

GENOTYPE BY ENVIRONMENT INTERACTION ESTIMATED  
BY USING REACTION NORMS IN CATTLE

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A Thesis present to  
the Faculty of the Graduate School  
at the University of Missouri – Columbia

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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science

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by  
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AUGUST 2008

The undersigned, appointed by the Dean of the Graduate School have examined the thesis entitled

GENOTYPE BY ENVIRONMENT INTERACTION ESTIMATED  
BY USING REACTION NORMS

Presented by Elizabeth Ann Maricle,

A candidate for the degree of Master of Science,

And hereby certify that in their opinion it is worthy of acceptance.

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## DEDICATION

To my parents, Keith and Mary Ann, who taught me  
to believe in myself and all of my dreams.

As in the words of my mother

“Your future is bright and the world is yours to see.  
So remember your roots, but don’t forget your wings”.

## ACKNOWLEDGEMENTS

The first person I want to thank for my educational experience here at Mizzou is Dr. Lamberson for being my advisor. He has been a great mentor and resource for teaching me the skills and thinking process to become a researcher. He taught me to use all of my resources, including multiple books, to answer my questions before asking for additional help. He believed and allowed me to take any opportunity that improved my education experience. I am truly grateful to have him as an advisor because he was more than an advisor. He gave me not only educational advice but life advice when I needed support. I thank Dr. Kristi Cammack who has been a key resource because she gave me great advice towards classes, what to expect as a graduate student, and assisted with my project. I want to also thank Dr. Miroslav Kaps for allowing me to ask multiple questions and assisting with my research. I would also like to thank my committee members, Drs. Robert Weaber and Timothy Holtford, for their guidance, support and time for being on my committee.

Along the route, several professors have taught me to not just accept what is told to me, but to question and find the truth. I am glad to have had the opportunity to either be taught, serve as a teaching assistant, or interact with many professors. I want to thank Drs. Timothy Safranski, Trista Strauch, Robert Weaber, Jim Spain, Mike Smith, Matt Lucy, Duane Keisler, H. Alan Garverick, and Rod Geisert for the time they spent with me to help me get to where I am today. I want to thank Drs. Julio de Souza and Ana Silvia Moura and families for hosting me during my 18 days in Brazil to experience the

livestock environment and their culture. I want to thank Cindy Glascock and Cinda Hudlow for always keeping me in line and helping me with whatever I needed.

I could not have the education or foundation to succeed here at Mizzou if it was not for Dr. Merlyn Nielsen, Dr. Rodger Johnson, and Sue Voss for being great mentors at the University of Nebraska – Lincoln. The three of them have always believed and challenged me to be the best person I could be. I want to thank you for supporting me to achieve great things and becoming friends along the way.

I know that I could not have stayed sane throughout these last few years without the love and support of my great friends. I am grateful for the Nebraska friends that randomly called me to make sure I was still a Husker at heart, was up for visitors, or ensuring that I was still alive and kicking. I personally want to thank Tim Anderson, Krista Holstein, Brynn Husk, Elizabeth Killinger, Crystal Klug, Lindsey Moore, Brent and Melissa Nelms, Bill and Lyndsey Pohlmeier, Shane Potter, Rachel Reuss, Jackie Snyder, Ryan Talley, and many other great Nebraskans that I know I am forgetting! I am grateful for the Mizzou gang which continues to grow. I am always amazed with the support I receive whether it is wondering how research and classes are going, what my future entails, or just how I am doing. I want to personally thank Jackie and Brandon Atkins, Ashley Brauch, Bethany Bauer, Matt and Stephanie Brooks, Jake Green, Nicole Green, Dan Mathew, Courtney McHughes, Allison Meyer, Joe Meyer, Mallory Risley, Megan Rolf, Erin Sellner, Amanda Williams, and Jay Wilson for all the laughs, concerns, and great friendships that I have made and hope to continue to have!

Last but not least, I want to thank my amazing family. I want to thank my siblings, Brian and Hilary, Kristin, and Laura for the random phone calls to always check

in on me and wondering when I am coming home next. Whether you teased me, cried with me, or just chatted away, I always knew I had your full support no matter what came my way. I want to thank my nephews and niece, Austin, Carson, Cody, and Cassidy, for the great laughs and hugs which makes it hard to be in Missouri but so enjoyable when I get to come home. I have to give the largest thanks to my parents Keith and Mary Ann who taught me to reach for the stars, believe in myself, and never to forget my roots but enjoy my wings. Due to them, I was able to find my true passion for the livestock industry while they gave me the best love and support I could ever ask or imagine.

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## CHAPTER ONE: LITERATURE REVIEW

### Introduction

Progress in the animal industry is directly proportional to technology and management techniques. In particular, a greater understanding of biological functions and proper management decisions due to research is able to increase a producer's profit and efficiency. Artificial insemination, embryo transfer, and other assisted reproductive techniques have increased in use due to potential genetic improvement and consequently increased production performance in superior animals. This improvement can be limited due to genotype by environment interaction. The purpose of this review is to discuss genotype by environment interaction and a way to measure the interaction by using reaction norms.

### Genotype by Environment Interaction

The interaction between an animal's genotype and its environment can play a major role in the animal's phenotype which can be measured in reproductive or production performances. This interaction has become a critical component in livestock production due to the ability to select genetically superior animals that have the potential

to improve the current performance level. Currently, producers are utilizing assisted reproductive techniques, such as artificial insemination (AI) and embryo transfer, to increase performance of their herds. These techniques allow germplasm to be distributed across multiple environments within countries and between countries. One complication is that animals' genetic merit fails to rank consistently across all environments. This can cause frustration to a producer that is selecting animals based upon a predicted performance but is not obtaining the expected results. Therefore, understanding the basis of genotype by environment interaction (GxE) and its influence on the livestock industry will assist in future animal production.

### History

A producer's goal, whether plant or animal, is to maximize profit. Producers today are selecting hybrids or breeding stock that they believe match their style of production and their production environment to create the strongest profit. However, when a producer selects a particular hybrid or sire, a result is expected based upon current predictions of genetic merit. A complication arises when the expected result is different from the actual performance in that producer's operation. This difference is recognized as GxE. Genotype by environment interaction has been defined as the change in relative performance of a characteristic expressed in two or more genotypes, when measured in two or more environments (Falconer, 1952). This definition can be simplified as a re-ranking or change of magnitude in differences of the genetic merit of individuals depending upon geographical areas and management systems. Mathematically, the contribution of GxE to phenotypic variance can be expressed in the equation:

$$V_P = V_G + V_E + 2\text{cov}_{GE} + V_{GE}$$

where  $V_P$  is the phenotypic variance,  $V_G$  is the genotypic variance,  $V_E$  is the environment variance,  $2\text{cov}_{GE}$  is the covariance between genotype and environment, and  $V_{GE}$  is the interaction variance between genotype and environment (Falconer, 1996). Inclusion of GxE variance is important when estimating the heritability of traits. It is known that a high GxE variance component will result in a low heritability (Kang, 2002). Estimating the genetic correlation of a trait between environments can help determine the GxE influence (Falconer, 1996). If the genetic correlation between traits is large, then there is slight GxE effect. However, if the correlation is small, GxE may strongly influence the performance. It is important to understand the potential magnitude of GxE when a producer is selecting animals for a particular region. For best performance, if GxE is large, it is recommended, if possible, to use the expected performance for the particular region in which the animal will produce progeny, instead of where performance measures were taken to estimate the genetic merit of the animal (Falconer, 1996). These specific predictions have not been fully developed for the animal industry. The lack of this tool may compromise the producer's ability to maximize his/her profit.

### Types of Interactions

Genotype by environment interaction has been measured for many traits in livestock species by using a variety of methods. Studies have focused on reproductive and production performance across different geographical locations which include cool and heat stress factors, management techniques, and breed composition.

### *Reproductive Performance*

Reproductive management is very crucial in livestock production. While the actual management decisions differ between operations, the important factors regarding productivity remain generally the same regardless of location. Reproductive traits are measured to help determine performance levels. Reproductive traits are lowly heritable, indicating that a large proportion of the variation is environmental (Dziuk and Bellows, 1983). Therefore, it is important to understand the production environment while making management decisions such as selecting breeds in a crossbreeding system since interactions may influence reproductive efficiency (Buttram and Willham, 1989; McCarter et al., 1991). Several factors will be discussed on how GxE influences the level of reproductive performance.

