

REGION-SPECIFIC ANALYSES OF BEEF CATTLE GROWTH AND IMPLEMENTATION
OF SINGLE-STEP GENOMIC BLUP WITH MANY GENOTYPED ANIMALS

by

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(Under the Direction of Ignacy Misztal)

ABSTRACT

Beef cattle are raised in a wide range of environmental conditions in the United States. Producers use calving seasons to help match the cows' nutritional needs throughout the year with forage quantity and quality in their production environment. As a result, some regions have large differences in calf weight depending on the calving season. One potential factor contributing to regional differences in beef production is heat stress. Heat stress causes economic losses for beef producers, and one way to mitigate the effects of heat stress is through genetic selection. Weaning and yearling weights were associated with the owner's zip code and the weigh date to determine retrospectively the weather conditions preceding the weigh date. Heat tolerance, the ability of an animal to grow despite heat stress, was heritable and could be incorporated into national cattle evaluations to enable producers to identify animals that best match their environment. Another issue for the livestock industries is the use of single-step genomic BLUP (ssGBLUP) when the number of genotyped animals makes implementation computationally prohibitive. The Algorithm for Proven and Young (APY) enables the use of ssGBLUP in such a scenario. Genotyped animals need to be partitioned into core and noncore subsets. Accuracy and bias for young animals were the same no matter which animals were selected as the core

animals. Livestock populations have limited effective population size, and this algorithm exploits the limited dimensionality of genomic information resulting in similar accuracies. Accuracy did not decrease as the relationship between the core and noncore animals decreased even though this result commonly occurs in multi-step methods. Randomly selecting core animals was consistently one of the most accurate and unbiased scenarios and is recommended for implementation of APY in ssGBLUP.

INDEX WORDS: genomic selection, heat stress, single-step GBLUP

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DEDICATION

To my parents, Rex and Bonnie Bradford.

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CHAPTER 1

INTRODUCTION

Since the domestication of animals, humans have selected animals to improve their quality of life and to meet their needs. This selection was based on phenotypes for millennia resulting in many changes to the phenotypes of livestock species. Greater genetic progress was made after the introduction of best linear unbiased prediction (BLUP) by Charles Henderson. This method enabled the prediction of breeding values to identify genetically superior animals. Since that development, the methodology has been extended to incorporate a variety of models applicable to livestock species. The number of traits being evaluated continues to increase as breeders begin phenotyping novel traits of economic importance. One of these novel traits is heat tolerance, the ability of an animal to perform during environmental heat stress. Genotype \times environment interactions can result in some genetics being better suited to specific environments. Reaction norms can be used to differentiate genetic merit across an environmental gradient such as heat stress. The objectives were to identify regional differences in beef production, quantify amounts of heat stress, and develop genetic evaluations for thermal tolerance for growth traits in Angus cattle.

Genomic information can be used in genetic evaluation to increase the accuracy of young animals' predictions and to shorten the generation interval. Recently, the sequencing of livestock genomes has enabled cost-effective, high-density genotyping. With the subsequent increase in the numbers of genotyped animals, the traditional single-step method could not be implemented for populations with the most genotyped animals. The Algorithm for Proven and Young (APY)

was a solution to the computational burden presented by large, genotyped populations. This algorithm makes use of the redundant information contained in genotypes to create a computationally efficient inverse for single-step genomic BLUP. Animals are divided into core and noncore subsets in APY, and the number of core animals is determined by eigenvalue decomposition of the genomic relationship matrix. The objective was to determine which animals should be selected as core animals to maintain accuracy and unbiasedness of genomic predictions.

CHAPTER 2

HEAT STRESS LITERATURE REVIEW

Because of the extensive nature of beef production, no single management scheme fits all conditions throughout the US. Cow-calf profitability depends on matching cow type and nutritional requirements to the environment (Dickerson, 1970; McMorris and Wilton, 1986; Adams et al., 1996). Thus, producers must identify the genetics that will succeed in the farm's specific environmental conditions. Robertson (1959) suggested a genetic correlation less than 0.80 was indicative of a biologically meaningful genotype \times environment interaction. When the same genetics are used in different regions, sires rank differently because of differences in adaptability to the regional environment. This interaction has consequences for selecting animals across environments based on national genetic evaluations.

Genotype \times environment interaction

Applied experiments have shown significant location effects on cattle growth. An experiment involving Hereford cattle adapted to Florida or Montana demonstrated that cattle were heavier and gained more in their native environment (Butts et al., 1971). Cattle adapted to the Florida environment weighed more than Montana cattle when both were raised in Florida. The opposite pattern occurred when both lines were raised in Montana. Forage type can also affect production. Angus and Brahman calves had lighter weaning weights (WW) when raised on endophyte-infected tall fescue instead of bermudagrass in Arkansas (Brown et al., 1997). Similar distinct regional differences have been observed for genetic evaluations. Genetic merit for Limousin sires varied by US region for WW (Bertrand et al., 1987) indicating regional

genetic evaluations for growth would be beneficial. In particular, producers from the Lower Plains and South would benefit most from region-specific genetic evaluations. Conversely, the Southeast and Northwest had strong direct genetic correlations but weaker maternal correlations between region and calving season in Angus (Williams, 2010). Environmental and management factors affected sire rankings for the maternal genetic component of WW. Thus, environmental adaptability can be important for weight traits in beef cattle.

Many genotype \times environment research projects have been conducted in the Southern US and evaluated the suitability of *Bos indicus* and their crosses for the region. *Bos indicus* cattle were more heat tolerant and resistant to environmental stressors than British and Continental *Bos taurus* breeds (Turner, 1980; Hammond et al., 1996), and *Bos indicus* crosses grew faster than *Bos taurus* crosses (Olson et al., 1991). Furthermore, breed group \times location interactions have been reported for weight traits in Florida and Nebraska (Olson et al., 1991) suggesting no single breed was best for all environments.

Heat Stress

Heat stress has been estimated to cost the US livestock industries \$2.4 billion annually (St-Pierre et al., 2003). Heat abatement strategies could reduce these losses in some industries but were not cost effective at eliminating the physiological consequences of heat stress. The beef industry had the second greatest losses behind dairy. Nearly \$87 million in losses was attributed to the negative effects of heat stress on reproduction in cow-calf production systems, and the remaining \$282 million was from reduced feed intake, reduced gain, and greater days on feed for finishing cattle (St-Pierre et al., 2003). While cow-calf production is dispersed throughout the US, feedlots are more concentrated in the central US with greater potential for heat stress in these states.

Physiological effects of heat stress

Heat stress causes greater respiration rate, greater rectal temperature, and behavioral modifications (Hahn, 1999; Roland et al., 2016). During hot temperatures, cattle spend more time seeking shade and less time grazing. Breed differences exist for adaptability to hot environments. Angus had greater rectal temperature, greater respiration rate, and consequently less gain than Brahman, Senepol, and Romosinuano (Hammond et al., 1996). With the large Angus influence in the national cow herd, reducing susceptibility to heat stress can be economically important.

Heat stress has negative consequences for production traits. Heat stressed animals had reduced dry matter intake and average daily gain resulting in more days on feed (Mitlöhner et al., 2002). Heifers with greater heat stress were more likely to be dark cutters and were less likely to grade Choice (Mitlöhner et al., 2002). The effects of heat stress on marbling deposition and days on feed were economically important to the beef industry. While shade or misting can be implemented in feedlots to reduce heat stress, these practices are not always realistic for cow-calf production. Thus, genetic selection can be used to improve adaptability of the national cow herd.

Characterization of heat stress

Weather information can be reconciled with a heat load function to quantify heat stress. Ravagnolo et al. (2000) examined different combinations of minimum, mean, and maximum temperature and humidity for modeling the decline in milk production traits associated with heat stress. Maximum temperature and minimum humidity fit data best when combined as a temperature-humidity index (**THI**). This THI is measured by:

$$\text{THI} = \text{temp} - (0.55 - 0.0055 * \text{rh}) * (\text{temp} - 58),$$

where temp was the maximum temperature (°F) and rh was the minimum relative humidity (%) for a given day. Additionally, a THI threshold existed, likely at the upper critical temperature of the thermal neutral zone, at which point production began to decline with greater heat stress. When THI was less than the threshold, THI had very little impact on production. Although many studies only evaluated THI specifically for heat stress, THI could be less than the lower critical temperature causing cold stress. Temperature-humidity index can be defined differently, but various indices had similar fit with the previous definition performing better in less humid environments (Bohmanova et al., 2007). Thus, a heat load function can be defined as:

$$H = \max(0, THI - THI_0),$$

where H was heat load, THI was defined previously, and THI_0 was the THI threshold at which phenotype began to decrease.

Freitas et al. (2006) demonstrated that off-farm weather data was just as useful as on-farm data for developing a heat load function. Weather station locations were 300 km from the farm and still provided consistent estimates for the THI threshold and change in production per unit change in THI. These results were specific for the Georgia terrain, but off-farm data can be used with careful selection of weather sources based on geography. Thus, heat load can be assessed on a regional or national scale using preexisting weather databases as a step toward genetic evaluations for heat tolerance.

While initial studies assumed phenotypes were affected by THI for 1 day (Ravagnolo et al., 2000; Ravagnolo and Misztal, 2002b), some traits could be affected by heat stress over time. Zumbach et al. (2008a) proposed heat stress affected weight for a period prior to the weigh date. Thus, heat load accumulated over time and could be defined as:

$$H_c = \max(0, \sum_{i=0}^n THI_i - THI_0),$$

where H_c was the cumulative heat load, THI_i was the THI on day i prior to the weigh date, THI_0 was the threshold, and n was the total number of days that heat stress affected phenotype. This model could apply to many traits and has been used for growth (Zumbach et al., 2008b; Fragomeni et al., 2015; Santana et al., 2016), reproduction (Schüller et al., 2014), and milk production (Carabaño et al., 2016; Nguyen et al., 2016).

Genetic evaluation

Livestock populations can be selected for improved heat tolerance if genetic variation exists for the phenotype associated with greater heat load. Genetic evaluations have been developed to identify those animals that are more robust to changes in THI. As weather patterns become more erratic and global warming continues, more robust animals will be more productive and profitable for farmers. Heat load information can be incorporated into genetic evaluations using reaction norms. These methods have been applied to dairy, swine, and beef cattle to create selection tools for heat tolerance.

Dairy

Numerous studies have assessed the effect of heat stress on milk production and component traits. Heritability was greatest for large heat loads (Ravagnolo and Misztal, 2000; Aguilar et al., 2009). Genetic correlations between environmental extremes, no or maximum heat load, were indicative of distinct traits (Ravagnolo and Misztal, 2000). Proven sires re-ranked when heat load was modeled instead of a traditional univariate approach (Bernabucci et al., 2014). Unproven sires may change rank between regions with different environments (Bohmanova et al., 2008).

Additionally, heat tolerance genetic merit may depend on parity with greater parities being more susceptible to heat stress (Aguilar et al., 2009; Bernabucci et al., 2014).

Reproductive heat tolerance has also been investigated. Initial studies assessed heat load for a single day with the day of insemination yielding the best results (Ravagnolo and Misztal, 2002b). Heat stress affecting pregnancy outcome during a period from initial follicle development to at least embryo implantation is more biologically plausible. Temperature-humidity index from 42 days before to 31 days after breeding affected conception with the period beginning with the previous estrous cycle until breeding being most sensitive (Schüller et al., 2014). These results were from a temperate environment, and heat tolerance may be important for reproductive ability in much of the continental US.

The genetic correlation between heat tolerance for milk and reproduction was near 0 (Ravagnolo and Misztal, 2002a) indicating selecting for heat tolerance based on a single trait was not sufficient to select more robust animals. Additionally, heat tolerance EBV were strongly negatively correlated with traditional EBV for the same trait (Nguyen et al., 2016). Selection for greater production should decrease heat tolerance, and producers would benefit from selection tools to balance production and heat tolerance in temperate and tropical climates.

Swine

Carcass weight heat tolerance has been evaluated in purebred and crossbred swine populations. Nucleus animals displayed little evidence of heat stress because of better management and environmental conditions compared with commercial animals (Fragomeni et al., 2016a; Fragomeni et al., 2016b). In the commercial populations from Zumbach et al. (2008b), weight was most heritable for the greatest heat load suggesting greater selection response. Rank correlations between minimum and maximum heat load were less than 0.20 indicating different

genetics would be selected in different environments. A univariate analysis of weight was most similar to intermediate heat load with the most re-ranking between univariate and maximum heat load.

Beef

Only one heat tolerance study is known for beef cattle. Santana et al. (2016) evaluated weaning weight heat tolerance in 3 breeds in Brazil with subtropical and tropical conditions. Heat load was defined using the average THI for the entire preweaning period even though heat stress early in life was likely compensated for closer to weaning when heat stress subsided. As in other studies, direct heritabilities were least for intermediate heat load; however, heritabilities were greatest for the least heat load. Selection in colder environments would result in greater response to selection based on heritability. Genetic correlations indicated direct and maternal WW were different traits depending on THI. For more tropically adapted breeds, direct correlations were stronger than maternal, and the opposite occurred for the less tropically adapted Brangus. Considerable re-ranking of Tropical Composite and Brangus sires occurred for direct effects with less re-ranking for Nelore.

Implications

Genetic variation exists for heat tolerance in a variety of traits and species. Regions with THI greater than 70 could have reduced animal production because of heat stress. Selection for greater production can negatively affect heat tolerance. With linear increases in performance in many livestock species, heat tolerance continues to be more relevant to the industries. Greater response to selection can be achieved by using environment-specific selection tools to reduce the use of heat susceptible animals in hot climates. Because of limited research on the relationships between heat tolerance of different traits, the best method is unclear for improving heat tolerance

of the animal as a whole. Heat tolerance for a primary production trait may be sufficient or heat tolerance for multiple economically relevant traits may need to be incorporated into an index.

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CHAPTER 3

GENOMIC SELECTION LITERATURE REVIEW

The availability of reference genome sequences for livestock species led to the identification of single nucleotide polymorphisms (SNP). These SNP could be genotyped relatively easily, and if enough SNP were genotyped, some SNP would be in linkage disequilibrium with the quantitative trait loci (QTL) that affect a given phenotype. Meuwissen et al. (2001) proposed methodology for whole-genome selection to introduce a new frontier in animal breeding by using SNP for genetic improvement. Since that seminal paper, many papers were published with efforts to identify the best genomic models for different species and traits. One group of these models is variance component based, and these methods will be addressed in further detail.

Genomic BLUP

VanRaden (2008) proposed several methods for calculating a genomic relationship matrix (**G**). The most commonly used is

$$\mathbf{G} = \frac{\mathbf{Z}\mathbf{Z}'}{2 \sum p_i(1-p_i)},$$

in which **Z** was a centered gene content matrix and p_i was the minor allele frequency of SNP i .

This matrix contains realized relationships that are approximated based on identity by state. One practical challenge with **G** is allele frequencies from the base population should be used to scale the matrix, but the population founders are typically not genotyped.

When all animals have genotypes, \mathbf{G} can be used as the relationship matrix to incorporate genomic information into EBV. This method is called genomic BLUP (GBLUP) with mixed model equations of

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

in which \mathbf{X} and \mathbf{Z} are incidence matrices relating observations in \mathbf{y} to fixed and random effects in $\boldsymbol{\beta}$ and \mathbf{u} , respectively, and α is the ratio of residual to genetic variances.

