THESIS

GENETIC PARAMETERS FOR FERTILITY AND PRODUCTION TRAITS IN RED ANGUS CATTLE

Submitted by

Ryan John Boldt

Department of Animal Sciences

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2017

Master's Committee:

Advisor: R. Mark Enns
Co-Advisor: Scott E. Speidel

Stephen Koontz

ABSTRACT

GENETIC PARAMETERS FOR FERTILITY AND PRODUCTION TRAITS IN RED ANGUS CATTLE

In beef cattle the ability of a herd to effectively reproduce is one of the most important factors that contributes to economic viability of an enterprise. However, genetic improvement for traits that relate to female reproductive capabilities have been slow when compared to other traits commonly under selection. Currently the Red Angus Association of America (RAAA) publishes 2 expected progeny differences (EPD) for fertility traits. These predictions include heifer pregnancy (HPG) which is the prediction of the ability of a female to conceive during her first breeding season, and stayability (STAY) which is a prediction of a female's ability to produce five consecutive calves by six years of age. While both traits are economically important to cattle producers, multiple hurdles arise when predicting genetic merit and in turn genetic progress in female reproductive traits. Some of the issues that commonly arise are the generally low heritability estimates associated with fertility phenotypes, which signifies that genetics have limited influence on fertility. Age of measurement of when phenotypes are recorded also limits the amount of genetic progress that is achieved. For HPG, phenotypes are not recorded on females until they are 2 years of age, and STAY phenotypes are collected at 6 years of age. Data is also limited for these traits because phenotypes can only be collected on females. Therefore, we hypothesized that traits that were recorded at younger ages and on both sexes would be genetically related to HPG and STAY. Thus, the main objective of our study was to determine the genetic relationships between HPG, STAY, and other more commonly recorded production trait phenotypes in the RAAA herd book. Production traits where genetic relationships were

studied for both HPG and STAY included: birth weight (BW), 205-d pre-weaning gain (direct and maternal; Pre-WG$_D$, Pre-WG$_M$), 205-d weaning weight (direct and maternal; WW$_D$, WW$_M$), 160-d post-weaning gain (Post-WG), 365-d yearling weight (direct and maternal YW$_D$,YW$_M$), ultrasound rib eye area (UREA), ultrasound backfat (UBF), ultrasound intramuscular fat (UIMF), scrotal circumference (SC), carcass rib eye area (REA), carcass backfat (BF), hot carcass weight (HCW), and carcass marbling score (MARB). Production traits that were evaluated for the genetic relationship for STAY only included: udder suspension (US), teat score (TS), mature weight (MW), and body condition score (BCS).

Data used for the analysis was extracted from animals that contained a valid HPG or STAY phenotype in the Winter 2014 RAAA national cattle evaluation. For HPG all phenotypes available were used in the analysis, whereas STAY observations were limited to females that were members of a contemporary group that contained 60 or more animals due to computational issues. To collect phenotypes on males and other females the RAAA association defined birth work group classification was used. This methodology yielded a list of 141,436 animals for all HPG analyses, and 152,376 animals for all STAY analyses.

Binary observations for HPG were formed by the RAAA based on a calving interval calculated from producer submitted breeding information. Observations for STAY are also binary in nature, were formed using calving information. For the production traits, Pre-WG, WW, Post-WG, YW, and SC phenotypes were pre-adjusted to age constant endpoints of 205 d, 205 d, 160 d, 365 d, and 365 d respectively. Phenotypes for MW were adjusted to a constant BCS of 5. If age of measurement, or phenotypic observations were outside 5 SD from the overall mean observations were removed from the analysis. Contemporary groups for all traits were formed in a similar fashion as to what was used in the national cattle evaluation. If an animal was

a member of a CG that exhibited no variation for a trait the contemporary group fixed effect was omitted. Based on the final data file for each two-trait analysis with HPG or STAY a three-generation pedigree was formed.

Genetic relationships for all traits were determined from (co)variance parameters, estimated using a series of two trait animal models and a REML procedure. Model fixed and random effects were consistent when a trait was evaluated with both HPG and STAY. These fixed effects include: appropriate contemporary group, as well as sex of animal for all weight, carcass, and ultrasound phenotypes, age of dam for all weight traits, and age of measurement for UREA, UBF, UIMF, REA, BF, MARB, HCW, BCS, TS, US, and MW. Random effects included: a direct genetic effect for all traits, maternal genetic effects for Pre-WG, WW, and YW, permanent environment of the dam for Pre-WG, and WW, and permanent environment of the individual for MW, BCS, TS, and US.

Results for the series of two trait analyses and HPG showed that the average heritability across all 12 analyses for 0.12± 0.01 (averaged across all analyses). Direct heritability estimates for production traits were 0.58 ± 0.01, 0.25 ± 0.01, 0.29 ± 0.01, 0.22 ± 0.01, 0.32 ± 0.01, 0.46 ± 0.02, 0.37 ± 0.07, 0.27 ± 0.06, 0.40 ± 0.06, 0.25 ± 0.06, 0.41 ± 0.01, 0.35 ± 0.01, and 0.38 ± 0.01 for BW, Pre-WG, WW, PWG, YW, SC, REA, BF, MARB, HCW, UREA, and UIMF, respectively. Heritability for maternal components of Pre-WG, WW, and YW were 0.11 ± 0.01, 0.10 ± 0.01, and 0.05 ± 0.01. Permanent environment of the dam estimates accounted for 0.10 ± 0.01 percent of the phenotypic variance for both Pre-WG and WW. Genetic correlations between Pre-WG$_{D}$ (0.24 ± 0.08), WW$_{D}$ (0.18± 0.08), YW$_{D}$ (0.20 ± 0.07), UREA (0.16 ± 0.08), and UBF (0.14 ± 0.08) with HPG were the strongest in magnitude. Genetic correlations between HPG and BW, SC, WW$_{M}$, Post-WG, YW$_{M}$, REA, BF, MARB, HCW, and UIMF had confidence

intervals that included or were near zero, suggesting minimal genetic relationship between the traits.

For the series of two trait analyses that included STAY and production traits the estimate of heritability for STAY averaged across all analyses was 0.10. Estimates for heritability of additive genetic effects were: 0.56 ± 0.01, 0.23 ± 0.01, 0.10 ± 0.01, 0.27 ± 0.01, 0.10 ± 0.01, 0.24 ± 0.01, 0.33 ± 0.01, 0.06 ± 0.01, 0.49 ± 0.03, 0.26 ± 0.08, 0.24 ± 0.07, 0.30 ± 0.08, 0.26 ± 0.07, 0.38 ± 0.02, 0.40 ± 0.02, 0.39 ± 0.02, 0.71 ± 0.02, 0.70 ± 0.02, 0.57 ± 0.02, and 0.27 ± 0.02 for BWT, Pre-WG$_{D}$, Pre-WG$_{M}$, WW$_{D}$, WW$_{M}$, PWG, YW$_{D}$, YW$_{M}$, SC, REA, BF, MARB, HCW, UREA, UBF, UIMF, TS, US, MW, and BCS, respectively. Permanent environment effects of the dam for Pre-WG and WW accounted for 0.13 ± 0.00 percent of the variance for both traits, whereas, permanent environment of the individual with multiple observations accounted for 0.00 ± 0.00, 0.00 ± 0.00, 0.16 ± 0.02, and 0.18 ± 0.01 percent of the variance for TS, US, MW, and BCS, respectively. Genetic correlations were highest in magnitude between STAY and Pre-WG$_{M}$ (0.54 ± 0.05), WW$_{M}$ (0.55 ± 0.05), YW$_{M}$ (0.36 ± 0.07), BF (0.53 ± 0.20), MARB (0.40 ± 0.20), UREA (0.19 ± 0.07), UBF (0.37 ± 0.07), TS (0.30 ± 0.11), and US (0.23 ± 0.11). Genetic correlations between STAY and direct components of weight traits were slightly negative, but contained standard errors that included or were near zero. Additionally, results of the analysis estimated that minimal genetic relationships between, SC, REA, HCW, UIMF, MW, and BCS and STAY.

Based on the results of these analyses we were able to accept the hypothesis that genetic relationships exist between HPG or STAY and other more highly recorded production traits. For national cattle evaluation, the trait Pre-WG could be included in a multiple trait model for HPG, and the trait UBF could be included in the STAY evaluation. Both traits are commonly recorded on both males and females, and at an age that is younger than when fertility phenotypes are recorded. Inclusion of these traits into genetic predictions for HPG and STAY will allow the ability to overcome several key issues that are faced when making genetic predictions for the fertility traits.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

INTRODUCTION

Effective reproduction can be defined as the ability for one generation to produce enough healthy offspring capable of perpetuating the species (Foote, 2003). In livestock species, this need is also combined with production of a product for human use/consumption. In the case of beef cattle, sufficient levels of reproduction can maintain herd size, but there is still a need for improved reproductive efficiency. Improving efficiency of reproduction will also improve performance in other traits. An improved reproductive rate provides more replacements to choose from which can boost selection intensity of replacements and in turn increase rate of genetic change.

The modern beef female is considered reproductively inefficient when 50 to 60% of cattle conceive each service is achieved (Parkinson, 2004). Modern beef production practices call for beef females to first calve as two years olds and subsequently maintain a 365-d calving interval each successive year. Failing to maintain this interval and then to rebreed is a major cause for culling decisions in beef cattle systems (Snelling, 1994). While in most cow/calf systems, primary emphasis is put on management practices to improve reproduction, little selection pressure has been applied to the measures of reproductive performance.

Historically, a multitude of different approaches were proposed to measure reproductive capabilities of beef females. Cammack et al. (2009) summarized genetic parameters for thirteen different measurements; however, only two were or have been adopted for national cattle evaluations. The first measurement was Heifer Pregnancy (HPG), which is the probability of a female conceiving at the end of her first breeding season (Crews and Enns, 2008b). The second measurement was stayability (STAY), which is defined as the probability of a female remaining in the herd to six years of age, given that she has had a calf at two years of age (Snelling et al., 1995).

The slow genetic improvement of reproductive traits is mainly a result of three factors. The first factor is the low heritability (< 0.30) often associated with measures of reproductive performance (Cammack et al., 2009). Secondly, most fertility observations are sex-limited, restricting, the amount of phenotype data available to make selection decisions. Lastly, many fertility outcomes are taken at considerably later ages than other performance traits. Due to the age of measurements, sires do not start receiving observations on daughter’s fertility traits until much later in life. Heifer pregnancy observations on sire’s daughters first accumulate when the sire is three years of age and for STAY observations at eight years of age. More effective ways for selection on reproductive traits that results in increased accuracy, and reduced generation interval are needed.

The incorporation of correlated traits has long been an accepted method to improve accuracy of prediction. Correlated traits offer the ability to include multiple traits in one genetic evaluation and add information to both trait evaluations simultaneously. In the context of reproductive research, the use of correlated traits in genetic evaluation offers the potential advantage of leveraging traits that are measured at younger ages. This approach could increase accuracy of selection for reproductive traits at younger ages than would be achievable by reproductive data collection alone.

We hypothesized that genetic relationships exist between HPG and STAY, and other production traits. The objective of our research is to examine the relationship between HPG and STAY, and their relationships with production traits more typically having higher reporting rates.

For this study, the production traits included: birth weight (BW), 205-d Pre weaning gain (direct and maternal, Pre-WG_D, Pre-WG_M), 205-d weaning weight (direct and maternal; WW_D, WW_M), 160-d post-weaning gain (Post-WG), 365-d yearling weight (direct and maternal YW_D ,YW_M), ultrasound rib eye area (UREA), ultrasound backfat (UBF), ultrasound intramuscular fat (UIMF), 365-d scrotal circumference (SC), carcass rib eye area (REA), carcass backfat (BF), hot carcass weight (HCW), carcass marbling score (MARB), udder suspension (US), teat score (TS), mature weight (MW), and body condition score (BCS).

