

**HERITABILITY ESTIMATION AND MODELING STRATEGIES UTILIZING RANDOM
REGRESSION FOR WEANING WEIGHT IN AMERICAN HEREFORD CATTLE**

A Dissertation

by

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ABSTRACT

Sufficiently accounting for genotype-environment interactions would enhance genetic merit prediction and parameter estimation for traits of economic prominence in beef cattle. The objective of this work was to utilize random regressions to estimate additive direct genetic variation, and milking ability intercepts expressed as maternal additive genetic, or maternal permanent environmental variances, each as proportions of total of phenotypic variance for weaning weight, denoted as h^2 , m^2 , and c^2 , respectively, across latitude or longitude coordinates within the continental United States. Records came from the American Hereford Association ($n = 226,845$), with pedigree of 383,426 animals. Analyses were conducted across the entire continental United States across latitude or longitude. An animal model, linear random regression, and quadratic random regression model were employed with latitude as the random covariate. Both an animal model, and linear random regression model were utilized with longitude as random covariate. From the animal model, direct, maternal, and maternal permanent environmental variances as proportions of phenotypic variance for latitude and longitude were 0.19 ± 0.008 , 0.04 ± 0.011 , and 0.17 ± 0.011 ; and 0.19 ± 0.008 , 0.04 ± 0.011 , and 0.17 ± 0.011 , respectively. For linear random regression across latitude or longitude, estimates of h^2 , m^2 , and c^2 were 0.09 to 0.20, 0.07 ± 0.010 , and 0.14 ± 0.011 ; and 0.15 to 0.26, 0.03 ± 0.009 , and 0.15 ± 0.010 , respectively. For the quadratic random regression across latitude, estimates of h^2 , m^2 , and c^2 were 0.08 to 0.23, 0.07 ± 0.010 , and 0.14 ± 0.010 , respectively. The quadratic random regression across latitude was the best fit model ($P < 0.001$) for the data. A quadratic random regression analysis across longitude was attempted, but failed to converge. Linear random regressions unique to regional subdivisions were attempted for latitude and longitude, but analyses failed to converge. Considerable differences in heritability estimates were observed in

different geographical zones as modeled by random regressions across the entire continental United States, when modeling intercepts of genetic and environmental components of maternal milking ability, across latitude or longitude.

DEDICATION

I would like to dedicate this dissertation work to God, and to my family.

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Contributors

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1. INTRODUCTION

It is important to the beef cattle industry to further develop genetic merit prediction strategies in beef cattle evaluation for economically important traits to further enhance the genetic merit of each successive generation of calves through trustworthy genetic selection. It is commonly known and accepted that certain breeds of cattle perform better, per their genetic potential, in the particular environments for which they are the most genetically suited. However, obstacles may arise when specific breeds, as well as specific genetic lines within breeds of livestock which vary in levels of genetic potential are reared in different environments. That is, environments for which they may be well-adapted and meet their genetic potential for performance in certain traits. In other cases, actual performance and ability to meet genetic potential for particular traits may be restricted by the environment. Made into separate paragraph below:

In these instances where genetic potential is restricted by the environment, it would be advantageous to account for genotype-environment interaction to the extent possible when performing genetic evaluations. Traditionally, genotype-environment interaction is defined as a situation where the difference in measured performance for a particular trait between different genetic groups is different across environments. Additionally, genotype-environment interaction can exist when the slope of the trajectory of heritability estimates, breeding values, or expected progeny differences from a random regression model across an environmental gradient (when environment is characterized as a continuous random covariate) for a single breed of cattle (that is, animals of the same genotype broadly categorized as a breed) has an absolute value greater than zero. In a more practical sense, genotype-environment interaction can be observed in a case of sires significantly reranking in terms of their genetic merit for traits of economic interest with

respect to environmental change across the United States. Random regression methodology offers the capability of working with longitudinal-type data in such a way as to model changes in additive genetic variation as a proportion of total phenotypic variation for particular traits for specific breeds of cattle across an environmental gradient. Therefore, the development of the most suitable random regression models presents a more reasonable approach to predict genetic merit for economically relevant traits for cattle, tailored to their production environment, and to more appropriately account for genotype-environment interaction, compared to the present genetic evaluation standard which does not currently utilize random regression, and does not account for genotype-environment interaction.

A random regression approach allows for the possibility to model genotype-environment interaction and achieve a higher level of precision for parameter estimates and genetic merit predictions for beef cattle traits of economic importance (Meyer, 2004). Furthermore, moving forward in consideration of the results from prior work conducted by Delgadillo et al. (2019), the objective of the current study was to develop and model random regressions of first order (linear), second order (quadratic), if possible, and an animal model to estimate additive direct genetic variation for weaning weight in American Hereford cattle across latitude or longitude coordinates as covariate within the continental United States, while modeling additive maternal and maternal permanent environmental variances each as a proportion of total phenotypic variance, to represent effects of maternal milking ability on weaning weight in American Hereford cattle. This may represent a novel methodology to identify and account for the presence and degree of genotype-environment interaction.

2. REVIEW OF LITERATURE

2.1 Historical importance of the Hereford breed

Hereford cattle were first cultivated as a breed around 300 years ago in Herefordshire, England. Three traits of supreme importance in the selection criteria for the earliest development of the breed were reproductive soundness, high yield, and overall efficient production. In the year 1817, Henry Clay of Kentucky first introduced Hereford cattle to the United States.

Hereford cattle then continued to gain popularity in the United States, and in the year 1840, the first recorded breeding herd of Hereford cattle in the country began in Albany, N. Y., by William Sotham and Erastus Corning. As time went on, and as the Hereford breed continued to grow in number, and in terms of genetic merit for traits of economic importance, Charles Gudgell and Thomas Simpson of Missouri became two of the most prominent Hereford breeders in the United States. They hit a home run in terms of successful breeding and contribution of favorable genetics to the Hereford breed in the United States with their importation of the bull, Anxiety the 4th, from England. Anxiety the 4th became one of the most influential sires in the Hereford breed in the United States. Of the calves Anxiety the 4th sired, he sired two sons who became highly influential in constructing the Hereford breed as it exists today, Don Carlos, and Don Quioté. As Hereford genetics became more conventional, and as breeders sprang up with new herds in various parts of the United States, a need began to arise for collaboration among breeders to exchange helpful ideas, as well as to genetically evaluate their cattle, and predict future offspring performance for traits pertinent to beef cattle production, and production efficiency.

Consequently, the first organized Hereford association was formed in Chicago, I. L. in 1881, the American Hereford Cattle Breeders Association (AHCBA). This organization later became what is now known as the American Hereford Association (AHA). As polled (genetically without

horns) Herefords began to gain favor among producers, numbers of these cattle began to rise, to the extent that another association was formed in the year 1910, the American Polled Hereford Association (APHA). However, as both horned and polled Hereford cattle grew both in number and in production and genetic quality, both associations merged in the year 1995, keeping the name, AHA, located in Kansas City, M. O. (Ward, 2017). In order to take advantage of potential benefits from hybrid vigor, as well as to avoid discounts at sale barns from selling red-haired cattle, Angus genetics were then incorporated into some Hereford herds to produce black-hided and black-haired “Herefords” to better satisfy the needs of producers when selling cattle in a “black dominant” market. After generations of experimenting with this breeding objective, John Gage of Eudora, K. S. established the American Black Hereford Association (ABHA) in the year 1994, in order to institute these black hided Herefords as an official breed, and to perpetuate the now black-hided and black-haired sector of the Hereford breed to better meet producer needs where the market demands these kinds of cattle (ABHA, home page). As it is today, the American Hereford Association and its breeders seek to satisfy market demands and producer interests in terms of survival, production, reproduction, and overall efficiency in Hereford cattle being produced, to a greater degree, through each successive generation of progeny produced and sold.

