REGION, SEASON, AND ALTITUDE AS SOURCES OF GENOTYPE BY ENVIRONMENT INTERACTIONS FOR GROWTH IN UNITED STATES BEEF CATTLE

by

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(Under the Direction of J. Keith Bertrand and Ignacy Misztal)

ABSTRACT

Identification of environmental factors important in genotype by environment (GxE) interactions will help producers in making the most optimal selection decisions given their management setting. Studies on growth in beef cattle have typically focused on genotype by region or genotype by country interactions. However, season is another environmental variable of interest because it encompasses potential environmental factors affecting growth such as forage quality and availability as well as temperature and humidity. The objective of the first study was to investigate the importance of genotype by region and season interactions for weaning weight in US Angus cattle. Altitude is known to be associated with brisket disease, a noninfectious cardiac pulmonary condition characterized by edema in the brisket and lower body. The objective of the second study was to determine if sires perform consistently across altitude and to quantify the genetic relationship between growth and survival at differing altitudes of Angus cattle born in Colorado.

Adjusted weaning weight (WW) records from 85,044 fall born calves in the Southeast, 64,389 winter born calves in the Southeast, 73,172 spring born calves in the Northwest, and 184,919 winter born calves in the Northwest were considered different, but genetically correlated traits in a multivariate analysis in order to investigate the presence of GxE. Genetic correlations ranged from 0.89 to 0.97 among direct effects and from 0.63 to 0.92 among maternal effects. Sires performed consistently across regions and seasons whereas maternal effects were variable across regions and seasons.

Growth records including 102,233 adjusted WW and 54,448 adjusted postweaning gain (PWG) were split into three traits, those measured at low, medium, and high altitude. A binary trait, survival (SV), accounted for censored records at yearling for each altitude. Genetic correlations between growth traits measured at different altitude were medium to high in magnitude, 0.47 to 0.83 for WW and 0.43 to 0.79 for PWG and indicate evidence for reranking of sires across altitude. Favorable positive genetic correlations were estimated between SV and PWG within the same altitude, suggesting that calves with genetics for increased growth from weaning to yearling also have increased genetic potential for SV at low, medium, and high altitude.

INDEX WORDS: Beef cattle, Brisket disease, Censored records, Genetic correlation, Genotype by environment interaction, Growth

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DEDICATION

I would like to dedicate this work to the loving memory of my father, Jim Lee, who always encouraged me to pursue my dreams. His life will forever serve as an example to me and my family.

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CHAPTER 1

INTRODUCTION

Widespread use of AI and embryo transfer has made it possible for sires to possess offspring in production under vastly different management systems and geographical areas. Problems arise when a sire's performance is inconsistent across different environments, defined as a genotype by environment interaction (**GxE**). Genetic evaluations traditionally regard a trait measured in different environments as the same trait, therefore published EPD are based on the performance of a sire's progeny in a number of environments and do not necessarily reflect his true merit in any one environment. Consequently, in the presence of GxE, producers basing their selection decisions on these genetic predictions may not obtain the performance they expect in their particular operation. Identification of environmental factors important in GxE will help producers in making the most optimal selection decisions given their management setting.

Studies investigating the existence of GxE in growth traits of beef cattle have generally focused on genotype by region or genotype by country interactions. However, some cattle may be more sensitive to seasonal changes than others implicating season as an environmental variable of interest. Season encompasses many potential environmental factors affecting growth such as forage quality and availability as well as temperature and humidity and has received little attention in studies on GxE.

High altitude is known to be associated with brisket disease, a noninfectious cardiac pulmonary condition characterized by edema in the brisket and lower body. This condition arises as pulmonary arteries thicken in response to low oxygen levels in the blood at high altitude, ultimately leading to a restriction in blood flow and possibly heart failure as blood accumulates in the veins and heart. Pulmonary arterial pressure can be used as an indicator trait for susceptibility to brisket disease given that elevated blood pressure is a reflection of a restriction in blood flow. Investigations into the genetic relationship between pulmonary arterial pressure and growth have revealed that selecting for growth at low altitude would increase pulmonary arterial pressure scores and susceptibility to brisket disease. Producers raising cattle in high altitude environments and basing their selection decisions on current genetic predictions may not obtain the performance they expect when the majority of a sire's offspring are maintained at low altitude. Therefore, reranking of sires in low and high altitude environments could be problematic for producers residing at high altitude.

The first objective of this study was to investigate the importance of genotype by region and season interactions for weaning weight in US Angus. The second objective of this study was to determine if sires perform consistently across altitude in the state of Colorado and to quantify the genetic relationship between growth and survival at differing altitudes.

CHAPTER 2

REVIEW OF LITERATURE

Introduction

Reproductive technologies available to beef producers, such as embryo transfer and artificial insemination have increased in popularity due to the potential amplified rate of genetic improvement obtained with such technologies. Consequently, genetic material can be widely distributed across very diverse regions and countries giving rise to bulls with progeny in production under vastly different environments. Therefore, it is important for cattle to adapt to a number of different environments without negatively affecting their performance.

Genotype by Environment Interactions

Genotype by environment interactions (GxE) occur when an animal does not perform consistently across different environments (Falconer, 1952). Falconer (1952) suggests that some individuals are more sensitive than others to environmental changes leading to more extreme changes in their performance in certain environments. Selecting individuals based on their performance in a favorable environment can lead to offspring which perform well in that environment, but perform poorly in a slightly less favorable one. Therefore, selecting individuals with superior performance in a less favorable environment will result in offspring that are less sensitive to environmental changes. The later situation would be preferable for producing robust cattle which perform consistently across a variety of environments.

Genotype by environment interactions can lead to either magnitude or rank changes depending upon how each sire behaves in each environment of interest (Bourdon, 2000). Figure 2.1 displays the two different changes with environmental value on the x-axis and phenotypic value on the y-axis. In Figure 2.1a, genotypes that show a magnitude change are depicted. Assuming one end of each line represents one environment and the other a different environment, it appears that all animals rank the same no matter which environment we look at. Although the differences between genotypes for performance are much smaller in the first as compared to the second environment, this type of GxE poses no problem from a selection standpoint because superior animals in one environment are still superior in the second environment (Lin and Togashi, 2002). In Figure 2.1b, genotypes exhibiting a rank change are presented. The lines now intersect and animals change in rank so that the best animal in one environment is now the worst animal in the second environment. In this case, selection of a sire based on his performance in one management setting could lead to unfavorable performance in a much different management setting.

Genetic evaluations traditionally regard a trait measured in different environments as the same trait, therefore published EPD are based on the performance of a sire’s progeny in a number of environments and do not necessarily reflect his true merit in any one environment (Bourdon, 2000). Consequently, in the presence of GxE, producers basing their selection decisions on these genetic predictions may not obtain the performance they expect in their particular operation. Therefore, understanding environmental factors important in GxE will help producers in making the most optimal selection decisions given their management setting.

The influence of GxE on a trait of interest can be determined through the use of three different types of statistical models (Bohmanova et al., 2008). In the past, an interaction term model has been used to investigate GxE. The interaction term model includes an effect of GxE and whether or not it is considered significant is an indicator of the presence of GxE; however this method does not allow for distinction between a magnitude or rank change (Strandberg, 2006). A more widely used method is a multiple trait model where records measured in different environments are considered different, but correlated traits. Robertson (1959) defined a genetic correlation of less than 0.80 between traits measured in two different environments as evidence for the presence of GxE of biological importance. Therefore, a large genetic correlation above 0.80 indicates a GxE of little effect whereas a small correlation would indicate that there is strong influence of GxE on the trait. More recently, a reaction norm model has been used that relates the mean phenotypic response of a genotype to a change in environment. These models illustrate how an individual's performance changes in relation to a change in environment on a continuous scale (Lynch and Walsh, 1998). The estimated slope from such a model indicates the degree of sensitivity of each genotype.

Types of Interactions

The presence of GxE has been investigated for many traits in beef cattle using a variety of the methods described previously. Environments of most interest for production traits have been different regions within the same country and different countries.

Between Regions within the Same Country

Several studies have focused on possible interactions between genotypes (sire or breed composition) and different locations (either across or within states) as a measure of a change in magnitude or a change in rank. Studies on GxE for growth traits have centered on birth, weaning, and yearling weights. Although the amount of environmental variation for growth traits is small in comparison to more lowly heritable traits, GxE still exist and identification of factors that can potentially cause reranking are important.

Birth weight often affects the economically relevant trait calving ease; therefore a great deal of reseach on GxE has focused on this trait. Burns et al. (1979) compared line by location interactions for birth weight among Hereford cattle. The first phase of their study included comparison of two unrelated lines of which one was selected for performance in Montana and the other in Florida (M1 and F6, respectively). Cattle from each line were transported to the location opposite of that from which they originated and their performances compared to that in their original location after 7 years of selection. Birth weights were 7.8 kg higher for M1 cattle evaluated in Montana than for M1 cattle in Florida. Similarly, birth weights of F6 cattle were 5.2 kg higher in Montana as compared to Florida suggesting there was an apparent advantage for the Montana location (Burns et al., 1979). In addition, birth weights were 1.3 kg higher on average in local groups as compared to introduced groups suggesting evidence for GxE. The second phase of their study included comparison of two related lines, M1 and F4, where F4 was selected in Florida, but came from a foundation of M1 cattle. Differences in performance between lines M1 and F4 were similar to those found between M1 and F6 in phase 1 (Burns et al., 1979). A similar study, conducted in the two very opposite environments of

Nebraska and Florida, reported a significant breed group by location interaction (Olson et al., 1991). Birth weight in calves from Bos indicus x Bos taurus dams was reduced by 6.9 kg in Florida relative to Nebraska whereas that of Bos taurus x Bos taurus dams was reduced by 9.0 kg. Alternatively to the previous studies, a study of Simmental sired calves across eight different regions of the United States revealed no sire by region interaction for birth weight (Nunn et al., 1978). These findings were confirmed by a study of Hereford sired calves in three different locations of North Carolina (Tess et al., 1984).

Strong emphasis is placed on weaning weight, especially by producers marketing cattle at weaning and interest in the influence of GxE on this trait is reflected in the literature. The study conducted by Burns et al. (1979), and described previously, revealed a significant line by location effect on weaning weight for both phases. Cattle local to the location of measurement were heavier on average than those introduced individuals by 16 kg in phase 1 and by 10 kg in phase 2 (Burns et al., 1979). Likewise, Olson et al. (1991) reported significant breed group by location effects. Dams of Zebu sires weaned calves with approximately equal weights in both Nebraska and Florida whereas Bos taurus crossbred dams weaned calves that were 28 kg heavier in Nebraska than in Florida. Nunn et al. (1978) also obtained a significant sire by region effect. Genetic correlations between weaning weight measured in eight different regions of the United States differed from unity and ranged from 0.73 to 0.78; however no significant region x sire interaction was reported for weaning weight within the state of Montana. Buchanan and Nielsen (1979) reported genetic correlations between breeding values across five regions of the United States (Northwest, Midwest, Southwest, Southeast, and

Northeast) ranging from 0.30 to 0.80 as evidence of significant sire by region interactions. Considering weight of Hereford calves in nine different regions of the United States as different traits, Bertrand et al. (1985) obtained an average genetic correlation of 0.64 and concluded that sire x region interactions were significant.

The GxE studies on weaning weight mentioned to this point would show strong evidence of GxE; however other studies have shown no significance. Tess et al. (1984) reported no significant sire x location interaction for weaning weight between what they classified as the Coastal Plain, lower Piedmont, and Mountain regions of North Carolina. Similary, Woodward and Clark (1950) reported no significant sire by location interaction for calves weaned in either Northern or Southern Montana, although they mention gains tended to be higher in Northern Montana. Insignificant genotype by region interactions have also been reported in a study by de Mattos et al. (2000) in which weaning weight in the Upper Plains-Corn Belt and the South-Gulf Coast of the United States were treated as different traits. A genetic correlation of 0.88 was estimated between weights in these two fairly diverse environments and is suggestive of a GxE of little biological importance (de Mattos et al., 2000).

Studies investigating the presence of GxE for weaning weight within one country have not been restricted to the United States. De Souza et al. (2003) evaluated the importance of genotype x region interaction effects of Nellore calves weaned across eight different regions of Brazil and reported significant interactions between all pairs of regions with the exception of Leiteira and Reconcavo Baiano. Analyzing weaning weight observations in three different areas (Mountain, Foothills, and Lowland) of the Czech Republic as different traits, Vostry et al. (2009) obtained genetic correlation estimates ranging from 0.82 to 0.98. They concluded that the animal by region interaction was not biologically significant and can be ignored in the Czech Republic genetic evaluation.

Yearling weight is another growth trait important to producers looking to retain replacements in their herd. It has been reported that a proportion of Brahman influence (0, 1/4, 1/2) by calving season interaction was not significant for yearling weight; however this interaction was significant for the closely related trait of postweaning daily gain (Bolton et al., 1987). Fall born heifers of each breed group gained at a faster rate from weaning to yearling than their spring born counterparts and daily gain increased with an increase in Brahman influence. Similar results were reported for heifers and steers of Angus, Brahman, Brahman x Angus, and Angus x Brahman breeding maintained on bermudagrass or endophyte-infected tall fescue. Interactions between dam breed, sire breed, and forage environment were not significant for yearling weight; however these interactions were significant for postweaning average daily gain (Brown et al., 1993). Pahnish et al. (1983), in a continuation of the study carried out by Burns et al. (1979), evaluated yearling weight differences in heifers when maintained in either Montana or Florida. These researchers discovered a significant line by location interaction in which heifers observed in their state of origin outperformed introduced individuals in both phases 1 and 2 of the study. In phase 1, a difference in fall yearling weight of 25 kg (in favor of M1) was observed between heifers of Montana and Florida origin measured in Montana and a difference of 12 kg (in favor of F6) was reported between the same groups in Florida (Pahnish et al., 1983). Similar results were obtained in phase 2; however differences between M1 and F4 (from M1 lineage) when evaluated in Montana were much smaller.

Between Countries

The widespread use of artificial insemination has made it possible for sires to possess offspring in many different countries around the world. Therefore, much interest has been centered on the possibility of combining data from multiple countries into one analysis to increase the accuracy of genetic predictions. Combining data from multiple countries into one international genetic evaluation assumes the populations from all countries are the same and that an animal's rank does not change across countries (Donoghue and Bertrand, 2004). However, this assumption is invalid in the presence of genotype by country interactions and research has been conducted to investigate the importance of such interactions.

Meyer (1995) treated growth traits of Angus cattle observed in New Zealand and Australia as different traits in a multivariate analysis to compare variance components for traits in each country. She found that variance components for birth, weaning, and yearling weight were in overall agreement between the two countries. Moreover, genetic correlations of 0.8 or higher between performance in Australia and New Zealand were estimated for birth, weaning, and yearling weight and gave no indication of a GxE of biological importance. Similarly, de Mattos et al. (2000) reported high direct genetic correlations of 0.86, 0.90, and 0.88 for Hereford weaning weights observed in United States-Canada, United States-Uruguay, and Canada-Uruguay combinations, respectively. Estimates of the genetic correlations for maternal effects were 0.82 for United States-Canada, 0.85 for United States-Uruguay, and 0.84 for Canada-Uruguay. They concluded that a joint genetic evaluation for Hereford cattle could be performed with a model that treats weaning weight data from Canada, Uruguay, and the United States as the same trait (de Mattos et al., 2000). A more recent study obtained genetic correlation estimates of 0.95 to 0.96 for weaning weight direct and estimates of 0.90 to 0.92 for weaning weight maternal between Charolais populations observed in Australia, Canada, New Zealand, and the United States (Donoghue and Bertrand, 2004). Additionally, estimates of the genetic correlation for postweaning gain ranged from 0.89 to 0.94 between observations in Australia, Canada, New Zealand, and the United States. Although sires would be expected to rank similarly for both traits in all four countries, these researchers mention an adjustment for heterogeneous variance parameters would be necessary before performance data from these four countries could be combined into one common analysis (Donoghue and Bertrand, 2004).

Results have also been reported that suggest genotype by country interactions may exist for some traits, but not others. As a follow up study to that conducted by de Mattos et al. (2000), Lee and Bertrand (2002) investigated birth weight, weaning weight, and postweaning gain observed in Argentina, Canada, Uruguay, and the United States as different traits to determine the importance of genotype by country interactions in Hereford cattle. High, positive genetic correlations between birth and weaning weights for all pairs of countries provided no evidence of genotype by country interactions and indicated a joint analysis for these traits would be possible. However, genetic correlations for postweaning gain among countries indicated gain in Argentina and Uruguay should be analyzed together and that between Canada and the United States should be analyzed as one trait whereas gain in Argentina and Uruguay should not be treated as the same trait as that of Canada and the United States. Postweaning gain is measured 345 days following weaning in Argentina and Uruguay and 160 days post weaning in Canada and the United States. This difference in definition could contribute to the mixed results observed for the presence of genotype by country interactions (Lee and Bertrand, 2002).

