INVESTIGATION OF INTERACTIONS IMPACTING GENETIC PARAMETER ESTIMATION AND GENETIC MERIT PREDICTIONS IN BEEF CATTLE

A Dissertation

by

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ABSTRACT

Increase in world population constantly raises the global demand for food. To respond to this demand, livestock systems require to constantly increase their production and/or efficiency. Improvement of beef production can be achieved using genetic and non-genetic strategies, however only with genetic improvement is possible to achieve accumulative improvements across time. Genetic improvement can be achieved by selection or crossbreeding. However, outcomes from both alternatives can be influenced by interactions between genotype and environmental factors, as well as between additive and non-additive genetic components.

This study evaluated three different interactions that could be acting on genetic merit predictions and parameter estimations in different cattle populations. First, the interaction between sire and progeny sex was evaluated for pre and post weaning weights and for intramuscular fat in Droughtmaster cattle (*Bos indicus-Bos taurus* composite breed). Sire by progeny sex interaction was significant for weight at ultrasound measurement (post weaning trait), indicating that it may be possible to achieve different rates of improvement across progeny sex, with intact males having the larger potential for improving this trait. Second, interaction between animals' additive and non-additive genetic components on birth weight and weaning weight was evaluated across different crossbreed scenarios involving Nellore and Angus influenced parents. The interaction was significant for both traits; thus, it may be possible to select sires given a specific type of cross, and to improve progeny performance due to achieving a

better combined effect between additive and non-additive genetic effects. Third, interaction between animals' additive genetic component and environments across a gradient of longitude or latitude coordinates within continental United States of America was evaluated for intramuscular fat in Hereford cattle. Results indicated large additive genetic variance and heritability differences across longitude or latitude coordinates, when evaluated at across-regions or within-region levels.

Results from this study support that genotype-environment interactions, as well as interaction between additive and non-additive genetic effects could introduce bias in genetic improvement programs if they are not accounted for in prediction equations. Further research is needed to corroborate findings from this study, in addition to further improve modeling strategies for these interactions in genetic prediction models.

DEDICATION

To my mother, Victoria Liberona, who taught me to never give up in life, and to always pursue my dreams.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

1.1. World Demand for Livestock Products

The world population is increasing, as is world food demand and corresponding production. The growth rate of global food production has been faster than the rate of population growth, which should make it possible to satisfy the food consumption needs. This has not occurred for many reasons, especially due to poverty around the world. It has been estimated that the human population could reach 9.15 billion by 2050 (Alexandratos and Bruinsma, 2012). This will challenge agricultural systems to produce food at rates to satisfy global increases in demand.

The increase in population and wealth in developed countries has been associated with increases in per capita food consumption and increased consumption of livestock products (Alexandratos and Bruinsma, 2012). This can also be observed in developing countries, but the increase in consumption of livestock products will probably not be as strong as what occurred in western developed countries (Alexandratos and Bruinsma, 2012). The estimated increase in population will result in increasing global demand for livestock products worldwide.

Cattle production for beef and milk is highly variable regarding production environments, cultural history, market expectations, and political importance. Total world beef and veal production reached 62,878,000 MT of carcass weight equivalent by 2018. The top contributors to this production were the United States, Brazil, the

European Union, China, and India (Table 1.1), and these had the largest numbers of animals (Table 1.2).

Table 1.1. Beef and veal production in the top 5 countries or groups of countries (1,000 MT carcass weight equivalent)

Country	Year 2015	2016	2017	2018	2019 April
United States	10,817	11,507	11,943	12,253	12,440
Brazil	9,425	9,284	9,550	9,900	10,200
European Union	7,684	7,880	7,869	8,030	7,820
China	6,169	6,169	6,346	6,440	6,575
India	4,100	4,200	4,250	4,300	4,340
Global total	59,179	59,659	60,651	62,193	62,593

USDA, 2019.

Table 1.2. Cattle inventory in the top 5 countries or groups of countries (1,000 head basis)

Country	Year 2015	2016	2017	2018	2019 April
India	301,100	302,600	303,600	305,000	306,400
Brazil	213,035	219,180	226,045	232,350	238,158
China	90,073	90,558	88,345	90,387	90,000
United States	89,143	91,918	93,705	94,298	94,760
European Union	88,406	89,152	89,152	88,819	87,508
Global total	969,259	978,770	984,528	996,361	1,002,722

USDA, 2019.

1.2. Classification of Cattle Breeds

Domesticated cattle breeds used in productive systems belong to the genus *Bos*, and either to the sub-species *Bos taurus* or *Bos indicus*. Breed characteristics from these two sub-species result in differing efficiency for unique production environments and, market expectations. *Bos taurus* breeds are the non-humped breeds that originated from

Middle East domestication events (Herring, 2014). Many breeds from this group are characterized by favorable carcass attributes such as increased marbling, tenderness, and meat yield, and improved weight-based production in temperate climates (Prado et al., 2008). *Bos indicus* (Zebu) breeds have their origin in Asia. *Bos indicus* cattle have a characteristic hump in the shoulder region. *Bos indicus* cattle have increased parasite and disease resistance, as well as higher heat tolerance, and are well-adapted to production in tropical and subtropical climates (Sanders, 1980; Turner, 1980; Jonsson, 2006; Prado et al., 2008; Herring, 2014).

Breeds investigated in this study include Angus, Droughtmaster, Hereford, and Nellore. Angus is a British breed (*Bos taurus*) developed in the Aberdeen and Angus Counties of Scotland; Angus cattle were imported to the United States in 1873 (American Angus Association, 2019). Hereford is a British breed (*Bos taurus*) developed in Herefordshire England, and were imported into the United States in 1817 (American Hereford Association, 2019). Droughtmaster is a stabilized composite developed in Australia and is 50% Shorthorn and 50% Brahman (Droughtmaster Stud Breeders Society, 2019). Shorthorn is a British breed (*Bos taurus*) developed in England and was distributed to many English colonies, among them American colonies in 1783 (Shorthorn Beef, 2019), and Australian colonies in 1800 (American Shorthorn Association, 2019). Brahman is a *Bos indicus* composite developed in the United States from four Asian *Bos indicus* breeds (Sanders, 1980). Nellore is one of these foundation breeds used to develop American Brahman; it is from the Ongole region of India

(Sanders, 1980) and it the predominant breed in Brazil (Oklahoma State University, 2019).

1.3. Improvement for Economically Relevant Traits

Genetic improvements in efficiency and productivity of beef cattle operations have followed two fundamental approaches, selection and crossbreeding (Herring, 2014). Selection, based on performance records and pedigree relationships, has been very efficient for improving traits with moderate to high heritability, such as growth and carcass traits (Falconer and Mackay, 1996; Herring, 2014). The use of genomic assisted selection (Meuwissen et al., 2001) incorporates high-density single nucleotide polymorphism genotypes into genetic prediction equations. This may result in increased accuracy of genetic merit predictions in comparison to that obtained using classic quantitative methodology with pedigree; this may permit selection of sires at younger ages (Schaeffer, 2006; Garrick, 2011).

The genetic improvement for traits with low heritability, such as reproduction and other fitness-related traits, has been associated with lower genetic gain per generation (Falconer and Mackay, 1996). Fitness-related traits may have negative correlations to at least some production traits, and therefore genetic improvement programs that do not incorporate these relationships into selection objectives may be indirectly selecting against them (Goddard, 2009). High selection intensity for production traits has been associated with inbreeding depression of fitness-traits in livestock populations (Goddard, 2009). Crossbreeding can be an effective alternative to improve these traits in commercial (non-purebred) herds by increasing the

heterozygosity of animals for benefits of direct and maternal hybrid vigor (Falconer and Mackay, 1996; Herring, 2014).

1.4. Hybrid Vigor Benefits and Concerns

Different domestication events led to the formation of the *Bos indicus* and *Bos taurus* breeds and provide the basis of their large genetic divergence (MacHugh et al., 1997). Crossing of breeds from these two cattle groups has been widely used due to large hybrid vigor (heterosis) effects in many economically relevant beef industry traits (Cartwright, 1980; Franke, 1980; Riley et al., 2007). Increased female fertility and longevity have been among the most important traits valued in *Bos indicus* x *Bos taurus* animals (Cartwright, 1980; Franke, 1980; Turner, 1980; Koger, 1980; Olson et al., 1990; Riley et al., 2001).

The effects of hybrid vigor are not equally beneficial for all traits. Heterosis for birth weight can be detrimental; higher weights are associated with a higher incidence of dystocia, which in turn can negatively impact dam and calf health, or even risk the survival of both (Dillon et al., 2015).

Intensive genetic selection can lead to reduction in genetic variability within a population; consequently, heritability and improvement by selection for traits under intensive selection is low (Falconer and Mackay, 1996). The use of crossbreeding may improve low heritability traits in progeny due to hybrid vigor effects.

1.5. Reciprocal Cross Differences for Growth and Carcass-Related Traits

The increase in birth weight, due to what some have previously considered being hybrid vigor, has shown to be unequal depending on the type of cross between *Bos*

indicus and *Bos taurus* as sire or dam breeds (description of crosses will indicate sire breed first followed by dam breed). Cartwright et al. (1964) evaluated birth weight differences between Brahman (*Bos indicus*) and Hereford (*Bos taurus*) reciprocal crosses (Brahman x Hereford dams and Hereford x Brahman). Cartwright et al. (1964) were the first to report higher birth weights of calves produced by Brahman sires and Hereford dams (37.8 kg) than calves produced by the reciprocal cross (29.1 kg). Other authors have found the same trend when evaluating other crosses of *Bos taurus* and *Bos indicus* breeds (Paschal et al., 1991; Chase et al., 2000; Holloway et al., 2002). This inheritance has been reported in studies evaluating *Bos indicus-Bos taurus* crossbred animals when the sire had a higher amount of *Bos indicus* in its genetic composition in relation to the amount of *Bos indicus* in the dam (Cartwright et al., 1964; Amen et al., 2007a).

Another unexplained characteristic of *Bos indicus* x *Bos taurus* crosses has been sexual dimorphism for birth weight: male calves produced by *Bos indicus* sires and *Bos taurus* dams had much larger birth weights than female calves (Cartwright et al., 1964). This sex difference is much greater than what is observed for calves out of the reciprocal cross (*Bos taurus* x *Bos indicus*), and those of *Bos taurus* x *Bos taurus* or *Bos indicus* x *Bos indicus* crosses (Long and Gregory, 1974; Thallman et al., 1993; Holloway et al., 2002; Riley et al., 2007; Bazzi, 2011; Fuad et al., 2014; Dillon et al., 2015). Thallman et al. (1993) first identified differences in birth weight between embryo transfer Brahman x Simmental (*Bos taurus*) calves that were twice as large between males and females as compared to Simmental x Brahman calves. Riley et al. (2007) evaluated crosses involving Angus, Romosinuano (tropically adapted *Bos taurus*) and Brahman, and found

Brahman x Angus calves expressed the greatest sexual dimorphism (males 5.7 kg heavier) in comparison to Brahman x Brahman (2.5 kg), Angus x Angus (1.8 kg), Angus x Brahman calves (-0.8 kg, with females heavier), Romosinuano x Angus calves (2.2 kg), and Angus x Romosinuano calves (1.7 kg). Brahman x Simmental male calves were 5 kg heavier at birth than female calves; Simmental x Brahman male calves only 0.7 kg heavier than females (Dillon et al., 2015). The sex difference in birth weight of *Bos indicus* x *Bos taurus* calves is much higher than that reported for *Bos indicus* breeds such as purebred Sistani (1.9 kg; Bazzi, 2011) and purebred Kedah-Kelantan cattle (0.77 kg; Fuad et al., 2014).

Reciprocal cross differences have been observed for weaning weight. Thallman et al. (1993) reported that Brahman x Simmental calves were x 23.7 kg heavier at weaning than Simmental x Brahman calves. Amen et al. (2007a) used information from backcrosses between F_1 Angus x *Bos indicus* (Brahman or Nellore) sires and dams to Angus, and *Bos indicus* animals, in order to assess the reciprocal backcross effects on weaning weight. Backcross animals whose sire had a greater percentage of *Bos indicus* in comparison to the dam (F_1-Angus and *Bos indicus*-F_1 animals) tended to be about 10 kg heavier at weaning (Amen et al., 2007a).

Sexual dimorphism differences for weaning weight have been observed in *Bos indicus* x *Bos taurus*. Studies using Brahman x Romosinuano (*Bos taurus* criollo breed), and Brahman x Angus reciprocal crosses indicated that sex difference (males – females) in Brahman-sired crosses was higher than the reciprocal crosses. These calf sex differences were 17.3 kg for Brahman x Romosinuano, 6.3 kg for Romosinuano x

Brahman, 17.4 kg for Brahman x Angus, and 11.2 kg for Angus x Brahman (Riley et al., 2007).

Other traits of *Bos indicus* x *Bos taurus* reciprocal crosses and backcrosses may have similar patterns of means as those for birth weight. Brown et al. (1993) reported yearling weights 18.7 kg heavier in Brahman x Angus calves than in Angus x Brahman calves. Amen et al. (2007b) found that carcasses in backcross animals whose sire had a greater percentage of *Bos indicus* in comparison to the dam (F_1-Angus and *Bos indicus*-F_1 animals) than the reciprocal crosses (Angus-F_1 and F_1-*Bos indicus* animals) tended to be heavier. F_1-Angus had carcasses that were 7.5 kg heavier than those of Angus- F_1, and *Bos indicus*-F_1 steers had carcasses 18.1 kg heavier than those of F_1-*Bos indicus* steers; however, these differences were not statistically significant. No similar trend was observed between reciprocal backcrosses for longissimus muscle area, intramuscular fat, and tenderness (Amen et al., 2007b).

1.6. Potential Parental Effects Over Reciprocal Crosses Differences

Differences observed between *Bos indicus* x *Bos taurus* reciprocal crosses were originally thought to be a consequence of maternal effects and were documented in natural service calves where the genetic dam also provided the uterine environment for the calf. However, research in embryo transfer calves has shown that the same patterns of reciprocal differences exist for birth weight (Thallman et al., 1993; Amen et al., 2007a; Dillon et al., 2015).

The inheritance of some growth-related traits in *Bos indicus* x *Bos taurus* reciprocal crosses does not follow the classical Mendelian pattern (Thallman et al.,

2014), where the expectation would be to have a similar phenotypic expression for these traits in animals sharing the same breed proportions in their genetic composition and subjected to similar environmental effects. Among the possible explanations for phenotypic differences observed between heterozygotes with an equal genetic contribution from both paternal breeds, is the hypothesis of differential expression of alleles depending inheritance from the male or female parent, a phenomenon known as parent-of-origin effect (Loschiavo et al., 2007; Vrana, 2007). This type of differential allele expression may be caused by genomic imprinting, where epigenetic modifications in DNA can trigger the complete or partial silencing of specific alleles (Reik and Walter, 2001; Li, 2002; Vrana, 2007; Shorter et al., 2012). In many situations the maternal genotype is confounded with progeny genotype, and it is difficult to distinguish maternal effects from parent-of-origin effects.

It has been observed in different livestock species that the main traits reported being under parent-of-origin control, through genomic imprinting, have been those associated with growth, development and behavior (Reik et al., 2003; Kim et al., 2007; Vrana, 2007), with results consistent with the observed differences in growth-related traits between *Bos indicus* x *Bos taurus* reciprocal crosses (Imumorin et al., 2011).

Clearly, parental breed composition has an impact over both phenotype and genotype of animals. A novel paradigm may be needed to examine the effect of different combinations of parental breeds involving *Bos taurus* and/or *Bos indicus* breeds on the additive genetic component of progeny. Such a novel approach could prove useful as information for selecting parents for use in specific crosses.

1.7. Genotype-Environment Interactions

The efficiency and profitability of a beef cattle operation are influenced by inheritance and by many non-genetic factors, such as feeding strategies, input costs, and various physical environmental conditions. The biological type, breed, family, or genotypes may interact with the production environment (Herring, 2014). Animals from the same breed, but reared under different environments could have differential expression of their genetic potential, leading to differences in their phenotypic performance (Butts et al., 1971; Souza et al., 2005). It may be beneficial to predict genetic merit for economically important traits relative to specific environments, especially when the genetic resources may be utilized in widely different environments.

Genotype-environment interactions can be of two forms: a change in scale across environments, or as a change in rank of animal phenotypes in different environments (Falconer and Mackay, 1996). Change in scale refers to an increase or reduction of the performance differences between genetic types when evaluated across 2 or more environments; the change in ranking indicates that some animals may outperform others in one environment but will underperform others in another environment. When considering genotype-environment interactions in the literature, "genotype" may refer to any non-environmental factor such as species, breed, family, or actual genomic genotype, and "environment" may indicate any non-genetic factor such as geographical location, or management aspects such as grazing system or parasite control.

Burns et al. (1979) reported genotype-environment interactions in Hereford cattle for birth weight, pre-weaning gain, estimated 205 d weight, body length, body condition

score, and annual production per cow. In that study Hereford cattle that had been in Florida and Montana for several generations, cattle from both groups were exchanged and both groups were evaluated in both locations. Hayes et al. (2016) supported the usefulness of incorporating genotype-environment interactions into livestock genetic evaluations, where genotypes could be evaluated as cattle subspecies (*Bos indicus* vs. *Bos taurus*), breeds, individual animals, or genotypes based on single nucleotide polymorphisms, and environments could be assessed as a variety of variables, either categorical (country, farming system, tropical vs. temperate climate, etc.) or continuous (temperature, humidity, altitude, average production level, average disease level, etc.).

Genetic variation within breed subpopulations reared in unique environments may have small to large differences depending upon the specific environment descriptor (Hayes et al., 2016). As an example, heritability for stayability (defined as cows having a calf at age 4 given they had a calf at age 2) in Red Angus ranged from 0.10 to 0.57 when evaluated across 9 regions defined by temperature and humidity indices within the United States (Fennewald et al., 2018). Distinct levels of genetic variation in different environments may lead to imprecise estimates of breeding values if predictions fail to account for the genotype-environment interaction.

1.8. Modeling of Genotype-Environment Interactions in Genetic Evaluations

Different modeling strategies have been used to account for genotype-environment interactions in livestock species. Those include the use of environmental groups such as country of origin (Wiggans and Van Vleck, 1978; Carabano et al., 1989; Stanton et al., 1991; De Mattos et al., 2000), herds across countries (Peterson, 1988;

Charagu and Peterson, 1998; Mwansa and Peterson, 1998), feed strategies (Brown et al., 1997; Cromie et al, 1998), or production levels (McDaniel and Corley, 1967). This approach makes it possible to identify scaling effects across environments, as well as potential changes in rankings of sires across environments (Falconer and Mackay, 1996).

The environment may be described as a continuous variable than as a categorical variable (Hayes et al., 2016). Random regression procedures are a different alternative to account for genotype-environment interactions in prediction models. Random regressions are also known as reaction norms. In such analyses, animal phenotype (or the additive genetic component of phenotypes) are regressed on a random covariate that represents an environmental gradient (Schaeffer, 2004; Bryant et al., 2005; Kolmodin et al., 2002). This procedure models these interactions, and may result in greater levels of precision for parameter estimates and genetic merit predictions (Cardoso et al., 2012; Kang et al., 2016).

The selection of appropriate random covariates is critical to obtain meaningful results in genetic parameter estimation and predictions of breeding values when using random regression. Two main random covariate categories have been reported in the literature: 1) deviations from the mean productive performance for a particular trait in a given environment (Falconer and Mackay, 1996; Kolmodin et al., 2002), and 2) continuous variables associated with environment descriptors that follow a gradient, such as temperature, humidity, rainfall, feed level, among others (Hammami et al., 2009; Hayes et al., 2016).

Kolmodin et al., (2002) identified the presence of genotype-environment interactions for protein production and days open in dairy cows, using random regression methodology and 4 Nordic dairy cattle breeds. When traits were regressed on deviations from herd-year averages across different countries, re-ranking of sires occurred, especially between the extreme environments (herd-year average ± 2.5 SD; Kolmodin et al., 2002). Pégolo et al. (2009) identified genotype-environment interactions for 450 d weight in Brazilian Nellore cattle, using standardized deviations from contemporary groups averages as the environmental variable. The latter experiment showed how re-ranking of sires not only could be observed when genotype-environment interactions are evaluated between countries, but also within the country (Pégolo et al., 2009).

Genotype-environment interactions have been investigated in the form of sire-environment interactions. Among these interactions, sire-sex interactions were investigated for growth and carcass traits in Hereford (Koger and Knox, 1945; Pahnish et al., 1961; Thrift et al., 1970), Polled Hereford (Wilson et al., 1969), Angus (Tanner et al., 1970), Simmental (Buchanan and Nielsen, 1979; Garrick et al., 1989) and Maine-Anjou (Buchanan and Nielsen, 1979). Significant sire-sex interactions were reported for birth weight and weaning weight in Simmental and Maine-Anjou (Buchanan and Nielsen, 1979) and in Simmental-influenced cattle (Garrick et al., 1989). Garrick et al. (1989) reported significant sire-sex interactions for post weaning gain in Simmental-influenced cattle. Sire-sex interactions are not included in most genetic evaluations, probably due to predominantly negative results and/or due to their modest practical effects (Notter et al., 1992).

Since genotype-environment interactions can affect many traits related to productivity and profitability of cattle operations and that favorable genes in some environments may not be equally beneficial in others (Via et al., 1995), it is important to identify "plastic" and "robust" genotypes among sires. A "plastic" genotype is one that corresponds to highly variable phenotypes across environments. "Robust" genotypes consistently result in phenotypes that have low variability across environments (De Jong et al., 2002). Selection of sires with robust genotypes would make it possible to increase the frequency of genes associated to adaptability across environments. Identification of plastic sires and the environments where their daughters will best perform would be of high value for beef producers.

1.9. Additive by Non-Additive Genetic Interactions

Improvement of economically relevant traits in beef cattle has followed two strategies, selection and crossbreeding (Herring, 2014). Selection is based on the ability of animals to transmit favorable genes into their progeny (Falconer and Mackay, 1996; Herring, 2014). Crossbreeding between different cattle breeds make it possible to realize benefits from hybrid vigor in progeny and dams (Cartwright, 1970; Falconer and Mackay, 1996; Herring, 2014).

Non-additive genetic effects have been widely studied for beef and dairy cattle; however, interactions between non-additive genetic effects and additive genetic effects has been limited to evaluate sire combining ability, in order to control inbreeding in a population (Allaire and Henderson, 1965; Henderson, 1989; DeStefano and Hoeschele, 1992). Crossbreeding is a widely used improvement strategy in many parts of the world.

Parameterization and characterization of its potential interaction with the additive genetic component may represent a new way of thinking in genetic improvement.

1.10. Summary

Different sources of variation influence phenotypic performance in beef cattle with either short- or long-term consequences. The interactions of genotype and environmental descriptors, and genotypes with parental breed crossbreeding may influence animal phenotype.