### *Beef Cattle*

Reproductive traits can be influenced by production environment. Azzam et al. (1989) completed a 12 year study (1972 to 1983) from Garst Co., Coon Rapids, IA where first service conception rates were observed on daughters of Simmental sires which showed a change of magnitude in first service conception rates. It was reported that the highest first service conception rate was from females that were inseminated during the winter following fall calving (0.76, 0.79, and 0.87 with age of breeding (year) at 1, 2, and 3, respectively). In contrast, females that were retained until the following spring had lower conception rates of 0.46, 0.58, and 0.80 for age at breeding of 1, 2, and 3, respectively. Similarly, females that were inseminated in the summer following spring calving had higher conception rates (0.57, 0.55, and 0.65 for age of breeding of 1, 2, and

3, respectively) compared to females calving in the spring and breeding in the fall (conception rates of 0.21, 0.39, and 0.44 of age of breeding for 1, 2, and 3, respectively). The authors suggest that fall calving with winter breeding has advantages over spring calving with summer breeding depending upon geographical region due to possible heat stress (Azzam et al., 1989).

Environmental heat stress during breeding has been a major concern because of its influence on fertility and conception rates. Dunlap and Vincent (1971) completed a study using purebred Hereford heifers to determine the effects of heat stress 72 hours immediately following breeding in treatments in which one chamber was set at 32.2 °C and 65% relative humidity with a second chamber set at 21.1 °C and 65% humidity. Heifers in the first treatment had a drastic decrease in conception rate with zero out of 23 females conceiving compared to the control group in which 12 of 25 females conceived (Dunlap and Vincent, 1971). This study agreed with previous research in which fertility decreased as females experienced heat stress (Fallon, 1962; Ulberg and Burfening, 1967). It has been shown that heat stress can influence pregnancy rate (Amundson et al., 2006; Sprott et al., 2001). Amundson et al. (2006) reported a negative association ( $P < 0.001$ ) between temperature and pregnancy rate and temperature humidity index in the first 21 and 42 days of the breeding season.

Buttram and Willham (1989) completed a study involving three different lines based on mature size (small, medium, and large) in two different herds (Rhodes research facility and McNay research facility) with different management techniques. Rhodes research facility is located in central Iowa while the McNay research farm is located in southern Iowa. The two farms differ in management with Rhodes breeding in June and

July with calving in the spring. Cows were on brome grass pasture during the breeding season with heat detection twice daily. These calves were weaned at 180 d of age. The McNay farm bred animals in November and December to calve in the fall. Cows were housed on dry lots and fed corn silage and ad lib hay during the breeding season. Heat detection occurred every 12 hours. Calves were weaned at 45 d of age. Calving rates of 83.7 and 64.8 for Rhodes and McNay managements, respectively, were significantly different in first parity dams (Buttram and Willham, 1989). This same study had significant interaction between lines and management which suggest that management techniques dictate the size of the breed in different situations.

It has been shown that pregnancy rates differed in Hereford cattle raised in Montana and Florida in a study in which location, line, and their interaction influenced pregnancy rates (Koger et al., 1979). Overall pregnancy rates for Montana and Florida were  $81.9 \pm 2.5$  and  $65.6 \pm 2.4$ , respectively ( $P = 0.01$ ; Koger et al., 1979). In this study, animal selection was based upon local or introduced animals to a region. A reversal of rankings occurred, showing an advantage to local line over the introduced line with pregnancy rates of  $79.6 \pm 1.9$  and  $68.0 \pm 3.5$ , respectively. Koger et al. (1979) believed with proper selection and culling procedures, genetic adaptation to the new environment is possible. It has also been shown that different breeds or proportion of specific breeds can influence pregnancy rates (Bolton et al., 1987). Bolton et al. (1987) reported that pregnancy rates obtained from cattle at the Southwestern Livestock and Forage Research Laboratory, El Reno, OK and two larger ranches in Texas from 1981 to 1983 were different ( $P < 0.01$ ) between spring and fall calving seasons. This season effect may be due to animals being under certain temperature stresses such as heat stress.

A study was completed on the weight of the heifer at attainment of puberty in Holstein and Hereford heifers (Grass et al., 1982). Season of birth was analyzed in this data set which showed that spring calves reached puberty at a lighter weight (278 kg) compared to winter calves (303 kg) ( $P < 0.01$ ; Grass et al., 1982). Similarly, Bolton et al. (1987) found season of birth differences ( $P < 0.05$ ) between spring and fall calving in crossbred heifers for age and weight of heifer at attainment of puberty ( $367 \pm 5$  and  $381 \pm 5$  days,  $296 \pm 5$  and  $256 \pm 6$  kg, respectively). However, this study showed that fall calves reached puberty at a smaller weight of  $256 \pm 6$  kg compared to  $296 \pm 5$  kg for spring calves. This difference may be due to different breeds used in the two studies.

#### *Dairy Cattle*

Similarly to beef cattle, dairy cattle reproductive traits can be influenced by management and environmental factors. It has been shown that corrective management decisions to compensate for the current environment has an influence on conception rate. Wolfenson et al. (1988) used four fans and a sprinkler system along with timed forced ventilation as the cooling system to analyze the differences between cooled and non-cooled females. Cooled cows had higher first service conception rates compared to the non-cooled females, 59% to 17%, respectively (Wolfenson et al., 1988). The same pattern was recognized ( $P < 0.01$ ) when all inseminations were used to compare cooled cows to non-cooled cows with rates of 57% versus 20%, respectively (Wolfenson et al., 1988).

Pregnancy rate is an important reproductive measurement as a composite of conception rate with estrous detection. A one percent difference in pregnancy rate is

equivalent to an addition or subtraction of four days open (VanRaden et al., 2004); a limited number of days open is a producer's focus. Pregnancy rate can be influenced by thermal stress, either heat or cold. Chebel et al. (2007) conducted a study on Holstein heifers to examine the effects of cold stress, no stress, and heat stress. Heifers exposed to cold stress were approximately 16% less likely to become pregnant compared to heifers that received no stress, while heat stress showed minimal effects (Chebel et al., 2007). This agrees with de Vries et al. (2005) who compared season (winter and summer), year, and breeding systems (natural service, artificial insemination, and mixed) for Holstein cows in Florida and Georgia. Effects were reported for year, season, breeding system x season ( $P < 0.001$ ) and breeding system ( $P < 0.05$ ). Overall, the winter season (months of November to April) had higher ( $P < 0.001$ ) pregnancy rates of 17.9% compared to summer (months of May to October) which had only 9.0% (de Vries et al., 2005) which may be due to the use of natural service and possible decrease in bull fertility. The seasonal differences resulting in a change of magnitude may be due to having proper quality and quantity of nutrients available.

Age of puberty is a significant component to dairy production efficiency. A majority of producers want heifers calving at two years of age. However, if heifers have not reached puberty by 12 months, that goal is unattainable. Therefore, it is important to recognize factors that influence attainment of age of puberty. Menge et al. (2006) reported a study involving six sire lines with four different mating systems [outbred heifers from outbred dams (O-O), outbred heifers from inbred dams (O-I), inbred heifers from outbred dams (I-O), and inbred heifers from inbred dams (I-I)] to examine sire line, mating system, and season of birth effects on age at puberty. Differences were found

between mating systems and between sire lines with mating system I-O differing only from O-I (370 d versus 318 d;  $P < 0.01$ ) and sire lines 3 and 4 (318 and 314 days, respectively) differing ( $P < 0.05$ ) from all others sire lines which ranged from 351 to 370 days (Menge et al., 1960).

A more recent study compared age and weight at puberty of three strains of Holstein-Friesians, New Zealand 1970 (NZ70), New Zealand 1990 (NZ90), and North America 1990 (NA90) in which the percentage of North American Holstein-Friesian genetic contribution varied (NZ70 = 7%, NZ90 = 24%, and NA90 = 91%; Macdonald et al., 2007). For age at puberty, NZ70 was less ( $P < 0.05$ ) than NZ90 and NA90 with ages of  $329 \pm 6.7$ ,  $356 \pm 6.9$ , and  $373 \pm 6.0$  d, respectively. There was a trend towards a difference in age at attainment of puberty between NZ90 and NA90 ( $P = 0.07$ ). Likewise, the three strains differed ( $P < 0.05$ ) in body weight at attainment of puberty with weights of  $230 \pm 4.9$ ,  $253 \pm 4.9$ , and  $274 \pm 4.4$  kg for NZ70, NZ90, and NA90, respectively.

### *Growth Traits*

Producers have the ability to put more selection pressure on growth traits, such as birth, weaning, and yearling weights, than on reproductive traits due to higher heritabilities of the former. However, genotype by environment interaction still exists even though the amount of environmental variation is small in comparison to reproductive traits. The greater genetic contribution makes it especially important to recognize the potential of re-ranking or change of magnitude of genetic merit of bulls depending upon location.

## *Beef Cattle*

Several studies have been conducted to examine the possible interactions between genotype (sire, dam, or calf breed composition) and environment (different locations either across or within states) to measure a change in magnitude or a change or rank. Studies have focused on growth traits including birth, weaning, and yearling weights.