Single-step GBLUP

Livestock populations have large databases of pedigree and phenotypic information, which add accuracy to genetic evaluations. Incorporating all phenotypes, genotypes, and pedigree in a single evaluation maximizes the use of all available information and remains unbiased. Pedigree and genomic relationships were combined into a single covariance matrix, \mathbf{H} , by Misztal et al. (2009), and \mathbf{H} can be defined as

$$\mathbf{H} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} \\ \mathbf{A}_{21} & \mathbf{G} \end{bmatrix},$$

in which \mathbf{A} is partitioned into nongenotyped (1) and genotyped (2) individuals. The \mathbf{H}^{-1} was derived independently by Aguilar et al. (2010) and Christensen and Lund (2010) as

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}.$$

Finally, \mathbf{H}^{-1} can be substituted for \mathbf{A}^{-1} in the mixed model equations to obtain genetic predictions that include phenotypes, pedigree, and genotypes in a single analysis, referred to as single-step GBLUP (ssGBLUP).

ssGBLUP with the Algorithm for Proven and Young

Traditional ssGBLUP can only be implemented for at most 150,000 genotyped animals because \mathbf{G} must be directly inverted. Misztal et al. (2014) proposed a sparse inverse for \mathbf{G} based on recursions called the Algorithm for Proven and Young (APY). Animals are partitioned into core (c) and noncore (n) subsets with \mathbf{G} structured as

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{cc} & \mathbf{G}_{cn} \\ \mathbf{G}_{nc} & \mathbf{G}_{nn} \end{bmatrix}.$$

By theory, the TBV for core animals are functions of effective SNP effects, and the TBV for noncore animals are functions of the TBV for core animals. Thus, only \mathbf{G}_{cc} is inverted directly in APY, and remaining components are calculated by recursion. The APY \mathbf{G}^{-1} is

$$\mathbf{G}_{\text{APY}}^{-1} = \begin{bmatrix} \mathbf{G}_{cc}^{-1} + \mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1}\mathbf{G}_{nc}\mathbf{G}_{cc}^{-1} & -\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1} \\ -\mathbf{M}^{-1}\mathbf{G}_{nc}\mathbf{G}_{cc}^{-1} & \mathbf{M}^{-1} \end{bmatrix},$$

with

$$\mathbf{M}_{ii} = \mathbf{G}_{ii} - \mathbf{G}_{ic}\mathbf{G}_{cc}^{-1}\mathbf{G}_{ci},$$

in which \mathbf{M} was a diagonal matrix with dimensions equal to the number of noncore animals. The core size is typically small in relation to the total number of genotyped animals. Thus, the APY \mathbf{G}^{-1} is sparse because \mathbf{M} is diagonal and relatively large (dimensions equal the number of noncore animals). The APY enables the efficient implementation of ssGBLUP for millions of genotyped animals (Masuda et al., 2016).

Computational properties of APY

For traditional ssGBLUP, the \mathbf{G}^{-1} had quadratic storage and cubic computational requirements based on the number of genotyped animals. For APY, the storage for \mathbf{G}^{-1} was quadratic for the number of core animals and linear for the number of noncore animals

(Fragomeni et al., 2015a). In addition, the computational requirement for the APY \mathbf{G}^{-1} was cubic for the number of core animals and linear for the number of noncore animals (Fragomeni et al., 2015a). These time savings are substantial for large, genotyped populations. The ssGBLUP with APY has been successful in a dairy population with more than 500,000 genotyped animals (Masuda et al., 2016). The predicted time to run a similar genetic evaluation with 2 million genotyped animals was just more than 10 hours, and the predicted storage was 183 GB (Masuda et al., 2016), which eliminate computational and time constraints for the foreseeable future.

Core size in APY

Genomic information has a limited dimensionality because of the small effective population sizes in livestock species. This dimensionality is limited by the minimum of the number of independent SNP, independent chromosome segments, and number of genotyped animals. Eigenvalue decomposition of \mathbf{G} can be used to determine the appropriate core size in a given population (Pocrnic et al., 2016a). The core size should equal the number of largest eigenvalues explaining 98% of the variation in \mathbf{G} (Pocrnic et al., 2016a; Pocrnic et al., 2016b) to maintain the accuracy of ssGBLUP with the traditional \mathbf{G}^{-1} . In some cases, ssGBLUP with APY was more accurate than traditional ssGBLUP (Pocrnic et al., 2016a; Pocrnic et al., 2016b). These results suggest that APY removes some redundant information from \mathbf{G} .

The core size is connected to the effective population size. For smaller effective population sizes, fewer core animals are needed to achieve the same accuracy (Pocrnic et al., 2016a; Pocrnic et al., 2016b). Cattle populations required 10,000 to 15,000 core animals (Fragomeni et al., 2015a; Lourenco et al., 2015; Masuda et al., 2016) and swine and chicken populations required 4,000 core animals (Pocrnic et al., 2016b) which reflect the differences in effective population sizes among these species. The smaller populations have fewer effective

SNP (independent chromosome segments), and fewer core animals are needed to estimate the effective SNP effects. The TBV for the core animals are functions of the effects of these effective SNP effects, and the TBV for noncore animals are functions of the TBV for core animals.

Core definition in APY

APY was originally theorized with proven core animals and young noncore animals resulting in TBV for young animals being functions of TBV for proven animals (Misztal et al., 2014). Traditional and APY ssGBLUP had nearly identical accuracies for EBV in simulation when using a proven core definition (Fragomeni et al., 2015b). A random core definition was as accurate as the proven core for dairy (Fragomeni et al., 2015a; Masuda et al., 2016) and beef (Lourenco et al., 2015) cattle. In addition, using young animals instead of random produced very similar EBV (Fragomeni et al., 2015a). Based on these studies, the choice of core animals appears arbitrary, given a large enough core size. Ostersen et al. (2016) found differences in EBV for some core definitions. Using only the oldest or youngest as core animals resulted in a decrease in the EBV correlation with traditional ssGBLUP in swine. These results suggest that not all core definitions are equally desirable. Using older core animals could result in a decrease in accuracy over time.

Conclusions

Genomic selection enables more rapid genetic improvement in livestock species (Schaeffer, 2006). Genomic information can be used to increase the accuracy of genetic predictions for unproven animals. Unproven animals have few or no progeny and may not have their own phenotypic record. Any additional information on these animals improves the accuracy of estimated breeding values (EBV), and genomics can be one potential source of information. In

addition, genomic selection is especially valuable for traits that are expensive or difficult to measure as phenotypic data are often limited. Using genomic data decreases the generation interval because the best animals can be more accurately identified early in life. Breeders do not have to wait to progeny test sires, which is expensive and time-consuming, especially when selecting dairy bulls for milk production traits. Thus, genomic selection is a tool to increase genetic progress in livestock breeding programs.

As breeders began to appreciate the value of genomic selection, greater numbers of animals in all livestock species have been genotyped annually. In some beef and dairy situations, the numbers of genotyped animals exceeds the computational capabilities of traditional ssGBLUP. The development of APY was a crucial step in overcoming this limitation and implementing genomic selection in the largest genotyped populations. In addition, APY may enable as frequent or more frequent genetic evaluations given the savings in computational time. These factors result in greater genetic improvement in livestock species that have implemented genomic selection.

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CHAPTER 4

REGIONAL AND SEASONAL ANALYSES OF WEIGHTS IN GROWING ANGUS
CATTLE¹

¹ Bradford, H. L., B. O. Fragomeni, J. K. Bertrand, D. A. L. Lourenco, and I. Misztal. 2016. *Journal of Animal Science*. 94:4369-4375.
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Abstract

This study evaluated the impact of region and season on growth in Angus seedstock. To assess geographic differences, the United States (US) was partitioned into 9 regions based on similar climate and topography related to cow-calf production. Seasonal effects were associated with the month that animals were weighed. The American Angus Association provided growth data, and records were assigned to regions based on the owner's zip code. Most Angus cattle were in the Cornbelt, Lower Plains, Rocky Mountain, Upper South, and Upper Plains regions, with proportionally fewer Angus in Texas compared with the national cow herd. Most calves were born in the spring, especially February and March. Weaning weights (WW; $n = 49,886$) and yearling weights (YW; $n = 45,168$) were modeled with fixed effects of age-of-dam class (WW only), weigh month, region, month-region interaction, and linear covariate of age. Random effects included contemporary group nested within month-region combination and residual. The significant month-region interaction ($P < 0.0001$) was expected because of the diverse production environments across the country and cyclical fluctuations in forage availability. Additionally, significant seasonal contrasts existed for several regions. Fall-born calves were heavier ($P < 0.01$) than spring-born calves in the hot and humid Lower South region coinciding with fall being the primary calving season. The North and Upper Plains regions had heavier, spring-born calves ($P < 0.01$), more than 90% spring calving, and colder climates. Interestingly, no seasonal WW or YW differences existed between spring- and fall-born calves in the Upper South region despite challenging environmental conditions. Angus seedstock producers have used calving seasons to adapt to the specific environmental conditions in their regions and to optimize growth in young animals.

Introduction

Numerous factors affect the success, production, and profitability of cow-calf operations. It is well known that feed costs comprise two-thirds of enterprise expenses (McBride and Mathews, 2011). In addition, matching cow nutritional status to the environment by altering the calving season to align maximum cow requirements with peak forage quality has well documented effects on profitability (Adams et al., 1996). The ideal calving season varies due to seasonal fluctuations in cattle markets and the diverse geographic and climatic landscape of the United States (US). This diversity contributes to genotype \times environment interactions and complicates identifying the ideal cow type and most profitable management practices.

Many studies have focused on either regional or seasonal impacts on cattle production but not both on a comprehensive, national scale. Producer surveys characterize beef enterprises on regional and national scales but are subject to non-response bias. Animal experiments require substantial time and monetary investment to investigate regional, seasonal, or both effects. Moreover, much of the peer-reviewed research occurred decades ago. Modern Angus cattle have changed drastically from the Angus cow in the 1990s because of selection for greater milk production and growth (AAA, 2016). Consequently, modern cattle have greater nutritional needs, which could affect environmental fitness. The beef industry would benefit from a reevaluation of regional and seasonal factors associated with calf growth.

The purpose of this observational study was to quantify regional and seasonal weight differences for growing cattle. These factors were characterized using a large, breed association dataset to better understand regional and seasonal aspects of calving distributions and calf growth in Angus herds on a national scale. The results have economic implications for users of Angus genetics to maximize profit for specific management and environmental conditions.

Materials and methods

Animal Care and Use Committee approval was not needed because data were obtained from existing databases. The American Angus Association (AAA; St. Joseph, MO) provided weaning and yearling data in August 2015. All records met AAA data quality requirements for use in their national cattle evaluation. Contemporary groups consisted of sex, owner-defined group codes, weigh date, and herd; yearling contemporary group also included weaning contemporary group. Data were edited to include only animals located in the continental US, multiple-sire contemporary groups, minimum contemporary group size of 5 animals, weigh years in 2005 or later, and an owner zip code. Embryo transfer calves were removed because of extensive use of cooperator herds in the Angus breed and potential inaccuracies from assigning these animals to regions based on the owner's zip code. Additionally, records were removed if the owner's zip code was known to be different from the primary herd location. Inaccuracies in assigning locations may occur for cattle raised far from the farm headquarters including satellite ranches, bull test stations, heifer development centers, and feed intake facilities. The resulting dataset contained 2,194,339 weaning weights (WW) from 7,665 herds and 1,133,706 yearling weights (YW) from 4,921 herds, and was used to quantify the numbers of records and calving distributions by region.

The continental US was partitioned into 9 regions based on similar geography and environmental conditions including temperature and precipitation. Region definitions were similar to those in Leighton et al. (1982), and producers were assigned to regions based on the zip code associated with each weight record. Region boundaries are shown in Fig. 1, and regional record counts are presented in Figure 4.2. For the season component, month corresponded to the month of the animal's weigh date and differed for WW and YW analyses.

To evaluate phenotypic weight differences between seasons and regions, the data were further refined to reduce dimensionality by randomly selecting 25 contemporary groups per month-region combination for both WW and YW. If fewer than 25 groups existed in a month-region combination, all contemporary groups were included with a minimum of 10 contemporary groups per combination for WW and YW. All animals within the chosen contemporary groups were included in the analyses. This procedure ensured that selection based on contemporary group size did not introduce bias and that all month-region combinations were represented in the final data despite differences in calving seasonality across regions. The final dataset contained 49,886 WW from 1,482 herds, and 45,168 YW from 1,258 herds.

Regional and seasonal weight differences were evaluated using the following linear mixed model implemented in the NLME package (Pinheiro et al., 2015) in R (R Core Team, 2015):

$$y_{ijklmn} = \beta_1 a_i + aod_j + m_k + r_l + mr_{kl} + c_{klm} + e_{ijklmn},$$

where y_{ijklmn} was the weight for animal n , β_1 was the regression coefficient for age, a_i was age of the animal on the weigh date (120 to 280 d for WW and 320 to 620 d for YW), aod_j was the fixed age-of-dam class effect for WW only (2, 3, 4, 5 to 10, or ≥ 11 yr; BIF, 2008), m_k was the fixed month effect corresponding to the weigh date (January through December), r_l was the fixed effect for one of the 9 regions defined previously (Figure 4.1), mr_{kl} was the fixed interaction effect between month k and region l , c_{klm} was the m^{th} random contemporary group effect within the k^{th} month and l^{th} region combination, and e_{ijklmn} was the random residual for animal n . Contemporary groups were assumed to be normally distributed with variance:

$$\text{Var}(\mathbf{c}) = \sigma_c^2 \mathbf{I}_n,$$

where σ_c^2 was the contemporary group variance and \mathbf{I}_n had dimension equal to the number of animals for WW or YW. This model was used separately for WW and YW analyses. Orthogonal contrasts were constructed to compare the difference between spring and fall weights within each region. Spring was defined as January through June, and fall was defined as July through December.

Results and discussion

Characterization of the growth database

Based on the number of records per region (Figure 4.2), the majority of Angus cattle were raised in the Cornbelt, Lower Plains, Rocky Mountain, Upper South, and Upper Plains regions of the US. The Lower South, North, and Pacific had little practical impact on Angus seedstock production and corresponded to areas with greater population densities and lesser agricultural production. The Rocky Mountain region had many records despite the effect of altitude on growth and survival (Williams et al., 2012). Interestingly, many Angus cattle were raised in the Upper South region despite being less heat tolerant than *Bos indicus* and tropically adapted *Bos Taurus* breeds (Hammond et al., 1996) potentially resulting in economic losses for beef producers (St.-Pierre et al., 2003). In contrast, the Lower South and West regions, both containing states with hot climates, had substantially fewer weight records suggesting that either Angus were less adaptable to these environments or the areas had less overall cow-calf production. Limited research existed on the national distribution of beef cattle breeds for comparison at the time of this study. According to USDA surveys from 2005 to 2015, Texas had the most beef cows on inventory with 15% of the national cow herd while Montana had only 5% (USDA, 2016). Comparing those results with the results of this study, Texas had only 4% of all WW records while Montana had 13%. The distribution of weights across different regions in

Figure 4.2 suggested that Southern producers raised other purebreds, composites, or crossbreds that were more adapted to the hotter climate, but Angus genetics were well adapted to colder Northern climates.