Genetic merit prediction equations incorporate relevant environmental factors, as well as non-additive genetic descriptors when crossbreed populations are evaluated in order to make accurate and useful predictions. Such interactions have not been considered within current livestock genetic prediction efforts. The use of categorical variables, random regression procedures, or a combination of both may help to improve genetic merit predictions and parameter estimation.

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CHAPTER II

INVESTIGATION OF SIRE BY PROGENY SEX INTERACTIONS FOR GROWTH-RELATED TRAITS AND INTRAMUSCULAR FAT IN DROUGHTMASTER CATTLE

2.1. Introduction

Productivity and profitability of beef cattle operations are influenced by several factors, some of which are more directly associated with genetics, and others are more related to non-genetic or environmental effects (Falconer and Mackay, 1996).

Crossbreeding between *Bos taurus* and *Bos indicus* breeds has been widely used in beef cattle operations to achieve large hybrid vigor (heterosis) effects in many economically relevant traits, due to the large genetic divergence between these two cattle subspecies (MacHugh et al., 1997). Droughtmaster is an example of a composite *Bos taurus-Bos indicus* breed (50% Shorthorn and 50% Brahman), which has its origin in northern Queensland, Australia. This tropically adapted breed is suitable to perform under the climate conditions of northern Australia (Droughtmaster Stud Breeders Society, 2019).

Some environmental factors may interact directly with animal genotype, modulating its expression and the phenotypic performance of economically relevant traits (Burns et al., 1979; Hayes et al., 2016; Fennewald et al., 2017). Some sires are used as breeders in widely different environments, and these genotype-environment

interactions may introduce bias for expected progeny performance (Butts et al., 1971; Souza et al., 2005).

From the late 1970s to mid 1990s genotype-environment interactions were investigated primarily as sire additive genetic merit with herd effects and/or region effects. Tess et al. (1979) found significant interaction effects between sire and herd within regions in the USA for weaning weight in Simmental cattle, and a near significant interaction between sire and region. Similarly, Bertrand et al. (1985) identified a significant interaction between sire and herd, as well as interaction between sires and regions within the USA for weaning weight using Polled Hereford records. Similar results were also identified in Australian Angus cattle, where significant sire by herd interactions were found for weaning weight (Notter et al., 1992).

Interactions between sire and year have also been described for weaning weight in Simmental cattle. The inclusion of this interaction in the prediction equation reduced the additive genetic covariance between the direct and maternal genetic component by 62%, reducing the magnitude of the genetic correlation between these components (Lee and Pollak, 1997).

Previously, from the mid-1940s to late 1980s, researchers investigated the effect of sire by sex interaction on growth and carcass traits in Hereford (Koger and Knox, 1945; Pahnish et al., 1961; Thrift et al., 1970), Polled Hereford (Wilson et al., 1969), Angus (Tanner et al., 1970), Simmental (Buchanan and Nielsen, 1979; Garrick et al., 1989) and Maine-Anjou (Buchanan and Nielsen, 1979) cattle in the USA. Sire-sex interaction was mostly found to be not significant in these studies, with exception for

birth weight and weaning weight in American Simmental and American Maine-Anjou (Buchanan and Nielsen, 1979), as well as in Simmental-influenced cattle (Garrick et al., 1989). Additionally, Garrick et al. (1989) identified significant sire-sex interaction for post weaning gain in Simmental-influenced cattle.

Since 1990 the scientific community stopped researching sire-sex interaction in cattle, as studies shown predominant non-significant results or modest practical effects for this interaction (Notter et al., 1992).

Many assume that genetic prediction comparisons among sires should be the same in purebred and in crossbred progeny. Composite breeds that are based on *Bos taurus*-*Bos indicus* crossbred foundations may useful to evaluate for potential sire interactions.

In Droughtmaster cattle, sire-sex interactions are a potential influence that could introduce bias in genetic merit predictions if they exist but are not considered in prediction equations. Assessment of the presence of sire-sex interactions for growth and carcass traits within this composite breed could help identify robust sires whose progeny could perform better for a given trait in all sex categories (Via and Lande, 1985; Agrawal, 2001; De Jong et al., 2002).

The objective of this study was to assess the presence of sire-sex interactions for weights at branding, weaning, and ultrasound scan, as well as for intramuscular fat in Droughtmaster heifers, steers and intact males. Single trait models and all potential bivariate model alternatives between these 4 traits (6 in total) were evaluated using 2 different modeling strategies: 1) modeling the random effect of sire within progeny sex

category, and, 2) modeling a linear random regression of sire genotype on progeny sex category.

2.2. Materials and Methods

2.2.1. Records

Weight traits and ultrasound measurements of carcass quality were obtained from a single Australian Droughtmaster operation across 4 years (2009 to 2012). Weights were recorded at branding (BRW; average age 125 d), weaning (WW; average age of 200 d), and at time of ultrasound measurement (ULW; average age of 546 d). Ultrasound measurement under evaluation was intramuscular fat percentage (IMF; recorded at an average age of 550 d). Records with complete information about season of birth, contemporary group, age at measurement, and sex type were kept in the database. Records considered unreasonable biologically were removed. Records greater than 4 SD above or below the mean were considered outliers and removed. The total number of records in the edited data for branding weight, weaning weight, weight at ultrasound measurement, and intramuscular fat were 1,876, 1,352, 1,770, and 1,794, respectively. The pedigree used for the analyses included information from 3,344 animals, with a total of 53 sires represented.

2.2.2. Statistical Analyses

Two set of analyses were performed to assess the potential interaction between sire and progeny sex category. The first set of analysis modeled sex as a categorical variable with 2 levels for BRW and WW analyses (females and intact males), and 3 levels for ULW and IMF analyses (females, steers, and intact males). All males not

selected as bulls were castrated after weaning. In the second set of analyses, sex was modeled as a continuous variable (linear covariate): values of 1 and 2 were assigned to females and intact males, respectively, in BRW and WW analyses; values of 1, 2, and 3 were assigned to females, steers, and intact males, respectively, for ULW and IMF analyses. The total number of records per sex category is indicated in Table 2.1.

Table 2.1. Number of records by sex category for analysis of branding weight, weaning weight, weight at ultrasound measurement, and intramuscular fat

	Sex category		
	Female	Steer	Intact male
Branding weight	884	--	1,032
Weaning weight	884	--	1,032
Weight at ultrasound measurement	884	411	621
Intramuscular fat	884	411	621

For each set of analyses (sex as categorical variable or as linear covariate), single-trait models were assessed for each trait as well as each possible bivariate model (6 in total). Fixed effects in models corresponded to season of birth (categorical), contemporary group (categorical), age in days at measurement (covariate), and sex (categorical or as linear covariate).

Random components for BRW and WW models corresponded to maternal additive genetic effect, and the interaction between sire and progeny sex category or the a linear random regression of sire on progeny sex category (first order Legendre polynomial), depending if sex was used as categorical variable or as linear covariate in the fixed component of the models, respectively. For ULW and IMF analyses, the

random component was as described for BRW and WW but without including maternal additive genetic effects.

2.2.2.1. Single-Trait Models with Sex as Categorical Variable

The single-trait models for BRW and WW using sex as categorical variable followed the form:

$$y = X\beta + Zu + Wc + e$$

where *y* was a vector of BRW or WW records, β was the vector of estimated fixed effects, *u* was the vector of random additive genetic effects for sires within each level of sex in the model, *c* was the vector of additive genetic effects of the dam, *e* was the vector of residuals, and *X*, *Z*, and *W* were incidence matrices relating observations in *y* to values in β, *u*, and *c* vectors, respectively.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows:

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G_F & G_{FM} & 0 & 0 \\ G_{FM} & G_M & 0 & 0 \\ 0 & 0 & C & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

in which $G_F = A\sigma^2_{a_F}$, $G_M = A\sigma^2_{a_M}$, $G_{FM} = A\sigma_{(a_F,a_M)}$, where *A* was the numerator relationship matrix constructed with the pedigree information, $\sigma^2_{a_F}$ is the additive genetic variance for sires when progeny is female, $\sigma^2_{a_M}$ is the additive genetic variance for sires when progeny is intact male, and $\sigma_{(a_F,a_M)}$ is the additive genetic covariance between sires when progeny is female and when progeny is intact male; $C = A\sigma^2_c$, where σ^2_c is the additive genetic variance for dams; $R = I\sigma^2_e$, and σ^2_e is the residual variance.

The single-trait models for ULW and IMF using sex as categorical variable followed the form:

$$y = X\beta + Zu + e$$

where *y* was a vector of ULW or IMF records, β was the vector of estimated fixed effects, *u* was the vector of random additive genetic effects for sires within each level of sex in the model, *e* was the vector of residuals, and *X* and *Z* were incidence matrices relating observations in *y* to values in β, and *u*.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follow:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G_F & G_{FS} & G_{FM} & 0 \\ G_{FS} & G_S & G_{SM} & 0 \\ G_{FM} & G_{SM} & G_M & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

in which components as described previously in addition to $G_S = A\sigma^2_{a_S}$, $G_{FS} = A\sigma_{(a_F,a_S)}$, and $G_{SM} = A\sigma_{(a_S,a_M)}$, where $\sigma^2_{a_S}$ is the additive genetic variance for sires when progeny is steer, $\sigma_{(a_F,a_S)}$ is the additive genetic covariance between sires when progeny is female and when progeny is steer, and $\sigma_{(a_S,a_M)}$ is the additive genetic covariance between sires when progeny is steer and when progeny is intact male.

2.2.2.2. Bivariate Models with Sex as Categorical Variable

Bivariate models using sex as categorical variable and including BRW and WW followed the form:

$$y = X\beta + Zu + Wc + e$$

where *y* corresponded to the vector of BRW and WW records; β was the vector of fixed effects for BRW and WW; u was the vector of sire additive genetic effects for BRW and WW; c was the vector of maternal additive genetic effects for BRW and WW; e was the vector of residual effects for BRW and WW records; X, Z, W are incidence matrices relating BRW and WW values in *y* to corresponding effects in β, u, and c.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G_{BRW_F} & & & & & & & \\ G_{BRW_{(F,M)}} & G_{BRW_M} & & & & & & \\ G_{(BRW_F,WW_F)} & G_{(BRW_M,WW_F)} & G_{WW_F} & & & & & \\ G_{(BRW_F,WW_M)} & G_{(BRW_M,WW_M)} & G_{WW_{(F,M)}} & G_{WW_M} & & & & \\ 0 & 0 & 0 & 0 & C_{BRW} & & & \\ 0 & 0 & 0 & 0 & C_{(BRW,WW)} & C_{WW} & & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{BRW} & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{(BRW,WW)} & R_{WW} \end{bmatrix}$$

where BRW and WW subscripts indicate branding weight and weaning weight variance and covariance components. Components G, C, and R were described previously, and now are included in covariances as well.

Bivariate models using sex as categorical variable and including BRW or WW (V1) with either ULW or IMF (V2) followed the form:

$$y = X\beta + Zu + Wc + e$$

where *y* corresponded to the vector of V1 and V2 records; β was the vector of fixed effects for V1 and V2; u was the vector of sire additive genetic effects for V1 and V2; c was the vector of maternal additive genetic effects for V1; e was the vector of residual effects for V1 and V2 records; X, Z, W were incidence matrices relating V1 and V2 values in *y* to corresponding effects in β, u, and c.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G_{V1_F} & & & & & & & \\ G_{V1_{(F,M)}} & G_{V1_M} & & & & & & \\ G_{(V1_F,V2_F)} & G_{(V1_M,V2_F)} & G_{V2_F} & & & & & \\ G_{(V1_F,V2_S)} & G_{(V1_M,V2_S)} & G_{V2_{(F,S)}} & G_{V2_S} & & & & \\ G_{(V1_F,V2_M)} & G_{(V1_M,V2_M)} & G_{V2_{(F,M)}} & G_{V2_{(S,M)}} & G_{V2_M} & & & \\ 0 & 0 & 0 & 0 & 0 & C_{V1} & & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{V1} & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{(V1,V2)} & R_{V2} \end{bmatrix}$$

where V1 and V2 subscripts indicate branding weight or weaning weight and weight at ultrasound measurement or intramuscular fat variance and covariance components, respectively. G, C, and R as described previously, with the addition of covariances within G, and R components.

Bivariate models using sex as categorical variable and including ULW and IMF followed the form:

$$y = X\beta + Zu + e$$

where *y* corresponded to the vector of ULW and IMF records; β was the vector of fixed effects for ULW and IMF; u was the vector of sire additive genetic effects for ULW and IMF; e was the vector of residual effects for ULW and IMF records; X and Z are incidence matrices relating ULW and IMF values in *y* to corresponding effects in β, and u.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G_{ULW_F} & & & & & & & \\ G_{ULW_{(F,S)}} & G_{ULW_S} & & & & & & \\ G_{ULW_{(F,M)}} & G_{ULW_{(S,M)}} & G_{ULW_M} & & & & & \\ G_{(ULW_F,IMF_F)} & G_{(ULW_S,IMF_F)} & G_{(ULW_M,IMF_F)} & G_{IMF_F} & & & & \\ G_{(ULW_F,IMF_S)} & G_{(ULW_S,IMF_S)} & G_{(ULW_M,IMF_S)} & G_{IMF_{(F,S)}} & G_{IMF_S} & & & \\ G_{(ULW_F,IMF_M)} & G_{(ULW_S,IMF_M)} & G_{(ULW_M,IMF_M)} & G_{IMF_{(F,M)}} & G_{IMF_{(S,M)}} & G_{IMF_M} & & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{ULW} & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{(ULW,IMF)} & R_{IMF} \end{bmatrix}$$

where ULW and IMF subscripts indicate weight at ultrasound measurement and intramuscular fat variance and covariance components, respectively. G and R as matrices and covariance components described previously.

2.2.2.3. Single-Trait Models with Sex as Random Linear Covariate

The single-trait models for BRW and WW using a random linear regression to model sex followed the form:

$$y = X\beta + Zu + Wc + e$$

where *y* was a vector of BRW or WW records, *u* was the vector of random regression coefficients for sire additive genetic effects, and *β*, *c*, *e*, *X*, *Z*, and *W* as described for BRW and WW models using sex as categorical variable.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follow:

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & C & 0 \\ 0 & 0 & R \end{bmatrix}$$

where *G* was the covariance matrix of additive genetic regression coefficients with order 2 (intercept and linear random regression coefficient), and *A*, *C* and *R* as described previously for BRW and WW models. The *G* matrix used in the linear random regression models included the estimation of the variances and covariances of the intercept and the regression coefficient.

The single-trait models for ULW and IMF using sex as linear covariate followed the form:

$$y = X\beta + Zu + e$$

where *y* was a vector of ULW or IMF records, u, β, e, X, and Z as described previously for BRW and WW models using sex as linear covariate.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follow:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 \\ 0 & R \end{bmatrix}$$

where G, A, and R as described for BRW and WW models using sex as linear covariate.

2.2.2.4. Bivariate Models with Sex as Random Linear Covariate

Bivariate model using sex as random linear covariate and including BRW and WW followed the form:

$$y = X\beta + Zu + Wc + e$$

where *y* corresponded to the vector of BRW and WW records; β was the vector of fixed effects for BRW and WW; u was the vector of random regression coefficients for sire additive genetic effects; c was the vector of maternal additive genetic effects for BRW and WW; e was the vector of residual effects for BRW and WW records. As before, X, Z, and W were incidence matrices relating BRW and WW values in *y* to corresponding effects in β, u, and c.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G_{BRW_{\beta_0}} & & & & & & & \\ G_{BRW_{(\beta_0,\beta_1)}} & G_{BRW_{\beta_1}} & & & & & & \\ G_{(BRW_{\beta_0},WW_{\beta_0})} & G_{(BRW_{\beta_1},WW_{\beta_0})} & G_{WW_{\beta_0}} & & & & & \\ G_{(BRW_{\beta_0},WW_{\beta_1})} & G_{(BRW_{\beta_1},WW_{\beta_1})} & G_{WW_{(\beta_0,\beta_1)}} & G_{WW_{\beta_1}} & & & & \\ 0 & 0 & 0 & 0 & C_{BRW} & & & \\ 0 & 0 & 0 & 0 & C_{(BRW,WW)} & C_{WW} & & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{BRW} & \\ 0 & 0 & 0 & 0 & 0 & 0 & R_{(BRW,WW)} & R_{WW} \end{bmatrix}$$

where BRW and WW subscripts indicate branding weight and weaning weight variance and covariance components, respectively. G, C, and R as described previously, with the addition of covariances within G, C, and R components. Subscripts β_0 and β_1 indicate variance and covariance components associated to random intercept and to linear random regression coefficient, respectively.

Bivariate models using sex as random linear covariate and including BRW or WW (V1) with either ULW or IMF (V2) followed the form:

$$y = X\beta + Zu + Wc + e$$

where y corresponded to the vector of V1 and V2 records; β is the vector of fixed effects for V1 and V2; u was the vector of random regression coefficients for sire additive genetic effects; c was the vector of maternal additive genetic effects for V1; e is the vector of residual effects for V1 and V2 records; X, Z, W are incidence matrices relating V1 and V2 values in y to corresponding effects in β, u, and c.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G_{V1_{\beta_0}} & & & & & & \\ G_{V1_{(\beta_0,\beta_1)}} & G_{V1_{\beta_1}} & & & & & \\ G_{(V1_{\beta_0},V2_{\beta_0})} & G_{(V1_{\beta_1},V2_{\beta_0})} & G_{V2_{\beta_0}} & & & & \\ G_{(V1_{\beta_0},V2_{\beta_1})} & G_{(V1_{\beta_1},V2_{\beta_1})} & G_{V2_{(\beta_0,\beta_1)}} & G_{V2_{\beta_1}} & & & \\ 0 & 0 & 0 & 0 & C_{V1} & & \\ 0 & 0 & 0 & 0 & 0 & R_{V1} & \\ 0 & 0 & 0 & 0 & 0 & R_{(V1,V2)} & R_{V2} \end{bmatrix}$$

where V1 and V2 subscripts indicate branding weight or weaning weight and weight at ultrasound measurement or intramuscular fat variance and covariance components, respectively, and all other terms as previously described.

Bivariate models using sex as random linear covariate and including ULW and IMF followed the form:

$$y = X\beta + Zu + e$$

where *y* correspond to the vector of ULW and IMF records; β was the vector of fixed effects for ULW and IMF; u was the vector of random regression coefficients for sire additive genetic effects; e was the vector of residual effects for ULW and IMF records; X, and Z are incidence matrices relating ULW and IMF values in *y* to corresponding effects in β, and u.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follows (matrix is symmetric; only diagonal elements on lower triangle of covariance terms presented):

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G_{ULW_{\beta_0}} & & & & & \\ G_{ULW_{(\beta_0,\beta_1)}} & G_{ULW_{\beta_1}} & & & & \\ G_{(ULW_{\beta_0},IMF_{\beta_0})} & G_{(ULW_{\beta_1},IMF_{\beta_0})} & G_{IMF_{\beta_0}} & & & \\ G_{(ULW_{\beta_0},IMF_{\beta_1})} & G_{(ULW_{\beta_1},IMF_{\beta_1})} & G_{IMF_{(\beta_0,\beta_1)}} & G_{IMF_{\beta_1}} & & \\ 0 & 0 & 0 & 0 & R_{ULW} & \\ 0 & 0 & 0 & 0 & R_{(ULW,IMF)} & R_{IMF} \end{bmatrix}$$

where subscripts indicate ULW and IMF variance and covariance components, respectively, and additional terms as previously described.

2.2.2.5. Animal Models

In addition to the single-trait and bivariate models, two animal models were evaluated for each trait; first, using sex as a fixed categorical variable, and then with sex as fixed linear covariate.

Models for BRW and WW had the following form:

$$y = X\beta + Zu + Wc + e$$

where *y* was the vector of BRW or WW records; β was the vector of fixed effects; u was a vector animal breeding values; c was the vector of maternal additive genetic effects; e was the vector of residual effects; *X*, *Z*, and *W* were incidence matrices relating BRW or WW values in *y* to corresponding effects in β, u, and c.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follow:

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ cov_{(G,C)} & C & 0 \\ 0 & 0 & R \end{bmatrix}$$

in which $G = A\sigma_a^2$, $C = A\sigma_c^2$, $cov_{(G,C)} = A\sigma_{(a,c)}$, where *A* was the numerator relationship matrix constructed with the pedigree information, σ_a^2 was the animal additive genetic variance, σ_c^2 was the maternal additive genetic variance, and $\sigma_{(a,c)}$ was the additive genetic covariance between the animal and maternal additive genetic effects; $R = I\sigma_e^2$, and σ_e^2 was the residual variance.

Models for ULW and IMF had the following form:

$$y = X\beta + Zu + e$$

where y was the vector of ULW or IMF records; β, u, e, X, and Z as described for BRW and WW animal models.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as follow:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}$$

in which G and R as described for BRW and WW animal models.

2.2.2.6. Analytical Tools

Analyses were performed using ASReml (Gilmour et al., 2009). Additionally, sire variance proportion (proportion of the phenotypic variance explained by the sire additive genetic variance), Pearson correlation coefficients between sire effects across sex categories, and corresponding SE were calculated directly using ASReml. Variance component estimates from the linear random regression of sire on progeny sex were used to plot gradients of sire variance proportions for each trait (Schaeffer, 2016) in single-trait and bivariate models.

2.2.2.7. Likelihood-Ratio Tests

Likelihood-ratio tests were conducted between final single-trait or bivariate models and reduced model counterparts to determine if sire-sex interaction was significant to incorporate in the models ($P < 0.05$). Random components in reduced models included the additive genetic effect of the sire (for BRW, WW, ULW and IMF

related models), and the additive genetic effect of the dam (for BRW and WW related models).

2.3. Results

2.3.1. Analyses Using Sex as Categorical Variable

2.3.1.1. Branding Weight Models

Preliminary analyses for the single trait model indicated that season of birth was not significant ($P = 0.08$) and, therefore, it was not kept in final models of any kind. Fixed effects included in the final models for BRW were contemporary group, age at measurement, and sex (categorical). Sire variance by sex as proportions of the phenotypic variance for BRW from single-trait model and bivariate models are presented in Table 2.2. These were similar in magnitude for each sex and model.

Table 2.2. Sire variance proportion (Sh^2) estimates for branding weight across models[1] using sex as categorical variable

	Models			
Parameter	Single-trait	BRW-WW	BRW-ULW	BRW-IMF
Sh^2 Female[2]	0.06 ± 0.02	0.07 ± 0.03	0.07 ± 0.03	0.07 ± 0.03
Sh^2 Intact male	0.06 ± 0.02	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02
Sh^2 RM	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sire variance proportion when progeny is female, intact male, or estimated with the reduced model (RM; sire and maternal additive effects as unique random components); for reference, heritability estimated from animal model was 0.26 ± 0.08.

Correlations between sire effects across sex categories for single-trait model and bivariate models are presented in Table 2.3. Across models, high correlations were obtained between sire effects when progeny is female and when progeny is intact male, ranging from 0.95 to 0.99.

