - Estimation of variance components using double hierarchical generalized linear models. *Genet. Sel. Evol.* 42:1–10. doi:10.1186/1297-9686-42-8/FIGURES/1.
- Rönnegård, L., M. Felleki, W. F. Fikse, H. A. Mulder, and E. Strandberg. 2013. Variance component and breeding value estimation for genetic heterogeneity of residual variance in Swedish Holstein dairy cattle. *J. Dairy Sci.* 96:2627–2636. doi:10.3168/JDS.2012-6198.
- Ros, M., D. Sorensen, R. Waagepetersen, M. Dupont-Nivet, M. SanCristobal, J. C. Bonnet, and J. Mallard. 2004. Evidence for Genetic Control of Adult Weight Plasticity in the Snail *Helix aspersa*. *Genetics*. 168:2089. doi:10.1534/GENETICS.104.032672.
- Rowe, S. J., I. M. White, S. Avendaño, and W. G. Hill. 2006. Genetic heterogeneity of residual variance in broiler chickens. *Genet. Sel. Evol.* 38:617. doi:10.1186/1297-9686-38-6-617.
- Sae-Lim, P., J. H. Jakobsen, and H. A. Mulder. 2018. Uniformity in birth weight is heritable in Norwegian White Sheep. In: *Proceedings of the World Congress on Genetics Applied to Livestock Production*. Auckland.
- Sae-Lim, P., A. Kause, M. Janhunen, H. Vehviläinen, H. Koskinen, B. Gjerde, M. Lillehammer, and H. A. Mulder. 2015. Genetic (co)variance of rainbow trout (*Oncorhynchus mykiss*) body weight and its uniformity across production environments. *Genet. Sel. Evol.* 47:1–10. doi:10.1186/S12711-015-0122-8/TABLES/3.
- Sae-Lim, P., A. Kause, M. Lillehammer, and H. A. Mulder. 2017. Estimation of breeding values for uniformity of growth in Atlantic salmon (*Salmo salar*) using pedigree relationships or single-step genomic evaluation. *Genet. Sel. Evol.* 49:1–12. doi:10.1186/S12711-017-0308-3/TABLES/3.
- SanCristobal-Gaudy, M., L. Bodin, J.-M. Elsen, and C. Chevalet. 2001. Genetic components of litter size variability in sheep. *Genet. Sel. Evol.* 2001 333. 33:1–23. doi:10.1186/1297-9686-33-3-249.
- SanCristobal-Gaudy, M., J.-M. Elsen, L. Bodin, and C. Chevalet. 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. *Genet. Sel. Evol.* 1998 305. 30:1–29. doi:10.1186/1297-9686-30-5-423.
- Sell-Kubiak, E. 2021. Selection for litter size and litter birthweight in Large White pigs: Maximum, mean and variability of reproduction traits. *Animal*. 15:100352.

doi:10.1016/J.ANIMAL.2021.100352.

Sell-Kubiak, E., P. Bijma, E. F. Knol, and H. A. Mulder. 2015a. Comparison of methods to study uniformity of traits: Application to birth weight in pigs. *J. Anim. Sci.* 93:900–911. doi:10.2527/JAS.2014-8313.

Sell-Kubiak, E., N. Duijvesteijn, M. S. Lopes, L. L. G. Janss, E. F. Knol, P. Bijma, and H. A. Mulder. 2015b. Genome-wide association study reveals novel loci for litter size and its variability in a Large White pig population. *BMC Genomics.* 16:1–13. doi:10.1186/S12864-015-2273-Y/FIGURES/4.

Sell-Kubiak, E., E. F. Knol, and H. A. Mulder. 2019. Selecting for changes in average “parity curve” pattern of litter size in Large White pigs. *J. Anim. Breed. Genet.* 136:134–148. doi:10.1111/JBG.12372.

Sell-Kubiak, E., S. Wang, E. F. Knol, and H. A. Mulder. 2015c. Genetic analysis of within-litter variation in piglets’ birth weight using genomic or pedigree relationship matrices. *J. Anim. Sci.* 93:1471–1480. doi:10.2527/JAS.2014-8674.

Silva, A. A., D. A. Silva, C. R. M. Pereira, C. P. Abreu, G. Caetano, J. T. Paiva, F. F. Silva, P. S. Lopes, and R. Veroneze. 2021. Exploring the use of residual variance for uniformity of body weight in meat quail lines using Bayesian inference. *Br. Poult. Sci.* 62:474–484. doi:10.1080/00071668.2021.1894320.

Sitz, T., H. DelCurto-Wyffels, M. Van Emon, S. Wyffels, K. Retallick, E. Tarpoff, K. Kangas, and T. DelCurto. 2023. Importance of Foot and Leg Structure for Beef Cattle in Forage-Based Production Systems. *Animals.* 13:495. doi:10.3390/ANI13030495/S1.

Sonesson, A. K., J. Ødegård, and L. Rönnegård. 2013. Genetic heterogeneity of within-family variance of body weight in Atlantic salmon (*Salmo salar*). *Genet. Sel. Evol.* 45:1–8. doi:10.1186/1297-9686-45-41/TABLES/4.

Sorensen, D., and R. Waagepetersen. 2003. Normal linear models with genetically structured residual variance heterogeneity: a case study. *Genet. Res. (Camb).* 82:207–222. doi:10.1017/S0016672303006426.

Southwood, O. I., and B. W. Kennedy. 1991. Genetic and environmental trends for litter size in swine. *J. Anim. Sci.* 69:3177–3182. doi:10.2527/1991.6983177X.

Starling, J. M. C., R. G. da Silva, M. Cerón-Muñoz, G. S. S. C. Barbosa, and M. J. R. Paranhos da Costa. 2002. Análise de algumas variáveis fisiológicas para avaliação do grau de adaptação de ovinos submetidos ao estresse por calor. *Rev. Bras. Zootec.* 31:2070–2077. doi:10.1590/S1516-35982002000800022.

Vandenplas, J., C. Bastin, N. Gengler, and H. A. Mulder. 2013. Genetic variance in micro-environmental sensitivity for milk and milk quality in Walloon Holstein cattle. *J. Dairy Sci.* 96:5977–5990. doi:10.3168/jds.2012-6521.

- Van Vleck, L. D. 1968. Variation of Milk Records Within Paternal-Sib Groups. *J. Dairy Sci.* 51:1465–1470. doi:10.3168/JDS.S0022-0302(68)87213-3.
- Wellmann, R. 2023. Selection index theory for populations under directional and stabilizing selection. *Genet. Sel. Evol.* 55:1–17. doi:10.1186/S12711-023-00776-4/FIGURES/4.
- Wilson, H. R. 1991. Interrelationships of egg size, chick size, posthatching growth and hatchability. *Worlds. Poult. Sci. J.* 47:5–20. doi:10.1079/WPS19910002.
- Wittenburg, D., V. Guiard, F. Teuscher, and N. Reinsch. 2008. Comparison of statistical models to analyse the genetic effect on within-litter variance in pigs. *Animal.* 2:1559–1568. doi:10.1017/S1751731108002851.
- Wolc, A., J. Arango, P. Settar, J. E. Fulton, N. P. O’Sullivan, R. Preisinger, D. Habier, R. Fernando, D. J. Garrick, W. G. Hill, and J. C. M. Dekkers. 2012. Genome-wide association analysis and genetic architecture of egg weight and egg uniformity in layer chickens. *Anim. Genet.* 43:87–96. doi:10.1111/J.1365-2052.2012.02381.X.
- Wolc, A., M. S. White, S. Avendano, and W. G. Hill. 2009. Genetic variability in residual variation of body weight and conformation scores in broiler chickens. *Poult. Sci.* 88:1156–1161. doi:10.3382/PS.2008-00547.
- Yang, Y., O. F. Christensen, and D. Sorensen. 2011. Analysis of a genetically structured variance heterogeneity model using the Box-Cox transformation. *Genet. Res. (Camb).* 93:33–46. doi:10.1017/S0016672310000418.
- Zaalberg, R. M., T. T. Chu, H. Bovbjerg, J. Jensen, and T. M. Villumsen. 2023. Genetic parameters for early piglet weight, litter traits and number of functional teats in organic pigs. *animal.* 17:100717. doi:10.1016/J.ANIMAL.2023.100717.
- Zeidler, G. 2002. Processing and Packaging Shell Eggs. *Commer. Chick. Meat Egg Prod.* 1129–1161. doi:10.1007/978-1-4615-0811-3_58.
- Zhang, T., L. G. Wang, H. B. Shi, H. Yan, L. C. Zhang, X. Liu, L. Pu, J. Liang, Y. B. Zhang, K. Bin Zhao, and L. X. Wang. 2016. Heritabilities and genetic and phenotypic correlations of litter uniformity and litter size in Large White sows. *J. Integr. Agric.* 15:848–854. doi:10.1016/S2095-3119(15)61155-8.
- Zygoyiannis, D. 2006. Sheep production in the world and in Greece. *Small Rumin. Res.* 62:143–147. doi:10.1016/j.smallrumres.2005.07.043.

**Chapter 3: GENETIC HETEROGENEITY OF RESIDUAL VARIANCE FOR
GROWTH TRAITS IN AMERICAN ANGUS CATTLE**

ABSTRACT

Economic incentives have increased the demand for more uniform animal production, making uniformity of beef production a prospective phenotype in genetic studies. Recent studies on genetic heterogeneity of residual variance have provided evidence for genetic control of residual variance, enabling reduction of variability through selection. However, research on genetic heterogeneity of residual variance in the American Angus population is limited. Therefore, the objectives of this study were 1) to investigate the extent of genetic heterogeneity of residual variances on three growth traits: birth weight (BW), weaning weight (WW), and yearling weight (YW) in Angus cattle, 2) to compare genetic homogeneity (M1) and genetic heterogeneity of residual variance models: double hierarchical generalized linear model (DHGLM, M2) and a genetically structured environmental variance model (M3), and 3) to evaluate the effectiveness of power transformation to account for scale differences. The comparison was based on the estimated genetic parameters for mean and residual variance. A total of 75,000 BW, 74,975 WW, and 49,803 YW records were used in the analysis. M1 and M2 used average information restricted maximum likelihood, and M3 used Markov chain Monte Carlo. Our results showed the presence of genetic heterogeneity of residual variances on growth traits and the possibility of selection as measured by the genetic coefficient of variation of residual variance (0.90 to 0.92 in M2 and 0.31 to 0.38 in M3 for BW; 0.64 in M2 and 0.01 to 0.29 in M3 for WW; and 0.67 to 0.63 in M2 and 0.25 to 0.31 in M3 for YW) using untransformed and Box-Cox transformed data. The low heritability estimates for residual variance were obtained in M2 (0.08 and 0.08 for BW, 0.06 and 0.001 for WW, and 0.09 for YW, using the untransformed and transformed data, respectively). Our

study found both negative and positive genetic correlations between mean and residual variance, depending on the traits, untransformed or transformed data, and models used. The negative genetic correlations between mean and residual variance found for BW (-0.49 for untransformed data in M3), WW (-0.04 for transformed data in M2), and YW (-0.46 for transformed data in M3) indicate the possibility of increasing the means of these traits while decreasing their variances. On the other hand, the estimated positive genetic correlations indicate that the genetic response to selection for production uniformity may be limited when increasing the mean of BW, WW, and YW, unless a selection index is used. Data transformation reduced the skewness of the data and consequently the mean-variance relationship, but genetic heterogeneity of residual variances persisted beyond scale effects. When comparing estimates between the DHGLM and genetically structured Bayesian approaches, the Bayesian approach resulted in higher estimates of additive genetic variance for residual variance. Our results demonstrate the potential to reduce variability through selection and represent a first step in exploring the possibility of incorporating uniformity of growth traits into breeding goals.

Keywords: beef cattle, birth weight, double hierarchical generalized linear model, genetic heterogeneity of residual variance, uniformity of production, weaning weight, yearling weight

INTRODUCTION

Genetic improvement of beef cattle considers several traits of economic importance, such as live weight traits (i.e., birth, weaning, and yearling weights) as indicators of growth performance (Archer and Bergh, 2000; Koknaroglu et al., 2005). Understanding the factors that determine variation in these phenotypes has been of ongoing interest to geneticists and animal breeders because variability is the basis for breeding programs.

Genetic variation is essential for progress in breeding successive generations and is needed to meet production demands in different environments, to enable continuous genetic improvement, and to facilitate rapid adaptation to changing breeding objectives (Notter, 1999). In terms of economic returns, more uniform animal performance and products have become increasingly relevant in the livestock industry, mainly through bonus programs to encourage farmers to deliver more homogeneous products (Hennessy, 2005; Merks et al., 2012; de Oliveira et al., 2017). In the case of beef cattle, producers may receive different payments for specific standards of carcass weight and fat thickness. Hence, the lack of uniformity can result in economic losses, such as 1) lower birth weight resulting in weaker or higher birth weight resulting in dystocia (Zaborski et al., 2009), 2) increased management practices to place calves with similar weaning weights in management groups, and 3) longer feeding periods due to lower growth rates resulting in increased input costs to reach market weight (Murray, 1980; Thonney et al., 1981; Archer and Bergh, 2000). In addition to economic losses, studies in various livestock and aquaculture species have reported that lack of homogeneity can lead to competition (affecting feed efficiency and potentially causing mortality) (Gilmour et al., 2005), increased stress, and delays in processing (Milligan et al., 2002).

Recent studies have provided evidence for genetic control of residual variance, making uniformity a potential phenotype to be explored in animal genetic studies. Mackay and Lyman (2005) and Mulder et al. (2007) reported empirical evidence that different genotypes respond differently to environmental variation, resulting in genetic differences in residual variance. A standard quantitative genetic model usually assumes that residual variance between genotypes is constant, suggesting that genotypes differ only in their mean effects (Falconer and Mackay, 1996). However, given evidence that residual variance may also be under genetic control, new models can be used to account for potential genotypic differences in residual variance (Sancristobal-Gaudy et al., 1998; Sorensen and Waagepetersen, 2003; Hill and Zhang, 2004; Ros et al., 2004; Mulder et al., 2007; Mulder et al., 2009a; Felleki et al., 2012).

Although uniformity of growth traits is a relevant with potential for inclusion in beef cattle breeding programs, there is still limited information on the presence of genetic variation for residual variance in birth, weaning, and yearling weights (Neves et al., 2011; Neves et al., 2012; Iung et al., 2017). Therefore, the objectives of this study were 1) to investigate the genetic heterogeneity of pedigree level residual variance for growth traits in American Angus cattle, 2) to compare the results of different genetic heterogeneity models, and 3) to evaluate the effectiveness of the Box-Cox transformation to account for possible scale differences.

MATERIAL AND METHODS

Ethics Statement

Institutional Animal Care and Use Committee approval was not required for this study because the data were obtained from the American Angus Association database.

Data

The dataset was provided by Angus Genetics Inc. and included phenotypic information for three growth traits: birth weight (BW), weaning weight (WN), and yearling weight (YW). During data cleaning, only records within 3 standard deviations from the mean were retained for analysis. Descriptive statistics of the data are presented in Table 1.

Table 1. Descriptive statistics for growth traits.

Trait	N¹	Minimum (lb)	Maximum (lb)	Mean±SD	Skewness	Kurtosis
Birth weight	75,000	75.00	139.00	117.5 ± 9.33	-0.24	-0.02
Weaning Weight	74,975	500.00	1,066.00	641.9 ± 81.82	0.67	0.52
Yearling Weight	49,803	1,272	1,600	1,476 ± 62.17	0.01	-0.72

N¹= Number of records.

WW was measured around 208 days of age, with a minimum of 120 days and a maximum of 280 days, and YW was measured around 392 days of age, with a minimum of 315 days and a maximum of 618 days. Animals were born between 1986 and 2013 and raised in different ecoregions of the United States. Contemporary groups (CG) were formed by concatenating sex, herd, year, and season of birth. CG with at least 100 animals for YW and 200 animals for BW and WW were retained for analysis. Table 2 shows the data structure after data cleaning.

Table 2. Data structure for growth traits.

	Trait		
	BW	WW	YW
Number of Records	75,000	74,975	49,803
Number of Animals in Pedigree	133,405	125,714	90,122
Number of Contemporary Groups	318	307	422
Number of Sires	3,967	3,315	3,652
Number of Dams	54,438	47,424	36,667
Average Number of Progeny per Sire	18.91	22.62	13.64
Average Number of Animals per CG	235.85	244.22	118.02

BW: Birth Weight. WW: Weaning Weight. YW: Yearling Weight. CG: Contemporary Group.