CHAPTER II

LITERATURE REVIEW

BACKGROUND

The Red Angus Association of America (RAAA) was established in 1954 (Marquez et al., 2010). Throughout its history the RAAA has positioned itself as focusing on adoption of scientific approaches to improve efficient cattle production. In 1995, the stayability (STAY) EPD was adopted as a published selection tool for improvement of reproductive fitness in RAAA. Stayability is classically defined as the probability that a female has had 5 calves by age 6 given that she had a calf as a two year old (Snelling et al., 1995). This measurement was chosen because it provides the opportunity to select for females that have a higher probability of remaining in the herd to a calculated break-even age of six years old. This measurement is more intuitive compared to a similar measurement termed longevity which is defined as the productive life of a female. One issue that often arises with using the longevity measurement is that animals do not receive observations until they leave the herd. This late life measurement increases generation interval, decreases accuracy as an observation does not occur until the end of the productive life of an animal, both of which in turn, slow genetic progress.

A second trait that was introduced to improve fertility in Red Angus cattle was heifer pregnancy (HPG), which is defined as the probability of a female conceiving during her first breeding season (Crews and Enns, 2008b), typically as a yearling. The genetic relationships between these traits and other economically relevant traits have not been extensively examined.

ECONOMIC IMPORTANCE OF REPRODUCTIVE EFFICENCY

Fertility has long been considered an important trait for selection for cow/calf producers. Melton (1995) classified reproductive traits as 3.24 times more important than end product traits to profitability of a cow/calf producer that markets calves at weaning. The most limiting factor to producing the greatest number of calves each year on a herd-wide basis is reproduction of the cow. In cow/calf production a common practice is to cull cows that are not diagnosed pregnant following the breeding season (Snelling, 1994). Culling a higher percentage of females due to reproductive failure increases replacement retention, and in turn, results in higher overall development costs per year. Additionally, after cows enter the breeding herd the goal for those is to maintain a 365-d calving interval and produce a calf each year (Short et al., 1990). However, average conception rate per exposure for the modern beef female is 50 to 60% (Parkinson, 2004) resulting in the need for multiple exposures for a successful pregnancy.

The economic impact of fertility is also seen in management considerations of when to first expose females. Heifers that calve at two years of age have the ability to be more productive and wean more calves over their lifetime (Cundiff et al., 1974). Breeding heifers as yearlings allows them to have a calf at a younger age and did not cause them to be removed from the herd at a younger age than heifers that first calved as 3 year olds (Cundiff et al., 1974). Timing of when heifers conceive during their first breeding season is also important for future calves. Heifers that conceive and calve early in their first reproductive cycle tend to continue to calve early in successive years (Lesmeister et al., 1973). By having the ability to calve earlier, calves are older and therefore on average are heavier when marketed.

The highest cost for a beef producer each year is the feeding of the cow for their maintenance requirements. To offset this cost, calves are marketed at weaning and sold on a weight basis with calves that are heavier at weaning being of a higher monetary value. From that perspective, calves that are born from older cows tend to be heavier at weaning compared to calves born from younger dams (Rumph and Van Vleck, 2004). Therefore, having a higher percentage of older dams retained in the commercial herd should create higher average weaning weights for the calf crop and greater overall income. Rumph and Van Vleck (2004) found that weaning weights of a dam's progeny increased until 5 years of age and BIF Guidelines for age of dam adjustments (BIF, 2011) also reflect these differences. Having cattle fall out of the herd before this time, results in production inefficiencies because the inputted protein into the cow is not rewarded with higher weaning weights until after 5 years of age. Having a higher percentage of mature cows in the herd helps to stabilize the economic viability of many beef cattle production systems.

While most income from commercial cattle production comes from the sale of calves each year, proper marketing of cull cows can also affect profitability. Salvage value of a cow is important at culling as it partially offsets development and maintenance costs. Snelling et al. (1995) used estimates obtained by Dalsted and Gutierrez (1989) for cow salvage value and net returns per calf to determine the number of calves required to breakeven for various cow production scenarios. Assuming a \$50 to \$100 annual return per cow and \$100 to \$200 dollar difference between development cost and salvage value, 4 to 8 calves are required to breakeven (Snelling et al., 1995). This results in a cow that is 6 to 10 years of age when she leaves the herd, assuming that she first calved as a two-year-old to break even. However, the cattle industry is repeatedly going through periods of expansion and consolidation. These signals as well as geographic location where cattle are marketed have a large effect on prices received for cull cows and market calves. Prices for processed grains used in heifer development programs are just as volatile. The difference in development costs and cull prices is constantly changing and is not consistent. Based on this the number of calves required to break even can also change based on the value of cull cows, the calves themselves, and costs of production.

Overall, the importance of fertility for cattle production is the ability of a producer to efficiently produce the maximum pounds of weaned calf, while minimizing the amount of money spent to prepare females to reproduce each year. Based on evidence presented in this section, the ability for a female to produce a calf early in the breeding season first as a 2 year old and continue to do so throughout her life allows an advantage in terms of efficiency. Additionally, allowing a cow to remain in the herd for an extended period of time allows the ability for her to offset her development cost, and more cows that are older allows more pounds of calf to be produced which intern increases profitability.

FACTORS AFFECTING HEIFER PREGNANCY

The ability for a heifer to become pregnant during her first breeding season is of utmost importance to beef cattle producers as it influences both costs of development for the heifers and income through the number calves for sale from a system (i.e. fewer replacement heifers needed, more saleable calves). There are a multitude of management decisions and physiological benchmarks that must be met for a female to become pregnant during her first breeding season. Genetic differences play a role in these benchmarks and differences also exist between females relative to their ability to become pregnant. Effective management and selection for improved reproductive performance should result in a higher percentage of females conceiving during their first breeding season. The process involved with a successful conception and pregnancy is complex as will be outlined in this section.

Managerial Components. Nutritional management post-weaning can have a major influence on a heifer's ability to become pregnant during the breeding season. The objective of heifer development programs is to feed heifers to improve their ability to become pregnant during their first breeding season. Historically heifer development systems focused on feeding heifers to reduce their age of puberty with the belief that females would reach puberty at a genetically predetermined time or weight. An inverse relationship was commonly found between post weaning growth rate and age of puberty (Wiltbank et al., 1969). Therefore, intensive feeding programs were established to allow heifers to reach their target breeding weight. Recommendations based on research conducted from the 1960's to 1980's called for heifers to be developed to 65% of their mature weight at the beginning of the breeding season (Patterson et al., 1992). In order to achieve this target, heifers were often placed in a dry lot and fed high-energy diets. In research settings, pregnancy rates for these systems with heifers on a high-energy diet ranged from 88% to 92% (Freetly et al., 2001; Funston and Deutscher, 2004; Roberts et al., 2009). Reproductive rates for these systems are high and have been successful preparing heifers for their first breeding season.

More recently, researchers have examined less intensive systems for heifer development. These systems call for heifers to be grown on pasture or corn residues with minor supplementation (Summers et al., 2014) and correspondingly reach 5 to 10% lower target body weights at the beginning of the breeding season compared to animals on the more intensive programs (Summers et al., 2014). The main benefits of these less intensive systems are that development costs are reduced (Funston and Deutscher, 2004; Martin et al., 2008) while maintaining similar reproductive rates to more intensive methods (Funston and Deutscher, 2004; Martin et al., 2008; Roberts et al., 2009). Summers et al. (2014) examined the reproductive differences between heifers grazed on corn stalks for 148 days and subsequently on range, versus heifers maintained on winter range only in the sand hills of Nebraska. Both of these methods are considered less intensive compared to previously described methods. A non-significant difference in pregnancy rate between the two methods (*P* = 0.29) was found. Both groups developed had pregnancy rates above 80%, however, heifers on the winter range tended (*P* = 0.11) to have a higher average daily gain before breeding.

Age of Puberty Related Factors. In order for a heifer to have the ability to become pregnant she must first experience puberty. In mammals, the reproductive system is the last physiological system to develop (Patterson et al., 1992). Overall pregnancy rates in heifers are directly influenced by the proportion of heifers showing estrous prior to the beginning of the breeding season (Funston et al., 2012). In beef cattle, age of puberty is defined as the point at which ovulation is accompanied by visual signs of estrus and initiation of normal luteal function (Perry, 2012). Measurement of age of puberty was proposed in the 1960's as an indicator of females that had a higher probability of becoming pregnant in a restricted breeding season (Wiltbank et al., 1966). The pubertal estrous cycle is less fertile than successive cycles and thus heifers should experience multiple cycles before the beginning of the breeding season to ensure higher probability of conception (Perry et al., 1991a). The struggle for producers is the need for heifers to achieve puberty at a lower age due to the common practice of breeding heifers before the mature cow herd in an effort to concentrate labor requirements at heifer calving (Larson, 2007).

Plane of nutrition, body composition, and age are highly related to body weight and the onset of puberty. Wiltbank et al. (1969) examined the differences between crossbred and straight bred heifers fed at low and high levels of nutrition. They reported that the average age of puberty for heifers on the high plane of nutrition was 381 days for both crossbred and straight bred animals compared to 424 and 572 for the same groups on those levels of nutrition respectively.

Roberts et al. (2009) found similar but less dramatic results comparing composite heifers of consistent breed composition that were fed ad libitum versus heifers on a restricted feed diet. Age of puberty was 7 to 30 days longer ($P < 0.01$) in heifers on the restricted diet compared to the controls on free choice feed. Pregnancy rates of females on a restricted diet were 87.4% compared to 91.9% to heifers on a control diet. Nonetheless, the savings on feed costs for animals fed the restricted diet was $33.28 per head and yielded a 27% reduction in harvested feed requirements.

Instead of feeding heifers to a constant weight, the body composition of heifers experiencing puberty has also been investigated. Hall et al. (1995) measured different body composition indicators pre and post mortem and compared those measurements between two groups of heifers fed at high and low levels of energy. Significant differences ($P < 0.01$) were found between the two groups for age, weight, body condition score, heart girth, weight: height ratio, and longissimus muscle area when puberty was achieved. Heifers on the high-energy diet achieved puberty at a lower age (386.3 days), were heavier (394.5 kg) with more backfat (6.8 mm), had a higher body condition score (6.7), larger heart girth (174.1 cm), higher weight: height ratio (3.2), and larger Longissimus muscle area (59.6 cm^2) compared to the heifers on the low energy diet at 415.3 days, 341.3 kg, 5.1 mm, 5.7 163.3 cm, 2.8, and 51.7 cm^2 respectively.

Multiple genetic components have been shown to exist for age of puberty. Different breeds have been shown to have different ages and weights at puberty (Laster et al., 1979; Ferrell, 1982; Freetly and Cundiff, 1998). Crossbreeding also plays a role with Wiltbank et al. (1969) examining the differences of age of puberty between crossbred heifers and Angus or Herford straight bred heifers fed at two levels of nutrition. No differences were reported between crossbreds and straight bred animals; however, at low levels of nutrition crossbreds experienced puberty on average 148 days earlier than the straight bred heifers. The biggest difference in age of puberty however is between *Bos Indicus* and *Bos Taurus* cattle. Gregory et al. (1979) reported that the mean age of puberty for calves born to Angus and Hereford dams was 398 ± 5.8, 383 ± 6.4, 303 ± 5.7, 318 ± 6.3 days for Brahman, Sahiwal, Pinzgauer, and Tarentaise sired calves, respectively. The two *Bos Inducus* breeds (Brahman and Sahiwal) were the highest in the average age of puberty. More recent age of puberty estimates ranged from 332 to 357 for *Bos Taurus* cattle which is compared to the 405 days which was predicted for the *Bos Indicus* breed Nelore (Tallman et al., 1999).