Table 2.3. Pearson correlation coefficients between sire effects within females and intact males (r F-M) for branding weight across models

	Models[1]			
Parameter	Single-trait	BRW-WW	BRW-ULW	BRW-IMF
r F-M	0.95 ± 0.14	0.99 ± 0.12	0.96 ± 0.10	0.98 ± 0.11

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits

2.3.1.2. Weaning Weight Models

Preliminary analyses for the single trait model indicated that season of birth was not significant ($P = 0.20$) and was removed from the final models. Fixed effects in the final models for WW were contemporary group, age at measurement, and sex (categorical).

Sire variance proportion estimates for WW from single-trait model and bivariate models are presented in Table 2.4. Across models, sire variance proportions had similar values within females, and within intact males; additionally, sire variance proportions across models were similar, with sire variance proportion from the reduced models showing a slightly larger range across models (0.08 to 0.11).

Table 2.4. Sire variance proportion (Sh^2) estimates for weaning weight across models using sex as categorical variable

	Models[1]			
Parameter	Single-trait	BRW-WW	WW-ULW	WW-IMF
Sh^2 Female[2]	0.06 ± 0.02	0.08 ± 0.03	0.08 ± 0.03	0.07 ± 0.03
Sh^2 Male	0.06 ± 0.02	0.09 ± 0.03	0.09 ± 0.03	0.07 ± 0.03
Sh^2 RM	0.08 ± 0.03	0.10 ± 0.03	0.11 ± 0.03	0.08 ± 0.03

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sire variance proportion when progeny is female, intact male, or estimated with the reduced model (RM; sire and maternal additive effects as unique random components); for reference, heritability estimated from animal model was 0.29 ± 0.10.

Correlations between sire effects across sex categories for single-trait model and bivariate models were unity in all analyses (Table 2.5).

Table 2.5. Pearson correlation coefficients between sire effects within females and intact males (r F-M) for weaning weight across models

	Models[1]			
Parameter	Single-trait	BRW-WW	WW-ULW	WW-IMF
r F-M	1 ± 0.17	1 ± 0.08	1 ± 0.07	1 ± 0.14

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.

2.3.1.3. Weight at Ultrasound Measurement Models

Preliminary analysis for the single-trait model indicated that season of birth, contemporary group, age at measurement, and sex (categorical) were significant ($P < 0.01$) and, therefore, they were kept in the final analyses for the animal model, single-trait model, and bivariate models including ULW.

Sire variance proportion estimates for ULW from single-trait model and bivariate models are presented in Table 2.6. Across models, the largest estimates of sire variance proportion were obtained within intact males, with the smallest estimates within steers, and with intermediate values within females. Sire variance proportions across models were similar, except for sire variance proportion within intact males, which ranged from 0.14 to 0.21 across models.

Table 2.6. Sire variance proportion (Sh^2) estimates for weight at ultrasound measurement across models using sex as categorical variable

	Models[1]			
Parameter	Single trait	BRW-ULW	WW-ULW	ULW-IMF
Sh^2 Female[2]	0.07 ± 0.02	0.06 ± 0.02	0.07 ± 0.02	0.07 ± 0.02
Sh^2 Steer	0.02 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
Sh^2 Intact male	0.14 ± 0.04	0.21 ± 0.04	0.18 ± 0.03	0.15 ± 0.04
Sh^2 RM	0.12 ± 0.03	0.12 ± 0.03	0.12 ± 0.03	0.12 ± 0.03

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sire variance proportion when progeny is female, steer, intact male, or estimated with the reduced model (RM; sire effect as sole random component); for reference, heritability estimated from animal model was 0.40 ± 0.07.

Correlations between sire effects across sex categories for single-trait model and bivariate models indicated essentially complete correspondence (Table 2.7), regardless of the model or analysis.

Table 2.7. Pearson correlation coefficients between sire effects within females and steers (r F-S), within females and intact males (r F-M), and within steers and intact males (r S-M) for weight at ultrasound measurement across models

	Models[1]			
Parameter	Single-trait	BRW-ULW	WW-ULW	ULW-IMF
r F-S	0.97 ± 0.25	0.98 ± 0.18	0.98 ± 0.18	0.99 ± 0.21
r F-M	0.98 ± 0.12	0.98 ± 0.07	0.98 ± 0.07	0.99 ± 0.11
r S-M	0.97 ± 0.27	0.98 ± 0.18	0.98 ± 0.16	0.98 ± 0.23

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.

2.3.1.4. Intramuscular Fat Models

Preliminary analyses for the single trait model indicated that season of birth, contemporary group, age at measurement, and sex (categorical) were significant ($P < 0.01$) and, therefore, they were included in the final models of all analyses of IMF.

Sire variance proportion estimates for IMF from single-trait model and bivariate models are presented in Table 2.8. Across models, sire variance proportions had similar

values within females, steers, and intact males, with sire variance proportions within intact males being slightly lower than the rest. Estimated sire variance proportions were similar or the same across models.

Table 2.8. Sire variance proportion (Sh^2) estimates for intramuscular fat across models using sex as categorical variable

	Models[1]			
Parameter	Single-trait	BRW-IMF	WW-IMF	ULW-IMF
Sh^2 Female[2]	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02
Sh^2 Steer	0.06 ± 0.02	0.07 ± 0.03	0.06 ± 0.02	0.07 ± 0.02
Sh^2 Intact male	0.05 ± 0.03	0.05 ± 0.03	0.05 ± 0.03	0.05 ± 0.03
Sh^2 RM	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02	0.07 ± 0.02

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sire variance proportion when progeny is female, steer, intact male, or estimated with the reduced model (RM; sire effect as sole random component); for reference, heritability estimated from animal model was 0.25 ± 0.06.

Correlations between sire effects across sex categories for single-trait model and bivariate models are presented in Table 2.9. Across models, high correlations were obtained between sire effects when progeny is female and when progeny is steer, ranging from 0.88 to 0.91. On the other hand, correlations between sire effects when progeny is female and when progeny is intact male were small, ranging from 0.32 to 0.40. Intermediate values were obtained for correlations between sire effects when progeny is steer and when progeny is intact male, with a range of 0.68 to 0.71.

Table 2.9. Pearson correlation coefficients between sire effects within females and steers (r F-S), within females and intact males, and within steer and intact male for intramuscular fat across models

	Models[1]			
Parameter	Single-trait	BRW-IMF	WW-IMF	ULW-IMF
r F-S	0.91 ± 0.17	0.89 ± 0.19	0.88 ± 0.19	0.90 ± 0.18
r F-M	0.40 ± 0.33	0.37 ± 0.34	0.32 ± 0.34	0.39 ± 0.33
r S-M	0.71 ± 0.31	0.70 ± 0.31	0.68 ± 0.31	0.71 ± 0.30

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.

2.3.1.5. Likelihood-Ratio Tests

Results from likelihood-ratio tests between models including sire-sex interaction and equivalent models without the interaction are presented in Table 2.10. Results indicated that sire-sex interaction was significant for BRW-ULW ($P < 0.01$) and for WW-ULW ($P = 0.01$) bivariate models.

Table 2.10. Likelihood-ratio tests between full[1] and reduced[2] models using sex as categorical variable.

	Log-Likelihood		
Models	Full model	Reduced model	*P*-value
Branding weight	-6,229.29	-6,229.03	1
Weaning weight	-4,679.09	-4,679.01	1
Weight at ultrasound measurement	-6,872.24	-6,876.48	0.13
Intramuscular fat	-550.42	-554.62	0.14
BRW-WW[3]	-10,110.20	-10,109.70	1
BRW-ULW	-12,842.13	-12,858.49	< 0.01
BRW-IMF	-6,776.75	-6,782.78	0.44
WW-ULW	-11,237.50	-11,250.10	0.01
WW-IMF	-5,226.56	-5,233.53	0.30
ULW-IMF	-7,417.67	-7,428.16	0.28

[1]With sire-sex interaction in the random component of the model
[2]Without sire-sex interaction in the random component of the model
[3]Bivariate models between branding weight and weaning weight (BRW-WW), branding weight and weight at ultrasound measurement (BRW-ULW), branding weight and intramuscular fat (BRW-IMF), weaning weight and weight at ultrasound measurement (WW-ULW), weaning weight and intramuscular fat (WW-IMF), weight at ultrasound measurement and intramuscular fat (ULW-IMF).

2.3.2. Analyses Using Sex as Random Linear Covariate

2.3.2.1. Branding Weight Models

Preliminary analyses for the single-trait model indicated that season of birth was not significant ($P = 0.09$); therefore, fixed effects in final BRW related models were contemporary group, age at measurement, and sex (linear fixed regression).

Variance and covariance estimates for analyses of BRW are presented in Table 2.11. Estimates of variance for linear random regression coefficient were small in single-trait and BRW-ULW analyses, and practically zero in BRW-WW and BRW-IMF analyses. Sire variance proportion estimates across the gradient of sex categories for analyses of BRW using single-trait and BRW-ULW models are presented in Figure 2.1, as well as sire variance proportion estimate from the corresponding reduced model analysis (without sire-sex interaction, just sire and maternal additive effects as random components). No slope was detected for analyses of BRW using BRW-WW and BRW-IMF models. Estimates for sire variance as a proportion of phenotypic variance from the different analyses of BRW are presented in Table 2.12.

Table 2.11. Estimates of variance from linear random regression analyses of branding weight[1]

	Intercept	Linear	Maternal additive	Residual
Single-trait				
Intercept	**54.01 ± 18.00**			
Linear	-1.55 ± 3.97	**1.10 ± 1.57**		
Maternal additive			**87.88 ± 11.70**	
Residual				**234.59 ± 10.41**
BRW-WW				
Intercept	**23.66 ± 8.86**			
Linear	$-3.64 \times 10^{-10} \pm 0$	**$3.07 \times 10^{-8} \pm 0$**		
Maternal additive			**92.66 ± 11.71**	
Residual				**237.50 ± 10.32**
BRW-ULW				
Intercept	**61.63 ± 19.88**			
Linear	3.30 ± 3.93	**1.35 ± 1.40**		
Maternal additive			**42.14 ± 7.55**	
Residual				**274.23 ± 11.18**
BRW-IMF				
Intercept	**55.06 ± 18.41**			
Linear	$-1.62 \times 10^{-11} \pm 0$	**$3.41 \times 10^{-7} \pm 0$**		
Maternal additive			**87.73 ± 11.65**	
Residual				**234.79 ± 10.34**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of maternal additive effects and residual with other terms were assumed to be 0.

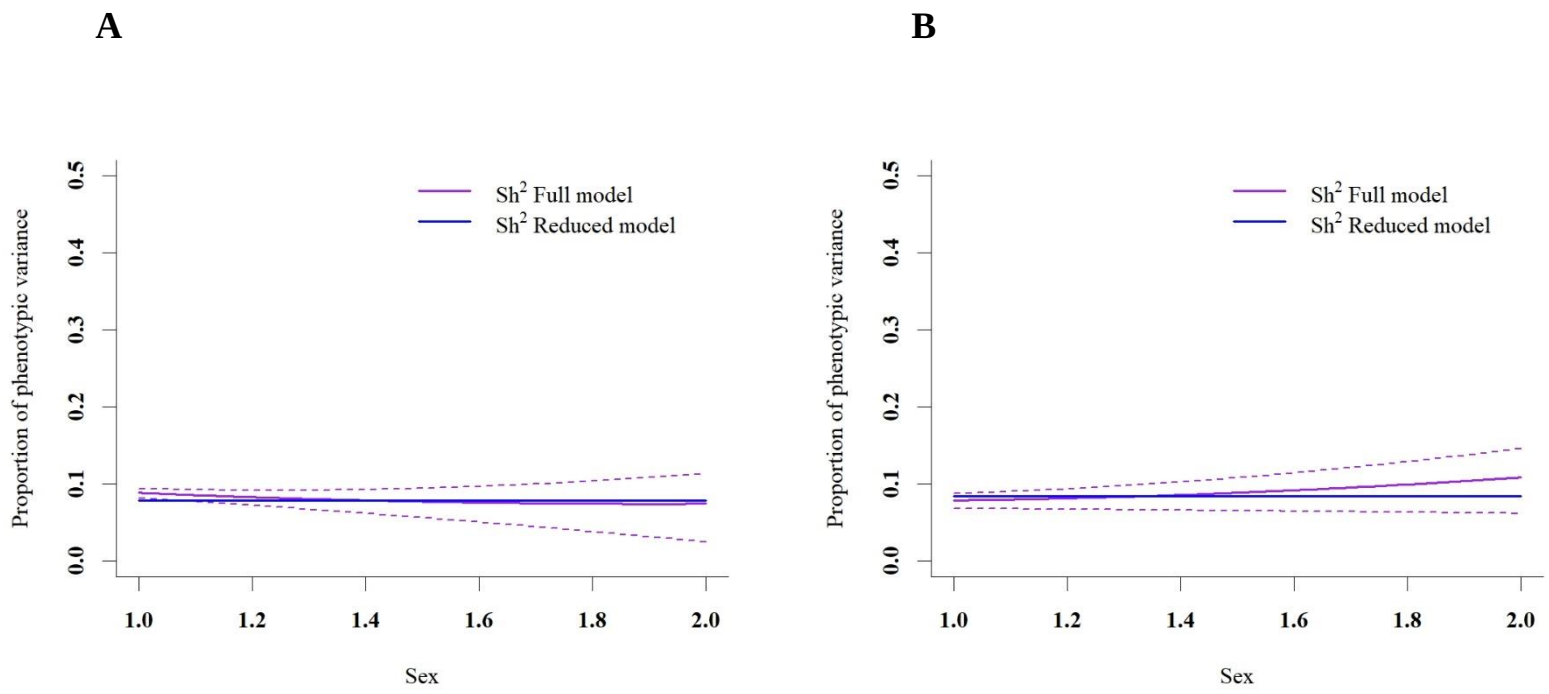

Figure 2.1. Sire variance proportions for branding weight from linear random regression models (Sh^2 Full model; dashed lines indicate ± 1 SE) and sire variance proportion estimates from equivalent models without random sire-sex interaction (Sh^2 Reduced model). A: single-trait model; B: branding weight-weight at ultrasound measurement bivariate model; Sex "1": female; Sex "2": intact male.

Table 2.12. Sire variance proportion (Sh^2) estimates from linear random regression models across branding weight models

	Model[1]			
Parameter	Single-trait	BRW-WW	BRW-ULW	BRW-IMF
Sh^2 Range[2]	0.07 – 0.09	0.03	0.08 – 0.11	0.08
Sh^2 for females	0.09	0.03	0.08	0.08
Sh^2 for intact males	0.07	0.03	0.11	0.08

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sole values indicate constant value across progeny sex categories.

2.3.2.2. Weaning Weight Models

Single-trait model analysis indicated that season of birth was not significant (P = 0.22), thus, it was removed from the final analyses for the animal model, single-trait model, and bivariate models including WW. Fixed effects used in the final analyses were contemporary group, age at measurement, and sex (linear fixed covariate).

Estimates of variance for the linear random regression coefficient were zero or close to zero in single-trait, BRW-WW, and WW-IMF analyses of WW (Table 2.13). Gradient of sire variance proportion estimates for WW from WW-ULW model, and sire variance proportion estimate from the corresponding reduced model analysis (no random sire-sex interaction, just sire and maternal additive genetic effects) are presented in Figure 2.2. Additionally, estimates for sire variance proportions across models for WW are presented in Table 2.14.

Table 2.13. Estimates of variance from linear random regression analyses of weaning weight[1]

	β_0	β_1	Maternal additive	Residual
Single-trait				
β_0	**78.16 ± 29.06**			
β_1	$1.30 \times 10^{-3} \pm 0$	**9.94×10^{-8} ± 0**		
Maternal additive			**185.47 ± 22.05**	
Residual				**275.10 ± 15.48**
BRW-WW				
β_0	**43.56 ± 15.50**			
β_1	$1.57 \times 10^{-11} \pm 0$	**3.97×10^{-10} ± 0**		
Maternal additive			**197.37 ± 21.06**	
Residual				**289.93 ± 14.72**
WW-ULW				
β_0	**87.39 ± 29.03**			
β_1	10.70 ± 5.66	**5.87 ± 3.35**		
Maternal additive			**96.90 ± 12.68**	
Residual				**338.56 ± 16.33**
WW-IMF				
β_0	**75.91 ± 28.33**			
β_1	$1.57 \times 10^{-11} \pm 0$	**0.99 ± 2.10**		
Maternal additive			**182.99 ± 21.94**	
Residual				**275.29 ± 15.63**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of maternal additive effects and residual with other terms were assumed to be 0.

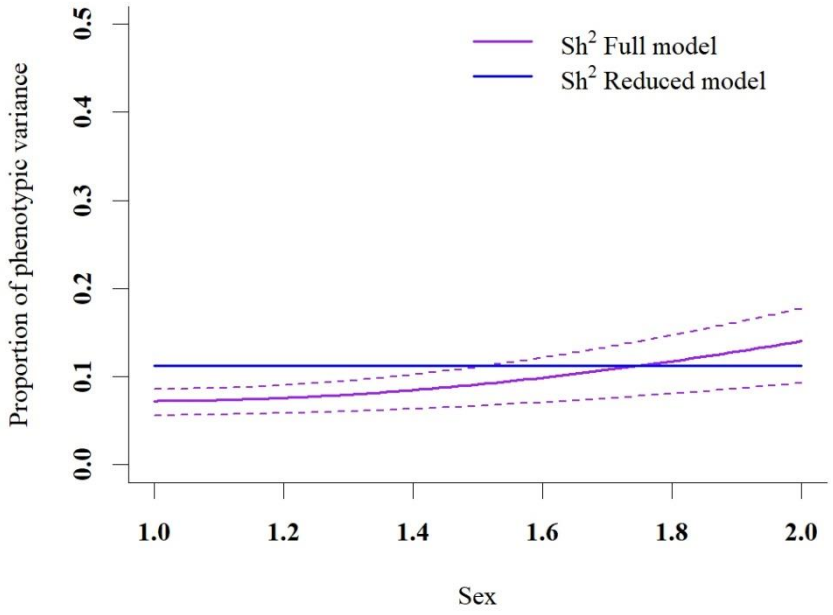

Figure 2.2. Sire variance proportion estimates for weaning weight from WW-ULW linear random regression model (Sh² Full model; dashed lines indicate ± 1 SE) and sire variance proportion estimates from equivalent model without random sire-sex interaction (Sh² Reduced model). Sex "1": female; Sex "2": intact male.

Table 2.14. Sire variance proportion (Sh²) estimates from linear random regression models across weaning weight models

	Model[1]			
Parameter	Single-trait	BRW-WW	WW-ULW	WW-IMF
Sh² Range[2]	0.08	0.07	0.07 – 0.14	0.08
Sh² for female	0.08	0.07	0.07	0.08
Sh² for intact male	0.08	0.07	0.14	0.08

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sole values indicate constant value across progeny sex categories.

2.3.2.3. Weight at Ultrasound Measurement Models

Significant fixed effects from single-trait model analysis were season of birth ($P = 0.015$), contemporary group ($P < 0.001$), age at measurement ($P < 0.001$), and sex (linear fixed covariate; $P < 0.001$), therefore, they were kept in the final analyses for the animal model, single-trait model, and bivariate models including ULW.

Analyses of ULW estimated variances for linear random regression coefficients different than zero for single-trait, BRW-ULW, WW-ULW, and ULW-IMF models (Table 2.15). Sire variance proportion estimates for ULW across the gradient of sex categories as well as sire variance proportion estimates from the corresponding reduced model analyses are presented in Figure 2.3. Estimates for sire variance proportion across models for ULW are presented in Table 2.16.

Table 2.15. Estimates of variance from linear random regression analyses of weight at ultrasound measurement[1]

	β_0	β_1	Residual
Single-trait			
β_0	**444.34 ± 130.69**		
β_1	126.39 ± 48.43	**65.79 ± 25.60**	
Residual			**1043.21 ± 36.34**
BRW-ULW			
β_0	**516.67 ± 146.78**		
β_1	156.37 ± 51.61	**66.28 ± 24.19**	
Residual			**1058.69 ± 36.84**
WW-ULW			
β_0	**352.91 ± 103.80**		
β_1	78.52 ± 30.08	**43.08 ± 15.78**	
Residual			**1063.86 ± 37.00**
ULW-IMF			
β_0	**442.02 ± 129.25**		
β_1	123.95 ± 47.13	**64.59 ± 24.75**	
Residual			**1042.49 ± 36.27**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of residual with other terms were assumed to be 0.

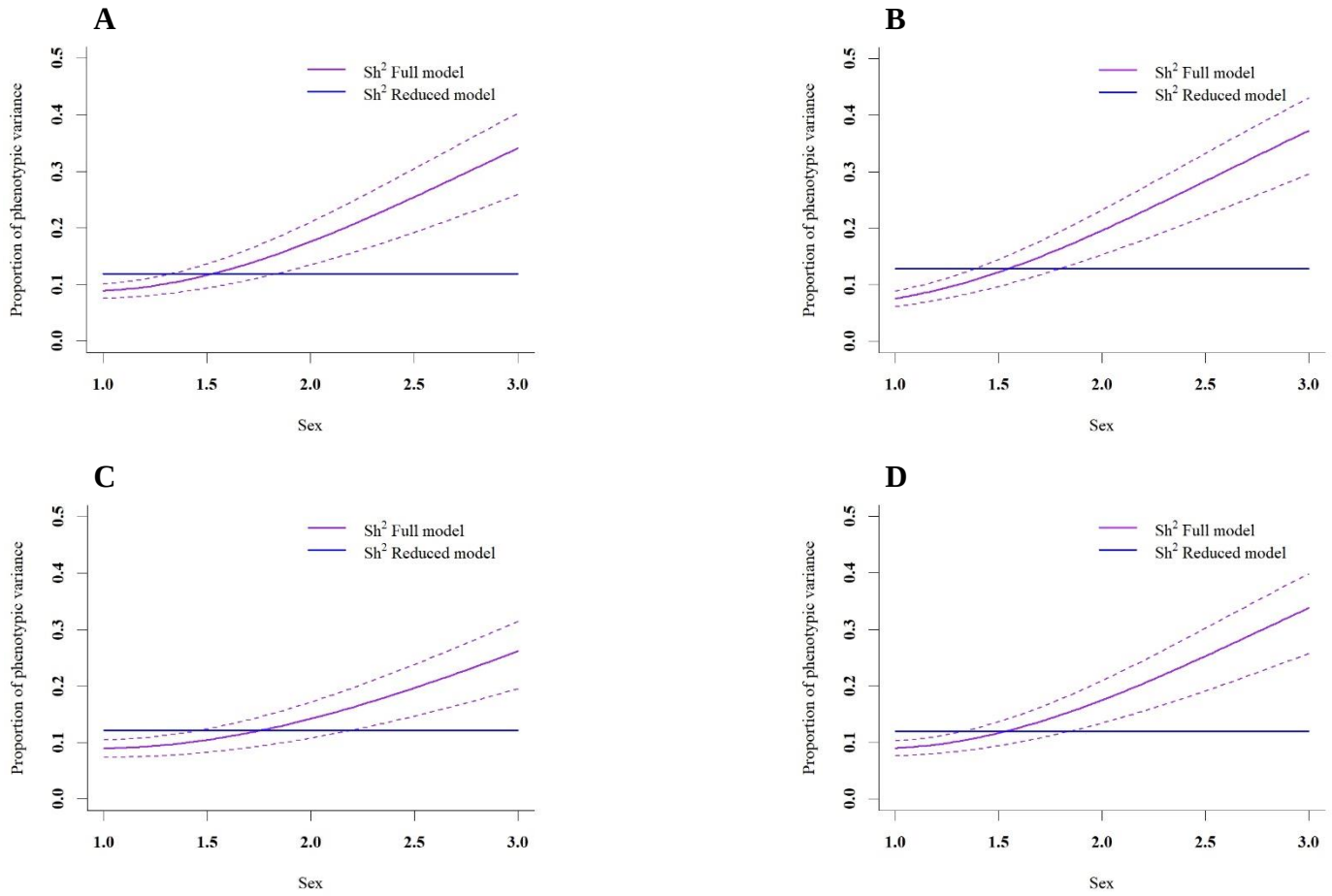

Figure 2.3. Sire variance proportion estimates for weight at ultrasound measurement from linear random regression models (Sh^2 Full model; dashed lines indicate ± 1 SE) and sire variance proportion estimates from equivalent models without random sire-sex interaction (Sh^2 Reduced model). A: Single-trait model; B: branding weight-weight at ultrasound measurement bivariate model; C: weaning weight-weight at ultrasound measurement bivariate model; D: weight at ultrasound measurement-intramuscular fat bivariate model; Sex "1": female; Sex "2": steer; Sex "3": intact male.