A Hereford study by Burns et al. (1979) compared line by location interactions in two phases. The first phase used two unrelated lines of which one was developed in Montana and the other in Florida (M1 and F6, respectively). Birth weights varied between M1 in MT, F6 in MT, M1 in FL, and F6 in FL ( $36.8 \pm 0.17$ ,  $35.0 \pm 0.22$ ,  $29.0 \pm 0.19$ , and  $29.8 \pm 0.27$ , respectively;  $P < 0.05$ ; Burns et al., 1979). The second phase included two related lines, M1 and F4, where F4 was developed in Florida, but came from M1 lineage. Lines M1 and F4 differed in performance in relatively the same pattern as phase one (Burns et al., 1979). A similar experiment was conducted in two sections evaluating crossbred versus purebred calves. Study one used Angus and Hereford bulls in seven states (AL, AR, FL, KY, LA, NC, and VA) while the second study used Brahman, Angus, and Hereford bulls in Florida and Louisiana (Northcutt et al., 1990). Breed of sire by location interaction ( $P < 0.01$ ) was evident in both studies. In the first study, Hereford sired calves were on average 2.3 kg heavier at birth than Angus sired calves across all seven location with crossbred calves weighing 1.3 kg more than purebred calves while the magnitude of variation depended upon location (Northcutt et al., 1990). Results from the second study showed that Brahman influenced calves had heavier birth weights (2.4 kg) compared to British sired calves, but resulting in a similar

trend with crossbred cattle weighing more than purebred cattle (Northcutt et al., 1990). In contrast to the two previous studies, a study of Hereford sired calves born in three different locations across North Carolina over a six year period revealed no sire by environment interaction (Tess et al., 1984).

Weaning weight, also denoted as 205 d weight, has been analyzed to examine genotype by environment interaction. The study conducted by Burns et al. (1979), and described above, showed a line by location effect ( $P < 0.01$ ) for both phases. Phase two, experimental design as described previously, showed that M1 and F4 had different weaning weights depending upon line and location with all four line by location combinations differing (M1 in MT, M1 in FL, F4 in MT, and F4 in FL with weaning weights (kg) of  $203 \pm 1.8$ ,  $158 \pm 3.8$ ,  $193 \pm 3.1$ , and  $167 \pm 2.0$ , respectively; Burns et al., 1979). Likewise, Northcutt et al. (1990) reported significant breed of sire by location effects. Hereford sired calves were heavier in Alabama, Florida, and Louisiana, but lighter in Arkansas, North Carolina, and Virginia compared to Angus sired calves. Weaning weight differed between crossbred and purebred calves in which crossbred animals were on average 15 kg heavier in the first study and on average 27 kg heavier in the second study compared to purebred calves (Northcutt et al., 1990). While these results would show strong genotype by environment interaction, other studies have shown no significance (Tess et al., 1984). It was reported by Tess et al. (1984) that no significant sire x location interactions were present for birth weight, preweaning average daily gain, and weaning weight in North Carolina among three locations (Mountain, Piedmont, and Coastal Plain regions of the Southeast).

Yearling weight is another growth trait that is utilized as a selection tool by producers who are interested in feeder cattle. It has been reported that proportion of Brahman influence (0, ¼, or ½) and calving season were significant for yearling weight, while the interaction between the two was not significant (Bolton et al., 1987). Similar results were found in Angus (AA), Brahman (BB), Angus x Brahman (AB), and Brahman by Angus (BA) heifers raised on bermudagrass or endophyte infected tall fescue pastures. Dam breed and sire by dam breed effects were significant, while the interactions between sire breed, dam breed, and environment were not (Brown et al., 1993). In contrast, Pahnish et al. (1983) in a continuation from the study conducted by Burns et al. (1979), evaluated yearling weight differences in the two phase study involving Hereford heifers in Florida and Montana (Phase 1 lines are M1 and F6; Phase 2 lines are M1 and F4). Line by location interaction for spring yearling weight (kg) and fall yearling weight (kg) (M1 in MT, F4 in MT, M1 in FL, and F4 in FL were  $248 \pm 2.4$ ,  $245 \pm 5.0$ ,  $227 \pm 5.9$ , and  $246 \pm 2.3$  for spring and  $359 \pm 2.5$ ,  $359 \pm 5.3$ ,  $275 \pm 6.2$ ,  $300 \pm 2.4$  for fall weights, respectively) and local versus introduced lines in spring and fall yearling weights (kg) (local =  $247 \pm 1.7$  and introduced =  $236 \pm 3.9$ ; local =  $330 \pm 1.7$  and introduced =  $317 \pm 4.1$ , respectively) were significant for both phases (Pahnish et al., 1983).

### *Dairy Cattle*

The GxE concerns in the dairy industry focus more on milk production and related traits (Beerda et al., 2007; Calus and Veerkamp, 2003). Therefore, the amount of studies regarding birth, weaning, and yearling weight are limited. Other studies focus on nutritional value and feed with interaction of the genotype (Berry et al., 2003). However,

the study of interest involves birth, weaning, and yearling weights in different environments.

Macdonald et al. (2007) was able to evaluate the influence of North American Holstein-Friesen genetics in the New Zealand dairy herd population. In 1970, only seven percent of North American Holstein-Friesen genetics existed in the New Zealand population (Macdonald et al., 2007). However, by 1990 the New Zealand Holstein-Friesen population consisted of 24% North American genetics while the North American Holstein-Friesen population consisted of 91% of original genetics. The influence of genetics showed a significant difference in change of magnitude between the New Zealand 1970 birth weight (kg) ( $37.5 \pm 1.59$ ) and the 1990 New Zealand and North American genetics ( $41.9 \pm 1.38$  and  $41.8 \pm 1.30$ , respectively). The study also examined the difference in the three strains for yearling weight. The 1970 New Zealand, 1990 New Zealand, and 1990 North American yearling weights (kg) were  $239.2 \pm 3.51$ ,  $248.8 \pm 2.69$ ,  $257.6 \pm 2.62$ , respectively ( $P < 0.05$ ) (Macdonald et al., 2007).

### *Between Countries*

The use of artificial insemination is increasing the use of germplasm between countries. Therefore, research is being conducted to determine the proper analyses for traits between countries. Zwald et al. (2003) evaluated factors to improve the use of Holstein sire selection across several countries. Records for test day milk weights from 17 countries (Australia, Austria, Belgium, Canada, Czech Republic, Estonia, Finland, Germany, Hungary, Ireland, Israel, Italy, The Netherlands, New Zealand, South Africa, Switzerland, and the United States) were used to evaluate the contributed difference. It

was found that the percentage of North American Holstein genes was not a useful selection criterion while maximum monthly temperature had significant variation between herds found in warm versus cool climates. Zwald et al. (2003) recommended grouping animals by sire PTA milk, rainfall, fat to protein ratio, and standard deviation of milk yield instead of by country borders. This has the potential to increase genetic progress by increasing the accuracy for such international genetic selection programs.

The use of sires across multiple countries within the dairy industry has an effect on milk yield, age at first calving, and milk fat (Ceron-Munoz et al., 2004a; Ceron-Munoz et al., 2004b; Cienfuegos-Rivas et al., 2006; Costa et al., 2000). The genetic correlations for milk yield and age at first calving were inconsistent between Mexico and the United States in the study conducted by Cienfuegos-Rivas et al. (2006). A negative correlation existed between milk yield and age at first calving when analyzed within countries, but the correlation was positive when analyzed between countries (Cienfuegos-Rivas et al., 2006). Ceron-Munoz et al. (2004a.) completed a study to determine if GxE had an effect on age of first calving between the countries of Brazil and Colombia. These results showed that the Brazilian Holstein cows were calving earlier than the Colombian cows ( $29.5 \pm 4.0$  versus  $32.1 \pm 3.5$  in months, respectively; Ceron-Munoz et al., 2004a). Due to the possibility of re-ranking of bulls between countries, a method to group or cluster the animals is under consideration (Ceron-Munoz et al., 2004b).

In the beef industry results are not consistent for determining if genotype by environment interactions are significant enough to be treated differently across countries. Some studies have shown significant interactions (Bertrand et al., 1985; Bertrand et al., 1987; Notter et al., 1992) while others have shown the opposite (Tess et al., 1979).

Studies involving birth and weaning weights and post weaning gain have compared performance among four regions (Upper Plains, Cornbelt, South, and Gulf Coast) of the United States, among Canada, Uruguay, and United States, and among Argentina, Canada, Uruguay, and the United States (de Mattos et al., 2000; Lee and Bertrand, 2002). In the study conducted by Lee and Bertrand (2002), birth and weaning weights were not significantly different which allows the data from Argentina, Canada, Uruguay, and the United States to be treated as the same trait. However, post weaning gain needs to be analyzed separately. Argentina and Uruguay are able to be analyzed together and Canada and the United States can be analyzed as one trait while Argentina and Uruguay cannot be treated as the same trait with Canada and the United States (Lee and Bertrand, 2002). One possible contributor could be that Canada and United States measure post weaning gain 160 day after weaning while Argentina and Uruguay measure 345 days post weaning (Lee and Bertrand, 2002).