2.2 Genetic prediction, past to present

In the early years of livestock breeding, Jay Lush studied animal breeding and genetics at Texas A&M University, and later developed a highly prestigious graduate program in animal breeding and genetics at Iowa State University in the 1930s. With the help of his colleague, L. N. Hazel, they jointly developed selection index principals for genetic selection purposes for traits

of economic importance in livestock. Furthermore, Lush wrote and published much of his work into a well-known and highly referenced book in the world of livestock breeding and academia “Animal Breeding Plans”. In the early 1940s, Hazel introduced the concept of genetic correlation, and demonstrated how these correlation estimates could be used to compute multi-trait selection indices. (Hill, 2014). Selection index theory became a highly effective method of genetic prediction. However, a fundamental assumption of selection index theory was that the performance data to be analyzed would come from genetically similar contemporary groups. This can become a problem when contemporary groups in a dataset happen to be genetically different. In the early 1960s, C. R. Henderson presented a solution to this deficiency in the selection index theory by developing the mixed model equations (MME), which would produce best linear unbiased predictions (BLUP). The MME and BLUP contained the flexibility to perform genetic evaluations while accommodating contemporary groups that were genetically different. This was a major accomplishment. Furthermore, in the early 1980s, mathematical algorithms and computer programming capabilities had evolved to the extent that prevalent utilization of BLUP for genetic parameter estimation and breeding value prediction became feasible then, and customary to this day. (Bourdon, 2000). In addition to BLUP, genomic information is currently being used to further enhance genetic predictions for traits of economic importance in beef cattle.

2.3 Importance of genotype-environment interaction

The potential impact of genotype-environment interaction on economically relevant traits could yield variations of genetic merit predictions across environments. An archetypal study conducted by Burns et al. (1979), observed genotype-environment interaction in Hereford cattle

where cattle that were adapted to their local geographical locations, either Florida or Montana, had advantages for birth weight, pre-weaning gain, estimated 205-d weight, body length, body condition score, and annual production per cow, when cattle were compared in different locations. In a much more recent study, Hayes et al. (2016) recognized the value of accounting for genotype-environment interaction in genetic evaluations of livestock. More recently, in Red Angus cattle, Fennewald et al. (2017) identified genotype-environment interaction from observing reranking of sires for birth weight and weaning weight in the southwestern and southcentral United States, compared to the rest of the country. Others have reported the importance of accounting for genotype-environment interaction in beef cattle for weaning weight (Bertrand et al. 1985; Notter et al. 1992; Williams et al. 2012), calving ease (Burfening et al. 1982), and pre-weaning gain (MacNeil et al. 2017). However, due to findings such as those reported by Tess et al. (1979, 1984), and Bertrand et al. (1987) of sires not reranking in terms of breeding values for traits of economic importance across the US, to date, genotype-environment interaction has not been modeled in the US National Cattle Evaluation strategies. Nevertheless, Hayes et al. (2016), and MacNeil et al. (2017) supported the notion of accounting for genotype-environment interaction in beef cattle genetic evaluation. Particularly, when using a random regression approach where environment is characterized as a continuous random variable over which to predict the response of a particular genotype to their specific environment.

2.4 Usefulness of random regression

Random regression modeling procedures allow for the possibility to model genotype-environment interaction for particular genetic groups of animals for traits of economic relevance, particularly with the use of longitudinal data. To date, there have been many different uses of

random regression in livestock applications, as well as in other disciplines. The capability of a random regression model to appropriately account for the variation in the correlation structure has been shown to result in an increase in genetic merit prediction accuracy of 5.9%, compared to a multivariate model (Meyer, 2004). Meyer (2004) compared genetic merit predictions from a multi-trait model and a random regression model for growth in beef cattle and found that the random regression model was better, and facilitated the inclusion of additional weight records.

Legarra et al. (2004) constructed covariance functions for random regression models for growth in Gelbvieh beef cattle, and estimated additive direct and maternal genetic effects, and maternal permanent environmental effects. These authors further explained that random regression modeling (compared to multiple-trait modeling currently used in the beef cattle genetic evaluation) would allow for the flexibility of using all available records without pre-adjustment, and would produce estimated breeding values for any age, along the continuous age gradient. Riley et al. (2007) assessed the genetic influence of, and estimated genetic parameters for: body weight, hip height, and ratio of body weight to hip height in Brahman feedlot cattle over a 170-d feeding period by use of covariance function random regression models, which allowed for genetic variance components to be calculated for any point of time for which the cattle were on feed. Speidel et al. (2016) utilized random regression models to predict number of days to desired body weight, ultrasound ribeye area, and ultrasound backfat depth in Angus and Charolais influenced feedlot cattle in order to reduce the number of days to a desired endpoint for economically pertinent traits for terminal cattle through genetic selection. Nobre et al. (2003) utilized random regression to estimate growth curves accounting for additive direct and maternal genetic effects, and permanent environmental and maternal permanent environmental effects in Nellore cattle. Aziz et al. (2005) used random regression to estimate additive direct and maternal

genetic effects, and maternal permanent environmental effects for weights from birth to 356 days of age in Japanese Black (Wagyu) feedlot cattle.

Random regression has also been utilized for genetic evaluation of test day records in dairy cattle (Ptak and Schaeffer, 1993; Guo and Swalve, 1997; Brotherstone et al., 2000). Koivula et al. (2015) used random regression in single-step genomic evaluation using a multi-trait random regression model and test-day data for dairy cows. Random regression has been used to model pig growth (Andersen and Pedersen, 1996) as well as for genetic merit prediction for growth in sheep (Lewis and Brotherstone, 2002). In using a random regression approach, variance components can be determined for particular breeds of livestock at any point along an environmental gradient. Consequently, random regression modeling presents the capacity to account for genotype-environment interaction. This altogether presents the random regression modeling approach as considerably advantageous when compared with alternative methods of predicting genetic merit.

2.5 Random regression covariates used in prior literature

With regard to the premise that random regression modeling can utilize a unique set of values which pertain to some specific characterization of the environment, earlier random regression analyses for estimation of genetic parameters or genetic merit prediction have included a variety of covariates for random regression analyses. There has apparently been no attempt to include latitude or longitude coordinates as a random covariate. Aziz et al. (2005), utilized random regression to estimate additive direct, additive maternal, and permanent environmental effects for body weights of Japanese Black cattle across an age covariate from birth to 356 days of age. Riley et al. (2007) included a random covariate of days on feed, to

estimate genetic parameters for body weight, hip height, and ratio of body weight to hip height in Brahman feedlot cattle, utilizing random regression. Speidel et al. (2016) incorporated a random covariate of body weight to predict days to end body weight, ultrasound ribeye area, and ultrasound backfat thickness for Angus, Charolais, and Charolais-sired feedlot calves, in random regression analyses. Lyles et al. (2000) utilized a random covariate of time in years to estimate the presence of HIV RNA and fixed regression coefficients in different sub-groups of people within the United States, employing random regression analyses across time. Delgadillo et al. (2019) included a random covariate of either latitude or longitude coordinates using an animal, linear, and quadratic random regression model to estimate variance components for additive direct effects of ultrasound live intramuscular fat in American Hereford cattle across either latitude or longitude coordinates within the continental United States. Covariates used in random regression analyses should be those that are most biologically practical in terms of how they may influence the predicted response in the traits being evaluated.

2.6 Orders of polynomials in random regression

The proper random regression polynomial order utilized in random regression analyses should be determined by model comparison with a likelihood ratio significance test at the predetermined appropriate order of fixed regression common to each of the models being compared, as done by Speidel et al. (2016). In that work, no additional genetic variation was accounted for by the quadratic random regression relative to the linear random regression for each of days to weight, days to ultrasound ribeye area, and days to ultrasound backfat traits in beef feedlot cattle with respect to a covariate of body weight. Veerkamp et al. (2001) employed random regression models of order zero to four for body condition score in first-parity Holstein-

influenced dairy cows across days in milk for the covariate, and revealed that the third order random regression accounted for the most genetic variation in body condition score. However, Legarra et al. (2004) found that random regression polynomials of third order or greater for growth in Gelbvieh beef cattle (over a covariate of age in days) accounted only for marginally more additive genetic variation when compared to polynomials of first and second order, and that first and second order random regression polynomials may be both necessary and sufficient account for additive genetic variation. In contrast, Delgadillo et al. (2019) reported that the quadratic random regression accounted for additional genetic variation in live ultrasound intramuscular fat for American Hereford cattle when compared to the linear random regression model, with either latitude or longitude as covariate. Although, there was little observable difference in the first and second order random regression curves, or the respective heritability estimates.