Table 2.16. Sire variance proportion (Sh^2) estimates from linear random regression models across weight at ultrasound models

	Model[1]			
Parameter	Single-trait	BRW-ULW	WW-ULW	ULW-IMF
Sh^2 Range[2]	0.09 – 0.34	0.08 – 0.37	0.09 – 0.26	0.09 – 0.34
Sh^2 for female	0.09	0.08	0.09	0.09
Sh^2 for steer	0.17	0.19	0.14	0.17
Sh^2 for intact male	0.34	0.37	0.26	0.34

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.
[2]Sole values indicates constant value across progeny sex categories.

2.3.2.4. Intramuscular Fat Models

Preliminary analyses for the single-trait model indicated that season of birth, contemporary group, age at measurement, and sex (linear fixed covariate) were appropriate components ($P < 0.001$) for final IMF models analysis.

Variance estimates for linear random regression coefficients of IMF analyses were practically zero (Table 2.17). The trajectories of sire variance as a proportion of phenotypic variance across the numerical "gradient" of sex deviated only slightly from a slope of 0 (Figure 2.4). Estimates for sire variance proportions of phenotypic variance from the various analyses of IMF are presented in Table 2.18.

Table 2.17. Estimates of variance from linear random regression analyses of intramuscular fat[1]

	β_0	β_1	Residual
Single-trait			
β_0	**0.09 ± 0.03**		
β_1	-0.01 ± 0.01	**0.01 ± 0.01**	
Residual			**0.62 ± 0.02**
BRW-IMF			
β_0	**0.09 ± 0.03**		
β_1	-0.01 ± 0.01	**0.01 ± 0.01**	
Residual			**0.62 ± 0.02**
WW-IMF			
β_0	**0.09 ± 0.03**		
β_1	-0.01 ± 0.01	**0.01 ± 0.01**	
Residual			**0.61 ± 0.02**
ULW-IMF			
β_0	**0.10 ± 0.03**		
β_1	-0.01 ± 0.01	**0.01 ± 0.01**	
Residual			**0.61 ± 0.02**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of residual with other terms were assumed to be 0.

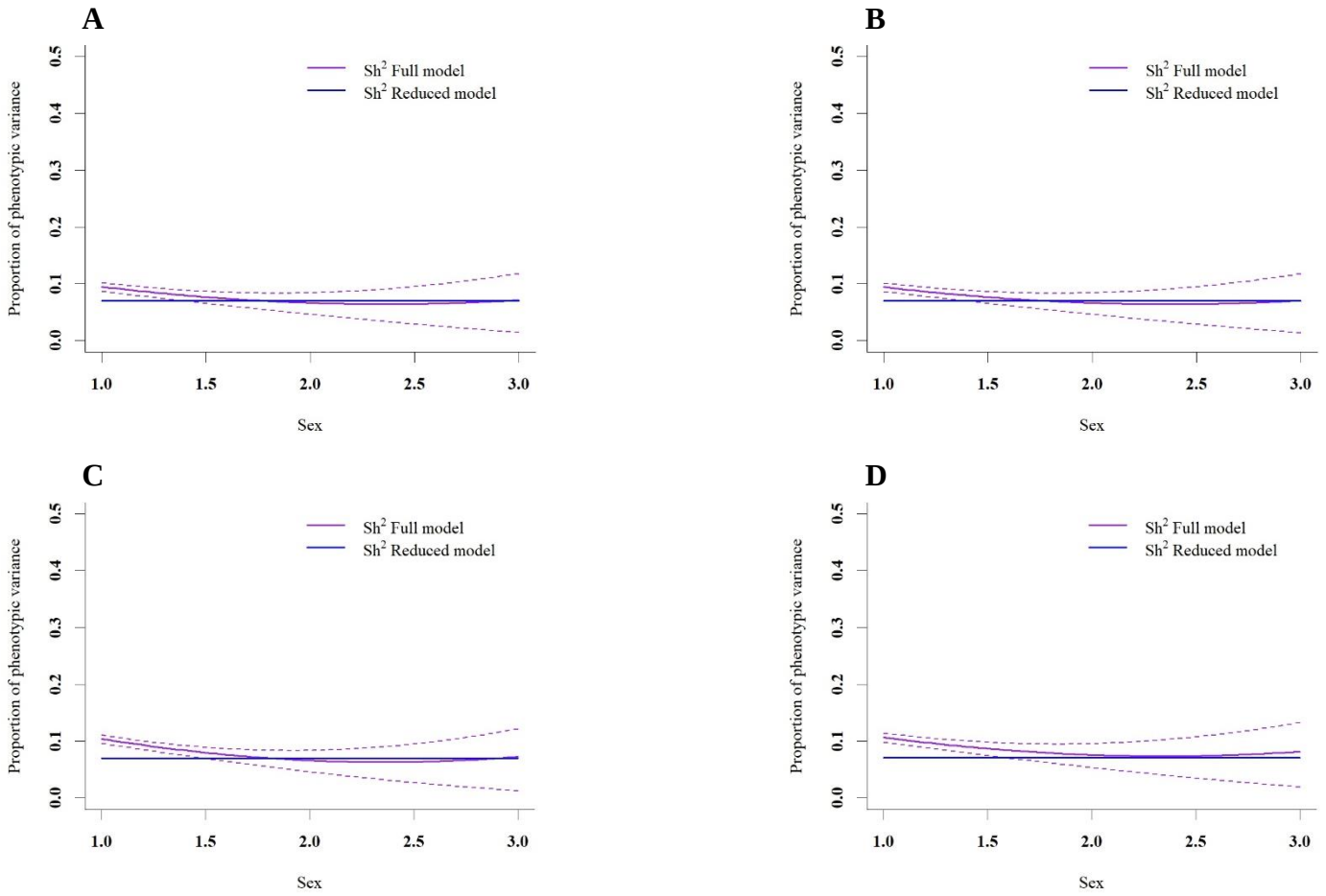

Figure 2.4. Sire variance proportion estimates for intramuscular fat from linear random regression models (Sh^2 Full model; dashed lines indicate ± 1 SE) and sire variance proportion estimates from equivalent models without random sire-sex interaction (Sh^2 Reduced model). A: Single-trait model; B: branding weight-intramuscular fat bivariate model; C: weaning weight- intramuscular fat bivariate model; D: weight at ultrasound measurement-intramuscular fat bivariate model; Sex "1": female; Sex "2": steer; Sex "3": intact male.

Table 2.18. Sire variance proportion (Sh^2) estimates from linear random regression models across intramuscular fat models

	Model[1]			
Parameter	Single-trait	BRW-IMF	WW-IMF	ULW-IMF
Sh^2 Range	0.06 – 0.09	0.06 – 0.09	0.06 – 0.10	0.07 – 0.11
Sh^2 for female	0.09	0.09	0.10	0.11
Sh^2 for steer	0.07	0.07	0.07	0.08
Sh^2 for intact male	0.07	0.07	0.07	0.08

[1]Models with labels for two traits separated by a hyphen indicate bivariate model between those traits.

2.3.2.5. Likelihood-Ratio Tests

Results from likelihood-ratio tests between models including sire-sex interaction (as a linear random regression), and equivalent models without the interaction are presented in Table 2.19. Results indicated that the linear random regression of sire on progeny sex categories was significant for ULW single-trait model ($P < 0.01$), and for BRW-ULW ($P < 0.01$) and ULW-IMF ($P < 0.01$) bivariate models.

Table 2.19. Likelihood-ratio tests between full[1] and reduced[2] models using sex as linear covariate

	Log-Likelihood		
Models	Full model	Reduced model	*P*-value
Branding weight	-6,230.51	-6,229.92	1
Weaning weight	-4,679.90	-4,679.90	1
Weight at ultrasound measurement	-6,995.73	-7,009.43	< 0.01
Intramuscular fat	-551.74	-554.61	0.06
BRW-WW[3]	-10,136.20	-10,111.50	1
BRW-ULW	-12,933.23	-12,954.65	< 0.01
BRW-IMF	-6,781.31	-6,783.94	0.15
WW-ULW	-11,339.50	-11,342.10	0.27
WW-IMF	-5,227.79	-5,234.50	0.06
ULW-IMF	-7,542.02	-7,562.86	< 0.01

[1]With sire-sex interaction in the random component of the model (linear random regression).
[2]Without sire-sex interaction in the random component of the model.
[3]Bivariate models between branding weight and weaning weight (BRW-WW), branding weight and weight at ultrasound measurement (BRW-ULW), branding weight and intramuscular fat (BRW-IMF), weaning weight and weight at ultrasound measurement (WW-ULW), weaning weight and intramuscular fat (WW-IMF), weight at ultrasound measurement and intramuscular fat (ULW-IMF).

2.4. Discussion

The investigation of genotype by environment interactions can be affected by different factors, including how the environment is modeled in prediction equations and how boundaries between environments are defined (Fikse et al., 2003).

To date, sire-sex interactions have not been sufficiently influential for genetic merit predictions when evaluated for weaning weight in different cattle breeds (Koger and Knox, 1945; Pahnish et al., 1961; Wilson et al., 1969; Tanner et al., 1970; Thrift et al., 1970). There may not be compelling reasons to include significant sire-sex interactions in genetic evaluation of growth traits in cattle because they have not been practically influential on predictions (Notter et al., 1992).

The present study evaluated two alternative strategies to model sex as an environmental descriptor and to assess its effect as an interaction with the additive genetic component of sires in Australian Droughtmaster cattle. Bivariate models were included in these analyses to assess the influence of covariances between trait components, and whether their inclusion could improve either the detection of sire-sex interactions or to support the lack of relevance of this interaction for a given trait.

The inclusion of sex as a fixed categorical variable and modeling sire additive effect within sex category resulted in similar estimates for sire variance proportions (of phenotypic variance) across sexes within analyses of BRW (Table 2.2), WW (Table 2.4), and IMF (Table 2.8). This suggests that this parameterization of these effects had little impact on analyses of these traits. Analyses of ULW indicated differences in sire variance proportion estimates across sex categories in single-trait and bivariate models.

The highest sire variance proportion estimate for this trait was for sire within intact males, and the lowest within steers, with sire variance proportion within females being an intermediate value between estimates within intact males and steers (Table 2.6). However, none were particularly strong, likely as a consequence of numbers of records.

Likelihood-ratio tests indicated that the interaction between sire and sex category was significant for BRW-ULW and WW-ULW models (Table 2.10), but not for any of the corresponding single-trait models. Considering sire variance proportion estimates, as well as estimates of linear regression coefficient variance for traits within these bivariate models, is possible to infer that the interaction within the ULW part of the bivariate models was the responsible of giving the whole model a better fit for the data in comparison to the equivalent model without the interaction (reduced model). Results from this study indicate that there is not an important sire-sex interaction effect acting on animal weights measured earlier in life; however, it may be that this interaction has a significant effect over weights measured later in life, at least in these Droughtmaster cattle. This would be consistent with results of Garrick et al. (1989), in which Simmental-sired females had higher heritability than males for post weaning gain, although there were substantial modeling differences between the present study and that of Garrick et al. (1989).

The larger sire variance proportion estimates for ULW within intact male progeny may suggest that selection may be improved if genetic evaluation was conducted within sex. Conclusions about WW analyses in the present study were consistent with others (Koger and Knox, 1945; Pahnish et al., 1961; Wilson et al., 1969;

Tanner et al., 1970; Thrift et al., 1970). Exceptions appeared to be results from Buchanan and Nielsen (1979) and Garrick et al. (1989), in which where a significant interaction between sire and sex was found in Simmental and Maine-Anjou cattle, and Simmental influenced cattle, respectively. Additionally, both of those groups reported significant sire-sex interaction for birth weight. However, there have not been additional studies evaluating the effect of sire-sex interactions on weights measured close to birth or weights measured after weaning; thus, further research is needed to validate findings in this study, especially considering the number of records available for analyses and the complexity of the models.

Additive genetic correlations between sire effects across sex categories indicated large positive correspondence in BRW (Table 2.3), WW (Table 2.5), and ULW (Table 2.7) analyses ($r \geq 0.95$). According to Robertson (1959), any correlation over 0.8 would indicate a non-significant interaction from a biological point of view. Thus, the impact of sire-sex interaction on these traits should be low (Hayes et al., 2003) or not existent, and, genetic improvement for these traits would not be unique within sex category (Yamada, 1962). Results from IMF analyses identified lower positive additive correlations (Table 2.9), suggesting that there may be traits for which the breeding merit of a sire would depend on progeny sex. This may indicate that phenotypic plasticity (phenotypic differences across environments due to genotype-environment interactions; De Jong et al., 2002) across sex categories for IMF would be higher than for BRW, WW, and ULW. Nevertheless, SE in correlations analyses were very large for each trait across models. This may be a consequence of a combined effect between the number of records used for

each analysis and the number of variance components incorporated in each model, especially for models including ULW and IMF where 3 extra (co)variance components were estimated in comparison to BRW and WW models.

The use of sex as an environmental gradient for a linear random regression of sire effects on sex category is a nonconventional method of assessment. Results from analyses of BRW, WW, and IMF indicated that this method was not useful or necessary. Analyses of ULW suggested differential sire merit by sex, particularly for intact males as compared with that of females. However, this is all interpreted in a relatively small data set context, and the model is complex.

Weight at ultrasound measurement seems to be the sole trait in this study that may benefit the most from incorporating sire-sex interaction in the models as linear random regression. This methodology may help to identify sires which genetic merit could further improve ULW, especially in intact males; however, larger databases are needed to validate findings from this study.

2.5. Conclusion

Analyses which included random sire-sex interactions as sire effects nested in sex categories or as linear random regressions provided similar evidence. Weight at ultrasound measurement was the only trait in which either method seemed feasible. Results suggest that there may be a larger potential for improvement of ULW in intact males; however, these results are very subject to low numbers of individuals overall and especially for females.

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CHAPTER III

MODELING OF GENETIC COMPONENTS FOR BIRTH WEIGHT AND WEANING WEIGHT ACROSS DIFFERENT PARENTAL INFLUENCES OF NELLORE AND ANGUS THROUGH RANDOM REGRESSIONS

3.1. Introduction

Genetic improvement for economically relevant traits in beef cattle operations has followed two strategies, selection and crossbreeding (Herring, 2014). The development of genetic merit prediction equations made possible to select animals to be parents based on their ability to transmit favorable genes into their progeny (Falconer and Mackay, 1996; Herring, 2014). The use of crossbreeding between different cattle breeds combines complementary strengths from those breeds and takes advantage of direct and maternal hybrid vigor (heterosis) for a variety of important traits (Cartwright, 1970; Falconer and Mackay, 1996; Herring, 2014).

These two improvement approaches are often evaluated through separate genetic evaluations. Genetic merit predictions accounting simultaneously for non-additive genetic effects and interactions between additive and non-additive effects have mainly been directed to assess sires combining ability to reduce inbreeding in a population (Allaire and Henderson, 1965; Henderson, 1989; DeStefano and Hoeschele, 1992). However, non-additive genetic effects due to crossbreeding and their interaction with additive effects have not been introduced into prediction equations. Consequently, genetic merit predictions for specific sires may not provide the expected outcomes in

progeny from different crossbreeding scenarios, where different non-additive effects may be influential.

Bos indicus and *Bos taurus* breeds were developed though different domestication events, which has produced large genetic divergence between these subspecies (MacHugh et al., 1997). This genetic divergence has been widely used to the benefit of beef cattle operations due to the large hybrid vigor achieved when *Bos indicus* and *Bos taurus* breeds are crossed (Cartwright, 1980; Franke, 1980; Riley et al., 2007). *Bos indicus* and *Bos taurus* breeds have complementary attributes that can be blended in crossbred animals, making them more or less efficient depending on the production environment, and relative market expectations (Sanders, 1980; Turner, 1980; Jonsson, 2006; Prado et al., 2008; Herring, 2014).

Bos indicus x *Bos taurus* reciprocal crosses express differences in birth and weaning weights, where calves produced by *Bos indicus* sires and *Bos taurus* dams are much heavier than calves produced by *Bos taurus* sires and *Bos indicus* dams at birth and weaning (Cartwright et al., 1964; Thallman et al., 1993; Chase et al., 2000; Holloway et al., 2002). These reciprocal crosses differences also have been identified when breeding *Bos indicus-Bos taurus* crossbred animals, when the proportion of *Bos indicus* in the sire is larger than in the dam (Cartwright et al., 1964; Amen et al., 2007).

Therefore, in addition to the “regular” non-additive genetic effects affecting crossbred populations (i.e., dominance or epistatic effects; Falconer and Mackay, 1996) there may be additional non-additive effects, such as parent-of-origin effects, affecting

progeny performance depending on the reciprocal cross type between parental breeds (Loschiavo et al., 2007; Vrana, 2007).

The objective of this study was to evaluate the interaction between additive and non-additive genetic effects and its potential contribution for selecting breeding animals according to specific crossbreeding scenarios. The interaction was evaluated in a mixed population of Nellore (*Bos indicus*), Angus (*Bos taurus*), and Nellore-Angus crossbred animals using random regression methodology.

3.2. Materials and Methods

3.2.1. Records

Birth weight and weaning weight records were obtained from the Texas A&M AgriLife Research Center at McGregor, TX, and from Texas A&M University Beef Cattle Systems Research Unit near College Station. Calves with records were out of crosses involving either Nellore or Angus sires and dams, or crossbred parents with Nellore and Angus in their genetic composition. Records for birth weight and weaning weight had complete information about calf year of birth, dam age, sex, and sire and dam breeds; additionally, records for weaning weight also included information about age at weaning. For both traits, records considered to be biologically unreasonable values were removed. Records greater or less than 4 SD relative to the mean were considered outliers and removed. After editing, a total of 5,591 and 4,721 records were available for birth weight and weaning weight analyzes, respectively. Pedigree information for 11,900 animals was available.

Frequency tables for birth weight and weaning weight records by year of birth, sex, dam age, sire breed and dam breed are presented in Tables 3.1, 3.2, 3.3, and 3.4.

Table 3.1. Birth weight and weaning weight records by birth year

	Birth weight		Weaning weight	
Year	Count	Frequency	Count	Frequency
2000	147	2.63	136	2.88
2001	199	3.56	157	3.33
2002	283	5.06	233	4.94
2003	294	5.26	221	4.68
2004	300	5.37	244	5.17
2005	291	5.20	239	5.06
2006	342	6.12	300	6.35
2007	345	6.17	297	6.29
2008	237	4.24	205	4.34
2009	335	5.99	309	6.55
2010	171	3.06	136	2.88
2011	380	6.80	275	5.83
2012	490	8.76	432	9.15
2013	583	10.43	529	11.21
2014	510	9.12	434	9.19
2015	684	12.23	574	12.16

Table 3.2. Birth weight and weaning weight records by calf sex and dam age

	Birth weight		Weaning weight	
Calf sex	Count	Frequency	Count	Frequency
Female	2,976	53.23	2,626	55.62
Male	2,615	46.77	2,095	44.38
Dam age (yr)	Count	Frequency	Count	Frequency
2	990	17.71	816	17.28
3	1,009	18.05	910	19.28
4	804	14.38	696	14.74
5 to 10	2,326	41.60	1,909	40.44
≥ 11	462	8.26	390	8.26

Table 3.3. Birth weight and weaning weight records by sire breed

	Birth weight		Weaning weight	
Sire breed[1]	Count	Frequency	Count	Frequency
Angus (An)	3,188	57.02	2,725	57.72
Nellore (Ne)	199	3.56	166	3.52
AnNe[2]	1,582	28.30	1,332	28.21
¾ An-¼ Ne	409	7.32	297	6.29
⅝ An-⅜ Ne	213	3.81	201	4.26

[1]Numbers represent the contribution of each breed to the sire breed.
[2]F_1 An-Ne, F_1 Ne-An, F_2 Ne-An, or F_3 Ne-An.

Table 3.4. Birth weight and weaning weight records by dam breed

	Birth weight		Weaning weight	
Dam breed[1]	Count	Frequency	Count	Frequency
Angus (An)	1,393	24.92	1,201	25.44
Nellore (Ne)	348	6.22	296	6.27
AnNe[2]	2,972	53.16	2,469	52.30
13/16 An-3/16 Ne (G1)[3]	42	0.75	32	0.68
13/16 An-3/16 Ne (G2)[4]	19	0.34	10	0.21
29/32 An-3/32 Ne	10	0.18	8	0.17
¾ An-¼ Ne	201	3.60	164	3.47
⅝ An-⅜ Ne (G1)	457	8.17	411	8.71
⅝ An-⅜ Ne (G2)	149	2.66	130	2.75

[1]Numbers represent the contribution of each breed to the dam breed.
[2]F_1 An-Ne, F_1 Ne-An, F_2 Ne-An, or F_3 Ne-An.
[3]First generation cross.
[3]Second generation cross.

The proportion of Nellore in the sire (sire-Ne) and dam (dam-Ne), and the difference between sire-Ne and dam-Ne (△Ne) were calculated for each calf, in both databases, using the parental breed composition information. The difference △Ne was adjusted by adding one unit to the respective value in order to keep the parameter space for this variable from 0 to 2 inclusive (i.e., values of 0 correspond to Angus bulls crossed to Nellore dams; values of 1 correspond to bulls and dams with and equal Nellore percentage in their genetic composition, and values of 2 correspond to Nellore bulls crossed to Angus dams). These values were used as explanatory variables in analyses; example values for common crosses in these data are shown in Table 3.5. Frequency tables for all combinations of sire and dam breeds in birth weight and weaning weight databases, and corresponding △Ne are presented in Table 3.6.