Conclusion

Studies conducted to explore the existence of GxE have differing conclusions. Generally, results from studies comparing sire performance across different states have suggested significant GxE effects (Buchanan and Nielsen, 1979; Burns et al., 1979; Olson et al., 1991) whereas studies comparing sire performance within the same state indicate GxE of no significance (Tess et al., 1984; Woodward and Clark, 1950). In addition, there are discrepancies among studies evaluating performance across regions of a country with some reporting a GxE of biological importance (Bertrand et al., 1985) and others reporting no evidence for reranking of sires (de Mattos et al., 2000). These inconsistencies imply that additional research in the area of GxE and the identification of environmental factors that lead to GxE is needed.

Potential Environmental Factors of Importance

Growth traits in beef cattle can be modified by several different environmental factors. Knowledge of the various environmental factors which modify growth traits is important before we can identify the presence of GxE. Environmental factors such as parasite levels, season, forage type, and altitude may play a role in GxE; however little research has been reported in these areas.

Parasite Levels

Parasites such as ticks can have a negative impact on performance, especially in tropical environments. Seifert (1971a) compared control cattle infested with ticks to a group of cattle dipped for ticks and reported 40 kg lower gains in the untreated British cattle. In a similar study, Wilkinson (1962) selected cattle for tick resistance and split cattle into resistant and susceptible groups based upon those with the smallest and largest numbers of ticks, respectively. Weight gains were reported as being similar between the two groups; however the author mentioned gains would have probably been significantly higher in the resistant group if tick infestations on the susceptible cattle had been allowed to reach higher levels before treatments were given. Resistance to ticks appears to be moderately to highly heritable with reported estimates of 0.34 to 0.82 (Mackinnon et al., 1991; Seifert, 1971b), suggesting that there is substantial genetic variability for this trait. Perhaps bulls susceptible to ticks could have offspring which perform well in temperate regions, but poorly in tropical regions potentially leading to GxE.

Season

Some cattle may be more sensitive to seasonal changes than others implicating season as an environmental variable of interest in GxE. Season encompasses many potential environmental factors affecting growth such as temperature and humidity as well as forage quality and availability. Temperature and forage quality can also interact with one another to elicit a reduction in growth performance.

The United States consists of many diverse regions from extensive arid range conditions such as the Great Basin to highly productive pasture conditions in the Midwest to tropical conditions characterized by high levels of heat and humidity (Ewing et al., 1999). The high levels of heat and humidity, particularly in the Southern United States, can be detrimental to cattle and often lead to heat stress. Heat stress is a combination of both climatic and non-climatic factors which lead to either heat gains by the body or to a limitation of the dissipation of heat from the body of animals (Leithead and Lind, 1964). Air temperature, radiation, humidity, and wind velocity tend to displace internal equilibrium which gives rise to heat stress (Blackshaw and Blackshaw, 1994). Thermal stress from the environment can have significant effects on production and reproduction of beef cattle especially with the recent increase in animal production in warmer climates of the United States. Annual production losses attributed to heat stress in the US beef industry are estimated at $370 million (St-Pierre et al., 2003).

The thermoneutral zone (TNZ), also known as the zone of thermal comfort, represents that range in ambient (air) temperature where an animal is comfortable and performance and health are at their optimal levels (Figure 2.2). The TNZ is defined by a lower critical temperature and an upper critical temperature. Temperatures slightly exceeding optimum levels reach a warm zone where thermoregulatory response mechanisms (sweating, panting) are used to dissipate heat from the body. However, once temperatures exceed the upper critical temperature the effects of heat stress become apparent and more drastic means of dissipating heat are necessary (NRC, 1981).

The digestion of consumed feed requires the production of metabolic heat; therefore reducing feed intake is a common response to decrease the amount of internal heat that needs to be dissipated by heat stressed cattle (Mitlohner et al., 2001). In fact, metabolism has been estimated to generate about one third of the heat load of an animal in a hot environment so any means of reducing this type of heat production is beneficial

(Blackshaw and Blackshaw, 1994). Unfortunately, reduced intake leads to a decline in growth rate and weight gain, two very important aspects of beef production. Feedlot heifers decreased their feed intake by 2% under heat stress conditions which were defined as having a maximum temperature over 35°C (Brown-Brandl et al., 2006). Similarly, Pereira et al. (2008) found that heifers of Limousine and Alentejana breeding maintained in a 36°C environment had feed intakes which decreased by 9.6% and 10%, respectively.

Quantitative genetic research pertaining to heat stress in cattle has predominately involved applications to dairy cattle. Ravagnolo and Misztal (2000) combined performance data of Holsteins with public weather data and discovered there was sufficient genetic variability for heat stress to allow for the selection of heat tolerant individuals. These findings suggest some individuals may be more heat tolerant than others and this can be important when sires are selected for use in thermally stressful environments and expected to perform as they would in a more temperate climate.

Forage quality can be negatively impacted by high seasonal temperatures. High temperatures cause the maturation process of grasses (specifically in tropical regions) to occur rapidly which in effect leads to a rise in cell wall content (NRC, 1981). Greater cell wall content results in a decrease in the digestibility of dry matter and a lower feed intake (Laredo and Minson, 1973). Goetsch and Johnson (1999) noticed that organic matter digestibility in sheep was similar in the summer and fall when high quality forages were provided however digestibility was 6% greater in the fall when low quality forages were fed during these same seasons. Summer seasons in the United States are often characterized by drought which can lead to low quality forage and these findings suggest high temperatures can cause the digestion process to slow down. As digestion begins to protract animals tend to become full more quickly resulting in a reduction in feed intake and consequently a decrease in performance (Beede and Collier, 1986). Therefore, forage in the United States is typically of highest quality in the winter and spring and of lowest quality in the late summer and early autumn (Hoveland, 1986).

Forage Type

Forage types vary considerably from the Western and Southern United States due to climate constraints. The predominate forages in the Western United States are wheatgrass and bermudagrass whereas those in the Southern portion of the country are largely fescue and ryegrass. Grasses in the south are typically of much lower quality than those temperate grasses growing under cooler conditions in the west (Reid and Klopfenstein, 1983).

Tall fescue is a grass which was brought into North America from Europe and comes in many different varieties. Kentucky 31 tall fescue is the most popular type due to its ability to grow well on moist or waterlogged areas and is grown mainly in the area between the temperate North and mild South of the U.S. (Buckner and Bush, 1979). Some species of Kentucky 31 are infected with a fungus and are referred to as endophyte-infected fescue due to its symbiotic relationship with a fungus. The fungus receives nutrients and protection from the fescue and the plant receives protection from grazing animals (Bacon and Siegel, 1988). Unfortunately, the endophyte-infected version of the fescue is toxic to cattle and its effects have been well documented.

Aldrich et al. (1993) compared the effects of endophyte-infected and endophyte free tall fescue seed on Holstein steers under high (32°C) and low (22°C) temperatures and found rectal temperatures to be similar amongst the two treatments at 22°C; however at 32°C temperatures were 0.32°C higher in the endophyte infected treatment group. Additionally, feed intake of steers consuming endophyte infected seed was reduced by 10% compared with steers consuming endophyte free seed. A similar deduction was provided by Browning (2004) in comparing the effects of orchardgrass and endophyte-infected fescue on Hereford and Senepol steers. He determined that respiration rates ranged from 22 to 48 breaths per minute higher during the hottest month in those individuals consuming tall fescue regardless of breed. In addition, he observed that the Hereford steers on the tall fescue experienced a weight loss of 578 grams per day while individuals of the same breed on orchardgrass gained 312 grams per day. Clearly, this fescue intensifies the effects of heat stress on animals consuming it during the warmest months of the year.

Endophyte-infected fescue has negative impacts on cow calf enterprises as well. Schmidt and Osborn (1993) reported weight loss and reduced pregnancy rates in cows grazing an infected fescue pasture as well as slower gains and lighter weaning weights in their calves as compared to their contemporaries on an endophyte free pasture. They also found infected fescue reduced milk production by as much as 45% in beef cows providing some justification for the lighter weaning weights previously mentioned.

Altitude

Altitude could be another environmental variable of interest in GxE due to its known association with brisket disease. Brisket disease, also known as high altitude disease, occurs in domestic cattle frequently less than one year of age at altitudes above 1,524 m and is a noninfectious cardiac pulmonary condition characterized by edema in the brisket and lower body (Alexander and Jensen, 1959). This condition, first reported by Glover and Newsom (1915), arises as pulmonary arteries thicken in response to low oxygen levels in the blood at high altitude, ultimately leading to a restriction in blood flow and possibly heart failure as blood accumulates in the veins and heart (Will and Alexander, 1970). Recovery from brisket disease has been reported when affected cattle are moved to a lower altitude; however these cattle will once again be afflicted with the disease upon their return to high altitude (Alexander and Jensen, 1959). Approximately 1.5 million head of cattle in the United States are raised at high altitude and 5% of annual death losses in these areas have been attributed to brisket disease (Holt and Callan, 2007). These figures translate into an annual loss of 75,000 head worth more than $60 million.

A common observation found upon necropsy of cattle with brisket disease is hypertrophy of the right ventricle of the heart. The right ventricle of the heart is responsible for pumping unoxygenated blood to the lungs for gaseous exchange and an increased work load is placed upon this portion of the heart when pulmonary circulation is impeded (Alexander and Jensen, 1959). The lack of oxygen at high altitude triggers the constriction of pulmonary arteries which prevents the heart from pumping blood forward to the tissues. This lack of blood flow results in increased pulmonary arterial pressure, an indicator trait commonly used to measure susceptibility of cattle to brisket disease (Schimmel and Brinks, 1982).

Pulmonary arterial pressure scores are moderately to highly heritable with reported estimates ranging from 0.34 to 0.78 (Schimmel and Brinks, 1982; Shirley et al., 2008). These estimates suggest there is sufficient genetic variability to select for lower pressure scores at high altitude. In addition, growth and pulmonary arterial pressure are influenced by some of the same genes. Investigating the genetic relationship between pulmonary arterial pressure and growth, Shirley et al. (2008) concluded that selecting for growth at low altitude would increase pulmonary arterial pressure scores and susceptibility to brisket disease. Therefore, AI sires used extensively at low altitude may have poor performing offspring when utilized at high altitude.

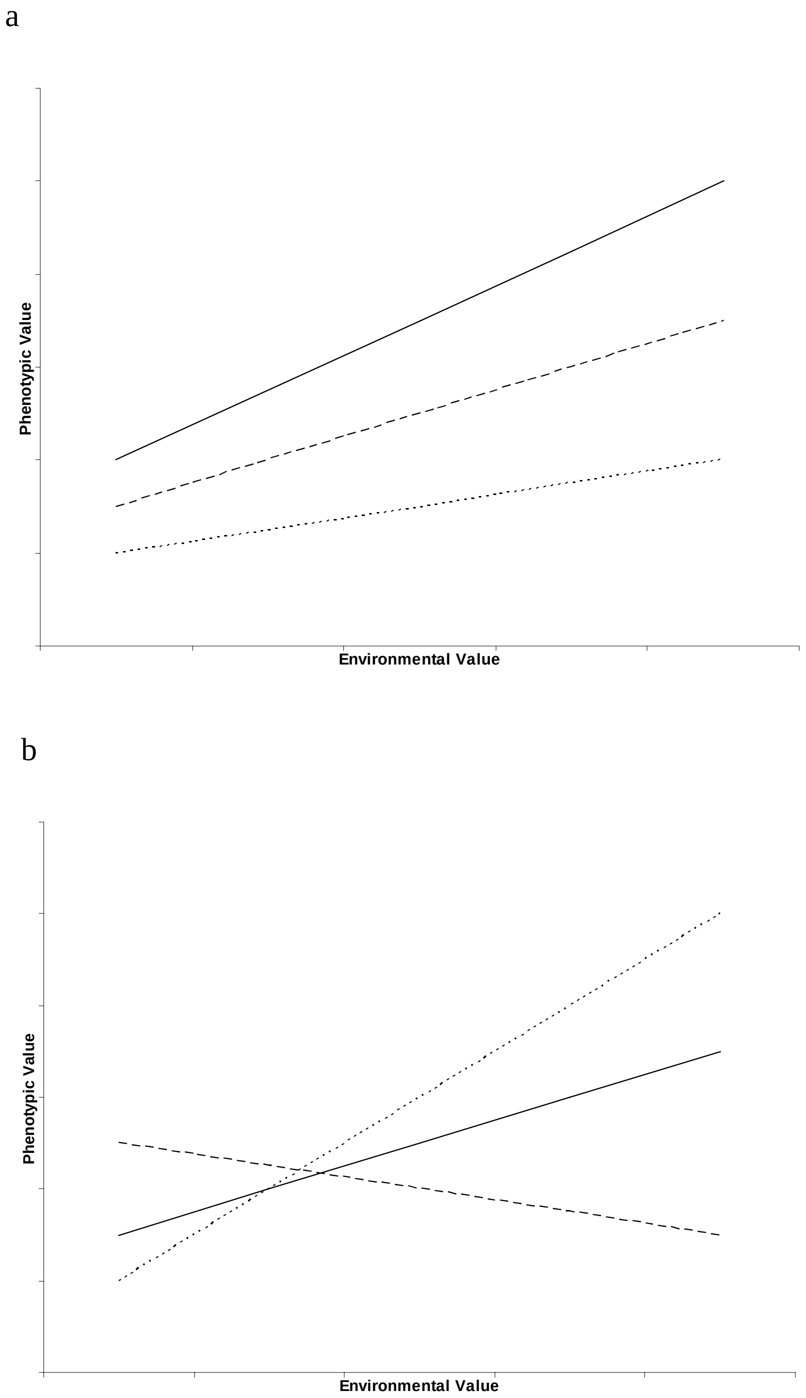

Figure 2.1. Examples of genotype by environment interactions. (Adapted from Bourdon, 2000)

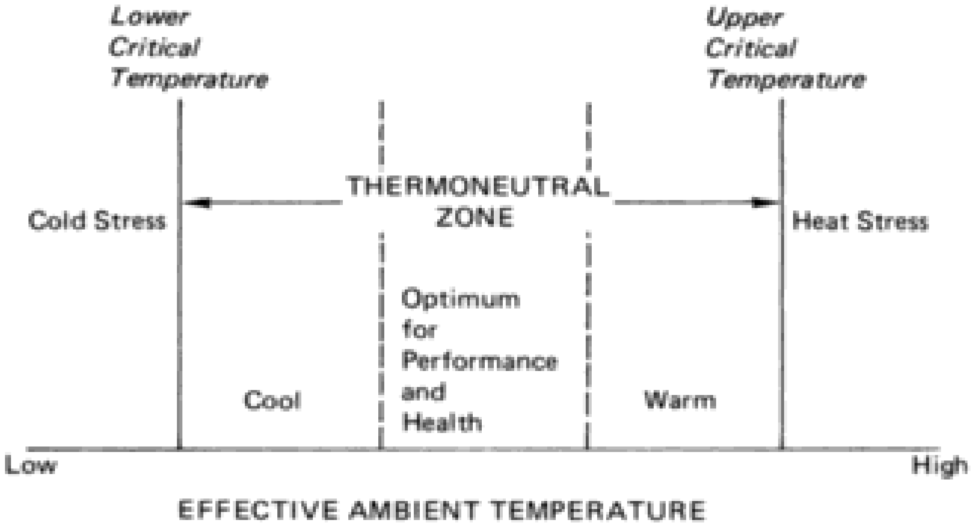

Figure 2.2. Schematic representation showing relationship of thermal zones and temperatures (source: (NRC, 1981))

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CHAPTER 3

GENOTYPE BY REGION AND SEASON INTERACTIONS ON WEANING WEIGHT IN UNITED STATES ANGUS CATTLE[1]

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[1] J.L. Williams, M. Łukaszewicz, J.K. Bertrand, and I. Misztal. 2010. Submitted to *Journal of Animal Science.*

ABSTRACT: The objective of this study was to determine if a sire's weaning weight performance is consistent across different environments and calving seasons in the United States. Data and pedigree information were provided by the American Angus Association. Weaning weights observed in the Southeast (SE) and Northwest (NW) were the focus of this study as these regions are perceived as opposite extremes in climate. The two most represented calving seasons in each region were fall and winter in the SE and spring and winter in the NW. The original datafile was edited to remove weaning weight records outside of two standard deviations from the overall mean and all single sire contemporary groups. The final dataset included a total of 407,524 weaning weight records with 85,044 coming from fall born calves in the SE, 64,389 from winter born calves in the SE, 73,172 from spring born calves in the NW, and 184,919 from winter born calves in the NW. Weaning weights adjusted to 205 days of age in each region-season class were considered different, but genetically correlated traits in a multivariate analysis in order to investigate the presence of genotype by environment interactions. The sole fixed effect in the model was weaning contemporary group and random effects included direct, maternal, maternal permanent environment, and a residual. Estimates of heritability for direct effects were 0.20 and 0.22 for weight in fall and winter born calves in the SE, respectively. Direct heritability for weight in the NW was 0.24 and 0.28 for spring and winter born calves, respectively. Maternal heritability estimates ranged from 0.10 to 0.12 for weight in winter born calves in the NW and for fall born calves in the SE, respectively. Genetic correlations ranged from 0.89 to 0.97 among direct effects and from 0.63 to 0.92 among maternal effects. Sires performed consistently across regions and seasons. Maternal effects were variable across regions and seasons within different regions suggesting a dam’s ability to produce milk, which contributes to her calf’s weaning weight, can change based on the region where she is in production and on the calving season she falls into. Selection decisions should be based on a specific production environment in order to obtain the growth performance expected.