Data Transformation

To account for possible scale effects (i.e., higher means associated with higher variances) and to reduce the mean-variance relationship, a Box-Cox transformation (Box and Cox, 1964) was performed for all traits (Yang et al., 2011). The transformed data were obtained as:

$$y^\lambda = \left[\frac{(y^\lambda - 1)}{\lambda} \right]$$

where y is the phenotypic records of BW, WW, and YW, and λ is a transformation parameter. To obtain the optimal λ for BW, YW, and WW, a model including the fixed

effects of CG and age of dam (for BW and WW) or age of animal (for YR) as a covariate (linear) was fitted using the MASS package (Venables and Ripley, 2002) in R (R Development Core Team, 2023).

Estimation of variance components

Three models were fitted to estimate genetic parameters using restricted maximum likelihood (REML) and Bayesian approaches. The first was a homoscedastic best linear unbiased prediction model (M1), which is the traditional additive genetic model including the assumption of homogeneity of residual variance, where REML was used to infer variance components. The second (M2) and third (M3) models assumed that residual variance is heterogeneous and partially under genetic control. A REML-based double hierarchical generalized linear model (DHGLM) (Rönnegård et al., 2010) and a Bayesian genetically structured model (SanCristobal-Gaudy et al. 1998) were used in M2 and M3, respectively. M1 and M2 were implemented using the average information REML module of the DMU package (Madsen and Jensen, 2013), while M3 was implemented using the GSEVM software (Ibáñez-Escriche et al., 2010).

Homoscedastic Residual Variance Model (M1)

The following standard animal model for BW and WW, assuming homogeneous residual variance, was fitted for M1:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{W}\mathbf{c} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of observations (BW or WW); $\mathbf{b}$ is a vector of fixed effects including CGs and dam age at calving as a linear covariate; $\mathbf{a}$ is a vector of direct additive genetic

effects; $\mathbf{m}$ is a vector of maternal additive genetic effects; $\mathbf{c}$ is a vector of maternal permanent environmental effects; $\mathbf{e}$ is a vector of residuals; and $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, and $\mathbf{W}$ are incidence matrices relating $\mathbf{b}$, $\mathbf{a}$, $\mathbf{m}$, and $\mathbf{c}$ to $\mathbf{y}$, respectively. It was assumed that:

$$E = \begin{bmatrix} y \\ a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{Xb} \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}; V \begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{I}_d \sigma_c^2 & 0 \\ 0 & 0 & \mathbf{I}_n \sigma_e^2 \end{bmatrix}$$

where $\mathbf{G} = \begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix}$ is a matrix of genetic covariances between direct and maternal effects; σ_a^2 is the additive genetic variance; σ_m^2 is the maternal additive genetic variance; σ_{am} is the covariance between maternal and direct additive genetic effects; $\mathbf{A}$ is the pedigree-based relationship matrix; $\mathbf{I}_d$ is the identity matrix of order equal to the number of dams; σ_c^2 is the maternal permanent environmental variance; $\mathbf{I}_n$ is the identity matrix equal to the number of observations; and σ_e^2 is the residual variance.

The following standard animal model was used for YW:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of phenotypes, $\mathbf{X}$ is an incidence matrix of systematic effects; $\mathbf{b}$ is a vector of systematic effects (CGs including animals born on the same farm, in the same year, and from the same management group at yearling, and age at yearling as a linear covariate); $\mathbf{Z}$ is an incidence matrix relating individuals to phenotypic records; $\mathbf{a}$ is the additive genetic variance with $\mathbf{a} \sim N(0, \mathbf{A}\sigma_a^2)$; and $\mathbf{e}$ is a vector of residuals, assuming $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$.

Heterogeneous Residual Variance Models

Model (M2)

Genetic heterogeneity of residual variance has been studied under various models, such as DHGLM. This approach is an extension of generalized linear models (Lee and Nelder, 1996). DHGLM handles non-normal data by assuming a gamma distribution (a flexible probability distribution often used to model positively skewed data) for the squared residuals (Rönnegård et al., 2010). During each iteration, the model fits the gamma distribution to the squared residuals and updates the parameter estimates, aiming to address the non-normality issue by modeling the squared residuals rather than the raw data, or in other words, to transpose the non-normality issue by using squared residuals. Later, the DHGLM approach was extended by simultaneously fitting the trait (also referred to as the mean) and residual variance within a bivariate model as follows (Felleki et al., 2012):

$$\begin{bmatrix} \mathbf{y} \\ \boldsymbol{\psi} \end{bmatrix} = \begin{bmatrix} \mathbf{X} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_v \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{b}_v \end{bmatrix} + \begin{bmatrix} \mathbf{Z} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_v \end{bmatrix} \begin{bmatrix} \mathbf{a} \\ \mathbf{a}_v \end{bmatrix} + \begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix}$$

where $\mathbf{y}$ is the trait (BW, WW, or YW) and $\boldsymbol{\psi}$ is the linearized response variable for the residual variance and is defined as:

$$\psi_i = \log(\hat{\sigma}_{e_i}^2) + \left(\left[\hat{e}_i^2 / (1 - h_i) \right] - \hat{\sigma}_{e_i}^2 \right) / \hat{\sigma}_{e_i}^2$$

Here, $\hat{\sigma}_{e_i}^2$ is the predicted residual variance for observation i from the previous iteration; $\hat{e}_i^2$ is the squared residual from the mean model estimated for observation i ; and h_i is the leverage for observation i that is the i^{th} diagonal element of the hat matrix (Hoaglin and Welsch, 1978); $\mathbf{Xb}$ and $\mathbf{X}_v \mathbf{b}_v$ are fixed effects for the mean and residual variance parts, respectively; $\mathbf{Za}$ and $\mathbf{Z}_v \mathbf{a}_v$ are the additive genetic effects for the mean and residual variance parts, respectively; and $\mathbf{e}$ and $\mathbf{e}_v$ are residuals for the mean and residual variance parts, respectively. The other effects in the model are the same as those described previously for M1. Further, it was assumed that

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{a}_v \end{bmatrix} \sim N(0, \begin{bmatrix} \sigma_a^2 & \sigma_{a,a_v} \\ \sigma_{a,a_v} & \sigma_{a_v}^2 \end{bmatrix} \otimes \mathbf{A})$$

and

$$\begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix} \sim N(0, \begin{bmatrix} \mathbf{W}^{-1}\sigma_e^2 & 0 \\ 0 & \mathbf{W}_v^{-1}\sigma_{e_v}^2 \end{bmatrix} \otimes \mathbf{I})$$

where $\mathbf{W} = \text{diag}(\hat{\Psi}^{-1})$ and $\mathbf{W}_v = \text{diag}\left(\frac{1-h}{2}\right)$ are the residual variance per observation, because σ_e^2 and $\sigma_{e_v}^2$ are scaling variances that are expected to be equal to 1. Ψ , $\mathbf{W}$, and $\mathbf{W}_v$ were updated in each iteration until the algorithm converged. Convergence was assumed when the relative difference in the estimates of the variance components between iterations was less than 10^{-6} .

Model 3 (M3)

Model 3 followed a genetically structured variance model proposed by SanCristobal-Gaudy et al. (1998), which assumes that residual variance is heterogeneous and partially under genetic control. M3 for BW and WW was:

$$y_i = \mathbf{x}_i \mathbf{b} + \mathbf{z}_i \mathbf{a} + \mathbf{w}_i \mathbf{c} + e^{\frac{1}{2}(\mathbf{x}_i \mathbf{b}^* + \mathbf{z}_i \mathbf{a}^* + \mathbf{w}_i \mathbf{c}^*)} \varepsilon_i$$

And for YW:

$$y_i = \mathbf{x}_i \mathbf{b} + \mathbf{z}_i \mathbf{a} + e^{\frac{1}{2}(\mathbf{x}_i \mathbf{b}^* + \mathbf{z}_i \mathbf{a}^*)} \varepsilon_i$$

where * indicates parameters associated with residual variance; $\mathbf{b}$ and $\mathbf{b}^*$ are the vectors of systematic effects, $\mathbf{a}$ and $\mathbf{a}^*$ are the vectors of direct genetic effects; $\mathbf{c}$ and $\mathbf{c}^*$ represent

the vectors associated with permanent environmental effects (BW and WW); and $\mathbf{x}_i$, $\mathbf{z}_i$, and $\mathbf{w}_i$ are the same as those described previously for M1 and M2.

Moreover, $\mathbf{a}$ and $\mathbf{a}^*$ are assumed to be Gaussian and jointly distributed:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{a}^* \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \rho\sigma_a\sigma_{a^*} \\ \rho\sigma_a\sigma_{a^*} & \sigma_{a^*}^2 \end{bmatrix} \otimes \mathbf{A}\right)$$

where $\mathbf{A}$ represents the numerator relationship matrix, σ_a^2 is the additive genetic variance; $\sigma_{a^*}^2$ is the additive genetic variance that influences the residual variance of the trait; ρ is the correlation coefficient between σ_a^2 and $\sigma_{a^*}^2$; and $\otimes$ denotes the Kronecker product.

Also, $\sigma_{a^*}^2$ was directly compared to σ_{av}^2 in M2 in the following sections.

Lastly, $\mathbf{c}$ and $\mathbf{c}^*$ were assumed to be independent:

$$\mathbf{c} \sim N(\mathbf{0}, \mathbf{I}_c \sigma_c^2)$$

$$\mathbf{c}^* \sim N(\mathbf{0}, \mathbf{I}_c \sigma_{c^*}^2)$$

where $\mathbf{I}_c$ is an identity matrix of the same order as the number of animals recorded for BW and WW, and σ_c^2 and $\sigma_{c^*}^2$ are the permanent environmental variances affecting the mean and residual variance, respectively. M3 was implemented using the GSEVM program (Ibáñez-Escriche et al., 2010). For each trait, the Markov chain Monte Carlo run consisted of 500,000 iterations with a burn-in period of 50,000 iterations. The Geweke criterion (Geweke, 1991) was used to diagnose the chains at a 5% significance level using the boa package (Smith, 2007) in R (R Development Core Team, 2021).

Genetic Parameters for the Mean and Residual Variance

The variance components obtained from M1, M2, and M3 were used to estimate genetic parameters for BW, WW, and YW. For M2, two genetic parameters were calculated for the residual variance: the heritability of the residual variance (h_v^2) and the

genetic coefficient of variation, GCV_E (Mulder et al., 2007). h_v^2 is used to determine the accuracy of the estimated breeding values (EBV) for the residual variance, which is calculated as follows:

$$h_v^2 = \frac{\sigma_{a_v,add}^2}{(2\sigma_p^4 + 3\sigma_{a_v,add}^2)}$$

where $\sigma_{a_v,add}^2$ is the additive genetic variance estimated for the residual variance on the additive scale and σ_p^4 is the squared phenotypic variance. Here, $\sigma_{a_v,add}^2$ and the standard error of h_v^2 were obtained according to Mulder et al. (2016). GCV_E evaluates the potential response to selection for residual variance as follows:

$$GCV_E = \frac{\sigma_{av,add}}{\bar{\sigma}_e^2}$$

where $\sigma_{a_v,add}$ is the standard deviation of the additive genetic variance for the residual variance on the additive scale. GCV_E was calculated as described in (Mulder et al., 2007; Hill and Mulder, 2010).

Under M3, heritability estimates of the mean of BW, WW, and YW are not unique because they depend on the value of the residual variance, which is influenced by different levels of environmental effects (represented by $\mathbf{b}^*$) (Ibáñez-Escriche et al., 2008; Formoso-Rafferty et al., 2017):

$$\text{Var}[y_i | \mathbf{b}, \mathbf{b}^*] = \sigma_a^2 + \sigma_c^2 + \exp((Xb^*)_i + \sigma_{a^*}^2/2 + \sigma_{c^*}^2/2).$$

Therefore, heritability estimates (h_i^2) were obtained for each combination of levels of systematic effects $(Xb^*)_i$ (Sorensen and Waagepetersen, 2003; Ros et al., 2004), as follows:

$$h_i^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \exp((Xb^*)_i + \frac{\sigma_{a^*}^2}{2} + \frac{\sigma_{c^*}^2}{2})}.$$

Lastly, we obtained the genetic correlation between the mean and the residual variance (r_{mv}). This is a genetic parameter that guides selection for uniformity, and it ranges from -1.0 to 1.0.

RESULTS

Data Transformation

The estimated optimal λ values for BW, WW, and YW were 1.95, -0.10, and 0.85, respectively. The scale effects on the mean of BW, WW, and YW reduced the linear dependence of the variance on the mean after Box-Cox transformation (Figure 1). In addition, the skewness of the untransformed data set was partially removed after data transformation, resulting in distributions closer to normal.

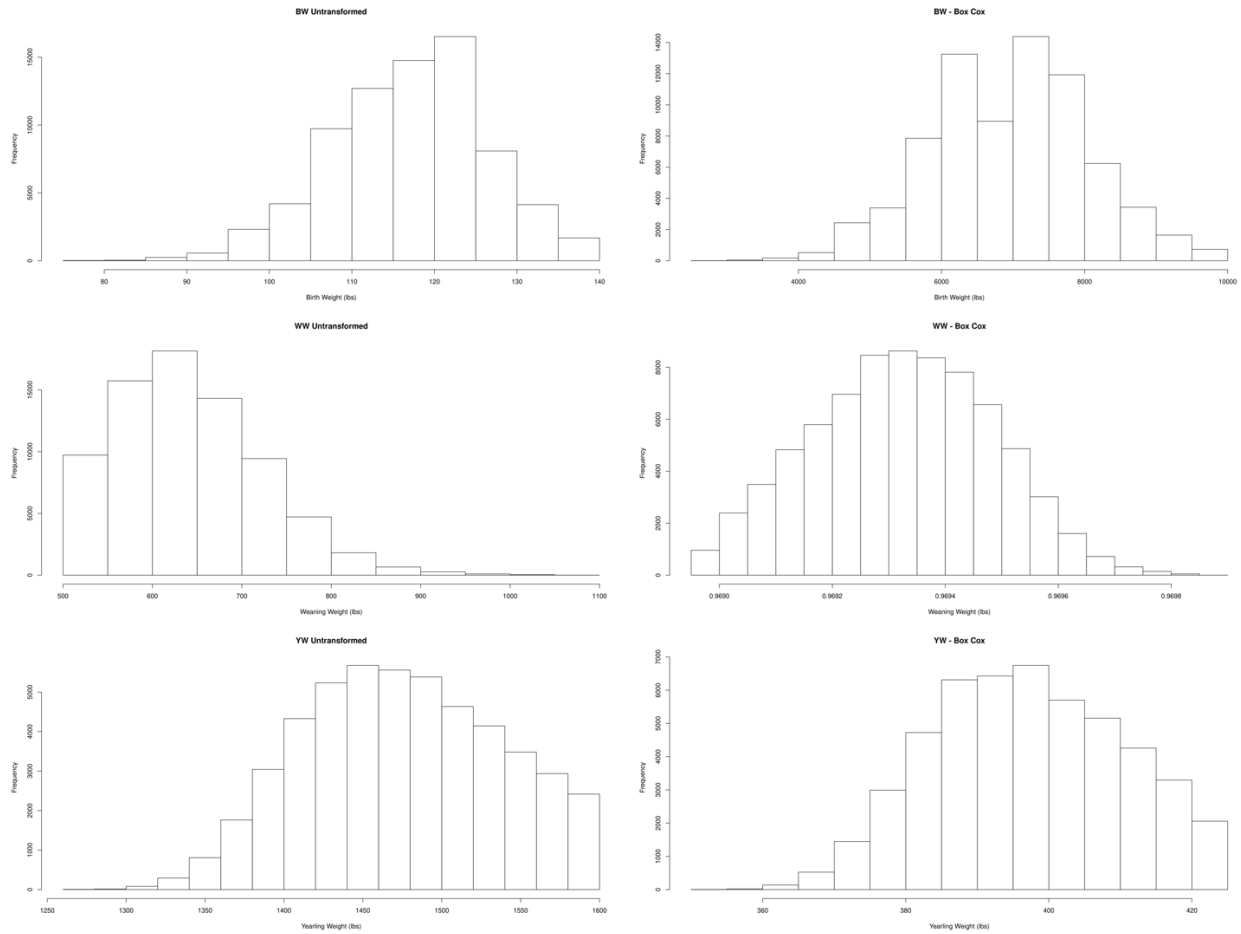


Figure 2. Distribution of Birth Weight (BW), Weaning Weight (WW) and Yearling Weight (YW) before (left) and after (right) Box-Cox Transformation.

Estimates of Variance Components and Genetic Parameters

Estimates of variance components and genetic parameters under the three models for BW, WW, and YW using untransformed and transformed data are presented in Tables 3 and 4.

Homoscedastic Residual Variance Model (M1)

In general, similar heritability estimates were obtained for untransformed and transformed data. For BW, heritability estimates were moderate ranging from 0.35 to

0.44. Heritability estimates for WW and YW were also moderate and similar ranging from 0.19 to 0.36 for WW and 0.20 to 0.26 for YW. The estimated distribution of the residuals is shown in Figure 2.