The objective of the current work was to develop and model random regression polynomials of first and second order, and an animal model to estimate additive direct genetic variation for weaning weight in American Hereford cattle across latitude or longitude coordinates as covariate within the continental United States, while modeling additive maternal and maternal permanent environmental variances each as a proportion of total phenotypic variance, to represent the contribution of maternal milking ability toward weaning weight in American Hereford cattle. Furthermore, this may be a new and viable method to identify and account for the presence and degree of genotype-environment interaction.

3. MATERIALS AND METHODS

3.1 Records

Individual adjusted weaning weight records were supplied by the American Hereford Association (AHA). The adjustments on weaning weight are AHA adjustments for age of calf and age of dam. Latitude and longitude coordinates were determined for each weaning weight record using the United State Postal Service zip code linked to the location within the continental United States associated with each individual herd which weaning weight records came from (<http://federalgovernmentzipcodes.us/>). Records with no zip code, and records with no contemporary group were removed. As defined by AHA, contemporary group designation was comprised of herd, sex, management group, and birth date of each individual animal. Records beyond ± 4 standard deviations of the mean were considered outliers and removed. The final edited dataset utilized 226,845 weaning weight records. The pedigree file consisted of 383,426 animals, nine generations back. Table 1, Figure 1, Figure 2 and Figure 3, below provide a description of the data.

Table 1. Description of American Hereford Association weaning weight data[†]

Parameter	Estimate
No. of animals	286,845
No. of sires	25,704
No. of dams	155,396
No. of contemporary groups	90,646
Average weaning weight (standard deviation)	257.1 (43.95) kg

[†]Each animal in the dataset has a single weaning weight record (as calves are only weaned once in their lifetime); standard deviation for weaning weight in parentheses beside the average weaning weight value

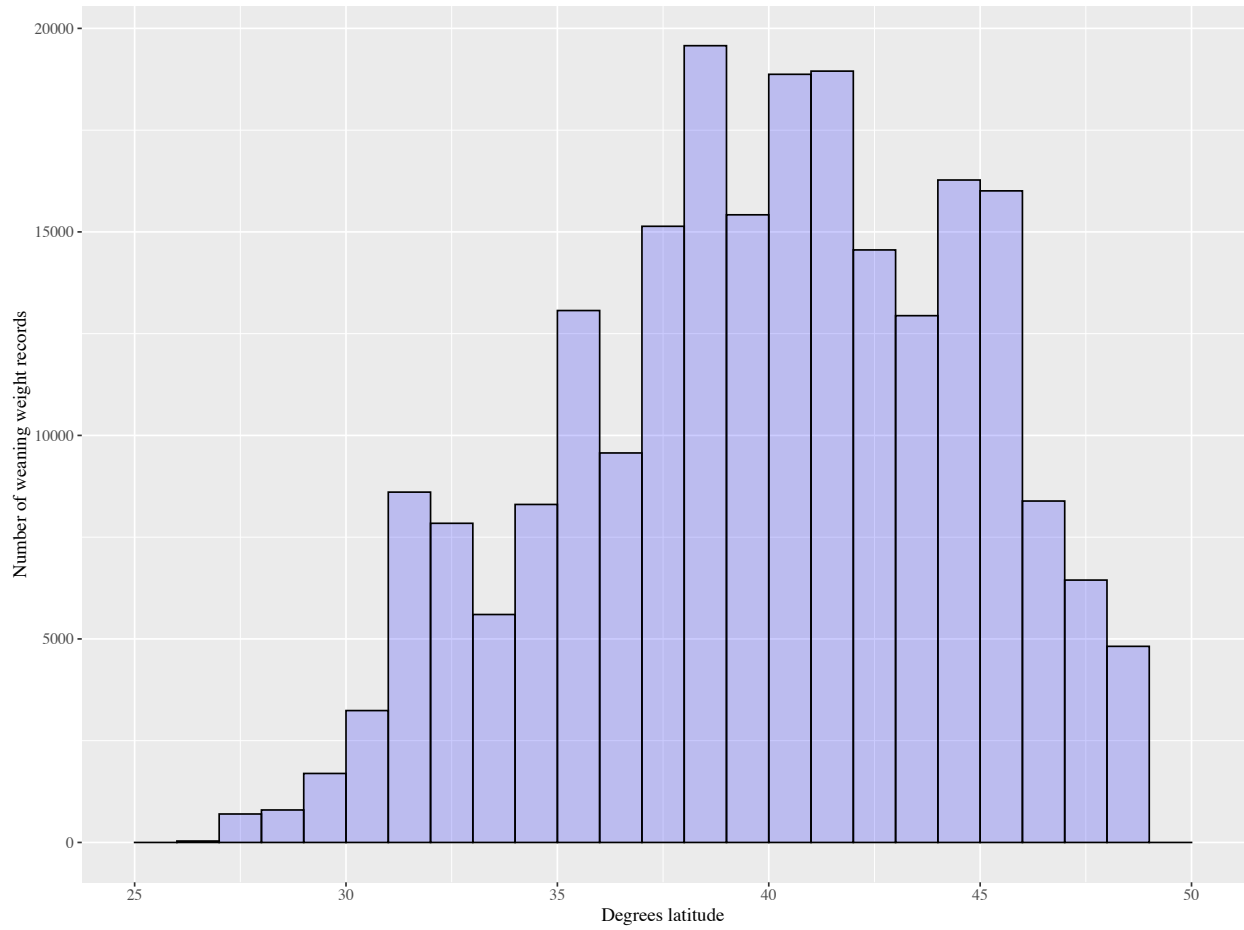


Figure 1. Histogram illustrating the distribution of weaning weight records across latitude coordinates within the United States