Genetics. Heritability estimates for heifer pregnancy have varied. Heritability estimates for heifer pregnancy have been reported and range from 0.05 to 0.68 (Koots et al., 1994a; Snelling, 1994; Snelling et al., 1995; Doyle et al., 2000; Eler et al., 2002; Eler et al., 2004; McAllister et al., 2011; Fortes et al., 2012). Within these estimates *Bos Taurus* cattle tended to have a lower heritability compared to *Bos Indicus*. These differences were attributed to differences in management techniques based on different breed averages for age of puberty, and intern a greater amount of genetic variability (Eler et al., 2002). Different and more appropriate analysis techniques to accurately estimate genetic parameters for categorical traits can lead to differences in heritability estimates (Snelling et al., 1995) as well. This can be seen with the more recent estimates in *Bos Indicus* cattle to be higher than more historical estimates in *Bos Taurus* cattle (Eler et al., 2002).

Different methods have been proposed to increase the genetic response to selection. Measurements that are taken on a phenotype and then used for the selection of a second genetically correlated phenotype have been defined as indicator traits (Bourdon, 1997). The idea of using indicator traits has long been adopted in genetic improvement programs. There are many traits that are of economic importance that are either hard to measure; occur later in life, or are only measureable in a single sex—all of which in some way limit the ability to collect phenotypic data on animals.

Indicator traits have also been used for evaluation of traits that are hard to measure or can only be measured on a single sex. Bull yearling scrotal circumference is used as an indicator for age of puberty in female offspring (Evans et al., 1999; Martinez-Velazquez et al., 2003; McAllister et al., 2011). Scrotal circumference is easily measured and can be used as a predictor for not only male fertility, but also for female pubertal traits as well. The idea of using scrotal circumference as an indicator for female reproductive traits was first introduced by Brinks et al. (1978), who reported a -0.71 genetic correlation between scrotal circumference and age of puberty in female half siblings. Similar results were reported by King et al. (1983), who found a strong negative correlation between scrotal circumference and age of puberty in Hereford cattle. While these two estimates may reduce the age of puberty, the relationship between scrotal circumference and a heifer's ability to become pregnant during her first breeding season has been more disputed.

More recently, several studies reported a weak to no genetic relationship between scrotal circumference and heifer pregnancy. Evans et al. (1999) studied the relationship between scrotal circumference and heifer pregnancy in Herford cattle. Heritability estimates were 0.24 ± 0.12 and 0.78 ± 0.16 for heifer pregnancy and scrotal circumference, respectively. The reported genetic correlation between heifer pregnancy and scrotal circumference was 0.002 ± 0.45. Similar results were reported by Martinez-Velazquez et al. (2003) using data on 12 *Bos Taurus* breeds. Heritability estimates for pregnancy status following the first breeding season were 0.14 ± 0.03 and 0.02 ± 0.01 for direct and maternal effects, respectively. Genetic correlations between scrotal circumference and pregnancy status following the first breeding season were 0.00 and 0.12 for direct and maternal effects of pregnancy status, respectively.

Eler et al. (2004) examined the relationship between HPG and scrotal circumference in Nellore cattle. Heritability estimates were reported as 0.68 ± 0.09 and 0.61 ± 0.10 for heifer pregnancy based on two different contemporary group definitions. Scrotal circumference heritability was reported as 0.57 ± 0.03 for both contemporary group definitions. The genetic correlations between heifer pregnancy and scrotal circumference were 0.20 ± 0.12 and 0.20 ± 0.13 for the different contemporary definitions. The increase in the genetic correlation for analysis involving *Bos Indicus* breeds is a result of the increased genetic variability of pregnancy at 14 months of age compared to *Bos Taurus* where puberty is commonly experienced before that age (Eler et al., 2004) .

Genetic correlations between HPG and carcass traits were also examined. In beef cattle the prioritization of energy occurs in the following order: basal metabolism, activity, growth, basic energy reserves, pregnancy, lactation, additional energy reserves, estrous cycle and initiation of pregnancy, and excess reserves (Short et al., 1990). Excess energy reserves are accumulated as intramuscular and subcutaneous fat. These excess fat measurements can serve as indicators as to which females are in the proper nutritional state to experience estrous and maintain pregnancy. In Red Angus cattle, McAllister et al. (2011) examined IMF and MARB in relation to HPG. Heritability estimates were 0.17 ± 0.01, 0.29 ± 0.01, and 0.35 ± 0.06 for HPG, IMF, and MARB, respectively. Genetic correlations between HPG, and IMF and MARB were 0.13 ± 0.09 and 0.10 ± 0.15, respectively. These results suggest that measurements of excess fat reserves are favorably related to HPG, but are poor predictors of a heifer's ability to become pregnant during her first breeding season.

Fortes et al. (2012) reported REML, genomic heritability, and genetic correlation estimates for HPG and different production traits in Brangus cattle. Heritability estimates using REML analysis were reported as 0.48 ± 0.12, 0.48 ± 0.11, 0.55 ± 0.15, 0.52 ± 0.14, 0.28 ± 0.08, 0.63 ± 0.11, 0.42 ± 0.10, 0.30 ± 0.09, 0.06 ± 0.05, and 0.07 ± 0.06 for 205-day body weight (BW_{205}), 365-day body weight (BW_{365}), 205-day height (HT_{205}), 365-day height (HT_{365}), average daily gain (ADG), rib eye area (LM Area), intramuscular fat (IMF), backfat (BFT), first service conception (FSC), and HPG respectively. Heritability estimates for weight and carcass traits were higher than what was reported by (Koots et al., 1994a); however they remain reasonable. Genetic correlations using a REML and genome-wide SNP effects are summarized in Table 2.1. Weight and height measurements were low to moderately negatively correlated with HPG. Meaning animals that had a higher genetic propensity for growth had a lower probability to become pregnant during the first breeding season. Genomic correlations using SNP effects show low positive correlations for BW_{205} and HT_{205} as well as, BW_{365}. Height at 365 days was lowly negatively correlated with heifer pregnancy. Carcass traits are lowly positively correlated in the REML analysis. Intramuscular fat was negatively correlated with HPG in the genomic correlation analysis. In both analyses a high positive genetic correlation was estimated between FSC and HPG. A successful FSC observation would also lead to a successful heifer pregnancy observation and therefore this high correlation is not surprising.

Table 2.1 Genetic correlations between heifer pregnancy, growth, average daily gain, and ultrasound carcass traits in Brangus heifers adapted from (Fortes et al., 2012).

Traits	Genomic Correlation	REML Correlation
	Heifer Pregnancy	Heifer Pregnancy
BW205	0.17	-0.28 ± 0.38
HT205	0.05	-0.39 ± 0.39
BW365	0.10	-0.14 ± 0.35
HT365	-0.05	-0.23 ± 0.36
ADG	0.08	0.20 ± 0.38
LM Area	0.18	0.17 ± 0.34
BFT	0.11	0.27 ± 0.38
IMF	-0.01	0.11 ± 0.35
FSC	0.73	0.66 ± 0.40

BW205 & 365 = BW at 205 and 365 d of age, respectively; HT205 & 365 = hip height at 205 and 365 d of age, respectively; BFT = backfat; IMF = percent intramuscular fat; FSC = first service conception; HPG = heifer pregnancy

FACTORS AFFECTING STAYABILITY

After a beef female enters the mature cowherd her main purpose is to raise a marketable calf each year for as long as possible. In order to do this, she must conceive during a shortened breeding season promptly after calving each year. Having females stay in the herd for multiple years allow them to help recuperate the cost of their development, as well as pay for cows that have fallen out of the herd. Additionally, older cattle wean heavier calves that are more valuable. It is important to understand the different factors that control a female’s ability to stay within the productive mature cow herd.

Post-Partum Interval. After a cow has given birth she experiences a short period of anestrous. The length of this period can affect her ability to rebreed and calve the following year. In order for a cow to maintain a 365-d calving interval she must rebreed within 80 days post calving. Suckling and nutrition are the two biggest factors that influence the length of a cow’s post-partum interval (PPI) (Short et al., 1990). Suckling determines the amount of milk that is produced by the cow in order to feed her calf. Cows that produce more milk require more energy and an increase in these energy requirements can stimulate an increase in the negative feedback to the hypothalamus that results in the resumption of estrous being prolonged. Therefore, nutrition plays a vital role in a cow's ability to resume estrous following parturition. The late gestation and early lactation periods are considered the most energy expensive times during a cow's yearly production cycle. When feed is restricted just before giving birth, the PPI is increased (Perry et al., 1991b). Therefore, proper nutritional management is imperative for continued reproductive success.

Body condition scoring (BCS) is a tool available to producers that assesses the nutritional status of the herd and individuals within the herd. Scores in the system range from 1 (severely emaciated) to 9 (very obese; BIF, 2011). Scores are determined via visual appraisal of external fat indicators focusing on the last half of the ribs, spinous processes, and the hooks and pins. From a reproductive perspective, all cows within a herd should ideally receive scores that range from 5 to 7 (Eversole et al., 2009). Cows that are scored within this range generally have the highest probability of having reproductive success during the breeding season as they are in a positive energy balance. The excess energy can then be allocated to a lower energy priority such as reproduction. Body condition scoring is a more accurate measurement for determining the nutritional status of a cow as compared to weight alone. Mature cow weight can vary greatly with frame size and is generally considered a poor predictor of the nutritional status of the beef female.

Culling. When a cow is removed from the herd she is considered "culled". In beef cattle production, the most common causes for culling include reproductive failure, mortality, and physical impairments (Greer et al., 1980; Nunez-Dominguez et al., 1991; Snelling, 1994). Common beef cattle practices call for cattle that are open following the breeding season to be culled from the herd (Snelling, 1994). Using this approach, the largest dropout of females typically occurs at 3 to 4 years of age. During this time, cattle experience all of the energy demands associated with resuming estrous and rebreeding as well as with their own growth, due to the fact that cattle do not reach mature weight until at least five years of age (Goldberg and Ravagnolo, 2015).

Another common criteria for culling cows is based on udder characteristics. When udders are not correctly sized, calves have difficulty nursing and receiving colostrum, which is imperative for good calf survival rates (Wythe, 1970; Edwards, 1982; Frisch, 1982; Ventorp and Michanek, 1992). Udder conformation is a trait that has a larger effect on older cows because as they age the conformational changes occur. Greer et al. (1980) found the probability of a cow being culled for udder characteristics increased with age. Within the study the probability for culling due to a bad udder was 0.0000, 0.0012, 0.0000, 0.0029, 0.0023, 0.0000, 0.0144, 0.0563, and 0.0667 for 2 to 10 year old dams, respectively. For these age classes the probability of being culled due to udder soundness was less then 2 percent for 2 to 7-year-old dams then increased to over 5 percent for dams that were 9 and 10 years old.

Rogers et al. (2004) looked at several factors that affect longevity (i.e. total time that a cow stays in the herd) in a composite population in Montana. They found that cows that experienced dystocia had a 58% greater risk ($P < 0.01$) of being culled compared to cows that had an unassisted birth. Cows that first calved at an age $\leq$ 730 days tended to have a lower probability of being culled ($P = 0.08$). As the breeding value (BV) for cow weight increased the probability of being culled decreased ($P < 0.01$). Increasing BV for the maternal effect of weaning weight also caused a higher probability of the cow being culled ($P < 0.05$). The rationale behind these results was that cows that produced less milk maintained better condition to weaning and thus weighed more.

Forabosco et al. (2004) examined phenotypic relationships between type traits and longevity in Italian Chianina cattle. The highest contributors to the likelihood of culling were herd-year effect, production trait levels, herd variation, age at first calving, and type traits, respectively. Out of the type traits analyzed, muscle traits contributed the most to the log likelihood of the analysis. Body size characteristics were the next highest contributor, followed by structural traits and lastly refinement. These results suggest that most of the culling decisions made by producers were due to personal preference and not driven by economic considerations.

Greer et al. (1980) examined the probability for culling cows that range from 2 to 10 years of age in the Livestock and Range Research Station herd in Miles City, Montana. They found that, across all age classes, management criteria produced the highest probabilities for cows being culled ranging from 0.1031 for 7-year-old cows to 0.3560 for 10-year-old cows. Within these management considerations, reproductive performance was included as all non-pregnant animals were culled, as well as, culling decisions based on soundness or other health issues. The death or missing as a reason for culling was similar for all age classes with probability of culling ranging from 0.0095 to 0.0165. Probability of culling due to other physical impairments tended to increase with age, ranging from a probability of 0.0048 for 2-year-olds to 0.1089 for ten year olds.