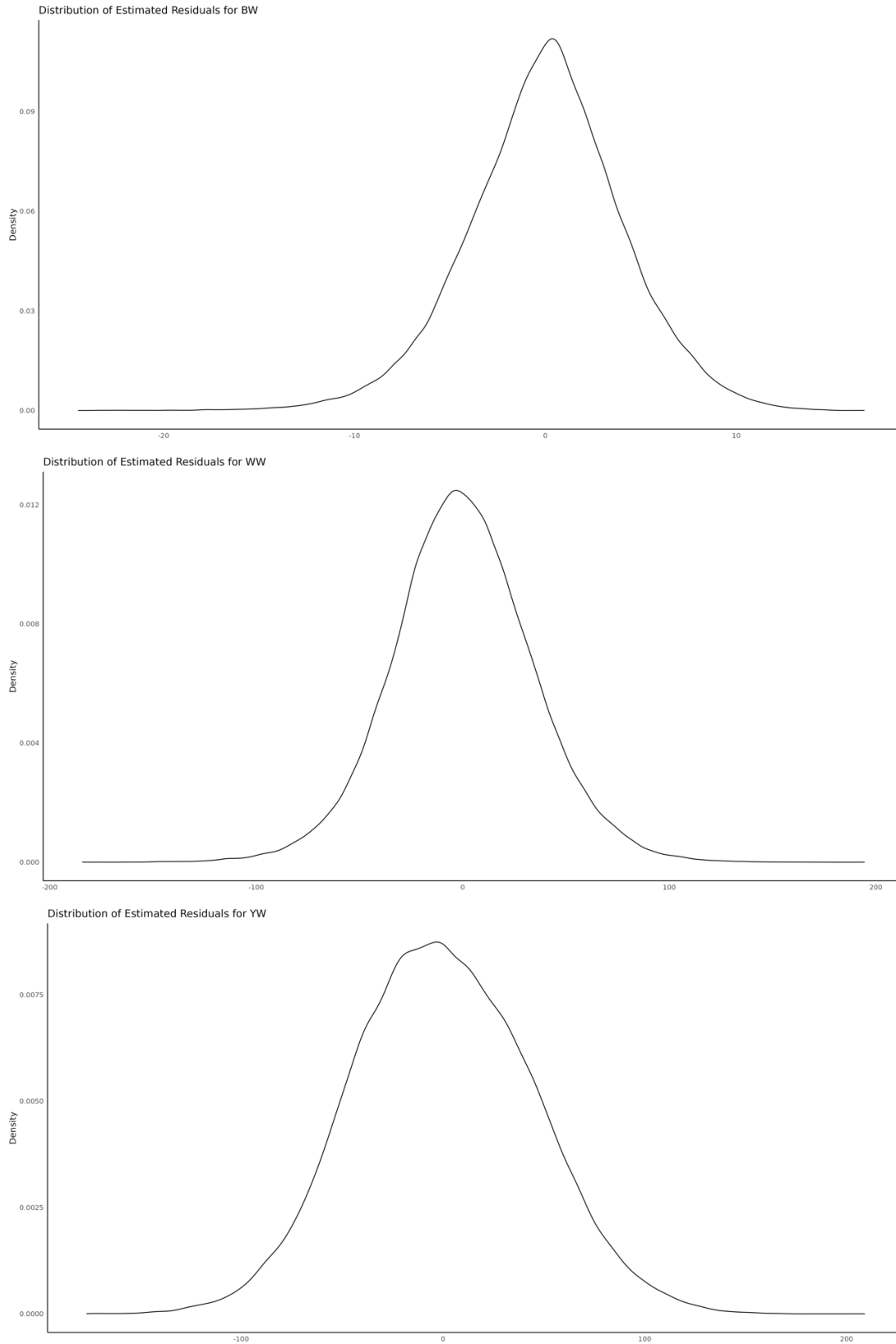


Figure 3. Distribution of estimated residuals based on the homoscedastic model (M1) for body weight (BW), weaning weight (WW), and yearling weight (YW).

Heterogeneous Residual Variance Models (M2 and M3)

Regarding the additive genetic variance for the mean (σ_a^2), M2 gave similar estimates of σ_a^2 compared to M1 for BW (27.17 for M1 and 25.74 for M2) and YW (473.33 for M1 and 462.32 for M2) using the untransformed data. In contrast, the WW estimates of σ_a^2 in M2 were lower for the untransformed data (791.78 for M1, 662.73 for M2), and when using the transformed dataset, the M2 estimates were lower compared to M1 (5.43×10^{-6} for M1 and 2.98×10^{-6} for M2). As for M3, the estimates of σ_a^2 were lower than M1 and M2 for BW (18.77) and higher than M1 for WW (942.28) and YW (1,633.66) for the untransformed data. Similar estimates were obtained for the transformed data.

The parameters influencing the genetic control of the residual variances were estimated with M2 and M3. In M2, σ_{av}^2 was 1.21×10^{-3} for BW, 6.54×10^{-7} for WW, and 9.08×10^{-7} for YW using the untransformed dataset, and 1.35×10^{-11} for BW, 5.73×10^{-13} for WW, and 2.01×10^{-2} for YW using the transformed dataset. As for M3, the posterior means of σ_{av}^2 were 0.14 for BW, 0.08 for WW, and 0.06 for YW for the untransformed dataset, and 0.10 for BW, 2.53×10^{-5} for WW, and 0.09 for YW for the transformed dataset.

For heritability estimates of residual variance in M2, low h_v^2 (< 0.1) were obtained for BW, WW, and YW. Estimates of h_v^2 from the untransformed and transformed data were 0.08 and 0.08 for BW, 0.06 and 0.001 for WW, and 0.09 and 0.09 for YW, respectively. Overall, estimates of GCV_E were moderate to high for all traits in M2. For M2, GCV_E estimates were 0.90 and 0.92 for BW, 0.64 and 0.64 for WW, and 0.67 and 0.63 for YW using the untransformed and transformed data, respectively. Estimates of

GCV_E obtained from M3 were 0.38 and 0.31 for BW, 0.29 and 0.01 for WW, and 0.25 and 0.31 for YW using the untransformed and transformed data, respectively. These estimates were lower than those for M2.

Lastly, the relationship between EBV of the mean and residual variance (r_{mv}) was calculated for M2 and M3. Overall, positive estimates were observed before Box-Cox transformation, except for BW in M3. The r_{mv} estimates in M2 were 0.88 and 0.86, 0.23 and 0.77, and 0.01 and 0.73 for BW, WW, and YW using the untransformed and transformed data, respectively. For M3, the r_{mv} estimates were -0.49 and 0.15 for BW, 0.50 and -0.04 for WW, and 0.39 and -0.46 for YW using the untransformed and transformed data, respectively.

Table 3. Variance component estimates and genetic parameters for mean and residual variance for **untransformed** phenotypes for body weight (BW), weaning weight (WW), and yearling weight (YW) under three different models.

Trait	Model	σ_a^2	σ_m^2	σ_c^2	σ_e^2	${}^2\sigma_{av}^2$	σ_{c*}^2	h^2	h_v^2	GCV _E	r _{mv}
BW	M1	27.17 (0.90)	4.03 (0.72)	0.17×10^{-5} (0.71)	30.16 (0.61)	-	-	0.44 (0.01)	-	-	-
	M2	25.74 (0.77)	4.89 (1.04)	0.23×10^{-5} (0.80)	31.61 (0.59)	1.21×10^{-3} (2.00×10^{-3})	-	0.41 (0.01)	0.08 (1.00×10^{-3})	0.90 (0.01)	0.88 (0.11)
	¹ M3	18.77 (3.48)	-	22.35 (1.90)	-	0.14 (0.01)	0.57 (0.31)	0.39		0.38	-0.49 (0.02)
WW	M1	791.78 (35.50)	154.89 (28.97)	146.08 (28.87)	1,876.31 (25.65)	-	-	0.26 (0.01)	-	-	-
	M2	662.73 (33.25)	337.09 (37.20)	268.60 (29.97)	1,915.92 (790.96)	6.54×10^{-7} (1.00×10^{-3})	-	0.22 (4.00×10^{-3})	0.06 (1.00×10^{-3})	0.64 (0.06)	0.23 (0.03)
	¹ M3	942.28 (72.84)	-	3,888.43 (317.49)	-	0.08 (0.01)	1.75 (3.41)	0.19	-	0.29	0.50 (0.04)
YW	M1	473.33 (25.82)	-	-	1,661.24 (23.13)	-	-	0.22 (9.00×10^{-2})	-	-	-
	M2	462.32 (24.44)	-	-	1,547.08 (260.91)	9.08×10^{-7} (1.00×10^{-3})	-	0.23 (0.03)	0.09 (2.00×10^{-3})	0.67 (0.01)	0.01 (0.01)
	¹ M3	1,633.66 (17.03)	-	-	-	0.06 (0.01)	-	0.26	-	0.25	0.39 (0.04)

BW: body weight. WW: weaning weight. YW: yearling weight. M1: Homoscedastic residual variance model. M2: Heteroscedastic model (DHGLM). M3: Heteroscedastic model (structured model). σ_a^2 and σ_{av}^2 are the additive genetic variance for the means and residual variances. σ_c^2 and σ_{c*}^2 are the permanent environmental variances for the means and residual variances. σ_m^2 is the maternal genetic variance. σ_e^2 is the residual variance. h^2 and h_v^2 are the heritability estimates for the means and residual variances. GCV_E is the genetic coefficient of variation for the residual variance; r_{mv} is the genetic correlation between the estimated breeding values of the means and residual variances; standard errors are given in parentheses.

¹Mean and SD (in parentheses) of the marginal posterior distribution. ²For M3, σ_{av}^2 represents σ_{a*}^2

Table 4. Variance component estimates and genetic parameters for mean and residual variance for **transformed** phenotypes for body weight (BW), weaning weight (WW), and yearling weight (YW) under three different models.

Trait	Model	σ_a^2	σ_m^2	σ_c^2	σ_e^2	$^2\sigma_{av}^2$	σ_{c*}^2	h^2	h_v^2	GCVE	r_{mv}
BW	M1	252.719.02 (8,439.99)	36,181.54 (6,571.87)	0.36×10^{-4} (1.51×10^{-4})	280,448.80 (5,721.78)	-	-	0.44 (0.01)	-	-	-
	M2	240,314.69 (7,172.00)	28,730.91 (9,433.75)	0.55×10^{-4} (9,433.75)	293,573.45 (5,573.16)	1.35×10^{-11} (1.00×10^{-3})	-	0.42 (0.01)	0.08 (1.00×10^{-3})	0.92 (0.01)	0.86 (0.13)
	¹ M3	41,281.17 (58,859.04)	-	310,313.02 (25,671.29)	-	0.10 (9.00×10^{-2})	10.42 (3.41)	0.35	-	0.31	0.15 (0.03)
WW	M1	5.43×10^{-6} (7.80×10^{-6})	3.89×10^{-6} (9.92×10^{-6})	2.34×10^{-6} (6.40×10^{-6})	3.29×10^{-6} (4.16×10^{-6})	-	-	0.36 (0.05)	-	-	-
	M2	2.98×10^{-6} (2.76×10^{-6})	7.87×10^{-6} (5.63×10^{-6})	2.17×10^{-6} (4.18×10^{-6})	1.17×10^{-6} (1.65×10^{-5})	5.73×10^{-13} (5.60×10^{-4})	-	0.20 (3.00×10^{-3})	1.00×10^{-3} (1.00×10^{-4})	0.64 (0.06)	0.77 (0.05)
	¹ M3	1.67×10^{-4} (0.01)	-	3.72×10^{-4} (0.02)	-	2.53×10^{-5} (1.13×10^{-4})	4.94×10^{-6} (0.02)	0.19	-	0.01	-0.04 (0.05)
YW	M1	0.06 (3.50×10^{-3})	-	-	0.23 (3.00×10^{-3})	-	-	0.21 (9.00×10^{-3})	-	-	-
	M2	0.05 (3.00×10^{-3})	-	-	0.22 (0.03)	2.01×10^{-2} (4.00×10^{-4})	-	0.20 (0.03)	0.09 (3.00×10^{-3})	0.63 (1.00×10^{-3})	0.73 (0.05)
	¹ M3	1.06×10^{-1} (0.01)	-	-	-	0.09 (9.00×10^{-3})	-	0.22	-	0.31	-0.46 (0.01)

BW: body weight. WW: weaning weight. YW: yearling weight. M1: Homoscedastic residual variance Model. M2: Heteroscedastic model (DHGLM). M3: Heteroscedastic model (structured model). σ_a^2 and σ_{av}^2 are the additive genetic variance for the means and residual variances. σ_c^2 and σ_{c*}^2 are the permanent environmental variances for the means and residual variances. σ_m^2 is the maternal genetic variance. σ_e^2 is the residual variance. h^2 and h_v^2 are the heritability estimates for the means and residual variances. $GCVE$ is the genetic coefficient of variation for the residual variance; r_{mv} is the genetic correlation between the estimated breeding values of the means and residual variances; standard errors are given in parentheses.

¹Mean and SD (in parentheses) of the marginal posterior distribution. ²For M3, σ_{av}^2 represents σ_{a*}^2

DISCUSSION

Genetic variances and parameters for the mean

The h^2 estimates for BW (0.44 in M1, 0.41 in M2, and 0.39 in M3) obtained in this study using the untransformed data were lower than those observed by Smith et al. (2022) (0.51) and slightly higher than those of Lourenco et al. (2015) (0.41). The h^2 estimates for WW (0.26 in M1, 0.22 in M2, and 0.19 in M3) were consistent with those reported by Smith et al. (2022) (0.25) and slightly higher than those of Lourenco et al. (2015) (0.20) using the untransformed data. For YW, our estimates (0.22 in M1, 0.23 in M2, and 0.26 in M3) using the untransformed data were lower than the genomic heritability estimates reported by Smith et al. (2022) (0.42) in Red Angus cattle and Schiermiester et al. (2015) (0.38-0.39) in a multibreed dataset including Angus cattle. The lower h^2 values obtained for YW could be explained by two reasons: 1) only a subset of the whole American Angus population and 2) pedigree information was used in the analysis. Therefore, there is a possibility that the dataset for YW used in this study may not be a representative sample of the national herd.

Genetic variances and parameters for the variance

M2 and M3 assume that there are genes controlling not only the mean of a trait but also its residual variance (Lee and Nelder, 2006, SanCristobal-Gaudy et al., 1998). Our results show the presence of additive genetic variances for the means (σ_a^2) of untransformed and transformed BW, WW, and YW and their variances (σ_{av}^2) in both models.

Low estimates of h_v^2 were observed for all traits, consistent with the range reported in the literature. For example, Neves et al. (2011) performed genetic heterogeneity of residual variance analysis for over fifteen traits in Nellore cattle by analyzing the log squared residuals of each phenotypic observation using an animal model. Estimates of genetic variances and parameters were obtained using a two-step approach consisting of first fitting a model to the mean, and then using the log-transformed squared estimated residuals as a measure of residual variance in the second step. For BW, they reported pedigree-based h_v^2 estimates of 0.09 (± 0.01), which is similar to our study (0.08). Using DHGLM in pigs, Sell-Kubiak et al. (2015a) found h_v^2 estimates for BW ranging from 0.008 to 0.01. In chickens, Yousefi Zonuz et al. (2019) reported h_v^2 for BW ranging from 0.08 (± 0.002) to 0.09 (± 0.003), and Sae-Lim et al. (2018) showed that h_v^2 for BW in sheep was 0.07.

To our knowledge, this is the first study to report the extent of genetic control of residual variance for WW in livestock species. Estimates of h_v^2 obtained were 0.06 (± 0.001) and 0.001 (± 0.001) using the untransformed and transformed data, respectively. The closest trait reported in the literature for cattle is weight gain from birth to weaning. For example, Neves et al. (2011) reported h_v^2 estimates of 0.02 (± 0.003) for birth to weaning weight gain. Similarly, Neves et al. (2012) used three different datasets (male, female, and combined) to investigate the genetic heterogeneity of residual variance of various weight traits in Nellore cattle using a two-step approach. The h_v^2 estimates for weight gain from birth to weaning were 0.03 for males, 0.05 for females, and 0.03 for combined data.

Yearling weight is a key breeding goal for beef cattle because it reflects the performance of the animal at an age when there is a high volume of animal trade. Our

estimates of h_v^2 were 0.09 using the untransformed and transformed data. These estimates were higher than those reported by Neves et al. (2012), who reported h_v^2 estimates for YW of 0.03 for females, 0.05 for males, and 0.02 for combined data. More recently, Lung et al. (2017) investigated genetic heterogeneity of residual variance in YW in a Nellore cattle population using a two-step approach and DHGLM for untransformed and Box-Cox transformed phenotypes. For untransformed data, they reported h_v^2 estimates of 0.01 (± 0.002) for females, 0.003 (± 0.001) for males, and 0.07 (± 0.001) for combined data using the DHGLM approach. After transformation, the h_v^2 estimate was reduced to 0.003 (± 0.001) for combined data. In both scenarios, the estimates in our study are higher for YW compared to the full data of Lung et al. (2017).