Key Words: beef cattle, genetic correlation, genotype by environment, weaning weight

INTRODUCTION

Widespread use of AI and embryo transfer has made it possible for sires to possess offspring in production under vastly different management systems and geographical areas. Problems arise when a sire’s performance is inconsistent across different environments, defined as a genotype by environment interaction (**GxE**) (Lynch and Walsh, 1998). Genetic evaluations traditionally regard a trait measured in different environments as the same trait, therefore published EPD are based on the performance of a sire’s progeny in a number of environments and do not necessarily reflect his true merit in any one environment (Bourdon, 2000). Consequently, in the presence of GxE, producers basing their selection decisions on these genetic predictions may not obtain the performance they expect in their particular operation. Identification of environmental factors important in GxE will help producers in making the most optimal selection decisions given their management setting.

Previous studies investigating the existence of GxE in growth traits of United States (**US**) cattle have generally defined environment based upon region with differing conclusions. Tess et al. (1979) reported sire by region interactions of little importance whereas Bertrand et al (1987) found significant sire by region interactions that would lead to considerable reranking among sires. The relative importance of region with regard to GxE for growth is unclear.

Some cattle may be more sensitive to seasonal changes than others implicating season as an environmental variable of interest. Season encompasses many potential environmental factors affecting growth such as forage quality and availability (Waterman et al., 2007) as well as temperature and humidity (Ray et al., 1969) and has received little attention in studies on GxE. The objective of this study was to investigate the importance of genotype by region and season interactions for weaning weight in US Angus cattle.

MATERIALS AND METHODS

Data

Field data from an existing database was used in this study, therefore Animal Care and Use Committee approval was not obtained. The American Angus Association (**AAA**) provided raw and adjusted weaning weight records on 5,224,034 individual animals born from 1972 to 2008 and pedigree records on 6,257,706 animals. Weaning weights were adjusted to 205 d according to Beef Improvement Federation guidelines (BIF, 2002). In addition, the AAA allowed determination of the specific location associated with each observation by providing pertinent state, city, and zip code information for each herd. Data analysis was limited to observations from the contiguous US and required the removal of weights measured in Canada, Alaska, and Hawaii. Further edits included removal of weaning weight observations outside of two standard deviations from the overall mean and all contemporary groups represented by a single sire. Weaning contemporary groups were formed based on herd, wean date, lot id, management code, and sex.

The US was partitioned into regions by grouping together states with similar climate and geography (Figure 3.1). This resulted in five different regions which were the Northwest (**NW**), Southwest, Midwest, Southeast (**SE**), and Northeast. Weaning weights from calves located in the SE and NW were the focus of this study as these regions are perceived as opposite extremes in climate; therefore observations from all other regions were excluded from the analysis.

Calving seasons were based on standard definitions so that winter included the months of December through February, spring included March through May, summer included June through August, and fall included September through November. The number of calves born in each birth month for the NW and SE are presented in Figure 3.2. The largest seasons of birth were spring and winter in the NW and fall and winter in the SE with very few calves born in the summer in either region. Thus, calving seasons of interest were reduced to the fall and winter in the SE and the spring and winter in the NW.

The final dataset was further reduced by including only animals whose sire had at least ten offspring in each of the four region-season categories to obtain a more accurate estimate of the genetic correlation between environments. There were 471 sires in common between the four region-season combinations. The final dataset following all edits consisted of 407,524 weaning weight observations in 61,264 contemporary groups. A 3-generation pedigree was compiled from the animals remaining in the dataset and contained 690,054 individuals.

Statistical Analysis

Weaning weight in each region-season category was analyzed using a multiple trait, multiple component animal model presented in scalar notation as:

$$y_{ijklm} = wcg_{im} + dir_{jm} + mat_{km} + mpe_{lm} + e_{ijklm}$$

where y is the observation for trait m (weaning weight of fall born calves in the SE, winter born calves in the SE, spring born calves in the NW, or winter born calves in the NW), wcg_{im} is the fixed weaning contemporary group effect i for trait m, dir_{jm} is the random additive direct genetic effect of animal j for trait m, mat_{km} is the random additive maternal genetic effect of dam k for trait m, mpe_{km} is the random additive maternal permanent environmental effect of dam k for trait m, and e_{ijklm} is the random residual effect for trait m. Direct and maternal genetic effects for all traits were assumed correlated. Maternal permanent environmental effects were also assumed correlated in the analysis because some dams had offspring measured in all four region-season combinations. Residual effects were assumed uncorrelated because calves were not observed in more than one environment. Variance components were estimated with the GIBBS2F90 program (Misztal et al., 2002), which uses a Bayesian approach via a Gibbs sampling algorithm to estimate the posterior distribution of the data. Posterior means and standard deviations for (co)variance components were calculated from 300,000 samples after discarding 50,000 samples as burn in.

RESULTS AND DISCUSSION

Summary statistics for weaning weight in each environmental classification are reported in Table 3.1. The NW clearly has a greater population of beef cattle when comparing the number of records in each region. The mean weaning weight of calves observed in the NW (273 kg) was approximately 13 kg heavier than those observed in the SE (260 kg) suggesting there is some advantage for growth in the NW. Within the NW winter born calves had slightly heavier weights on average than spring born and within the SE fall born calves had equally greater weights over winter born. These summary statistics indicate there may be differences in weights observed between regions and seasons.

Heritability estimates for direct and maternal effects for weaning weight in each environment are presented in Table 3.2. Estimates for direct effects ranged from 0.20 to 0.28 and were close to the value of 0.20 used by AAA in their genetic evaluation. Maternal values ranged from 0.10 to 0.12 and were slightly lower than the value of 0.14 used in the estimation of breeding values by AAA. Estimates published in the literature for direct and maternal effects on weaning weight were in agreement with those calculated in this study. Robinson (1996) reported a similar direct effect estimate of 0.20 in Australian Angus cattle and a lower estimate of 0.09 for maternal effects. Similarly, the investigation of Dodenhoff et al. (1999) into the inclusion of grand maternal effects yielded direct effect estimates of 0.22 and 0.25 and maternal estimates of 0.11 for Angus cattle. Conversely, larger estimates of 0.53 and 0.18 for direct and maternal effects, respectively, were reported when genetically correlated traits were combined with weaning weight into one analysis (Kaps et al., 2000).

There was an apparent advantage in terms of heritability for direct effects on weaning weight in the NW as compared to the SE. This difference was due to the larger direct genetic (129 kg^2 vs. 115 kg^2) and lower residual (254 kg^2 vs. 300 kg^2) variances associated with weaning weight in the NW, indicating there is less environmental variation in the NW as compared to the SE. Environmental effects may have less influence on weaning weight in the NW due to the lower variation in annual temperature typical for this region as evidenced by the smaller range in number of heat stress degrees per year (Bohmanova et al., 2008).

Within regions, direct effects on weaning weight of winter born calves were more highly heritable in the NW compared to NW spring born calves whereas heritabilities were very similar between seasons in the SE. Environmental effects likely have the same influence on fall and winter born calf weaning weights in the SE because these calves are given the opportunity to consume forage of equal quality during the winter and spring, respectively (Hoveland, 1986). Alternatively, differences in forage quality can likely provide an explanation for dissimilar heritability estimates between weaning weights for spring and winter born calves in the NW. Calves born in the spring must consume mid to late summer forage whereas those born in the winter have the opportunity to graze spring pasture. Summer grasses are known to have greater cell wall content than cool season grasses due to the rapid rate of maturation brought about by high summer temperatures (NRC, 1981). This higher cell wall content can impact weaning weight by decreasing the animal's ability to digest the forage which leads to reduced feed intake (Laredo and Minson, 1973).

Heritability estimates for maternal effects were very similar across regions and seasons within region. Similar findings of consistent maternal heritability across environments were reported by Speidel et al. (2007) in which weaning weight of calves was classified into good or poor environments based upon above or below average BW gain of their dams from the previous year. In contrast, de Mattos et al. (2000) found a difference in maternal heritability of 0.08 between what they classified as the Upper Plains and Corn Belt regions of the US; however they did not consider this difference to be significant.

Direct genetic correlations from the 4-trait analysis of weaning weight are shown in Table 3.3. An upper limit of 0.80 for genetic correlations between the same trait in different environments was defined by Robertson (1959) to indicate a GxE of little biological importance. Estimates presented here are very close to unity and indicate weaning weight observations in these four environments may not be different traits. Similarly, de Mattos et al. (2000) regarded weaning weight observations as different traits in three pairs of US regions and reported genetic correlations ranging from 0.87 to 0.88. Tess et al. (1984) explored GxE between different regions of North Carolina and obtained a genetic correlation estimate of 0.91. Collectively, these results reflect the absence of GxE and indicate that there should be no reranking of sires across environments.

Although there was no strong evidence for GxE among direct effects, it was noted that seasons in the SE (0.93) were not as highly correlated as seasons in the NW (0.97) suggesting more variability exists between seasons in the SE. As previously mentioned, temperatures in the SE tend to fluctuate more than those in NW; therefore this observation was not unexpected. It was additionally noted that calving seasons in each region with the greatest correlations between them were also those with the heaviest and lightest mean weaning weight in each region (NWwi and SEfa, NWsp and SEwi). This finding implies that these pairs of environments are very similar and the genes affecting weaning weight are not being differentially expressed.

Maternal genetic correlations between the four different environments are provided in Table 3.4. Estimates ranged from 0.63 to 0.92 with the highest correlations being between seasons in the same region. A similar tendency is observed with the maternal as was noted with the direct correlations where seasons in the SE (0.83) are more lowly correlated than those in the NW (0.92). All correlations involving different regions are much lower than were obtained for direct effects and ranged from 0.63 to 0.76. These results suggest that maternal effects on weaning weight are not consistent across regions or seasons within different regions and that there is evidence for GxE. Maternal effects relate to the amount of milk a dam will produce to contribute to her calf's weaning weight and these correlations suggest that a dam's ability can change based upon the region where she is in production and on the calving season she falls into. The SE in comparison to the NW is characterized not only by poorer forage quality, but also by higher parasite loads which have been reported to negatively affect weight gain (Seifert, 1971a). Furthermore, lactating cows exhibit reduced resistance to parasites (Seifert, 1971b) and likely suffer more severe losses in weight gain which could lead to a loss in milk production when cows raise their calves in the SE as opposed to the NW. Analyzing weaning weight observations in three different areas (Mountain, Foothills, and Lowland) of the Czech Republic as different traits, Vostry et al. (2009) obtained maternal genetic correlation estimates ranging from 0.50 to 0.65. Although these researchers mention their estimates may not be very reliable due to high standard errors, the estimates in the present study were associated with much lower standard deviations indicating the correlations presented here are significant. Similarly, Brown et al. (1993) found evidence that maternal effects for growth vary with nutritional environment.

Direct-maternal genetic correlations for weaning weight from each region-season classification are shown in Table 3.5. The negative estimates obtained in this study confirm those of previous studies (Eler et al., 1995; Meyer et al., 1994; Splan et al., 2002). Correlations involving the maternal effect for winter born calves in the SE were the lowest of all correlations and nearly zero. Speidel et al. (2007) noted similar tendencies between direct and maternal effects in a less favorable environment. Calves born in the winter in the SE are weaned following a hot humid summer; therefore this is likely the least favorable of all environments analyzed in this study. A larger difference existed for correlations between maternal weaning weight and its direct counterparts in the SE (-0.27 and -0.04) in comparison to those in the NW (-0.30 and -0.27). Perhaps direct-maternal correlation differences are less obvious in the NW where the climate is much milder than that in the SE. With the exception of those correlations involving winter born calves in the SE, estimates between direct effects in one environment and maternal effects in another environment were very similar.

Maternal permanent environmental effects for the four traits in the analysis are included in Table 3.6. Maternal permanent environment accounted for a similar proportion of variation in all four environments ranging from 0.15 to 0.18. These estimates are very similar to those reported by de Mattos et al. (2000) and Vostry et al. (2009) when considering the same trait in different regions within a single country as separate traits. In the current study, correlations were strongest amongst seasons in the same region (0.90 and 0.89). The small standard deviations associated with these estimates indicate a large number of dams had offspring represented in both seasons within the same region. However, correlations between different regions were coupled with larger standard deviations reflecting that there were fewer dams with offspring in both regions and suggest these estimates may be less reliable.

In conclusion, genetic correlations between direct effects for weaning weight indicated no evidence of GxE and suggest sires should not rerank across regions of the US or calving seasons. However, more environmental variation was found for weaning weight in the SE as compared to the NW. Genetic correlations between maternal effects were below 0.80 indicating GxE may exist and that a dam's ability to produce milk for her calf changes based upon the region of the country where she is in production and on the calving season she falls into. Given that differences in performance exist between seasons and regions, producers should base their selection decisions upon characteristics of their specific production environment.

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Table 3.1. Summary statistics for weaning weight observations in each environment classified by season of birth and region of observation

Region-season[1]	Records, n	Mean Weaning Weight, kg	SD, kg
SEfa	85,044	262.4	38.6
SEwi	64,389	257.6	38.1
NWsp	73,172	270.7	34.5
NWwi	184,919	276.0	32.5

[1] SEfa= fall born calves observed in the Southeast, SEwi= winter born calves observed in the Southeast, NWsp= spring born calves observed in the Northwest, and NWwi= winter born calves observed in the Northwest.

Table 3.2. Posterior mean heritability estimates (± SD) for weaning weights of calves classified into environments based upon their season of birth and region of the US where they were observed

Trait[1]	Heritability
$SEfa_d$	0.20 ± 0.02
$SEwi_d$	0.22 ± 0.02
$NWsp_d$	0.24 ± 0.02
$NWwi_d$	0.28 ± 0.02
$SEfa_m$	0.12 ± 0.01
$SEwi_m$	0.12 ± 0.01
$NWsp_m$	0.11 ± 0.01
$NWwi_m$	0.10 ± 0.01

[1] Weaning weight direct (d) and maternal (m) for fall born calves observed in the Southeast (SEfa), winter born calves in the Southeast (SEwi), spring born calves in the Northwest (NWsp), and winter born calves in the Northwest (NWwi).

Table 3.3. Posterior mean direct genetic correlation estimates (± SD) for weaning weight of calves classified into environments based upon their season of birth and region of the US where they were observed

	$\mathrm{SEfa_d}^1$	$\mathrm{SEwi_d}^1$	$\mathrm{NWsp_d}^1$	$\mathrm{NWwi_d}^1$
$\mathrm{SEfa_d}$		0.93 ± 0.02	0.89 ± 0.02	0.92 ± 0.01
$\mathrm{SEwi_d}$			0.93 ± 0.03	0.92 ± 0.02
$\mathrm{NWsp_d}$				0.97 ± 0.01

[1] Weaning weight direct (d) for fall born calves observed in the Southeast (SEfa), winter born calves in the Southeast (SEwi), spring born calves in the Northwest (NWsp) and winter born calves in the Northwest (NWwi).

Table 3.4. Posterior mean maternal genetic correlation estimates (± SD) for weaning weight of calves classified into environments based upon their season of birth and region of the US where they were observed

	$SEfa_m$[1]	$SEwi_m$[1]	$NWsp_m$[1]	$NWwi_m$[1]
$SEfa_m$		0.83 ± 0.03	0.67 ± 0.05	0.76 ± 0.05
$SEwi_m$			0.63 ± 0.05	0.71 ± 0.04
$NWsp_m$				0.92 ± 0.02

[1] Weaning weight maternal (m) for fall born calves observed in the Southeast (SEfa), winter born calves in the Southeast (SEwi), spring born calves in the Northwest (NWsp) and winter born calves in the Northwest (NWwi).