Genetics. Selection for improved female reproductive traits has long been of interest to help increase the efficiency of beef cattle production. Throughout previous research, STAY has taken on multiple definitions. The main difference between STAY definitions is what determines "success" and whether it occurs with cows reaching a certain age or, alternatively, producing a certain number of progeny. These differences in the definition introduce problems with comparisons of research results. In herds that commit to strict culling of all females that do not produce a calf each year differences in definition of STAY no longer exist. Heritability estimates for STAY based on number of calves produced ranged from 0.019 to 0.35 (Snelling et al., 1995; Martinez et al., 2005; Van Melis et al., 2007; Jamrozik et al., 2013). Differences in heritability estimates, are attributed to differences in computational methods as well as, differences between the populations studied. Although there is a large range of heritability estimates all the researchers concluded that STAY is a heritable trait that can be used as a tool to improve the productive life of females within a herd.

Snelling et al. (1995) first introduced the idea of using calving data as a measurement of reproductive performance in beef cattle. The experiment examined the heritability of four different definitions of STAY including S(2 | 1), S(5 |1), S(8 | 1), S(11 | 1) representing the probability that a cow will have 2, 5, 8 or 11 calves, respectively, given that she has had one calf. Data was analyzed using three different variance component estimation methods and the Colorado State University Beef Improvement Center (BIC) and Beckton Stock Farm (BSF) herds' historical databases. Heritability estimates from these analyses are summarized in Table 2.2. Stayability estimates tended to be low with the exception of the sire model in BIC for S(5|1), S(8|1), and S(11|1). The high heritability estimates for the sire models were contributed to a confounding of birth year and sire effects that lead to an over estimation of heritability and unreliable results. Computational limitations at the time of the paper's publishing led to the recommendation of using Method R (Reverter et al., 1994) for variance component estimation. The highest heritability estimate with the sire models eliminated was achieved for S(5 | 1) at

0.227 ± 0.010. This measurement was also convenient because it aligned with the average breakeven age of cows as previously indicated.

Table 2.2 Heritability estimates of measures of stayability of dams adapted from Snelling et al. (1995).

Trait	BSF	BIC
	Animal Model Marginal Likelihood	
S(2 | 1)	0.93	0.19
S(5 | 1)	0.105	0.143
S(8 | 1)	0.070	0.091
S(11 | 1)	0.195	0.068
	Sire Model Marginal Likelihood	
S(2 | 1)	0.080	0.072
S(5 | 1)	0.121	0.708
S(8 | 1)	-	0.628
S(11 | 1)	-	0.680
	Animal Model Method R[A]	
S(2 | 1)	0.208 ± 0.044	0.025 ± 0.007
S(5 | 1)	0.123 ± 0.028	0.227 ± 0.010
S(8 | 1)	0.163 ± 0.018	0.188 ± 0.044
S(11 | 1)	-	0.192 ± 0.022

[A] Mean and SE of five 50% subsamples

One issue continually faced for the effective use of STAY EPD is that females do not receive observations until they are 6 years of age. To improve the effectiveness and adoption rates, traits expressed at earlier ages have been investigated to help improve accuracy of STAY estimates at younger ages. Using a random regression analysis, Jamrozik et al. (2013) estimated heritability, genetic, and phenotypic correlations of calving records at different ages and their relationship to other measures of consecutive calvings for Canadian Simmental cattle. The data used included observations that ranged from two to eight consecutive calvings. Heritability estimates were 0.36, 0.23, 0.19, 0.16, 0.15, 0.13, 0.12 for 2, 3, 4, 5, 6, 7, and 8 consecutive calvings respectively. Genetic correlations between 5 consecutive calvings and 2, 3, 4, 6, 7, and 8 consecutive calvings were 0.83, 0.94, 0.98, 0.98, 0.95, and 0.86, respectively. The high genetic correlations achieved show that early life calving performance is a good predictor of future calving performance. While these correlations are strong, for sires the issue remains that observations on their daughters are not recorded until they are 5 years of age assuming that the daughters calve first as 2-year-old.

Considerable research has also focused on *Bos Indicus* cattle and potential for improvements in reproductive performance. Some of these studies have also focused on genetic correlations between traits measured at younger ages and STAY. Using Bayesian methodology, Buzanskas et al. (2010) achieved an average heritability for STAY of 0.03. Genetic correlations between STAY and age of first calving, body weight at 420 days of age and scrotal circumference at 420 days of age were -0.63 ± 0.20, -0.09 ± 0.11, and 0.45 ± 0.21, respectively. Using a similar methodology Eler et al. (2014) reported a heritability estimate for STAY of 0.19 with genetic associations between STAY and HPG, age at first calving, PWG, and hip height at 18 months of age of 0.73, -0.60, 0.23, and -0.05, respectively. Within these breeds of cattle moderate to strong genetic relationships exist between age at first calving and STAY. Based on these results a genetic relationship exists between scrotal circumference and post weaning gain in *Bos Indicus* cattle breeds. Both of these traits can be measured at younger ages than STAY for use as indicator traits for these breeds.

At a young age, and before observations are recorded, cattle are given parental average EPDs. For traits such as STAY this parental estimate may be of low accuracy and therefore the progeny EPD is likely not accurate. Saatchi et al. (2012) examined the efficiency of selecting animals for different traits using genomic breeding values (GBV) for Simmental and Limousin cattle. The analysis was performed by de-regressing an animal’s estimated breeding value (DEBV) and performing a two trait animal model to estimate the genetic correlation between

DEBV and GBV. For STAY, the correlation between the trait and DEBV was 0.39 ± 0.06 and 0.58 ± 0.06 for Limousin and Simmental, respectively. Efficiency of selection using the DGV was calculated using the following equation:

$$Efficiency = \frac{Accuracy\ of\ DGV}{Accuracy\ of\ Parental\ Averages} = \frac{r_{g\,(T,DGV)}}{\sqrt{R_{PA}^{2}}}$$

Efficiency values were 0.69, 1.39, and 1.48 for genotyped Limousin, genotyped Simmental, and young Simmental animals, respectively. Efficiency values greater than one indicate that selection on GBV will result in greater genetic gains than selection based on parental averages. Based on this, Simmental breeders should have the ability to make greater genetic progress using GBV than by selection based solely on more traditional breeding value estimates as a result of pedigree estimates. However, Limousin breeders would be more successful when selecting on more traditional methods. Genomic breeding values can be a valuable tool for producers that wish to estimate the genetic potential for STAY for animals at younger ages than would be achieved through more traditional methods (Saatchi et al., 2012).

GENETIC EVALUATION OF REPRODUCTIVE TRAITS

Genetic improvement of reproductive traits has long been of interest of researchers and producers. However, early national cattle evaluations focused on weight traits such as BW, WW, and PWG (Golden et al., 2009) primarily because data were available and had been recorded for years. As technology advanced, and computational limits decreased, more traits were added into the genetic evaluation of cattle. Currently the Red Angus, Simmental, Limousin, and Gelbvieh breed associations publish a STAY EPD, whereas, Red Angus, Angus, and Gelbvieh associations also publish a HPG EPD.

In order for a breed association to maximize the accuracy of a STAY EPD, a total herd reporting (THR) system must be established. Total herd reporting systems call for the collection of data on why animals exit from the herd. For an EPD that represents fertility, it is important to establish why females leave the herd to establish a STAY observation. For HPG, exposure, and pregnancy diagnosis, either palpation or ultrasound; or calving information can be used to form the observation. Both of these traits are binary necessitating model specifications that are different from what is assumed in the genetic evaluation of continuous traits.

Scrotal circumference is a moderately heritable trait (Bourdon and Brinks, 1986) that can be used to predict reproductive performance in males. In order for a bull to pass a breeding soundness exam, a bull’s testicles must meet a threshold depending on age. Scrotal circumference has shown to be favorably correlated with seminal traits in male cattle (Smith et al., 1989) as well as with age of puberty in female offspring (Brinks et al., 1978). For some time, it served as the only selection tool for the improvement of reproductive traits in females.

Threshold Model. Both HPG and STAY observations are binary in nature. The genetic evaluation of such traits lends itself to the use of threshold models which were designed to evaluate traits that have an ordered categorical response such as calving difficulty and litter size. The theory of threshold traits was originally described by Wright (1934) studying the number of digits present in guinea pigs. However, statistical methodologies for handling these threshold traits were not developed until much later. Categorical traits violate assumptions of normality, and variance homogeneity using the best linear unbiased prediction (BLUP) of Henderson (1975) (Gianola, 1982). Threshold models overcome this by assuming underlying normally distributed liabilities that become discrete (observed scale) with known fixed thresholds that define the boundaries for observed categories (Wright, 1934; Falconer, 1965). Equivalent threshold models for the analysis of categorical traits were developed by Gianola and Foulley (1983) using Bayesian methodology and Harville and Mee (1984) using BLUP methodology.

The implementation of the threshold model requires a higher computational cost than traditional continuous trait, linear methodologies. This cost was estimated by Misztal et al. (1989) to be three to five times higher for the threshold models. This cost stems from the fact that solutions using threshold methodology must be solved iteratively and during each round a linear set of equations must be solved (Misztal et al., 1989). Another issue faced by threshold models is the extreme case problem (ECP), where observations for the fixed effect fall into the same category (i.e. all observations 0 or 1). This causes poor convergence criteria for these fixed effects as solutions approach ± ∞ or 0 (Misztal et al., 1989). In order to overcome this, Harville and Mee (1984) recommended to treat these fixed effects as random variables or to delete observations experiencing ECP.

Multiple Trait Model. Genetic evaluation for multiple traits simultaneously can be accomplished using models first proposed by Henderson and Quaas (1976) using genetic and residual variances and covariance between traits (Mrode, 2014). This methodology was first applied to weight traits. Genetic and residual relationships exist between weight measurements that are taken across cattle's lifetime and make this approach possible. Currently most National Cattle Genetic Evaluation (NCE) preform genetic analysis for weight traits as genetically correlated traits. For example, BW and WW are analyzed as separate but genetically correlated traits. The matrix form of the multiple trait model as described by Mrode (2014) is shown below:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

In the above equation $\boldsymbol{y_i}$ was a vector of observations, $\mathbf{b_i}$, $\mathbf{u_i}$, and $\mathbf{e_i}$ were vectors of fixed effects, random genetic effect, and random residual effect solutions, respectively**.** $\mathbf{X_i}$ and $\mathbf{Z_i}$ are incidence matrices that relate fixed and random effects to observations in **y**. The model assumes that the mean of the observations in y are equal to **Xb** and random effects have a mean of zero and genetic variance structure of:

$$var\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \sigma_{g_1}^2 & \sigma_{g_{1},g_2} \\ \sigma_{g_2,g_1} & \sigma_{g_2}^2 \end{bmatrix} \otimes \boldsymbol{A}$$

and a residual variance structure of:

$$var\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I\sigma_{e_1}^2 & I\sigma_{e_{1},e_2} \\ I\sigma_{e_{2},e_1} & I\sigma_{e_2}^2 \end{bmatrix}.$$

where $\sigma_{g_1}^2$, $\sigma_{g_2}^2$, σ_{g_{1},g_2}, σ_{g_2,g_1} are the additive genetic variances and covariance between y_1 and y_2. Similarly, $\sigma_{e_1}^2$, $\sigma_{e_2}^2$, σ_{e_{1},e_2}, σ_{e_{2},e_1} are the residual error variances and covariances between y_1 and y_2. The **A** represents Wright's numerator relationship matrix and **I** is an identity matrix with the order of n x n with a dimension of n which is the number of animals in the set of equations with observations for each trait. The relationship between genetic and residual effects are assumed 0.