The low estimates of h_v^2 obtained in this study and other work in different species (Hill and Mulder, 2010; Lung et al., 2020) suggest the need for larger data to predict EBV_v (Mulder et al., 2007). Several factors may explain the low h_v^2 estimates found in our study. The primary issue is that h_v^2 in M2 and M3 are defined at the level of individual single records. Estimating variance from single phenotypes can be challenging because the sampling variance of a variance estimate typically exceeds that of a mean, and these sampling problems tend to occur when environmental effects affect variability (Lung et al., 2017). However, several studies suggest that selective breeding can improve uniformity. For example, early selection experiments have successfully reduced residual variance in body weight and litter size in rabbits (Garreau et al., 2008; Blasco et al., 2017) and birth weight in mice (Formoso-Rafferty et al., 2016).

Opportunities for Genetic Improvement

GCV_E evaluates the potential response to selection for residual variance, and although h_v^2 estimates were not high in our study, GCV_E estimates show that improving

uniformity for BW, WW, and YW through selection is feasible. In all scenarios studied, GCV_E estimates in M2 were higher than those of GCV_E in M3.

For BW, the estimated GCV_E found in our study was higher than that of Neves et al. (2011), who reported GCV_E of 0.69 in Nellore cattle, Sell-Kubiak et al. (2015) in pigs (0.20-0.24), and Sae-Lim et al. (2018) in sheep (0.58). We found that the estimates of GCV_E for WW was 0.64 using both untransformed and transformed data in M2, and 0.29 0.01 using untransformed and transformed data in M3, respectively. Our results are in line with the estimates reported for weight gain from birth to weaning in Neves et al. (2011) and Neves et al. (2012) (0.18 to 0.65). Lastly, the estimate of GCV_E for YW was slightly smaller than that in Neves et al. (2012), which was 0.43 for females, 0.79 for males, and 0.43 for the combined data. The estimates in Iung et al. (2017) were smaller than our results and those of Neves et al. (2012). They reported 0.20 for females, 0.10 for males, and 0.17 for the combined data, and 0.12 after Box-Cox transformation.

Our results for GCV_E based on M2 suggest that a change of 1 genetic standard deviation would change the residual variance by 90 to 92% for BW, 64 % for WW, and 63 to 67% for YW. For M3, a change of 1 genetic standard deviation would change the residual variance by 31 to 38% for BW, 1 to 29% for WW, and 25 to 31 % for YW. The estimates in this study for M2 and M3 were within the range previously reported for other species (Hill and Mulder, 2010; cIung et al., 2020). This suggests that the genetic heterogeneity of residual variance is sizeable, indicating the potential for selection to alter residual variance.

r_{mv} is a genetic parameter that can be used to guide selection for uniformity. It ranges from -1.0 to 1.0, and in general, negative values of r_{mv} are preferred if the

objective is to increase the mean while decreasing the variance. Otherwise, the mean and residual variance must be included in a selection index to obtain the desired response (Mulder et al., 2008; Berghof et al., 2019). In our study, BW based on M3 showed a negative moderate genetic correlation (-0.49) between the mean and residual variance. Similarly, WW showed a negative low genetic correlation of -0.04 (M3), and a negative moderate correlation of -0.46 for YW (M3). Estimates of r_{mv} for BW reported in the literature are 0.42 in cattle (Neves et al., 2011), 0.39 in sheep (Sae-Lim et al., 2018), 0.53 to 0.62 in chickens (Sell-Kubiak et al., 2015a; Sell-Kubiak et al., 2015b), -0.02 for weight gain from birth to weaning in beef cattle (Neves et al., 2011), and 0.21 to 0.27 for the same trait in beef cattle (Neves et al., 2012). In other scenarios, all r_{mv} estimates were positive, meaning that the residual variance tended to increase with increasing EBV.

Data Transformation and Scale Effects

Typically, animals with higher genetic means also have higher variances, partly due to scaling. Yang et al. (2011) showed that data transformation is an alternative to reduce scaling effects on genetic heterogeneity of residual variance, reporting that Box-Cox transformation considerably affected r_{mv} . Our study shows that Box-Cox transformation was able to reduce the dependence of the variance on the mean, resulting in lower estimates of h_v^2 and GCV_E . However, it did not eliminate the presence of genetic heterogeneity of residual variance. In addition, we observed changes in the sign and magnitude of r_{mv} after data transformation. These changes are not atypical and have been reported in other studies of genetic heterogeneity of residual variance. For example, Yang et al. (2011) reexamined litter size data for rabbits and pigs using a Box-Cox transformation and observed differences from the original findings. The relationship between additive genetic effect on mean and variance was reversed for

rabbits (original data: -0.73, transformed data: 0.28) and pigs (original data: -0.64, transformed data: 0.70). Additionally, Sae-Lim et al. (2015) found a significant shift in the genetic correlation between mean and residual variance in rainbow trout (*Oncorhynchus mykiss*), from 0.30 to -0.62 after logarithmic transformation. Our results highlight the importance of considering scale effects when examining genetic heterogeneity in residual variances.

REML and Bayesian Approaches

Modeling genetic heterogeneity of residual variance assumes the presence of genes that influence mean performance and variability under changing environmental conditions. SanCristobal-Gaudy et al. (1998) proposed a model based on the expectation maximization algorithm to estimate genetic parameters. Since then, alternative models have been introduced, including the two-step approach (Garreau et al., 2008; Mulder et al., 2009b), DHGLM (Rönnegård et al., 2010; Felleki et al., 2012), and the structured approach (Sorensen and Waagepetersen, 2003).

In our study, we assessed variance components and genetic parameters for residual variance using REML (DHGML) and Bayesian (structured) approaches. The Bayesian approach showed higher estimates of σ_{av}^2 compared to the REML approach. Due to software limitations, the Bayesian approach was not able to account for maternal effects, as it can only fit additive and permanent environmental effects. However, it is assumed that $\mathbf{c}$ and $\mathbf{c}^*$ also capture most of the maternal effects, as observed in Ibáñez-Escriche et al. (2008). The authors included both litter and maternal genetic effects in a study of the environmental variability of weight gain in mice and found that these effects were confounded and could not be clearly separated, therefore the maternal

effects were not completely ignored in the model but were accounted for by the litter effect.

Estimates of GCV_E and r_{mv} varied between the two approaches but were within the ranges reported in the literature for different species. Studies using both REML and Bayesian approaches on the same data have reported similar estimates of σ_{av}^2 (Wolc et al., 2009; Rönnegård et al., 2010). However, similar to our findings, Gutiérrez et al. (2006) found different estimates between REML and Bayesian approaches in the same data when examining genetic heterogeneity for litter size, litter weight, and individual birth weight in mice. Further studies with real and simulated data should evaluate these methods in repeated observations on the same individual or with larger family (Iung et al., 2020).

In terms of computational time in this study, the REML approach (M2) took approximately 8 hours to complete for each trait, while the Bayesian approach (M3) took an average of 16 hours per trait. The Bayesian approach is computationally expensive due to its complex sampling techniques, using combinations of Gibbs sampling and Metropolis-Hastings algorithms, which are essential for estimating all parameters because the full conditional distributions do not conform to standard forms (Sorensen and Waagepetersen, 2003; Ibáñez-Escriche et al., 2010).

Future Developments

The advent of genomic selection has improved selection responses in many livestock species (Meuwissen et al., 2001; Hayes et al., 2009; Goddard et al., 2010). However, to date, genomic approaches to quantify genetic heterogeneity of residual variance are scarce, likely because DHGLM is computationally demanding to fit high-dimensional genomic data. In this study, genomic data were not used because the model

failed to converge. Recently, Berghof et al. (2019) presented an alternative way to define uniformity (or resilience) traits by measuring deviations from expected production levels over a period of time. The authors presented several indicators for uniformity, including variance of deviations, skewness of deviations, slope of reaction norms, and autocorrelation of deviations. Finally, digital phenotyping technologies have become popular for collecting large amounts of data at a faster rate than traditional methods (Morota et al., 2018), providing an excellent opportunity to record new phenotypes based on longitudinal data, and therefore contributing to the study of uniformity (Iung et al., 2017; Berghof et al., 2019).

CONCLUSION

Our study presented genetic parameter estimates associated with residual variances for economically important growth traits in American Angus cattle and the potential to alter them through selection using the GCV_E of residual variance. Interpretation of these values should also consider the magnitude of genetic variance, the heritability of residual variance, and the genetic correlation between mean and residual variance, as they may limit the genetic response to selection for uniformity of production when simultaneously aiming to increase the mean of BW, WW, or YW.

Data transformation reduced the mean-variance relationship, yet genetic heterogeneity of residual variance persisted beyond scale effects. The Bayesian approach resulted in higher estimates of additive genetic variance for the residual variance than the REML approach. The REML approach was the least computationally expensive and provided estimates of the heritability of residual variance. Because of the observed difference in genetic parameter estimates for residual variance, further

studies with real and simulated data should be conducted to evaluate these methods when applied to repeated observations on the same individual or within larger family groups.

To our knowledge, this is one of the first studies of genetic heterogeneity of residual variance in American Angus cattle, and to compare DHGLM and structured approaches to estimate genetic variance for growth weight uniformity, constituting the first steps to investigate the possibility of including these traits in breeding goals.

BIBLIOGRAPHY

Archer, J. A., and L. Bergh. 2000. Duration of performance tests for growth rate, feed intake and feed efficiency in four biological types of beef cattle. *Livest. Prod. Sci.* 65:47–55. doi:10.1016/S0301-6226(99)00181-5.

Berghof, T. V. L., M. Poppe, and H. A. Mulder. 2019. Opportunities to improve resilience in animal breeding programs. *Front. Genet.* 10:410180. doi:10.3389/FGENE.2018.00692/BIBTEX.

Blasco, A., M. Martínez-Álvaro, M. L. García, N. Ibáñez-Escriche, and M. J. Argente. 2017. Selection for environmental variance of litter size in rabbits. *Genet. Sel. Evol.* 49:1–8. doi:10.1186/S12711-017-0323-4/FIGURES/6

Box, G. E. P., and ; D R Cox. 1964. An Analysis of Transformations. *J. R. Stat. Soc. Ser. B.* 26:211–252.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Pearson.

Felleki, M., D. Lee, Y. Lee, A. R. Gilmour, and L. Rönnegård. 2012. Estimation of breeding values for mean and dispersion, their variance and correlation using double hierarchical generalized linear models. *Genet. Res. (Camb)*. 94:307–317. doi:10.1017/S0016672312000766.

Formoso-Rafferty, N., I. Cervantes, N. Ibáñez-Escriche, and J. P. Gutiérrez. 2016. Genetic control of the environmental variance for birth weight in seven generations of a divergent selection experiment in mice. *J. Anim. Breed. Genet.* 133:227–237. doi:10.1111/JBG.12174.

Formoso-Rafferty, N., I. Cervantes, N. Ibáñez-Escriche, and J. P. Gutiérrez. 2017. Modulating birth weight heritability in mice. *J. Anim. Sci.* 95:531–537. doi:10.2527/JAS.2016.1169.

Garreau, H., G. Bolet, C. Larzul, C. Robert-Granié, G. Saleil, M. SanCristobal, and L. Bodin. 2008. Results of four generations of a canalising selection for rabbit birth weight. *Livest. Sci.* 119:55–62. doi:10.1016/J.LIVSCI.2008.02.009.

Geweke, J. F. 1991. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. Staff Rep.

Gilmour, K. M., J. D. DiBattista, and J. B. Thomas. 2005. Physiological Causes and Consequences of Social Status in Salmonid Fish. *Integr. Comp. Biol.* 45:263–273. doi:10.1093/ICB/45.2.263.

- Goddard, M. E., B. J. Hayes, and T. H. E. Meuwissen. 2010. Genomic selection in livestock populations. *Genet. Res. (Camb)*. 92:413–421. doi:10.1017/S0016672310000613.
- Gutiérrez, J. P., B. Nieto, P. Piqueras, N. Ibáñez, and C. Salgado. 2006. Genetic parameters for canalisation analysis of litter size and litter weight traits at birth in mice. *Genet. Sel. Evol.* 38. doi:10.1186/1297-9686-38-5-445/METRICS.
- Hayes, B. J., P. J. Bowman, A. J. Chamberlain, and M. E. Goddard. 2009. Invited review: Genomic selection in dairy cattle: Progress and challenges. *J. Dairy Sci.* 92:433–443. doi:10.3168/jds.2008-1646.
- Hennessy, D. A. 2005. Slaughterhouse Rules: Animal Uniformity and Regulating for Food Safety in Meat Packing. *Am. J. Agric. Econ.* 87:600–609. doi:10.1111/J.1467-8276.2005.00750.X.
- Hill, W. G., and H. A. Mulder. 2010. Genetic analysis of environmental variation. *Genet. Res. (Camb)*. 92:381–395. doi:10.1017/S0016672310000546.
- Hill, W. G., and X. S. Zhang. 2004. Effects on phenotypic variability of directional selection arising through genetic differences in residual variability. *Genet. Res. (Camb)*. 83:121–132. doi:10.1017/S0016672304006640.
- Hoaglin, D. C., and R. E. Welsch. 1978. The hat matrix in regression and anova. *Am. Stat.* 32:17–22. doi:10.1080/00031305.1978.10479237.
- Ibáñez-Escriche, N., M. Garcia, and D. Sorensen. 2010. GSEVM v.2: MCMC software to analyze genetically structured environmental variance models. *J. Anim. Breed. Genet.* 127:249–251. doi:10.1111/J.1439-0388.2009.00846.X.
- Ibáñez-Escriche, N., A. Moreno, B. Nieto, P. Piqueras, C. Salgado, and J. P. Gutiérrez. 2008. Genetic parameters related to environmental variability of weight traits in a selection experiment for weight gain in mice; signs of correlated canalised response. *Genet. Sel. Evol.* 40:279. doi:10.1186/1297-9686-40-3-279.
- Ibáñez-Escriche, N., D. Sorensen, R. Waagepetersen, and A. Blasco. 2008. Selection for Environmental Variation: A Statistical Analysis and Power Calculations to Detect Response. *Genetics*. 180:2209–2226. doi:10.1534/GENETICS.108.091678.
- Iung, L. H. de S., R. Carneiro, H. H. de R. Neves, and H. A. Mulder. 2020. Genetics and genomics of uniformity and resilience in livestock and aquaculture species: A review. *J. Anim. Breed. Genet.* 137:263–280. doi:10.1111/JBG.12454.

Iung, L. H. S., H. H. R. Neves, H. A. Mulder, and R. Carvalheiro. 2017. Genetic control of residual variance of yearling weight in Nellore beef cattle. *J. Anim. Sci.* 95:1425–1433. doi:10.2527/JAS.2016.1326.

Koknaroglu, H., D. D. Loy, D. E. Wilson, M. P. Hoffman, and J. D. Lawrence. 2005. Factors Affecting Beef Cattle Performance and Profitability. *Prof. Anim. Sci.* 21:286–296. doi:10.15232/S1080-7446(15)31220-1.

Lee, Y., and J. A. Nelder. 1996. Hierarchical Generalized Linear Models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 58:619–656. doi:10.1111/J.2517-6161.1996.TB02105.X. Available from: <https://dx.doi.org/10.1111/j.2517-6161.1996.tb02105.x>

Lourenco, D. A. L., S. Tsuruta, B. O. Fragomeni, Y. Masuda, I. Aguilar, A. Legarra, J. K. Bertrand, T. S. Amen, L. Wang, D. W. Moser, and I. Misztal. 2015. Genetic evaluation using single-step genomic best linear unbiased predictor in American Angus. *J. Anim. Sci.* 93:2653–2662. doi:10.2527/JAS.2014-8836.

Mackay, T. F. C., and R. F. Lyman. 2005. *Drosophila* bristles and the nature of quantitative genetic variation. *Philos. Trans. R. Soc. B Biol. Sci.* 360:1513–1527. doi:10.1098/RSTB.2005.1672.

Madsen, P., and J. Jensen. 2013. A user's guide to DMU. Version 6, release 5.2. Danish Institute of Agricultural Sciences, Research Centre Foulum, Denmark.

Merks, J. W. M., P. K. Mathur, and E. F. Knol. 2012. New phenotypes for new breeding goals in pigs. *animal.* 6:535–543. doi:10.1017/S1751731111002266.

Meuwissen, T. H. E., B. J. Hayes, and M. E. Goddard. 2001. Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps. *Genetics.* 157:1819–1829.