Calving seasonality has not been characterized with data encompassing the entire US. In the present study, spring and fall calving seasons were clearly distinguished based on counts by birth month (Figure 4.3). The spring calving season contained more than 75% of calves, primarily born in February and March. Summer calving was rare in this dataset, and fall calving peaked in September. Less spring calving occurred in the Lower South and Upper South regions where heat stress can occur from mid-April until mid-September (Figure 4.4). The Pacific and West regions had an intermediate proportion of spring calving, which was probably because these two regions spanned a large range in latitudes. Meanwhile, the North, Rocky Mountain, and Upper Plains regions had at least 90% spring calving. These regions have very cold winters and producers most likely needed to align cow requirements during lactation with the peak quantity and quality of grazed forages. Cow-calf producers reported similar patterns in an earlier study, where producers in states associated with the Pacific, Rocky Mountain, West, and Upper Plains regions reported predominately spring calving and producers in the Upper South and Lower South regions reported more year-round calving (USDA, 2010b). In another USDA survey, 25% of cow-calf producers selected weather as the most important factor affecting the breeding season (USDA, 2010a). Seasonal fluctuation in feeder calf prices also affected the best calving strategy in this study. Overall, regional differences existed for the choice of calving season and producers appeared to determine the calving season that was optimal for their specific production environment.

Statistical analyses for a subset of the database

For the phenotypic weight analyses, age, age-of-dam class (WW only), month, region, and month-by-region interaction were all significant ($P < 0.0001$). The interaction was expected and resulted from the diverse combinations of topography and climate, which caused variation in feed resources, management practices, and cattle performance. These results are important for the design and interpretation of livestock field trials and experiments, as findings may not be generalizable to other seasons or regions.

Contrasts were summarized as the difference between spring and fall WW and YW (Figure 4.5). Positive contrasts indicated spring weights were heavier than fall weights, corresponding with heavier fall-born calves than spring-born calves for WW and heavier spring-born calves than fall-born calves for YW. Fall-born calves had lighter WW ($P < 0.05$) in three regions (Cornbelt, North and Rocky Mountains), all located in colder climates. These findings were similar to results of a lesser magnitude observed in the Nebraska Sandhills (Griffin et al., 2012). Lighter WW for fall-born calves could be caused by feeding poorer-quality, harvested forages to lactating cows during their greatest nutritional demand, which coincided with harsh winters in this region. Only the Lower South region had fall-born calves with heavier WW ($P < 0.05$) coinciding with fall being the predominant calving season. Earlier studies showed similar results but to a lesser extent in Louisiana and Texas, where fall-born calves were heavier at weaning and consumed better quality cool-season grasses than their spring-born counterparts (Bagley et al 1987; Gaertner et al., 1992). In this region, fall-born calves would experience less heat stress, resulting in greater weights. Based on these results, seasonal WW differences existed in regions with either very cold winters or very hot, humid summers.

The Lower South and West regions had heavier YW for fall-born calves ($P < 0.05$), and the Upper Plains had heavier YW for spring-born calves ($P < 0.05$). The Lower South and West had dramatically different climates with the Lower South being much more humid than the West; yet, both had fall-born calves with 100 kg heavier YW (Figure 4.5). Fall-born calves were expected to have lighter YW in these two regions due to the negative impact of heat stress on summer weight gain (Mitlöhner et al., 2001). Alternatively, spring-born calves were heavier at yearling in the Upper Plains, which had a colder climate and substantial snowfall. The 100 to 150 kg YW contrasts (Figure 4.5) could be caused by seasonal differences in feeding strategies for some regions. Few researchers have investigated seasonal effects for YW in seedstock or even stocker cattle. Carcass weights were heavier for spring-born calves in Iowa (Janovick Guretzky et al., 2005), but these animals were managed differently than seedstock bulls and replacement heifers.

One unexpected result was the lack of significant seasonal weight differences ($P > 0.10$) in the Upper South region. The Lower Plains region also had no significant weight difference ($P > 0.10$) between seasons and was a western extension of the Upper South region. Many factors contributed to the expectation of differences in either WW or YW in the Upper South region. The southern portion of the Upper South region should have a similar climate to the Lower South, where Angus heifers suffer from greater heat stress than heifers from other breeds (Hammond et al., 1996). Additionally, the primary forage base in the northern part of the Upper South region probably consisted of endophyte-infected tall fescue (West, 1998), which has been shown to increase body temperature causing more severe heat stress and decreasing calf WW (Brown et al., 1997; Paterson et al., 1995; Caldwell et al., 2013). Previously, fall-born calves were heavier at weaning than spring-born calves in Arkansas, one of the characteristic states in

this environment (Caldwell et al., 2013). Despite these factors, the environmental conditions in the Upper South region did not cause significant seasonal differences in WW or YW in this analysis. From this study, producers in the Upper South region appeared to have identified the genetics and production systems best suited to where they resided within this region, or cattle were receiving supplementation to maintain consistent weights throughout the year. The current study had no information regarding forage type and could not specifically identify weight differences attributed to endophyte-infected tall fescue. With yearly variation in temperature and precipitation, a year \times month \times region interaction may provide valuable insight into forage quantity and quality fluctuations.

Some regions had a single calving season that was heavier for WW and YW. For the Lower South region, cattle born in the fall were heavier than spring-born cattle at weaning and as yearlings. On the other hand, spring-born cattle tended to be heavier than fall-born cattle for WW and YW in the North and Upper Plains regions, which were characterized by colder winters with significant snowfall. Based on these results, the heaviest calves were born in the primary calving season, indicating that producers had embraced the success of this calving season. Systematic environmental and management factors were contributing to the WW and YW differences, highlighting the importance of the environment for cattle production.

Some seasonal weight contrasts were greater than 100 kg and may have a substantial economic impact for cattlemen. Earlier studies found significant seasonal effects with a magnitude of 10 to 25 kg, although some were from previous decades (Bagley et al., 1987; Gaertner et al., 1992; Griffin et al., 2012; Caldwell et al., 2013). The modern beef cow is biologically very different from the cow of the 1990s, and the offspring have greater genetic potential for growth. The current study represented a sample of the Angus population for a 10-

year period, and part of the large magnitude in weight differences could be attributed to sampling. This period might not be long enough to average out effects of significant weather events, such as the Texas drought (2011 to 2014).

In recent decades, breeders have selected Angus cattle for increased production traits with correlated increases in mature size, milk production, and feed requirements (AAA, 2016). With feed being one of the largest production costs and agricultural acreage being lost to development, matching animal production to the environment becomes even more important. The most profitable herds have lesser feed costs, irrespective of region (Dunn, 2002; Ramsey et al., 2005). Body size and milk production potential affect nutritional demand and thus, feed costs, and require optimization for specific production systems (Dickerson, 1970; McMorris and Wilton, 1986). Thus, matching cow type and nutritional status with seasonal forage fluctuations is critical for the profitability of cow-calf enterprises.

Climatic characteristics affect growth differently depending on the region. Heat stress has been shown to cost the beef industry more than an estimated \$350 million annually (St.-Pierre et al., 2003) through reduced feed intake, less weight gain, reduced milk production, and greater reproductive failure in males and females. In addition, hide color has been shown to impact weight gain with dark-hided cattle growing less because of greater susceptibility to heat stress (Finch et al., 1994). Differences in humidity between the Lower South and West regions cause differing responses to these hot environments in dairy cattle (Bohmanova et al., 2007). On the other extreme, cold temperatures and wet conditions cause greater calf death (Sprott et al., 2001) in some regions but contribute to greater growth in other regions (Olson et al., 1991). These differential responses further highlight the need for region-specific production schemes.

Genotype \times environment interactions exist both within and across beef cattle breeds. Many studies have examined breed \times environment interactions, particularly comparing breed performance in cooler versus hotter climates in the US. *Bos indicus* cattle are more heat tolerant and resistant to environmental stressors than Angus (Turner, 1980; Hammond et al., 1994), and *Bos indicus* crosses grow faster than *Bos taurus* crosses in subtropical conditions (Olson et al., 1991). Within-breed genotype \times environment interactions have also been documented for growth traits (Butts et al., 1971; Bertrand et al., 1987). Thus, cattle were not expected to perform uniformly across regions in this study. Although Angus perform well in temperate conditions, other breeds may have better growth potential in Southern areas, which may explain the lesser representation of Angus in Texas.

Conclusions

Most Angus calves are born in the spring, though fall calving is more common in the Lower South and Upper South regions than in other regions. Regions differ in the effect of season on WW and YW. Colder regions appear suitable for spring calving based on the frequency of spring calving and heavier calf weights in this dataset. Fall calving appears advantageous for producers in the hot, humid Lower South region to increase calf weight. Potentially, Southern Angus producers would benefit from genetic selection tools to improve adaptability and heat tolerance. Further research is needed to establish a genetic evaluation for these traits.

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Figures

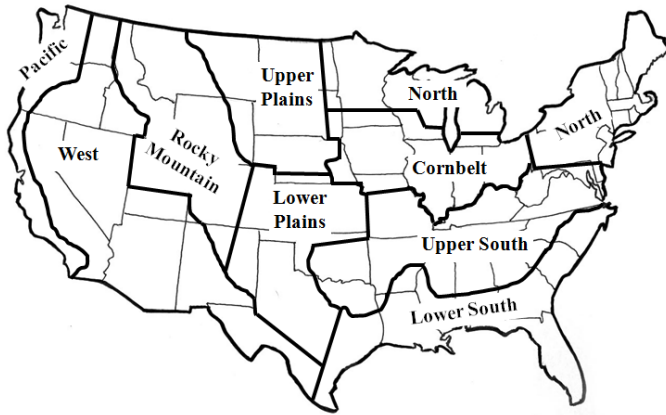


Figure 4.1. Boundaries for region assignments in the United States. These boundaries were based on Leighton et al. (1982).

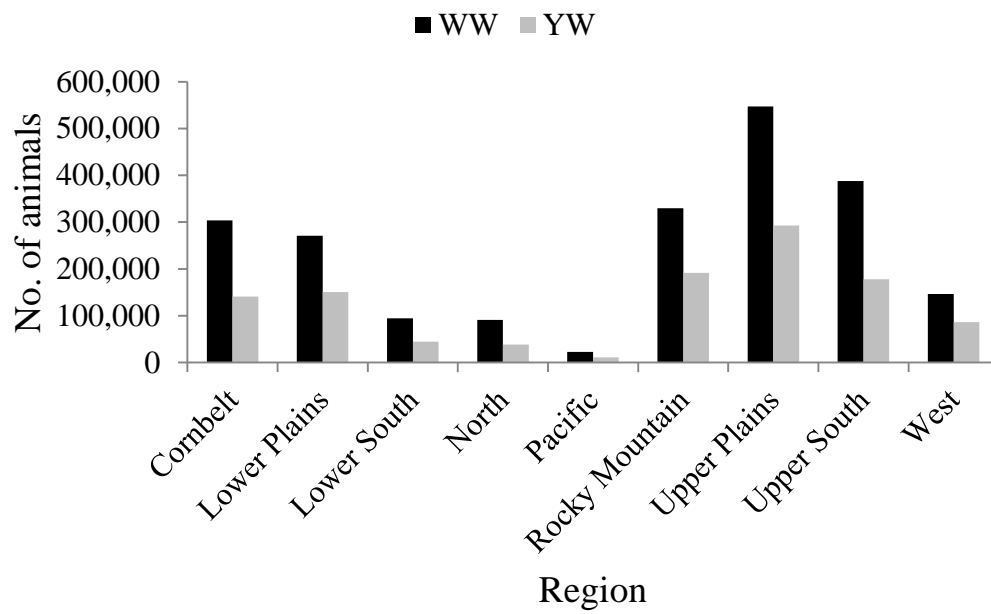


Figure 4.2. Number of Angus weaning weights (WW) and yearling weights (YW) by geographic region.

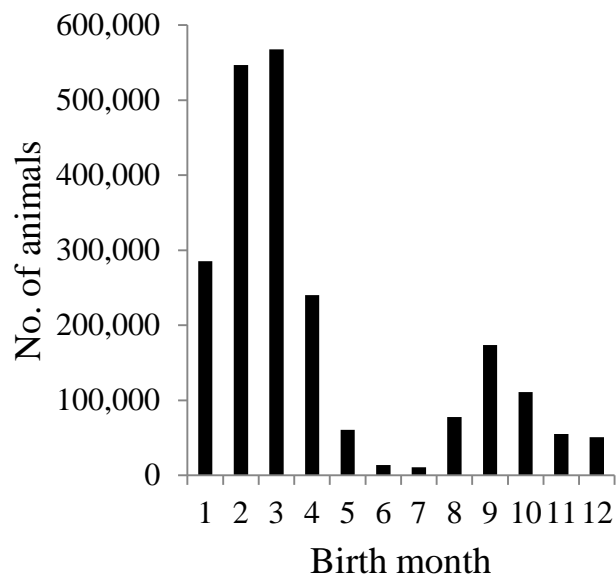


Figure 4.3. Birth month of Angus calves with weaning weight records.

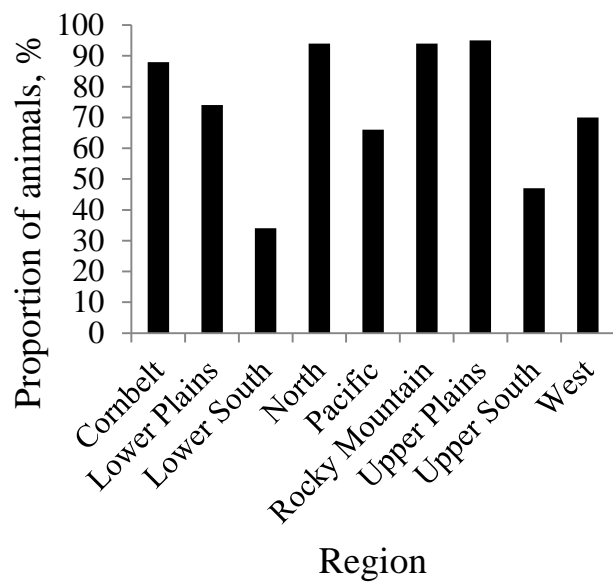


Figure 4.4. Incidence of spring calving (January through June) by geographic region for Angus calves with weaning weight records.