A bivariate analysis using a threshold and a continuous trait was first described by Foulley and Thompson (1983) using a Bayesian approach. This methodology however relied on equal design matrices and only animals with both observations included. This situation is often not present in field data where animals have missing observations. Therefore the methodology was extended by Janss and Foulley (1993) who presented a system of equations that allowed for unequal design matrices and for the inclusion of animals with missing observations.

Generalized linear mixed model procedures can be used for the analysis of binomial and continuous traits. Several link functions are available for the analysis of bivariate data in this scenario. Link functions relate the mean of the response to predictors in the model. The differences between the different functions are the underlying distributional assumptions that are used to relate observations. The logit link function relates the observations to a logistic distribution and the probit link transforms the data to a standard normal distribution (Kutner et al., 2005). Differences between the two procedures come from the differences in implicit residual variances on the underlying scale. The residual variance for the logit model is $\pi^2/_3$ where π is equal to the probability of a successful observation, while probit models have a residual variance equal to 1 (Gilmour et al., 2009). Both models are appropriate for the analysis of bivariate data.

Genetic Parameters for Production Traits. In this study, commonly recorded production traits are examined to determine their genetic relationship with the fertility traits of interest. Genetic parameters for production traits have been some of the most studied traits in literature. Additionally, many of the production traits are the basis of many selection programs in beef cattle. Due to this determining the relationships between heifer pregnancy or stayability and the different production traits can not only help to identify traits that can be incorporated into multiple trait models, but can additionally be used to discover if selection for a trait has a negative impact on reproductive performance.

Heritability estimates for sixteen production traits are summarized in Table 2.3 along with the references for these estimates. Weight traits are some of the most reported estimates in literature, are easily and cheaply recorded and have been the focus of genetic improvement in many herds.

Carcass traits are also important production traits for genetic improvement as those traits influence eating characteristics and value of harvest offspring. Originally carcass evaluations were performed on animals that had actual carcass measurements. However, this is not an ideal situation because breeding animals are not able to receive observations resulting in limited numbers of observations. Therefore, ultrasound measurements are also included as predictors for carcass characteristics. Genetic correlations between actual and ultrasound carcass measurements are high (Crews et al., 2003). Heritability estimates for carcass and ultrasound traits have been estimated to be low to moderate (Koots et al., 1994a). Therefore, the inclusion of both measurements can be used for the improvement of carcass characteristics of harvest progeny.

Table 2.3. Summary of heritability estimates (h^2) for production traits in cattle.

Trait	h^2	References
Birth Weight	0.31 to 0.69	Winder et al. (1990);Koots et al. (1994a);BIF (2011)
Weaning Weight	0.18 to 0.44	Winder et al. (1990);Koots et al. (1994a) Williams et al. (2009); BIF (2011)
Post Weaning Gain	0.18 to 0.40	Winder et al. (1990);Koots et al. (1994a); Williams et al. (2009);BIF (2011)
Yearling Weight	0.13 to 0.40	Winder et al. (1990); Koots et al. (1994a);Meyer (1992)
Ultrasound Rib Eye Area	0.34 to 0.51	Reverter et al. (2000);Crews et al. (2003)
Ultrasound Backfat	0.09 to 0.69	Reverter et al. (2000);Crews et al. (2003)
Ultrasound Intramuscular Fat	0.12 to 0.52	Reverter et al. (2000);Crews et al. (2003); McAllister et al. (2011)
Rib Eye Area	0.26 to 0.57	Koots et al. (1994a);Reverter et al. (2000); Crews et al. (2003);Nephawe et al. (2004)
Backfat	0.23 to 0.46	Koots et al. (1994a);Reverter et al. (2000); Crews et al. (2003);Nephawe et al. (2004)
Marbling Score	0.27 to 0.54	Koots et al. (1994a);Crews et al. (2003); McAllister et al. (2011)
Hot Carcass Weight	0.20 to 0.54	Koots et al. (1994a);Reverter et al. (2000); Nephawe et al. (2004)
Scrotal Circumference	0.31 to 0.53	Bourdon and Brinks (1986); Koots et al. (1994a); McAllister et al. (2011)
Udder Suspension	0.32	Bradford et al. (2015)
Udder Teat Score	0.28	Bradford et al. (2015)
Cow Mature Weight	0.44 to 0.66	Nephawe et al. (2004);Williams et al. (2009)
Body Condition Score	0.16	Nephawe et al. (2004)

More recently, selection for traits that focus on the mature cow characteristics has been made possible with new genetic evaluations that can be included in selection programs. For instance, teat and udder scores are measurements that are taken to improve the maternal environment that is provided to a calf. The scoring system evaluates udder suspension and teat size separately with each having 9 categories of scores. Udder suspension scores range from 1 (very pendulous, broken floor) to 9 (very tight); teat scores are evaluated similarly with a score of 1 (very large balloon shaped teats) and 9 (very small teats) (BIF, 2011). If teat size is extreme or cows possess pendulous udders, calves can have difficulty nursing (Ventorp and Michanek, 1992) and this scoring system is designed to be used to reduce this incidence. Selection for mature cow weight has also been introduced as a method to select more efficient mature females. Metabolic requirements can be calculated using functions of cow body weight and milk production (Williams et al., 2009). The concern is that selection for increased weight at younger ages has caused an increase of mature cow weight and in turn higher maintenance requirements (Williams et al., 2009). Another cow-associated trait, body condition score, has been developed as a tool to evaluate the metabolic state of cattle. A scoring system was developed to assign scores to females based on external indicators of fat deposition. Scores range from 1 (severely emaciated) to 9 (very obese) (BIF, 2011).

LITERATURE CITED

Beef Improvement Federation. 2011. Guidelines for uniform beef improvement programs. Internet site: www. beefimprovement. org/library/06 guidelines. pdf (Accessed August 1 2016).

Bourdon, R.M., and J.S. Brinks. 1986. Scrotal circumference in yearling Hereford bulls: adjustment factors, heritabilities and genetic, environmental and phenotypic relationships with growth traits. J. Anim. Sci. 62: 958-967.

Bourdon, R. 2000. Understanding Animal Breeding. 2nd ed. Prentice-Hall, Upper Saddle River, NJ.

Bradford, H.L., D.W. Moser, J. Minick Bormann, and R.L. Weaber. 2015. Estimation of genetic parameters for udder traits in Hereford cattle. J. Anim. Sci. 93: 2663-2668.

Brinks, J.S., M.J. McInerney, and P.J. Chenoweth. 1978. Relationship of age at puberty in heifers to reproductive traits in young bulls. Proc. West. Sect. Am. Soc. Anim. Sci. 29:28-30.

Buzanskas, M. E., D. A. Grossi, F. Baldi, D. Barrozo, L. O. C. Silva, and R. A. A. Torres. 2010. Genetic associations between stayability and reproductive and growth traits in Canchim beef cattle. Livest. Prod. Sci. 132:107–112.

Cammack, K.M., M.G. Thomas, and R.M. Enns. 2009. Review: reproductive traits and their heritabilities in beef cattle. Prof. Anim. Sci. 25: 517-528.

Crews, D.H., and R.A. Kemp. 2001. Genetic parameters for ultrasound and carcass measures of yield and quality among replacement and slaughter beef cattle. J. Anim. Sci. 79: 3008-3020.

Crews, D.H., E.J. Pollak, R.L. Weaber, R.L. Quaas, and R.J. Lipsey. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. J. Anim. Sci. 81: 1427-1433.

Crews, D. H., and R. M. Enns. 2008b. Genetic Improvement of Heifer Pregnancy and Performance in Beef Cattle. http://beefrepro.unl.edu/proceedings/2008ftcollins/12_csu_genetics_crews.pdf. (Accessed August 1, 2016).

Cundiff, L.V., K.E. Gregory, and R.M. Koch. 1974. Effects of heterosis on reproduction in Herford, Angus and Shorthorn cattle. J. Anim. Sci. 38: 711.

Dalsted, N.L., and P.H. Gutierrez. 1989. How long do you keep her? BEEF Spring:15.

Doyle, S.P., B.L. Golden, R.D. Green, and J.S. Brinks. 2000. Additive genetic parameter estimates for heifer pregnancy and subsequent reproduction in Angus females. J. Anim. Sci. 78: 2091-2098.

Edwards, S.A. 1982. Factors affecting the time to first suckling in dairy calves. Anim. Prod. 34: 339-346.

Eler, J.P., A.B. Bignardi, J.B.S. Ferraz, and M.L. Santana Jr. 2014. Genetic relationships among traits related to reproduction and growth of Nelore females. Theriogenology 82: 708-714.

Eler, J.P., J.A. II V. Silva, J.L. Evans, J.B.S. Ferraz, F. Dias, and B.L. Golden. 2004. Additive genetic relationships between heifer pregnancy and scrotal circumference in Nellore cattle. J. Anim. Sci. 82: 2519-2527.

Eler, J. P., J.A. II V. Silva, J.B.S. Ferraz, F. Dias, H.N. Oliveria, J.L. Evans, and B.L. Golden. 2002. Genetic evaluation of the probability of pregnancy at 14 months for Nellore heifers. J. Anim. Sci. 80: 951-954.

Evans, J.L., B.L. Golden, R.M. Bourdon, and K.L. Long. 1999. Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77: 2621-2628.

Eversole, D.E., M.F. Browne, J.B. Hall, and R.E. Dietz. 2009. Body condition scoring beef cows. http://hdl.handle.net/10919/50710. (Accessed 9/1/2016).

Falconer, D. S. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. Ann. Hum. Genet. 29: 51-76.

Ferrell, C.L. 1982. Effects of postweaning rate of gain on onset of puberty and productive performance of heifers of different breeds. J. Anim. Sci. 55: 1272-1283.

Foote, R. H. 2003. Fertility estimation: a review of past experience and future prospects. Anim. Reprod. Sci. 75: 119-139.

Forabosco, F., A.F. Groen, R. Bozzi, J.A.M Van Arendonk, F. Filippini, P. Boettcher, and P. Bijma. 2004. Phenotypic relationships between longevity, type traits, and production in Chianina beef cattle. J. Anim. Sci. 82: 1572-1580.

Fortes, M.R., W.M. Snelling, A. Reverter, S.H. Nagaraj, S.A. Lehnert, R.J. Hawken, K.L. DeAtley, S.O. Peters, G.A. Silver, G. Rincon, J.F. Medrano, A. Islas-Trejo, and M.G. Thomas. 2012. Gene network analyses of first service conception in Brangus heifers: use of genome and trait associations, hypothalamic-transcriptome information, and transcription factors. J. Anim. Sci. 90: 2894-2906.

Foulley, J.L. D. Ginanola, and R. Thompson. 1983. Prediction of genetic merit from data on bianry and qualatitative variates with an application to calving difficulty, birth weight, and pelvic opening. Gent. Sel. Evol. 15: 401-424.

Freetly, H.C., and L.V. Cundiff. 1998. Reproductive performance, calf growth, and milk production of first-calf heifers sired by seven breeds and raised on different levels of nutrition. J. Anim. Sci. 76: 1513-1522.

Freetly, H.C., C.L. Ferrell, and T.G. Jenkins. 2001. Production performance of beef cows raised on three different nutritionally controlled heifer development programs. J. Anim. Sci. 79: 819-826.

Frisch, J.E. 1982. The use of teat-size measurements or calf weaning weight as an aid to selection against teat defects in cattle. Anim. Prod. 35: 127-133.

Funston, R.N., and G.H. Deutscher. 2004. Comparison of target breeding weight and breeding date for replacement beef heifers and effects on subsequent reproduction and calf performance. J. Anim. Sci. 82: 3094-3099.

Funston, R. N., J. L. Martin, D. M. Larson, and A. J. Roberts. 2012. PHYSIOLOGY AND ENDOCRINOLOGY SYMPOSIUM: Nutritional aspects of developing replacement heifers1. J. Anim. Sci. 90: 1166-1171.