Milligan, B. N., D. Fraser, and D. L. Kramer. 2002. Within-litter birth weight variation in the domestic pig and its relation to pre-weaning survival, weight gain, and variation in weaning weights. *Livest. Prod. Sci.* 76:181–191. doi:10.1016/S0301-6226(02)00012-X.

Morota, G., R. V. Ventura, F. F. Silva, M. Koyama, and S. C. Fernando. 2018. BIG DATA ANALYTICS AND PRECISION ANIMAL AGRICULTURE SYMPOSIUM: Machine learning and data mining advance predictive big data analysis in precision animal agriculture. *J. Anim. Sci.* 96:1540–1550. doi:10.1093/JAS/SKY014.

Mulder, H. A., P. Bijma, and W. G. Hill. 2007. Prediction of Breeding Values and Selection Responses With Genetic Heterogeneity of Environmental Variance. *Genetics.* 175:1895. doi:10.1534/GENETICS.106.063743.

Mulder, H. A., P. Bijma, and W. G. Hill. 2008. Selection for uniformity in livestock by exploiting genetic heterogeneity of residual variance. *Genet. Sel. Evol.* 40:37–59. doi:10.1051/GSE:2007034.

- Mulder, H. A., W. G. Hill, A. Vereijken, and R. F. Veerkamp. 2009a. Estimation of genetic variation in residual variance in female and male broiler chickens. *Animal*. 3:1673–1680. doi:10.1017/S1751731109990668.
- Mulder, H. A., W. G. Hill, A. Vereijken, and R. F. Veerkamp. 2009b. Estimation of genetic variation in residual variance in female and male broiler chickens. *Animal*. 3:1673–1680. doi:10.1017/S1751731109990668.
- Mulder, H. A., J. Visscher, and J. Fablet. 2016. Estimating the purebred-crossbred genetic correlation for uniformity of eggshell color in laying hens. *Genet. Sel. Evol.* 48:1–13. doi:10.1186/S12711-016-0212-2/TABLES/6.
- Murray, D. M. 1980. The effect of three different growth rates on feed utilization of cattle. *Aust. J. Agric. Res.* 31:1139–1145. doi:10.1071/AR9801139.
- Neves, H. H. R., R. Carneiro, and S. A. Queiroz. 2012. Genetic and environmental heterogeneity of residual variance of weight traits in Nellore beef cattle. *Genet. Sel. Evol.* 44:1–12. doi:10.1186/1297-9686-44-19/TABLES/5.
- Neves, H. H. R., R. Carneiro, V. M. Roso, and S. A. Queiroz. 2011. Genetic variability of residual variance of production traits in Nellore beef cattle. *Livest. Sci.* 142:164–169. doi:10.1016/J.LIVSCI.2011.07.010.
- Notter, D. R. 1999. The importance of genetic diversity in livestock populations of the future. *J. Anim. Sci.* 77:61–69. doi:10.2527/1999.77161X.
- de Oliveira, G. M., S. M. de Queiroz, C. F. da Cunha, and M. Puperi. 2017. Value appropriation in Brazilian cattle industry. *Br. Food J.* 119:2089–2101. doi:10.1108/BFJ-10-2016-0478/FULL/PDF.
- Rönnegård, L., M. Felleki, F. Fikse, H. A. Mulder, and E. Strandberg. 2010. Genetic heterogeneity of residual variance - Estimation of variance components using double hierarchical generalized linear models. *Genet. Sel. Evol.* 42:1–10. doi:10.1186/1297-9686-42-8/FIGURES/1.
- Ros, M., D. Sorensen, R. Waagepetersen, M. Dupont-Nivet, M. SanCristobal, J. C. Bonnet, and J. Mallard. 2004. Evidence for Genetic Control of Adult Weight Plasticity in the Snail *Helix aspersa*. *Genetics*. 168:2089. doi:10.1534/GENETICS.104.032672.
- Sae-Lim, P., J. H. Jakobsen, and H. A. Mulder. 2018. Uniformity in birth weight is heritable in Norwegian White Sheep. In: *Proceedings of the World Congress on Genetics Applied to Livestock Production*. Auckland.
- Sae-Lim, P., A. Kaase, M. Janhunen, H. Vehviläinen, H. Koskinen, B. Gjerde, M. Lillehammer, and H. A. Mulder. 2015. Genetic (co)variance of rainbow trout

(*Oncorhynchus mykiss*) body weight and its uniformity across production environments. *Genet. Sel. Evol.* 47:1–10. doi:10.1186/S12711-015-0122-8/TABLES/3.

Sancristobal-Gaudy, M., J.-M. Elsen, L. Bodin, and C. Chevalet. 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. *Genet. Sel. Evol.* 423–451.

Schiermister, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. *J. Anim. Sci.* 93:46–52. doi:10.2527/JAS.2014-8493.

Sell-Kubiak, E., P. Bijma, E. F. Knol, and H. A. Mulder. 2015a. Comparison of methods to study uniformity of traits: Application to birth weight in pigs. *J. Anim. Sci.* 93:900–911. doi:10.2527/JAS.2014-8313.

Sell-Kubiak, E., S. Wang, E. F. Knol, and H. A. Mulder. 2015b. Genetic analysis of within-litter variation in piglets' birth weight using genomic or pedigree relationship matrices. *J. Anim. Sci.* 93:1471–1480. doi:10.2527/JAS.2014-8674.

Smith, B. J. 2007. *boa: An R Package for MCMC Output Convergence Assessment and Posterior Inference*. *J. Stat. Softw.* 21:1–37. doi:10.18637/JSS.V021.I11.

Smith, J. L., M. L. Wilson, S. M. Nilson, T. N. Rowan, R. D. Schnabel, J. E. Decker, and C. M. Seabury. 2022. Genome-wide association and genotype by environment interactions for growth traits in U.S. Red Angus cattle. *BMC Genomics* 2022 231. 23:1–22. doi:10.1186/S12864-022-08667-6.

Sorensen, D., and R. Waagepetersen. 2003. Normal linear models with genetically structured residual variance heterogeneity: a case study. *Genet. Res. (Camb)*. 82:207–222. doi:10.1017/S0016672303006426.

Thonney, M. L., E. K. Heide, D. J. Duhaime, A. Y. M. Nour, and P. A. Oltenacu. 1981. Growth and Feed Efficiency of Cattle of Different Mature Sizes. *J. Anim. Sci.* 53:354–362. doi:10.2527/JAS1981.532354X.

Wilson, A., and N. Norden. 2021. *The R Project for Statistical Computing* The R Project for Statistical Computing. URL <http://www.r-project.org/254>. 3:1–9.

Wolc, A., M. S. White, S. Avendano, and W. G. Hill. 2009. Genetic variability in residual variation of body weight and conformation scores in broiler chickens. *Poult. Sci.* 88:1156–1161. doi:10.3382/PS.2008-00547.

Yang, Y., O. F. Christensen, and D. Sorensen. 2011. Analysis of a genetically structured variance heterogeneity model using the Box-Cox transformation. *Genet. Res. (Camb)*. 93:33–46. doi:10.1017/S0016672310000418.

Yousefi Zonuz, A., S. Alijani, and S. A. Rafat. 2019. Genetic heterogeneity of residual variance of hatch weight in Mazandaran native chicken. *Br. Poult. Sci.* 60:366–372. doi:10.1080/00071668.2019.1614527.

Zaborski, D., W. Grzesiak, I. Szatkowska, A. Dybus, M. Muszynska, and M. Jedrzejczak. 2009. Factors Affecting Dystocia in Cattle. *Reprod. Domest. Anim.* 44:540–551. doi:10.1111/J.1439-0531.2008.01123.X.

**Chapter 4: GENETIC HETEROGENEITY OF RESIDUAL VARIANCE FOR
FUNCTIONAL TRAITS IN AMERICAN ANGUS CATTLE**

ABSTRACT

Foot conformation is one of the main breeding goals in recent beef cattle breeding programs because it directly affects productivity, economic losses, animal welfare, and longevity. Genetic heterogeneity of residual variance can be used to improve production uniformity in animal breeding programs because recent studies have shown that residual variance is partially under genetic control, allowing reduction of variability through selection. Despite being an important breeding goal, research on genetic heterogeneity of residual variance for conformation traits, such as foot angle and foot claw is still scarce in livestock species. The objectives of our study were 1) to investigate the extent of genetic heterogeneity of residual variances on two conformation traits: foot angle (FA) and claw set (CS) in Angus cattle using genetic homogeneity (M1) and two genetic heterogeneity of residual variance models, including a double hierarchical generalized linear model (DHGLM, M2) and a genetically structured environmental variance model (M3). Genetic parameters for means and residual variances were estimated using M2 and M3. The dataset included 45,667 phenotypic records for FA and CS (scores from 1 to 9 with 5 being ideal) of American Angus cattle recorded from 2009 to 2021. M1 and M2 were fitted using average information restricted maximum likelihood and M3 was fitted using Markov chain Monte Carlo. Heritability estimates for the means of FA (0.19 ± 0.01 for M1 and 0.11 ± 0.02 for M2) and CS (0.16 ± 0.01 for M1 and 0.08 ± 0.03 for M2) were within the range reported in the literature, but M2 estimates were lower than M1. Genetic heterogeneity of residual variance was assessed using three parameters: heritability for residual variance, genetic coefficient of variation, and correlation between mean and residual variance. Although heritability estimates for residual variance in M2 were low

(0.07 for FA and 0.05 for CS), our results suggest that residual variance is partially under genetic control. The genetic coefficients of variation estimates were 0.48 (M1) and 0.42 (M2) for FA, and 0.40 (M1) and 0.44 (M2) for CS, indicating that selection on the trait mean would also change the residual variance. Our results for FA and CS showed high positive genetic correlations in M2 (0.86 for FA and 0.73 for CS) and low positive genetic correlations in M3 (0.29 for FA and 0.27 for CS) between mean and residual variance. Positive correlations may limit the response to selection unless other breeding strategies, such as selection indices, are used. FA and CS are promising traits for uniformity or resilience indicators because they are phenotypes that can be collected throughout the production cycle using traditional or digital data recording systems. Our results demonstrate the potential to modulate variability through breeding strategies and present an opportunity to evaluate the uniformity of foot score traits in beef cattle.

Keywords: beef cattle, claw set, foot angle, foot scores, genetic heterogeneity of residual variance.

INTRODUCTION

Hoof structure is a major concern in global dairy and beef cattle production and is critical for optimal animal performance, health, and longevity (Giess et al., 2021).

Identifying structural disorders is critical to animal welfare because they can lead to lameness, which can result in economic losses due to reduced production, fertility issues, and veterinary costs (Van Dorp et al., 2004). In addition, Oliveira et al. (2020) reported that approximately 6% of cows are culled due to structural problems, which has a direct impact on the longevity of the animal.

Traditionally, beef cattle breeding programs have focused on production and reproduction traits because these are the primary profit drivers for the industry. However, the North American and Australian Angus Associations have defined foot conformation (structural soundness) as one of the top three breeding goals (Bell et al., 2019; Santos et al., 2019). Selection for hoof structure can be performed using the foot scoring system, with foot angle (FA) and claw set (CS) being the key indicators of structural disorders. Recently, efforts from both associations have spurred interest in the genetic evaluation of foot score traits (Alvarenga et al., 2023), drawing attention to the evaluation of animals in different environments and the potential re-ranking of breeding candidates for specific environmental conditions due to genotype-by-environment interactions (Hayes et al., 2016) or microenvironmental sensitivity.

Uniformity of production has become an important breeding goal in several livestock species (Iung et al., 2020) because of the economic returns that more uniform animal production can bring through differentiated payment according to optimal trait ranges or specific industry standards. In addition, lack of uniformity has been associated

with economic losses in many species (Wilson, 1991; Milligan et al., 2002; Abiola et al., 2008; Mee, 2008; Pardo et al., 2013). Breeding strategies, such as mating systems and selection play an important role in influencing trait variability within animal populations. Recently, numerous studies have shown that residual variance may be under genetic control (Hill and Mulder, 2010; Iung et al., 2017), which can potentially be used to enhance the uniformity of foot score traits. Genetic control of uniformity, also referred to as genetic heterogeneity of residual variance or genetic variance in microenvironmental sensitivity, can provide insight into how genotypes respond differently to unknown microenvironmental factors (Falconer and Mackay, 1996; Ehsaninia et al., 2019).

Several approaches have been developed to study genetic heterogeneity of residual variance (Felleki et al., 2012; Mulder et al., 2009; Rönnegård et al., 2010; SanCristobal-Gaudy et al., 1998), providing solutions for response variables at the level of mean and residual variance. However, there is still a lack of studies on genetic heterogeneity of residual variance in beef cattle (Neves et al., 2012, 2011; Iung et al., 2017), and no reports on structural traits such as FA and CS. Therefore, the objectives of our study were 1) to investigate the extent of heterogeneity in residual variance for foot score traits in American Angus cattle and 2) to compare the results of pedigree-based REML and Bayesian approaches.

MATERIAL AND METHODS

Ethics Statement

Institutional Animal Care and Use Committee approval was not required for this study because the data were obtained from an existing American Angus Association database.

Data

The dataset was provided by Angus Genetics Inc. and included phenotypic information for two foot score traits: FA and CS. The foot scoring system, developed by the American Angus Association, are subjective measurements ranging from 1 to 9, as shown in Figure 1. A score of five is optimal for both FA and CS.

For FA, an animal with a score of five would have a 45-degree angle in the pastern along with a satisfactory heel depth. For CS, a score of five reflects claws that are straight and even (symmetrical). Phenotypes were collected at the yearling stage (one year of age) or older. It is recommended that repeated measurements be taken prior to hoof trimming. Additionally, the association advises that FA and CS be recorded on the worst foot when contemporary animals are handled, with a single handler recording all scores within a contemporary group (Retallick, 2019).

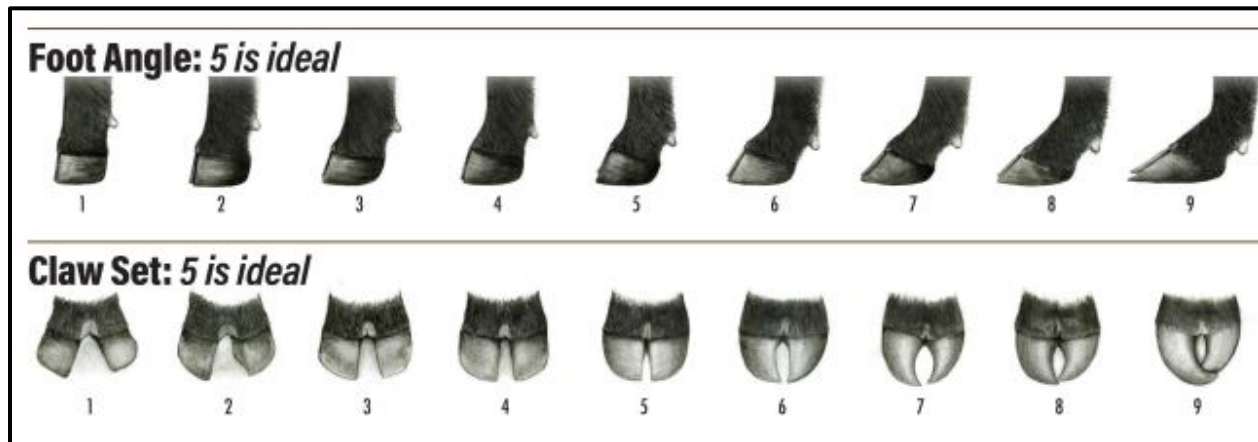


Figure 4. Foot score guidelines developed by the American Angus Association. Picture Source: American Angus Association (Retallick, 2019).

Contemporary groups (CG) consisted of a concatenation of the following systematic effects: weaning and yearling herd, lot identification, measurement date, management code (e.g., creep feeding system), diet type (i.e., low concentrate diet < 50%, high concentrate diet > 50%, or pasture), herd, and date of foot score collection.

The phenotypic datasets included data from registered purebred Angus cattle. A total of 190,140 phenotypes (118,828 animals recorded from December 2008 to October 2022) from the USA were available for analysis. The datasets were edited to maintain sufficient variation within each level of CG (at least 20 records and two foot score categories) and age from 321 to 7,796 days.

Variance components estimation

Variance components for the mean and residual variance of FA and CS were estimated using three models. The first model is a homoscedastic model (M1), which follows a traditional additive genetic framework in which the residual variance is homogeneous. The subsequent models, M2 and M3, jointly estimate parameters for the mean and residual variance.