Table 3.5. Posterior mean direct-maternal genetic correlation estimates (± SD) for weaning weight of calves classified into environments based upon their season of birth and region of the US where they were observed

	$SEfa_m{}^1$	$SEwi_m{}^1$	$NWsp_m{}^1$	$NWwi_m{}^1$
$SEfa_d{}^1$	-0.27 ± 0.05	-0.07 ± 0.06	-0.23 ± 0.05	-0.21 ± 0.05
$SEwi_d{}^1$	-0.14 ± 0.05	-0.04 ± 0.06	-0.25 ± 0.05	-0.18 ± 0.05
$NWsp_d{}^1$	-0.20 ± 0.05	-0.01 ± 0.06	-0.30 ± 0.04	-0.20 ± 0.05
$NWwi_d{}^1$	-0.32 ± 0.05	-0.10 ± 0.05	-0.29 ± 0.05	-0.27 ± 0.04

[1] Weaning weight direct (d) and maternal (m) for fall born calves observed in the Southeast (SEfa), winter born calves in the Southeast (SEwi), spring born calves in the Northwest (NWsp) and winter born calves in the Northwest (NWwi).

Table 3.6. Posterior mean estimates of maternal permanent environmental variance as a fraction of the phenotypic variance for weaning weight and genetic correlations (± SD) between maternal permanent environmental effects of calves classified into environments based upon their season of birth and region of the US where they were observed

	SEfa[1]	SEwi[1]	NWsp[1]	NWwi[1]
SEfa	**0.17 ± 0.01**			
SEwi	0.89 ± 0.05	**0.15 ± 0.01**		
NWsp	0.52 ±0.11	0.65 ± 0.13	**0.18 ± 0.01**	
NWwi	0.58 ± 0.11	0.66 ± 0.12	0.90 ± 0.03	**0.15 ± 0.00**

[1] Fraction of weaning weight phenotypic variance accounted for by maternal permanent environmental variance for fall born calves observed in the Southeast (SEfa), winter born calves in the Southeast (SEwi), spring calves in the Northwest (NWsp), and winter born calves in the Northwest (NWwi) indicated by bold type on the diagonal. Genetic correlations for maternal permanent environmental effects are below the diagonal.

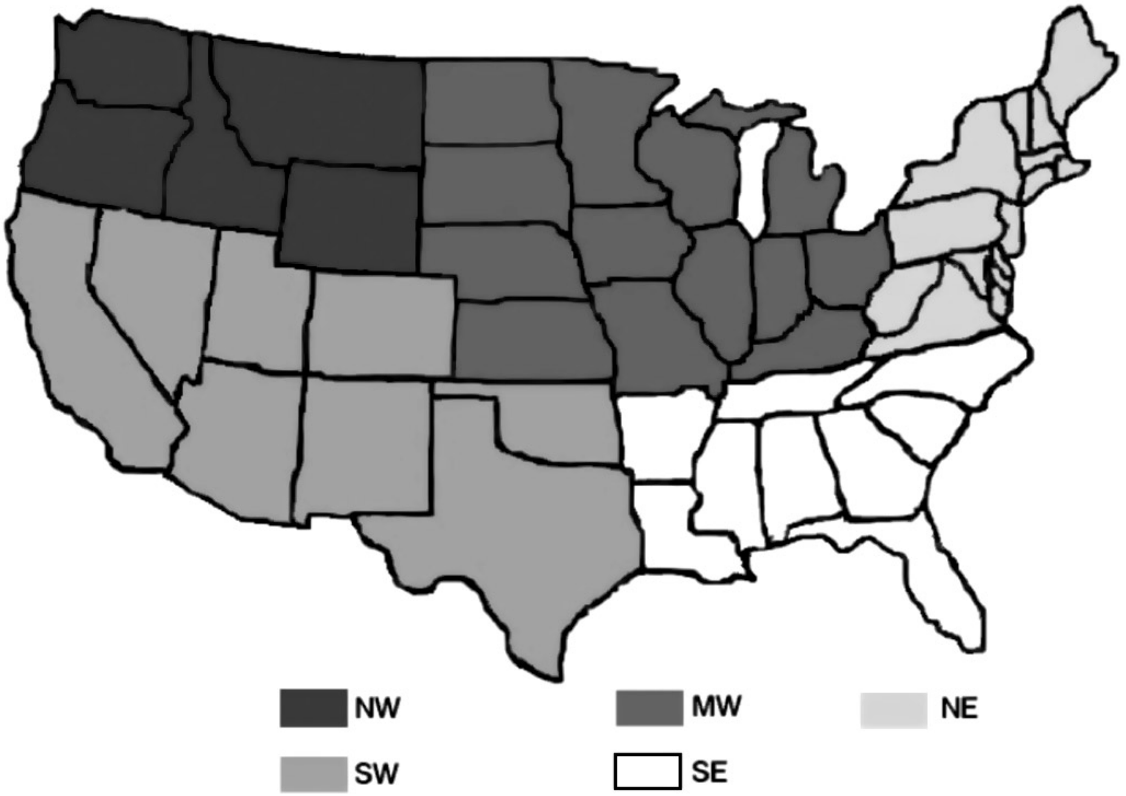

Figure 3.1. Distribution of the United States by region: Northwest (NW), Southwest (SW), Midwest (MW), Southeast (SE), and Northeast (NE). (Oseni et al., 2003)

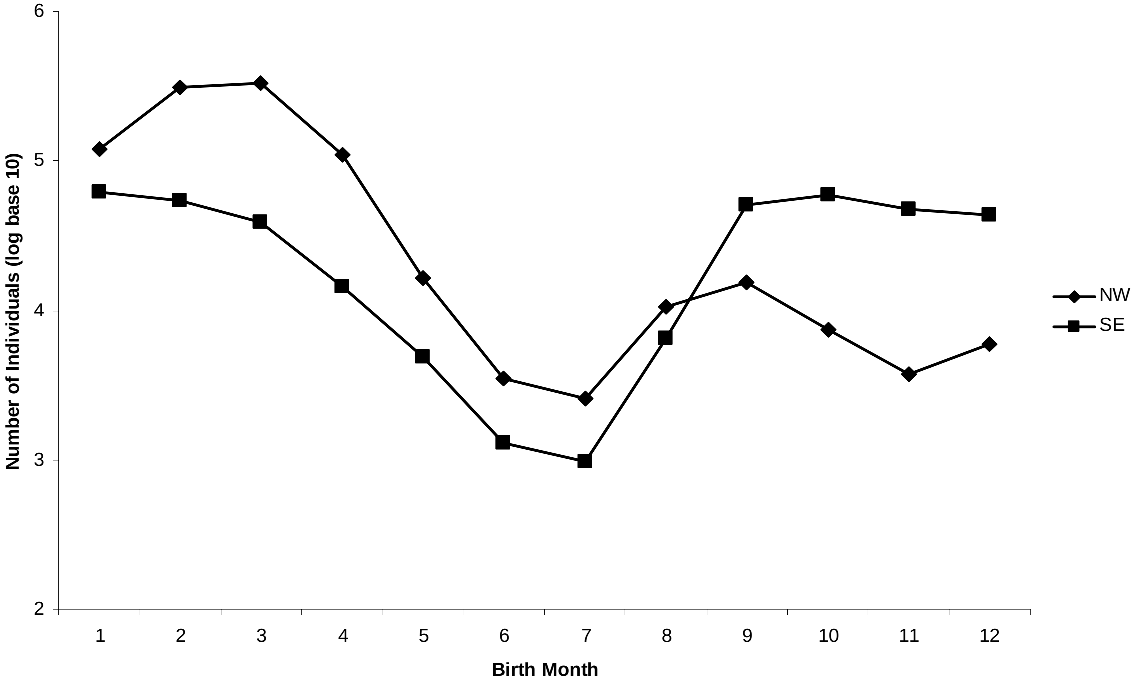

Figure 3.2. Plot of the number of calves born in each birth month for the Northwest and Southeast.

CHAPTER 4

GENOTYPE BY ENVIRONMENT INTERACTION FOR GROWTH DUE TO ALTITUDE IN COLORADO ANGUS CATTLE[1]

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[1] J.L. Williams, J.K. Bertrand, and I. Misztal. To be submitted to *Journal of Animal Science*.

ABSTRACT: The objectives of this study were to determine if sires perform consistently across altitude and to quantify the genetic relationship between growth and survival at differing altitudes. Growth records from the American Angus Association included weaning weight (WW) adjusted to 205 (n = 102,233) and yearling weight adjusted to 365 (n = 54,448) days of age from 102,233 purebred Angus cattle born in Colorado between 1972 and 2007. Postweaning gain (PWG) was calculated by subtracting adjusted WW from adjusted yearling weight. Altitude was assigned to each performance record based upon the zipcode associated with each herd in the database. Records for WW and PWG were each split into three traits, those measured at low, medium, and high altitude. A binary trait, survival (SV), accounted for censored records at yearling for each altitude. It was assumed that individuals missing a yearling weight either suffered heart failure and died or required relocation to a lower altitude due to brisket disease, a condition common at high altitude. Model 1 considered WW and PWG measured at three altitudes as separate traits. Model 2 considered PWG and SV measured at three altitudes as separate traits. Models included the effects of weaning contemporary group, age of dam, animal additive genetic effects, and residual. Maternal genetic and maternal permanent environmental effects were included for WW. Estimates of heritability for WW in model 1 ranged from 0.26 to 0.28, with greater values in low altitude. Estimates of heritability for PWG ranged from 0.18 to 0.25, with greater values in low altitude. Genetic correlations between growth traits measured at different altitude were medium to high in magnitude, 0.47 to 0.83 for WW and 0.43 to 0.79 for PWG and indicate evidence for reranking of sires across altitude. In model 2, heritabilities ranged from 0.18 to 0.26 for PWG and from 0.20 to 0.23 for SV. Genetic correlations between PWG measured at different altitude varied between 0.27 and 0.77. Favorable positive genetic correlations were estimated between SV and PWG within the same altitude, suggesting that calves with genetics for increased growth from weaning to yearling also have increased genetic potential for survival at low, medium, and high altitude. Heterogeneous genetic variances for growth across altitude should be accounted for in a national evaluation to aid producers selecting bulls for use in high altitude environments.

Key words: beef cattle, brisket disease, censored records, genotype by environment interaction, growth

INTRODUCTION

Brisket disease, also known as high altitude disease, occurs in domestic cattle frequently less than one year of age at altitudes above 1,524 m and is a noninfectious cardiac pulmonary condition characterized by edema in the brisket and lower body (Gjermundson, 2000). This condition, first reported by Glover and Newsom (1915), arises as pulmonary arteries thicken in response to low oxygen levels in the blood at high altitude, ultimately leading to a restriction in blood flow and possibly heart failure as blood accumulates in the veins and heart (Will and Alexander, 1970). Approximately 1.5 million head of cattle in the United States are raised at high altitude and 5% of annual death losses in these areas have been attributed to brisket disease (Holt and Callan, 2007). These figures translate into an annual loss of 75,000 head worth more than $60 million.

Studies have used pulmonary arterial pressure as an indicator trait for susceptibility to brisket disease given that elevated blood pressure is a reflection of a restriction in blood flow (Holt and Callan, 2007). Investigating the genetic relationship between pulmonary arterial pressure and growth, Shirley et al. (2008) concluded that selecting for growth at low altitude would increase pulmonary arterial pressure scores and susceptibility to brisket disease. Genetic predictions for growth are based on the performance of a sire's progeny in a number of environments and do not necessarily reflect his true merit in any one environment (Bourdon, 2000). Producers raising cattle in high altitude environments and basing their selection decisions on these predictions may not obtain the performance they expect when the majority of a sire's offspring are maintained at low altitude. The objectives of this study were to determine if sires perform consistently across altitude and to quantify the genetic relationship between growth and survival at differing altitudes.

MATERIALS AND METHODS

Data

Performance data in this study was obtained from an existing database, therefore Animal Care and Use Committee approval was not warranted.

Growth records for weaning weight (WW) adjusted to 205 and yearling weight adjusted to 365 days of age according to BIF Guidelines ((BIF, 2002) were obtained from the American Angus Association (**AAA**; St. Joseph, MO). Records were from purebred Angus cattle born between 1972 and 2007 in Colorado. Postweaning gain (PWG) was calculated by subtracting adjusted WW from adjusted yearling weight. Contemporary groups were defined based upon herd, process date, lot identification, management code, and sex resulting in 5,134 unique groups each containing an average of 20 individuals. Contemporary groups represented by a single sire as well as individuals with an age of dam greater than 12 years were not included in analyses. In addition, analyses were limited to large herds with greater than 200 animals represented in the data. Zipcode information provided by AAA referred only to the herd location at weaning; thus zipcodes pertaining to yearling herds were unavailable for those individuals changing herds from weaning to yearling. Animals in this situation were removed from the data because an appropriate altitude could not be assigned in this case. Following edits, a 3-generation pedigree file of 140,529 animals was extracted for 102,233 individuals with 102,233 WW and 54,448 yearling weight records. The number of records, mean, and SD for WW and PWG are summarized in Table 4.1.

Colorado has been the focus of a number of studies investigating brisket disease due to its very diverse geography. The eastern half of the state is considered high plains and ranges between 900 and 1,830 m in altitude whereas the western half is comprised of the Rocky Mountain range and has an altitude of 1,830 to 3,658 m (Figure 4.1). Performance records were assigned an altitude based upon the zipcode associated with each herd in the database. Altitudes associated with records in the data ranged from 914 to 2743 m. Three altitude groups (low, medium, and high), each comprised of 600 m, were formed and WW and PWG records were categorized based on these altitude groups. Weaning weight observed at low altitude (WWL) consisted of those individuals measured at altitudes ranging from 914 to 1523 m, weaning weight observed at medium altitude (WWM) consisted of measurements taken at altitudes ranging from 1524 to 2133 m, and weaning weight observed at high altitude (WWH) consisted of measurements taken at altitudes ranging from 2134 to 2743 m. Similarly, PWG measured at low, medium, and high altitude were coded as PWGL, PWGM, and PWGH, respectively. There were 142 sires in common among PWG measured at the three levels of altitude and

204 sires in common among WW measured at each altitude to allow for accurate estimation of the correlations between the traits measured at each altitude.

A trait measuring survival (SV) at each of the three altitudes (SVL, SVM, and SVH) was developed to account for the presence or absence of yearling weights among animals in the same weaning contemporary group. Individuals in the data with yearling weight observations were coded as 2=survive whereas animals missing a yearling weight were coded either 1=not survive or 0=missing. Animals coded as missing were members of a weaning contemporary group in which none of their contemporaries possessed a yearling weight and were assumed to belong to a herd which did not routinely report yearling weights. Individuals coded as not surviving were in a weaning contemporary group where some individuals had a yearling weight reported. It was assumed that these animals either suffered heart failure and died or required relocation to a lower altitude due to brisket disease.