Table 3.5. Examples to determine △Ne coefficients from sire and dam combinations

Sire breed[1]	Dam breed[1]	Sire-Ne	Dam-Ne	Difference (sire - dam) Ne	Coefficient (△Ne)
Angus (An)	Nellore (Ne)	0	1	–1	0
An	½ An-½ Ne	0	0.50	–0.50	0.5
½ An-½ Ne	½ An-½ Ne	0.50	0.50	0	1
⅝ An-⅜ Ne	⅝ An-⅜ Ne	0.38	0.38	0	1
½ An-½ Ne	¾ An-¼ Ne	0.50	0.25	0.25	1.25
Ne	An	1	0	1	2

[1]Numbers represent the contribution of each breed to the sire or dam breed.

Table 3.6. Birth weight and weaning records by type of parental cross and corresponding △Ne coefficients

		Birth weight		Weaning weight		
Sire breed[1]	Dam breed[1]	Count	Frequency	Count	Frequency	△Ne
Angus (An)	Nellore (Ne)	230	4.11	193	4.09	0
An	AnNe[2]	1,022	18.28	877	18.58	0.50
An	5/8 An-3/8 Ne (G_1)[3]	241	4.31	207	4.39	0.63
An	5/8 An-3/8 Ne (G_2)[4]	143	2.56	125	2.65	0.63
An	3/4 An-1/4 Ne	169	3.02	135	2.86	0.75
3/4 An-1/4 Ne	AnNe	409	7.32	297	6.29	0.75
An	13/16 An-3/16 Ne (G_1)	42	0.75	32	0.68	0.81
An	13/16 An-3/16 Ne (G_2)	19	0.34	10	0.21	0.81
An	29/32 An-3/32 Ne	10	0.18	8	0.17	0.91
An	An	1,312	23.47	1,138	24.11	1
Ne	Ne	118	2.11	103	2.18	1
AnNe	AnNe	1,541	27.56	1,295	27.43	1
5/8 An-3/8 Ne (G_1)	5/8 An-3/8 Ne (G_1)	207	3.70	196	4.15	1
5/8 An-3/8 Ne (G_1)	5/8 An-3/8 Ne (G_2)	6	0.11	5	0.11	1
AnNe	5/8 An-3/8 Ne (G_1)	9	0.16	8	0.17	1.13
AnNe	3/4 An-1/4 Ne	32	0.57	29	0.61	1.25
Ne	An	81	1.45	63	1.33	2

[1]Numbers represent the contribution of each breed to the sire or dam breed.
[2]F_1 An-Ne, F_1 Ne-An, F_2 Ne-An, or F_3 Ne-An.
[3]First generation cross.
[4]Second generation cross.

3.2.2. Statistical Analyses

3.2.2.1. Principal Component Analysis

Principal component analyses were used to evaluate associations between variables within birth weight and weaning weight data. Potential correlated variables within birth weight database were birth weight, sire-Ne, and dam-Ne. Weaning weight database, variables investigated in principal component analyses included weaning weight, birth weight, weaning age, sire-Ne, and dam-Ne. Associations among variables

within each group were evaluated by estimating correlations between them and the first 2 principal components. Observations were plotted using their weighted value for the first 2 principal components. Clusters among observations were evaluated according to calf sex, birth year, and dam age.

3.2.2.2. Prediction Models

Two set of genetic merit prediction models were evaluated for birth weight and weaning. Linear random regression models (first order Legendre polynomials) were evaluated, where the additive genetic component of animals was modeled across a gradient corresponding to the parameter space for △Ne. Higher order Legendre polynomials were not evaluated, as the estimation of a larger number of variance and covariance components would be too demanding given the current databases. Traditional animal models were evaluated for each trait for comparison to the linear random regression results.

Fixed effects in linear random regression models and animal models for birth weight and weaning weight included birth year (categorical; ranging from 2000 to 2015), dam age (categorical; ages were considered individually from 2 to 4 years, ages ranging from 5 to 10 years were grouped together, as well as ages greater than 11 years), sex (categorical; females and males), and △Ne (linear fixed covariate). Age in days (linear fixed covariate) was also included in analyses of weaning weight.

Random effects in linear random regression models for birth weight and weaning weight were the linear random regression of animal additive genetic effects on △Ne, maternal additive genetic effect (as a single variance), and maternal permanent

environment effect (as a single variance). Random effects in the traditional animal models included additive genetic, maternal additive genetic, and maternal permanent environment effects.

Random regression models followed the form:

$$y = X\beta + Zu + Wm + Qc + e$$

where *y* was a vector of birth weight or weaning weight records, β was the vector of estimated fixed effects, *u* was the vector of random regression coefficients for animal additive genetic effects, *c* was the vector of additive genetic effects of the dam, *p* was the vector of maternal permanent environment effects, *e* was the vector of residuals, and *X*, *Z*, *W*, and *Q* were incidence matrices relating observations in *y* to values in β, *u*, *m*, and *c*, respectively.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as:

$$Var\begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 & 0 \\ 0 & M & 0 & 0 \\ 0 & 0 & C & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

where *A* was the numerator relationship matrix constructed from the pedigree information, and *G* was the covariance matrix of additive genetic regression coefficients with order 2 (intercept and linear random regression coefficient); $M = A\sigma_m^2$, where σ_m^2 is the additive genetic variance for dams; $C = I\sigma_i^2$, where σ_i^2 is the variance of maternal permanent effects; $R = I\sigma_e^2$, and σ_e^2 is the residual variance.

Animal models followed the form:

$$y = X\beta + Zu + Wm + Qc + e$$

where *y* was a vector of birth weight or weaning weight records, *u* was the vector of animals' predicted breeding values; *β*, *m*, *c*, *e*, *X*, *Z*, *W*, and *Q* were the same as described for the random regression models.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure as:

$$Var\begin{bmatrix} u \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 & 0 \\ 0 & M & 0 & 0 \\ 0 & 0 & C & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

in which $G = A\sigma_a^2$, σ_a^2 was the animal additive genetic variance, and *A*, *M*, *C* and *R* were as described for the random regression models. No additive genetic covariance between direct and maternal effects was included in birth weight or weaning weight animal models in order to obtain results comparable to those of linear random regression models.

3.2.2.3. Likelihood-Ratio Tests

Likelihood-ratio tests were conducted between linear random regression models and corresponding animal models in order to assess which model had the better fit for birth weight and weaning weight analyses. This is possible because the traditional animal model may be thought of as a random regression model of order 0 (intercept only) and therefore the models are nested.

3.2.2.4. Analytical Tools

Principal component analyses were conducted using R project (R Core Team, 2018). Analyses for linear random regression as well as for animal models were conducted using ASReml (Gilmour et al., 2009). Heritability estimates and

corresponding SE of animal models were calculated directly with ASReml. Gradients of heritability estimates for birth weight and weaning weight across the parameter space △Ne were estimated using variance component estimates (Schaeffer, 2016).

3.3. Results

3.3.1. Principal Component Analyses

Eigenvectors and the most important principal components from analyses of birth and weaning weight databases are presented in Tables 3.7 and 3.8, respectively.

Table 3.7. Principal component analysis eigenvectors and descriptors for birth weight database

	PC1[1]	PC2	PC3
Birth weight	0.02	0.95	-0.33
Sire-Ne[2]	-0.71	0.24	0.67
Dam-Ne[3]	-0.71	-0.22	-0.67
Standard deviation	1.17	1.02	0.76
Proportion of variance	0.46	0.35	0.19
Cumulative proportion	0.46	0.81	1

[1]First, second, or third principal component.
[2]Proportion of Nellore in sire.
[3]Proportion of Nellore in dam.

Table 3.8. Principal component analysis eigenvectors and descriptors for weaning weight database

	PC1[1]	PC2	PC3	PC4	PC5
Birth weight	0.13	-0.51	0.70	-0.07	-0.47
Weaning weight	0.42	-0.63	-0.13	-0.15	0.62
Sire-Ne[2]	-0.49	-0.43	-0.11	0.75	0.05
Dam-Ne[3]	-0.46	-0.38	-0.46	-0.57	-0.32
Weaning age	0.60	-0.10	-0.51	0.29	-0.53
Standard deviation	1.25	1.19	1.03	0.78	0.57
Proportion of variance	0.31	0.28	0.21	0.12	0.07
Cumulative proportion	0.31	0.60	0.81	0.93	1

[1]First, second, or third principal component.
[2]Proportion of Nellore in sire.
[3]Proportion of Nellore in dam.

In analysis of birth weight database, the first 2 principal components explained 81% of the joint variability associated with birth weight, sire-Ne, and dam-Ne. For analysis of weaning weight database, the first 2 principal components explained 60% of the joint variability between weaning weight, birth weight, weaning age, sire-Ne, and dam-Ne.

Correlations between evaluated variables and the first 2 principal components are presented in Table 3.9 and Table 3.10 for analysis of birth weight and weaning weight databases, respectively. For birth weight database analysis, results indicate that higher values for the first principal component are associated with lower sire-Ne and dam-Ne values. Larger values for the second principal component were associated with greater birth weight and sire-Ne, and with lower dam-Ne values. For analysis of weaning weight database, results indicated that higher values for the first principal component were associated with greater weaning weights, birth weights, and weaning ages, and with lower sire-Ne and dam-Ne. Lower values for the second principal component were associated with greater weaning weight, birth weight, sire-Ne, and dam-Ne.

Table 3.9. Principal components correlations for birth weight analysis

	PC1[1]	**PC2[1]**
Birth weight	0.02	0.97
Sire-Ne[2]	-0.82	0.25
Dam-Ne[3]	-0.83	-0.23

[1]First or second principal component.
[2]Proportion of Nellore in sire.
[3]Proportion of Nellore in dam.

Table 3.10. Principal components correlations for weaning weight analysis

	PC1[1]	PC2[1]
Birth weight	0.17	-0.61
Weaning weight	0.52	-0.76
Sire-Ne[2]	-0.62	-0.52
Dam-Ne[3]	-0.58	-0.45
Weaning Age	0.75	-0.12

[1]First or second principal component.
[2]Proportion of Nellore in sire.
[3]Proportion of Nellore in dam.

Cluster analyses for birth weight database by sex (Figure 3.1), birth year (Figure 3.3), and dam age (Figure 3.5) indicated no clusters for observations distributed according the first and second principal components. For weaning weight database, cluster analyses by sex (Figure 3.2), birth year (Figure 3.4), and dam age (Figure 3.6) also did not determine any clear clusters between observations.

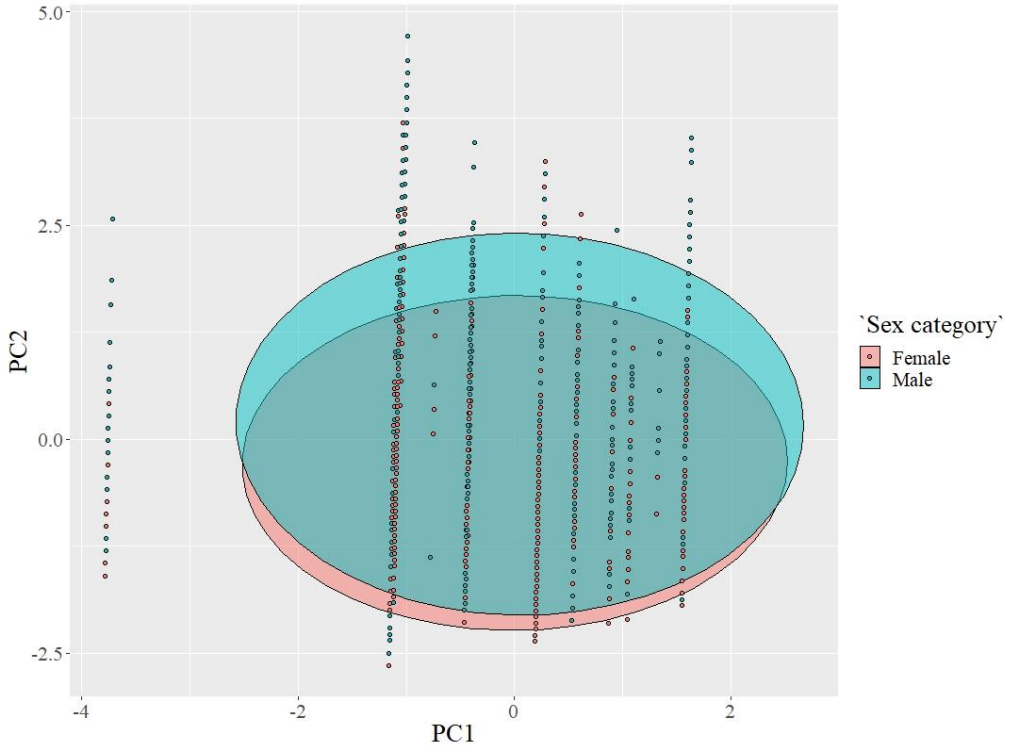

Figure 3.1. Clusters by sex category for observations distributed accordengly to the first 2 principal components from birth weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, sire-Ne, and dam-Ne.

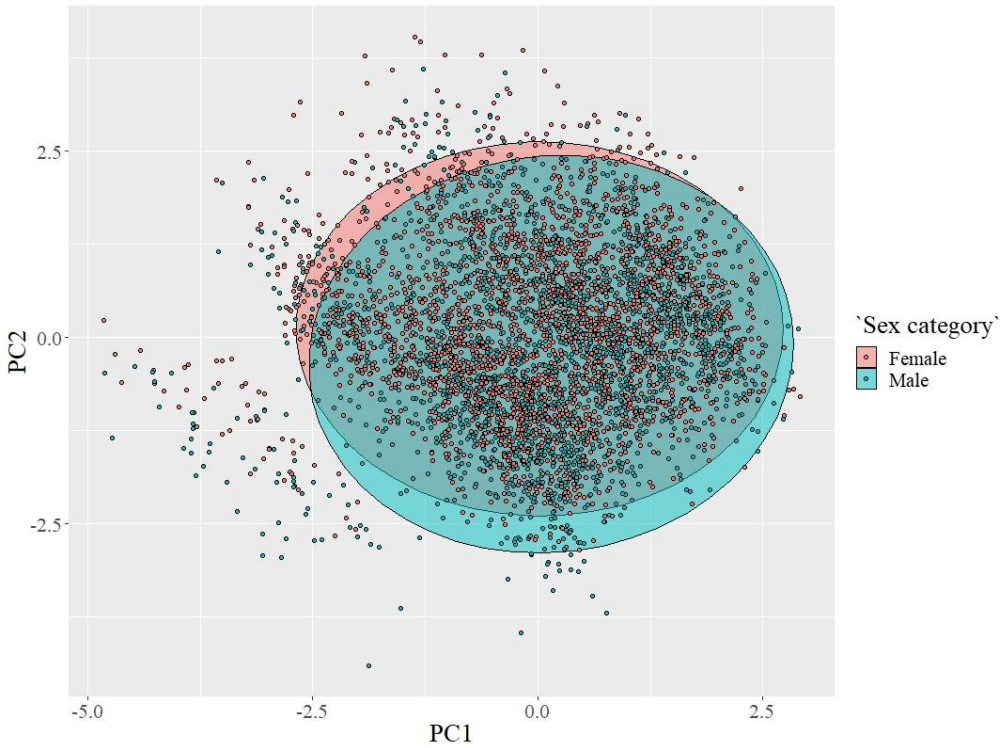

Figure 3.2. Clusters by sex category for observations distributed accordengly to the first 2 principal components from weaning weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, weaning weight, weaning age, sire-Ne, and dam-Ne.

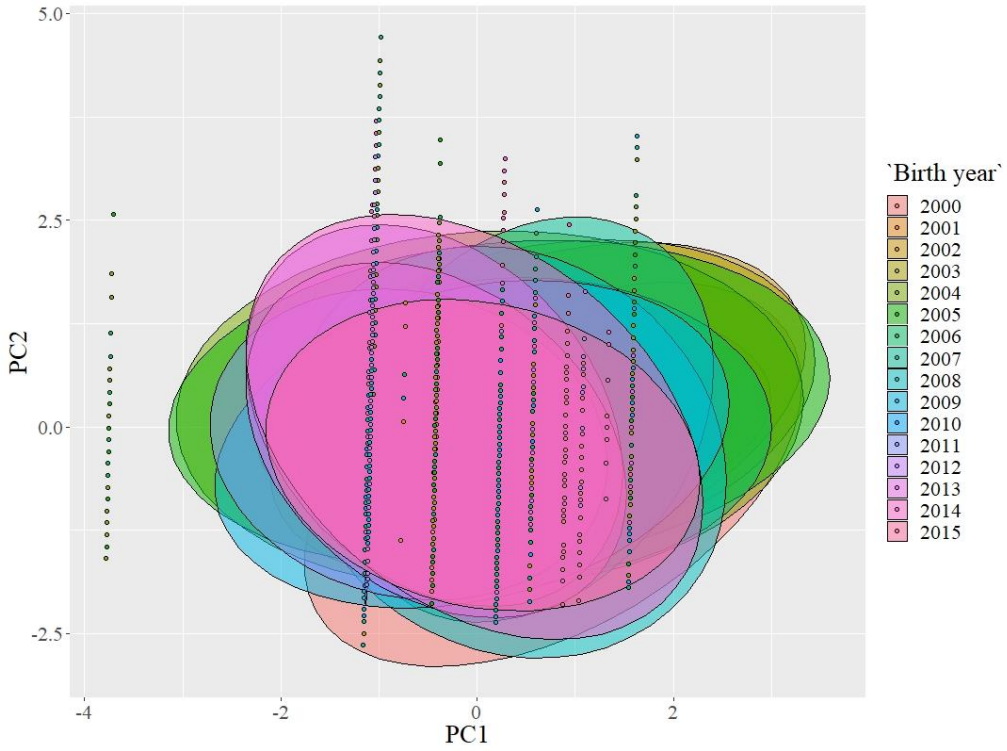

Figure 3.3. Clusters by birth year for observations distributed accordengly to the first 2 principal components from birth weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, sire-Ne, and dam-Ne.

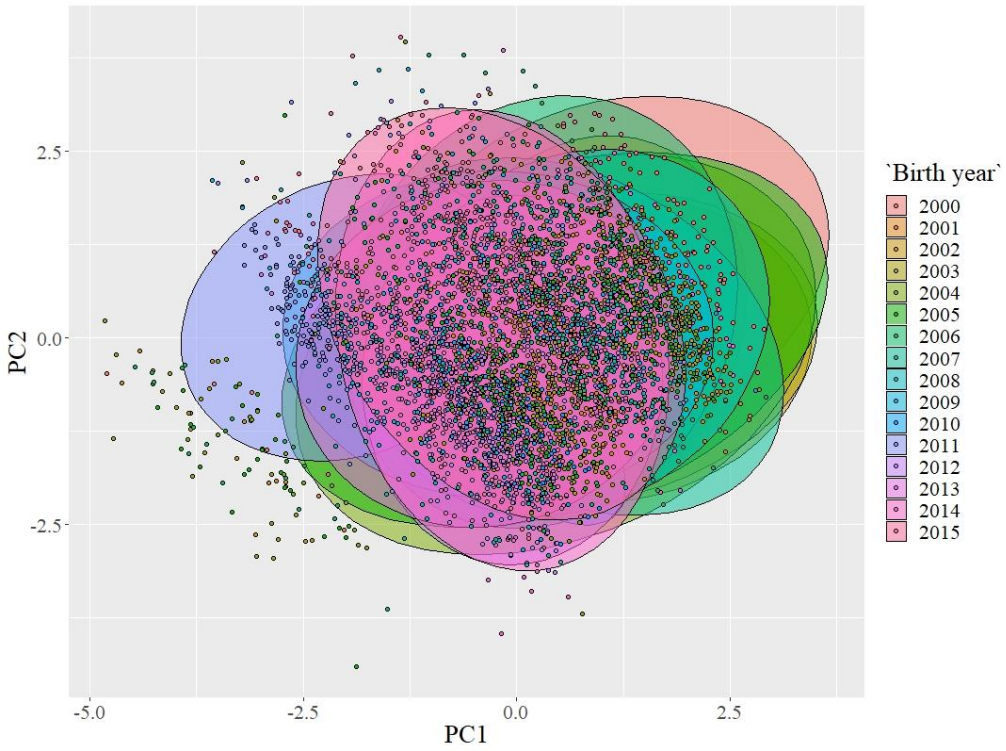

Figure 3.4. Clusters by birth year for observations distributed accordengly to the first 2 principal components from weaning weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, weaning weight, weaning age, sire-Ne, and dam-Ne.

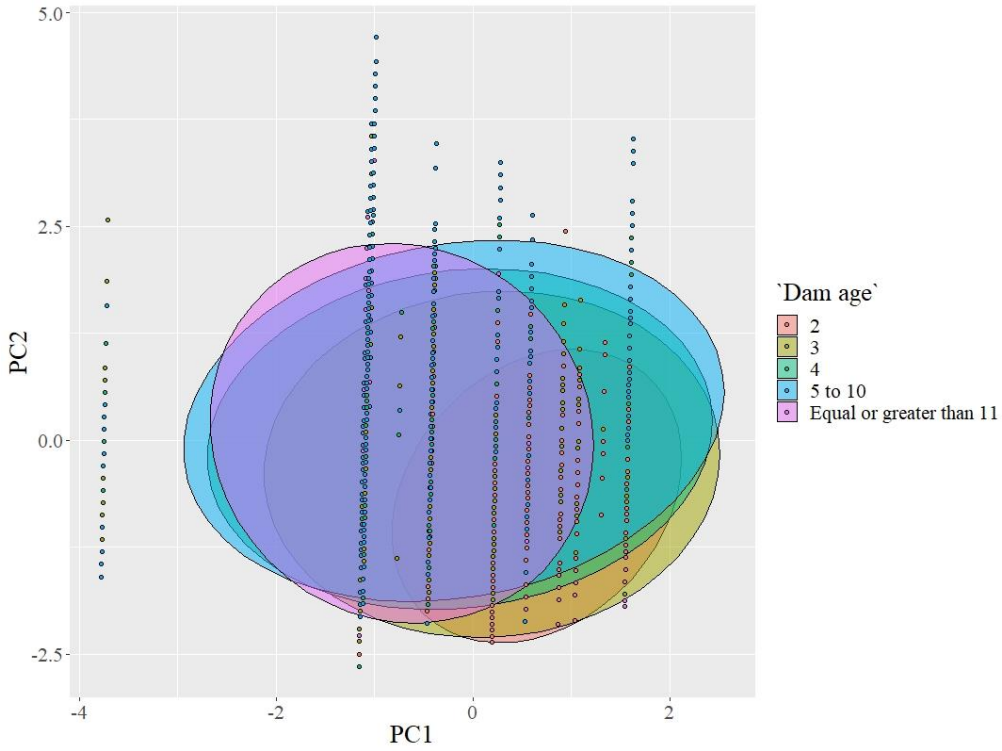

Figure 3.5. Clusters by dam age for observations distributed accordengly to the first 2 principal components from birth weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, sire-Ne, and dam-Ne.