### *Conclusion*

Results vary for genotype by environment studies. Several studies which involved multi-state distribution of genotypes typically reported significant effects of GxE (Burns et al., 1979; Northcutt et al., 1990; Olson et al., 1991; Pahnish et al., 1983; Pahnish et al., 1985), while comparison within the same state were not significant (Brown et al., 1997, 1993; Tess et al., 1984). This suggests that GxE is more prevalent in comparison across regions in production environment, while within states similar climate and management practices reduces the magnitude of GxE. The inconsistency between

regions and specific traits leads to the need for additional research to determine the effect of genotype by environment interaction.

### Reaction Norms

The ability to put a quantitative number to the measurement of the GxE interaction would be a great assistance in countries that strongly differ in climate or management systems. This may be achieved through the use of reaction norms, which are a mathematical function relating the mean phenotypic response of a genotype to a change in environment. Reaction norms have been utilized in plant science, neuroscience and behavior science in which an intercept and slope are used to compare differences between individuals. Reaction norm graphs are used to view the magnitude and direction of GxE. Lynch and Walsh (1998) described four graphs each containing three lines to explain reaction norms across two environments. The first graph had three lines that were parallel to one another (same slope) represent a no GxE effect. The second graph has three lines that do not interact (no change in rank) but have different slopes from one another. This GxE effect is due to a change in scale. The third and fourth graphs show GxE with a change in rank with different slopes between the two environments. The greatest concern is the changing of ranks for sires in different environments. The influence and use of reaction norms are growing within the animal industry, in particular for genotype by environment studies. It is believed the best way to evaluate the environments using this technique is if the environments are arranged based upon climate

(temperature-humidity index), geographical location (elevation), and average herd production (Schaeffer, 2004).

### *History*

The idea of the reaction norm is thought to have originated in 1909 by Richard Woltereck from Germany in his work with the *Daphnia* and *Hyalodaphnia* species from German lakes (Fuller et al., 2005; Kolmodin et al., 2004; Sarkar, 1999). He recognized morphological differences between pure lines in response to environmental differences. He began drawing “phenotypic curves” which he coined the term “Reaktionsnorm” (Sarkar, 1999). In 1926, Theodius Dobzhansky from the Soviet Union believed that traits were not inherited but the generalized idea of a norm of reaction was inherited (Sarkar, 1999). Dobzhansky introduced this concept to the United States of America when he moved here in 1927. The term for this concept has been a reaction range, environmental plasticity, environmental sensitivity, norm of reaction, and reaction norm (Falconer, 1996; Fuller et al., 2005; Kolmodin et al., 2004; Sarkar, 1999). The depiction of a reaction norm in a graph has some significant value. The graph gives a visual for how the subject of interest’s phenotype differs across environments by the evaluation of the slope of the line. The first graph using the reaction norm concept in the United Kingdom is believed to be from Falconer’s 1947 research involving three inbred strains and examining affects of environmental manipulation on litter size and litter weight at 12 d of age, although he did not use the term reaction norm (Fuller et al., 2005). Others have evaluated performance of different strains or lines in multiple environments. For instance, Davis and Lamberson (1991) analyzed performance of six genetic groups of

mice across three different environments. Their graphs depict a regression of each genetic group's performance against an environmental index for the traits ovulation rate, number of implantations, number of fetuses, and age at vaginal opening.

### *Application*

Within the animal industry, reaction norms are being used in dairy (conformation traits, body condition scores, feed intake and heart girth measurements), swine (weights, back fat, and litter size), and beef cattle (weights and back fat) (Schaeffer, 2004). The potential application could be used for wool yield in sheep, sperm production and quality in male reproduction, lifetime milk production in dairy, and female reproduction (Schaeffer, 2004).

Kolmodin et al. (2002) reported a study in Nordic dairy cattle (Danish Red Dairy Breed, Finnish Ayrshire, Norwegian Dairy Cattle, and Swedish Red and White Breed) in which the amount and pattern of GxE in production and fertility traits were analyzed. A linear random regression statistical model was used to produce reaction norms for individual bulls ( $n = 3847$ ) from 927,927 records for 305 day kg protein production and days open in first lactation (Kolmodin et al., 2002). It was found that the slopes were significantly different with larger differences between extreme environments and the average environment (Kolmodin et al., 2002). A continuation of this study was completed to describe possible effects of GxE and fixed effects for the environmental variables: geographical location, herd size, herd levels of protein yield and days open, monthly rainfall, average summer temperature, average temperature in January, and average radiation from the sun during the summer on protein yield and days open

(Kolmodin et al., 2004). First lactation data on Swedish Red and White dairy cattle included 412,385 cows in 14,976 herds after selection criteria were used to estimate reaction norms via a random regression sire model. It was shown that GxE interaction exists between protein yield and average herd year protein yield, protein yield and herd size, and days open and average herd year days open. However, it is recognized that the correlations between the phenotypic values in average and deviating environment was  $> 0.94$  which means there is a small effect on reranking of sires. It is important to recognize if the correlation is high, then there is little difference among animals resulting in no re-ranking of animals.

Reaction norms, estimated by using random regression models (RRM), are being evaluated for estimating genetic merit of beef cattle by comparing models (Arango et al., 2004; Bohmanova et al., 2005; Legarra et al., 2004; Nobre et al., 2003; Sanchez et al., 2008a; Sanchez et al., 2008b). Nobre et al. (2003) completed a study to determine if the RRM estimates expected progeny differences (EPD) more accurately compared to the multiple-trait model (MTM) for large beef cattle populations. It was reported that the RRM was more accurate in predicting the EPD in comparison with the MTM. One concern for using the RRM is that parameter estimates have a large influence on the accuracy of the technique.

Bohmanova et al. (2005) compared accuracy differences between the random regression models with cubic Legendre polynomials (RRML) and linear splines with three knots (RRMS) and MTM. An important note in this study is that the parameters for RRMS were the same as for MTM. Four different data sets were compiled for records to include 1, 205, and 365 d (3EXACT); 1, 160 to 250, and 320 to 410 d (3SPREAD); 1,

100, 205, 300, and 365 d (5EXACT); and 1, 55 to 145, 160 to 250, 275 to 325, and 320 to 410 d (5SPREAD). The first data (3EXACT) set had similar accuracies for all three models (Bohmanova et al., 2005). The second data set (3SPREAD) differed with the RRML and RRMS models being similar while the accuracy of MTM was 1.5% lower (Bohmanova et al., 2005). The accuracy for the third data (5EXACT) set was 2.4% higher than for the first data set, with the fourth data set (5SPREAD) being 2.5% higher compared to the second data set (Bohmanova et al., 2005). It was once again recognized that parameter estimates are an important component to a successful use of RRM.

### Conclusion

Geographical location and management techniques influence animal performance (Buttram and Willham, 1989; Koger et al., 1979). The ability to improve the prediction of a performance would be a great benefit to all livestock producers. Reaction norms, by use of a random regression model, are one way to produce a quantitative measurement for comparing differences between animals with use of appropriate parameter estimates. The reaction norm is able to show how animals differ across environments. Other models are able to identify that a GxE exist. A reaction norm is able to express where a change in rank occurs and to what magnitude.

CHAPTER TWO: GENOTYPE BY ENVIRONMENT INTERACTION MEASURED  
BY USING REACTION NORMS IN U.S. ANGUS BEEF CATTLE

Abstract

The influence of genotype by environment interaction (GxE) on animal performance complicates selection decisions. Reaction norms are a statistical technique used to characterize GxE. The objective of this study was to evaluate GxE by comparing reaction norms among Angus bulls from the United States. Dependent variables were weight at birth, 205 d weaning, and 365 d yearling. Weights were adjusted according to American guidelines of the American Angus Association. Environments were defined as progeny groups with a common herd based upon location of data record. For data to be included, the following criteria had to be met: each bull must have had at least 100 progeny, with at least six progeny per environment, in at least five environments per bull, and at least six bulls having progeny in each environment. The average performance of all progeny within each herd environment was defined as the environmental mean. Average performance of progeny of a sire within an environment was defined as the progeny mean. Four statistical models were analyzed evaluating single traits and random regression model using herd environment or environmental mean for estimating breeding values and heritabilities. Fixed effects for all models included year–season, contemporary group (processing date and lot id), and sex. Herd environment was fitted as a categorical effect in models designated categorical (CM) and genotype by environment (GEM). Environmental means were fitted as a continuous effect in models

designated continuous environment (CEM) and random regression (RRM). Models CM and CEM included sire as the random variable. The GEM model included sire and sire by herd environment interaction as the random variables. In model RRM reaction norms for each bull were calculated by regressing progeny means within an environment on environment means. Regression coefficients from RRM were fitted to an ANOVA model including bull and environmental mean. Regression coefficients differed among bulls for all traits ( $P < 0.0001$ ). The reaction norm model had the best fit. Heritabilities were estimated for all traits in SAS and ASREML. Heritability estimates ranged from 0.293 to 0.401 for birth weight; 0.141 to 0.289 for weaning weight; and 0.147 to 0.259 for yearling weight across all models. These results suggest that bulls differ in the consistency of their progeny's performance across environments. Estimates of genetic merit of regressions from reaction norms may be a useful selection tool for ranking bulls to be used across diverse environments.