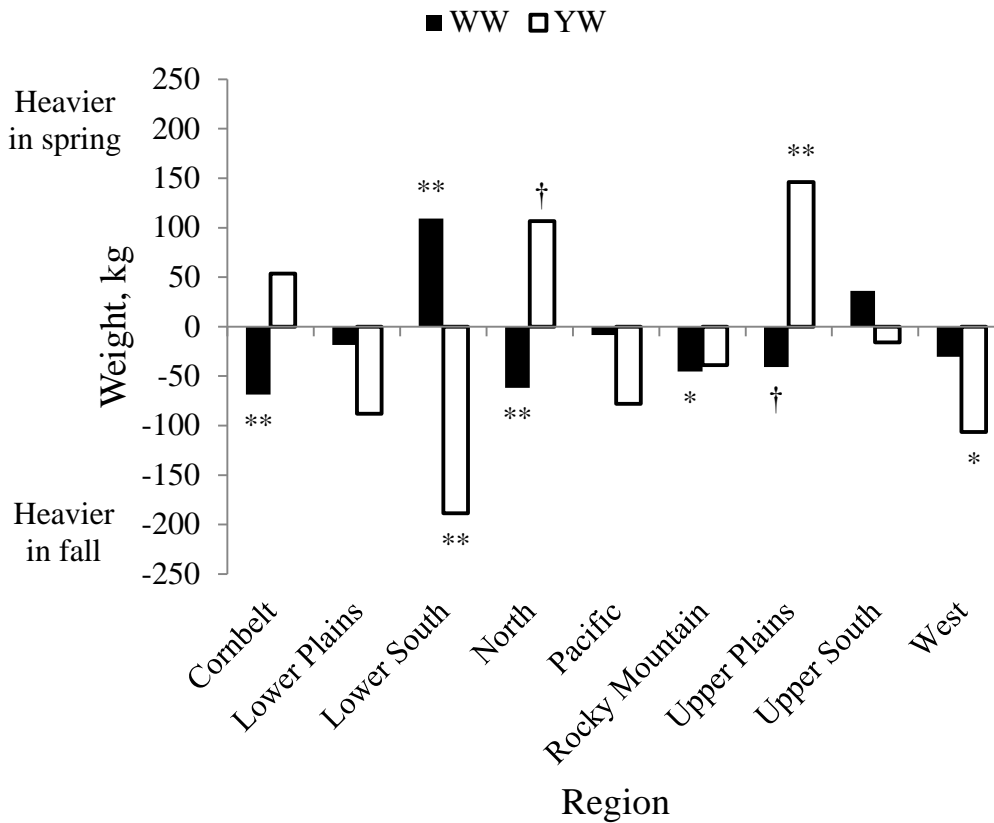


Figure 4.5. Contrasts were evaluated between spring (January through June) and fall (July through December) weaning weights (WW) and yearling weights (YW) in Angus cattle by geographic region. Positive contrasts indicated spring weights were heavier than fall weights, corresponding with heavier fall-born calves than spring-born calves for WW and heavier spring-born calves than fall-born calves for YW. † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

CHAPTER 5

GENETIC EVALUATIONS FOR GROWTH HEAT TOLERANCE IN ANGUS CATTLE²

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Abstract

The objectives were to assess the impact of heat stress and to develop a model for genetic evaluation of growth heat tolerance in Angus cattle. The American Angus Association (AAA) provided weaning weight (WW) and yearling weight (YW) data, and records from the Upper South region were used because of the hot climatic conditions. Heat stress was characterized by a weaning (yearling) heat load function defined as the mean degrees of temperature-humidity index (THI) greater than 75 °F (70 °F) for 30 (150) days prior to the weigh date. Thus, a weaning (yearling) heat load of 5 °F matched to a mean THI of 80 °F (75 °F) for the corresponding period prior to the weigh date. For all analyses, 82,669 WW and 69,040 YW were used with 3 ancestral generations in the pedigree. Univariate models were a proxy for the Angus growth evaluation, and reaction norms using 2 B-splines for heat load were fit separately for weaning and yearling heat loads. For both models, random effects included direct genetic, maternal genetic, maternal permanent environment (WW only), and residual. Fixed effects included a linear age covariate, age-of-dam class (WW only), and contemporary group for both models and fixed regressions on the B-splines in the reaction norm. Direct genetic correlations for WW were strong for modest heat load differences but decreased to less than 0.50 for large differences. Re-ranking of proven sires occurred for only WW direct effects for the reaction norms with extreme heat load differences. Conversely, YW results indicated little effect of heat stress on genetic merit. Thus, weaning heat tolerance was a better candidate for developing selection tools. Maternal heritabilities were consistent across heat loads, and maternal genetic correlations were greater than 0.90 for nearly all heat load combinations. No evidence existed for a genotype \times environment interaction for the maternal component of growth. Overall, some evidence exists for

phenotypic plasticity for the direct genetic effects of WW, but traditional national cattle evaluations are likely ranking sires adequately for non-extreme environmental conditions.

Introduction

Because beef cattle are raised in extensive conditions, growth can vary across production environments. Genotype x environment interactions have been reported for weaning weight (WW) and yearling weight (YW; Butts et al., 1971; Bertrand et al., 1987). Part of this interaction could be attributed to genetic differences in heat tolerance, an economically important trait for livestock producers in some regions. In the beef industry, total economic losses from heat stress are estimated to be greater than \$360 million annually (St.-Pierre et al., 2003). Heat stress reduces feed intake, growth, milk production, and pregnancy percentage (Nardone et al., 2006). Angus has been reported to experience greater physiological effects of heat stress than *Bos indicus* and tropically adapted *Bos taurus* breeds (Hammond et al., 1996). With Angus dominating the United States (US) beef industry, improving heat tolerance can have a large economic impact nationally and can increase the use of Angus genetics in regions with greater heat stress.

Currently, selection tools for improving heat tolerance or adaptability are not routine in US national cattle evaluations. Hair shedding scores were proposed as an indicator trait for heat tolerance (Gray et al., 2011) but are not commonly collected. Producers have limited options for decreasing heat stress in cow-calf production systems, and with intense selection for production traits in Angus cattle (AAA, 2016), the consequences for adaptability are unknown. Heat stress has been characterized using methods developed by Ravagnolo and Misztal (2000) and has been implemented successfully in dairy (Bohmanova et al., 2007; Freitas et al., 2006; Aguilar et al., 2009) and swine (Zumbach et al., 2008a; Fragomeni et al., 2015). The purpose of this study was

to investigate the existence of heat stress on growth in Angus cattle and to develop a model for genetic evaluation using routinely measured, economically relevant traits to improve heat tolerance.

Materials and methods

Animal Care and Use Committee approval was not needed as data were obtained from pre-existing databases.

Animal Data

The American Angus Association (AAA; St. Joseph, MO) provided WW and YW data in August 2015. Contemporary groups were the concatenation of sex, owner-defined group codes, weigh date, and herd. Yearling contemporary group also included weaning contemporary group. Data were edited to include weights recorded in 2005 or after, multiple-sire contemporary groups with at least 35 animals for WW or 20 animals for YW, and a known owner zip code. Embryo transfer calves were removed because of extensive use of cooperator herds in the Angus breed, and some of those calves' geographic locations would be inaccurate. Phenotyped animals had 3 ancestral generations included in the pedigree.

Based on Leighton et al. (1982), records were assigned to regions of the US to coincide with similar climate and environmental conditions (Figure 5.6). Bradford et al. (2016) used the same region boundaries and presented more detailed regional and seasonal data descriptions. Data from the Upper South region were used for genetic analyses because of the number of records (Bradford et al., 2016) and the expectation of meaningful heat stress in this area. Data descriptions are summarized in

Tables

Table 5.1.

Weather Data

Freitas et al. (2006) demonstrated that off-farm weather data were adequate for approximating on-farm weather conditions. Airport weather stations were assigned to herds based on the owner's zip code. Minimum, mean, and maximum distances of the weather station from the herds were 4, 61, and 140 km for WW and 4, 59, and 144 km for YW, respectively. Based on the weather station associated with each contemporary group, maximum daily temperature (Fahrenheit; °F) and minimum relative humidity (%) were obtained for a given number of days prior to the weigh date using the weatherData (Narasimhan, 2014) package in R (R Core Team, 2015). Data were used to calculate daily temperature-humidity index (THI):

$$THI_i = temp_i - (0.55 - 0.0055 * rh_i) * (temp_i - 58),$$

where THI_i was THI for the i^{th} day prior to the weigh date, $temp_i$ was maximum temperature (°F), and rh_i was minimum relative humidity (%). This index adjusted temperature based on the relative humidity.

Heat load functions were developed to quantify weaning and yearling heat stress (Ravagnolo and Misztal, 2000). For these functions, a common threshold represented the THI at which growth began to decrease, and heat stress effects were assumed cumulative for a number of days prior to data collection. The threshold and days were determined as in Zumbach et al. (2008a) by selecting the combination with the greatest R^2 for each trait (data not shown). The threshold THI were 75 and 70 °F for WW and YW, respectively. Heat load accumulated for 30 days before weaning and 150 days before yearling weigh dates. Thus, WW and YW heat loads were defined, respectively:

$$H_{Wj} = \max(0, \sum_{i=0}^{30} THI_{ij} - 75),$$

$$H_{Yj} = \max(0, \sum_{i=0}^{150} THI_{ij} - 70),$$

where H_{Wj} ($^{\circ}\text{F}$) was the weaning (H_{Yj} was yearling) heat load for contemporary group j and THI_{ij} was the THI on the i^{th} day prior to the weigh date. When THI was less than the threshold, heat stress was not expected to affect growth. Thus, if average THI was less than the threshold, the contemporary group had 0 heat load. If the mean THI was greater than the threshold, the entire contemporary group had a positive heat load. Heat load was greater than 0 for 46% of WW and 44% of YW.

Univariate Models

Separate univariate models were used for WW and YW as a proxy for the Angus growth national cattle evaluation. The model for WW was:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{W}\mathbf{m} + \mathbf{M}\mathbf{p} + \mathbf{e},$$

where \mathbf{y} was a vector of WW; $\boldsymbol{\beta}$ contained solutions for fixed effects of linear age covariate (d), age-of-dam class (2, 3, 4, 5 to 10, or ≥ 11 yr; BIF, 2008), and weaning contemporary group; \mathbf{u} was a vector of direct genetic effects; \mathbf{m} was a vector of maternal genetic effects; \mathbf{p} was a vector of maternal permanent environmental effects; \mathbf{e} was a vector of random residuals; and \mathbf{X} , \mathbf{Z} , \mathbf{W} , and \mathbf{M} were incidence matrices relating records to fixed, direct genetic, maternal genetic, and maternal permanent environmental effects, respectively. Likewise, the model for YW was:

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

where \mathbf{y} was a vector of YW; $\boldsymbol{\beta}$ contained solutions for fixed effects of linear age covariate (d) and yearling contemporary group, and all other effects were the same as previously

defined. Maternal permanent environment was not significant ($P < 0.01$) for YW. For all models, the covariance between direct and maternal genetic effects was assumed to be 0 as used by AAA. Variance components were estimated with animal models using Average Information REML (AIREML) implemented in the BLUPF90 family of programs (Misztal et al., 2015).

Reaction Norm Models

Reaction norms were used to determine how genetic predictions changed as a function of heat load. Heat load was transformed to first degree B-splines with an interior knot at 0 and no explicit intercept. The knot was placed at 0 because more than half of the heat loads were 0. Thus, the first spline functioned as the intercept, and the second was the linear slope for heat load. The B-splines were modeled as:

$$S_{0ij} = \frac{H_{i\max} - H_{ij}}{H_{i\max}} I(H_{ij} \neq 0) + I(H_{ij} = 0),$$

$$S_{1ij} = \frac{H_{ij}}{H_{i\max}} I(H_{ij} \neq 0),$$

where S_{0ij} was the heat load intercept for trait i and contemporary group j , S_{1ij} was the heat load slope, $H_{i\max}$ was the maximum heat load for the trait, H_{ij} was the heat load, $I(H_{ij} = 0)$ was an indicator variable equal to 1 if heat load was 0 and equal to 0 otherwise, and $I(H_{ij} \neq 0)$ was an indicator variable equal to 1 if heat load was greater than 0 and equal to 0 otherwise.

The following random regression model was used:

$$y_{ijkl} = \text{fixed}_i + \sum_{a=0}^1 F_a S_{aj} + \sum_{a=0}^1 D_a S_{aj} + \sum_{a=0}^1 M_{ak} S_{aj} + \sum_{a=0}^1 P_{ak} S_{aj} + e_{ijkl},$$

where y_{ijkl} was the WW for animal l with fixed effects i , heat load j , and dam k ; fixed_i were the fixed effects for linear age covariate (d), age-of-dam class (2, 3, 4, 5 to 10, or ≥ 11 yr; BIF, 2008), and contemporary group; a was the degree of the B-spline for heat load (0 intercept,

1 linear slope); S_{aj} was the heat load B-spline; F_a was a fixed regression coefficient; D_{al} was a direct genetic random regression coefficient; M_{ak} was a maternal genetic random regression coefficient; P_{ak} was a maternal permanent environmental random regression coefficient; and e_{ijkl} was a random residual. The YW model was the same but with fixed effects of linear age covariate (d) and contemporary group, and no maternal permanent environmental effects.

Direct WW heritabilities were calculated as:

$$h^2 = \frac{\mathbf{z}'\mathbf{V}_d\mathbf{z}}{\mathbf{z}'\mathbf{V}_d\mathbf{z} + \mathbf{z}'\mathbf{V}_m\mathbf{z} + \mathbf{z}'\mathbf{V}_p\mathbf{z} + v_e},$$

where h^2 was the heritability for a specific heat load (0 to 10); \mathbf{z} was a vector containing the intercept and slope B-splines for the given heat load; \mathbf{V} were covariance matrices for the direct genetic (d), maternal genetic (m), and maternal permanent environmental (p) effects; and v_e was the residual variance. Maternal heritabilities were calculated with the maternal variance components in the numerator. Heritabilities for YW were calculated without the maternal permanent environmental variance components.

Validation

Validations used predictivity for the direct effect in all models as in Legarra et al. (2008). Validation data included young animals born in 2012 or after, and analyses had 18,474 and 13,683 young animals for WW and YW, respectively. Of those young animals, 7,763 and 6,341 had a heat load greater than 0 for WW and YW, respectively. Phenotypes were corrected for all fixed effects for a given model, and the corrected phenotypes were correlated with EBV from an evaluation excluding young animals' phenotypes. For the reaction norm, EBV were calculated based on the actual heat load each young animal experienced. Additionally, proven sires ($n = 1,048$ for WW and 878 for YW) with at least 25 progeny were used to compare rankings

between models. For both direct and maternal effects, Spearman rank correlations were evaluated across models and within the reaction norm using different heat loads.

Results and discussion

Heat load distributions are illustrated for WW and YW (Figure 5.7). A WW heat load of 1 °F corresponded to 76 °F THI, and the same YW heat load matched to 71 °F THI. Thus, heat load values were not directly comparable between traits. No heat load was observed for more than half of WW and YW, and heat stress was not expected to negatively affect the growth of those animals. Few records had large heat loads; consequently, results for large heat loads were less accurate because few producers raised cattle in these conditions. More extreme yearling heat loads were expected because the threshold THI was less than for weaning, but weaning heat loads were more extreme when considering the underlying THI.

One challenge was appropriately quantifying heat stress in beef cattle. The methods used to define heat load have been used successfully in dairy cattle (Ravagnolo and Misztal, 2000; Aguilar et al., 2009) and swine (Zumbach et al., 2008b; Fragomeni et al., 2015). These species were both raised in confinement systems with less variation in production environments from farm to farm than existed for beef cattle. Because beef cattle typically harvest their own forages, heat load was confounded with seasonal changes in forage type, quantity, and quality including fescue toxicosis (Paterson et al., 1995). Confounding may also exist between calving season and heat load because of the seasonality of calving in some regions (Bradford et al., 2016). Yearling weight was used instead of actual postweaning gain. The number of days between weaning and yearling weigh dates were the same for all animals in a postweaning gain contemporary group and were confounded with heat load. Approaches exist to distinguish heat load and contemporary group but require assuming heat load accumulates for the animal's lifetime (Santana et al.,

2015). Although heat stress may decrease growth for a period, animals will likely have compensatory gain after the heat stress has subsided. In addition, off-farm weather data were used as an approximation for on-farm conditions. On-farm data were not available to validate this estimate although off-farm data were acceptable for more intensively managed dairy cattle (Freitas et al., 2006).