Homoscedastic Residual Variance Model (M1)

The first model was a standard animal model for FA and CS, which is a classical additive genetic model including the assumption of homogeneity of residual variance. For both traits, M1 was:

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

where $\mathbf{y}$ is a vector of phenotypes (FA or CS); $\mathbf{X}$ is an incidence matrix of systematic effects; $\mathbf{b}$ is a vector of systematic effects (CG as previously defined); $\mathbf{Z}$ is an incidence matrix relating individuals to phenotypic records; $\mathbf{a}$ is the additive genetic effect with $\mathbf{a} \sim N(0, \mathbf{A}\sigma_a^2)$, where $\mathbf{A}$ is the numerator relationship matrix and σ_a^2 is the additive genetic variance; and $\mathbf{e}$ is a vector of residuals, assuming that $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$, where $\mathbf{I}$ is an identity matrix and σ_e^2 is the residual variance. M1 was solved using the Average Information Restricted Maximum Likelihood (AI-REML) module of the DMU package (Madsen and Jensen, 2013).

Heterogeneous Residual Variance Models

Double Hierarchical Generalized Linear Model (M2)

A double hierarchical generalized linear model (DHGLM) is an extension of generalized linear models (Lee and Nelder, 1996), which can handle non-normal data by assuming a gamma distribution for the squared residuals (Rönnegård et al., 2010). The algorithm iterates using a bivariate analysis by fitting the mean and residual variance as follows (Felleki et al., 2012):

$$\begin{bmatrix} \mathbf{y} \\ \boldsymbol{\psi} \end{bmatrix} = \begin{bmatrix} \mathbf{X} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_v \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{b}_v \end{bmatrix} + \begin{bmatrix} \mathbf{Z} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_v \end{bmatrix} \begin{bmatrix} \mathbf{a} \\ \mathbf{a}_v \end{bmatrix} + \begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix}$$

where $\mathbf{y}$ and $\boldsymbol{\psi}$ are vectors of response variables for the trait (FA or CS) and residual variance, respectively. $\boldsymbol{\psi}$ is defined as:

$$\psi_i = \log(\hat{\sigma}_{e_i}^2) + \left(\left[\hat{e}_i^2 / (1 - h_i) \right] - \hat{\sigma}_{e_i}^2 \right) / \hat{\sigma}_{e_i}^2,$$

where $\hat{\sigma}_{e_i}^2$ is the predicted residual variance for observation i from the previous iteration; $\hat{e}_i^2$ is the squared residual from the mean model estimated for observation i ; h_i is the leverage defined as the i^{th} diagonal element of the hat matrix $\mathbf{H}$ corresponding to the i^{th} individual (Hoaglin and Welsch, 1978); $\mathbf{Xb}$ and $\mathbf{X_v b_v}$ are fixed effects for the mean and residual variance parts, respectively; $\mathbf{Za}$ and $\mathbf{Z_v a_v}$ are the additive genetic effects for the mean and residual variance parts, respectively; and $\mathbf{e}$ and $\mathbf{e_v}$ are residuals for the mean and residual variance parts, respectively. The other effects in the model are the same as those described above for M1. It was also assumed that:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{a_v} \end{bmatrix} \sim N(0, \begin{bmatrix} \sigma_a^2 & \sigma_{a,a_v} \\ \sigma_{a,a_v} & \sigma_{a_v}^2 \end{bmatrix} \otimes \mathbf{A})$$

The residuals $\mathbf{e}$ and $\mathbf{e_v}$ were independent and followed a normal distribution:

$$\begin{bmatrix} \mathbf{e} \\ \mathbf{e_v} \end{bmatrix} \sim N(0, \begin{bmatrix} \mathbf{W}^{-1}\sigma_e^2 & 0 \\ 0 & \mathbf{W_v}^{-1}\sigma_{e_v}^2 \end{bmatrix} \otimes \mathbf{I})$$

where $\mathbf{W} = \text{diag}(\hat{\boldsymbol{\psi}}^{-1})$ and $\mathbf{W_v} = \text{diag}\left(\frac{1-h}{2}\right)$ are the residual variance per observation, since σ_e^2 and $\sigma_{e_v}^2$ are scaling variances that are expected to be equal to 1.

Estimation of the variance components was performed using the iterative AI-REML algorithm in the DMU software (Madsen and Jensen, 2013). The parameters, $\boldsymbol{\psi}$, $\mathbf{W}$, and $\mathbf{W_v}$, were updated at each iteration until the algorithm converged.

Convergence was assumed when the relative difference in the estimates of the variance components between iterations was less than 10^{-6} .

Genetically Structured Variance Model (M3)

The quantitative genetic model for M3 is the exponential model (SanCristobal-Gaudy et al., 1998), which is an extension of M1. The residual variance is assumed to be heterogeneous and partially under genetic control:

$$y_i = \mathbf{x}_i \mathbf{b} + \mathbf{z}_i \mathbf{a} + e^{\frac{1}{2}(\mathbf{x}_i \mathbf{b}^* + \mathbf{z}_i \mathbf{a}^*)} \varepsilon_i$$

where y_i is FA or CS of the i^{th} individual; * indicates parameters associated with the residual variance; $\mathbf{b}$ and $\mathbf{b}^*$ are the vectors of systematic effects; $\mathbf{a}$ and $\mathbf{a}^*$ are the vectors of direct genetic effects; $\mathbf{x}_i$, $\mathbf{z}_i$, are the same as previously described for M1 and M2; and $\varepsilon_i \sim N(0,1)$ is the residual of animal i .

The genetic effects $\mathbf{a}$ and $\mathbf{a}^*$ are jointly distributed and assumed to be Gaussian:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{a}^* \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \rho \sigma_a \sigma_{a^*} \\ \rho \sigma_a \sigma_{a^*} & \sigma_{a^*}^2 \end{bmatrix} \otimes \mathbf{A} \right)$$

where $\mathbf{A}$ is the numerator relationship matrix; σ_a^2 is the additive genetic variance; $\sigma_{a^*}^2$ is the additive genetic variance for the residual variance; ρ is the coefficient of correlation between σ_a^2 and $\sigma_{a^*}^2$; and $\otimes$ denotes the Kronecker product.

M3 was fit using the GSEVM program (Ibáñez-Escriche et al., 2010). The results of M3 were obtained by averaging the results of Markov chain Monte Carlo samples

after 500,000 iterations with a burn-in period of 50,000 iterations. The Geweke criterion (Geweke, 1991) was used to diagnose chains at a 5% significance level using the *boa* package (Smith, 2007) in R (R Development Core Team, 2021). Inferences were based on probabilities obtained from marginal posterior distributions of the parameters or their combinations. The means of the marginal posterior distributions were taken as estimates, and $\sigma_{a^*}^2$ was compared to $\sigma_{a_v}^2$ from M2.

Genetic parameters associated with residual variance

Three genetic parameters were calculated to interpret the genetic heterogeneity of residual variance in our study: heritability of residual variance (h_v^2), genetic coefficient of variation of residual variance (GCV_E), and genetic correlation between mean and residual variance (r_{mv}).

The h_v^2 can be used to evaluate the accuracy of the estimated breeding values for the residual variance. h_v^2 was estimated as defined by Mulder et al. (2007):

$$h_v^2 = \frac{\sigma_{a_v,add}^2}{(2\sigma_p^4 + 3\sigma_{a_v,add}^2)}$$

where $\sigma_{a_v,add}^2$ is the additive genetic variance estimated for the residual variance on the additive scale and σ_p^4 is the squared phenotypic variance. Here, $\sigma_{a_v,add}^2$ and the standard error of h_v^2 were obtained following Mulder et al. (2016).

GCV_E infers how much the residual variance could be changed by selection (Mulder et al., 2016) and was calculated as:

$$GCV_E = \frac{\sigma_{a_v,add}}{\bar{\sigma}_e^2}$$

where $\sigma_{a_v,add}$ is the standard deviation of the additive genetic variance for the residual variance on the additive scale. GCV_E in M3 was calculated as described in Rönnegard et al. (2013).

The genetic correlation between mean and residual variance (r_{mv}) was estimated as:

$$r_{mv} = \frac{\sigma_{a,a_v}}{\sqrt{\sigma_a^2 \sigma_{a_v}^2}}$$

where σ_{a,a_v} , σ_a^2 , and $\sigma_{a_v}^2$ were previously defined for M2.

RESULTS

After quality control, 45,667 records (45,667 animals recorded from October 2009 to November 2021) remained for further analysis. Tables 1 and 2 present the data structure and descriptive statistics. The distribution of foot scores after data cleaning is shown in Figure 2.

Table 1. Data structure of foot score traits after data cleaning.

<i>Data Structure</i>	Foot Angle and Claw Set
Number of Records	45,667
Number of Animals in Pedigree	80,808
Number of CG ¹	1,111
Number of Sires	3,069
Number of Dams	32,072

Average Number of Progeny per Sire	16.81
Average Number of Animals per contemporary groups	46.46

CG¹: Contemporary Group

Table 2. Descriptive statistics of foot score traits.

<i>Descriptive Statistics</i>	Foot Angle	Claw Set
Minimum	3.00	3.00
Maximum	9.00	9.00
Mean±SD	5.45 ± 0.71	5.55 ± 0.73
Skewness	0.77	0.78
Kurtosis	1.38	1.31

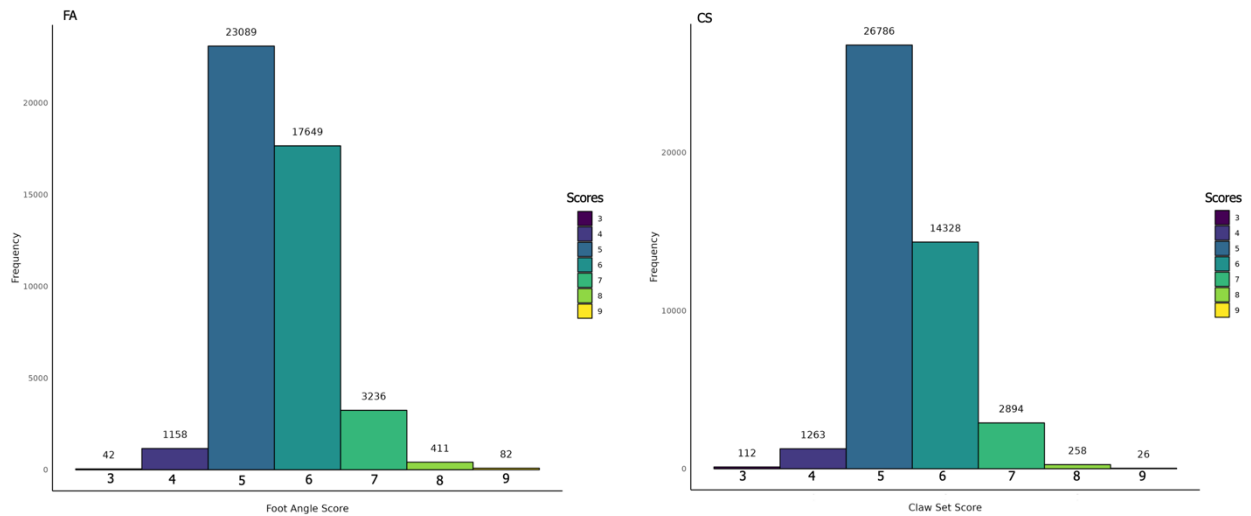


Figure 5. Distribution of foot angle (FA) and claw set (CS) scores after data cleaning.

Homoscedastic Residual Variance Model (M1)

Estimates of variance components and genetic parameters obtained from the three models for FA and CS are presented in Table 3. Heritability estimates were low ranging from 0.19 (± 0.01) for FA to 0.16 (± 0.01) for CS. The estimated residual distributions are presented in Figures 3 and 4.

Table 3. Variance component estimates and genetic parameters for mean and residual variance for FA and CS using three different models.								
Trait	Model	σ_a^2	σ_e^2	σ_{av}^2	h^2	$^2h_v^2$	GCV_E	r_{mv}
FA	M1	0.07 (3.00×10^{-3})	0.30 (3.10×10^{-3})	-	0.19 (7.00×10^{-3})	-	-	-
	M2	0.04 (1.00×10^{-3})	0.32 (0.08)	0.02 (6.00×10^{-3})	0.11 (0.02)	0.07 (7.00×10^{-3})	0.48 (0.03)	0.86 (0.05)
	¹ M3	1.85 (2.10×10^{-5})	-	0.17 (0.02)	-	-	0.42	0.29 (0.17)
CS	M1	0.04 (4.00×10^{-3})	0.24 (4.00×10^{-3})	-	0.16 (5.00×10^{-3})	-	-	-
	M2	1.00×10^{-3} (1.00×10^{-4})	0.01 (6.00×10^{-3})	3.87×10^{-5} (2.10×10^{-5})	0.08 (0.03)	0.05 (5.00×10^{-3})	0.40 (0.03)	0.73 (0.06)
	¹ M3	1.79 (3.22×10^{-7})	-	0.20 (1.40×10^{-7})	-	-	0.44	0.27 (4.37×10^{-7})

FA: Foot Angle

CS: Claw Set

M1: Homoscedastic residual variance model. M2: Heteroscedastic model (DHGLM). M3: Heteroscedastic model (structured model). σ_a^2 and σ_{av}^2 are additive genetic variances for the means and residual variances. σ_e^2 is the residual variance. h^2 and h_v^2 are heritability estimates for the means and residual variances. GCV_E is the genetic coefficient of variation for the residual variance; r_{mv} is the genetic correlation between the estimated breeding values of the means and the residual variance; standard errors are given in parentheses.

¹Mean and SD (in brackets) of the marginal posterior distribution.

²For M3, σ_{av}^2 represents $\sigma_{a^*}^2$

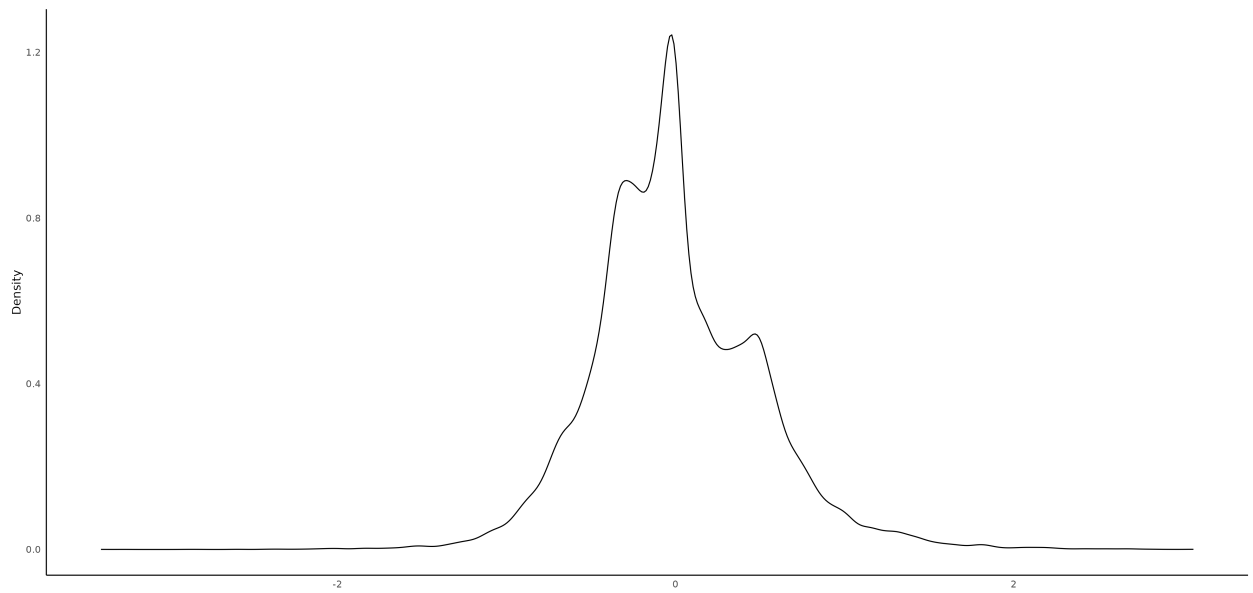


Figure 6. Estimated residual distribution for foot angle using M1.