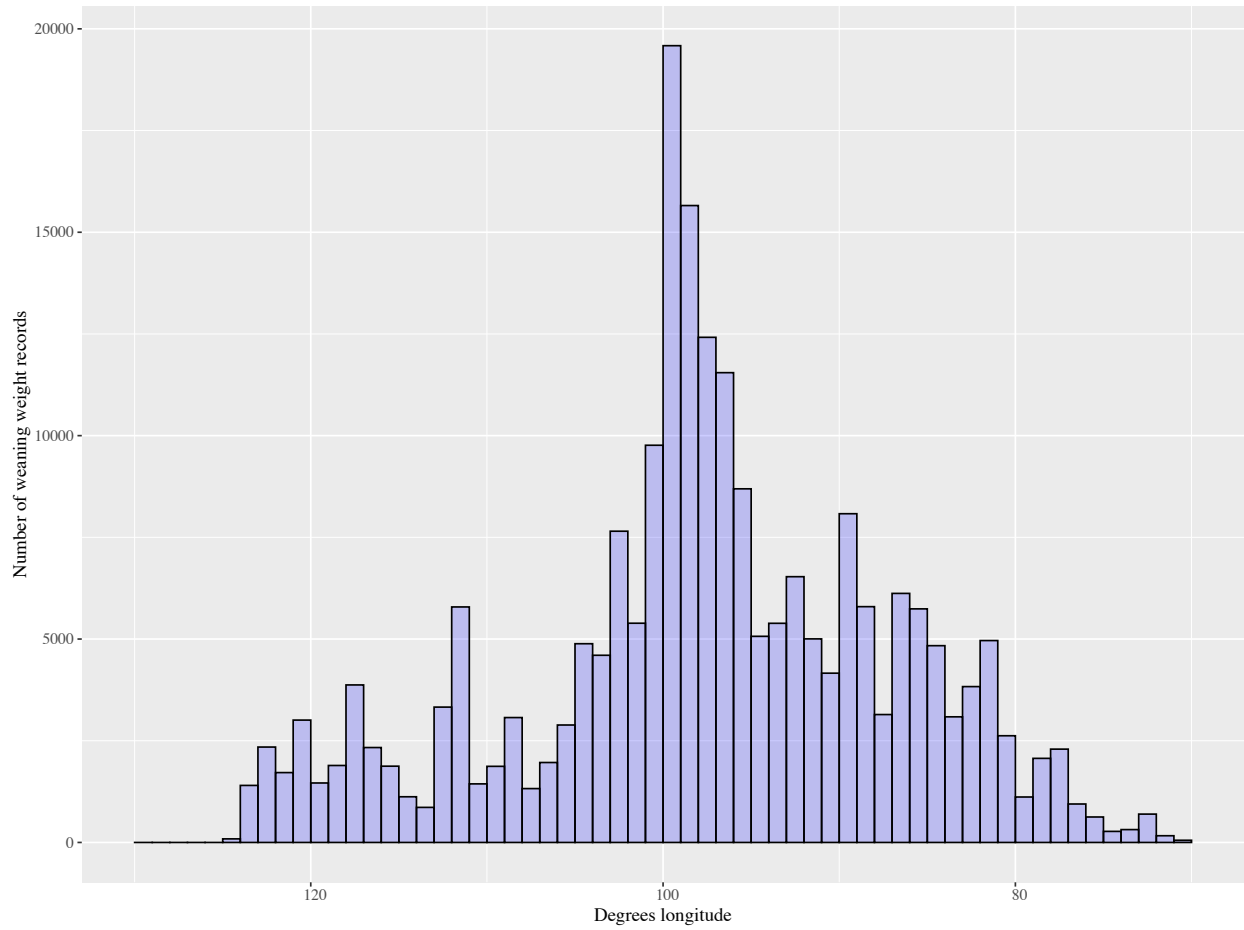


Figure 2. Histogram illustrating the distribution of weaning weight records across longitude coordinates within the United States

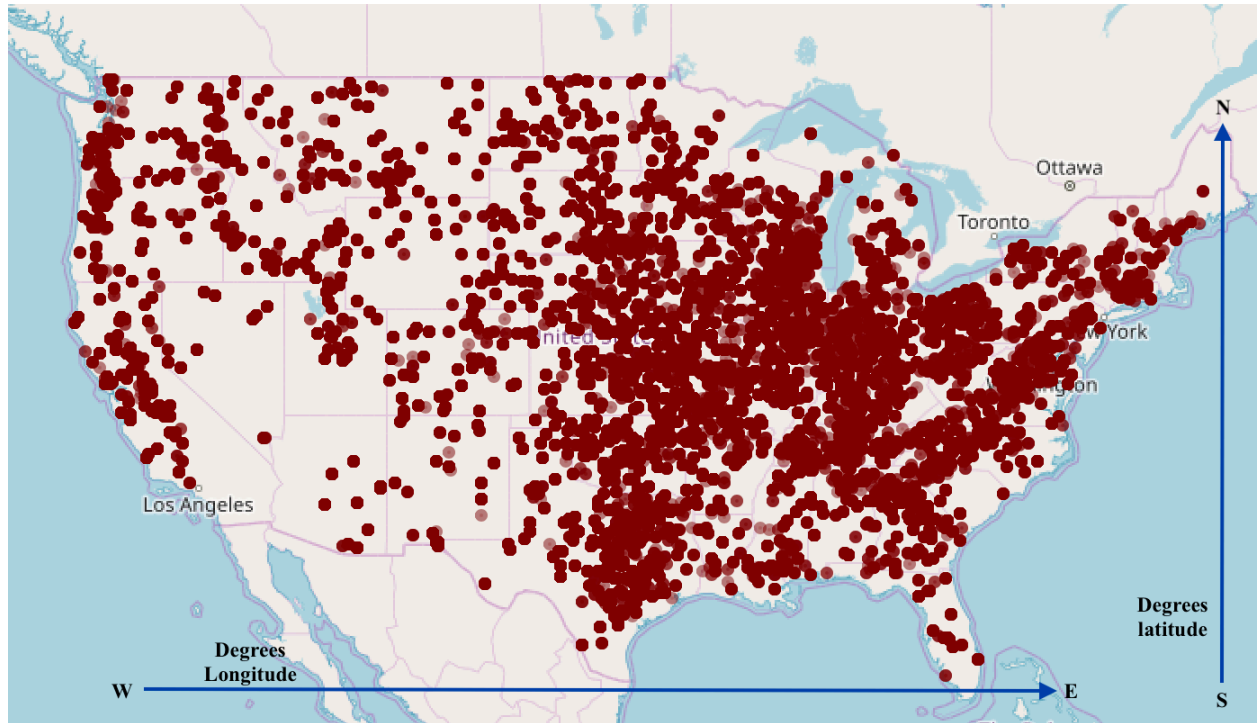


Figure 3. Map displaying a visual distribution of weaning weight records across the United States (maroon dots), also showing the direction of the latitude and longitude random regressions indicated by the vertical and horizontal arrows, respectively

3.2 Statistical analyses

Three different single-trait models were employed in analyses of weaning weight: a simple animal model with no random regression (which will be referred to as the animal model, in this work), and a linear, and quadratic random regression model. The animal model included additive direct genetic, as well as additive maternal genetic, and maternal permanent environmental effects, with no random regression components. The animal model was similar to the animal model from Maniatis and Pollott (2003) for early growth in sheep, such that it included additive maternal genetic effects and maternal permanent environmental effects, as also shown in Schaeffer (2016). There were sufficient records to estimate the covariance between additive direct and additive maternal genetic effects. The linear and quadratic random regression models were similar to those used by Delgadillo et al. (2019), which were developed considering those in Speidel et al. (2016). The current project incorporated additive maternal genetic, and maternal permanent environmental effects. For additive direct genetic effects, parameters estimated were single variances which were considered to correspond to random regression intercept coefficients, and all covariances involving random regression coefficients and intercepts, according to the order of random regression polynomial used. The models in the present work were used in two distinct sets of analyses in ASReml software program (Gilmour, 2009), and the Texas A&M University High Performance Research Computing Service, across the continental United States. One set of analyses included an animal, linear, and quadratic random regression which utilized latitude coordinates as the covariate, within the continental United States. The other set of analyses included an animal, and linear random regression which utilized longitude coordinates as the covariate, within the continental United States.

For the linear and quadratic random regression models across latitude, a likelihood ratio test was conducted to determine the best fit model for the data.

For random regression models employed in the current work, the number of covariances to be estimated in each analysis was determined in this sequence. The analysis procedure began with the attempt to estimate all covariances among random regression coefficients. Upon failure, certain covariances were fixed to zero, or to a close reasonable start value. Covariances to be either estimated or dropped from the analysis were selected or culled in accordance with their ranking of importance, similar to the process done by Delgadillo et al. (2019). The covariances of foremost importance were those between random regression coefficients and their associated intercepts. The second-most important covariances were those between random regression coefficients. The third-most important covariances were those between intercepts. The least important covariances were those between a random regression coefficient of one order and an intercept associated with a random regression coefficient of a different order. In Delgadillo et al. (2019), this similar process entailed a great amount of trial and error to determine the maximum number of covariances ASReml could compute for each model, with the given number of effects in each model. All (co)-variances were set at the specified starting values used from estimates of (co)-variance for weaning weight in Hereford cattle in Torres-Vásquez and Spangler (2016), and were designated as free to change. That is, to be estimated in the analysis procedure. Consequently, all possible covariances have been estimated (with corresponding correlation coefficient estimates) in this study.