Heritabilities were estimated with univariate and reaction norm models. Univariate direct heritabilities (SD) were 0.24 (0.01) for WW and 0.32 (0.01) for YW. Previous estimates were greater for both traits in Angus (Costa et al., 2011), but our WW direct result was closer to the 0.20 heritability used by AAA (AAA, 2016). The univariate results were most similar to the reaction norms with intermediate heat loads (Figure 5.8). Weights were most heritable for no heat load and least heritable for intermediate heat load. Other beef cattle studies also had greater heritability for more favorable environmental conditions (Cardoso and Templeman, 2012; Santana et al., 2015). Conversely, carcass weight during heat stress was most heritable in swine (Zumbach et al., 2008b; Fragomeni et al., 2015). The heritability estimates from the current study indicated breeders could make genetic improvement by selecting for the direct genetic component of weight in heat stressed conditions.

Maternal heritabilities increased with increasing heat load (Figure 5.8). Univariate maternal heritabilities (SD) were 0.07 (0.01) for WW and 0.12 (0.01) for YW, and reaction norm heritabilities were similar, especially with little or no heat load. Previous estimates were greater for WW and similar for YW (Costa et al., 2011). The AAA uses a WW maternal heritability of 0.14 (AAA, 2016). In Brazilian beef breeds, maternal WW heritabilities from the reaction norm were similar in magnitude but quadratic in shape (Santana et al., 2015). Differences in the definition and amount of heat load could contribute to the dissimilarities between studies. In

dairy cattle, milk production also had greater heritability with increasing heat stress (Ravagnolo and Misztal, 2000; Aguilar et al., 2009).

Correlations between slope and intercept were all positive and indicative of a favorable relationship between greater growth in environments both with and without heat stress. The direct genetic correlations (SD) were 0.30 (0.002) for WW and 0.71 (0.06) for YW, and the maternal genetic correlations (SD) were 0.87 (0.001) for WW and 0.96 (0.07) for YW. The correlations indicated greater growth without heat stress was positively related to growth during heat stress with a very strong relationship for the maternal effects. These correlations were previously reported to be moderately negative for WW direct ($r = -0.30$ to -0.43) and negative or no different from 0 for WW maternal ($r = -0.17$ to -0.37 ; Santana et al., 2015), which suggested phenotypic plasticity existed for growth traits. Differences between studies could result from differences in breeds, random regression models, heat load definitions, or the complexity of modeling maternal traits. Selecting Angus cattle for greater growth should result in increased weight across environmental temperatures in the Upper South region.

Direct genetic correlations are summarized as a heat map for the WW and YW reaction norms (Figure 5.9). Weaning weight correlations were strong when heat load differed by at most 5 °F, but for large heat load differences, direct correlations were less than 0.50 indicating growth was not the same trait between these environments. Conversely, results for YW indicated no environmental differences for the direct effect. Phenotypic analyses of these data suggested no seasonal differences for WW or YW in the Upper South region (Bradford et al., 2016). These results align well with the lack of genotype \times environment interaction for YW. Heat load was defined for a longer period for YW, and cattle may have acclimatized to heat stress during the 150 days (Robinson et al., 1986) resulting in no detectable genotype \times environment interaction.

Santana et al. (2015) studied three beef breeds with similar WW direct results for Brangus, stronger correlations for Nellore, and weaker correlations for Tropical Composite. The correlation strength may be related to the adaptability of the breed to hot environments causing weaker correlations for less-adapted breeds. Weaning weight was only considered distinct traits for no heat load or large heat load; however, few seedstock animals were raised in these extreme environments.

Results for maternal correlations differed from the direct correlations (Figure 5.9), and WW and YW had similar results. All maternal correlations were greater than 0.85, indicating little change in the maternal component across heat loads. Strong genetic correlations existed for dairy milk production across a similar range of THI (Ravagnolo and Misztal, 2000). Dairy and beef cows have a large difference in their genetic potential for milk production, and heat stress was expected to affect dairy cows more resulting in weaker genetic correlations in dairy cattle because of their greater production. Although one component of the maternal genetic effect is milk production, this effect included other genetic factors associated with the growth of the dam's offspring such as nurturing ability and milk quality. Additionally, the calf could be compensating for any decrease in milk production by consuming creep feed or other forages to maintain weight gain (McMorris and Wilton, 1986). Conversely, Santana et al. (2015) had weaker maternal genetic correlations than direct genetic for two of three breeds. Santana et al. (2015) had data from fewer farms and did not include the maternal permanent environmental effect for one breed because of limited repeated records per dam. The breed with no maternal permanent environmental effect had the strongest maternal genetic correlations (Santana et al., 2015); so, perhaps our model was not sufficiently distinguishing between maternal genetic and maternal permanent environmental effects as a result of relatively few offspring per dam

(average no. = 1.7). These results indicate selection for the maternal genetic component of weight should be effective despite any environmental heat stress.

Rank correlations were strong between the univariate and reaction norm (Table 5.2), and proven sires ranked nearly identically between models for the maternal effects. Some re-ranking occurred between the univariate and reaction norm with extreme heat load for WW direct, and selection decisions for the direct effect could slightly differ depending on the heat load for WW. Carcass weights in swine had slightly weaker correlations between the univariate and reaction norm models and substantially weaker correlations within the reaction norm, suggesting swine had a greater physiological response to heat stress (Zumbach et al., 2008b). Rank correlations were stronger for YW than WW, potentially resulting from the lesser yearling THI threshold and selection after weaning. The single-trait YW models did not account for sequential culling after weaning. Despite some re-ranking of sires, the univariate models were adequately identifying the best growth sires across environmental conditions.

Reaction norms for proven bulls were inspected to visualize how EBV changed as a function of heat load. From the univariate evaluation, 10 proven bulls were chosen with the largest and smallest WW EBV, and the same procedure was used for YW. The bulls with the largest EBV were important to the breed as producers would be considering these bulls when selecting for greater growth. The two groups of bulls were distinct across heat loads for both traits (Figure 5.10). Although both traits have a similar amount of re-ranking, WW had a greater magnitude difference between EBV for minimum and maximum heat load. Generally, the expected WW for these bulls' offspring would be different during heat stress resulting in regional or seasonal differences in progeny performance.

Predictivity was used to compare the models' accuracies. Predictive abilities for the univariate and reaction norm based on the actual heat load were $r = 0.17$ and 0.20 , respectively, for WW and $r = 0.22$ and 0.20 , respectively, for YW. The univariate WW correlation was less than in Lourenco et al. (2015) for traditional, multiple-trait BLUP ($r = 0.34$) in the same Angus population. No predictivity difference was expected because heritability estimates were similar between models. Only the direct genetic effect could be assessed using predictivity as difficulties arise for a maternal effect, because the maternal genetic effect was one generation back and required corrected phenotypes for the dam instead of the individual (Lourenco et al., 2015). Based on predictive abilities, the univariate model was performing well for WW and YW.

For producers with operations in extreme heat stress conditions, opportunities exist to make greater genetic progress with environment-specific WW EBV. Genetic correlations between environments indicate WW was not the same trait depending on heat stress. Although rank correlations were strong across environments, progeny of some proven bulls in Figure 5.10 would be expected to have a greater than 20 kg WW difference between no heat load and maximum heat load, and this difference would have a large economic impact for producers who market calves at weaning. Thus, some breeders could use a heat tolerance genetic evaluation to fine-tune selection decisions in the Upper South region. Identifying the elite bulls for hot environments would enable Angus producers to stimulate demand for these genetics and to market those bulls to commercial cattlemen in the Upper South, potentially for a premium.

Many considerations exist for the implementation of a heat tolerance genetic evaluation for growth traits in beef cattle. The weatherData package (Narasimhan, 2014) has data retrieval inconsistencies, which are concerning for large-scale, routine heat load calculations. Occasionally, weather information was available, but the package reported no data and located

the data on another attempt. If heat tolerance was implemented, the opportunity could exist for producers to submit zip codes specific to where cattle were raised to reduce the inevitable inaccuracies in assigning cattle to geographic locations. Another issue is the presentation of the EPD as publishing the slope coefficients creates difficulty in interpretation because solutions are based on splines. Ideally, heat tolerance EPD would be disseminated to producers through decision support tools to customize predictions to an individual environment. Beef producers are not accustomed to obtaining genetic predictions in this manner, and the alternative is to provide EPD based on pre-selected heat load(s). Publishing both traditional and heat tolerance WW EPD could create additional confusion for cattlemen when comparing the two results. Either way, a large education effort would be needed for successful implementation.

In modern beef production enterprises, cattlemen consider many economically relevant traits in their breeding objectives. The methodology from this study requires heat tolerance to be assessed by trait. Between WW and YW, WW was better for assessing growth heat tolerance because of weaker genetic correlations across environments and more producers marketing calves at weaning than yearling. Carcass traits are important to the industry, but breed associations do not typically have information regarding the geographic location of animals during the finishing phase limiting the ability to evaluate heat tolerance. On the other hand, heat stress is expected to affect female and male reproductive traits making these traits a logical next step for evaluating heat tolerance. Yet, female reproduction is best assessed when whole herd reporting is used to consistently account for every female. Ideally, heat tolerance for all of these traits could be combined into an index to provide producers with comprehensive, easy-to-use selection tools.

Conclusions

Selection tools for improving heat tolerance in growth traits were developed in Angus cattle. Some evidence exists for phenotypic plasticity for the WW direct genetic effects indicating potential for users of Angus genetics in extreme environments to make greater genetic improvement by using environment-specific genetic predictions. The maternal component of growth can be selected with similar selection response despite environmental heat stress. Further research is needed for the heat tolerance of other traits in beef cattle to develop a systematic understanding of the genetic mechanisms controlling adaptability. These conclusions assume that heat load directly quantifies the amount of heat stress.

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Tables

Table 5.1. Descriptive statistics for weaning weights (WW) and yearling weights (YW) for Angus in the Upper South region

Item	WW	YW
Mean (kg)	255	430
SD (kg)	48	90
Animals	82,669	69,040
Pedigree animals	169,291	149,963
Contemporary groups	1,549	2,071

Table 5.2. Spearman rank correlations for sires with at least 25 progeny for direct genetic (above diagonal) and maternal genetic (below diagonal) effects for weaning and yearling weights using univariate or reaction norm models for Angus in the Upper South region

		Reaction norm ¹		
Model	Uni ²	H = 0	H = 5	H = 10
Weaning weight (<i>n</i> = 1,048)				
Uni		0.98	0.98	0.79
H = 0	0.99		0.95	0.71
H = 5	0.98	0.99		0.89
H = 10	0.96	0.97	0.99	
Yearling weight (<i>n</i> = 878)				
Uni		0.99	0.99	0.95
H = 0	0.99		0.98	0.91
H = 5	0.99	0.99		0.98
H = 10	0.99	0.99	0.99	

¹Reaction norm model with heat loads (H) of 0, 5, or 10 °F

²Uni = univariate model

Figures

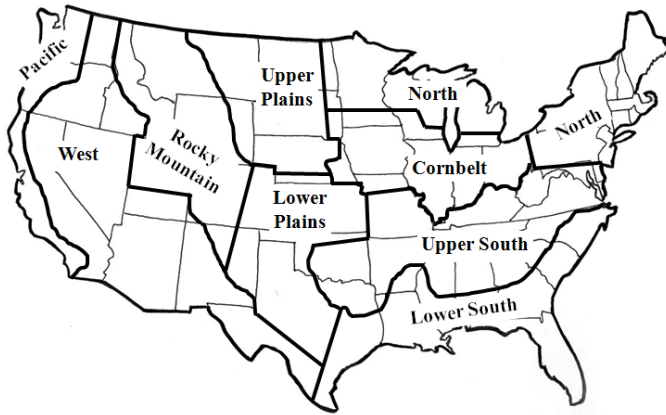
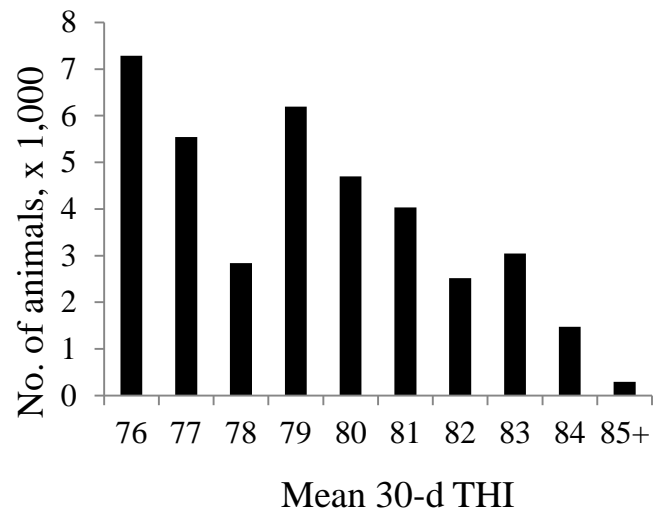


Figure 5.6. Boundaries for region assignments in the United States.

A. Weaning weight



B. Yearling weight

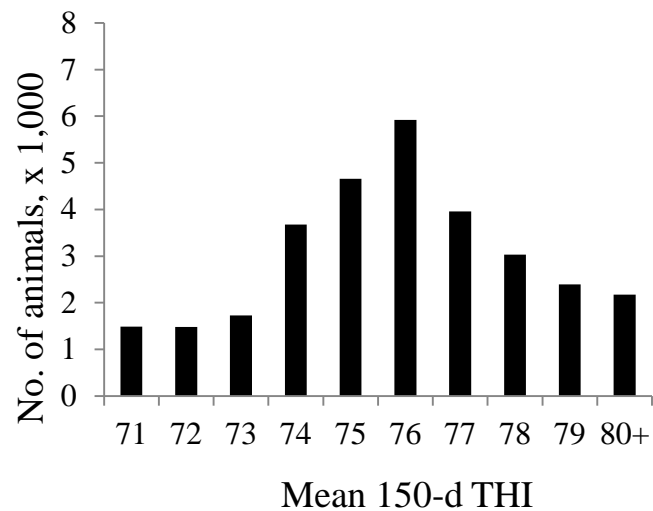


Figure 5.7. Distributions of mean temperature-humidity index (THI) for weaning (A) and yearling (B) weights for Angus in the Upper South region. Graphs exclude 44,747 weaning and 38,540 yearling weights with mean THI less than the respective threshold.