Key Words: Beef Cattle, Genotype x Environment Interaction, Reaction Norm

### Introduction

Animals perform differently across geographical locations and/or under different management systems. The variation in performance can be partitioned into genotype, environment, and the genotype by environment interaction (GxE) components. Genotype by environment interaction is defined as the change in relative performance of a characteristic expressed in two or more genotypes, when measured in two or more environments (Falconer, 1952). This definition can be simplified as a re-ranking of the

genetic merit of individuals depending upon geographical areas and management systems in which performance is recorded. This interaction has become a critical component in livestock production due to producers selecting sires for improved performance which is not being observed in the performance in the offspring.

Plant scientists have evaluated GxE when selecting hybrids for use in specific soils by use of reaction norms, which are mathematical functions measuring the stability of performance of a genotype to changes in environment. Reaction norms can be graphed to compare the slopes of the individuals of interest (Kolmodin et al., 2002; Lynch and Walsh, 1998). A slope greater than one indicates the individual is more responsive than average to positive environmental factors, while a slope less than one shows relative stability of performance across environments. The livestock industry has begun to utilize the reaction norms to select for individual traits (Bohmanova et al., 2005; Kolmodin et al., 2004; Kolmodin et al., 2002; Legarra et al., 2004; Nobre et al., 2003; Sanchez et al., 2008a; Schaeffer, 2004).

Model comparisons have been used to determine if traits across regions or countries should be analyzed separately or together when estimating the genetic parameters and predicting genetic merit (Bertrand et al., 1985; Ceron-Munoz et al., 2004a; Ceron-Munoz et al., 2004b; Costa et al., 2000; de Mattos et al., 2000; Lee and Bertrand, 2002; Tess et al., 1979; Zwald et al., 2003). Model type can affect accuracy of measuring GxE which impacts predicting animals' performance.

The purpose of this study was to determine the magnitude of genotype by environment interaction by comparing reaction norms among Angus bulls from the United States population. Four different models were evaluated to determine efficiency

of estimating heritabilities of birth, weaning, and yearling weights and to evaluate the benefit of including reaction norms in estimation of genetic merit. If important and heritable, slopes of reaction norms could be used as a selection criterion to choose animals that produce progeny robust to changes in the environment.

### Materials and Methods

#### *Data*

Birth, weaning, and yearling weights were provided by the American Angus Association. The birth weight data set consisted of 236,239 records, weaning weight had 241,401, and yearling weight had 140,589, before records missing data were deleted. All weights were adjusted using American Angus Association guidelines. Weights more than two standard deviations from the mean were considered outliers and deleted.

The three traits (birth, weaning, and yearling weights) were considered separately. Each farm/ranch was identified as a herd environment to group animals together based upon location. For data to be included in the analysis each sire was required to have at least 100 progeny, with at least six progeny per environment in five or more environments, and each environment must have had calves from at least six qualifying bulls. The mean performance of progeny of all qualifying bulls within each environment was denoted as the environmental mean. The mean performance of progeny of a sire within multiple environments was designated as the progeny mean. A contemporary group was defined as the processing date and lot id for birth, weaning, and yearling

weights. A year–season effect was defined as a fixed effect to reduce the amount of computational time.

The final data set for each trait consisted of animal ID, sire ID, sex, adjusted weight, year–season, herd environment, contemporary group, and environmental and progeny mean. The number of animals pre and post criteria selection, number of sires, and number of herd environments are presented in table 2.1. Pedigree files which included the sire, dam, paternal grandsire, and paternal granddam were defined for each trait.

### *Models*

Four models were developed to estimate genetic parameters to determine the effect of GxE on parameter estimates. Dependent variables were adjusted birth, weaning, or yearling weight. The herd environment was fitted as a categorical effect for models denoted categorical (CM) and genotype by environment (GEM). Environmental mean was fitted as a continuous effect in models denoted continuous environment (CEM) and random regression (RRM). Sire was included as a random variable in models CM and CEM. Model GEM included sire and sire by herd environment as random variables. Model RRM included a simple linear random regression by bull of progeny means in environment on the environmental means. The regressions represent stability of performance of a bull’s progeny across a set of environments compared to the theoretical “average” bull. All models included year x season, contemporary group, and sex as fixed effects.

Model CM was represented by:

$$y_{ijk} = \mu + HE_i + fixed_j + sire_k + e_{ijk},$$

where  $y_{ijk}$  is the animal's weight,  $\mu$  is the overall mean,  $HE_i$  is the herd environment (defined as a class variable),  $fixed_j$  are the fixed effects as described above,  $sire_k$  is the random sire effect, and  $e_{ijk}$  is the error. This is the common sire model.

Model GEM is similar to categorical model but adds an interaction component represented by:

$$y_{ijk} = \mu + HE_i + fixed_j + sire_k + (sire*HE)_{ij} + e_{ijk}$$

where  $y_{ijk}$  is the animal's weight,  $\mu$  is the overall mean,  $HE_i$  is the herd environment (defined as a class variable),  $fixed_j$  are the fixed effects as described above,  $sire_k$  is the random sire effect, and  $(sire*HE)_{ij}$  is the sire x herd interaction, and  $e_{ijk}$  is the error.

There is an overall sire effect, and also the effect of sire for each defined herd.

Model CE differs by replacing the HE by the environmental mean (EM) fitted as a continuous effect as shown below:

$$y_{ijk} = \mu + b(EM_i) + fixed_j + sire_k + e_{ijk},$$

where  $y_{ijk}$  is the animal's weight,  $\mu$  is the overall mean, EM denotes the environmental mean (herd progeny means),  $b$  is regression coefficient of  $y_{ijk}$  on an environmental mean,  $fixed_j$  are the fixed effects as described above,  $sire_k$  is the random sire effect, and  $e_{ijk}$  is the error. This model is the common sire model, with the effect of environment defined as a regression. Sire effects are constant across environment (herds).

Model RRM is the random regression model as represented below:

$$y_{ijk} = \mu + \beta(EM_i) + fixed_j + sire_k + e_{ijk},$$

where  $y_{ijk}$  is the animal's weight,  $\mu$  is the overall mean,  $\beta$  is regression coefficient of  $y_{ijk}$  on an environmental mean,  $fixed_j$  are the fixed effects as described above,  $sire_k$  is the random sire effect explained as a random linear function of herd mean, that is:

$sire_k = b0_k + b1_k EM_i$ , where  $b0_k$  and  $b1_k$  are random intercept and slope, respectively, of the regression of progeny performance on the environmental mean for sire  $k$ ; and  $e_{ijk}$  is the error. This model was based upon an unstructured covariance model.

To estimate regression coefficients, a phenotypic model is represented below:

$$y_{ijk} = \mu + \beta EM_i(sire_k) + fixed_j + sire_k + e_{ijk},$$

where  $y_{ijk}$  is the animals weight,  $\mu$  is the overall mean,  $\beta$  is regression coefficient of  $y_{ijk}$  on a environmental mean by sire,  $fixed_j$  are the fixed effects as described above,  $sire_k$  is the sire effect, and  $e_{ijk}$  is the error.

### *Analyses*

All three traits were analyzed first via SAS 9.1 (SAS Inst., Inc., Cary, NC). Data were then analyzed using ASREML 2.0 (VSN International Ltd, Hemel Hempstead, HP1 1ES, UK) with the addition of pedigree information. Heritability estimates were based upon sire model calculations. Heritabilities were calculated as four times the sire variance component divided by the sum of the sire plus the residual variance components for models CM and CEM:

$$h^2 = (4 * \text{Sire Var}) / (\text{Sire Var} + \text{Residual Var}).$$

Heritabilities from GEM were estimated with the formula:

$$h^2 = [4 * (\text{Sire Var} + \text{Interaction Var})] / (\text{Sire Var} + \text{Interaction Var} + \text{Residual Var}).$$

Heritabilities from RRM were estimated by calculating the sire variance first as:

$$\text{Sire Var} = \text{Var}(b_0) + x_i^2 \text{Var}(b_1) + 2 x_i \text{Cov}(b_0, b_1)$$

Where,  $\text{Var}(b_0) = \sigma_{b_0}^2$  = variance of the intercept  $b_0$ ;  $\text{Var}(b_1) = \sigma_{b_1}^2$  = variance of the slope  $b_1$ ;  $\text{Cov}(b_0, b_1)$  = covariance between intercept and the slope; and  $x_i$  is the average herd weight. The heritability is calculated as:

$$h^2 = [4 * (\text{Sire Var})] / (\text{Sire Var} + \text{Residual Var}).$$

The models were compared based upon Akaike information criterion (AIC) which is defined as  $-2(\log\text{-REML Likelihood} - \text{number of parameters})$ .