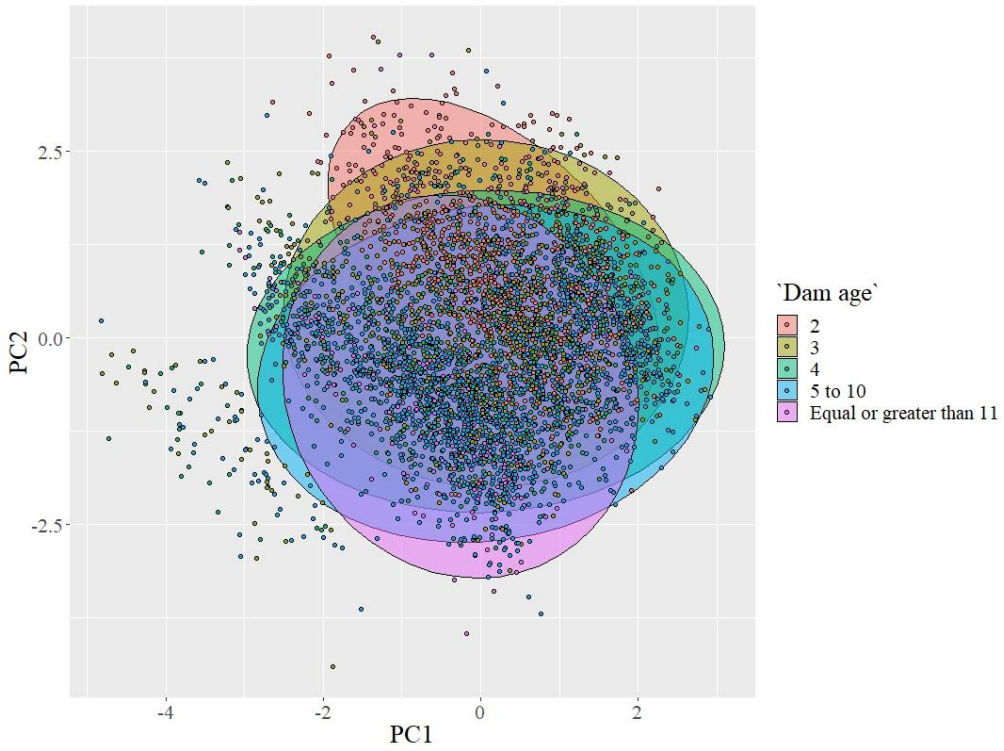

Figure 3.6. Clusters by dam age for observations distributed accordengly to the first 2 principal components from weaning weight database analysis. PC1: first principal component; PC2: second principal component. The X and Y axis represent standardized values for observations weighted according to PC1 and PC2, respectively, and centered around a mean equal 0. Variables weighted in PC1 and PC2 were birth weight, weaning weight, weaning age, sire-Ne, and dam-Ne.

3.3.2. Prediction Models

3.3.2.1. Fixed Effects

Year of birth, dam age, sex, and the linear regression of birth weight on △Ne were significant ($P < 0.01$) in both linear random regression and animal models for birth weight analyses. Similarly, year of birth, dam age, sex, linear regression of weaning weight on weaning age, and linear regression of weaning weight on △Ne were significant ($P < 0.01$) for both linear random regression and animal models for weaning weight analyses.

3.3.2.2. Random Effects

The relevance of including the maternal permanent environment effect in linear random regression analyses for birth weight and weaning weight was evaluated with a likelihood-ratio tests (comparing models with and without the effect). Maternal permanent environment was significant in linear random regression models for birth weight and weaning weight ($P < 0.01$); therefore, it was kept in the final analyses for the linear random regression models. Maternal permanent environment effect was also kept in animal models for birth weight and weaning weight analyses in order to compare them to linear random regression models through likelihood-ratio tests. Variance component estimates for birth weight and weaning weight analyses are presented in Table 3.11 and Table 3.12, respectively.

Table 3.11. Estimates of variance from birth weight analyses[1]

Linear random regression model

	β_0[2]	β_1[3]	MG[4]	MPE[5]	Res[6]
β_0	**164.00 ± 15.68**				
β_1	46.90 ± 8.80	**52.77 ± 12.44**			
MG			**1.76 ± 3.38**		
MPE				**5.58 ± 2.69**	
Res					**55.02 ± 5.64**

Animal model

	DG[7]	MG	MPE	Res
DG	**66.38 ± 7.24**			
MG		**2.30 ± 3.48**		
MPE			**5.91 ± 2.75**	
Res				**64.35 ± 5.48**

[1]Variances are on diagonal and in bold type, and covariances are below that diagonal. Covariances not specified were assumed to be 0.
[2]Random intercept.
[3]Random linear regression coefficient.
[4]Maternal additive genetic.
[5]Maternal permanent environment.
[6]Residual.
[7]Direct additive genetic.

Table 3.12. Estimates of variance from weaning weight analyses[1]

Linear random regression model					
	β_0[2]	β_1[3]	MG[4]	MPE[5]	Res[6]
β_0	**2,332.17 ± 388.70**				
β_1	852.88 ± 157.94	**856.39 ± 219.03**			
MG			**409.85 ± 147.43**		
MPE				**807.94 ± 123.92**	
Residual					**917.91 ± 142.09**

Animal model				
	DG[7]	MG	MPE	Res
DG	**1,062.96 ± 180.16**			
MG		**372.00 ± 141.44**		
MPE			**726.93 ± 117.44**	
Res				**985.13 ± 134.58**

[1]Variances are on diagonal and in bold type. Covariances not specified were assumed to be 0.
[2]Random intercept.
[3]Random linear regression coefficient.
[4]Maternal additive genetic.
[5]Maternal permanent environment.
[6]Residual.
[7]Direct additive genetic.

3.3.2.3. Heritability Estimates for Birth Weight and Weaning Weight

Heritability estimates from the animal model as well as proportions of phenotypic variance explained by maternal additive genetic variance, and by maternal permanent environment are presented in Table 3.13 for birth weight and weaning weight.

Table 3.13. Proportions of phenotypic variance explained by direct additive genetic (h^2), maternal additive genetic (m^2), and maternal permanent environment (c^2) for birth weight and weaning weight

	Birth weight	Weaning weight
h^2	0.48 ± 0.05	0.34 ± 0.06
m^2	0.02 ± 0.03	0.12 ± 0.04
c^2	0.04 ± 0.02	0.23 ± 0.04

Heritability estimates from the random regression model ranged from 0.5 to 0.8 for birth weight (Figure 3.7). The smallest estimates were observed for △Ne values near 0.49 (i.e., dam with 49% more Nellore in her breed composition than the sire), and largest estimates were associated to △Ne values of 2 (i.e., Nellore sires to Angus dams).

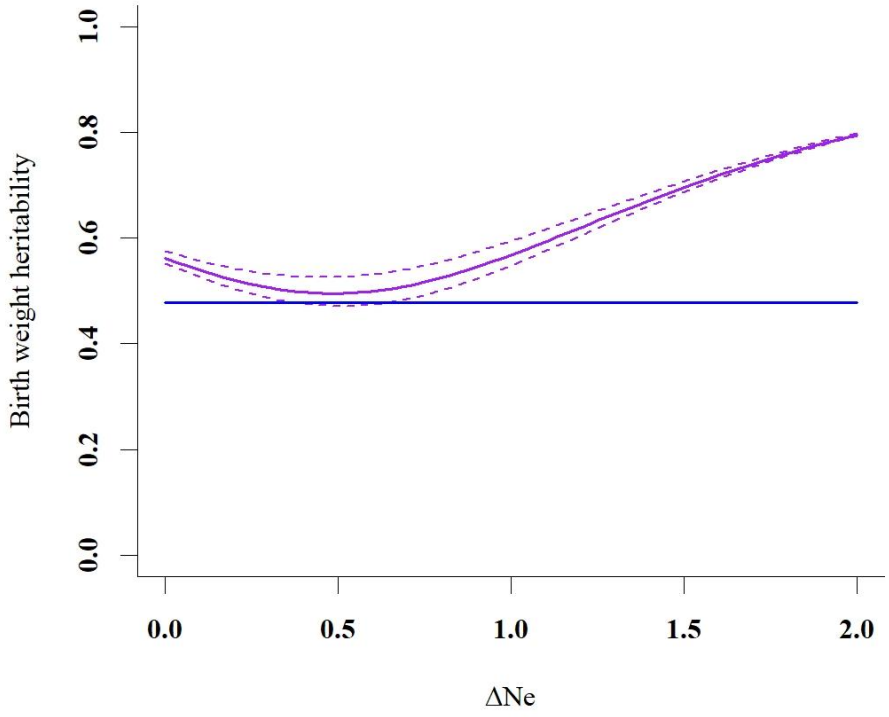

Figure 3.7. Heritability estimates for birth weight from linear random regression model (purple line; dashed lines indicate ± 1 SE) and from animal model (blue line).

Heritability estimates from the random regression model ranged from 0.26 to 0.65 (Figure 3.8) for weaning weight. The smallest estimates were observed near △Ne values of 0.42 (i.e., dam with 42% more Nellore in her breed composition than the sire),

and largest estimates were associated with △Ne values of 2, which correspond to Nellore x Angus cross (sire breed listed first, followed by dam breed).

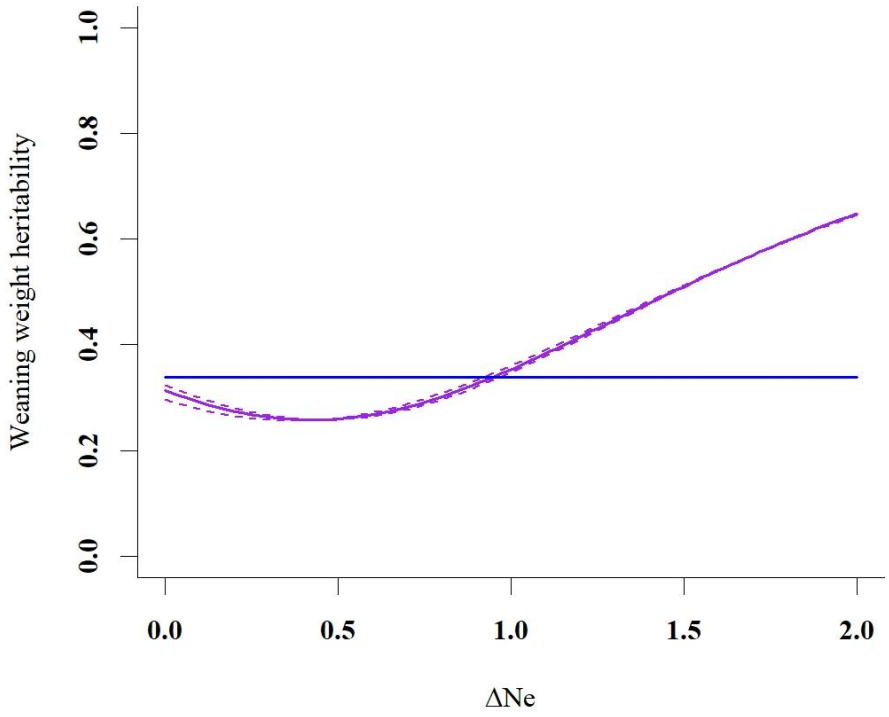

Figure 3.8. Heritability estimates for weaning weight from linear random regression model (purple line; dashed lines indicate ± 1 SE) and from animal model (blue line).

3.3.2.4. Likelihood-Ratio Test

Comparing linear random regression models to corresponding animal models through likelihood-ratio tests determined that the linear random regression of animal additive genetic effects on △Ne was relevant for analyses of birth weight ($P < 0.01$) and weaning weight ($P < 0.01$).

3.4. Discussion

Exploratory analyses though principal components made it possible to identify relationships between observations within birth weight and weaning weight databases, and to assess how continuous variables in those databases were explaining variability across observations.

The first and second principal components explained 46% and 35% of the total variability in birth weight database, respectively. The first principal component was negatively influenced by sire-Ne and dam-Ne, with no practical association to birth weight (Table 3.7). The second principal component was highly and positively associated with birth weight and had a lower association to sire-Ne and dam-Ne, which were weighted similarly but with a positive association with sire-Ne and a negative association with dam-Ne (Table 3.7). Overall, the 46% of data variation explained by the first principal component was mainly associated with changes in sire-Ne and dam-Ne, where lower values of sire-Ne and dam-Ne were associated to higher values for the first principal component. The 35% of variation explained by the second principal component was highly influenced by birth weight; however, besides heavier weights at birth, a greater sire-Ne and a lower dam-Ne were also associated to increase the values of the second principal component, but in a lower degree.

Results from principal component analysis using weaning weight database indicated that the first and second principal components explained 31% and 28% of data variability, respectively (Table 3.8). The variability explained by these two principal components results were lower than the one explained by the 2 first principal

components from principal component analysis of birth weight database; however, sire-Ne and dam-Ne had also a high correlation with the first principal component in comparison to the other variables in the analysis (Table 3.10). Additionally, birth weight had a low positive correlation to the first principal component, just as it was observed for principal component analysis using birth weight data. The variable with the greatest (and positive) correlation to the first principal component was weaning age. The second principal component was negatively correlated to all the variables in the analysis, with the greatest negative correlations associated to weight variables (birth weight and weaning weight), followed by sire-Ne and dam-Ne, and with the lowest correlation associated to weaning age. Thus, variability explained by the first and second principal components were lowly influenced by birth weight and weaning age, respectively.

Principal component analyses for birth weight and weaning weight databases agreed in identifying important associations between sire-Ne and dam-Ne to the respective first principal components, meaning that an important part of the variability across observations was influenced by these variables. Observations distributed with respect to the first two principal components of analyses of birth weight and weaning weight databases did not show a clear cluster pattern by calf sex (Figure 3.1 and Figure 3.2, respectively), calf birth year (Figure 3.3 and Figure 3.4, respectively), and dam age (Figure 3.5 and Figure 3.6, respectively). This means that highly or lowly weighted observations across the first and second principal component from both analyses were not dependent on these classification variables. However, some observations distributed across the first two principal components seems to depart from rest, as can be observe in

the left lower corner of Figures 3.2 to 3.8. This may indicate that a different source of variation could be responsible of this potential cluster pattern.

The influence of sire-Ne and dam-Ne with on the variability of databases designed specifically for birth weight and weaning weight analyses is interesting considering what has been described in the literature. Experiments involving crossbreeding between *Bos indicus-Bos taurus* crossbred animals have showed that higher birth weights were observed when the amount of *Bos indicus* in the sire was greater than the amount of *Bos indicus* in the dam (Cartwright et al., 1964; Amen et al., 2007); similar results were found for weaning weight in backcrosses between F_1 Angus x *Bos indicus* (Brahman or Nellore) sires and dams to Angus or *Bos indicus* animals, where Angus-*Bos indicus* x Angus calves, and *Bos indicus* x Angus-*Bos indicus* calves were heavier at weaning than Angus x Angus-*Bos indicus* calves, and Angus-*Bos indicus* x *Bos indicus* calves (Amen et al., 2007).

Principal component analyses findings supported the potential inclusion of sire-Ne and dam-Ne for birth weight and weaning weight genetic predictions. Moreover, to incorporate them into prediction equations as genotype by parental cross type interaction could have a high practical relevance to operations using Nellore-Angus (and other *Bos indicus-Bos taurus*) crossbred animals.

Random regression was utilized to model genotype-parental cross type information into prediction equations. As such, genetic merit can be predicted across a gradient of continuous values, such as sire-Ne and dam-Ne. However, in order to minimize parametrization, a variable was created combining the information from sire-

Ne and dam-Ne (△Ne). This is a novel approach to assessment of mating systems; the additive genetic component could be affected depending on specific types of parental breed combinations. This is of major importance for breeders of specific types of crosses.

Heritability estimates for birth weight from the linear random regression model had a large range: 0.5 to 0.8 (Figure 3.7); the largest values are very large relative to most other reported estimates for this trait. Estimates of heritability for birth weight from mostly traditional animal models ranged from 0.22 to 0.70 for Angus cattle (0.22, Elzo and Wakeman, 1998; 0.29, Cardoso et al., 2001; 0.27, Trus and Wilton, 1988; 0.41, Alenda and Martin, 1987; 0.42, Brown et al., 1990, and Johnson et al., 1992; 0.45, Rasali et al., 2005; 0.51, Alenda and Martin, 1987; 0.51, Rasali et al., 2005; 0.70, Knights et al., 1984), and from 0.10 to 0.33 in Nellore cattle (0.10, 0.14, 0.21 and 0.33, Nobre et al., 2003; 0.28 and 0.32, Albuquerque and Meyer, 2001; 0.29, Eler et al., 1995). The largest estimates from the current study were observed for high values of the "environmental" gradient, which represents a high proportion of Nellore in sires and a low proportion of Nellore in dams—this is "contextual heritability" with respect to genetic background, and may represent a unique quantitative modeling opportunity for a clearly non-Mendelian mode of inheritance above the effects of heterosis (Thallman et al., 1993; Thallman et al., 2014). This random regression parameterization likely encompasses both the non-additive genetic effects as well as the non-Mendelian inheritance.

The range of estimates of heritability for weaning weight from random regression analyses was larger (0.26 to 0.65; Figure 3.8), although the highest values were not as

large. Reported estimates of heritability for weaning weight were similar (0.19, Shepard et al., 1996; 0.20, 0.21 and 0.32 Dodenhoff et al., 1999; 0.21 and 0.30, Alenda and Martin, 1987; 0.25, Elzo and Wakeman, 1998; 0.30 and 0.40 Schaeffer and Wilton, 1981; 0.46, Knights et al., 1984; 0.53, Kaps et al., 1999; 0.63, Brown et al., 1990; 0.63, Johnson et al., 1992; 0.70, Rasali et al., 2005), but the largest values from the current random regression analysis were higher than estimates reported for Nellore cattle (0.14, Eler et al., 1995; 0.15, 0.23 and 0.26, Magnabosco et al., 2000; 0.26, 0.28, and 0.33, Ribeiro et al., 2006).

Modeling the genotype of animals across a gradient associated with parental breed composition information implies an interaction between the additive genetic component of animals with non-additive genetic effects associated to specific △Ne from different parental combinations. These non-additive genetic effects could correspond to either dominance effects, epistatic effects, parent-of-origin effects, or combinations among these (Falconer and Mackay, 1996; Loschiavo et al., 2007; Vrana, 2007). Heritability estimates in this study should be interpreted as a contextual parameter, that is, the specific △Ne associated to parental cross types, and the corresponding average non-additive effects acting on birth weight and weaning weight phenotypic values.

Results from the linear random regression model for birth weight indicated that the greatest estimate of heritability ($h^2 = 0.8$; Figure 3.7) was associated with F_1 calves with Nellore sires and Angus dams (△Ne = 2). Heritability estimated for calves out of the reciprocal cross (Angus x Nellore; △Ne = 0), was somewhat smaller (0.56). Heritability estimated from both Nellore x Angus reciprocal crosses were higher than

heritability estimated using the animal model ($h^2 = 0.48 \pm 0.05$). Furthermore, across the gradient of △Ne values, all heritability estimates were higher than the estimated value from the animal model, probably due to relocation of part of the residual variance associated to non-additive effects into the random regression (co)variance components. The minimum estimate of heritability ($h^2 = 0.5$) was obtained for △Ne of 0.5, which is associated to crosses where dams have 50% more Nellore content in their breed composition than sires, such as Angus x ½ Angus-½ Nellore cross. Estimates of heritability for crosses with △Ne of 1.5 (Nellore content in sires 50% higher than in dams; e.g., ½ Angus-½ Nellore x Angus cross) had an intermediate value of 0.69. Thus, heritability estimates were greater for crosses where the sire had a higher amount of Nellore than the dam, and as such may be accommodating dominance variation (heterosis) and non-Mendelian variation.

The trajectory of the weaning weight heritability gradient from random regression analyses was similar to that from the birth weight analysis. The highest heritability estimate ($h^2 = 0.65$) was obtained at △Ne of 2 (Nellore x Angus cross), and the smallest estimate ($h^2 = 0.26$) was around △Ne of 0.5 (Angus x ½ Angus-½ Nellore cross; Figure 3.8). Heritability estimate for △Ne equal 2 (Nellore x Angus cross) was almost twice as large as for △Ne equal 0 (Angus x Nellore cross) (0.65 vs. 0.31). Estimates of heritability for weaning weight were larger than the estimated value from the animal model (0.34 ± 0.06) for values of △Ne larger than 0.94 (e.g., Angus x Angus, Nellore x Nellore, ½ Angus-½ Nellore x ½ Angus-½ Nellore, ½ Angus-½ Nellore x ⅝ Angus-⅜ Nellore, and Nellore x Angus crosses). This may indicate that estimates from

animal models could be biased because the model is not accounting for heterosis effectively.

Prediction models for birth weight and weaning weight incorporate covariance estimates between direct and maternal additive genetics effects when the dataset is large enough to estimate all the covariance components; however, this covariance was not included in the present study for linear random regression models because the extra number of covariances would make the models too complicated for the current birth weight and weaning weight databases. Consequently, this covariance was also not included in animal models in order to make these models comparable to the linear random regression models though likelihood ratio tests. Likelihood-ratio tests determined that the linear random regression model for birth weight and weaning weight had a better fit for the data in comparison to the respective animal model.

It was not possible to identify is the non-additive effects acting over the phenotypic expression of birth weight and weaning weight corresponded to dominance, epistasis, or parent-of-origin effects; however, these results represent a novel approach with potential application for cattle operations based on crossbreeding strategies. Results from random regression analyses indicated that it may be possible to select sires that can increase progeny birth weight and weaning weight at different rates in the context of the type of cross, due to different average non-additive genetic effects interacting with sire's additive genetic component across different cross types. Much of US beef production is based on crossbreeding strategies. Those strategies mostly involve consideration of relative sire genetic merit only in a purebred context.

This novel approach may offer prediction advantages in *Bos indicus-Bos taurus* crosses, as the non-Mendelian inheritance of birth weight in those crosses (Cartwright et al., 1964; Paschal et al., 1991; Chase et al., 2000; Holloway et al., 2002) has enormous economic consequences. Selection methodology is needed in such crosses to reduce the negative impacts of birth weight increase and thereby reduce incidence of dystocia, preventing its negative impacts on calf health, and survival of both calf and dam (Dillon et al., 2015). This approach might be beneficial for crosses involving crossbred animals where the sire has a larger proportion of *Bos indicus* in his breed composition than the dam, as larger birth weight has also been identified for calves out of this type of crosses in comparison to progeny from the respective reciprocal cross (Cartwright et al., 1964; Amen et al., 2007). Extensions of this methodology to sex-specific predictions may permit selection of *Bos indicus* sires that sire male progeny with "safe" birth weights when the sires are used in a *Bos indicus* x *Bos taurus* crossbreeding scenario.