3.3 The animal model

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{u} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{mpe} + \mathbf{e}$$

In the animal model (similar to that of Maniatis and Pollott, 2003; Shaeffer, 2016), \mathbf{y} was the vector of single weaning weight records for each individual animal, $\boldsymbol{\beta}$ was the vector of estimated fixed effects: the mean, contemporary group, and fixed regression of first order; for a linear regression on either latitude or longitude coordinates as covariate, \mathbf{u} was the vector of random additive genetic effects, \mathbf{m} was the vector of random maternal additive genetic effects, \mathbf{mpe} was the vector of maternal permanent environmental effects, \mathbf{e} is the vector of residuals (random error). Incidence matrices \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 , relate individual weaning weight records in \mathbf{y} to values in $\boldsymbol{\beta}$, \mathbf{u} , \mathbf{m} , \mathbf{mpe} , and \mathbf{e} , respectively. The expectation of \mathbf{y} is $\mathbf{X}\boldsymbol{\beta}$, and the expectation of all random variables, \mathbf{u} , \mathbf{m} , \mathbf{mpe} , and \mathbf{e} is zero. The (co)-variance structure for this particular animal model is as follows:

$$\text{Var} \begin{bmatrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{mpe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{mpe}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where, \mathbf{A} in $\mathbf{A}\sigma_a^2$, $\mathbf{A}\sigma_m^2$, and $\mathbf{A}\sigma_{am}$ represent the numerator relationship matrix constructed with the pedigree information, and σ_a^2 , σ_m^2 , and $\mathbf{A}\sigma_{am}$ were the additive direct genetic variance, additive maternal genetic variance, and the direct-maternal covariance, respectively; the \mathbf{I} in $\mathbf{I}\sigma_{mpe}^2$, and $\mathbf{I}\sigma_e^2$, was an identity matrix and σ_{mpe}^2 , and σ_e^2 , were the maternal permanent environmental, and residual variances, respectively. The additive genetic-maternal additive

genetic covariance term ($\mathbf{A}\sigma_{am}$) was excluded from the final animal model in order to conduct likelihood ratio tests.

3.4 General model for linear and quadratic random regression

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Q}\mathbf{u} + \mathbf{Z}_1\mathbf{m} + \mathbf{Z}_2\mathbf{mpe} + \mathbf{e}$$

Where \mathbf{y} , $\boldsymbol{\beta}$, and \mathbf{e} vectors were as described for the animal model; \mathbf{u} was the vector of random regression coefficients for additive genetic effects, and similar to the animal model, \mathbf{m} was the vector of random maternal additive genetic effects, and \mathbf{mpe} was the vector of maternal permanent environmental effects. The incidence matrix, \mathbf{X} , was as described for the animal model; \mathbf{Q} was the incidence matrix which contained the latitude or longitude coordinate covariates, which related the weaning weight records in \mathbf{y} to the additive genetic random regression coefficients in \mathbf{u} ; and the number of columns in the \mathbf{Q} matrix is associated to the order of the random regression being employed (first, or first and second order, in the current work). As in the animal model, incidence matrices, \mathbf{Z}_1 and \mathbf{Z}_2 relate individual weaning weight records in \mathbf{y} to values in \mathbf{m} and \mathbf{mpe} , respectively. The expectation of \mathbf{y} was $\mathbf{X}\boldsymbol{\beta}$, and the expectation of all random variables, \mathbf{u} , \mathbf{m} , \mathbf{mpe} , and \mathbf{e} was zero. The (co)-variance structure for the linear random regression model was as follows (similar to that of Nobre et al., 2003):

$$\text{Var} \begin{bmatrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{mpe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}\sigma_m^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{mpe}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where \mathbf{A} was the numerator relationship matrix, and \mathbf{G} was the (co)-variance matrix of random regression coefficients for additive direct genetic effects with an order equal to the polynomial

modeled. For the linear and quadratic random regression models, the \mathbf{G} matrix included the variance estimation of the intercept, and the regression coefficients (first order, or first and second order), and all covariances.

4. RESULTS AND DISCUSSION

4.1 Fixed effects

The regression of weaning weight on either latitude or longitude as covariate, and contemporary group were important fixed effects ($P < 0.001$) in all analyses.

4.2 Animal model

Estimates of heritability, maternal heritability, and proportion of maternal permanent environmental variance to total phenotypic variance are presented in Table 2. Including either the fixed regression on latitude coordinates or longitude coordinates did not result in changed genetic variances or parameters. These were consistent with those used by the American Hereford Association (S. Sanders, personal communication). Other recent reports of heritability for this trait in Hereford cattle were larger (0.35 to 0.45; Dodenhoff et al., 1998; Torres and Spangler, 2016). Torres-Vázquez and Spangler (2016) reported estimates of maternal heritability and maternal permanent environmental effects as a proportion of phenotypic variance of 0.15, and 0.14, respectively. Dodenhoff et al. (1998) reported values of 0.1 and 0.01, respectively. It was reasonable to assert that lower heritability estimates in this work relative to those in Dodenhoff et al. (1998) and Torres-Vázquez and Spangler (2016) may be related to the current work not having estimated covariance between direct and maternal genetic effects, though it was estimated in the two prior studies. This covariance was not estimated in the current animal models due to failure of convergence when attempted to estimate in random regression models. Therefore, to preserve model consistency for comparison using a likelihood ratio test, this parameter was not estimated in any of the current models. Estimates of heritability, maternal heritability, and maternal permanent environmental variance from animal models in the current

work with the modeled covariance between direct and maternal genetic effects were 0.22, 0.14, and 0.16, respectively. The direct-maternal genetic correlation was moderate and negative in the current work (-0.56), and not different than the direct-maternal genetic correlation found in Torres-Vásquez and Spangler (2016) of -0.58 . Heritability, maternal heritability, and maternal permanent environmental proportion of phenotypic variance from the animal model where the direct-maternal genetic covariance was left in the model to be estimated (0.22, 0.14, and 0.16, respectively) were slightly different from those estimated by the current animal models which did not estimate the covariance between direct and maternal genetic effects, as seen in Table 1 (0.19, 0.04, and 0.17, respectively). The largest difference in proportions of phenotypic variance between the two animal models was observed in the maternal heritability (0.04 without the direct-maternal genetic covariance in the model, and 0.14 with this term in the model for estimation). This difference is not negligible, and due to the enormity of weaning weight records used in these analyses, it would be reasonable to assert that this difference is real and meaningful.

Table 2. Estimates of variance components and heritability (SE) using a single-trait animal model for weaning weight

Parameter ¹	Estimate
σ_a^2	632.4 (27.74)
σ_m^2	137.2 (35.73)
σ_c^2	580.3 (37.63)
σ_e^2	2010.9 (23.26)
σ_p^2	3360.8 (13.86)
h^2	0.19 (0.008)
m^2	0.04 (0.011)
c^2	0.17 (0.011)

¹ σ_a^2 = additive genetic variance; σ_m^2 = additive maternal genetic variance; σ_c^2 = maternal permanent environmental variance; σ_e^2 = residual variance; σ_p^2 = phenotypic variance; h^2 = direct heritability; m^2 = maternal heritability; c^2 = maternal permanent environmental variance as a proportion of phenotypic variance

4.3 Random regression analyses across latitude

Estimation of linear (first order) random regressions of the additive genetic component of weaning weight unique to subdivided regions was attempted, and did not converge. Linear and quadratic random regressions across latitude over the entire continental United States was accomplished. The quadratic random regression was the preferred model for the data ($P < 0.001$). Attempts to model either the maternal additive genetic, or the maternal permanent environmental components as random regressions were unsuccessful. This failure is most likely due to the lack of support for these effects (individual dams) in the data.

Nevertheless, upon observation of heritability estimates from both the linear and quadratic random regressions across latitude in the current work (as validated by similar observations in recent research involving random regression of intramuscular fat (IMF) across latitude in Delgadillo et al., 2019), only small differences were seen in heritability estimates and curves between the linear and quadratic random regressions across latitude. Additionally, larger standard errors were observed from the quadratic random regression for heritability estimates across latitude, particularly at the ends of the curves, both in the current work and in Delgadillo et al. (2019). This observed increase in variability at the ends of the random regression curves is likely due to reduced density of records near the ends of the country (and the curves) making the higher order polynomial behave in an unwieldy manner as to potentially accentuate records and inflate heritability estimates near the ends of the random regression curves beyond their true values (Speidel, 2011). Therefore, the linear random regression is likely the model of greatest precision for best practical use in genetic parameter estimation, given these data.

For analyses which utilized latitude coordinates as covariate, the random regression curves for estimates of heritability (h^2), and estimated maternal milking ability intercepts,

expressed as two distinct proportions: proportion of additive maternal genetic variance to total phenotypic variance (m^2 , maternal heritability), and the proportion of maternal permanent environmental variance to total phenotypic variance (c^2), were plotted across the continental United States (Figure 4). Estimates of heritability, maternal heritability, and c^2 from linear random regression results ranged from 0.15 to 0.26, 0.03 ± 0.009 , and 0.15 ± 0.010 , respectively (Table 3). For the quadratic random regression analysis, estimates of heritability, maternal heritability, and c^2 were from 0.08 to 0.23, 0.07 ± 0.010 , and 0.14 ± 0.010 , respectively (Table 4; Figure 5). Estimates of (co)-variances, and correlation coefficients from the quadratic random regression analysis across latitude are listed in Table 5.