Gianola, D. 1982. Theory and analysis of threshold characters. J. Anim. Sci. 54: 1079-1096.

Gianola, D., and J.L. Foulley. 1983. Sire evaluation for ordered categorical data with a threshold model. Gent. Sel. Evol. 15: 201-224.

Gilmour, A. R., B. Gogel, B. Cullis, R. Thompson, and D. Butler. 2009. ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK.

Goldberg, V., and O. Ravagnolo. 2015. Description of the growth curve for Angus pasture-fed cows under extensive systems. J. Anim. Sci. 93: 4285-4290.

Golden, B.L., D.J. Garrick, and L.L. Benyshek. 2009. Milestones in beef cattle genetic evaluation. J. Anim. Sci. 87:E3-E10.

Greer, R.C., R.W. Whitman, and R.R. Woodward. 1980. Estimation of probability of beef cows being culled and calculation of expected herd life. J. Anim. Sci. 51: 10-19.

Gregory, K.E., D.B. Laster, L.V. Cundiff, G.M. Smith, and R.M. Koch. 1979. Characterization of biological types of cattle—Cycle III: II. Growth rate and puberty in females. J. Anim. Sci. 49: 461-471.

Hall, J.B., R.B. Staigmiller, R.A. Bellows, R.E. Short, W.M. Moseley, S.E. Bellows. 1995. Body composition and metabolic profiles associated with puberty in beef heifers. J. Anim. Sci. 73: 3409-3420.

Harville, D.A., and R.W. Mee. 1984. A mixed-model procedure for analyzing ordered categorical data. Biometrics: 393-408.

Henderson, C.R., and R.L. Quaas. 1976. Multiple trait evaluation using relatives' records. J. Anim. Sci. 43: 1188-1197.

Henderson, C. R. 1975. Best linear unbiased estimation and prediction under a selection model. Biometrics: 423-447.

Jamrozik, J., S. McGrath, R.A. Kemp, and S.P. Miller. 2013. Estimates of genetic parameters for stayability to consecutive calvings of Canadian Simmentals by random regression models. J. Anim. Sci. 91: 3634-3643.

Janss, L.L.G., and J.L. Foulley. 1993. Bivariate analysis for one continuous and one threshold dichotomous trait with unequal design matrices and an application to birth weight and calving difficulty. Lives. Prod. Sci. 33: 183-198.

King, R.G., D.D. Kress, D.C. Anderson, D.E. Doornbos, and P.J. Burfening. 1983. Genetic parameters in Herefords for puberty in heifers and scrotal circumference in bulls. Proc. West. Sect. Anim. Sci. 34:ll.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr.62: 309-338.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62: 826-853.

Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2005. Applied Linear Statisical Models. 5th ed. McGraw-Hill/Irwin, Chicago.

Larson, R.L. 2007. Heifer development: reproduction and nutrition. Vet. Clin. North Am.: Food Anim. Pract. 23: 53-68.

Laster, D.B., G.M. Smith, L.V. Cundiff, and K. E. Gregory. 1979. Characterization of biological types of cattle (Cycle II) II. Postweaning growth and puberty of heifers. J. Anim. Sci. 48: 500-508.

Lesmeister, J.L., P.J. Burfening, and R.L. Blackwell. 1973. Date of first calving in beef cows and subsequent calf production. J. Anim. Sci. 36: 1-6.

Marquez, G.C., S.E. Speidel, R.M. Enns, and D.J. Garrick. 2010. Genetic diversity and population structure of American Red Angus cattle. J. Anim. Sci. 88: 59-68.

Martin, J.L. K.W. Creighton, J.A. Musgrave, T.J. Klopfenstein, R.T. Clark, D.C. Adams, and R.N. Funston. 2008. Effect of prebreeding body weight or progestin exposure before breeding on beef heifer performance through the second breeding season. J. Anim. Sci. 86: 451-459.

Martinez, G.E., R.M. Koch, L.V. Cundiff, K.E. Gregory, S.D. Kachman, and L.D. Van Vleck. 2005. Genetic parameters for stayability, stayability at calving, and stayability at weaning to specified ages for Hereford cows. J. Anim. Sci. 83: 2033-2042.

Martinez-Velazquez, G., K.E. Gregory, G.L. Bennett, and L.D. Van Vleck. 2003. Genetic relationships between scrotal circumference and female reproductive traits. J. Anim. Sci. 81: 395-401.

McAllister, C.M., S.E. Speidel, D.H. Crews, Jr., and R.M. Enns. 2011. Genetic parameters for intramuscular fat percentage, marbling score, scrotal circumference, and heifer pregnancy in Red Angus cattle. J. Anim. Sci. 89: 2068-2072.

Melton, B. 1995. Conception to consumption: The economics of genetic improvement. Proc. Beef Improvement Federation 27th Research Symposium and Annual Meeting. Sheridan, WY. 27: 40-71.

Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Lives. Prod. Sci. 31: 179-204.

Misztal, I., D. Gianola, and J.L. Foulley. 1989. Computing Aspects of a Nonlinear Method of Sire Evaluation for Categorical Data. J. Dairy Sci. 72: 1557-1568.

Mrode, R. A. 2014. Linear models for the prediction of animal breeding values. Cambridge:Cabi.

Nephawe, K.A., L.V. Cundiff, M.E. Dikeman, J.D. Crouse, and L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. J. Anim. Sci. 82: 647-653.

Nunez-Dominguez, R., L.V. Cundiff, G.E. Dickerson, K.E. Gregory, and R.M. Koch. 1991. Heterosis for survival and dentition in Hereford, Angus, Shorthorn, and crossbred cows. J. Anim. Sci. 69: 1885-1898.

Parkinson, T. J. 2004. Evaluation of fertility and infertility in natural service bulls. Vet. J. 168: 215-229.

Patterson, D.J., R.C. Perry, G.H. Kiracofe, R.A. Bellows, R.B. Staigmiller, and L.R. Corah. 1992. Management considerations in heifer development and puberty. J. Anim. Sci. 70: 4018-4035.

Perry, G.A. 2012. PHYSIOLOGY AND ENDOCRINOLOGY SYMPOSIUM: Harnessing basic knowledge of factors controlling puberty to improve synchronization of estrus and fertility in heifers. J. Anim. Sci. 90: 1172-1182.

Perry, R.C., L.R. Corah, R.C. Cochran, J.R. Brethour, K.C. Olson, and J.J. Higgins. 1991a. Effects of hay quality, breed, and ovarian development on onset of puberty and reproductive performance of beef heifers. J. of Prod. Agric. 4: 13-18.

Perry, R.C., L.R. Corah, R.C. Cochran, W.E. Beal, J.S. Stevenson, J.E. Minton, D.D. Simms, and J.R. Brethour. 1991b. Influence of dietary energy on follicular development, serum gonadotropins, and first postpartum ovulation in suckled beef cows. J. Anim. Sci. 69: 3762-3773.

Reverter, A., B.L. Golden, R.M. Bourdon, and J.S. Brinks. 1994. Method R variance components procedure: application on the simple breeding value model. J. Anim. Sci. 72: 2247-2253.

Reverter, A., D.J. Johnston, H.U. Graser, M.L. Wolcott, and W.H. Upton. 2000. Genetic analyses of live-animal ultrasound and abattoir carcass traits in Australian Angus and Hereford cattle. J. Anim. Sci. 78: 1786-1795.

Roberts, A.J., T.W. Geary, E.E. Grings, R.C. Waterman, and M.D. MacNeil. 2009. Reproductive performance of heifers offered ad libitum or restricted access to feed for a one hundred forty-day period after weaning. J. Anim. Sci. 87: 3043-3052.

Rogers, P.L., C.T. Gaskins, K.A. Johnson, and M.D. MacNeil. 2004. Evaluating longevity of composite beef females using survival analysis techniques. J. Anim. Sci. 82: 860-866.

Rumph, J.M., and L.D. Van Vleck. 2004. Age-of-dam adjustment factors for birth and weaning weight records of beef cattle: a review. Genet. Mol. Res.3: 1-17.

Saatchi, M., R.D. Schnabel, M.M. Rolf, J.F. Taylor, and D.J. Garrick. 2012. Accuracy of direct genomic breeding values for nationally evaluated traits in US Limousin and Simmental beef cattle. Genet. Sel. Evol. 44: 38.

Short, R.E., R.A. Bellows, R.B. Staigmiller, J.G. Berardinelli, and E.E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68: 799-816.

Smith, B.A., J.S. Brinks, and G.V. Richardson. 1989. Estimation of genetic parameters among breeding soundness examination components and growth traits in yearling bulls. J. Anim. Sci. 67: 2892-2896.

Snelling, W.M., B.L. Golden, and R.M. Bourdon. 1995. Within-herd genetic analyses of stayability of beef females. J. Anim. Sci. 73: 993-1001.

Snelling, W. M. 1994. Genetic analyses of binary stayability measures of beef females. PhD Diss. Colorado State Univ., Fort Collins.

Summers, A.F., S.P. Weber, H.A. Lardner, and R.N. Funston. 2014. Effect of beef heifer development system on average daily gain, reproduction, and adaptation to corn residue during first pregnancy. J. Anim. Sci. 92: 2620-2629.

Tallman, R.M., L.V. Cundiff, K.E. Gregory, and R.M. Koch. 1999. Germplasm Evaluation in Beef Cattle - Cycle IV: Postweaning Growth and Puberty of Heifers. J. Anim. Sci. 77: 2651-2659.

Van Melis, M. H., J.P. Eler, H.N. Oilvira, G.J.M. Rosa, J.A.V. Silva, J.B.S Ferraz, and E. Pereira. 2007. Study of stayability in Nellore cows using a threshold model. J Anim Sci 85: 1780-1786.

Ventorp, M., and P. Michanek. 1992. The importance of udder and teat conformation for teat seeking by the newborn calf. J. Dairy Sci. 75: 262-268.

Williams, J.L., D.J. Garrick, and S.E. Speidel. 2009. Reducing bias in maintenance energy expected progeny difference by accounting for selection on weaning and yearling weights. J. Anim. Sci. 87: 1628-1637.

Wiltbank, J.N., K.E. Gregory, L.A. Swiger, J.E. Ingalls, J.A. Rothlisberger, and R.M. Koch. 1966. Effects of heterosis on age and weight at puberty in beef heifers. J. Anim. Sci. 25: 744-751.

Wiltbank, J.N., C.W. Kasson, and J.E. Ingalls. 1969. Puberty in crossbred and straightbred beef heifers on two levels of feed. J. Anim. Sci. 29: 602-605.

Winder, J.A., J.S. Brinks, R.M. Bourdon, and B.L. Golden. 1990. Genetic analysis of absolute growth measurements, relative growth rate and restricted selection indices in red Angus cattle. J. Anim. Sci. 68: 330-336.

Wright, S. 1934. An analysis of variability in number of digits in an inbred strain of guinea pigs. Genet. 19: 506.

Wythe, L. D. 1970. Genetic and environmental effects on characters related to productive ability of the American Brahman. PhD Diss. Texas A&M Univ., College Station.