Models and Analyses

This study involved two separate multivariate analyses for the estimation of variance components for growth measured at three different levels of altitude. Model 1 was a six trait model considering WW and PWG at each altitude as different traits:

$$\mathrm{y}_{\mathrm{ijklm}} = \mathrm{wcg}_{\mathrm{im}} + \mathrm{aod}_{\mathrm{jm}} + \mathrm{a}_{\mathrm{km}} + \mathrm{m}_{\mathrm{lm}} + \mathrm{mpe}_{\mathrm{lm}} + \mathrm{e}_{\mathrm{ijklm}}$$

where y is the observation for trait m (WWL, WWM, WWH, PWGL, PWGM, and PWGH for 1 to 6) of weaning contemporary group i and age of dam group j; a_{km} is the random additive direct genetic effect of animal k for trait m, m_{lm} is the random additive maternal effect of dam l for trait m, $\mathrm{mpe}_{\mathrm{lm}}$ is the random maternal permanent environmental effect of dam l for trait m, and $\mathrm{e}_{\mathrm{ijklm}}$ is the random residual effect. Random maternal additive and maternal permanent environmental effects were excluded for PWG. For traits m = 1 to 6, the (co)variance structure was

$$\operatorname{var}\begin{bmatrix}\mathbf{a_1}\\ \mathbf{a_2}\\ \mathbf{a_3}\\ \mathbf{a_4}\\ \mathbf{a_5}\\ \mathbf{a_6}\\ \mathbf{m_1}\\ \mathbf{m_2}\\ \mathbf{m_3}\\ \mathbf{m_4}\\ \mathbf{m_5}\\ \mathbf{m_6}\end{bmatrix}=\begin{bmatrix}\sigma^2_{a_1} &&&&&&&&&&& \\ \sigma_{a_1,a_2} & \sigma^2_{a_2} &&&&&&&&&& \\ \sigma_{a_1,a_3} & \sigma_{a_2,a_3} & \sigma^2_{a_3} &&&& \text{Symmetric} &&&&& \\ \sigma_{a_1,a_4} & \sigma_{a_2,a_4} & \sigma_{a_3,a_4} & \sigma^2_{a_4} &&&&&&&& \\ \sigma_{a_1,a_5} & \sigma_{a_2,a_5} & \sigma_{a_3,a_5} & \sigma_{a_4,a_5} & \sigma^2_{a_5} &&&&&&& \\ \sigma_{a_1,a_6} & \sigma_{a_2,a_6} & \sigma_{a_3,a_6} & \sigma_{a_4,a_6} & \sigma_{a_5,a_6} & \sigma^2_{a_6} &&&&&& \\ \sigma_{a_1,m_1} & \sigma_{a_2,m_1} & \sigma_{a_3,a_{m_1}} & \sigma_{a_4,m_1} & \sigma_{a_5,m_1} & \sigma_{a_6,m_1} & \sigma^2_{m_1} &&&&& \\ \sigma_{a_1,m_2} & \sigma_{a_2,m_2} & \sigma_{a_3,a_{m_2}} & \sigma_{a_4,m_2} & \sigma_{a_5,m_2} & \sigma_{a_6,m_2} & \sigma_{m_1,m_2} & \sigma^2_{m_2} &&&& \\ \sigma_{a_1,m_3} & \sigma_{a_2,m_3} & \sigma_{a_3,a_{m_3}} & \sigma_{a_4,m_3} & \sigma_{a_5,m_3} & \sigma_{a_6,m_3} & \sigma_{m_1,m_3} & \sigma_{m_1,m_3} & \sigma^2_{m_3} &&& \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 && \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0\end{bmatrix}\otimes\mathbf{A}$$

, the maternal permanent environmental (co)variance structure was

$$\operatorname{var}\begin{bmatrix}\mathbf{mpe_1}\\ \mathbf{mpe_2}\\ \mathbf{mpe_3}\\ \mathbf{mpe_4}\\ \mathbf{mpe_5}\\ \mathbf{mpe_6}\end{bmatrix}=\begin{bmatrix}\sigma^2_{mpe_1} & 0 & 0 & 0 & 0 & 0\\ 0 & \sigma^2_{mpe_2} & 0 & 0 & 0 & 0\\ 0 & 0 & \sigma^2_{mpe_3} & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & 0 & 0\end{bmatrix}\otimes\mathbf{I},$$

and the residual (co)variance structure was

$$\operatorname{var}\begin{bmatrix}\mathbf{e_1}\\ \mathbf{e_2}\\ \mathbf{e_3}\\ \mathbf{e_4}\\ \mathbf{e_5}\\ \mathbf{e_6}\end{bmatrix}=\begin{bmatrix}\sigma^2_{e_1} & 0 & 0 & 0 & 0 & 0\\ 0 & \sigma^2_{e_2} & 0 & 0 & 0 & 0\\ 0 & 0 & \sigma^2_{e_3} & 0 & 0 & 0\\ 0 & 0 & 0 & \sigma^2_{e_4} & 0 & 0\\ 0 & 0 & 0 & 0 & \sigma^2_{e_5} & 0\\ 0 & 0 & 0 & 0 & 0 & \sigma^2_{e_6}\end{bmatrix}\otimes\mathbf{I}$$

where **A** is the average numerator relationship matrix and **I** is an identity matrix.

Model 2 was also a six trait model that considered PWG and SV at each altitude as different traits with the same effects as model 1, except for the exclusion of the maternal effects. The (co)variance structure was

$$\mathrm{var}\begin{bmatrix}\mathbf{a}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{G_0} & 0\\ 0 & \mathbf{I}\otimes\mathbf{R_0}\end{bmatrix}$$

where $\mathbf{G_0}$ is a 6x6 (co)variance matrix for the additive effects in the model and $\mathbf{R_0}$ is a diagonal matrix of residual variances corresponding to each trait. This approach was based on the methodology of Árnason (1999) in which racing performance (a linear trait) and racing status (a categorical trait) were combined to account for censoring of racing performance in Swedish Standardbred trotters. The similar model used in this study assumes PWG has been censored by the independent trait SV. Another model, which included WW, PWG, and SV measured at each altitude was of interest in order to determine the relationship between SV and WW; however time did not allow for convergence of a model of this size.

Multiple trait analyses were performed using the GIBBS2F90 (Misztal et al., 2002) program that implements a Gibbs sampling algorithm to estimate the posterior distribution of the data. A single chain of 300,000 samples was run with the first 50,000 samples discarded as burn-in for both models. Variance components for additive genetic, maternal permanent environment, and residual effects for each trait were calculated from the remaining 250,000 samples. Posterior means were calculated for each variance parameter and used to estimate genetic correlations. Convergence was determined graphically through inspection of the posterior chain and through the effective sample size of the parameter of interest.

RESULTS AND DISCUSSION

The number of records, mean, and SD for WWL, WWM, WWH, PWGL, PWGM, PWGH, SVL, SVM, and SVH are presented in Table 4.2. The largest number of records for WW, PWG, and SV occurred at the lowest altitude, indicating that the majority of cattle in Colorado are maintained at low altitude. The majority of cattle are likely maintained at low altitude due to a combination of factors (i.e. brisket disease, more rugged terrain, and poorer forage quality) associated with high altitude (Christen et al., 1996).

Mean WW and PWG were highest at low altitude whereas means were lowest at medium altitude. Means were expected to decrease with increasing altitude given that brisket disease is most common at altitudes above 1524 m. Although means increased slightly from medium to high altitude, the means at high altitude did not surpass those at low altitude. It is important to note that the zip codes provided by the AAA, which were used to identify altitude for each observation, corresponded to the mailing address on file and may not necessarily reflect where the herd is actually located. This means that observations appearing to come from extremely high altitude may actually be from a lower altitude and perhaps explain the increases in mean WW and PWG from medium to high altitude.

Incidence of survival codes for each altitude in the dataset are in Table 4.3. Differences were observed in the proportion of individuals coded as not surviving at each altitude. The proportion of individuals with a WW at low altitude that was not accompanied by a corresponding yearling weight was 22% whereas the proportion decreased to 18% for those measured at medium altitude, and then increased to 26% for those measured at high altitude. As expected, more selection appears to be occurring at high altitude as compared to low altitude. The stronger selection at high altitude could be due to the higher incidence of brisket disease observed in these areas.

Posterior mean variances from the multivariate analysis for WW and PWG in low, medium and high altitude are in Table 4.4. Additive genetic variances for WW were similar across the three levels of altitude with the largest difference being an increase of 12% from medium to high altitude. However, additive genetic variances for PWG were highest for low altitude and decreased by as much as 27% from low to medium altitude, suggesting that PWG may be more strongly affected by altitude than WW. The most rapid growth for cattle occurs during the period from weaning to yearling and rapid growth has been implicated as one of the factors contributing to the onset of brisket disease. Jensen et al. (1976) mention high rates of growth require constant acceleration of blood through the circulation system, which increases the work load on both ventricles of the heart and can lead to heart failure in susceptible individuals.

Posterior mean variances from the multivariate analysis for PWG and SV in low, medium, and high altitude are in Table 4.5. Additive genetic and residual variances for PWG were very similar to equivalent estimates displayed in Table 4.4. This suggests that the inclusion of the SV trait had little impact on the estimation of additive and residual variances. Similar genetic and residual variances were estimated for SVL, SVM, and SVH and would likely change if SV were treated as a binary rather than continuous trait.

Posterior means for heritabilities and genetic correlations from the multivariate analysis of WW and PWG at low, medium, and high altitude are in Table 4.6. Heritability for WW direct was very similar across the three altitudes and ranged from 0.26 to 0.28.

Estimates of heritability for PWG were moderate and ranged from 0.18 to 0.25. Average estimates in the literature are 0.27 and 0.31 for WW and PWG, respectively (Koots et al., 1994a). The heritability of maternal WW across the three altitudes ranged from 0.11 to 0.15. Values assumed in the AAA genetic evaluation for WW direct (0.20), WW maternal (0.14), and PWG (0.20) are in close agreement to the estimates obtained herein.

Estimates of the genetic correlation between the direct and maternal effect for WW were negative and low to moderate in magnitude within the same altitude (-0.46 to -0.19). Between different altitudes, estimates were close to zero (-0.14 to 0.17) indicating selection for direct WW had a slight negative to no effect on the maternal effect for growth. Negative values of the genetic correlation between direct and maternal effects for WW are prominent in the literature and an average estimate of -0.16 has been reported by Koots et al. (1994b). The genetic correlations between direct WW at each of the three levels of altitude ranged from 0.47 to 0.83. The largest correlation (0.83), which was between WWL and WWM, exceeds the value of 0.80 as defined by Robertson (1959) to suggest the presence of a genotype by environment interaction of little biological importance. Weaning weight measured at low and medium altitude would be considered the same trait; however the moderate correlations between WWL and WWH (0.47) and between WWM and WWH (0.49) indicate WW measured at low and high altitude as well as that measured at medium and high altitude should be considered different traits. Similarly, correlations between maternal effects for WW ranged from 0.42 to 0.63 and indicate that a dam’s ability to produce milk for her calf changes based upon the altitude where she is in production. Christen et al. (1996) also found that milk production varied with altitude and reported a 15.4 kg/d decrease in milk yield of dairy cows maintained on high altitude (2000 m) as compared to low altitude (400 m) pastures. In contrast, Bryant et al. (2007) concluded that there were no significant differences in milk yield across extreme altitude; however altitude in that study only ranged from 50 to 367 m.

Genetic correlation estimates of direct WW with PWG were low to moderate ranging from 0.13 to 0.44. Estimates between these traits at the same level of altitude ranged from 0.13 to 0.42 and suggest that calves with genetics for increased growth at weaning also have increased genetic potential for growth from weaning to yearling. This relationship, although smaller in magnitude, supports the findings of Bennett and Gregory (1996). In a review of studies published from 1940 to 1991, Koots et al. (1994b) reported a similar average estimate of 0.44. The genetic correlations between maternal WW and PWG ranged from 0.06 to 0.25 suggesting selection on dam milk production will lead to a corresponding increase in PWG. These low to moderate positive correlations are similar to the estimate of 0.11 reported by Koots et al. (1994b). Genetic correlations among PWG measured at the three levels of altitude followed a trend similar to that observed for WW. Postweaning gain measured at low altitude and PWGM exhibited a higher correlation (0.79) in comparison to that between PWGL and PWGH (0.62) and between PWGM and PWGH (0.43). These results suggest PWGL and PWGH as well as PWGM and PWGH should be considered different traits and indicate there may be significant reranking of sires for PWG across altitude. Live weight of dairy cows maintained at high altitude was found to be 28 kg lighter than that of cows maintained at low altitude providing additional evidence for differences in growth based on altitude (Christen et al., 1996). A smaller reduction in body weight of approximately 5 kg was reported in calves 3 months of age at an altitude of 4500 m as compared to those at a much lower altitude of 1600 m (Tucker et al., 1975). Investigating performance and pulmonary arterial pressure in cattle of uniform breeding, Will et al. (1962) found average weight gain in cattle maintained at high altitude (3048 m) for six months was less than half of the average gain of those maintained at low altitude (1524 m). Differences in performance between high and low altitude in individuals with similar breeding also provides evidence of possible reranking of sires.

Posterior means for heritability and genetic correlations from the multivariate analysis of PWG and SV at low, medium, and high altitude are in Table 4.7. Heritability estimates for PWG ranged from 0.18 to 0.26 and were very similar to those observed in Table 4.6. This finding is reflective of the similar genetic and residual variances obtained in both analyses. The addition of SV to the model was expected to explain more of the variation in PWG and lead to an increase in the heritability of PWG; however estimates changed very little. Perhaps treating SV as a categorical as opposed to a continuous trait would increase heritability (Urioste et al., 2007); however SV in this study was treated as linear for computational convenience because convergence problems were encountered when treating SV as categorical. Posterior means of the heritability of SV ranged from 0.20 to 0.23 and indicate SV is a moderately heritable trait that could be used as a selection tool for improving the chance of survival at low, medium, and high altitude.

Genetic correlations among PWG measured at different altitudes ranged from 0.27 to 0.77. The highest correlation was that between the highest and lowest altitudes and was unexpected because the highest correlation in the previous analysis with WWT was between PWGL and PWGM. This unexpected result could reflect some convergence issues with the inclusion of the survival trait in the model. Although correlations between

PWG measured at different altitude exhibited a trend unlike that from the previous analysis, estimates continued to differ from unity and provide evidence of genotype by environment interaction and possible reranking of sires (Robertson, 1959).

Estimates of the genetic correlation between PWG and SV measured at the same altitude were positive and ranged from 0.28 to 0.41. These estimates are moderate in magnitude and indicate that calves with genetics for increased growth from weaning to yearling also have increased genetic potential for survival at low, medium, and high altitude. Genetic correlations between PWG and SV measured at the same altitude were stronger at medium and high altitude as compared to low altitude and suggest that the chances of survival at higher altitudes are greater for those with greater gains from weaning to yearling. The majority of research focusing on the genetics of brisket disease centers on pulmonary arterial pressure as an indicator trait for susceptibility to brisket disease given that elevated blood pressure is a common symptom of the disease. Schimmel and Brinks (1982) reported a strong negative correlation of -0.46 between postweaning average daily gain and pulmonary arterial pressure suggesting that as producers select bulls for increased gain they are also indirectly selecting for lower susceptibility to brisket disease. These findings agree nicely with those reported here for PWG and SV indicating selection for greater gains, especially at higher altitudes, will also lead to better survival (reduced susceptibility).

Posterior mean genetic correlations between SV at each level of altitude were positive and moderate to high in magnitude. Estimates were highest between SVL and SVM and lowest between SVM and SVH. These correlations suggest that the genetic ability for SV is most similar between the lowest altitudes and less similar between the highest altitudes. Although brisket disease can occur at altitudes of less than 2134 m, the highest incidence tends to occur above this altitude (Will and Alexander, 1970) and may explain why the genetic ability to survive is most different when comparisons involve the highest altitude in the current study.

A very strong assumption made in this study was that animals missing yearling weights were either moved to lower altitudes or died of heart failure, both of which were associated with brisket disease. Disposal codes for calves at weaning would help in identifying the reason for an animal leaving the herd. In addition, measures of pulmonary arterial pressure on all individuals in the dataset could have assisted us in our assumption that animals leaving the herd at weaning were susceptible to brisket disease. Herd zipcodes that reflect the exact location of the cattle when performance was measured could have also been very useful in assigning weaning weights to the correct environment.

Pulmonary hypertension which results from hypoxia at high altitudes is a common symptom associated with individuals contracting brisket disease and is variable among and between species. The variation in magnitude of response to hypoxia has been attributed to the amount of smooth muscle in the small pulmonary arteries of the lung (Tucker et al., 1975). Tucker et al. (1975) compared species known to exhibit high pulmonary vascular reactivity (cattle and pigs) to those known to exhibit low reactivity (sheep) to hypoxia at high altitude and discovered that low reactors had much less pulmonary vascular smooth muscle than high reactors. These findings suggest that cattle able to withstand higher altitudes without contracting brisket disease may have less pulmonary vascular smooth muscle than those susceptible to the disease. Perhaps, through association analysis, SNP with the greatest impact on arterial smooth muscle of the lung can be identified and used to select for cattle resistant to dangerous increases in pulmonary arterial pressure associated with brisket disease.

In conclusion, genetic correlations between direct effects for WW and PWG measured at low, medium, and high altitude indicated evidence for genotype by environment interaction and suggested that sires may rerank in their performance across altitude. Selection for higher gains from weaning to yearling would be expected to increase survival, especially at higher altitudes. The results presented here suggest that WW and PWG in different altitudes should be considered different traits in a national evaluation to aid producers selecting bulls for use in high altitude environments.

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Table 4.1. Number of records, mean, and SD for weaning weight (WW) and postweaning gain (PWG)

Trait	No. of Records	Mean	SD
WW, kg	102,233	261.5	38.9
PWG, kg	54,448	149.7	66.4

Table 4.2. Number of records, mean, and SD for weaning weight (WW), postweaning gain (PWG), and survival (SV) measured at low (L), medium (M), and high (H) altitude

Trait	No. of Records	Mean	SD
WW, kg			
L	54,559	264.1	38.9
M	24,462	254.7	35.6
H	23,212	262.8	41.1
PWG, kg			
L	27,113	169.6	61.9
M	14,998	114.9	60.3
H	12,337	148.3	65.3
SV, 1 and 2			
L	34,837	1.78	0.17
M	18,190	1.82	0.14
H	16,734	1.74	0.19

Table 4.3. Culling rate and incidence of survival codes for each altitude in the dataset

	Survival Code[1]		
Altitude	1	2	Culling rate[2]
Low	7,724	27,113	22%
Medium	3,192	14,998	18%
High	4,397	12,337	26%

[1] Survival code 1= individuals with a weaning weight observation and no yearling weight observation. 2= individuals with both a weaning and yearling observation.