Table 3. Estimates of variance components and heritability (SE) using a single-trait linear random regression model for weaning weight

Parameter ¹	Latitude	Longitude
$\sigma_{\beta_0}^2$	583.9 (45.12)	1033.3 (58.08)
$\sigma_{\beta_0, \beta_1}$	- 34.4 (21.65)	- 102.0 (11.70)
$\sigma_{\beta_1}^2$	278.9 (38.78)	178.5 (21.07)
σ_m^2	276.4 (38.44)	132.3 (35.20)
σ_c^2	563.1 (41.01)	575.6 (37.26)
σ_e^2	2251.2 (18.81)	1978.4 (23.25)
σ_p^2	3919.1 (42.78)	3796.2 (38.36)
h^2	0.09 to 0.20	0.15 to 0.26
m^2	0.07 (0.010)	0.03 (0.009)
c^2	0.14 (0.011)	0.15 (0.010)

¹ $\sigma_{\beta_0}^2$ = additive direct genetic intercept variance; $\sigma_{\beta_0, \beta_1}$ = covariance between the additive direct genetic intercept and random regression coefficient; $\sigma_{\beta_1}^2$ = additive direct genetic random regression coefficient variance; σ_m^2 = additive maternal genetic variance; σ_c^2 = maternal permanent environmental variance; σ_e^2 = residual variance; σ_p^2 = phenotypic variance; h^2 = direct heritability from linear random regression; m^2 = maternal heritability; c^2 = maternal permanent environmental variance as a proportion of phenotypic variance

Table 4. Estimates of variance components and heritability (SE) using a single-trait quadratic random regression model for weaning weight, with latitude as covariate

Parameter ¹	Latitude
σ_m^2	276.3 (38.48)
σ_c^2	564.2 (41.00)
σ_e^2	2253.5 (18.82)
σ_p^2	4036.8 (62.02)
h^2	0.08 to 0.23
m^2	0.07 (0.010)
c^2	0.14 (0.010)

¹ σ_m^2 = additive maternal genetic variance; σ_c^2 = maternal permanent environmental variance; σ_e^2 = residual variance; σ_p^2 = phenotypic variance; h^2 = direct heritability; m^2 = maternal heritability; c^2 = maternal permanent environmental variance as a proportion of phenotypic variance

Table 5. Estimates of (co)variance components and correlation coefficients (SE) using a single-trait quadratic random regression model for weaning weight, with latitude as covariate¹

	β_0	β_1	β_2
β_0	747.3 (68.00)	- 0.05 (0.136)	0.58 (0.229)
β_1	- 9.43 (24.818)	44.97 (53.541)	- 0.26 (0.433)
β_2	117.7 (29.64)	- 12.88 (18.672)	55.21 (34.506)

¹Estimates of variance along the diagonal in bold; estimates of covariance below the diagonal; estimates of correlation coefficients above the diagonal

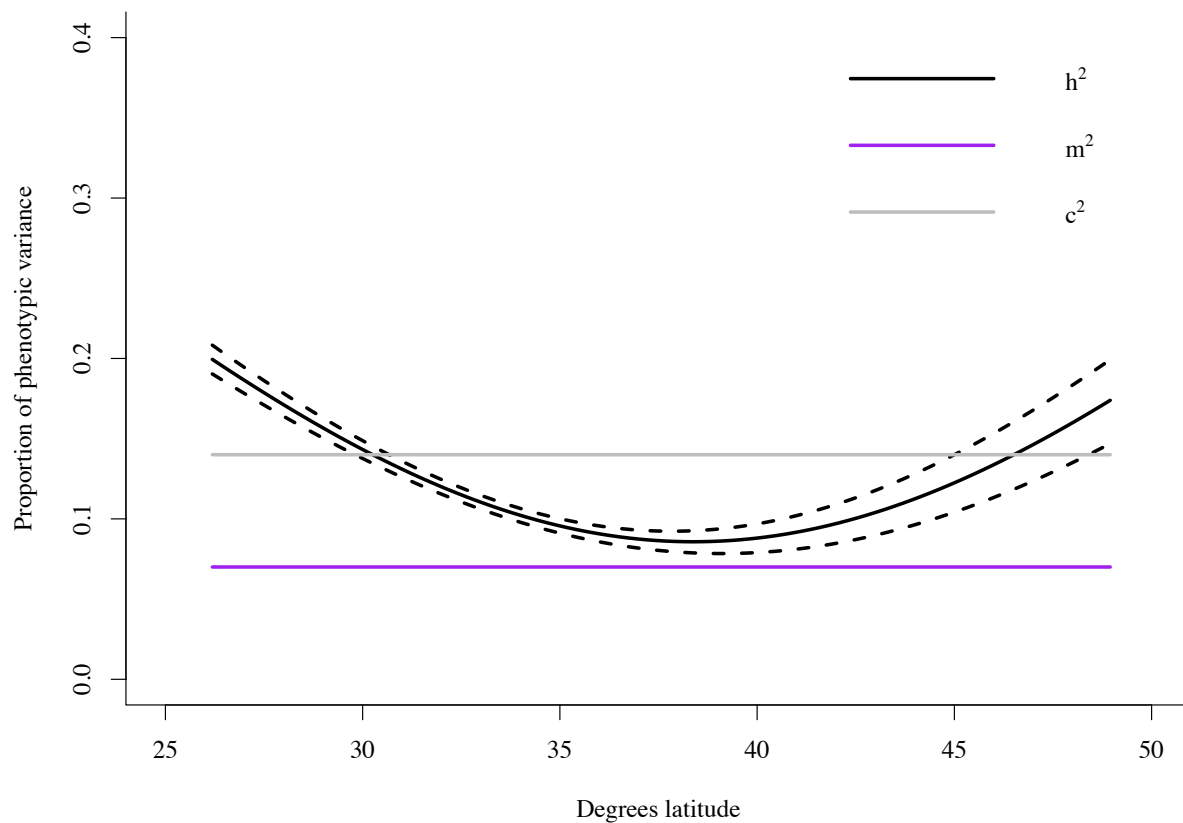


Figure 4. Estimates of heritability from linear random regression, with milking ability intercepts represented by additive maternal genetic, and maternal permanent environmental variance each as proportions of phenotypic variance for weaning weight across latitude coordinates (dashed lines indicate ± 1 SE)