## Results

Variance components are presented for CM without pedigree information and all models with pedigree information. The CM sire variance component became greater for birth weight with the addition of pedigree information (0.849 to 1.018; Table 2.2). The addition of environmental interaction decreased the residual from 11.688 to 11.449 for CM and GEM, respectively, and 11.785 to 11.775 for CEM and RRM, respectively (Table 2.5).

For weaning weight, residual variance decreased as model complexity increased from CM to GEM (572.973 to 555.804) and CEM to RRM (590.713 to 589.045; Table 2.4). Sire variance was higher without pedigree information compared to inclusion of pedigree information. Similarly to birth and weaning weights, the residual variance for yearling weight decreased as the models increased in complexity.

The RRM has the variance components for the intercept, slope, covariance between the intercept and slope, and the residual error for birth, weaning, and yearling weights and are presented in Table 2.5.

Heritabilities increased for all three traits for CM with the inclusion of pedigree information (birth weight = 0.260 and 0.321; weaning weight = 0.139 and 0.149; yearling weight = 0.142 and 0.147; Table 2.6). Heritabilities increased from CM to GEM with the inclusion of an environmental effect for all three traits (birth weight = 0.321 to 0.401; weaning weight = 0.149 to 0.289; yearling weight = 0.147 to 0.259; Table 2.6). Model RRM differs from CM, GEM, and CEM as the heritability estimate for CM, GEM, and CEM is of the weight trait while RRM is the heritability estimate is for the reaction norm slope for that trait. Heritabilities of weight and for reaction norm slopes from models CEM and RRM were similar. Birth weight and weaning weight heritabilities decreased slightly (0.297 to 0.293 and 0.146 to 0.141, respectively) while heritability of yearling weight increased (0.175 to 0.181).

Akaike information criterion (AIC) values are presented in Table 2.7 for birth, weaning, and yearling weights. It is important to recognize that CM and GEM utilize herd environments which is the farm/ranch while models CEM and RRM utilize continuous environmental means which is a weight value to compare differences. Therefore, models CM and GEM can be compared with one another and models CEM and RRM can be compared. The GEM was a better fit than categorical model for all three traits. Random regression was better compared to CEM (birth weight = 15,082.6 and 15098.9; weaning weight = 2,405.38 and 2,457.64; yearling = 15,643.3 and 15,706.4, respectively).

## Discussion

Heritability estimates (Table 2.6) for birth, weaning, and yearling weights were on average lower compared to the average beef heritability values of 0.31, 0.24, and 0.33, respectively (Bolton, 2008). Heritability estimates ranged from 0.260 to 0.401 for birth weight, 0.139 to 0.289 for weaning weight, and 0.142 to 0.259 for yearling weight. Heritabilities increased for categorical model with the inclusion of pedigree information for all traits (birth weight 0.260 to 0.321; weaning weight 0.139 to 0.149; yearling weight 0.142 to 0.146). That precision of an analysis increases with the use of pedigree information was previously reported by Cantet et al., (2000).

Model GEM fit the data better than CM based for all three traits when environments were fitted as a categorical variable while RRM was better than CEM based upon environments fitted as a continuous variable (Table 2.7). The major benefit of utilizing an environmental mean to group animals is because a larger portion of animals from different areas are able to be thought as one “environment”. This also allows for a continuous variable to determine how animals perform across different production weights. One advantage to RRM over CEM is the ability to estimate breeding values of the slope for reaction norms through regression analyses.

Models CM and CEM include sire as the only random variable component while GEM and RRM include sire and an environmental interaction component. The models that contain an environmental interaction component had a lower AIC value. Among the environmental mean models, the best method was RRM. The dairy and beef industries

have increased the use of RRM to analyze GxE (Bohmanova et al., 2005; Kolmodin et al., 2004; Nobre et al., 2003; Sanchez et al., 2008a; Schaeffer, 2004). Random regression models estimate an intercept and slope, a reaction norm, which can be used to compare sires in different environments.

Reaction norms show how sires differ across environments for birth weight, weaning weight, and yearling weight with the x-axis being a continuous weight while the y-axis is the mean of progeny (Figures 2.1, 2.2, and 2.3, respectively). Each graph contains sires that respond differently across environments. The sires depicted in Figure 2.1 show the wide variety of environmental sensitivity. Differences between sires can be shown based upon reaction norm graphs (Lynch and Walsh, 1998). The “average” sires that perform across environments are represented by the lines with a slope of one. Sires with a slope greater than one are more responsive to environmental effects allowing for a greater increase in production. The sires with a negative slope would decrease in production.

It is possible for sires to not change rank, but the difference in change of phenotypic magnitude shows that GxE is present. In particular, an increase in birth weight is correlated to an increase in calving difficulty. Therefore, producers would rather select animals with smaller birth weights than larger weights. The selection technique is opposite for weaning and yearling weights with greater weights being more desired. The sires for weaning weight presented in Figure 2.2 depict re-rank and change of magnitude for animals based upon the weight environment. The same trends can be shown in yearling weights (Figure 2.3) with re-ranking and changing in magnitude of sires. It is also important to recognize that certain sires perform uniformly across

environments. Sires with uniform performance would be a good selection choice for producers desiring the same results regardless of average herd weight. Reaction norms have been expressed similarly for number of days to 110 kg for lines of pigs (Knap and Wang, 2006), protein yield and days open in Swedish dairy cattle (Kolmodin et al., 2004), and protein yield based upon milk solid states for New Zealand dairy cattle (Bryant et al., 2006). This technique is increasing in use and has the potential to increase efficiency of livestock production.

Breeding values can be estimated for reaction norms (Knap and Wang, 2006). Frequencies of breeding values are depicted in figures 2.4, 2.5, and 2.6 for birth, weaning, and yearling weight, respectively. The majority of breeding values are centered around zero with a range of 0.10 to -0.20. A positive breeding value represents an environmental responsive sire while negative positive breeding values signify the stable animals across environments. The differences in breeding values allow for producers to select sires based upon desired goals respective to specific traits.

### Conclusion

Expected progeny differences for reaction norms estimated from random regression models may offer producers a method to select animals while minimizing the confounding effects of genotype by environment interaction. Additional research is needed to determine how to efficiently utilize expected progeny differences for reaction norms combined with contemporary group means before reaction norms are made available to producers for use as another selection criterion.

**Table 2.1:** Number of records pre and post criteria selection, number of sires, and number of herd environments for birth, weaning, and yearling weights.

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<u>Trait</u>	Number of Records			
	<u>Pre-Criteria</u>	<u>Post-Criteria</u>	<u>Sires</u>	<u>Herd Environments</u>
Birth Weight	236,329	66,725	176	289
Weaning Weight	241,401	68,000	180	293
Yearling Weight	140,589	38,160	128	188

**Table 2.2:** Birth weight variance components for categorical, continuous environment, and genotype by environment models: Sire, Sire by Herd Environment (Sire\*HE), and residual variances with standard errors (Std. Error).

	<b>Variance Components</b>					
	Sire	Std. Error	Sire*HE	Std. Error	Residual	Std. Error
<b>Categorical (without pedigree)</b>	0.849	0.100	-	-	12.206	0.067
<b>Categorical</b>	1.018	0.123	-	-	11.688	0.065
<b>Continuous Environment</b>	0.945	0.114	-	-	11.785	0.065
<b>Genotype by Environment</b>	0.908	0.117	0.368	0.031	11.449	0.065

**Table 2.3:** Weaning weight variance components for categorical, continuous environment, and genotype by environment models: Sire, Sire by Herd Environment (Sire\*HE), and residual variances with standard errors (Std. Error).

	<b>Variance Components</b>					
	Sire	Std. Error	Sire*HE	Std. Error	Residual	Std. Error
<b>Categorical (without pedigree)</b>	30.888	4.067	-	-	858.085	4.672
<b>Categorical</b>	22.193	2.983	-	-	572.973	3.148
<b>Continuous Environment</b>	22.307	2.994	-	-	590.713	3.239
<b>Genotype by Environment</b>	15.435	2.572	27.855	1.881	555.804	3.112

**Table 2.4:** Yearling weight variance components for models categorical, continuous environment, and genotype by environment models: Sire, Sire by Herd Environment (Sire\*HE), and residual variances with standard errors (Std. Error).