[2] Culling rate= number of individuals coded 1 divided by total number of individuals at each altitude.

Table 4.4. Posterior mean variances[1] (± SD) from the multivariate analysis for weaning weight (WW) and postweaning gain (PWG) in low (L), medium (M) and high (H) altitude

Item	σ^2_a	σ^2_m	σ^2_{mpe}	σ^2_e
WW, kg^2				
L	155 ± 10	61 ± 6	81 ± 4	299 ± 6
M	141 ± 14	68 ± 9	58 ± 5	279 ± 8
H	158 ± 17	89 ± 10	70 ± 6	349 ± 10
PWG, kg^2				
L	157 ± 11	-	-	479 ± 8
M	114 ± 11	-	-	441 ± 9
H	118 ± 13	-	-	527 ± 12

[1] σ^2_a, σ^2_m, σ^2_{mpe}, and σ^2_e are additive, maternal, maternal permanent environment, and residual variances.

Table 4.5. Posterior mean variances[1] (± SD) from the multivariate analysis for postweaning gain (PWG) and survival (SV) in low (L), medium (M) and high (H) altitude

Item	σ^2_a	σ^2_e
PWG, kg^2		
L	170 ± 11	472 ± 9
M	112 ± 14	444 ± 10
H	118 ± 14	529 ± 12
SV, 1 and 2		
L	0.03 ± 0.00	0.10 ± 0.00
M	0.03 ± 0.00	0.09 ± 0.00
H	0.03 ± 0.00	0.13 ± 0.00

[1] σ^2_a and σ^2_e are additive and residual variances.

Table 4.6. Posterior means for heritabilities (on the diagonal) and genetic correlations (above the diagonal) from the multivariate analysis of weaning weight (WW) and postweaning gain (PWG) at low (L), medium (M), and high (H) altitude with posterior SD in parentheses

	WWL$_D$[1]	WWM$_D$[1]	WWH$_D$[1]	PWGL	PWGM	PWGH	WWL$_M$[1]	WWM$_M$[1]	WWH$_M$[1]
WWL$_D$	0.28 (0.02)	0.83 (0.06)	0.47 (0.08)	0.19 (0.04)	0.28 (0.07)	0.18 (0.11)	-0.37 (0.05)	0.09 (0.09)	0.08 (0.08)
WWM$_D$		0.27 (0.02)	0.49 (0.11)	0.25 (0.12)	0.42 (0.05)	0.16 (0.11)	-0.14 (0.09)	-0.19 (0.08)	0.17 (0.10)
WWH$_D$			0.26 (0.03)	0.44 (0.09)	0.32 (0.13)	0.13 (0.06)	-0.06 (0.11)	0.02 (0.12)	-0.46 (0.05)
PWGL				0.25 (0.02)	0.79 (0.07)	0.62 (0.11)	0.23 (0.05)	0.10 (0.12)	0.07 (0.09)
PWGM					0.21 (0.02)	0.43 (0.17)	0.24 (0.11)	0.14 (0.08)	0.20 (0.12)
PWGH						0.18 (0.02)	0.23 (0.10)	0.06 (0.15)	0.25 (0.07)
WWL$_M$							0.11 (0.01)	0.49 (0.09)	0.63 (0.07)
WWM$_M$								0.13 (0.02)	0.42 (0.10)
WWH$_M$									0.15 (0.02)

[1] D and M subscripts indicate the direct and maternal effect for weaning weight, respectively.

Table 4.7. Posterior means for heritability (on the diagonal) and genetic correlations (above the diagonal) from the multivariate analysis of postweaning gain (PWG) and survival (SV) at low (L), medium (M), and high (H) altitude with posterior SD in parentheses

	PWGL	PWGM	PWGH	SVL	SVM	SVH
PWGL	0.26 (0.02)	0.72 (0.08)	0.77 (0.11)	0.28 (0.06)	0.35 (0.14)	0.49 (0.10)
PWGM		0.20 (0.02)	0.27 (0.15)	0.58 (0.13)	0.48 (0.08)	0.19 (0.14)
PWGH			0.18 (0.02)	-0.02 (0.11)	0.28 (0.22)	0.41 (0.09)
SVL				0.23 (0.01)	0.60 (0.11)	0.37 (0.15)
SVM					0.22 (0.02)	0.27 (0.18)
SVH						0.20 (0.02)

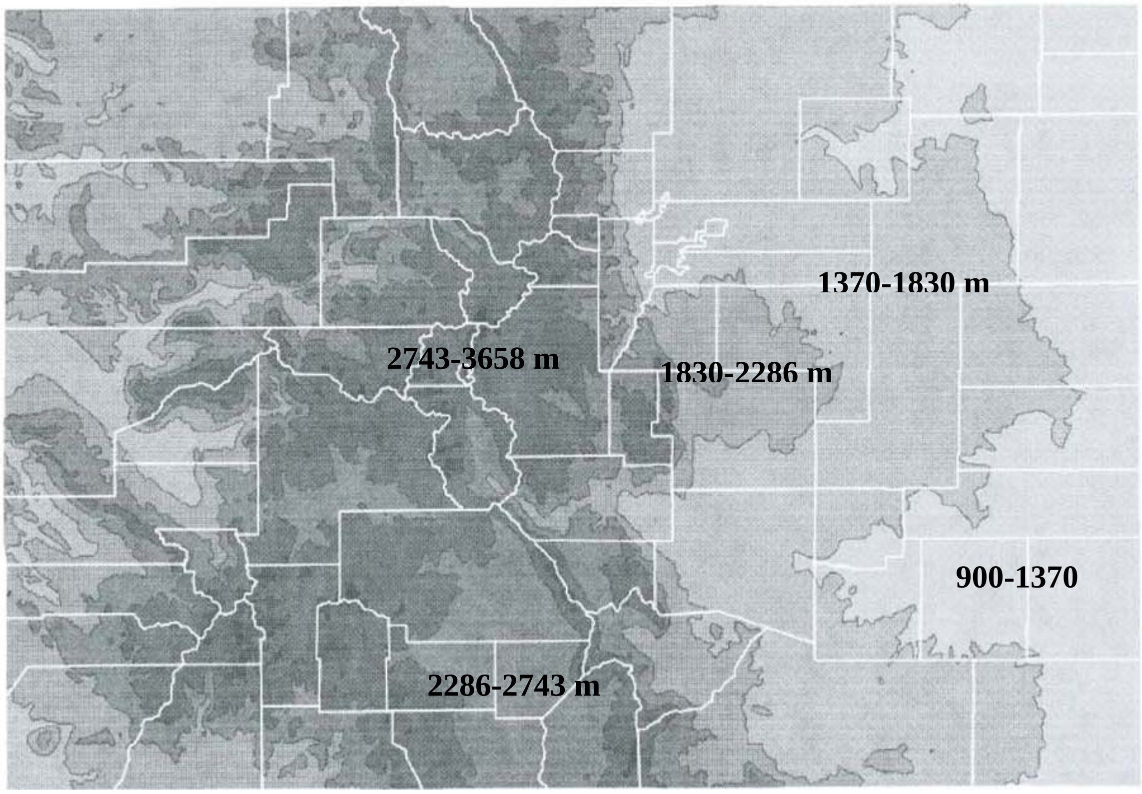

Figure 4.1. Elevation trends across the state of Colorado (Adapted from www.geology.com)

CHAPTER 5

PRELIMINARY ANALYSES ACCOMPANYING RESEARCH IN CHAPTER 4

INTRODUCTION

A series of preliminary analyses were undertaken prior to arriving at the preceeding analysis and this chapter summarizes those methods and results. The objective of this portion of the study was to investigate the relationship between altitude and weaning weight in Angus cattle born in Colorado. Brisket disease is a common problem for producers in Colorado. Pulmonary arterial pressure (PAP), an indicator trait for susceptibility to brisket disease, is reported to have a high negative correlation with growth. Perhaps weaning weight is stable at lower altitudes and begins to decrease at a certain altitude. The objective of this portion of the study was to investigate the presence of a height threshold at which weaning weight begins to decrease.

MATERIALS AND METHODS

Data

Weaning weight records adjusted to 205 days of age according to BIF guidelines were obtained from the American Angus Association (**AAA**). Data were from purebred Angus cattle born between 1972 and 2007 in Colorado. Contemporary groups were defined based upon herd, process date, lot identification, management code, and sex resulting in 5,134 unique contemporary groups. Individuals with an age of dam greater than 12 years and contemporary groups represented by a single sire were excluded from the study. In addition, analyses were limited to large herds with greater than 200 individuals represented in the data. A 3-generation pedigree file of 141,103 animals was extracted for 102,696 individuals.

The AAA allowed determination of the specific location associated with each weaning weight observation by providing pertinent city, and zip code information for each herd at weaning. Zip codes were used to assign each observation to an approximate altitude. Altitudes in the data ranged from 914 m to 2742 m and were divided into six classes, each consisting of 305 m of altitude. The number of weaning weight records and mean weaning weights by altitude class are in Table 5.1.

A height index, similar to the THI index developed by Ravagnolo et al. (2000), was developed to investigate the existence of a height threshold for weaning weight and was defined as

$$\mathrm{HI} = \begin{cases} 0 & \text{if altitude} \leq \text{altitude}_{\text{threshold}} \\ \text{or} & \\ \text{altitude-altitude}_{\text{threshold}} & \text{if altitude} > \text{altitude}_{\text{threshold}} \end{cases}$$

where $\text{altitude}_{\text{threshold}}$ was set at 914, 1219, 1524, 1829, 2134, and 2439 m in six different analyses to determine the appropriate threshold value for weaning weight.

Statistical Analysis

Potential threshold values were tested and used to divide weaning weight observations into those observed at low and high altitudes. The six different potential threshold values were tested with the following fixed effect model:

$$y_{ijkl} = aod_i + YMOB_j + sex_k + bHI_l + e_{ijkl}$$

where y_{ijkl} is the adjusted weaning weight for an individual with an age of dam i, born in year-month of birth j, of sex k, and at a height index of l; aod_i is the effect of age of dam on weaning weight; $YMOB_j$ is the effect of year-month of birth on weaning weight; sex_k is the effect of sex on weaning weight, bHI_l is a fixed regression of height on weaning weight; and e_{ijkl} is the residual. Each of the six potential threshold values was tested and the value with the highest R^2 was chosen as the true threshold.

Weaning weight observed in low and high altitudes were treated as different, but correlated traits in a two trait multiple component animal model presented in matrix notation as

$$\begin{bmatrix} \mathbf{y}_{\mathbf{L}} \\ \mathbf{y}_{\mathbf{H}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\mathbf{L}} & 0 \\ 0 & \mathbf{X}_{\mathbf{H}} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\mathbf{L}} \\ \mathbf{b}_{\mathbf{H}} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\mathbf{L}_{\mathbf{D}}} & \mathbf{Z}_{\mathbf{L}_{\mathbf{M}}} & \mathbf{Z}_{\mathbf{L}_{\mathbf{MPE}}} & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{Z}_{\mathbf{H}_{\mathbf{D}}} & \mathbf{Z}_{\mathbf{H}_{\mathbf{M}}} & \mathbf{Z}_{\mathbf{H}_{\mathbf{MPE}}} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{\mathbf{L}_{\mathbf{D}}} \\ \mathbf{u}_{\mathbf{L}_{\mathbf{M}}} \\ \mathbf{u}_{\mathbf{L}_{\mathbf{MPE}}} \\ \mathbf{u}_{\mathbf{H}_{\mathbf{D}}} \\ \mathbf{u}_{\mathbf{H}_{\mathbf{M}}} \\ \mathbf{u}_{\mathbf{H}_{\mathbf{MPE}}} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\mathbf{L}} \\ \mathbf{e}_{\mathbf{H}} \end{bmatrix}$$

where $\mathbf{y}_{\mathbf{i}}$ is a vector of observations for trait i; $\mathbf{X}_{\mathbf{L}}$ is a known incidence matrix relating weaning weight observations at low altitude to the fixed effects in $\mathbf{b}_{\mathbf{L}}$ (contemporary group, year-month of birth, and age of dam); $\mathbf{X}_{\mathbf{H}}$ is a known incidence matrix relating weaning weight observations at high altitude to the fixed effects in $\mathbf{b}_{\mathbf{H}}$ (contemporary group, year-month of birth, and age of dam); $\mathbf{Z}_{\mathbf{L}_{\mathbf{D}}}$ is a known incidence matrix relating weaning weight observations at low altitude to the random direct animal effects in $\mathbf{u}_{\mathbf{L}_{\mathbf{D}}}$; $\mathbf{Z}_{\mathbf{L}_{\mathbf{M}}}$ is a known incidence matrix relating weaning weight observations at low altitude to the random maternal effects in $\mathbf{u}_{\mathbf{L}_{\mathbf{M}}}$; $\mathbf{Z}_{\mathbf{L}_{\mathbf{MPE}}}$ is a known incidence matrix relating weaning weight observations at low altitude to the random maternal permanent environmental effects in $\mathbf{u}_{\mathbf{L}_{\mathbf{MPE}}}$; $\mathbf{Z}_{\mathbf{H}_{\mathbf{D}}}$ is a known incidence matrix relating weaning weight observations at high altitude to the random direct animal effects in $\mathbf{u}_{\mathbf{H}_{\mathbf{D}}}$; $\mathbf{Z}_{\mathbf{H}_{\mathbf{M}}}$ is a known incidence matrix relating weaning weight observations at high altitude to the random maternal effects in $\mathbf{u}_{\mathbf{H_M}}$; $\mathbf{Z}_{\mathbf{H_{MPE}}}$ is a known incidence matrix relating weaning weight observations at high altitude to the random maternal permanent environmental effects in $\mathbf{u}_{\mathbf{H_{MPE}}}$; and $\mathbf{e_i}$ is a vector of random residual effects for trait i. Variances and covariances for this two trait model are represented as

$$\mathrm{var}\begin{bmatrix}\mathbf{u}_{\mathbf{L_D}}\\ \mathbf{u}_{\mathbf{L_M}}\\ \mathbf{u}_{\mathbf{H_D}}\\ \mathbf{u}_{\mathbf{H_M}}\end{bmatrix}=\begin{bmatrix}\sigma^2_{L_D} & \sigma_{L_D,L_M} & \sigma_{L_D,H_D} & \sigma_{L_D,H_M}\\ \sigma_{L_D,L_M} & \sigma^2_{L_M} & \sigma_{L_M,H_D} & \sigma_{L_M,H_M}\\ \sigma_{L_D,H_D} & \sigma_{L_M,H_D} & \sigma^2_{H_D} & \sigma_{H_D,H_M}\\ \sigma_{L_D,H_M} & \sigma_{L_M,H_M} & \sigma_{H_D,H_M} & \sigma^2_{H_M}\end{bmatrix}\otimes\mathbf{A},$$

maternal permanent environment variances represented by

$$\mathrm{var}\begin{bmatrix}\mathbf{u}_{\mathbf{L_{MPE}}}\\ \mathbf{u}_{\mathbf{H_{MPE}}}\end{bmatrix}=\begin{bmatrix}\sigma^2_{\mathrm{L}} & \sigma_{\mathrm{L,H}}\\ \sigma_{\mathrm{L,H}} & \sigma^2_{\mathrm{H}}\end{bmatrix}\otimes\mathbf{I},$$

and residual variances as

$$\mathrm{var}\begin{bmatrix}\mathbf{e_L}\\ \mathbf{e_H}\end{bmatrix}=\begin{bmatrix}\sigma^2_{\mathrm{L}} & 0\\ 0 & \sigma^2_{\mathrm{H}}\end{bmatrix}\otimes\mathbf{I}$$

where **A** is the numerator relationship matrix, **I** is an identity matrix. The subscripts L_D, L_M, L_{MPE} ,H_D, H_M, H_{MPE} refer to weaning weight in low altitude direct, maternal, maternal permanent environment; and weaning weight in high altitude direct, maternal, and maternal permanent environment, respectively.