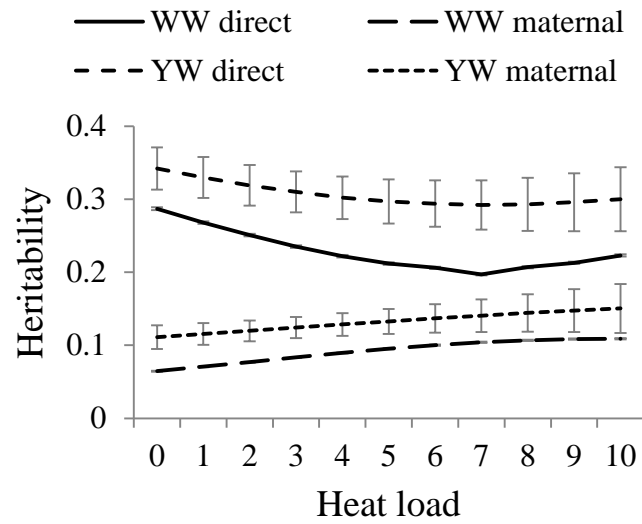
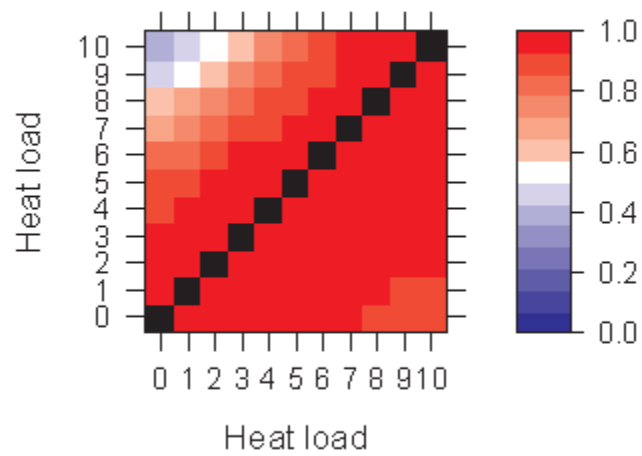


Figure 5.8. Direct and maternal heritabilities ± 2 SD for weaning weight (WW) and yearling weight (YW) using a reaction norm on heat load for Angus in the Upper South region.

A. Weaning weight



B. Yearling weight

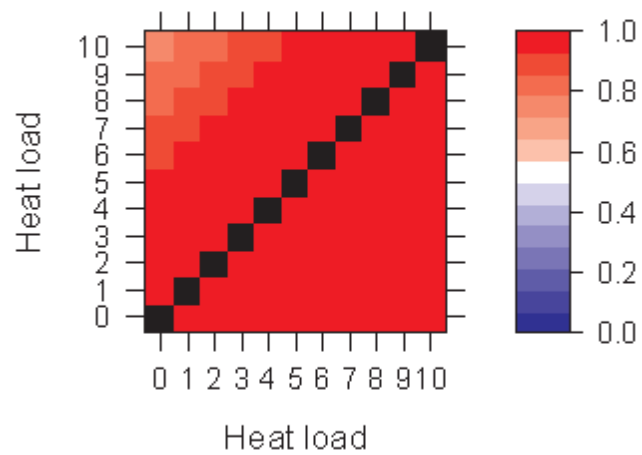
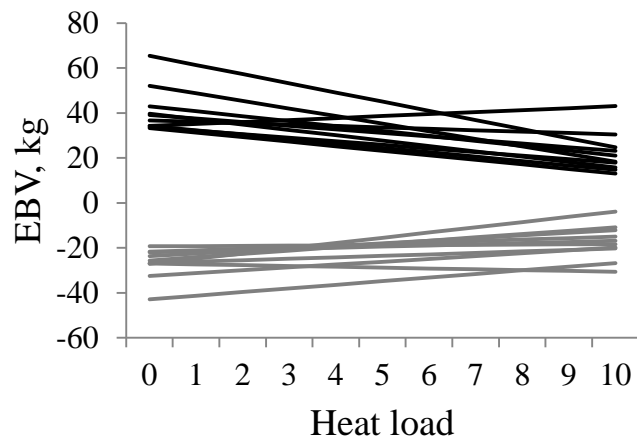


Figure 5.9. Heat map of direct (above diagonal) and maternal (below diagonal) genetic correlations from the reaction norm on heat load for weaning (A) and yearling (B) weight in Angus in the Upper South region.

A. Weaning weight



B. Yearling weight

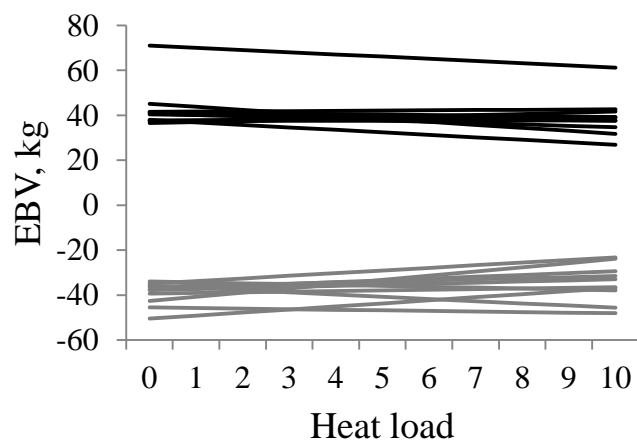


Figure 5.10. Reaction norms for the 10 proven bulls with the greatest (black) or least (grey) weaning (A) or yearling (B) weight direct EBV from the univariate analysis for Angus in the Upper South region.

CHAPTER 6

SELECTION OF CORE ANIMALS IN THE ALGORITHM FOR PROVEN AND YOUNG
USING A SIMULATION MODEL³

³ Bradford, H. L., I. Pocrníć, B. O. Fragomeni, D. A. L. Lourenco, and I. Misztal. 2017. *Journal of Animal Breeding and Genetics*. 2017:1-8. DOI: 10.1111/jbg.12276 (in press)
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Abstract

The Algorithm for Proven and Young (APY) enables the implementation of single-step genomic BLUP (ssGBLUP) in large, genotyped populations by separating genotyped animals into core and noncore subsets and creating a computationally efficient inverse for the genomic relationship matrix (**G**). Since APY became the choice for large-scale genomic evaluations in BLUP-based methods, a common question is how to choose the animals in the core subset. We compared several core definitions to answer this question. Simulations comprised a moderately heritable trait for 95,010 animals and 50,000 genotypes for animals across 5 generations. Genotypes consisted of 25,500 SNP distributed across 15 chromosomes. Genotyping errors and missing pedigree were also mimicked. Core animals were defined based on individual generations, equal representation across generations, and at random. For a sufficiently large core size, core definitions had the same accuracies and biases, even if the core animals had imperfect genotypes. When genotyped animals had unknown parents, accuracy and bias were significantly better ($P \leq 0.05$) for random and across-generation core definitions.

Introduction

Breeders have implemented genomic selection using single-step genomic BLUP (ssGBLUP) in many species worldwide (Aguilar et al., 2010; Christensen and Lund, 2010). The ssGBLUP combined pedigree, phenotypes, and genotypes into an analysis using the same framework as historical genetic evaluations. Traditionally, the blended genomic relationship matrix (**G**) was directly inverted; however, this matrix was dense and had dimensions equal to the number of genotyped animals. Inverting **G** was computationally feasible when the most advanced livestock populations had up to 150,000 genotyped animals. With increasing adoption of genotyping globally, the ssGBLUP methodology was adapted to efficiently incorporate

millions of genotyped animals into genetic evaluations. Misztal et al. (2014) solved this problem by developing the Algorithm for Proven and Young animals (APY).

To implement APY, the genotyped population is divided into core and noncore animals such that core animals contain most of the genomic information, and \mathbf{G} is partitioned into core and noncore animals. For APY \mathbf{G}^{-1} , only the core animals' partition is inverted directly. The APY \mathbf{G}^{-1} also includes relationships between core and noncore animals and diagonal elements for noncore animals. These other components are linear functions of the inverse for the core animals' partition, genomic relationships between core and noncore animals, and diagonal elements of \mathbf{G} for noncore animals.

The dimensionality of the genomic information is limited by the minimum of number of SNP, number of effective SNP markers (or independent chromosome segments), and number of genotyped animals. This dimensionality is related to the core size used in the implementation of APY (Pocrnic et al., 2016a; Pocrnic et al., 2016b). To assess dimensionality, eigenvalue decomposition of the original \mathbf{G} without blending (\mathbf{G}_0) is used to determine the number of largest eigenvalues explaining most of the variation in \mathbf{G}_0 , and this number of eigenvalues is used as the core size in APY. With a core size based on 98% of the variation in \mathbf{G}_0 , APY was at least as accurate as the traditional \mathbf{G}^{-1} in ssGBLUP. Thus, APY can replace traditional \mathbf{G}^{-1} in large, genotyped populations because of the limited dimensionality of the genomic information.

According to theory, the choice of core animals is generally unimportant because of the limited dimensionality. With adequate core size, the true breeding values (TBV) of core animals are functions of the effects of independent chromosome segments, and the TBV of noncore animals are functions of the TBV for core animals. This concept can be extended to ssGBLUP by using proven sires as core animals (Misztal et al., 2014). The estimated breeding values

(EBV) for young animals are then functions of the EBV for proven sires. When proven sires were used as core animals, APY was as accurate as traditional ssGBLUP (Fragomeni et al., 2015b). More recently, Ostersen et al. (2016) proposed that core definitions may have different accuracies. When selection is occurring, prediction accuracies for direct genomic values are known to decrease as the prediction and predicted populations become more distantly related (Muir, 2007; Saatchi et al., 2011). Thus, better understanding the importance of individual generations in APY is important for theoretical understanding and practical implementation. Since APY became the choice for large-scale genomic evaluations in BLUP-based methods, a common question is how to choose animals to be part of the core subset.

A limited number of core definitions have been investigated. Using proven animals (many progeny) as core resulted in nearly identical EBV and accuracies as using random core definitions in cattle (Fragomeni et al., 2015a; Lourenco et al., 2015; Masuda et al., 2016). In addition, random core definitions provided the same accuracy as the young core definition, which indicated that the core definition may be arbitrary (Fragomeni et al., 2015a). Recently, different EBV were reported for swine when using old or young core definitions (Ostersen et al., 2016). Our objectives for the current study were to investigate different core definitions, to quantify accuracy changes when core animals were older and less related to the youngest generation, and to ascertain why the random core definition worked well in implementation.

Materials and methods

Animal care and use committee approval was not needed because data were simulated.

Simulation

The population structure started with a founder population to generate initial linkage disequilibrium between SNP and QTL. The founder population began with 5000 individuals and

steadily decreased to 1000 individuals after 1000 generations. Then, the population size steadily increased for 250 generations to 5010 individuals, 10 males and 5000 females. Individuals in the last generation were parents for the first generation of the current population.

We simulated 10 non-overlapping generations for the current population undergoing selection on males. Selection was only for males to control the effective population size and to have a manageable number of genotyped animals. Individuals were randomly mated with 2 full-sibling offspring per mating (10,000 offspring per generation; equal sex ratio). From these offspring, 10 males were selected based on BLUP EBV along with all 5,000 females to be parents for the next generation. This process generated a pedigree with 105,010 individuals. Generations 0 to 9 had phenotypes ($n = 95,010$) for a moderately heritable trait ($h^2 = 0.30$), and generation 10 was used for validation. Five replicates were simulated using QMSim (Sargolzaei and Schenkel, 2009).

The simulations had small effective population sizes. The theoretical effective population size was 40 based on the formula given by Wright (1931). Mean realized effective population size (SE) was 26 (7.6) based on the amount of inbreeding per generation and defined by Falconer and Mackay (1996). The realized and theoretical effective population sizes differed because selection violated the assumptions of an idealized population, but both estimates indicated a small effective population size.

Generations 6 to 10 had genotypes ($n = 50,000$) based on the following assumptions. While less realistic, all animals in these generations were assumed to be genotyped; this simplification allowed for a better theoretical understanding of how to select core animals. The simulated genomes contained fifteen 1 M long chromosomes, 25,500 biallelic SNP, and 2550 biallelic QTL. The SNP and QTL were randomly positioned on the chromosomes with equal

numbers per chromosome. The simulations created a similar number of SNP per chromosome as medium-density genotyping typical in cattle. The QTL effects were simulated from the Gamma distribution (shape = 0.40, scaled internally for a genetic variance of 0.30) resulting in QTL with small effects and accounted for all the genetic variation in the trait. All SNP and QTL had 0.5 allele frequencies to begin the founder population. On average, 1 crossover occurred per chromosome with no interference, and the recurrent mutation was 2.5×10^{-5} mutations per meiosis per loci. Allele frequencies and linkage disequilibrium changed throughout the simulation. For linkage disequilibrium, mean (SE) pooled r^2 per chromosome was 0.38 (0.01) based on default calculations in QMSim (Sargolzaei and Schenkel, 2009).

Methodology

We constructed \mathbf{G}_0 following VanRaden (2008)

$$\mathbf{G}_0 = \frac{\mathbf{Z}\mathbf{Z}'}{2 \sum p_i(1-p_i)},$$

in which \mathbf{Z} was a centered gene content matrix and p_i was the minor allele frequency of SNP i . Allele frequencies were calculated from all observed genotypes. A blended \mathbf{G}_0 was used in implementation and was defined as

$$\mathbf{G} = 0.95\mathbf{G}_0 + 0.05\mathbf{A}_{22},$$

in which \mathbf{A}_{22} was the partition of the numerator relationship matrix corresponding to genotyped animals.

The traditional ssGBLUP involved replacing \mathbf{A}^{-1} , the inverse of the numerator relationship matrix, with \mathbf{H}^{-1} defined by Aguilar et al. (2010) as

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix},$$

in which \mathbf{G}^{-1} was calculated directly. This \mathbf{G}^{-1} becomes more computationally challenging as more animals are genotyped. Alternatively, a sparse \mathbf{G}^{-1} was created using APY (Miszta et al., 2014). For APY, animals were categorized as either core (c) or noncore (n) animals. Thus, \mathbf{G} was partitioned as

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_{cc} & \mathbf{G}_{cn} \\ \mathbf{G}_{nc} & \mathbf{G}_{nn} \end{bmatrix}.$$

The APY inverse was calculated as

$$\mathbf{G}_{\text{APY}}^{-1} = \begin{bmatrix} \mathbf{G}_{cc}^{-1} + \mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1}\mathbf{G}_{nc}\mathbf{G}_{cc}^{-1} & -\mathbf{G}_{cc}^{-1}\mathbf{G}_{cn}\mathbf{M}^{-1} \\ -\mathbf{M}^{-1}\mathbf{G}_{nc}\mathbf{G}_{cc}^{-1} & \mathbf{M}^{-1} \end{bmatrix},$$

with

$$\mathbf{M}_{ii} = \mathbf{G}_{ii} - \mathbf{g}_{ic}\mathbf{G}_{cc}^{-1}\mathbf{g}_{ci},$$

in which \mathbf{M} was a diagonal matrix with dimensions equal to the number of noncore animals.

Thus, the inverted matrices were a diagonal matrix and a small subset of \mathbf{G} . Miszta (2016) presented complete derivations and theory for APY. We analyzed all data using the BLUPF90 family of programs (Miszta et al., 2016).