Additional work is required to refine modeling of parental breed composition in the models to resolve some potential confounding effects from different cross types that can lead to equal △Ne values, such as Angus x Angus, Nellore x Nellore, and ½ Angus-½ Nellore x ½ Angus-½ Nellore crosses (△Ne = 1) or as ¾ Angus-¼ Nellore x ½ Angus-½ Nellore and Angus x ¾ Angus-¼ Nellore crosses (△Ne = 0.75). This represents the first attempt to characterize cattle genetic variance within a context for parental breed combination gradients through random regression. Results of these analyses could benefit cattle operations already realizing the benefits of both additive and non-additive genetic effects on birth weight and weaning weight through production of various *Bos*

indicus-Bos taurus crosses and could aid in genetic prediction for first generation crosses in *Bos indicus-Bos taurus* composite populations.

3.5. Conclusion

This study evaluated a novel strategy to model interactions between additive and non-additive genetic effects in genetic merit predictions equations for birth weight and weaning weight on a population involving Nellore and Angus influenced parents. There may be potential to select sires (or dams) based on their genetic merit predicted for specific crossbreeding scenarios. Therefore, improvement of progeny phenotypic performance for birth weight and weaning weight could be optimized for different type of parental crosses. However, current modeling strategy needs to consider additional features to remove confounding effects for some types of parental crosses, and to account for potential sex dimorphism effects on genetic merit predictions across crosses.

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CHAPTER IV

RANDOM REGRESSION OF HEREFORD PERCENTAGE INTRAMUSCULAR FAT ON GEOGRAPHICAL COORDINATES

4.1. Introduction

Genetic merit is likely contextual, and it may be beneficial to predict genetic merit for economically important traits across environments. Burns et al. (1979) revealed genotype-environment interactions (G x E) in Hereford cattle for birth weight, pre-weaning gain, estimated 205 d weight, body length, body condition score, and annual production per cow. Hayes et al. (2016) supported the usefulness of incorporating G x E into livestock genetic evaluations, and Fennewald et al. (2017) identified G x E for stayability in different regions within the United States (US) for Red Angus. Genetic variation within breed subpopulations reared in different environments has shown to impact heritability (Blackburn et al., 2017), and can lead to over- or underestimate breeding values if predictions across subpopulations are done without accounting for environment. Notter et al. (1992), Hayes et al. (2016), and MacNeil et al. (2017) support the use of G x E in beef cattle genetic evaluation. However, G x E has not been employed in US National Cattle Evaluation. Not accounting for G x E could lower the rate of genetic change for traits. The American Hereford Association has records to account for G x E in genetic merit predictions. Among relevant traits fit for this analysis strategy, intramuscular fat (IMF) impacts beef quality, and its improvement in post-natal

life via nutrition is governed by the genetic potential of the breed (Pethick et al., 2004; Hocquette et al., 2010).

Random regression procedures make it possible to model G x E and attain a greater level of precision for parameter estimates and genetic merit predictions (Cardoso et al., 2012). Accounting for ecozone would help producers select sires more fit to the environment in their operations. The objective of this study was to estimate genetic parameters for IMF in American Hereford cattle using random regressions across latitude or longitude coordinates within the continental US and to evaluate estimates differences.

4.2. Materials and Methods

4.2.1. Records

Records were provided by the American Hereford Association. Using open source databases (http://federalgovernmentzipcodes.us/), longitude and latitude coordinates were obtained for each IMF record using the U.S. Postal Service zip code of the ranch listed as the breeder. Contemporary groups were defined by the American Hereford Association, combining information related to herd, sex, management group, and birth date of the animals. Records without an associated zip code or with no contemporary group assignment were removed. Records greater than the mean +4 SD or less than the mean –4 SD were considered outliers and removed. After editing, the final data included 169,440 IMF records. The pedigree included 227,902 animals and 9 generations.

4.2.2. Statistical Analyses

Analysis assessed the benefits of using linear or quadratic random regressions of IMF on latitude or longitude coordinates versus traditional animal models in genetic parameters estimation, accounting for US as a unique geographic location. Additionally, linear random regressions were evaluated subdividing the US into 2 and 4 regions, in order to identify the impact of an increase in geographical subdivision of the country over genetic parameters estimation.

The animal model followed this form:

$$y = X\beta + Zu + Wc + e$$

where *y* was a vector of IMF records, β was a vector of estimated fixed effects for a linear regression on longitude or latitude coordinate, *u* was a vector of random additive genetic effects, *c* was a vector of random contemporary group effects, *e* was a vector of residuals, and *X*, *Z*, and *W* were incidence matrices relating observations in *y* to values in β, *u*, and *c*.

Expectation for the components in the random vector were equal to vectors of 0, with variance-covariance structure:

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} G & 0 & 0 \\ 0 & C & 0 \\ 0 & 0 & R \end{bmatrix}$$

in which $G = A\sigma_a^2$, where *A* was the numerator relationship matrix constructed with the pedigree information, and σ_a^2 is the additive genetic variance; $C = I\sigma_c^2$, where *I* is an identity matrix and σ_c^2 the contemporary group variance; $R = I\sigma_e^2$, and σ_e^2 is the residual variance.

The linear and quadratic random regression models followed the general form:

$$y = X\beta + Qu + Wc + e$$

in which *y*, *β*, *c*, and *e* vectors were as described for the animal model, and *u* was a vector of random regression coefficients for additive genetic effects. *X* and *W* were incidence matrices as described for the animal model, and *Q* was the design matrix containing the longitude or latitude coordinates as covariates, and relates the IMF records in *y* to the additive genetic random regression coefficients in *u*. The number of columns in the *Q* matrix is equal to the order of the random regression (2 or 3 for the linear and quadratic random regressions, respectively). Expectation of the random vectors were a vector of 0. The variance-covariance structure was:

$$Var\begin{bmatrix} u \\ c \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & C & 0 \\ 0 & 0 & R \end{bmatrix}$$

where *A* was the numerator relationship matrix, *G* the covariance matrix of additive genetic regression coefficients with an order equal to the polynomial modeled; *C* and *R* were matrices as described for the animal model. The *G* matrix used in the random regression models included the estimation of the variances and covariances of the intercept and the regression coefficients.

Models for analyses of regionally-subdivided data included a linear random regression of IMF on longitude or latitude coordinates unique by region (i.e., one linear random regression per each region in the model). Analyses of data subdivided into two regions included unique random regressions within North and South (longitude; Figure 4.1) or West and East (latitude; Figure 4.3) regions. Analyses of data divided into 4

regions included random regressions within North 1, North 2, South 1, and South 2 (longitude; Figure 4.2) and West 1, West 2, East 1 and East 2 (latitude; Figure 4.4) regions. Regional boundaries were designated at specific longitudes or latitudes which were chosen to evaluate an overall even land territory across regions, and to keep similar numbers of records in each region. The North and South regions were delineated at 40°N latitude, with 94,188 and 75,252 records, respectively (Figure 4.1). The boundary between West and East regions was set at 99°W longitude, with 84,340 and 85,100 records, respectively (Figure 4.3). Boundaries for analyses of random regression on longitude within 4 regions were set at 44.46°N (between North 1 and North 2), 40°N (between North 2 and South 1), and 36.46°N (between South 1 and South 2). Corresponding numbers of records were 42,403, 51,785, 42,927, and 32,325 for the North 1, North 2, South 1, and South 2 regions, respectively (Figure 4.2). The regional boundaries for random regression on latitude were set at 104.55°W (between West 1 and West 2), 99°W (between West 2 and East 1), and 92.22°W longitude (between East 1 and East 2), with 47,151, 37,949, 46,427, and 37,913 records represented in the West 1, West 2, East 1 and East 2 regions, respectively (Figure 4.4).

Figure 4.1. Regional subdivision of the US into North and South regions. Dashed line indicates boundary between North and South regions at 40° N. The value for "n" represents the number of IMF records within a region.

Figure 4.2. Regional subdivision of the US into North 1, North 2, South 1 and South 2 regions. Dashed lines from north to south indicate boundary between North 1 and North 2, North 2 and South 1, South 1 and South 2 regions at 44.46° N, 40° N, and 36.46° N, respectively. The value for "n" represents the number of IMF records within a region.

Figure 4.3. Regional subdivision of the US into West and East regions. Dashed line indicates boundary between West and East regions at 99° W. The value for "n" represents the number of IMF records within a region.

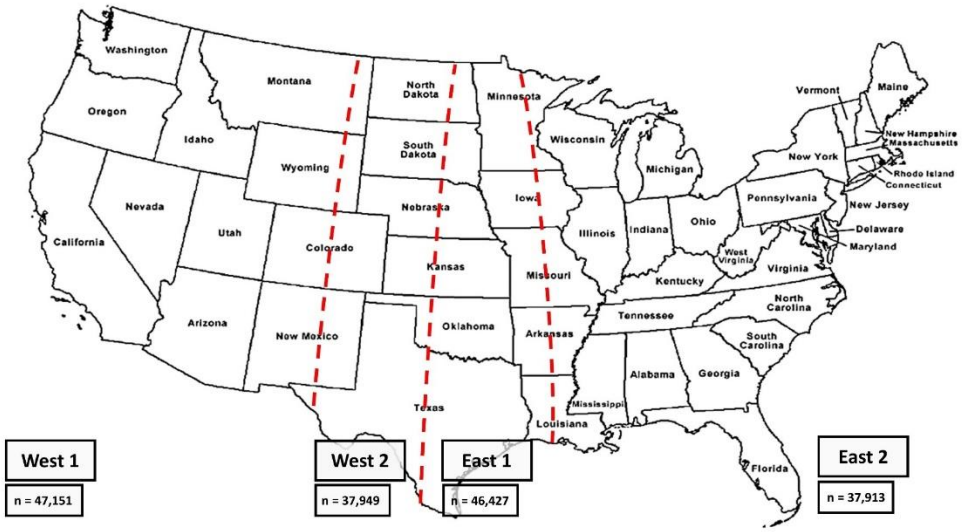

Figure 4.4. Regional subdivision of the US into West 1, West 2, East 1 and East 2 regions. Dashed lines from north to south indicate boundary between West 1 and West 2, West 2 and East 1, East 1 and East 2 regions at 104.55° W, 99° W, and 92.22° W, respectively. The value for "n" represents the number of IMF records within a region.

The analyses of unique random regressions per region were the same as the first set of random regression models with the same expectations for first and second moments. They differed in that *Q* is the incidence matrix containing the longitude or latitude coordinates covariate nested within regions and relates the IMF records in *y* to the additive genetic random regression coefficients in *u* for each region in the model. The number of columns in the *Q* matrix was associated with the order of the random regression amplified by the number of modeled regions (four for the 2-region subdivision, and eight for 4-region subdivision). The strategy for *G* matrix estimation was to first estimate variances of coefficients with all other covariances fixed at 0, and then incrementally add covariance components for estimation while holding previously estimated parameters constant; various analyses were attempted varying the set of parameters held constant. Analyses were repeated as necessary with estimation of previously fixed components. Non-estimable covariance components were fixed to zero and all other parameters were simultaneously estimated in final models. For analyses with two regions modeled, the *G* matrix included the estimation of variances for the intercept and the linear regression coefficient from both regions, as well as all covariance components between intercepts and linear regression coefficients from those two regions. In analyses with four regions the *G* matrix included the variances for intercepts and linear regression coefficients from each region, as well as the covariance between the intercept and the linear regression coefficient within each region. Estimation of other covariance components in the *G* matrix were prioritized in this order: 1) covariances between each pair of linear regression coefficients across regions, 2)

covariances between each pair of intercept coefficients across regions, 3) all other covariances.

Likelihood-ratio tests were conducted for analyses of the data without regional subdivisions. Differences in the structure of the analyses using the 2-region and 4-region models did not permit statistical comparison. Analyses were conducted using ASReml (Gilmour et al., 2009), and the Texas A&M University High Performance Research Computing Service.

From random regression analyses gradients of heritability for IMF across longitude or latitude coordinates were estimated using variance component estimates (Schaeffer, 2016).

4.3. Results

4.3.1. Fixed Effects

The fixed effect of linear regression of IMF on latitude coordinates was significant ($P < 0.001$) with latitude as covariate. The corresponding fixed regression on longitude coordinates was significant only in the quadratic random regression model analysis. Nevertheless, the fixed linear regression was kept in the animal and linear random regression models that utilized longitude as covariate to permit likelihood-ratio tests.

The fixed effect of region, as well as the linear random regression of IMF on latitude nested within region were significant ($P < 0.001$) when data was subdivided in either 2 or 4 regions. When longitude was used as covariate in the model, the previous effects were only significant ($P < 0.001$) when data was subdivided in 4 regions.

These effects were kept in random regression analyses regardless of significance in order to facilitate model comparison.

4.3.2. Across-Region Random Regression

Results from the likelihood ratio test between each pair of the three continental US models (animal model, linear random regression model, and quadratic random regression model), using either latitude or longitude coordinates as covariate, indicated that the quadratic random regression model has the better fit for these data ($P < 0.001$).

Heritability estimated using the animal model with either latitude or longitude coordinates as covariate was low (0.19 ± 0.004). Variances estimated for linear and quadratic random regression coefficients (latitude as a covariate) are shown in Table 4.1 and Table 4.2, respectively.

Table 4.1. Estimates of variance from linear random regression analyses[1]

	Contemporary group	Intercept	Linear	Residual
Latitude covariate				
Contemporary group	**0.38 ± 0.004**			
Intercept		**0.25 ± 0.006**		
Linear		0.04 ± 0.002	**0.02 ± 0.003**	
Residual				**0.23 ± 0.002**
Longitude covariate				
Contemporary group	**0.37 ± 0.004**			
Intercept		**0.25 ± 0.006**		
Linear		0.00 ± 0.003	**0.09 ± 0.005**	
Residual				**0.24 ± 0.002**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of contemporary group and residual with other terms were assumed to be 0.

Table 4.2. Estimates of variance from quadratic random regression analyses[1]

	Contemporary group	Intercept	Linear	Quadratic	Residual
Latitude covariate					
Contemporary group	**0.38 ± 0.004**				
Intercept		**0.20 ± 0.008**			
Linear		0.05 ± 0.002	**0.04 ± 0.006**		
Quadratic		–0.02 ± 0.003	0.00 ± 0.003	**0.01 ± 0.004**	
Residual					**0.23 ± 0.002**
Longitude covariate					
Contemporary group	**0.37 ± 0.004**				
Intercept		**0.26 ± 0.010**			
Linear		0.01 ± 0.003	**0.05 ± 0.009**		
Quadratic		0.02 ± 0.005	–0.02 ± 0.003	**0.03 ± 0.004**	
Residual					**0.23 ± 0.002**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal. Covariances of contemporary group and residual with other terms were assumed to be 0.

For analyses of latitude, heritability estimated with linear and quadratic random regression parameters resulted in similar ranges (0.08 to 0.27, linear; 0.12 to 0.27, quadratic). Plotted estimates of heritability from linear random regression on latitude appeared to increase from South to North (Figure 4.5). Estimates produced from the quadratic random regression were lower in southern latitudes, but higher in middle latitudes.

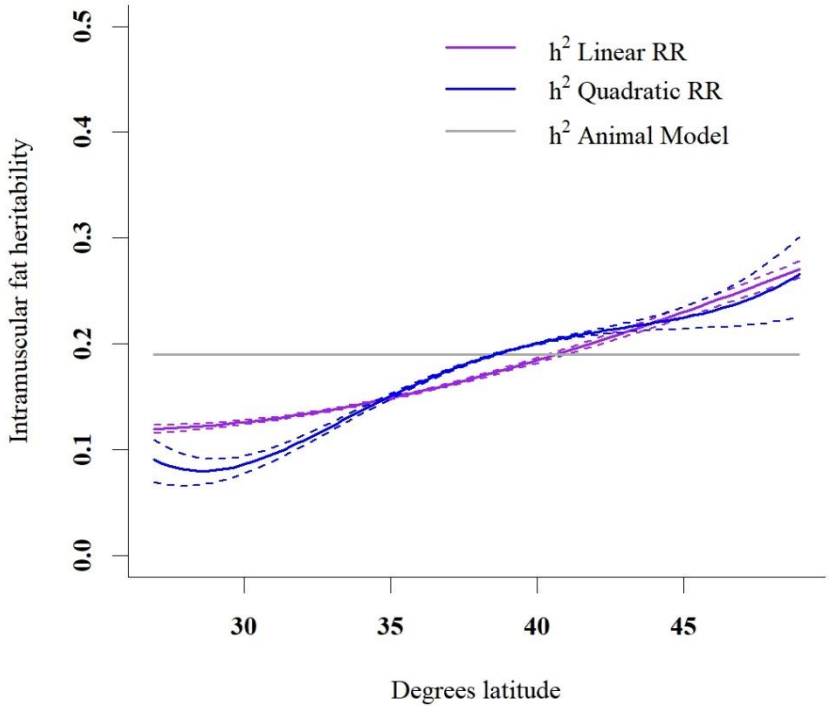

Figure 4.5. Estimates of heritability for IMF from the animal model, linear and quadratic random regression (RR) of IMF on latitude (dashed lines indicate ± 1 SE).

The variances estimated for the random regression coefficients using longitude as a covariate are shown in Table 4.1 and Table 4.2. These yielded estimates of heritability ranging from 0.17 to 0.30 (linear random regression only), and from 0.17 to 0.37 using the quadratic random regression (Figure 4.6). The curve of plotted estimates of heritability from the analysis that included only a linear random regression was fairly symmetric and positively parabolic, generally smooth, and indicated greater estimates of heritability at the two extremes of longitudinal coordinates (farthest West, and farthest East), with a minimum heritability in the middle of the regression. The curve of heritability estimates from analyses with a quadratic random regression was asymmetric,

with a single inflection less centered and positioned closer to the West than for the linear random regression (Figure 4.6).

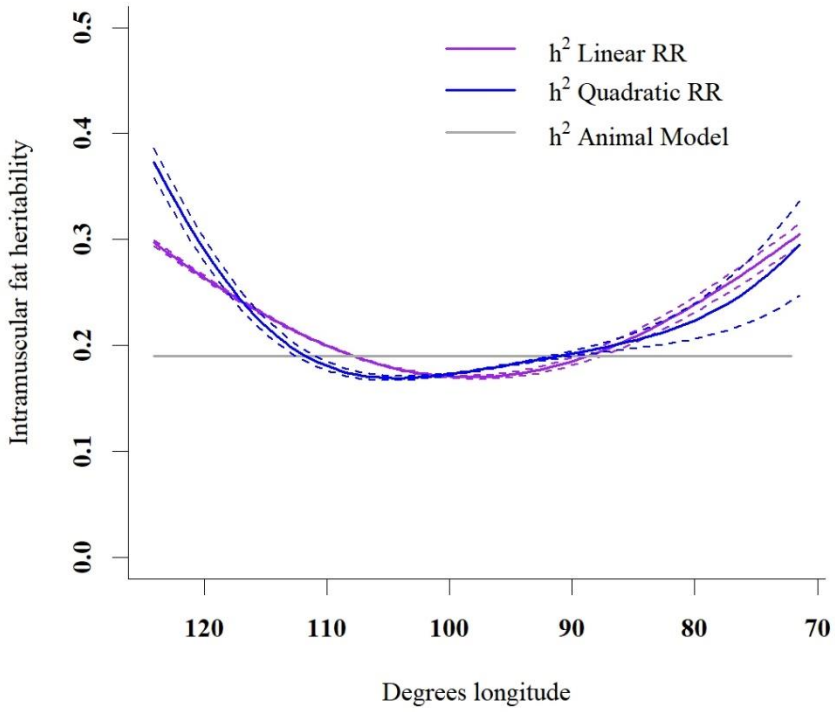

Figure 4.6. Estimates of heritability for IMF from the animal model, linear and quadratic random regression of IMF (RR) on longitude (dashed lines indicate ± 1 SE).

4.3.3. Unique Random Regressions by Region

Regions within the continental US present a range of environmental differences (Blackburn et al., 2017). Random regressions as used in the present study may be more appropriate to consider as unique to regions. This was done as an attempt to model North-South and East-West environmental changes simultaneously.

The continental US was subdivided into two major regions (North and South or West and East for latitude or longitude coordinates as covariate, respectively), with an

overall similar number of records and territory size covered. This approach made it possible to estimate variances for random intercepts and random regression linear coefficients and covariance components in analyses with latitude coordinates as was covariate (Table 4.3) and longitude coordinates as covariate (Table 4.4).

Table 4.3. Linear random regression (co)variance components estimates for IMF on latitude in 2 regions[1, 2]

	β_0 East	β_1 East	β_0 West	β_1 West
β_0 East	**0.27 ± 0.007**	0.77 ± 0.076	0.91 ± 0.031	0.37 ± 0.081
β_1 East	0.06 ± 0.004	**0.03 ± 0.005**	0.62 ± 0.115	0.41 ± 0.215
β_0 West	0.22 ± 0.009	0.05 ± 0.008	**0.22 ± 0.008**	0.34 ± 0.065
β_1 West	0.04 ± 0.009	0.01 ± 0.007	0.03 ± 0.004	**0.04 ± 0.007**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal and correlation coefficients are above.
[2]Data were divided into West and East regions at 99° W longitude.

Table 4.4. Linear random regression (co)variance components estimates for IMF on longitude in 2 regions[1, 2]

	β_0 North	β_1 North	β_0 South	β_1 South
β_0 North	**0.32 ± 0.008**	0.32 ± 0.020	0.78 ± 0.038	0.18 ± 0.085
β_1 North	0.07 ± 0.007	**0.17 ± 0.011**	0.06 ± 0.070	0.11 ± 0.148
β_0 South	0.20 ± 0.011	0.01 ± 0.013	**0.21 ± 0.006**	–0.03 ± 0.027
β_1 South	0.03 ± 0.016	0.02 ± 0.020	–0.01 ± 0.004	**0.11 ± 0.008**

[1]Variances are on diagonal and in bold type. Covariances are below that diagonal and correlation coefficients are above.
[2]Data were divided into North and South regions at 40° N latitude.

Increasing the order of the random regression to a quadratic polynomial (intercept, linear, and quadratic) was never accomplished when data were divided into regions due to computational limitations of ASReml when the additional covariances were included in the model, preventing convergence of parameter estimates. Variance of intercepts were similar in magnitude in random regressions of IMF on latitude or longitude; however, the variances of the linear random regression coefficients on

longitude (Table 4.4) were from two to five times larger than those from regression on latitude (Table 4.3). Correspondence of random regression coefficients (latitude) was positive and large, as correlations of those components ranged from 0.34 to 0.91 (Table 4.3); much lower correspondence of random regression coefficients (longitude) is shown in Table 4.4. As an exception, the correlation of intercept coefficients for the North and South regions was large ($r = 0.78 \pm 0.04$).

Random regression of IMF on latitude resulted in estimation of only variances of regression coefficients and within-region covariances of coefficients (Table 4.5). Intercept variances were similar in the central regions (West 2 and East 1) and between one half and two thirds of the magnitude of those on the extremes (West 1 and East 2). The West 1 region (furthest West) differed substantially from the other regions as the variance estimates of the linear regression coefficient was two to three times larger than all other regional variances of that coefficient. The West 1 region had a negative genetic correlation between the intercept and linear regression coefficients; all other regions were large and positive.