Potential threshold values were tested using the GLM procedure of SAS (SAS, 2008). Variance components were calculated using the Gibbs2F90 program (Misztal et al., 2002). A single chain of 200,000 samples was run with the first 40,000 samples discarded as burn-in. Additive genetic, maternal genetic, maternal permanent environmental, and phenotypic variances were estimated using the remaining 160,000 samples. Convergence was determined by graphical inspection of the posterior chain and the effective sample size of each parameter.

RESULTS AND DISCUSSION

Coefficients of determination for each height threshold value are presented in Figure 5.1. Little variation was observed between the R^2 values for each potential threshold and ranged from 0.2665 to 0.2667. We expected to obtain a significantly higher R^2 value for altitudes above 1524 m compared to those at lower altitude because brisket disease commonly occurs in susceptible cattle at altitudes above 1524 m (Gjermundson, 2000). The highest R^2 value was obtained for the threshold of 1829 m and was used to divide weaning weight observations in the dataset into those observed at low and high altitude.

The number of weaning weight records and mean weaning weights for observations classified as occurring in low or high altitude based on R^2 values obtained from the height index model are in Table 5.2. Seventy-four percent of the weaning weight observations in this study were classified as occurring in low altitude, suggesting the majority of cattle in Colorado are located at lower altitudes. Mean weaning weight of cattle observed at low altitude was approximately 4 kg lighter than those observed at high altitude indicating there may be some differences in growth between altitudes.

Posterior mean heritability and genetic correlation estimates for weaning weight classified as occurring at high or low altitude based on R^2 values obtained from the height index model are in Table 5.3. Heritability estimates for direct effects averaged 0.27 and were slightly higher than the value of 0.20 currently assumed in the AAA genetic evaluation. Maternal heritability estimates averaged 0.11, which is slightly lower than the value of 0.14 used by the AAA. Overall, direct and maternal estimates of heritability agreed closely with those in the literature (Dodenhoff et al., 1999; Robinson, 1996).

Heritability estimates for direct effects were higher at low altitude (0.28) as compared to high altitude (0.25) suggesting the presence of less environmental variation at low altitude. Brisket disease is reported to occur most frequently in cattle maintained above 1524 m (Alexander and Jensen, 1959), therefore, growth of susceptible cattle may be most affected at high altitude. Maternal heritability estimates exhibited the opposite situation in which estimates were higher at high altitude compared to those at low altitude indicating less influence of environment on maternal effects at high altitude.

The presence of genotype by environment interactions due to altitude was assessed by looking at the genetic correlation between weaning weights at high and low altitude. The estimated genetic correlation between the direct effects at low and high altitude (0.85) exceeded the value of 0.80 defined by Robertson as an upper limit to indicate a GxE of little biological importance. These results indicate that there is no evidence that sires will rerank based on low and high altitude environments. Similarly, the genetic correlation between the maternal effects in each altitude class also exceeded the upper limit and suggested that a dam's ability to produce milk to contribute to her calf's weaning weight does not change based upon the altitude at which she is in production.

Genetic correlation estimates between direct and maternal effects among both altitudes ranged from -0.44 to -0.26. All direct-maternal correlations were negative and not unexpected considering estimates between these effects in the literature are typically negative as well (Eler et al., 1995; Meyer et al., 1994).

In conclusion, there was no evidence of genotype by environment interaction on weaning weight at high and low altitudes based upon the genetic correlation estimated between weight at each altitude. This finding indicates that there should be no reranking of sires across altitude. Perhaps differences in weaning weight performance due to altitude are compensated for by the dam's milk production. An interesting follow up to this study would be a similar analysis using a non-maternally influenced trait, such as postweanin gain.

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SAS User's Guide: Statistics. Version 9.2 Edition 2008. SAS Inst. Inc., Cary, NC.

Table 5.1. Number of weaning weight records and mean weaning weights by altitude class

Altitude Class, m	Records, n	Mean Weaning Weight, kg	SD, kg
914-1218	14482	261.7	41.1
1219-1523	40372	265.0	38.1
1524-1828	20822	250.9	35.1
1829-2133	3663	276.4	30.2
2134-2438	20096	266.1	39.7
2439-2742	3261	242.6	43.9

Table 5.2. Number of weaning weight records and mean weaning weights for observations classified as occurring in high or low altitude based on R^2 values obtained from the height index model

Altitude Class[1]	No. Records, n	Mean Weaning Weight, kg	SD, kg
Low	75676	260.5	38.4
High	27020	264.7	40.1

[1] Low= weaning weights observed at altitudes of 914-1828 m and High= weaning weights observed at altitudes of 1829-2742 m.

Table 5.3. Posterior mean heritability (in bold on the diagonal) and genetic correlation (above the diagonal) estimates (± SD) for weaning weight classified as occurring at high or low altitude based on R^2 values obtained from the height index model

	WWL_D[1]	WWH_D[1]	WWL_M[1]	WWH_M[1]
WWL_D	**0.28 ± 0.01**	0.85 ± 0.05	-0.26 ± 0.04	-0.21 ± 0.09
WWH_D		**0.25 ± 0.02**	-0.26 ± 0.08	-0.44 ± 0.06
WWL_M			**0.09 ± 0.01**	0.82 ± 0.08
WWH_M				**0.12 ± 0.01**

[1] Weaning weight direct (D) and maternal (M) for calves observed at low (WWL) or high (WWH) altitude.

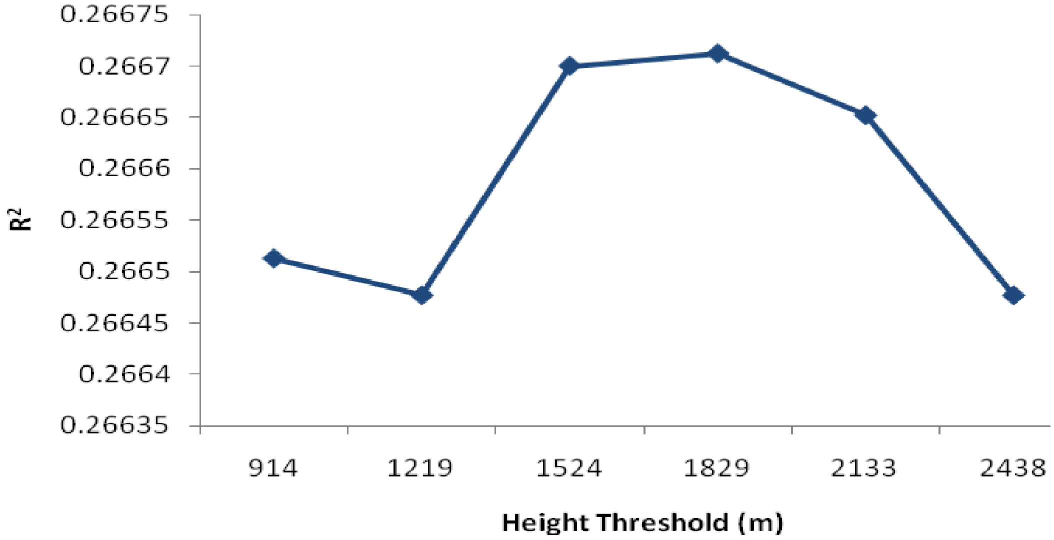

Figure 5.1. Coefficients of determination (R^2) for each height threshold value

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CONCLUSIONS

Genetic correlations between direct effects for weaning weight indicated no evidence of GxE and suggest sires should not rerank across regions of the United States or calving seasons. However, more environmental variation was found for weaning weight in the SE as compared to the NW. Genetic correlations between maternal effects were below 0.80 indicating GxE may exist and that a dam's ability to produce milk for her calf changes based upon the region of the country where she is in production and on the calving season she falls into. Given that differences in performance exist between seasons and regions, producers should base their selection decisions upon characteristics of their specific production environment.

Brisket disease is common at altitudes above 1524 m and motivated an investigation into differences in performance across altitude. Genetic correlations between direct effects for WW and PWG measured at low, medium, and high altitude indicated evidence for GxE and suggested that sires may rerank in their performance across altitude. Selection for higher gains from weaning to yearling would be expected to increase survival, especially at higher altitudes. The results presented in this study suggest that heterogeneous genetic variances for growth across altitude should be accounted for in a national evaluation to aid producers selecting bulls for use in high altitude environments.

APPENDIX A

ESTIMATION OF BREED AND HETEROSIS EFFECTS FOR GROWTH AND CARCASS TRAITS IN CATTLE USING PUBLISHED CROSSBREEDING STUDIES[1]

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[1] J.L. Williams, I. Aguilar, R. Rekaya, and J.K. Bertrand. 2010. *Journal of Animal Science*. 88:460-466.

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ABSTRACT: Current genetic evaluations are performed separately for each breed. Multiple breed genetic evaluations, however, assume a common base among breeds enabling producers to compare cattle of different breed makeup. Breed and heterosis effects are needed in a multi-breed evaluation because databases maintained by breed associations include few crossbred animals which may not be enough to accurately estimate these effects. The objective of this study was to infer breed effects (BE), maternal effects (ME), direct heterosis effects, and maternal heterosis effects for growth and carcass traits using least square means estimates from crossbreeding studies published in the literature from 1976 to 1996. The dataset was formed by recording each least square mean along with the breed composition, maternal breed composition, and direct and maternal heterozygosity. Each trait was analyzed using a single trait fixed effect model which included study as a fixed effect and breed composition and heterozygosity as covariates. Breed solutions for each trait were expressed relative to the Angus breed. Direct BE for weaning weight ranged from -7.0 ± 0.67 kg (British Dairy) to 29.3 ± 0.74 kg (Simmental) and ME ranged from -11.7 ± 0.24 kg (Hereford) to 31.1 ± 2.22 kg (Gelbvieh). Direct BE for birth weight ranged from -0.5 ± 0.14 kg (British Dairy) to 10.1 ± 0.46 kg (Continental Beef) and ME ranged from -7.2 ± 0.13 kg (Brahman) to 6.0 ± 1.07 kg (Continental Beef). Direct BE ranged from -17.9 ± 1.64 kg (Brahman) to 21.6 ± 1.95 kg (Charolais), from -6.5 ± 1.29 kg (Brahman) to 55.8 ± 1.47 kg (Continental Beef), from -8.1 ± 0.48 cm^2 (Shorthorn) to 21.0 ± 0.48 cm^2 (Continental Beef), and from -1.1 ± 0.02 cm (Continental Beef) to 0 ± 0.00 cm (Angus) for post weaning gain, carcass weight, rib eye area, and fat thickness, respectively. The use of literature estimates to predict direct and maternal breed and heterosis effects may

supplement their direct prediction in a multi-breed evaluation.

Key Words: Breed effects, Multi-breed evaluation, Heterosis

INTRODUCTION

The benefits of crossbreeding cattle are well documented (Fitzhugh et al., 1975; Gray et al., 1969; 1978) and include increased performance in both growth and carcass traits. Currently commercial producers trying to take advantage of some of these benefits are unable to compare bulls from different breeds due to the genetic evaluations available at this time. A multibreed evaluation which includes all crossbred and purebred individuals into a single analysis has been proposed as an alternative (Arnold et al., 1992). This type of evaluation would allow all progeny of an individual to influence its performance evaluation (Klei et al., 1996) and presumably lead to higher accuracies and less bias associated with the estimates.

Incorporating crossbred and purebred individuals into one analysis entails accounting for both direct and maternal breed and heterosis effects in the evaluation. These effects can either be estimated directly from the breed association data alone or this data can be combined with estimates calculated using results from crossbreeding studies in the scientific literature (Klei et al., 1996). Crossbreeding studies from the literature consist of larger numbers of crossbred animals and will likely yield more accurate estimates for these effects in comparison to available field data alone. The objective of this study was to calculate direct and maternal breed and heterosis effects for a number of growth and carcass traits in cattle using the results from several different crossbreeding studies found in the scientific literature.

MATERIALS AND METHODS

Data

This study involved an extensive literature review of crossbreeding studies in order to develop a dataset of crossbred and purebred records to use in the analysis. Therefore Animal Care and Use Committee approval was not obtained for this study. Least squares means reported in the literature from 1976 to 1996 for birth weight, weaning weight, postweaning gain, carcass weight, fat thickness, longissimus muscle area, and marbling score were used to develop the database utilized for the investigation of direct and maternal breed and heterosis effects. The majority of the scientific literature used was published between the years of 1976 to 1986 which represents a time period in which there was an absence of any strong change in genetic trend for the breeds and EPD were not readily available to producers. Preference for inclusion in this analysis was given to literature published in the Journal of Animal Science with the stipulation that each study include at least one group of crossbred individuals. Least squares means reported in these studies were used as dependent variables in our analyses. Following edits, the number of records and studies used in the analysis is presented in Table A.1. Citations for the studies from which the least squares means were collected are included in an electronic appendix and can be viewed along with this article on the online version of the Journal of Animal Science (http://jas.fass.org). For each least squares mean, direct and maternal breed percentages, direct and maternal heterozygosity percentages, standard errors reported for each mean, and the study associated with each mean were also recorded. The study was included to account for effects particular to each literature estimate such as management or environmental effects. Gregory et al. (1991) concluded that heterosis is primarily due to dominance effects; therefore direct and maternal breed and heterozygosity percentages in the current study were assumed to be the average amount of genes inherited from each breed.

Statistical Anlaysis

Direct and maternal breed and heterosis effects were included for both birth weight and weaning weight; however only direct breed and heterosis effects were included for post weaning gain, carcass weight, longissimus muscle area, fat thickness, and marbling score. Direct and maternal breed effects were based on the major breeds in terms of the studies reported in the literature and included Angus, Hereford, Shorthorn, Charolais, Limousin, Gelbvieh, Simmental, and Brahman. Four additional breed categories (British Beef, Continental Beef, British Dairy, and Continental Dairy) were added to encompass breeds with a smaller number of observations (Legarra et al., 2007). Devon, Chianina, Jersey, and Holstein, respectively, are examples of breeds that were placed into these categories.

Direct and maternal heterosis effects were based on biological type and defined by five different categories. Estimation of heterosis for each possible breed combination was not feasible; therefore breeds of similar origin were grouped together to form each biological type. A British x British cross was a British breed (Angus, Hereford, or Shorthorn) crossed with any other British breed, British x Continental heterosis was a British breed crossed with a Continental breed (Charolais, Limousin, Gelbvieh, or

Simmental), British x Zebu heterosis was a British breed crossed with a Zebu breed (Brahman), Continental x Continental heterosis was a cross between two Continental breeds, and Continental x Zebu was a cross between a Continental breed and a Zebu breed.

The single trait fixed effect model used to analyze the data for each trait is presented in scalar notation as:

$$y_{ijklm} = study_i + \sum_{j=1}^{12} f_j * de_j + \sum_{k=1}^{12} f_k * me_k + \sum_{l=1}^{5} f_l * dh_l + \sum_{m=1}^{5} f_m * mh_m + e_{ijklm}$$

where y_{ijklm} is the least squares means for the trait of interest (birth weight, weaning weight, postweaning gain, carcass weight, longissimus muscle area, fat thickness, or marbling score), $study_i$ is the effect of the i^{th} study group or management within study, f_j is the gene fraction for breed j for direct effects, de_j is the direct effect of the j^{th} breed, f_k is the gene fraction for breed k for maternal effects, me_k is the maternal effect of the k^{th} breed, f_l is the direct heterosis percentage from biological type combination l, dh_l is the direct heterosis effect of the l^{th} biological type combination, f_m is the maternal heterosis percentage from biological type combination m, mh_m is the maternal heterosis effect of the m^{th} biological type combination, and e_{ijklm} is the residual. The data was analyzed with this model using the Gibbsf90 (Misztal, 1999) program. In order to account for the uncertainty associated with the least squares estimates used as dependent variables in the model, each element of the vector **y** was sampled every round from a normal distribution with a mean equal to the least squares mean reported in the literature and a variance equal to the square of the standard error associated with the least squares mean. The Gibbs sampler was run for 100,000 iterations with a conservative burn in period of 40,000 rounds.

The Angus breed had the largest number of observations represented in the data and was used as the base breed. As a result the remaining breed effects were expressed as a deviation from Angus.

RESULTS AND DISCUSSION

Breed Effects

A summary of posterior direct and maternal breed effect solutions and associated standard deviations for birth weight, weaning weight, and post weaning gain is listed in Table A.2. Direct breed effects refer to the influence of the breed composition of the individual on the trait of interest and these effects for birth weight ranged from -0.51 kg for British Dairy to 10.13 kg for Continental Beef. Overall the larger framed Continental breeds were associated with the most positive effects while the smaller framed British breeds the most negative (Arango et al., 2002). Investigating direct breed effects in three multibreed populations of beef cattle Rodriguez-Almeida et al. (1997) reported estimates of 3.47 kg, 5.61 kg, 7.97 kg, and 10.63 kg for Hereford, Limousin, Charolais, and Simmental as deviations from Angus, respectively. Corresponding estimates in the current study were similar and in overall agreement. The highest standard deviations were associated with the British Beef (0.43) and Continental Beef (0.46) categories indicating fewer means were available for their estimation.