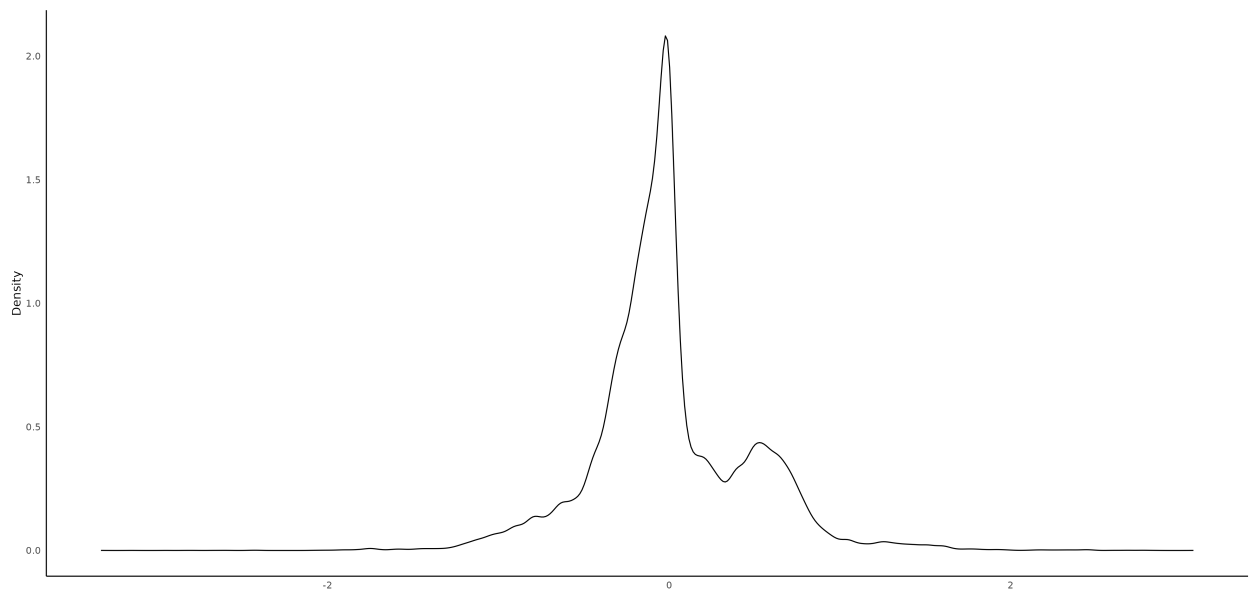


Figure 7. Estimated residual distribution for claw set using M1.

Heterogeneous Residual Variance Models

The additive genetic variance for the mean in M2 was similar but slightly lower than in M1 for FA ($\sigma_a^2 = 0.07$ in M1 and $\sigma_a^2 = 0.04$ in M2) and a similar pattern was observed for CS ($\sigma_a^2 = 0.04$ in M1 and $\sigma_a^2 = 1.00 \times 10^{-3}$ in M2). In contrast, the estimates of σ_a^2 in M3 were 1.85 for FA and 1.79 for CS, the highest among the three models in this study. Heritability estimates (h^2) for the mean in M2 were lower for FA (0.11 ± 0.02) and CS (0.08 ± 0.03) than in M1.

We estimated the parameters influencing the genetic control of the residual variance with M2 and M3. In M2, the genetic variance for the residual variance (σ_{av}^2) was 0.02 for FA and 3.87×10^{-5} for CS. In M3, the posterior means of σ_{av}^2 were 0.17 for FA and 0.20 for CS and were higher than those in M2.

The heritability estimates of the residual variance (h_v^2) were obtained using M2. Low estimates of h_v^2 (< 0.1) were obtained for both traits, ranging from 0.07 ± 0.01 for FA to 0.05 ± 0.01 for CS. Estimates of GCV_E were moderate for FA and CS in M2, ranging from 0.48 for FA to 0.40 for CS. The estimates of GCV_E in M3 were 15% lower (0.42) for FA than that of M2 and 10% higher for CS than that of M2 (0.44).

Finally, the genetic correlation between the mean and residual variance (r_{mv}) was estimated using M2 and M3. In both models, low to high positive correlations were found, and the highest values of r_{mv} were observed in M2, ranging from 0.86 for FA to 0.73 for CS. Lower positive correlations were obtained in M3 ranging from 0.29 to 0.27 for FA and CS, respectively.

DISCUSSION

Genetic Parameters for the mean

Hoof structure is crucial in beef cattle production, as poor feet and legs are among the most common reasons for culling beef cattle from a herd. Culling animals can be costly, especially in situations where raising or rearing an animal does not generate sufficient income to cover these production costs (Giess et al., 2021). Despite the economic importance of foot score traits in beef cattle, research on these traits remains scarce (Jeyaruban et al., 2012; Wang et al., 2017; Giess et al., 2021; Saad et al., 2021; Alvarenga et al., 2023).

First, it should be noted that some studies may report foot scores for both front and rear legs. However, it has been shown that front and rear leg scores are highly genetically correlated (~ 0.88 for FA and ~ 0.75 for CS) (Giess et al., 2021), meaning that only one record in the front or rear leg could be recorded and used to select individuals based on foot scores. Based on this high genetic correlation, the data analyzed in the current study collected one record (front or rear leg) from each animal instead of two records to optimize phenotype collection (Retallick, 2019). The estimates of h^2 for FA obtained in this study (0.19 in M1 and 0.11 in M2) were lower than those observed by Jeyaruban et al. (2012), who reported h^2 estimates of 0.32 and 0.29 for front and rear feet angle in Australian Angus. Our results were also lower than those reported by Wang et al. (2017) in the American Angus population, with animals ranging in age from 320 to 810 days (0.37) and by Saad et al. (2021) in a multibreed population with animals ranging in age from 8 months to 16 years (0.26). More recently, Alvarenga et al. (2023), in a study of foot score traits in American and Australian Angus cattle reported slightly higher h^2

estimates for FA in the US population (0.22) compared to estimates in M1. However, it is important to note that the dataset used in this study is a subset of the US dataset in Alvarenga et al. (2023), so lower h^2 estimates were expected in M1. Our estimates of h^2 for FA in M1 were higher than those found by Giess et al. (2021) for front and rear hoof angles measured at 1 to 2 years of age for bulls and 1 to 18 years of age for cows in Red Angus (0.18 and 0.17, respectively). The estimate of h^2 for FA in M2 (0.11) in our study was lower than all other estimates reported in the literature.

For CS, the range of heritability estimates in the different studies presented above was between 0.08 and 0.33. Our estimates for CS were higher than those of Giess et al. (2021) for front (0.08) and rear (0.15) CS in M1 and the same (0.08) for the front CS in M2. Compared to the other studies, our estimates in M1 and M2 were lower than those of Jeyaruban et al. (2012), who evaluated CS using only single records from animals younger than 750 days of age (0.33) and Saad et al. (2021) (0.29), who worked with a dataset of 4,333 single records per animal and repeated records per animal (865 repeated records for FA and 864 for CS), for a total of 12,179 observations in their multi-breed population of Black Angus, Red Angus, South Devon, British, Simmental, Charolais, Gelbvieh, Continental breeds, and others. In American Angus, Wang et al. (2017) used a subset of the dataset used in Alvarenga et al. (2023) (phenotypes collected up to 2016) and reported h^2 for CS of 0.25, which was higher than the recent work by Alvarenga et al. (2023) (0.21). Another possible reason why our heritability estimates were lower than those of the aforementioned studies is the presence of scores 3 and 4 in the dataset. Previous studies have observed the same trend of decreasing heritability estimates when these scores (<5) are included, which is why some studies (Wang et al., 2017; Saad et al.,

2021; Alvarenga et al., 2023) chose to remove these phenotypes for further analysis. Additionally, only a subset of the entire American Angus population and 2) pedigree information were used in the analysis, which may indicate that there is a possibility that the dataset for FA and CS used in this study may not be a representative sample of the national herd.

Genetic variances and parameters for the variance

In general, animals are born with good hoof structure. As they grow, the locomotor system is influenced by genetic factors that may or may not be expressed at different stages of the animal's life, which can alter its posture. Additionally, environmental factors, such as overfeeding, food and water availability, and the topography of the grazing environment, can have lasting effects on bones and joints (Boelling and Pollott, 1998a; Langova et al., 2020; Tranter and Morris, 1992).

To our knowledge, this is the first study to report the extent of genetic control of residual variance for FA and CS in beef cattle and therefore the discussion for these parameters will focus on other similar conformation-related traits in chicken and cattle. Our results show the presence of additive genetic variances for the mean (σ_a^2) of FA and CS and their variances (σ_{av}^2 and σ_{a+}^2). In particular, M3 resulted in an increase in σ_a^2 compared to M1 and M2 for both traits, similar to Ibáñez-Escriche et al. (2008) in a study of environmental variability of body weight traits in mice.

Estimates of heritability of residual variance (h_v^2) were low, ranging from 0.07 (± 0.01) for FA to 0.05 (± 0.01) for CS in M2. These estimates are within the range reported by Hill and Mulder (2010) and Iung et al. (2020) (between 0.05 and <0.1). Wolc et al. (2009) estimated genetic parameters for the residual variance of conformation

scores in chickens (where 1 was considered poor conformation and 5 was excellent conformation). The authors reported h_v^2 estimates for conformation scores of 0.03 (± 0.01) for females and 0.02 (± 0.004) for broilers. Similarly, in Nellore cattle, Neves et al. (2011) evaluated conformation scores (scale of 1 to 5) at weaning and yearling and reported 0.01 (± 0.004) for conformation score at weaning and 0.01 (± 0.002) for conformation score at yearling. These estimates were lower than those reported by Wolc et al. (2009).

Mulder et al. (2007) pointed out that large amounts of information are needed to accurately predict h_v^2 . Our low estimates for h_v^2 compared to other studies in the literature for conformation-related traits support this statement. Based on the estimated GCV_E values obtained from M2 and M3, the presence of a possible opportunity for genetic change in FA and CS through selection is suggested. The concept of GCV_E (also referred to as evolvability) was originally introduced by Houle (1992) as a measure of the genetic standard deviation relative to the mean of a trait, which is crucial for predicting the ability of a population to respond to selection. Our results indicate that a change of 1 genetic standard deviation would change the residual variance of FA by $\sim 48\%$ in M2 and $\sim 42\%$ in M3. For CS, a change in residual variance of $\sim 40\%$ in M2 and $\sim 44\%$ in M3 is expected. The GCV_E values obtained are higher than the range reported for conformation traits in chickens and cattle (0.15 to 0.31) (Neves et al., 2011; Wolc et al., 2009), but within the range of GCV_E reported for livestock and aquaculture species (0 – 0.86) (Hill and Mulder, 2010; Lung et al., 2020).

The genetic correlation between mean and residual variance is represented by r_{mv} . M2 showed the highest correlations of 0.86 for FA and 0.73 for CS. The range for

conformation-related traits in the literature is 0.15 to 0.40 (Neves et al., 2011; Wolc et al., 2009), which is within the range reported for various traits in cattle (-0.20 to 0.89) (Iung et al., 2020). The observed high r_{mv} values may also be related to pleiotropic effects, as most of the alleles of the mean of a trait may also act on its variance (Gavrilets and Hastings, 1994). On the other hand, r_{mv} estimates were positive but lower in M3 than in M2, where the corresponding r_{mv} was 0.29 for FA and 0.27 for CS. Combined with h_v^2 , the genetic correlation between mean and residual variance indicates the response to selection when the breeding goal is to increase uniformity. Our low estimates of h_v^2 and positive r_{mv} in M2 and M3 suggest that the response to selection may be limited if the desired response is to increase FA or CS scores and reduce their variability.

Implications for Breeding

Foot and leg scores have become an important part of the genetic evaluation of beef cattle worldwide because animals with undesirable proportions, foot angle, and fore and hind limbs may have problems with bones and hooves, which can affect their productive performance and reduce their longevity (Filho et al., 2010). Hoof alignment is directly related to the overall health of the animal and its longevity in the herd, as any postural irregularity can cause discomfort in different ways and degrees. In a study of dairy cows, Sewalem et al. (2004) reported that the longevity of cows with legs that were either too straight or too curved was negatively affected, resulting in a shorter productive life, even when the animals had favorable genetic potential for other economically important traits.

Based on our results, selection to simultaneously alter the mean and variance of FA and CS could be explored using index selection theory, which implies that mean and

residual variance should be considered as distinct traits (Ros et al., 2004 and Mulder et al. 2008). For example, if the mean of the trait is close to its optimum, a restricted index could be used to maintain the mean while reducing the residual variance. Similarly, Berghof et al. (2019) presented an alternative to include uniformity (resilience) in selection indices by using indicators based on their economic values (reduced labor and health costs). Given the importance and documented economic losses due to poor hoof structure (Boelling and Pollott, 1998b; Boettcher et al., 1998; Enting et al., 1997; Merks et al., 2012), including uniformity parameters in selection indices may be an appropriate approach. The authors also evaluated the inclusion of these indicators in simulated scenarios for pig and dairy cattle breeding systems. The results of these simulations indicated that the selection response was greater when the indicators were considered in selection, and therefore uniformity should be considered when calculating total merit indices of animals. Lastly, because FA and CS are recommended to be collected at different ages (covering different production periods) and are relatively easy to obtain, they can be used to calculate uniformity or resilience indicators to be evaluated genetically.

With the recent development of precision livestock farming (PLF) technologies, digital data recording is another alternative to collect phenotypes more frequently, in greater quantities, and at a much faster rate (Morota et al., 2018). Phenotype collection can be laborious, costly, and prone to human error. PLF technologies, such as imaging or sensors, can be used to assess different production traits. Digital phenotyping tools are being developed to minimize lameness in pigs by evaluating locomotion and front/rear legs (Psota, 2024). Research on digital data recording and investigation of the inclusion

of uniformity FA and CS should be explored to evaluate genetic and economic responses to breeding goals in beef cattle.

Lastly, genomic selection can potentially be used to predict uniformity parameters. The advantages of using genomic selection include increased accuracy of genetic value estimates, reduced generation intervals by identifying genetically superior animals before they express the phenotype of interest, and correcting for potential pedigree errors that would negatively affect the accuracy of estimates (Goddard et al., 2010). Additionally, genomic selection plays a role in increasing the reliability of EBV, especially for young animals. However, few studies have been published using genomic data to evaluate genetic heterogeneity of residual variance (Mulder et al., 2013; Sell-Kubiak et al., 2015; Sae-Lim et al., 2017), likely due to the complex task of fitting high-dimensional genomic data using DHGLM or the genetically structured variance model and the lack of software capable of incorporating genomic information in their evaluations. In our study, genomic data were not used because 1) the DHGLM model did not converge and 2) available software for fitting the genetically structured variance model does not yet support genomic data. Further research should be conducted to incorporate genomic data with different models to evaluate genetic heterogeneity of residual variance in economically important traits.

CONCLUSION

To our knowledge, this is one of the first studies of genetic heterogeneity of residual variance for foot score traits in beef cattle and to estimate genetic parameters for foot score uniformity. The results of this study suggest the presence of additive genetic

effects on residual variance for FA and CS, and the possibility of altering the residual variance through selection. The genetic coefficient of variation on M2 and M3 averaged 0.45 for FA and 0.42 for CS, indicating that changing the mean of FA or CS would also change the residual variance by 45% and 42% for FA and CS, respectively.

The low heritability estimates for residual variance were within the range reported in other studies in livestock species and reinforced the need for larger datasets to more accurately estimate heritabilities for residual variance. Additionally, positive genetic correlations between means and residual variances suggest that the genetic response to direct selection may be limited, but alternatives such as the development of uniformity indicators could be used in selection indices along with other breeding goals, such as growth, reproduction, and health traits. Further studies should be conducted to evaluate the incorporation of such indicators in breeding programs and to confirm the results obtained from the exploratory approach in this study.