A larger number of parameters were estimated in analyses of random regression on longitude in 4 regions (Table 4.6). Variances estimated for the intercept and linear regression terms were largest in the Northernmost region (North 1) and progressively smaller in each region to the South, which was similar to the pattern of variances from analyses of data in 2 regions (Table 4.4). Within-region correlations between the intercept and linear terms were large and positive in both North regions, but of low magnitude in both South regions, and that in the Southernmost region (South 2) was

negative (Table 4.4). Across-region correlations between the linear regression coefficient terms were large and positive for North 1 with North 2 and South 1 with South 2. That for North 2 with South 1 (these are adjacent regions) was less than half the magnitude. Correlations of linear regression coefficients of North 1 with South 1 and North 2 with South 2 did not differ from 0. The correlation between linear regression coefficients from the extreme regions (North 1 with South 2) was large and negative.

Random regression analyses of subdivided data indicated reasonably similar estimates of heritability for IMF at Northern latitudes (Figures 4.7 and 4.8). However, at Southern latitudes, modeling distinct random regressions in the Western US resulted in much higher estimates of heritability in the westernmost region (West 1; Figure 4.7).

Table 4.5. Linear random regression (co)variance components estimates for IMF on latitude in 4 regions[1, 2, 3]

	β_0 East 1	β_1 East 1	β_0 East 2	β_1 East 2	β_0 West 1	β_1 West 1	β_0 West 2	β_1 West 2
β_0 East 1	**0.24 ± 0.008**	0.49 ± 0.078						
β_1 East 1	0.04 ± 0.004	**0.03 ± 0.008**						
β_0 East 2			**0.37 ± 0.010**	0.92 ± 0.072				
β_1 East 2			0.15 ± 0.008	**0.07 ± 0.014**				
β_0 West 1					**0.35 ± 0.015**	–0.31 ± 0.044		
β_1 West 1					–0.07 ± 0.015	**0.14 ± 0.020**		
β_0 West 2							**0.19 ± 0.009**	0.64 ± 0.126
β_1 West 2							0.04 ± 0.004	**0.03 ± 0.008**

[1]Absence of a value indicates that estimation of this parameter was not accomplished and was fixed to 0.
[2]Variances are on diagonal and in bold type. Covariances are below that diagonal and correlation coefficients are above.
[3]Lower numbers indicate regions further West. Boundaries separating the four regions were 104.55° W (between West 1 and West 2), 99° W (between West 2 and East 1), and 92.22° W (between East 1 and East 2).

Table 4.6. Linear random regression (co)variance components estimates for IMF on longitude in 4 regions[1, 2, 3]

	β_0 North 1	β_1 North 1	β_0 North 2	β_1 North 2	β_0 South 1	β_1 South 1	β_0 South 2	β_1 South 2
β_0 North 1	**0.42 ± 0.014**	0.46 ± 0.033						
β_1 North 1	0.17 ± 0.022	**0.33 ± 0.033**		0.54 ± 0.094		0.02 ± 0.147		–0.63 ± 0.167
β_0 North 2			**0.30 ± 0.008**	0.49 ± 0.022				
β_1 North 2		0.13 ± 0.022	0.11 ± 0.007	**0.16 ± 0.013**		0.21 ± 0.143		–0.11 ± 0.202
β_0 South 1					**0.25 ± 0.008**	0.13 ± 0.030		
β_1 South 1		0.01 ± 0.033		0.03 ± 0.022	0.02 ± 0.006	**0.15 ± 0.010**		0.49 ± 0.202
β_0 South 2							**0.16 ± 0.008**	–0.11 ± 0.057
β_1 South 2		–0.10 ± 0.029		–0.01 ± 0.023		0.05 ± 0.023	-0.01 ± 0.007	**0.08 ± 0.016**

[1]Absence of a value indicates that estimation of this parameter was not accomplished and was fixed to 0.
[2]Variances are on diagonal and in bold type. Covariances are below that diagonal and correlation coefficients are above.
[3]Lower numbers indicate regions further North. Boundaries separating the four regions were 44.46° N (between North 1 and North 2), 40° N (between North 2 and South 1), and 36.46° N (between South 1 and South 2).

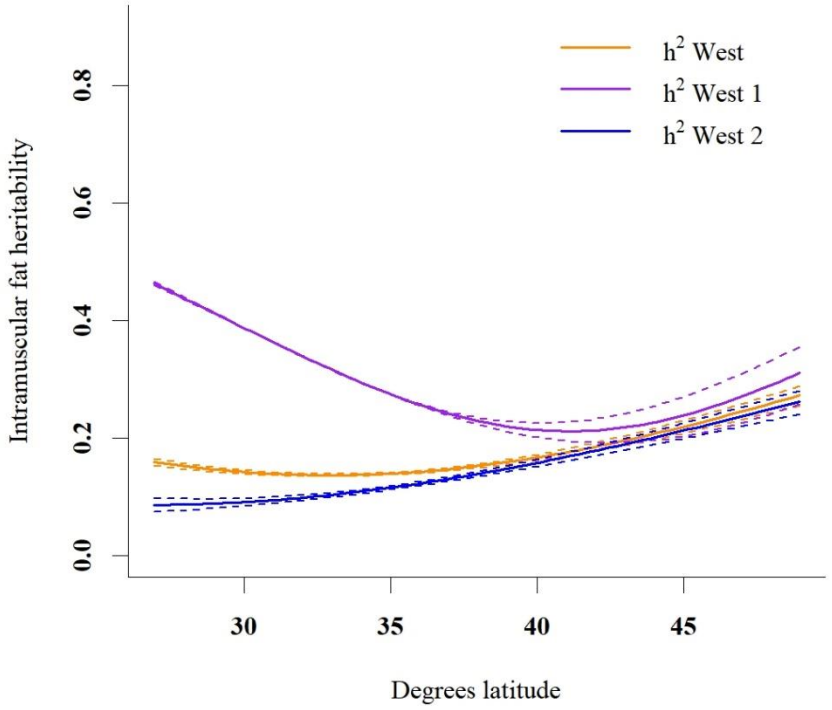

Figure 4.7. Estimates of heritability from linear random regression of IMF on latitude within the West region (data divided into West and East regions at 99° W), and within West 1 (furthest West subregion with boundary at 104.55° W) and West 2 regions (dashed lines indicate ± 1 SE).

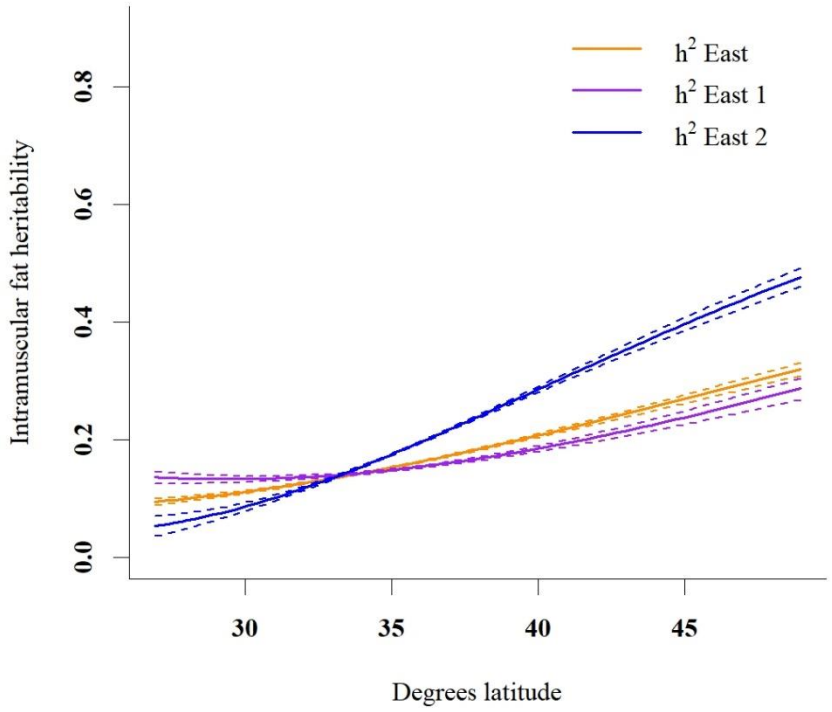

Figure 4.8. Estimates of heritability from linear random regression of IMF on latitude within the East region (data divided into West and East regions at 99° W), and within East 1 (furthest West subregion with boundary at 92.22° W) and East 2 regions (dashed lines indicate ± 1 SE).

Heritability estimates determined within the East and West regions ranged from 0.09 to 0.32, and 0.14 to 0.27, respectively. Heritability estimates in the West 1 and West 2 regions ranged from 0.21 to 0.46 and 0.09 to 0.26, respectively. Heritability estimates in the East 1 and East 2 regions ranged from 0.13 to 0.29 and 0.05 to 0.48, respectively. The curves of estimates of heritability obtained for the West, West 1, and West 2 regions differed in shape as well as in minimum and maximum values (Figure 4.7); particularly the curve obtained within the West 1 region, which had a shape more similar to a parabola in comparison to curves from the West and West 2 regions, which

appear linear. The minimum heritability value within the West 1 region was nearer to the center of the latitude coordinates evaluated (41° N), unlike the minimum value determined within the West, and West 2 regions, which was closer to the farther South coordinate (32.9 and 26.9° N, respectively).

Random regression analyses of data subdivided into 2 regions resulted in patterns of heritability of somewhat greater estimates in the Northern region (Figure 4.9), especially at the easternmost longitudes. Those estimates ranged from 0.19 to 0.47 and 0.15 to 0.31, for the Northern and Southern regions, respectively (Figures 4.9 and 4.10).

Analyses of data subdivided into 4 regions resulted in again larger estimates of heritability for IMF in eastern longitudes, especially in the northernmost region (North 1); or in other words, successively lower estimates in each region southward. Those estimates ranged from 0.22 to 0.63 (North 1; Figure 4.9), from 0.16 to 0.50 (North 2; Figure 4.9), from 0.17 to 0.40 (South 1; Figure 4.10) and from 0.12 to 0.28 (South 2; Figure 4.10).

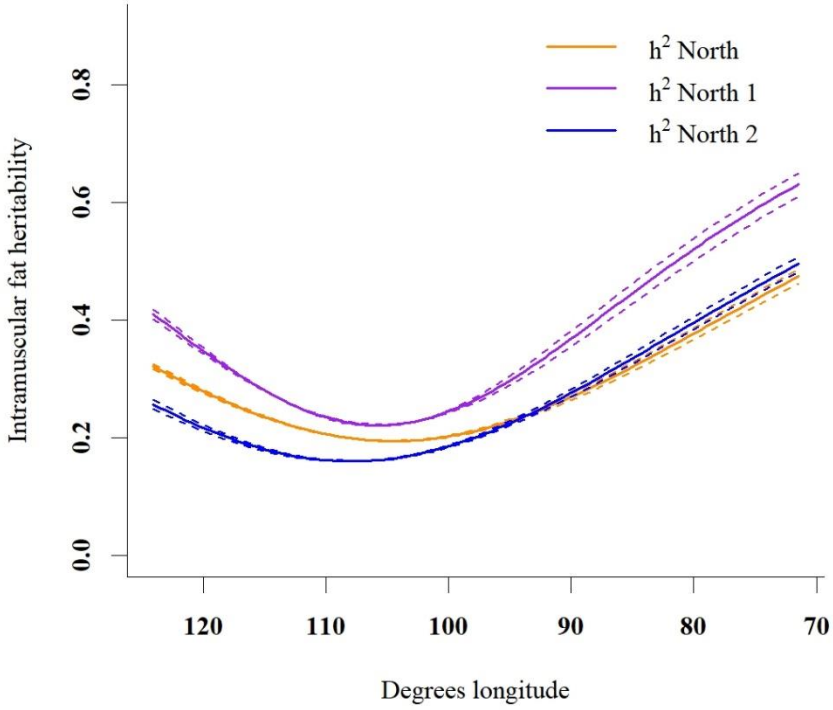

Figure 4.9. Estimates of heritability from linear random regression of IMF on longitude within the North region (data divided into North and South regions at 40° N), and within North 1 (furthest North subregion with boundary at 44.46° N) and North 2 regions (dashed lines indicate ± 1 SE).

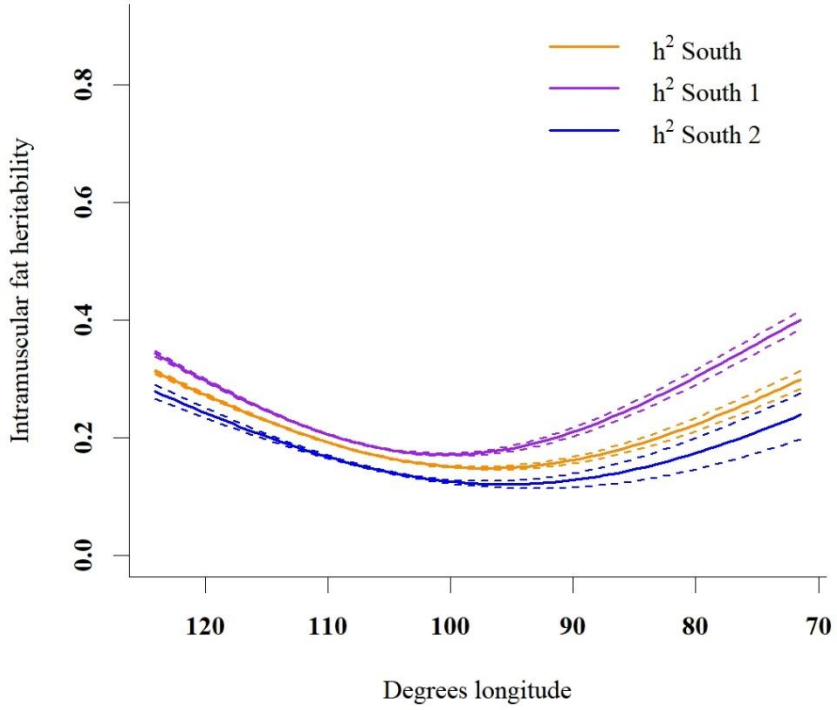

Figure 4.10. Estimates of heritability from linear random regression of IMF on longitude within the South region (data divided into North and South regions at 40° N), and within South 1 (furthest North subregion with boundary at 36.46° N) and South 2 regions (dashed lines indicate ± 1 SE).

The change in heritability estimates across longitude coordinates was similar in trajectory, where from West to East the heritability exhibited a decrease in value, achieving a minimum at longitude coordinates 104, 105, and 108° W for the North, North 1, and North 2 regions, respectively. With decreasing longitude (moving eastward), heritability estimates increased until achieving a maximum value at 71° W for North, North 1, and North 2 regions (Figure 4.9). Heritability estimates across longitude coordinates also decreased in the South, South 1 and South 2 regions (Figure 4.10); but reach a minimum value near the center of the evaluated longitude coordinates, and

higher values at the extremes of the respective curves. Differences at the extreme covariate values were less pronounced in the South (Figure 4.10) than those in Northern regions.

4.4. Discussion

Random regression methodology may provide an effective way to model the geographic-environmental complex. Likelihood ratio tests across models with data not subdivided into regions, using either latitude or longitude, indicated that the quadratic random regression better fit the data in comparison to the linear random regression and animal model. However, the variance components' estimates from the quadratic random regression model were low in comparison to estimates from the linear random regression using either latitude or longitude. Additionally, the extremes of the heritability curves estimated across latitude or longitude have larger standard errors when a quadratic random regression is modeled in comparison to the linear random regression. All this considered, maybe the use of a quadratic random regression is not necessarily the best alternative to model IMF with the current database, and more accurate estimations could be done using the linear random regression.

Heritability estimates using random regression of IMF on latitude coordinates (both linear and quadratic regressions) were greater in the northern and lower in the farthest South latitudes of the US. Random regression of IMF on longitude coordinates yielded heritability estimates that were lowest in the middle section of the country, and largest in the far west. Evaluation of linear random regression within four rather than two regions did not substantially impact the shapes of heritability curves from regions or

subdivided regions; but the minimum and maximum values for IMF heritability were influenced. In contrast, more restricted region size influenced the rate of change in the estimates of heritability across latitudes, especially in the western half of the country. In those analyses the maximum estimate of heritability in the furthest east region of 0.48 was noticeably greater than the other east subdivided region (0.32) and the overall (not subdivided) east region (0.29). The maximum estimate of heritability in the coastal west region was larger than the inland west region and the overall west region (0.46, 0.27, and 0.26, respectively), and this was the case for the minimum estimates of heritability in those same regions (0.21 vs 0.14 and 0.09 respectively). Results from random regression analyses on longitude and latitude jointly suggest that the greater heritability for IMF can be found in the coastal areas of the northern US, and the lowest values are found in the central south.

The range of IMF heritability estimated with the random regression models was similar to results out of traditional (not random regression) analysis (0.26 to 0.42) in Hereford cattle (0.26; Moser, 2006; 0.42; Su et al., 2017), suggesting that results are representative of the Hereford population in the US.

This current work suggests that the environment where animals were evaluated may impact the additive genetic estimates. Sire or other genetic components as an interaction with environment may merit inclusion in genetic evaluation (Bertrand et al., 1985; Bertrand et al., 1987). Genotype-environment interactions also have been studied for birth weight and weaning weight in Red Angus cattle using random regressions that evaluated sire's progeny within regions that differed in temperature and humidity indices

(Fennewald et al., 2017). Those authors concluded that genotype-environment interactions, although present, did not influence the rank of sire predictions of genetic merit for those traits.

There were substantially different regional heritability estimates (not random regression) for Red Angus birth weight (0.00 and 0.46, in the area near the Gulf Coast and the Upper Great Plains, respectively) and weaning weight (0.05 and 0.41, Gulf Coast and desert subregions; Fennewald et al., 2017).

The use of either longitude or latitude coordinates as an environmental gradient is a proxy for a combination of ambient and nutrition conditions. Those appeared to be most severe when considering covariance (of coefficients) differences from North to South and would at first consideration suggest differences in environment temperature or in forage species which are being consumed by the cattle. However, the large differences in estimates of variances from West to East were noteworthy, especially differences between the farther West region and the rest of the regions. Whether modeled through linear or quadratic random regressions, estimates of heritability (without modeling region) were lower in latitudes farther south (Figure 4.5). Linear random regressions on latitude (Figures 4.3 and 4.4) supported this with an exception of in the far West (West 1; Figure 4.7) in which estimates of heritability at lower latitudes were higher. North to South differences were also evident in the random regressions on longitude. Estimates of heritability were lower in the central (90 to 110º longitude) United States as indicated by either linear or quadratic random regression results (Figure 4.6). Random regression analysis within regions (linear random regression only) produced similar results (Figures

4.5 and 4.6) except that heritability estimates were much higher in the lowest longitudes of all regions, but especially the furthest North (Figure 4.9). Estimated correlation coefficients from random regression within regions supported positive correspondence of East-West regions in comparison to those from the North and South regions (0.41 vs. 0.11). This appropriately suggests greater difference between the environmental factors from northern and southern sections of the country. Adjacent regions often had positive correlations, and regions farther apart had negative correlations which became more negative with distance; that for the Northernmost and Southernmost was –0.63.

These results show the feasibility of using random regressions to account for genotype-environment interactions in genetic merit predictions with Hereford cattle. Furthermore, the use of this type of strategy would make it possible to select sires based on their location-specific genetic merit instead of an overall average across the country. This would lead to a more efficient genetic improvement of IMF, where the potential improvement per generation will depend on the genetic variability within specific geographic locations.

4.5. Conclusion

Considering the findings out of this project, the use of random regressions represents a promising modeling strategy to be considered by the American Hereford Association. Its use has the potential of providing producers with a better tool to select sires according to the specific environments where their operations are located. Nevertheless, further studies are needed in order to assess this methodology in additional economically relevant traits for this breed.

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CHAPTER V

CONCLUSIONS

Production and profitability in beef cattle operations are under the control of genetic and non-genetic factors, as well as interactions between them. Genetic sources of variation can be associated to breed type, as well as to genetic improvement strategies. On one hand, purebred cattle operations base their genetic improvement on selection, where animals' genetic merit for a set of relevant traits will determine which animals will be used as breeders. On the other hand, operations based on crossbreed animals base the improvement of the system on transmitting ability of animals as well as on the combining ability between breeds. Furthermore, crossbreed operations benefit from non-additive genetic effects by harvesting direct and/or maternal hybrid vigor.

Non-genetic factors affecting a cattle operation can have different origins, some of them are associated to the market and to the demand for specific products, and others associated to environmental conditions, such as temperature, humidity, feed resources, and level of productivity within a herd, among others. Moreover, some environmental descriptors can modulate the expression of the genetic potential of an animal, leading to changes in scale or ranking between animals' genetic merit when evaluated under different environments.

Additionally, interactions between genetics effects can also impact the performance of beef cattle when crossbreed populations are evaluated. These interactions are based on the association between additive and non-additive genetic

effects, where non-additive effects could correspond to dominance, epistasis, or even parent-of-origin effects.

In this study, interactions influencing genetic merit predictions and parameter estimation for growth- and carcass-related traits in beef cattle were evaluated using three different approaches. First, two modeling strategies were used to evaluate the effect of sire by progeny sex interaction on pre weaning and post weaning weight traits and intramuscular fat in Droughtmaster cattle. Both strategies indicated that improvement for weight at an average age of 546 d may be achieved at different rates across progeny sex categories, with intact males having the larger potential for improvement. Sire by sex interactions were not influential for weights measured earlier in life and intramuscular fat. Number of records for these analyses were small considering the complexity of the models and, thus, results may be subject to variation; however, the evaluated models may provide a good alternative to incorporate sire by sex interactions in prediction equations if larger databases are available.

Second, the interaction effect between animals' additive genetic component and non-additive genetic component on birth weight and weaning weight was evaluated across different crossbreed scenarios involving Nellore and Angus influenced parents. Results indicated that under specific type of crosses it may be possible to select sires that would improve birth weight and weaning weight at a higher rate than others. Therefore, the selection of sires (and dams) could be done more precisely according to the type of cross in which they will be used. Nevertheless, the proposed method requires additional

features to remove confounding effects between some parental crosses, as well as to account for potential sex effects on genetic predictions across different parental crosses.

Third, the interaction between additive genetic component and environments across longitude and latitude coordinates within the United States of America was evaluated for intramuscular fat in Hereford cattle. Results indicated that there was substantial additive genetic variance and heritability differences across the environment gradients determined by within-region longitude or latitude coordinates. Therefore, it may be possible to select sires that would increase the genetic gain for intramuscular fat on specific geographical environments, defined by latitude and longitude coordinates within the continental US.

Finally, the study of potential interactions affecting genetic merit predictions and parameter estimations is important for the beef industry, and to account for these interactions in genetic evaluations would provide more precise information to producers to select breeders according to the reality of their operations and, therefore, to increase the potential of the beef industry to respond to the increasing demand for food in the world.