	<b>Variance Components</b>					
	Sire	Std. Error	Sire*HE	Std. Error	Residual	Std. Error
<b>Categorical (without pedigree)</b>	59.762	9.427	-	-	1620.378	11.788
<b>Categorical</b>	40.918	6.763	-	-	1075.523	7.992
<b>Continuous Environment</b>	52.653	8.398	-	-	1150.857	8.534
<b>Genotype by Environment</b>	33.347	6.564	39.400	4.325	1052.163	7.970

**Table 2.5:** Random regression variance components: Random regression variances and standard errors (Std. Error) for the intercept, slope, covariance between the intercept and slope (Cov), and the residual birth, weaning, and yearling weights.

	<b>Variance Components</b>							
	Intercept	Std. Error	Slope	Std. Error	Cov(Int, Slope)	Std. Error	Residual	Std. Error
<b>Birth Weight</b>	7.44758	3.48014	0.00115	0.00004	-0.08687	0.04194	11.77517	0.06529
<b>Weaning Weight</b>	977.27273	229.40682	0.00279	0.00062	-1.63264	0.38244	589.04545	3.23450
<b>Yearling Weight</b>	1817.18182	506.17872	0.00188	0.00041	-1.82355	0.50517	1146.24380	8.51343

**Table 2.6:** Heritability estimates for birth, weaning, and yearling weights for the categorical model without pedigree information and all other models with pedigree information.

	<b>Birth Weight</b>	<b>Weaning Weight</b>	<b>Yearling Weight</b>
<b>Categorical (without pedigree)</b>	0.260	0.139	0.142
<b>Categorical</b>	0.321	0.149	0.147
<b>Continuous Environment</b>	0.297	0.146	0.175
<b>Genotype by Environment</b>	0.401	0.289	0.259
<b>Random Regression*</b>	0.293	0.141	0.181

\*Heritability of the slope of the reaction norm.

**Table 2.7:** Model comparison based upon AIC values (smaller the better) for birth, weaning, and yearling weights for all models with pedigree information.

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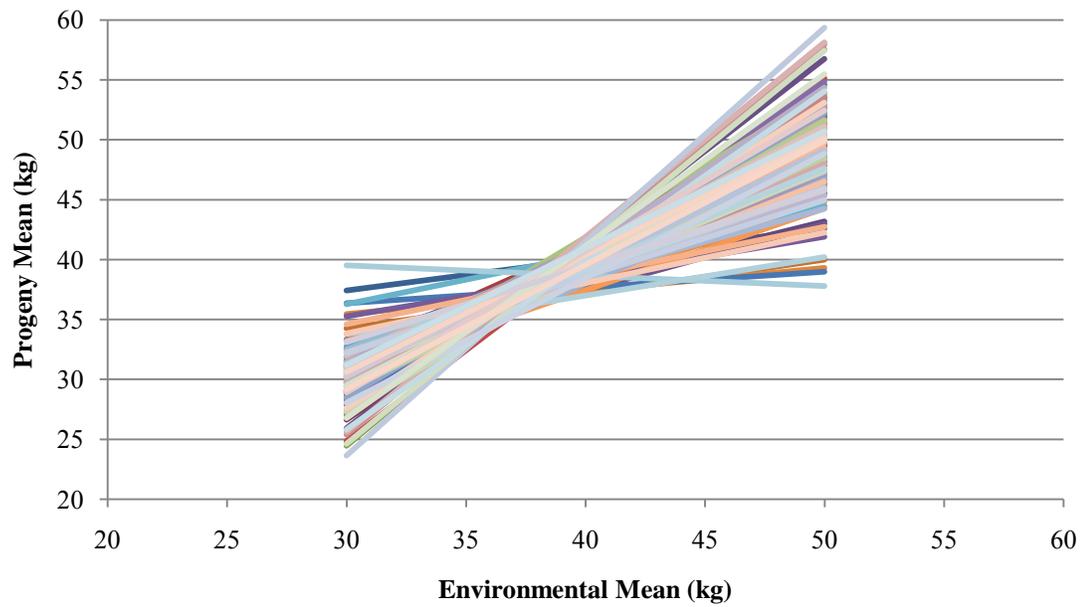
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	<b>Birth Weight</b>	<b>Weaning Weight</b>	<b>Yearling Weight</b>
<b>Categorical</b>	14,181.6	19,068.62	12,161.3
<b>Continuous Environment</b>	15,098.9	2,457.64	15,706.4
<b>Genotype by Environment</b>	13,836.6	18,476.40	11,983.8
<b>Random Regression</b>	15,082.6	2,405.38	15,643.3

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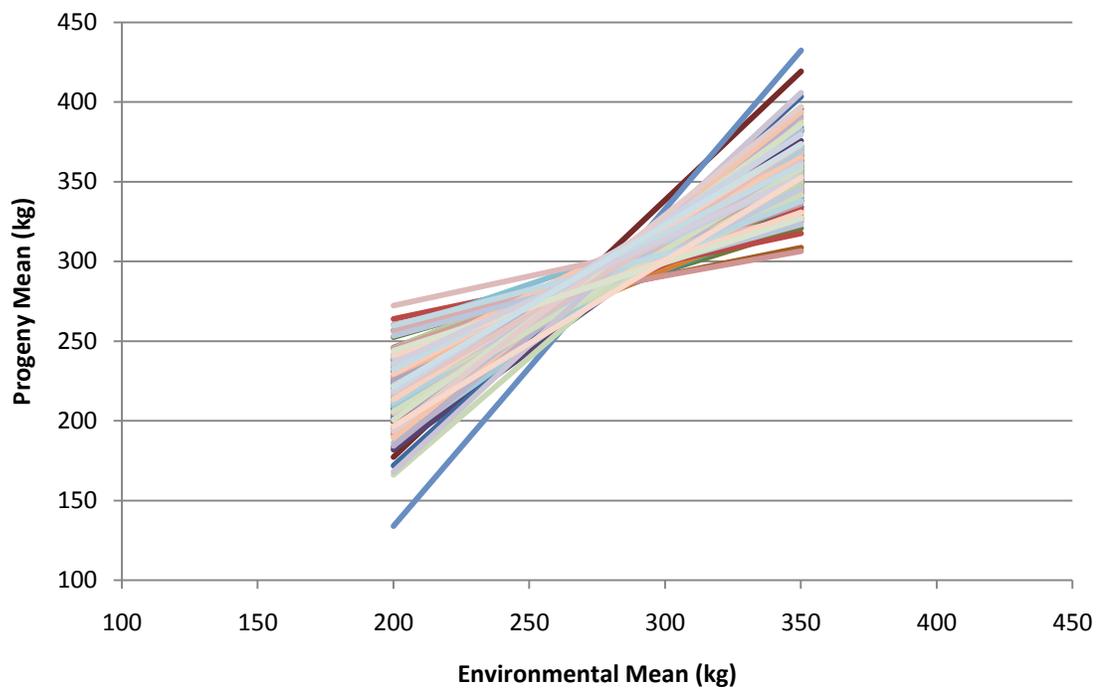
**Figure 2.1:** Birth weight reaction norms of bulls shown performance across variety of average herd birth weights (kg).

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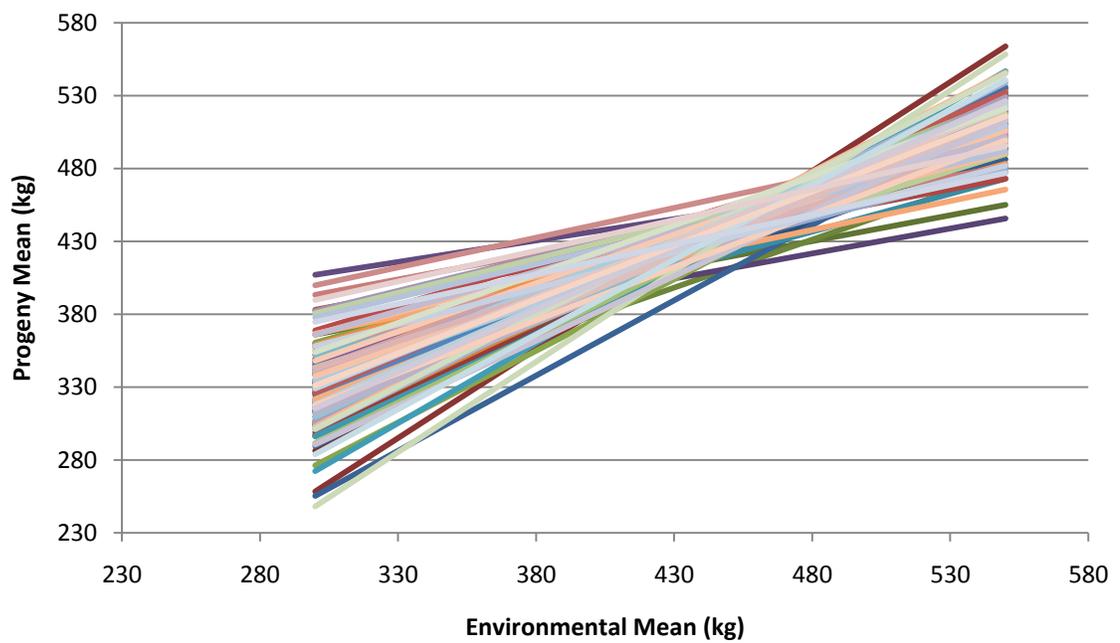


**Figure 2.2:** Weaning weight reaction norms of bulls shown performance across variety of average herd weaning weights (kg).