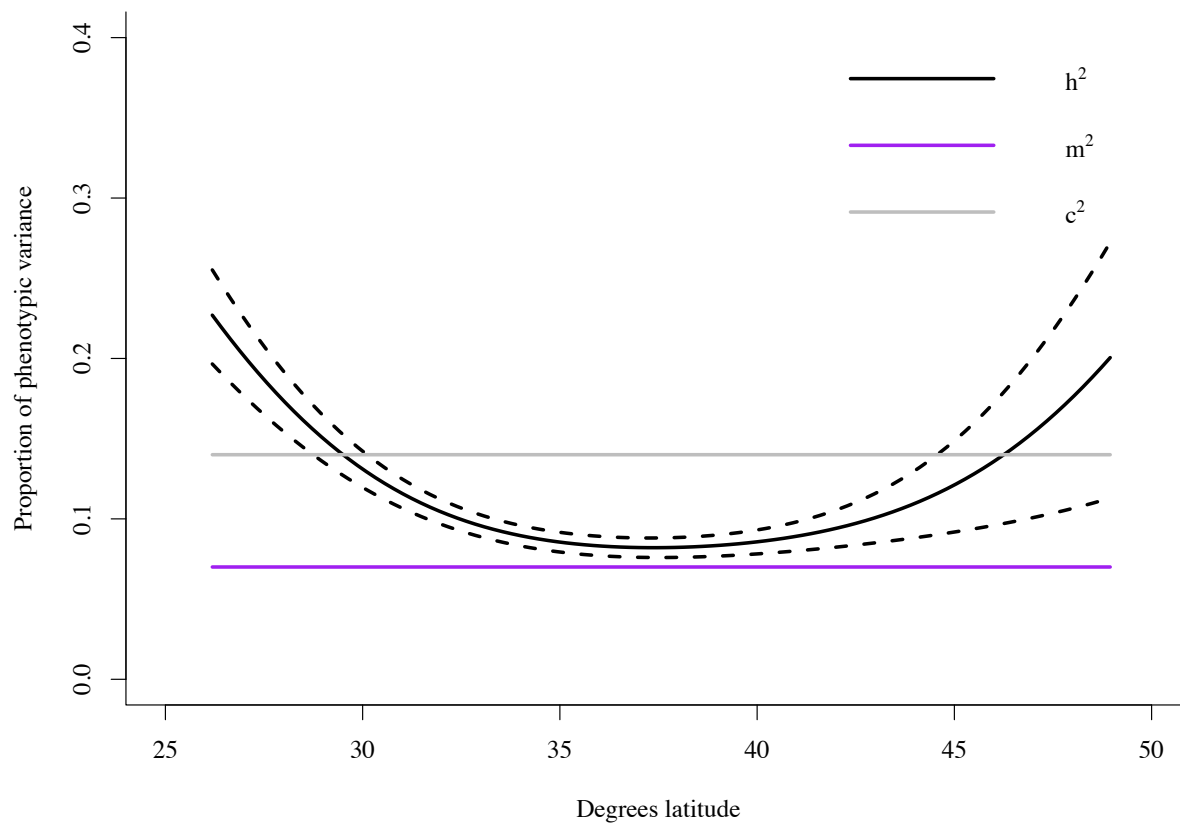


Figure 5. Estimates of heritability from quadratic random regression, with milking ability intercepts represented by additive maternal genetic, and maternal permanent environmental variance each as proportions of phenotypic variance for weaning weight across latitude coordinates (dashed lines indicate ± 1 SE)

4.4 Random regression analyses across longitude

As conducted with latitude as random covariate, estimation of linear random regressions of the additive genetic component of weaning weight unique to subdivided regions was attempted, but analyses failed to converge due to insufficient computing power in the super computer at maximum allowable workspace in ASReml. Also, a quadratic random regression across longitude over the entire continental United States was attempted, and convergence was not achieved. As concluded from the attempts with latitude, attempts to model either the maternal additive genetic, or the maternal permanent environmental components as random regressions across longitude were not successful. Similar to analyses for latitude, this failure is most likely due to insufficient support for these effects in the data, where dams are very likely to be more prominently localized at a limited set of covariate values.

Similar to analyses done across latitude, for analyses across longitude, the random regression curves for estimates of h^2 , m^2 , and c^2 , were plotted across the continental United States (Figure 6). For the linear random regression model with longitude as random covariate, these estimates were 0.09 to 0.20, 0.07 ± 0.010 , and 0.14 ± 0.011 , respectively (Table 3).

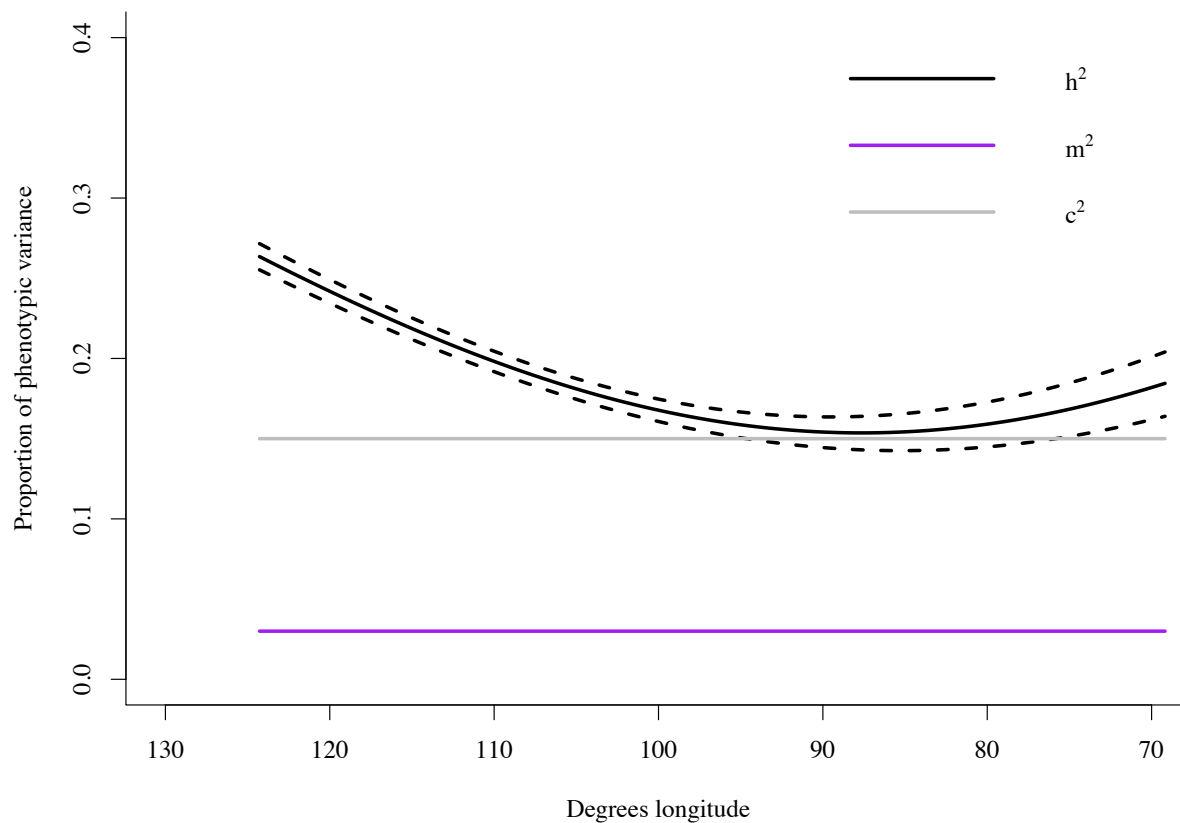


Figure 6. Estimates of heritability from linear random regression, with milking ability intercepts represented by additive maternal genetic, and maternal permanent environmental variance each as proportions of phenotypic variance for weaning weight across longitude coordinates (dashed lines indicate ± 1 SE)

4.5 Random regression results vs. animal model results, and prior work

As with the animal models in the current work, estimates for heritability from the current random regression models were in agreement with those estimated by the American Hereford Association, and lower than those found by both Dodenhoff et al. (1998), and Torres-Vásquez and Spangler (2016). Estimates of maternal heritability, and c^2 from the current random regression models were similar to those found by Torres-Vásquez and Spangler (2016), and greater than those found in Dodenhoff et al. (1998). While remaining consistent with weaning weight heritability estimates from the American Hereford Association, and with those in prior literature, change has been observed in heritability estimates as plotted in linear random regression analyses across latitude or longitude in the current work. It is apparent from these findings that genotype-environment interaction is indeed accounted for to some extent in the random regression for additive direct genetic effects for weaning weight across latitude or longitude. Furthermore, heritability estimates in the current work were conserved to a range of values consistent with those documented by trustworthy sources, and should be representative of the Hereford cattle population in the United States.