BIBLIOGRAPHY

- Abiola, S.S., Meshioye, O.O., Oyerinde, B.O., Bamgbose, M.A., 2008. Effect of egg size on hatchability of broiler chicks. *Arch. Zootec* 57, 83–86.
- Alvarenga, A.B., Retallick, K.J., Garcia, A., Miller, S.P., Byrne, A., Oliveira, H.R., Brito, L.F., 2023. Across-country genetic and genomic analyses of foot score traits in American and Australian Angus cattle. *Genet. Sel. Evol.* 55. <https://doi.org/10.1186/S12711-023-00850-X>
- Berghof, T.V.L., Poppe, M., Mulder, H.A., 2019. Opportunities to improve resilience in animal breeding programs. *Front. Genet.* 10, 410180. <https://doi.org/10.3389/FGENE.2018.00692/BIBTEX>
- Boelling, D., Pollott, G.E., 1998a. Locomotion, lameness, hoof and leg traits in cattle: II. Genetic relationships and breeding value. *Livest. Prod. Sci.* 54, 205–215. [https://doi.org/10.1016/S0301-6226\(97\)00173-5](https://doi.org/10.1016/S0301-6226(97)00173-5)
- Boelling, D., Pollott, G.E., 1998b. Locomotion, lameness, hoof and leg traits in cattle II.: Genetic relationships and breeding values. *Livest. Prod. Sci.* 54, 205–215. [https://doi.org/10.1016/S0301-6226\(97\)00173-5](https://doi.org/10.1016/S0301-6226(97)00173-5)
- Boettcher, P.J., Dekkers, J.C.M., Warnick, L.D., Wells, S.J., 1998. Genetic analysis of clinical lameness in dairy cattle. *J. Dairy Sci.* 81, 1148–1156. [https://doi.org/10.3168/JDS.S0022-0302\(98\)75677-2](https://doi.org/10.3168/JDS.S0022-0302(98)75677-2)
- Ehsaninia, J., Ghavi Hossein-Zadeh, N., Shadparvar, A.A., 2019. Estimation of genetic variation for macro- and micro-environmental sensitivities of milk yield and composition in Holstein cows using double hierarchical generalized linear models. *J. Dairy Res.* 86, 145–153. <https://doi.org/10.1017/S0022029919000293>
- Enting, H., Kooij, D., Dijkhuizen, A.A., Huirne, R.B.M., Noordhuizen-Stassen, E.N., 1997. Economic losses due to clinical lameness in dairy cattle. *Livest. Prod. Sci.* 49, 259–267. [https://doi.org/10.1016/S0301-6226\(97\)00051-1](https://doi.org/10.1016/S0301-6226(97)00051-1)
- Falconer, D.S., Mackay, T.F.C., 1996. *Introduction to quantitative genetics*. Pearson.
- Felleki, M., Lee, D., Lee, Y., Gilmour, A.R., Rönnegård, L., 2012. Estimation of breeding values for mean and dispersion, their variance and correlation using double hierarchical generalized linear models. *Genet. Res. (Camb)*. 94, 307–317. <https://doi.org/10.1017/S0016672312000766>
- Filho, W.K., de Albuquerque, L.G., Forni, S., de Vasconcelos Silva, J.A., Yokoo, M.J., de Alencar, M.M., 2010. Estimativas de parâmetros genéticos para os escores visuais e suas associações com peso corporal em bovinos de corte. *Rev. Bras. Zootec.* 39, 1015–1022. <https://doi.org/10.1590/S1516-35982010000500011>
- Gavrilets, S., Hastings, A., 1994. A Quantitative-Genetic Model for Selection on Developmental Noise. *Evolution (N. Y.)*. 48, 1478. <https://doi.org/10.2307/2410242>

- Geweke, J.F., 1991. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. Staff Rep.
- Giess, L.K., Jensen, B.R., Bormann, J.M., Rolf, M.M., Weaber, R.L., 2021. Genetic parameter estimates for feet and leg traits in Red Angus cattle. *J. Anim. Sci.* 99, 1–12. <https://doi.org/10.1093/JAS/SKAB256>
- Goddard, M. E., B. J. Hayes, and T. H. E. Meuwissen. 2010. Genomic selection in livestock populations. *Genet. Res. (Camb)*. 92:413–421. doi:10.1017/S0016672310000613.
- Hayes, B.J., Daetwyler, H.D., Goddard, M.E., 2016. Models for Genome $\times$ Environment Interaction: Examples in Livestock. *Crop Sci.* 56, 2251–2259. <https://doi.org/10.2135/CROPSCI2015.07.0451>
- Hill, W.G., Mulder, H.A., 2010. Genetic analysis of environmental variation. *Genet. Res. (Camb)*. 92, 381–395. <https://doi.org/10.1017/S0016672310000546>
- Hoaglin, D.C., Welsch, R.E., 1978. The hat matrix in regression and anova. *Am. Stat.* 32, 17–22. <https://doi.org/10.1080/00031305.1978.10479237>
- Houle, D., 1992. Comparing evolvability and variability of quantitative traits. *Genetics* 130, 195–204. <https://doi.org/10.1093/GENETICS/130.1.195>
- Ibáñez-Escriche, N., Garcia, M., Sorensen, D., 2010. GSEVM v.2: MCMC software to analyze genetically structured environmental variance models. *J. Anim. Breed. Genet.* 127, 249–251. <https://doi.org/10.1111/J.1439-0388.2009.00846.X>
- Ibáñez-Escriche, N., Moreno, A., Nieto, B., Piqueras, P., Salgado, C., Gutiérrez, J.P., 2008. Genetic parameters related to environmental variability of weight traits in a selection experiment for weight gain in mice; signs of correlated canalised response. *Genet. Sel. Evol.* 40, 279. <https://doi.org/10.1186/1297-9686-40-3-279>
- Iung, L.H. de S., Carvalheiro, R., Neves, H.H. de R., Mulder, H.A., 2020. Genetics and genomics of uniformity and resilience in livestock and aquaculture species: A review. *J. Anim. Breed. Genet.* 137, 263–280. <https://doi.org/10.1111/JBG.12454>
- Iung, L.H.S., Neves, H.H.R., Mulder, H.A., Carvalheiro, R., 2017. Genetic control of residual variance of yearling weight in Nellore beef cattle. *J. Anim. Sci.* 95, 1425–1433. <https://doi.org/10.2527/JAS.2016.1326>
- Jeyaruban, G., Tier, B., Johnston, D., Graser, H., 2012. Genetic analysis of feet and leg traits of Australian Angus cattle using linear and threshold models. *Anim. Prod. Sci.* 52, 1–10. <https://doi.org/10.1071/AN11153>
- Langova, L., Novotna, I., Nemcova, P., Machacek, M., Havlicek, Z., Zemanova, M., Chrast, V., 2020. Impact of Nutrients on the Hoof Health in Cattle. *Anim.* 2020, Vol. 10, Page 1824 10, 1824. <https://doi.org/10.3390/ANI10101824>
- Lee, Y., Nelder, J.A., 1996. Hierarchical Generalized Linear Models. *J. R. Stat. Soc. Ser.*

- B Stat. Methodol. 58, 619–656. <https://doi.org/10.1111/J.2517-6161.1996.TB02105.X>
- Mee, J.F., 2008. Prevalence and risk factors for dystocia in dairy cattle: A review. *Vet. J.* 176, 93–101. <https://doi.org/10.1016/J.TVJL.2007.12.032>
- Merks, J.W.M., Mathur, P.K., Knol, E.F., 2012. New phenotypes for new breeding goals in pigs. *animal* 6, 535–543. <https://doi.org/10.1017/S1751731111002266>
- Milligan, B.N., Fraser, D., Kramer, D.L., 2002. Within-litter birth weight variation in the domestic pig and its relation to pre-weaning survival, weight gain, and variation in weaning weights. *Livest. Prod. Sci.* 76, 181–191. [https://doi.org/10.1016/S0301-6226\(02\)00012-X](https://doi.org/10.1016/S0301-6226(02)00012-X)
- Morota, G., R. V. Ventura, F. F. Silva, M. Koyama, and S. C. Fernando. 2018. BIG DATA ANALYTICS AND PRECISION ANIMAL AGRICULTURE SYMPOSIUM: Machine learning and data mining advance predictive big data analysis in precision animal agriculture. *J. Anim. Sci.* 96:1540–1550. doi:10.1093/JAS/SKY014.
- Mulder, H.A., Bijma, P., Hill, W.G., 2008. Selection for uniformity in livestock by exploiting genetic heterogeneity of residual variance. *Genet. Sel. Evol.* 40, 37–59. <https://doi.org/10.1051/GSE:2007034>
- Mulder, H.A., Bijma, P., Hill, W.G., 2007. Prediction of Breeding Values and Selection Responses With Genetic Heterogeneity of Environmental Variance. *Genetics* 175, 1895. <https://doi.org/10.1534/GENETICS.106.063743>
- Mulder, H.A., Hill, W.G., Vereijken, A., Veerkamp, R.F., 2009. Estimation of genetic variation in residual variance in female and male broiler chickens. *Animal* 3, 1673–1680. <https://doi.org/10.1017/S1751731109990668>
- Mulder, H. A., R. E. Crump, M. P. L. Calus, and R. F. Veerkamp. 2013. Unraveling the genetic architecture of environmental variance of somatic cell score using high-density single nucleotide polymorphism and cow data from experimental farms. *J. Dairy Sci.* 96:7306–7317. doi:10.3168/JDS.2013-6818.
- Mulder, H.A., Visscher, J., Fablet, J., 2016. Estimating the purebred-crossbred genetic correlation for uniformity of eggshell color in laying hens. *Genet. Sel. Evol.* 48, 1–13. <https://doi.org/10.1186/S12711-016-0212-2/TABLES/6>
- Neves, H.H.R., Carneiro, R., Queiroz, S.A., 2012. Genetic and environmental heterogeneity of residual variance of weight traits in Nelore beef cattle. *Genet. Sel. Evol.* 44, 1–12. <https://doi.org/10.1186/1297-9686-44-19/TABLES/5>
- Neves, H.H.R., Carneiro, R., Roso, V.M., Queiroz, S.A., 2011. Genetic variability of residual variance of production traits in Nelore beef cattle. *Livest. Sci.* 142, 164–169. <https://doi.org/10.1016/J.LIVSCI.2011.07.010>
- Oliveira, H.R., Brito, L.F., Miller, S.P., Schenkel, F.S., 2020. Using Random Regression Models to Genetically Evaluate Functional Longevity Traits in North American Angus

Cattle. Anim. an Open Access J. from MDPI 10, 1–30.
<https://doi.org/10.3390/ANI10122410>

Pardo, C.E., Kreuzer, M., Bee, G., 2013. Effect of average litter weight in pigs on growth performance, carcass characteristics and meat quality of the offspring as depending on birth weight. animal 7, 1884–1892. <https://doi.org/10.1017/S1751731113001419>

Psota, E. 2024. *Never stop improving: Advancing pig genetics using digital phenotyping*. Advances in Genome Biology and Technology (AGBT). Phoenix, AZ.

Rönnegård, L., Felleki, M., Fikse, F., Mulder, H.A., Strandberg, E., 2010. Genetic heterogeneity of residual variance - Estimation of variance components using double hierarchical generalized linear models. Genet. Sel. Evol. 42, 1–10.
<https://doi.org/10.1186/1297-9686-42-8/FIGURES/1>

Rönnegård, L., Felleki, M., Fikse, W.F., Mulder, H.A., Strandberg, E., 2013. Variance component and breeding value estimation for genetic heterogeneity of residual variance in Swedish Holstein dairy cattle. J. Dairy Sci. 96, 2627–2636.
<https://doi.org/10.3168/JDS.2012-6198>

Ros, M., Sorensen, D., Waagepetersen, R., Dupont-Nivet, M., SanCristobal, M., Bonnet, J.C., Mallard, J., 2004. Evidence for Genetic Control of Adult Weight Plasticity in the Snail *Helix aspersa*. Genetics 168, 2089. <https://doi.org/10.1534/GENETICS.104.032672>

Saad, H.M., Enns, R.M., Thomas, M.G., Leachman, L.L., Speidel, S.E., 2021. Foot scores genetic parameters estimation in beef cattle. Transl. Anim. Sci. 5, S180–S184.
<https://doi.org/10.1093/TAS/TXAB170>

Sae-Lim, P., A. Kause, M. Lillehammer, and H. A. Mulder. 2017. Estimation of breeding values for uniformity of growth in Atlantic salmon (*Salmo salar*) using pedigree relationships or single-step genomic evaluation. Genet. Sel. Evol. 49:1–12.
doi:10.1186/S12711-017-0308-3/TABLES/3.

SanCristobal-Gaudy, M., Elsen, J.-M., Bodin, L., Chevalet, C., 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. Genet. Sel. Evol. 1998 305 30, 1–29. <https://doi.org/10.1186/1297-9686-30-5-423>

Sell-Kubiak, E., S. Wang, E. F. Knol, and H. A. Mulder. 2015. Genetic analysis of within-litter variation in piglets' birth weight using genomic or pedigree relationship matrices. J. Anim. Sci. 93:1471–1480. doi:10.2527/JAS.2014-8674.

Sewalem, A., Kistemaker, G.J., Miglior, F., Van Doormaal, B.J., 2004. Analysis of the Relationship Between Type Traits and Functional Survival in Canadian Holsteins Using a Weibull Proportional Hazards Model. J. Dairy Sci. 87, 3938–3946.
[https://doi.org/10.3168/JDS.S0022-0302\(04\)73533-X](https://doi.org/10.3168/JDS.S0022-0302(04)73533-X)

Smith, B.J., 2007. boa: An R Package for MCMC Output Convergence Assessment and Posterior Inference. J. Stat. Softw. 21, 1–37. <https://doi.org/10.18637/JSS.V021.I11>

Tranter, W.P., Morris, R.S., 1992. Hoof growth and wear in pasture-fed dairy cattle. N. Z.

Vet. J. 40, 89–96. <https://doi.org/10.1080/00480169.1992.35707>

Van Dorp, T.E., Boettcher, P., Schaeffer, L.R., 2004. Genetics of locomotion. *Livest. Prod. Sci.* 90, 247–253. <https://doi.org/10.1016/J.LIVPRODSCI.2004.06.003>

Walsh, B., Lynch, M., 2018. Evolution and Selection of Quantitative Traits 1. <https://doi.org/10.1093/OSO/9780198830870.001.0001>

Wang, L., Miller, S.P., Retallick, K.J., Moser, D.W., 2017. 203 Genetic parameter estimation for foot structure in American Angus cattle. *J. Anim. Sci.* 95, 100–100. <https://doi.org/10.2527/asasann.2017.203>

Wilson, A., Norden, N., 2021. The R Project for Statistical Computing The R Project for Statistical Computing [WWW Document]. URL <http://www.r-project.org/254>. URL <https://www.r-project.org/> (accessed 4.30.20).

Wilson, H.R., 1991. Interrelationships of egg size, chick size, posthatching growth and hatchability. *Worlds. Poult. Sci. J.* 47, 5–20. <https://doi.org/10.1079/WPS19910002>

Wolc, A., White, M.S., Avendano, S., Hill, W.G., 2009. Genetic variability in residual variation of body weight and conformation scores in broiler chickens. *Poult. Sci.* 88, 1156–1161. <https://doi.org/10.3382/PS.2008-00547>

GENERAL CONCLUSION

Uniformity in production is attractive to breeding programs and industry because it can result in reduced phenotypic variation. Recent studies on genetic heterogeneity of residual variance have provided insights into the possibility of reducing residual variance while increasing the mean phenotypic level of a trait of interest based on specific genetic parameters of residual variance.

This dissertation set out to investigate the extent of genetic heterogeneity of residual variance in growth and functional traits of American Angus cattle and to explore the applicability of these findings to improve uniformity in beef cattle breeding programs. Chapters 3 and 4 compared different genetic heterogeneity models, evaluated data transformation effectiveness in continuous traits, and addressed potential pitfalls of these methods.

Chapter 3 presented genetic parameter estimates for residual variances in key growth traits such as birth weight, weaning weight, and yearling weight. It was shown that selection using genetic coefficients of variation for residual variance could potentially alter these traits. However, the genetic response to selection for uniformity may be limited by the magnitude of genetic variance, the heritability of residual variance, and the genetic correlation between mean and residual variance. Despite reducing the mean-variance relationship through data transformation, genetic heterogeneity of residual variance persisted beyond scaling effects. The Bayesian approach provided higher estimates of additive genetic variance for residual variance compared to the REML approach, which was less computationally intensive and effective for estimating the heritability of residual variance. This study represents one of the first efforts to

investigate the genetic heterogeneity of residual variance in American Angus cattle, to compare DHGLM and structured approaches, and to lay the groundwork for the potential inclusion of these traits in breeding goals.

Chapter 4 investigated genetic heterogeneity of residual variance for a set of conformation traits: foot angle (FA) and claw set (CS). It identified additive genetic effects on residual variance for these traits, with genetic coefficients of variation around 45% for FA and 42% for CS. This suggests that altering the mean of these traits would proportionally change their residual variance. The low heritability estimates for residual variance, similar to those reported in other livestock studies and the findings in Chapter 3, highlighted the need for larger datasets to obtain more accurate estimates. Positive genetic correlations between means and residual variances indicated potential limitations in direct selection response. However, the development of uniformity indicators could be incorporated into selection indices alongside other ongoing breeding goals such as growth, reproduction, and health traits. Further research is recommended to evaluate the integration of such indicators into breeding programs and to validate the exploratory findings of this study.

Our findings indicate that selection for uniformity in growth and foot score traits may be limited depending on the model used (DHGLM or Genetically Structured Variance Models). This is due to the low heritability of residual variance and moderate to high positive genetic correlations between mean and residual variance, as reported for most traits in Chapters 3 and 4. Further studies are needed to address these challenges, such as exploring the use of genomic information to enhance the prediction accuracy of estimated breeding values (EBV) for residual. Although limited studies have examined

uniformity using genomic data, all have demonstrated improved accuracy of EBV for residual variance. Additionally, alternative methods for measuring uniformity, including different uniformity or resilience indicators, should be considered, especially in the era of phenomics. Precision livestock farming technologies offer the opportunity to collect extensive data on various production traits and should be integrated into the development of new uniformity indicators.

Finally, this dissertation has provided valuable insight into the genetic heterogeneity of residual variance in American Angus cattle for the first time. The findings emphasize the complexity of selecting for uniformity while improving mean traits and highlight the potential for using residual variance genetic parameters in breeding programs. Continued research in this area, with larger datasets, genomic information, and further methodological refinement, will be critical to advancing the application of these findings to improve uniformity and productivity in beef cattle breeding.