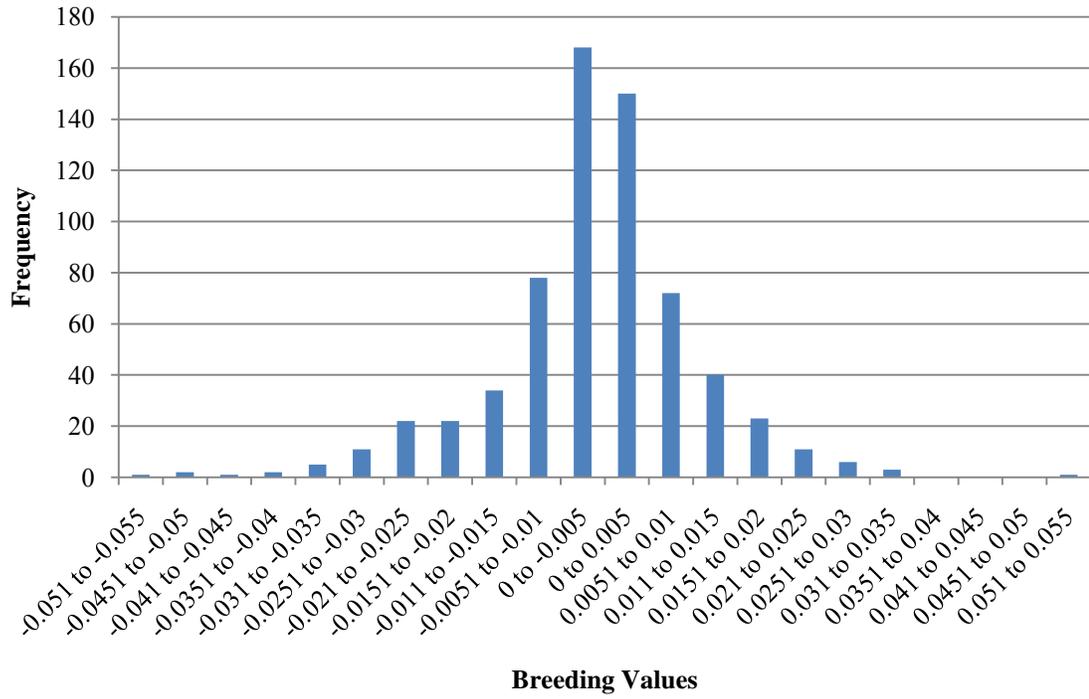
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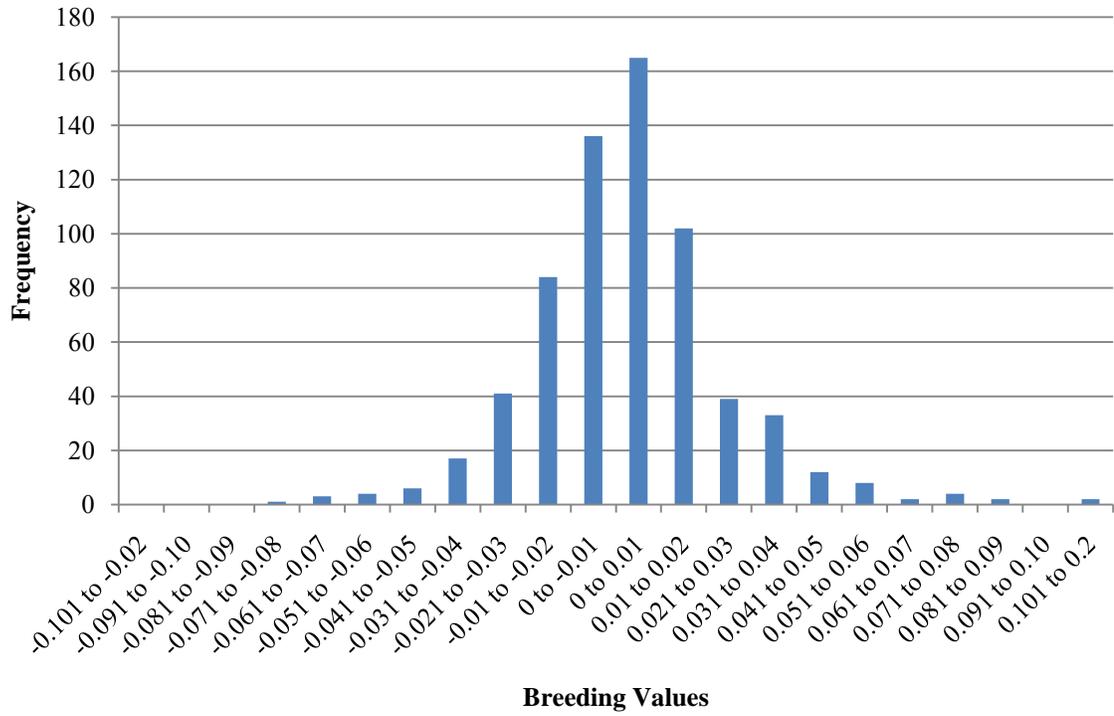
**Figure 2.3:** Yearling weight reaction norms of bulls shown performance across variety of average herd yearling weights (kg).



**Figure 2.4:** Histogram of breeding values for slopes of the birth weight reaction norm.

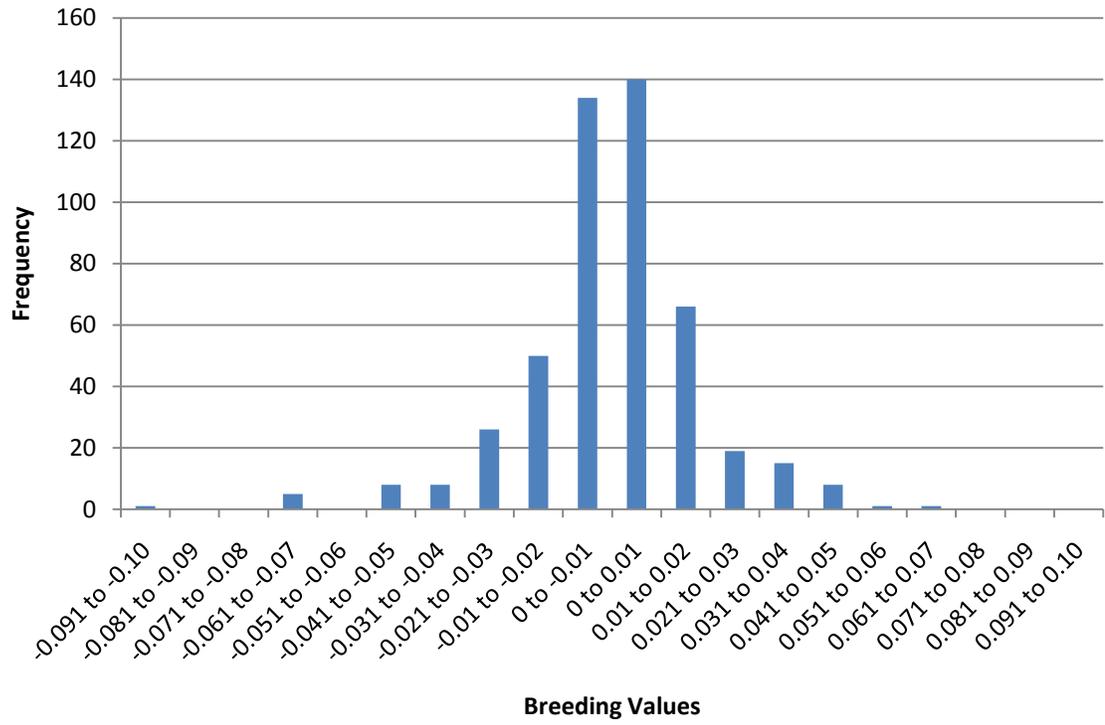


**Figure 2.5:** Histogram of breeding values for slopes of the weaning weight reaction norm.



**Figure 2.6:** Histogram of breeding values for slopes of the yearling weight reaction norm.

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