Similar to the linear random regression curves across longitude for additive direct genetic variation as a proportion of total phenotypic variation across the continental United States for IMF in Delgadillo et al. (2019), apparent change was also observed across either latitude or longitude as random covariate, in this work. The linear and quadratic random regression curves of plotted heritability for linear random regression for weaning weight in the current work (regardless of covariate) have their minimum heritability estimate nearer to middle of the curve (associated with the center of the country), and the greatest estimates of heritability appeared to consistently occur at the ends of the curves (the farthest south and north with latitude as

covariate; and the farthest west and east with longitude as covariate, in the present work). With latitude as random covariate, the minimum heritability estimate from the linear random regression for weaning weight was 0.09 at approximately 38.37° N, in the middle of the United States. Similarly, the quadratic random regression across latitude (Figure 5) had a minimum heritability estimate of 0.08 at approximately 37.45° N (central United States). Linear and quadratic random regression curves for weaning weight were generally parabolic in shape, and fairly symmetrical. With longitude as random covariate, the minimum heritability along the linear random regression curve for weaning weight was shifted only slightly east of central United States (0.15 at approximately 87.55° W; Figure 6). The linear random regression curve for weaning weight across longitude was skewed parabolic, with the minimum of the curve shifted slightly east of central United States. These results propose that greater estimates of heritability for weaning weight occur nearer to coastal areas of the United States. Lower estimates of heritability for weaning weight exist in the south-central United States. These findings advocate that genetic progress through selection for weaning weight in Hereford cattle may be realized most rapidly in coastal herds that select sires native to either coastline, and slower genetic progress may be actualized in herds located nearer the south-central United States which select sires therein.

This work showed a measurable effect of geographical location on additive direct genetic effects for weaning weight in American Hereford cattle. The use of latitude or longitude coordinates as random covariate served as a continuous characterization across the United States, for climatic and nutritional conditions (environment) for which Hereford cattle were reared. To that effect, these results therefore provide clear evidence of genotype-environment interaction as revealed by random regression analyses of weaning weight in the current study. These findings

were consistent with those from random regression work done with American Hereford IMF in Delgadillo et al. (2019).

Results from this study suggest the importance of a random regression modeling approach attempting to sufficiently account for genotype-environment interaction in genetic merit predictions in American Hereford cattle. Furthermore, the use of random regression to predict genetic merit may allow for the possibility of selecting sires based on their genetic merit specific to their environment, rather than a blanketed average across the whole continental United States. This could result in a more precise sire selection process, which could eventually lead to greater efficiency and productivity in genetic enhancement for weaning weight in beef cattle. Consequently, generational genetic progress would then depend upon the environment-specific genetic variability, by use of the genetic prediction methods suggested in the current work. Moving forward to incorporate random regression methodology into national cattle evaluation or breed association evaluations with use of random covariates such as latitude or longitude as a proxy for rearing environment and plane of nutrition, may be advantageous. Linear random regression analyses across either latitude or longitude appear to account for genotype-environment interaction, at least to some degree. It is nevertheless unclear as to which covariate has best accounted for genotype-environment interaction in the current work. Perhaps, a necessary follow-up study to help gain clearer direction as to practical applications of methods presented in this project (which covariate is most useful) would entail estimation of expected progeny differences (EPDs) from the current linear random regression analyses (across latitude or longitude), to compare with those currently estimated by the American Hereford Association. Consequently, it may prove necessary for the American Hereford Association (or national cattle evaluation) to then implement this methodology in parallel with their current means of

estimating expected progeny differences to provide producers some flexibility in their selection procedures. Producers would then be afforded the opportunity to use either EPDs estimated by the proposed new methods (random regression across either latitude or longitude coordinates) for genetic selection, or to continue to use the standard EPDs. Over generations of selection, the use of location-specific EPDs may prove to be more practical and useful to beef cattle producers than current blanketed selection methods. Nevertheless, further research is needed to more precisely adjust and refine the practical application of this approach of genetic parameter estimation and genetic merit prediction. Perhaps genetic parameter estimation and genetic merit prediction in other economically relevant traits for the Hereford breed, as well as additional beef cattle breeds, and the possible effect of regional subdivision of random regressions nested within regions would be advantageous pursuits, where records are sufficient, and where data would allow.

5. CONCLUSION

Findings from the present study revealed that a random regression modeling approach showed differences in estimates of heritability for weaning weight in American Hereford cattle in different longitude or latitude coordinate positions within the continental United States. A classic animal model might not sufficiently account for potential change in genetic variation for economically pertinent traits of livestock production performance in various livestock operations, across different environments. Nevertheless, using a random regression modeling approach for additive genetic variation in proportion to phenotypic variation, while attempting to account for milking ability of dams in genetic parameter estimation, and genetic merit prediction analyses for weaning weight may very well have the potential to advance the American Hereford Association genetic evaluations, as it appears to embody a considerably more flexible and suitable representation of additive genetic variation, and changes in additive genetic variation conditional to locational or environmental differences. Furthermore, the inclusion of genomic information may effectively compliment and further enhance the proposed random regression approach to genetic parameter estimation and genetic merit prediction in the current work. Nevertheless, in order to validate that the current approach is sufficiently accounting for all major sources of environmental effects influencing genotype, a reasonable next step would be to compare EPDs from random regression analyses to those from the animal models in the current study, and with those estimated by the American Hereford Association.

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APPENDIX

ASREML COMMAND FILE CODE FOR RANDOM REGRESSION ANALYSES

Linear random regression across latitude

```
!WORKSPACE 32000
RANDOM_REGRESSION_WW
id                !P
sire              !P
dam              !P
ww_adj           !M -9999
ww_group         !I 90646
scanwt_adj       !M -9999
scanwt_group     !I 11447
scanimf_adj      !M -9999
scanimf_group    !I 13385
ce_group         !I 11921
lat              !M -9999
long             !M -9999
zipcode          !I 3027
Ped_WW_SHORT.ped !SKIP 1
WW_SHORT.dat     !SKIP 1 !MVREMOVE !DDF !FCON !MAXIT 5000 !CONTINUE !STEP 0.01
#####
# MODEL = WW
#####
ww_adj !SIGMAP ~ mu ww_group leg(lat,1),
!r !{ leg(lat,1).id nrm(dam) !} ide(dam)
#####
0 0 3
#
leg(lat,1).id 2
leg(lat,1) 0 US !GPPP
327.9
-77.0 327.9
id 0 AINV
#
nrm(dam) 2
1 0 US !GP
141.1
nrm(dam) 0 AINV
#
ide(dam) 2
1 0 US !GP
130.8
ide(dam)
```


Quadratic random regression across latitude

```
!WORKSPACE 32000
RANDOM_REGRESSION_WW
id          !P
sire        !P
dam         !P
ww_adj      !M -9999
ww_group    !I 90646
scanwt_adj  !M -9999
scanwt_group !I 11447
scanimf_adj !M -9999
scanimf_group !I 13385
ce_group    !I 11921
lat         !M -9999
long        !M -9999
zipcode     !I 3027
Ped_WW_SHORT.ped !SKIP 1
WW_SHORT.dat      !SKIP 1 !MVREMOVE !DDF !FCON !MAXIT 5000 !CONTINUE !STEP 0.01
#####
# MODEL = WW
#####
ww_adj !SIGMAP ~ mu ww_group leg(lat,2),
!r !{ leg(lat,2).id nrm(dam) !} ide(dam)
#####
0 0 3
#
leg(lat,2).id 2
3 0 US !GP
327.9
-77.0 327.9
-77.0 -77.0 327.9
id 0 AINV
#
nrm(dam) 2
1 0 US !GP
141.1
nrm(dam) 0 AINV
#
ide(dam) 2
1 0 US !GP
130.8
ide(dam)
```

Linear random regression across longitude

```
!WORKSPACE 32000
RANDOM_REGRESSION_WW
id !P
sire !P
dam !P
ww_adj !M -9999
ww_group !I 90646
scanwt_adj !M -9999
scanwt_group !I 11447
scanimf_adj !M -9999
scanimf_group !I 13385
ce_group !I 11921
lat !M -9999
long !M -9999
zipcode !I 3027
Ped_WW_SHORT.ped !SKIP 1
WW_SHORT.dat !SKIP 1 !MVREMOVE !DDF !FCON !MAXIT 5000 !CONTINUE !STEP 0.01
#####
# MODEL = WW
#####
ww_adj !SIGMAP ~ mu ww_group leg(long,1),
!r !{ leg(long,1).id nrm(dam) !} ide(dam)
#####
0 0 3
#
leg(long,1).id 2
leg(long,1) 0 US !GPPP
327.9
-77.0 327.9
id 0 AINV
#
nrm(dam) 2
1 0 US !GP
141.10
nrm(dam) 0 AINV
#
ide(dam) 2
1 0 US !GP
130.8
ide(dam)
```