Maternal breed effects refer to the influence of the breed composition of the dam on the trait of interest and these effects for birth weight ranged from -7.22 kg for Brahman to 5.99 kg for Continental beef. Franke et al. (2001) obtained a similar estimate for the Brahman maternal effect of -6.9 kg, which is not surprising considering the fact that Brahman are known to have a low maternal effect for birth weight (Roberson et al., 1986). Although a numerically smaller difference, Shorthorn and Simmental also had maternal effects below that of Angus which was a similar finding to that reported by Rodriguez-Almeida et al. (1997).

Gelbvieh and Simmental had the most positive effects for weaning weight direct with values of 27.14 kg and 28.00 kg, respectively. These two breeds are known for their large frames and high growth potentials therefore these results are not unexpected (Arango et al., 2002). There was a difference between these two breeds of only 0.86 kg which is slightly lower than that of 7.19 kg found by Rodriguez-Almeida et al. (1997), but in close agreement with that of 1.6 kg assumed by Legarra et al. (2007). Shorthorn, British Beef, Brahman, and British Dairy had effects less than that of Angus indicating these breeds have slower pre-weaning growth rates. A similar trend to that previously observed with birth weight was also detected with weaning weight in which Continental breeds had more positive and British breeds more negative effects.

Maternal breed effects for weaning weight were most positive for Continental Dairy (31.30 kg) and Gelbvieh (28.84 kg) and most negative for Hereford (-11.44 kg) and Continental Beef (-14.27 kg). A number of studies have reported low maternal effects for Hereford with similar magnitude (Franke et al., 2001; Legarra et al., 2007; Rodriguez-Almeida et al., 1997). The difference of 14.82 kg observed between the maternal effects for Simmental and Gelbvieh was slightly inflated in comparison to estimates of 2 to 8 kg found in the literature (Legarra et al., 2007; Rodriguez-Almeida et al., 1997). However, the higher standard deviation associated with the Gelbvieh estimate indicates that there were fewer means available for estimation of this effect.

Direct effects for postweaning gain ranged from -17.85 kg for Brahman to 21.57 kg for Charolais. Few estimates from the literature for postweaning gain were available for comparison, however a similar trend was found by Legarra et al. (2007), although in their case Simmental had the most positive effect, whereas it had the second most positive effect in the current study. As expected from the traits previously discussed, there was an overall trend with British breeds having the most negative effects and Continental breeds having the most positive effects.

Direct breed effects and their corresponding standard deviations for carcass weight, longissimus muscle area, fat thickness, and marbling score are summarized in Table A.3. Breed effects for carcass weight ranged from -6.48 kg for Brahman to 55.77 kg for Continental Beef. Breeds of English origin (Angus, Hereford, Shorthorn, and British Dairy) had the most negative effects while breeds of European origin (Charolais, Simmental, Gelbvieh, Limousin, and Continental beef) had the most positive. This tendency for Continental breeds to have the most positive effect seems reasonable given these breeds are known to be larger framed which is typically associated with heavier carcasses (Arango et al., 2002). Rios-Utrera et al. (2006) noted a similar trend for hot carcass weight with estimates ranging from -10.18 kg for Hereford to 33.63 kg for Simmental using Angus as the base breed. Additionally, Hassen et al. (1999) found the effect of hot carcass weight in Simmental to be larger than that in Angus by 36.51 kg, an estimate very close to that obtained in the current study.

Estimates of direct effects for longissimus muscle area ranged from -8.10 cm^2 for Shorthorn to 20.98 cm^2 for Continental Beef. Rios-Utrera et al. (2006) obtained a higher direct effect for Gelbvieh in comparison to Charolais; however in the current study

Charolais was found to have a slightly more positive effect. The standard deviations from the present study appear smaller than those of Rios-Uterra et al., indicating a larger number of animals were available for more accurate estimations.

The Angus breed had the overall most positive effect for fat thickness. British breeds in general tended to have the most positive effects while Continental breeds the most negative which was expected due to leaner carcasses typical of Continental breeds (Johnson et al., 1988). Estimates ranged from 0 cm for Angus to -1.08 cm for Continental Beef. A similar tendency was also observed by Hassen et al. (1999) in which they noted that Simmental had an overall estimate of 0.79 cm below that of Angus. Estimates of -0.79, -0.79, -0.81, and -0.84 were reported for Simmental, Limousin, Charolais, and Gelbvieh, respectively and are very similar to the relevant estimates in the current study (Rios-Utrera et al., 2006).

Breed effects for marbling score like fat thickness were most positive for the Angus breed and most negative for Continental Beef (-1.68). Johnson et al. (1988) also found that higher marbling scores were associated with British rather than Continental breeds. Similarly, Rios-Utrera et al. (2006) found effects for marbling score to be lowest among Continental breeds with Limousin (-1.18) having the lowest effect.

The direct and maternal breed effects for growth estimated in the current study best reflect differences between the respective breeds in the late 1970s and 1980s due to the fact that most of the studies reviewed were performed in this time period. Breed differences for current populations of beef cattle may have changed due to selection practiced over time by breeders within each breed. For example, the Angus genetic trend (American Angus Association, 2008) for weaning and yearling weight from the 1980s to the present is 1.5 times greater than that of the Limousin breed (North American Limousin Foundation, 2008) and 3 times greater than that of the Gelbvieh breed (American Gelbvieh Association, 2008) during the same time period. Therefore, the breed differences reported in this study are representative of differences in the 1970’s and 1980’s; however, due to selection practiced by breeders, the breed differences reported in this study are not as representative of differences between breeds after 1990. The breed differences provided in the current study can be used in a multibreed genetic evaluation as prior breed-of-founder effects for the time period between the mid 1970’s to mid 1980’s prior to the wide spread use of EPD within most breeds as described by Legarra et al. (2007) and applied by Sanchez et al. (2008).

Heterosis Effects

A summary of individual and maternal heterosis solutions and associated standard deviations for birth weight, weaning weight, and postweaning gain is listed in Table A.4. Individual heterosis estimates for birth weight ranged from 0.63 kg for the Continental x Continental cross to 2.43 kg for the British x Zebu cross. Similar large positive heterosis effects of 5.1 kg, and 5.3 kg were obtained for Brahman crosses investigated by Franke et al. (2001). Maternal heterosis estimates for birth weight ranged from 0.57 kg for the British x British cross to 1.53 for the British x Zebu cross. Individual heterosis effects for weaning weight ranged from 3.47 kg for the Continental by Continental cross to 25.93 kg for the Continental x Zebu cross. The effects were highest for Zebu crosses and lowest for British and Continental crosses. A similar trend was noted by Franke et al. (2001), however they obtained slightly higher estimates compared to those presented here.

Maternal heterosis effects for weaning weight were highest for the British x Zebu (22.09 kg) and Continental x Continental (15.63 kg) crosses, although the large standard deviation associated with the Continental x Continental cross indicates this estimate may be slightly less reliable.

Heterosis effects for postweaning gain ranged from 1.49 kg for the Continental x Zebu cross to 14.68 kg for the British x Zebu cross. The low estimate obtained for the Continental x Zebu cross was unexpected considering this cross had the highest effect for all other growth traits. Approximately forty percent of the least squares means used to calculate the Continental x Zebu heterosis effect came from crossbreeding studies performed at the Meat Animal Research Center in the cool, temperate state of Nebraska and the remainder were carried out in the hot humid Southeastern states which are more ideal for Brahman cattle. Least squares means from studies in Nebraska were on average 40 kg lower and were based on a larger number of gain observations compared to those in the Southeast. This suggests that the large number of Brahman cattle contributing records to the current analysis were unable to gain at their optimum level in the cooler climate of Nebraska which consequently lead to a reduced heterosis estimate. Studies conducted in more extreme regions such as Louisiana and Georgia have reported higher heterosis estimates of 6.3 kg and 4.8 kg, respectively for post weaning gain in Brahman x Continental crosses (Comerford et al., 1988; Damon et al., 1961).

Overall there was more heterosis for growth in the British x Zebu and Continental x Zebu crosses than any of the remaining crosses. Individual heterosis estimates for growth were often lower for British x Continental crosses in comparison to British x British crosses which was an unexpected result considering the fact that British and

Continental breeds are different biological types while British breeds are of the same biological type. A possible explanation could be that British and Continental breeds are more closely related evolutionarily than typically thought and perhaps Continental breeds are the result of grading up from British breeds. Wiener et al. (2004) using microsatellite markers discovered breeds similar in their genetic makeup are not necessarily of similar geographic origin. In fact, these researchers established Ayrshire cattle (British breed) to be more closely related to Friesian cattle (Continental breed) than to any other British breed in their study.

Direct heterosis effects and associated standard deviations for carcass weight, longissimus muscle area, fat thickness, and marbling score are listed in Table A.5. Effects for carcass weight ranged from 10.34 kg for British x British to 42.04 kg for British x Zebu crosses. Similarly, DeRouen et al. (1992) reported a range of 39.4 to 59.6 kg for Zebu crosses and a range of 12.3 to 27.7 kg for British x Continental crosses. Estimates for longissimus muscle area ranged from 2.40 cm^2 for British x British to 6.57 cm^2 for British x Zebu crosses. Comparable estimates of 2.4 and 5.8 cm^2, respectively were presented by DeRouen et al. (1992). Heterosis for fat thickness was near zero for both British x Continental and Continental x Continental crosses indicating that there is no heterosis for fat thickness in these two biological type combinations. British x Zebu and Continental x Zebu crosses had the highest effects for fat thickness with values of 0.20 cm and 0.16 cm, respectively. Continental x Continental heterosis for marbling score was near zero indicating no increase in marbling associated with this cross. The highest estimates for marbling score were associated with the Continental x Zebu (0.30) and British x British (0.17) crosses. With the exception of marbling score, the Zebu crosses had the highest heterosis effects for the carcass traits analyzed in this study which is in overall agreement with findings from other studies (Rios-Utrera et al., 2006). Heterosis effects among British x British, British x Continental, and Continental x Continental crosses were similar and also tended to be the lowest estimates obtained for carcass traits.

In summary, hundreds of cattle breeds exist in the United States today with many more composites still being added. A research project involving crosses of all of these breeds is not very likely due to the large amount of labor that would be involved in maintaining the different breed groups. In addition, field data where purebreds and crossbreds of a variety of breeds are represented by a substantial number of observations is highly unlikely. A meta-analysis such as the one described in this study where information from various crossbreeding studies can be combined presents a practical alternative. Direct and maternal breed and heterosis effect estimates obtained in this manner can be used to aid in their prediction from breed association data.

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Table A.1. Summary of the number of means and studies from the literature for growth and carcass traits

	Birth Weight	Weaning Weight	Postweaning Gain	Carcass Weight	Fat Thickness	Longissimus muscle area	Marbling Score
No. Means	541	646	426	360	394	376	352
No. Studies	68	78	43	32	33	32	31

Table A.2. Posterior means and standard deviations (SD) for direct and maternal breed effects as deviations from Angus for birth weight, weaning weight, and postweaning gain

	Birth Weight, kg		Weaning Weight, kg		Postweaning Gain, kg
Breed	Direct Breed Effect	Maternal Breed Effect	Direct Breed Effect	Maternal Breed Effect	Direct Breed Effect
Angus	0	0	0	0	0
Hereford	3.04 (0.09)	0.25 (0.06)	4.27 (0.41)	-11.44 (0.22)	6.81 (0.71)
Shorthorn	2.39 (0.27)	-0.75 (0.22)	-4.02 (1.14)	1.20 (0.81)	2.59 (1.23)
Charolais	9.00 (0.18)	0.77 (0.16)	24.30 (0.81)	9.56 (0.68)	21.57 (1.95)
Limousin	6.08 (0.27)	0.44 (0.26)	11.40 (1.11)	0.51 (1.34)	3.05 (1.43)
Gelbvieh	6.74 (0.37)	1.81 (0.54)	27.14 (1.58)	28.84 (2.37)	9.59 (1.73)
Simmental	8.89 (0.23)	-0.04 (0.23)	28.00 (0.87)	14.02 (1.19)	15.81 (1.26)
Brahman	8.21 (0.17)	-7.22 (0.13)	-3.15 (0.77)	6.63 (0.58)	-17.85 (1.64)
British Beef	1.78 (0.43)	2.26 (0.92)	-3.62 (1.78)	-2.09 (3.51)	-16.73 (1.98)
Continental Beef	10.13 (0.46)	5.99 (1.07)	26.49 (1.64)	-14.27 (4.44)	7.24 (2.41)
British Dairy	-0.51 (0.14)	1.45 (0.12)	-7.48 (0.66)	15.42 (0.54)	-11.04 (1.26)
Continental Dairy	7.89 (0.16)	3.06 (0.14)	20.59 (0.74)	31.30 (0.65)	10.70 (1.07)

Table A.3. Posterior means and standard deviations (SD) for direct breed effects as deviations from Angus for carcass weight, longissimus muscle area, fat thickness, and marbling score

Breed	Carcass Weight, kg	Longissimus muscle area, cm^2	Fat Thickness, cm	Marbling Score[1]
Angus	0	0	0	0
Hereford	-1.91 (0.79)	-2.13 (0.22)	-0.15 (0.01)	-0.58 (0.02)
Shorthorn	-3.86 (1.60)	-8.10 (0.48)	-0.02 (0.03)	-0.11 (0.04)
Charolais	53.40 (1.32)	14.67 (0.38)	-0.77 (0.02)	-1.00 (0.03)
Limousin	24.92 (1.45)	17.43 (0.56)	-0.82 (0.03)	-1.42 (0.07)
Gelbvieh	41.22 (1.81)	13.69 (0.54)	-0.90 (0.02)	-1.14 (0.05)
Simmental	35.49 (1.09)	11.29 (0.43)	-0.84 (0.02)	-1.01 (0.05)
Brahman	-6.48 (1.29)	-4.15 (0.42)	-0.51 (0.02)	-1.39 (0.04)
British Beef	1.68 (2.41)	3.05 (0.78)	-0.55 (0.03)	-0.72 (0.08)
Continental Beef	55.77 (1.47)	20.98 (0.48)	-1.08 (0.02)	-1.68 (0.10)
British Dairy	-2.66 (1.50)	-3.02 (0.51)	-0.57 (0.02)	-0.20 (0.04)
Continental Dairy	39.87 (1.08)	10.41 (0.32)	-0.83 (0.01)	-0.78 (0.03)

[1] Marbling score was measured from practically devoid (2.0-2.9) to abundant (10.0-10.9)

Table A.4. Posterior means and standard deviations (SD) for individual and maternal heterosis effects for birth weight, weaning weight, and postweaning gain by biological type combination

Biological Type Combination	Birth Weight, kg		Weaning Weight, kg		Postweaning Gain, kg
	Individual Heterosis	Maternal Heterosis	Individual Heterosis	Maternal Heterosis	Individual Heterosis
British x British	0.90 (0.06)	0.57 (0.07)	8.22 (0.25)	8.33 (0.35)	6.30 (0.42)
British x Continental	0.70 (0.05)	0.83 (0.08)	5.79 (0.25)	7.41 (0.38)	7.90 (0.43)
British x Zebu	2.43 (0.11)	1.53 (0.13)	23.02 (0.54)	22.09 (0.66)	14.68 (1.00)
Continental x Continental	0.63 (0.23)	1.12 (0.69)	3.47 (1.28)	15.63 (3.54)	9.10 (2.04)
Continental x Zebu	2.00 (0.30)	1.10 (0.48)	25.93 (1.20)	10.66 (1.47)	1.49 (2.59)

Table A.5. Posterior means and standard deviations (SD) for individual heterosis effects for carcass weight, longissimus muscle area, fat thickness, and marbling score by biological type combination

Biological Type Combination	Carcass Weight, kg	Longissimus muscle area, cm^2	Fat Thickness, cm	Marbling Score[1]
British x British	10.34 (0.48)	2.40 (0.16)	0.11 (0.01)	0.17 (0.01)
British x Continental	13.13 (0.48)	2.62 (0.15)	-0.02 (0.01)	0.06 (0.01)
British x Zebu	42.04 (1.07)	6.57 (0.35)	0.20 (0.01)	0.09 (0.03)
Continental x Continental	16.44 (1.57)	3.18 (0.47)	-0.01 (0.02)	-0.05 (0.06)
Continental x Zebu	24.63 (1.47)	4.43 (0.51)	0.16 (0.02)	0.30 (0.04)

[1] Marbling score was measured from practically devoid (2.0-2.9) to abundant (10.0-10.9)