CHAPTER III

GENETIC PARAMETERS FOR PRODUCTION TRAITS AND HEIFER PREGNANCY IN RED ANGUS CATTLE

SUMMARY: Heifer pregnancy (HPG) EPD is a prediction of the probability that a female will conceive during her first breeding season. An inherent issue in the genetic prediction of HPG is that phenotypes can only be collected on females limiting the amount of information available to improve accuracy of genetic prediction. To overcome this, inclusion of traits recorded on both sexes could be used to improve accuracy of HPG predictions. Therefore, the objective of this study was to estimate the genetic relationship between HPG and commonly recorded performance traits including birth weight (BW), 205-d pre weaning gain (direct and maternal Pre-WG$_{D}$, Pre-WG$_{M}$), 205-d weaning weight (direct and maternal, WW$_{D}$, WW$_{M}$), 160-d post weaning gain (Post-WG), 365-d yearling weight (direct and maternal, YW$_{D}$, YW$_{M}$), scrotal circumference (SC), rib eye area (REA), backfat (BF), marbling score (MARB), hot carcass weight (HCW), ultrasound rib eye area (UREA), ultrasound backfat (UBF), and ultrasound percent intramuscular fat (UIMF). The data set contained records on 142,146 animals from the Red Angus Association of America. Genetic relationships, (co)variances, were estimated with multiple, two-trait animal models using a REML procedure. Appropriate contemporary groups were formed and modeled either as the only fixed effect or jointly with sex for BW, WW, PWG, YW, REA, BF, MARB, HCW, UREA, UBF, and UIMF. Furthermore, the effect of age of dam was also modeled in the analysis of BW, WW, PWG, and YW; whereas, the effect of age of measurement was included for HPG, REA, BF, MARB, HCW, UREA, UBF, and UIMF. Random effects consisted of direct genetic effects for all traits, maternal genetic effects for WW and YW, and permanent environment of the dam for Pre-WG, and WW. Results revealed direct heritability estimates of 0.58 ± 0.01, 0.25 ± 0.01, 0.29 ± 0.01, 0.22 ± 0.01, 0.32 ± 0.01, 0.46 ± 0.02, 0.37 ± 0.07, 0.27 ± 0.06, 0.40 ± 0.06, 0.25 ± 0.06, 0.41 ± 0.01, 0.35 ± 0.01, 0.38 ± 0.01 and 0.12 for BW, Pre-WG, WW, PWG, YW, SC, REA, BF, MARB, HCW, UREA, UIMF, and HPG (averaged across all analyses on the underlying scale), respectively. Genetic association for Pre-WG direct (0.24 ± 0.08), WW direct (0.18± 0.08), YW direct (0.20 ± 0.07), UREA (0.16 ± 0.08), and UBF (0.14 ± 0.08) with HPG were the strongest. Genetic correlations between HPG and BW, SC, WW maternal, Post-WG, YW maternal, REA, BF, MARB, HCW, and UIMF had confidence intervals that included or were near zero, suggesting minimal genetic relationship between the traits. These results suggest that genetic relationships exist between HPG and other more highly recorded production traits and could be used to increase accuracy of selection for HPG.

Key Words: beef cattle, genetic correlation, heifer pregnancy

INTRODUCTION

Traits that have a direct influence on cost or revenue of a beef cattle enterprise can be classified as economically relevant (Golden et al., 2000). In the context of the cow-calf sector of the beef industry, traits that relate to the reproductive capabilities of females have been shown to be the largest drivers of profitability (Melton, 1995). One of the first measurements that can contribute to the prediction of reproductive performance in cattle is the heifer pregnancy **(HPG)** phenotype, which is defined as the ability of a beef female to conceive during her first breeding season (Crews and Enns, 2008b), typically as a two-year-old. However, collection of phenotypes for HPG are restricted to only females that are retained as replacements in the breeding herd. Additionally, HPG heritability estimates are typically low to moderate in magnitude (Cammack et al., 2009). Consequently, many progeny are needed to produce high accuracy HPG genetic predictions. To overcome the difficulty of producing high accuracy genetic predictions for HPG, correlated traits have suggested as a means to increase accuracy. In the context of genetic improvement of reproductive traits, the use of correlated traits offers the potential advantage of including traits that are measured at younger ages, and on both sexes. Traits that would be most beneficial for inclusion in genetic predictions are traits that are measured before culling decisions are made, or phenotypes that can be measured on both culled and retained individuals of both sexes.

The objective of this study was to estimate the genetic parameters for HPG, and other production measures to determine the genetic relationship between the traits in an effort to use these results in future genetic evaluation.

MATERIALS AND METHODS

Data used in this study was obtained from the existing database of the Red Angus Association of America (RAAA, Denton, TX), therefore, animal care and use committee approval was not obtained.

Pedigree and performance records on animals born from 1986 to 2012 were used in the analysis. Production traits used in the analyses included: birth weight (**BW**), 205-d pre-weaning gain (**direct and maternal, Pre-WG$_D$, Pre-WG$_M$**), 205-d weaning weight **(direct and maternal, WW$_D$, WW$_M$**), 160-d post weaning gain (**Post-WG**), 365-d yearling weight (**direct and maternal, YW$_D$, YW$_M$**), scrotal circumference (**SC**), rib eye area (**REA**), backfat (**BF**), marbling score (**MARB**), hot carcass weight (**HCW**), ultrasound rib eye area (**UREA**), ultrasound backfat (**UBF**), and ultrasound percent intramuscular fat (**UIMF**). Data from animals that were members of the same birth work group as females with a HPG observation were included in this study. Birth work group is an RAAA defined category that contains both males and females from the same ranch or herd. Binary observations for HPG were based on calving intervals calculated from producer submitted breeding season information (McAllister et al., 2011). An observation of 1 represents a female that successfully became pregnant during her first breeding season; whereas, an observation of 0 corresponds to a female that was unsuccessful. For the production traits, phenotypic observations were discarded, if either the age at measurement was greater than 5 SD from the overall mean, or the observations were greater than 5 SD from the overall mean.

Contemporary groups **(CG)** were formed in accordance with current standards used in the RAAA genetic evaluations. Breed code (**BC**) represented four subcategories 87.5 percent Red Angus or greater, animals between 50 percent and 87.4 percent Red Angus, and animals with the same Red Angus percentage but also having some Brahman influence. Birth contemporary group (**BCG**) was defined as BC, birth work group, a producer defined birth management group, as well as season and year of birth. Weaning contemporary group (**WCG**) was defined as BC, a breed association defined weaning work group, a producer defined weaning management code, birth work group, and weaning date. Yearling contemporary group (**YCG**) was defined as all components that comprised the WCG, as well as a breed association defined yearling work group, and a producer defined yearling management group. Heifer pregnancy contemporary group was defined as YCG and a producer defined heifer pregnancy management code. Carcass contemporary group was defined as owner and harvest date. Ultrasound contemporary groups were defined as YCG, a producer defined ultrasound management group, and ultrasound date. If there was no variation for observations in a particular CG, then the CG was omitted from the analysis. The total number of unique CG for HPG, BW, Pre-WG, WW, Post-WG, YW, SC, REA, BF, MARB, HCW, UREA, UBF, and UIMF were 5494, 4349, 4351, 5451, 5415, 5424, 1210, 83, 84, 77, 84, 2573, 2574, and 2589, respectively. Average contemporary group size for HPG was 14 animals, 26 animals for BW, 31 animals for Pre-WG and WW, 19 animals for Post-WG and YW, 17 animals for SC, 29 animals for all carcass traits, and 15 animals for all ultrasound traits.

A series of two-trait animal models were used to estimate the genetic and residual (co)variance components between HPG and the other performance traits. Contemporary groups were modeled as fixed effects. For BW, sex was included in the model with 2 categories, bull and heifer. Whereas, sex classification for WW, PWG, YW, REA, BF, MARB, HCW, UREA, UBF, and UIMF, was included using the three levels of bull, heifer, and steer. The fixed effect of age of dam was included as a categorical effect (2, 3, 4, 5 to 9, 10, ≥ 11; BIF, 2011) for BW, WW, PWG, and YW. A linear covariate for age of measurement was included for HPG, carcass, and ultrasound traits. Age of measurement for HPG was determined as the age when the female was initially exposed for breeding, whereas, the age of measurement for other production traits was calculated using the date the phenotype was recorded. The WW, PWG, YW, and SC phenotypes were adjusted to an age constant point in accordance with BIF guidelines (BIF, 2011). Maternal genetic effects of the dam were included in the models for WW and YW. Weaning weight and Pre-WG analysis included a random, permanent environmental effect of the dam. A 3-genertation pedigree was formed based on animals from the final data set. A summary of the pedigree used in each analysis is presented in Table 3.1.

Due to the binary nature of HPG phenotypes, observations were converted to an underlying normal distribution using a probit link function, which limits the residual variance of the trait to 1 (Harville and Mee, 1984; McAllister et al., 2011). Residual covariances between several traits used in the analysis were constrained to 0 because both phenotypes could not be measured on the same individual. These trait pairs included HPG and SC, as well as, HPG and all carcass traits: HCW, BF, REA, and MARB. Variance parameters and SE for all traits were calculated using ASREML 3.0 (Gilmour et al., 2009).

RESULTS AND DISSCUSSION

Table 3.2 presents summary statistics for all traits. The average success rate for HPG was 0.77, which is equivalent to an average of 77% of heifers successfully becoming pregnant during their first breeding season. These results were consistent with published results of McAllister et al. (2011) of 0.80 in Red Angus cattle, Peters et al. (2013) of 0.78 in Brangus cattle, and Evans et al. (1999) of 0.78 in Hereford cattle. Winder et al. (1990) reported mean weights of 34.1 kg, 231.8 kg, 134.7 kg, and 366.6 kg for BW, WW, PWG, and YW in Red Angus cattle, respectively. Phenotypic averages in the current study were higher than these previous estimates which was not surprising given the genetic trends in the RAAA population (http://www.redangus.org/). The average scrotal circumference was consistent with the averages of 35.24 cm and 32.59 ± 2.97 cm reported by McAllister et al. (2011) and Martinez-Velazquez et al. (2003), respectively. Average HCW and BF in this analysis were both higher, and MARB was consistent with published estimates from Crews et al. (2003) in Simmental cattle, Peters et al. (2014) in crossbred cattle, and Nephawe et al. (2004) for cattle in the Germ Plasm Evaluation at the Meat Animal Research Center. Our estimated averages of UREA and UBF were higher than those reported by Crews and Kemp (2001) from cross bred bulls and heifers at a year of age. Average UIMF was consistent with estimates published by McAllister et al. (2011) in Red Angus cattle.

Table 3.3 summarizes parameter variance, heritability, and total variance explained by permanent environment effects, for all studied traits. Because HPG was included in a two-trait model with each of the other production traits, multiple heritability estimates were calculated for HPG (n=12). The results shown in the table (0.12) was calculated by averaging the estimates obtained from each of the separate two-trait analyses of HPG with all production traits. The current heritability estimate was lower than the heritability estimate of 0.17 ± 0.01 obtained by McAllister et al. (2011) using a sire model in Red Angus cattle. The difference in heritability using similar data sets likely is the results of the use of a sire model in the previous analysis, compared to the animal model in the current analyses. For production traits, direct heritability estimates were generally moderate to high in magnitude. Permanent environment variance accounted for 0.14 ± 0.00 of the total variance in both the Pre-WG and WW analyses. Genetic correlations between the direct and maternal components of Pre-WG, WW, and YW were -0.31± 0.03, -0.29 ± 0.03 and 0.02 ± 0.05, respectively. Estimates of direct and maternal correlations are consistent with ranges established in previous research (Meyer, 1992). Birth weight heritability was higher than estimates reported by Winder et al. (1990) of 0.46 ± 0.02 and weighted and unweighted average estimates by Koots et al. (1994a) of 0.31 and 0.35, respectively. Pre-weaning gain direct heritability estimates were higher and maternal heritability was lower than MacNeil and Mott (2006) in Line 1 Hereford cattle. However, estimates in the study for Pre-WG_D and Pre-WG_M are in agreement with previous ranges established using sire models (Brown et al. 1990, Hetzel et al. 1990). The trait Pre-WG has not been studied extensively in recent literature and therefore is unique to this study. Post weaning gain heritability was similar to estimates published in the BIF guidelines for Red Angus (BIF, 2011). Estimates for heritability of WW_D (0.26 ± 0.02), WW_M (0.14 ± 0.02), and variance accounted for by permanent environment effects of the dam (0.19 ± 0.01) were similar to those published previously published in Red Angus cattle (Speidel et al., 2007). Yearling weight direct and maternal heritability estimates were consistent with the estimates of 0.32 and 0.06 in Angus cattle where random effects were similar to the model used here (Meyer, 1992). Scrotal circumference heritability estimate was consistent with the reported estimate of 0.51 ± 0.02 (Crews and Enns, 2008a) from RAAA. Estimates for carcass and ultrasound parameters were consistent with the parameters in Simmental cattle of 0.37, 0.29, 0.33, 0.43, 0.40, 0.44, 0.44 for CWT, BF, REA, MARB, UBF, UREA, and UIMF, respectively (Su et al., 2016) and for the weighted averages from Koots et al. (1994a) were 0.23 (BF), 0.20 (HCW), 0.27 (MARB), 0.40 (REA).