Scenarios

The core size has been linked to the dimensionality of the genomic information. A limited number of effective SNP markers or independent chromosome segments exist in livestock populations; so, adding more genotyped animals contributes less and less new information about the population. Enough core animals were needed to account for most of the variation in \mathbf{G} and to ultimately obtain accurate EBV. The core size was determined through eigenvalue decomposition of \mathbf{G}_0 (Pocrnic et al., 2016a). Core sizes were the numbers of largest eigenvalues explaining 98, 95, or 90% of the variation in \mathbf{G}_0 . The core size was calculated for each simulation replicate, and the same core size (98, 95, or 90%) was used for scenarios within

the replicate. Hence, core sizes differed across replicates but were based on the same proportion of variation in \mathbf{G}_0 . We focused on the effect of core size for one group of analyses, and all remaining analyses used a core size equal to the number of largest eigenvalues explaining 98% of the variation in \mathbf{G}_0 for each replicate. This value was selected based on previously reported accuracies (Pocrnic et al., 2016a; Pocrnic et al., 2016b).

The core definition was investigated by analyzing the same dataset with ssGBLUP but using different core animals in APY, and the core animals were selected based on specific subsets of the genotyped animals (Table 1). The core animals were randomly selected from parents in one generation (generations 6 to 9) and from young animals (generation 10). In addition, an across-generation core was defined by randomly selecting 20% of core animals from each of the 5 genotyped generations (only parents in generations 6 to 9). Core animals were also randomly selected from all genotyped animals (random) to make comparisons with previous studies. The restriction of using parents when selecting core animals from specific generations maintained consistency in the type of core animals among generations and replicates.

We considered additional factors to assess the utility of core definitions in less ideal situations. We investigated genotype accuracy as a source of variation potentially affecting the best core definition because genotype errors may impact the dimensionality of \mathbf{G} . Genotypes were modified to be 98% accurate to emulate imputed genotypes for all animals in generations 9 and 10. These modified genotypes were referred to as imputed genotypes throughout this study. Thus, imputed genotypes were core animals for some scenarios and noncore animals for others. The original genotypes were used in the eigenvalue decomposition to select the core size resulting in a smaller core size than using the imputed genotypes for eigenvalue decomposition.

For another scenario, we evaluated pedigree completeness for any interaction with the core definition. To investigate different ancestral pedigree depths for genotyped animals, 25% of animals were randomly selected from generations 1 to 5, and we removed their sires. These animals with unknown sires had phenotypes, and progeny were the closest possible genotyped relatives. In addition, we considered the consequences of genotyping animals with no pedigree information. We randomly removed both parents from 80% of genotyped animals.

Validation

We modeled the simulated phenotype using an animal model with the overall mean as a fixed effect and direct additive genetic and residual as random effects. For validation, we assessed accuracy and bias for animals born in generation 10; these 10,000 animals had genotypes but no phenotypes. We measured accuracy as the correlation between TBV and EBV and bias as the regression of TBV on EBV. Also, we considered rounds to convergence using a convergence criterion of 10^{-12} . Within each analysis, we compared pairwise means for 8 core definitions using Tukey's honest significant difference test (Tukey, 1949) to detect differences in accuracy, bias, and rounds to convergence.

Results and Discussion

Number of core animals

Accuracy and bias are presented in Figures

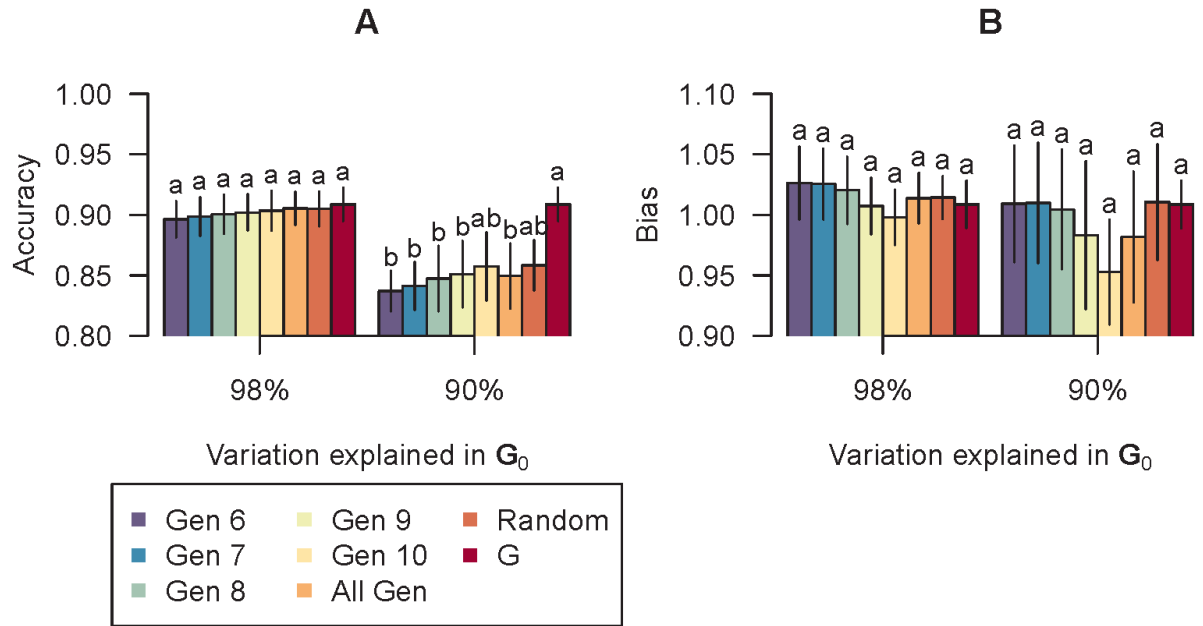


Figure 6.11 for different core sizes (numbers of largest eigenvalues for G_0) and core definitions. Core definitions included individual generations (6 to 10), equal representation across generations, and random. The core size is approximately 75% smaller when 90% instead of 98% of the variation in G_0 is used. All scenarios were very accurate, and the accuracy may have resulted from the strong selection and corresponding large linkage disequilibrium in the simulation. For the larger core size (98%), accuracy and bias for APY are no different from traditional G^{-1} ($P > 0.05$) meaning solutions are robust to core definition. Within the APY core definitions, accuracies differ by less than 0.01, and biases differ by less than 0.03. The more recent single-generation core definitions typically had numerically greater accuracy than core definitions with older generations, and the random core definition was more accurate than any single-generation core definitions. For the smaller core size (90%), validation accuracies significantly decrease when core definitions are based on a single generation (6 to 9) or across generations when compared with traditional G^{-1} ($P \leq 0.05$). On average, accuracies are 0.06 less

for APY with the smaller core size (90%) than for traditional \mathbf{G}^{-1} . A decrease in accuracy is expected because the smaller core size accounts for less variation in \mathbf{G}_0 . A few core definitions do not differ from traditional \mathbf{G}^{-1} , but we expect them to differ with more replicates and greater power. Although accuracy is less for the smaller core size (90%), accuracies do not differ across the core definitions for APY with a range in accuracy of 0.02, and the greatest accuracy was for the random core definition. The smaller core size has no bias differences across the core definitions ($P > 0.05$) with a range of 0.06. Results are intermediate to those presented in Figures

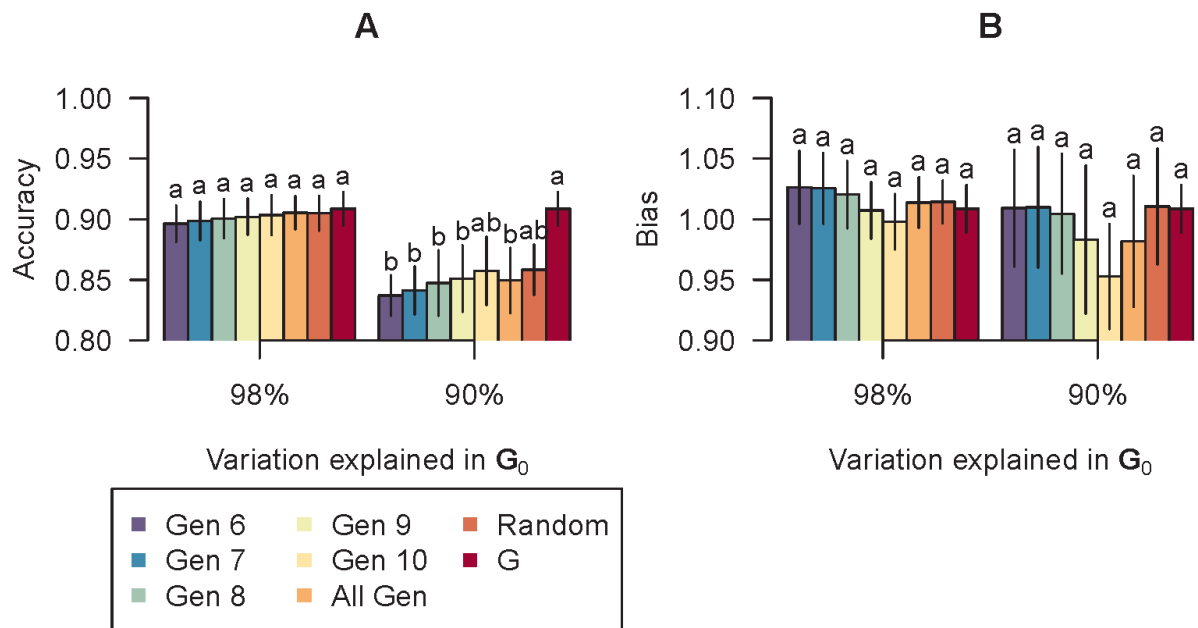


Figure 6.11 when core size is associated with 95% of the variation in \mathbf{G}_0 . Using fewer core animals in APY decreases accuracy but may not affect bias.

The mean (SE) numbers of largest eigenvalues (core sizes) explaining 98, 95, and 90% of the variation in \mathbf{G}_0 were 2521 (107), 1194 (69), and 603 (44), respectively. Each replicate used the number of eigenvalues calculated from the \mathbf{G}_0 for that specific replicate. Most of the genomic variation was contained in 2000 of the 50,000 genotyped animals. Thus, instead of directly

inverting a \mathbf{G} with dimensions of 50,000, a small matrix can be inverted when calculating an APY \mathbf{G}^{-1} . The APY \mathbf{G}^{-1} substantially reduces computing time and memory compared with \mathbf{G}^{-1} (Masuda et al., 2016). When using APY in large, genotyped populations, breeders can implement ssGBLUP for a reasonable computational requirement.

Pocrnic et al. (2016a) suggested modifying formulas from Stam (1980) to make the core size a function of genome length and effective population size. Combining an effective population size (N_e) of 40 and a genome length (L) of 15 Morgans with their formulas, predictions are 2,400 (98%; $4N_eL$), 1,200 (95%; $2N_eL$), and 600 (90%; N_eL) largest eigenvalues in \mathbf{G}_0 depending on the amount of variation explained. The predictions are similar to the actual numbers of eigenvalues if theoretical effective population size is used. Realized effective population size underestimates the numbers of eigenvalues because the approximations were derived from random mating populations but we included strong selection. In populations undergoing selection, theoretical effective population size is the better measure for predicting the numbers of eigenvalues to use as the core size.

EBV comparisons are important for practical implementation. For all replicates and core sizes, EBV correlations for all animals were greater than 0.99 between ssGBLUP with traditional \mathbf{G}^{-1} and APY with different core definitions. These outcomes differ from a previous study in which the EBV correlation decreased for some core definitions (Ostersen et al., 2016). These differences can result from the strong, single-trait selection in the simulation. On a population-wide scale, EBV from APY are comparable to traditional ssGBLUP. For validation animals, EBV correlations between methods follow the same pattern as accuracies. For sufficient core size (98%), correlations between APY and traditional ssGBLUP were greater than 0.99 for all core definitions. Correlations for the smaller core size (90%) range from 0.91 to 0.94 and are

slightly weaker ($r \geq 0.89$) than a simulation by Pocrnic et al. (2016a). Livestock populations are typically selected for multiple traits; so, correlations may be stronger because of less intensive selection in those populations.

The numbers of rounds to convergence were presented in

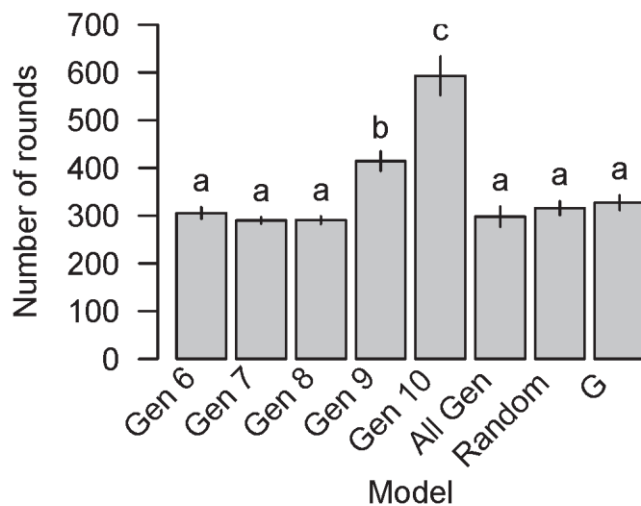


Figure 6.12 for the core size associated with 98% of the variation in \mathbf{G}_0 . Most core definitions had similar numbers of rounds as traditional \mathbf{G}^{-1} , but the number of rounds began to increase for generation 9 and doubled for the generation 10 core definition. In all analyses, the number of rounds displayed a similar pattern. Animals in generation 10 are young animals with genotypes, no phenotypes, and no progeny. Animals in generation 9 have genotypes, phenotypes, genotyped progeny, and no phenotyped progeny. The number of rounds also increased when young dairy cattle were used as core animals (Fragomeni et al., 2015a). To avoid convergence problems in practice, core animals should not primarily consist of animals without phenotypes. In a previous study, all animals had genotypes and phenotypes, and the number of rounds was actually less for the young core definition (Ostersen et al., 2016). Possibly, numerical stability improves when the core includes animals with phenotypes and phenotyped progeny. In addition,

convergence differences could be caused by slight changes in scaling of \mathbf{G} with different core subsets in relation to the scaling of \mathbf{A}_{22} in the default implementation in BLUPF90 (Misztal et al., 2016).

Imputation

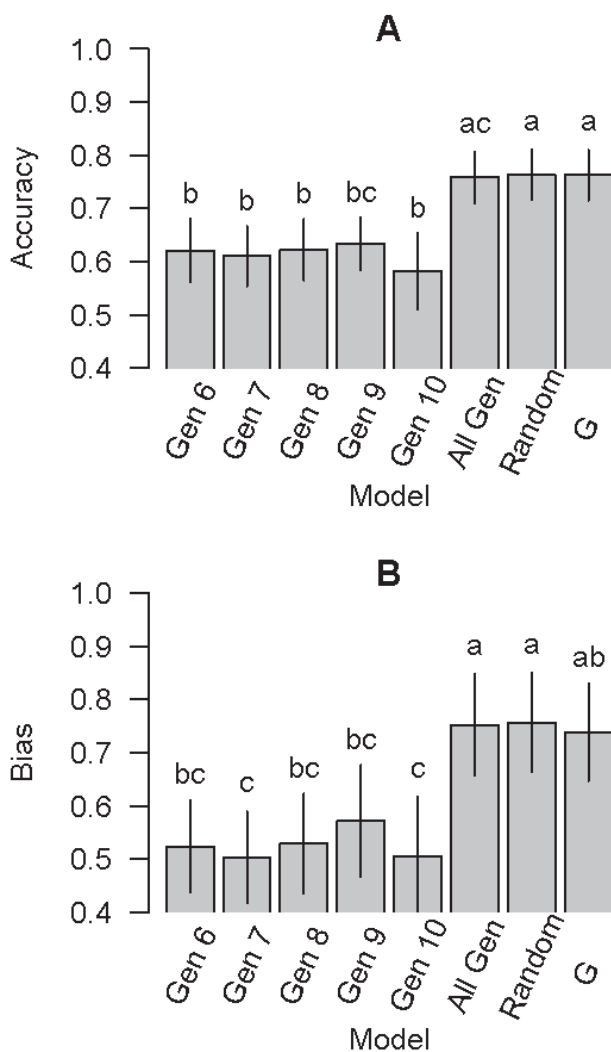
Because genotype accuracy affects the dimensionality of genomic information (results not shown), we considered imputation as a contributing factor for selecting the core definition. When genotypes imputed with 98% accuracy are included, accuracy and bias did not differ ($P > 0.05$) across core definitions. Accuracies (SE) ranged from 0.89 (0.01) to 0.90 (0.01), and biases (SE) ranged from 0.99 (0.01) to 1.04 (0.02). No differences occur despite generations 9 and 10 ($n = 20,000$) having accurately imputed genotypes and being used as core animals. Thus, the best core definition is not affected by the presence of accurately imputed genotypes in simulation. In practice, any core differences will be smaller because eigenvalue decomposition will be used for the imputed not the actual genotypes and core size will increase. The small amount of genotype errors do not dramatically affect the dimensionality of the genomic information or independent chromosome segments based on the accuracies. If imputation accuracy is less than 98%, including those imputed genotypes as core animals might affect EBV. Imputation is increasing because of the cost effectiveness of low-density genotyping panels. The importance of imputation needs to be studied in livestock populations because including imputed genotypes as young, core animals previously affected EBV (Ostersen et al., 2016). Nonetheless, the current study finds no effect of imputation on the core definition.

Incomplete pedigree

We examined two scenarios with incomplete pedigree information and found different conclusions. The first scenario was incomplete ancestral pedigrees that created different pedigree

depths for genotyped animals. We altered pedigree depths by removing sires for 25% of non-genotyped animals. Incomplete ancestral pedigrees do not affect accuracy or bias for different core definitions ($P > 0.05$). Accuracies (SE) ranged from 0.90 (0.01) to 0.91 (0.01), and biases (SE) ranged from 0.99 (0.01) to 1.02 (0.02). Thus, incomplete ancestral pedigrees do not affect EBV when using different core definitions. Core definitions should be robust across species with different degrees of pedigree depth.

Conversely, the core definition matters when most genotyped animals have unknown



parents (

Figure 6.13). Accuracy is less and bias is greater than traditional \mathbf{G}^{-1} for single-generation core definitions ($P \leq 0.05$). Random core definitions perform well as expected from previous research (Fragomeni et al., 2015a; Lourenco et al., 2015; Masuda et al., 2016; Ostersen et al., 2016). In addition, the across-generation core definition is as accurate as the random core definition and traditional \mathbf{G}^{-1} . The mean accuracy for random and across-generation cores is 0.76 compared with a mean accuracy of 0.61 for single-generation cores (range 0.05). Correlations between EBV from the 2 methods follow a similar pattern with random and across-generation cores greater than 0.99 and single-generation cores ranging from 0.89 to 0.93. We consider this accuracy difference to be meaningful and recommend the use of multi-generational core definitions (random or equal representation across generations). These results indicate that the random core definition is effective because the core animals represent multiple generations. Interestingly, core definitions including 2 or 3 generations increase accuracy but are still numerically less accurate than using all generations. The across-generation core definition would be applicable for species with multi-sire breeding cohorts or no pedigrees for genotyped animals. Again, differences between core definitions can be attributed to differences in scaling of \mathbf{G} .

Interpretation

The simulation assumptions affect the dimensionality of \mathbf{G}_0 as the simulation has more genotyped animals (50,000) than the number of SNP ($< 25,500$). In livestock populations, medium-density genotyping is common ($\sim 50,000$ SNP), and APY is needed when the number of genotyped animals ($\sim 100,000$ to $150,000$) is at least twice the number of SNP for these populations. We expect 2400 independent chromosome segments (Stam, 1980) in this population. Our number of SNP is 9 to 10 times greater than the number of independent chromosome segments, which is less than the 12 times needed to capture all the junctions

between segments (MacLeod et al., 2005). Thus, either the number of SNP or the number of independent chromosome segments limits the dimensionality of \mathbf{G}_0 . Doubling the genome size would cause a smaller proportional increase in the number of largest eigenvalues. Our conclusions are not expected to change with different simulation parameters because our core sizes would account for a large percentage of the variation in \mathbf{G}_0 .

Given the simulated scenario with selection, the generational core definitions are robust even for smaller core size. For the 5 generational core definitions, no pairwise comparisons differ for accuracy or bias in any scenario. Accuracy does not decrease as the relationships between core and validation animals decrease as previously proposed (Ostersen et al., 2016). Potentially, the independent chromosome segments present in generation 6 are applicable for generation 10. The accuracies indicate that the same core definition can be used for multiple generations unless pedigrees are incomplete. With incomplete pedigrees, across-generation core definitions may better represent the independent chromosome segments in the core animals. Because these differences are not seen in the other scenarios, the results are more likely caused by the genomic relationships between core animals correcting for the lack of pedigree connectedness across generations. In datasets with incomplete pedigree, metafounders can be used to better account for the missing pedigree relationships and need to be investigated (Legarra et al., 2015).

Accuracy differences are expected for generational core definitions based on the research by Ostersen et al. (2016). When comparing traditional and APY ssGBLUP, the EBV correlations were least with old or young core definitions. The core size can affect their conclusions as the study was published concurrently to the implementation of eigenvalue decomposition for core size. Their core size was approximately 90 or 95% of the variation in a different commercial swine population with similar number of genotyped animals and SNP (Pocrnic et al., 2016b).

The EBV correlations were similar for the 2 studies when comparing traditional and APY ssGBLUP with a random core definition (Ostersen et al., 2016; Pocrnic et al., 2016b). In practice, more core animals can increase correlations because computation time was reasonable and the core size was smaller than the optimal number of eigenvalues explaining 98% of the variation in \mathbf{G}_0 .

Conclusions

The core definition is robust to the core size, accurate imputation, and incomplete ancestral pedigree. The core definitions become more important when genotyped animals have incomplete pedigrees. When genotyped animals have unknown parents, the core definition is more important, and the core needs to include multiple generations to maintain accuracy and unbiasedness. In this scenario, random or across generation core definitions are appropriate to include all generations. These ideas need to be applied to livestock populations, particularly those with incomplete pedigrees to assess accuracy changes with different core definitions.

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Table

Table 6.1. Criteria for randomly selecting core animals for different core definitions in the Algorithm for Proven and Young

Core	Criteria for selection as core animals
Gen 6	Born in generation 6 with offspring in generation 7
Gen 7	Born in generation 7 with offspring in generation 8
Gen 8	Born in generation 8 with offspring in generation 9
Gen 9	Born in generation 9 with offspring in generation 10
Gen 10	Born in generation 10
All Gen	20% from each of generations 6 to 10, meets above criteria
Random	All animals in generations 6 to 10

Figures

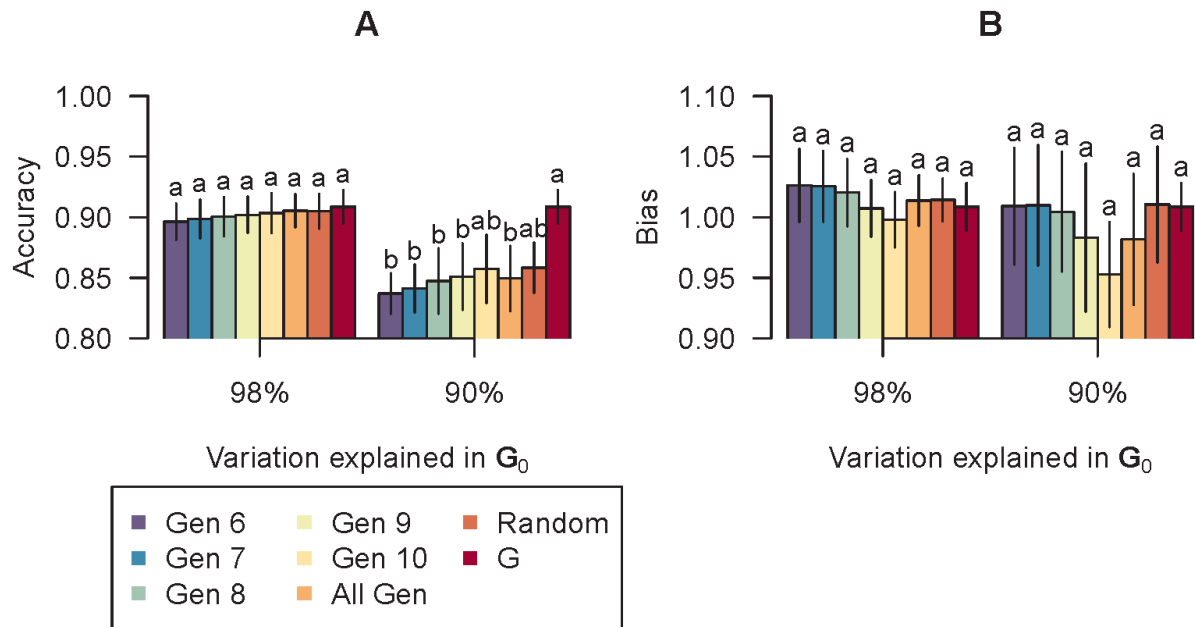


Figure 6.11. Accuracy (A) and bias (B) for traditional single-step genomic BLUP (G) and for different Algorithms for Proven and Young core definitions based on core sizes equal to the numbers of largest eigenvalues explaining 98 or 90% of the variation in G_0 . Accuracy was defined as the correlation between true and estimated breeding values. Bias was measured as the regression of true on estimated breeding value. Results with the same core size and no common letters differed significantly ($P \leq 0.05$). Error bars were ± 2 SE.

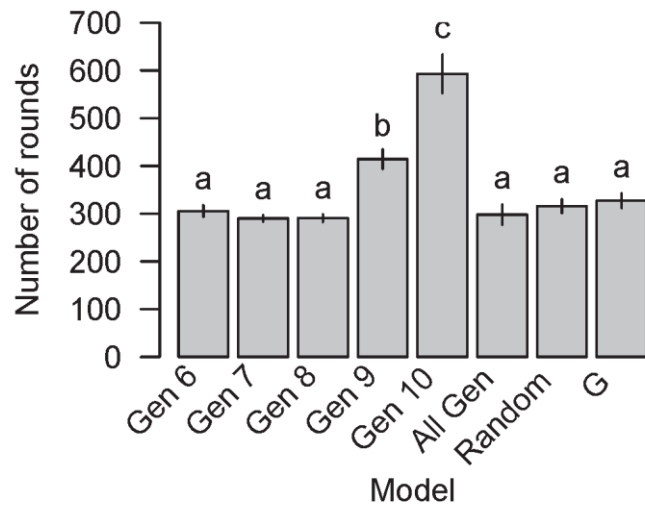


Figure 6.12. Numbers of rounds to convergence (10^{-12}) for traditional single-step genomic BLUP (G) and different Algorithm for Proven and Young core definitions. Results with no common letters differed significantly ($P \leq 0.001$). Error bars were ± 2 SE.

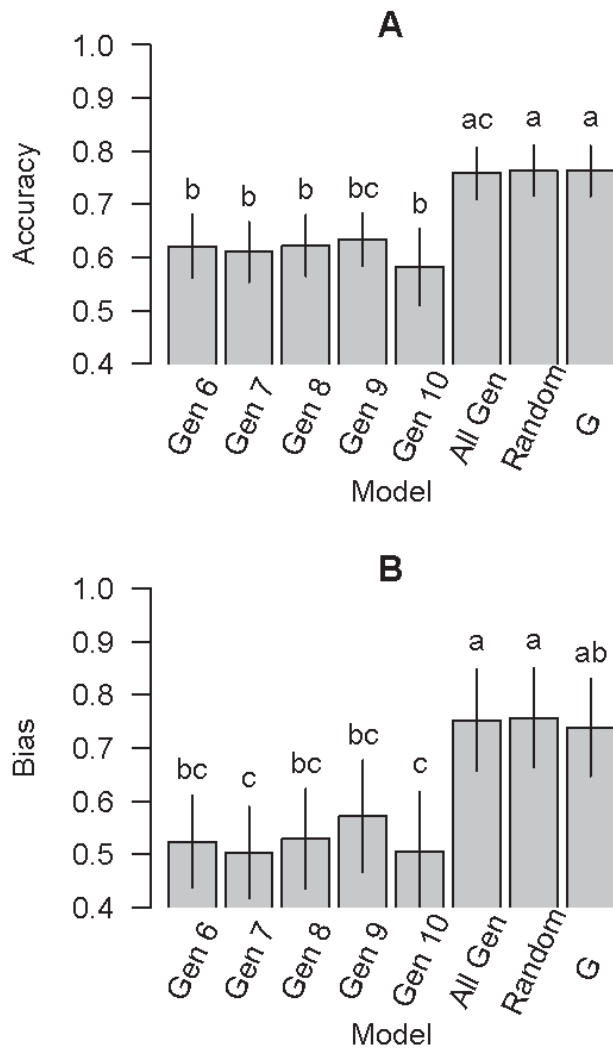


Figure 6.13. Accuracy (A) and bias (B) for traditional single-step genomic BLUP (G) and different Algorithm for Proven and Young core definitions when genotyped animals had unknown parents. Accuracy was defined as the correlation between true and estimated breeding values. Bias was measured as the regression of true on estimated breeding value. Results with no common letters differed significantly ($P \leq 0.05$). Error bars were ± 2 SE.

CHAPTER 7

CONCLUSIONS

With a focus on economically relevant traits, genetic evaluations for novel traits are being developed to meet industry needs. One of these traits includes heat tolerance, the ability to maintain performance in hot and humid environments. Because beef cattle are raised in extensive conditions, profitability depends on selecting the right genetics for the environment. Evidence exists for a genotype \times environment interaction for growth based on the environmental temperature. There was no evidence of the same interaction for the maternal genetic contribution to calf growth. Thus, any effects of heat stress in the dam may not be severe enough to result in a measurable difference in calf performance. Beef producers can use this information to better select sires that fit their specific production system and environment.

In addition to novel traits, genomic selection is another popular area of research. One method for implementing genomic selection is single-step genomic BLUP (ssGBLUP). As more and more animals are genotyped, the computational burden for ssGBLUP becomes too large. The Algorithm for Proven and Young was a solution to this problem and enabled genomic selection for nearly unlimited numbers of genotyped animals. The core animals for this algorithm can be selected at random or from a single generation with equal accuracy and unbiasedness; however, convergence properties were worse when the youngest animals were used as core. In addition, cores with animals from many generations should be used when datasets have incomplete pedigree information for genotyped animals. These results aid in the implementation of genomic selection for large genotyped populations.

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