Table 3.4 summarizes the estimated genetic and residual covariance, and correlations between HPG and production traits. The genetic correlation with the highest magnitude was between HPG and Pre-WG_D at 0.24 ± 0.08. While previous estimates of genetic correlations between the traits were not available, results from Roberts et al. (2009) showed that increases of 0.1 kg/d in pre-weaning average daily gain increased the percentage of heifers achieving puberty during a post weaning treatment of restricted and ab-libitum control diets by 11.6 ± 2.6 percentage points. Additionally, in a review by Patterson et al. (1992) multiple studies from the 1950’s through the 1970’s were cited that suggested pre-weaning growth was a greater influence on age of puberty **(AOP)** than post weaning growth rate (Wiltbank et al. 1966; Swierstra et al. 1977). While these results compared pre-weaning growth rate to AOP, in populations where a significant number of heifers do not reach puberty before the start of the breeding season, AOP would have an effect on HPG during the first breeding season. Heifers that have the ability to reach puberty at younger ages have the opportunity to have multiple ovulation cycles before the breeding season with later cycles being more fertile than the pubertal estrus (Perry et al., 1991). Therefore, it is not unreasonable to assume that the benefits of higher Pre-WG would extend to the HPG phenotype as well.

The genetic correlations between HPG and WW_D and YW_D were moderate and positive at 0.18 ± 0.08 and 0.20 ± 0.07, respectively. Fortes et al. (2012) examined REML and genomic correlations for HPG and weight traits in Brangus cattle. The REML correlation estimates in the study were -0.28 ± 0.38 for 205-d weight, and -0.14 ± 0.35 for 365-d weight. Additionally, Pearson's genomic correlations were calculated using an associated weight matrix. Correlations between HPG, and 205-d weight and 365-d weight were 0.17 and 0.10, respectively (Fortes et al., 2012). The differences between the current study and previous literature may arise from the small sample size (n = 835) in the Brangus analysis. Moreover, *Bos Indicus* cattle, traditionally, achieve puberty at a later age, which might also bias these estimates and cause a non-zero correlation.

Genetic correlations between HPG, UBF, and UREA were low but positive in nature. In Brangus cattle positive correlations were also estimated between UREA, and UBF (Fortes et al., 2012). All carcass traits and UIMF also showed to have little to no genetic relationship with HPG. This might be due to the relatively few records available on carcass traits. These few records resulted in large standard error estimates that caused the genetic correlations to not be different from 0. For Red Angus cattle, McAllister, et al. (2011), found a stronger positive correlation (0.13 ± 0.09) between HPG and UIMF. While the estimate in the current analysis is lower in magnitude both estimates are within the range of the standard errors and therefore can be considered equivalent.

Generally, correlations between HPG and BW, Post-WG, and SC were near zero. These results suggest that little genetic relationship exists between the traits. There are no published genetic correlations between BW and HPG. The current estimate suggests that heifers that were born with heavier birth weights have a lower chance of conceiving during their first breeding season. Alternatively, Cushman et al. (2009) showed that heifers with higher birth weights had a higher antral follicle count and higher HPG rates ($P = 0.05$). Post weaning gain also has negligible relationship with HPG. Previous research has shown that a phenotypic increase in heifer's PWG can help to reduce the AOP (Wiltbank et al., 1969). This was then developed into what is now known as heifer development programs. The objective of the development programs are to feed heifers so that they can achieve weights that are 65 percent of their mature weight at the start of the of the breeding season (Patterson et al., 1992). While a phenotypic relationship may exist between AOP and Post-WG, this relationship does not extend to the genetic relationship of HPG and Post-WG.

Scrotal circumference has also been a suggested tool to improve reproductive performance. Brinks et al. (1978) showed that the genetic correlation between SC and AOP was negative. More recently, however, the relationship between SC and HPG has been disputed, in which multiple studies have found negligible genetic relationship between the traits. (Evans et al., 1999; McAllister et al., 2011). This could be the result of selection and changes in performance in the intervening period. In the current study, a slight negative association between these traits was estimated. This may partially be explained by the fact that if all heifers reach puberty at an age before breeding, then heifers that reach this point earlier have no advantage because all females are successfully cycling at the beginning of the breeding season (Martin et al. 1992).

Overall residual correlations between HPG and the production traits were positive and weak. The strongest correlation was between HPG and YW (0.14 ± 0.03). These results suggest that an environment that promotes a higher YW will also increase the probability of a female to become pregnant during their first breeding season. The effect of the previously mentioned heifer development programs may be seen through this correlation.

Summary statistics for BIF accuracy values for a single trait analysis that contained only HPG phenotypes, and the multiple trait model that included HPG and Pre-WG are contained in Table 3.5. Overall, an increase in accuracy values can be seen for the multiple trait model compared to the single trait model. For all animals average accuracy values increased 12%, parents of animals with observations accuracy values increased 2%, and non-parents average accuracy values increased 13%.

The genetic evaluation of HPG using information from correlated traits has the most promise with Pre-WG as it had the strongest genetic relationship with HPG. This trait can be used in routine genetic evaluation as a correlated trait to improve the accuracy of HPG genetic predictions. Pre-weaning gain lends itself to be an ideal indicator trait because it can be easily and cheaply recorded, measured on both sexes, and occurs before culling decisions are made; maximizing the amount of data that is available for the evaluations. An additional outcome of this study is that selection for improving weight and carcass traits should not have a negative effect on the ability of a female to become pregnant during her first breeding season.

Table 3.1 Description of pedigree used for two-trait analyses with heifer pregnancy and production traits in Red Angus Cattle.

Trait	Total number of animals	Number of unique sires	Number of unique dams
Birth weight	248,082	17,104	111,258
Pre-weaning gain	236,506	16,697	107,216
Weaning weight	236,507	15,378	107,216
Post weaning gain	190,981	15,428	91,569
Yearling weight	192,849	12,354	92,324
Scrotal circumference	117,314	11,655	63,626
Rib eye area	90,960	11,655	53,716
Backfat	90,933	11,653	53,723
Marbling score	90,791	11,656	53,689
Hot carcass weight	91,000	12,536	53,726
Ultrasound rib eye area	128,833	12,536	67,806
Ultrasound backfat	128,881	12,536	67,826
Ultrasound intramuscular fat	128,834	12,536	67,809

Table 3.2 Summary statistics for heifer pregnancy (HPG), birth weight (BW), weaning weight (WW), post weaning gain (PWG), yearling weight (YW), scrotal circumference (SC), rib eye area (REA), backfat (BF), marbling score (MARB), hot carcass weight (HCW), ultrasound rib eye area (UREA), ultrasound backfat (UBF), ultrasound intramuscular fat (UIMF) in Red Angus cattle used in this analysis.

Trait	n	Mean	S.D.	Minimum	Maximum
HPG, %	29,322	0.77	0.42	0.00	1.00
BW, kg	141,436	36.08	5.46	11.00	63.00
Pre-WG, kg	134,202	220.07	38.00	68.00	409.00
WW, kg	134,202	256.19	40.16	90.26	454.05
Post-WG, kg	101,916	160.00	63.84	1.00	477.00
YW, kg	103,334	418.51	83.64	158.30	809.21
SC, cm	20,389	35.34	2.77	21.64	49.33
REA, cm^2	2,372	81.51	9.40	35.48	119.35
BF, mm	2,404	14.01	4.03	0.51	30.48
MARB	2,234	5.44	1.08	1.24	9.60
HCW, kg	2,409	369.96	39.74	233.60	510.29
UREA, cm^2	39,227	71.06	13.43	24.52	124.52
UBF, mm	39,274	5.60	2.24	0.51	16.76
UIMF, %	39,113	3.56	0.97	0.59	8.37

Table 3.3 Estimates of parameter variance, phenotypic variance, heritability (h^2 ± S.E.), and permanent environment effects (c^2 ± S.E.) for production traits and heifer pregnancy in Red Angus cattle.

Trait	Parameter variance	Phenotypic variance	h^2	c^2
HPG_{D}	0.14[2]	1.14[2]	0.12 ± 0.01[2]	
BW_{D}	27.25	46.65	0.58 ± 0.01	
Pre-WG_{D}	360.09	1,431.13	0.25 ± 0.01	
Pre-WG_{M}	151.15	1,431.13	0.11 ± 0.01	
$\text{Pre-WG}_{\text{PE}}$	199.72	1,431.13		0.14 ± 0.00
WW_{D}	442.35	1,508.69	0.29 ± 0.01	
WW_{M}	154.30	1,508.69	0.10 ± 0.01	
WW_{PE}	212.53	1,508.69		0.14 ± 0.00
$\text{Post-WG}_{\text{D}}$	344.49	1,532.42	0.22 ± 0.01	
YW_{D}	987.04	3,056.03	0.32 ± 0.01	
YW_{M}	166.38	3,056.03	0.05 ± 0.01	
SC_{D}	2.43	5.25	0.46 ± 0.02	
REA_{D}	3.56	9.74	0.37 ± 0.07	
BF_{D}	0.14	0.52	0.27 ± 0.06	
MARB_{D}	0.32	0.80	0.40 ± 0.06	
HCW_{D}	482.69	1,969.41	0.25 ± 0.06	
UREA_{D}	3.33	8.19	0.41 ± 0.01	
UBF_{D}	0.03	0.10	0.35 ± 0.01	
UIMF_{D}	0.18	0.50	0.38 ± 0.01	

[1] HPG_{D} = heifer pregnancy direct (%); BW_{D} = birth weight direct (kg); Pre-WG_{D} = Pre weaning gain direct (kg); Pre-WG_{M} = Pre weaning gain maternal (kg); $\text{Pre-WG}_{\text{PE}}$ = Pre weaning gain permanent environment of the dam (kg); WW_{D} = weaning weight direct (kg); WW_{M} = weaning weight maternal (kg); WW_{PE} = weaning weight permanent environment if the dam (kg); $\text{Post-WG}_{\text{D}}$ = post weaning gain direct (kg); YW_{D} = yearling weight direct (kg); YW_{M} = yearling weight maternal (kg); SC_{D}= scrotal circumference direct (cm); REA_{D} = rib eye area direct (cm^2); BF_{D} = backfat direct (mm); MARB_{D} = marbling score direct; HCW_{D} = hot carcass weight direct (kg); UREA_{D} = ultrasound rib eye area direct (cm^2); UBF_{D} = ultrasound backfat direct (mm); UIMF_{D} = ultrasound intramuscular fat direct (%).

[2] Reported as the average of heritability estimates and largest S.E. of all two-trait analyses between heifer pregnancy and production traits.

Table 3.4 Estimates of genetic covariance, residual covariance, genetic correlation, and residual correlation between heifer pregnancy (HPG) and production traits in Red Angus cattle.

Trait	Genetic covariance	Residual covariance	Genetic correlation	Residual correlation
$\mathrm{BW_D}$	-0.08	0.02	-0.06 ± 0.05	0.01 ± 0.01
$\mathrm{Pre\text{-}WG_D}$	1.12	0.79	0.24 ± 0.08	0.04 ± 0.01
$\mathrm{Pre\text{-}WG_M}$	0.00	0.79	0.00 ± 0.09	0.04 ± 0.01
$\mathrm{WW_D}$	0.94	0.80	0.18 ± 0.08	0.04 ± 0.01
$\mathrm{WW_M}$	0.07	0.80	0.02 ± 0.09	0.04 ± 0.01
$\mathrm{Post\text{-}WG_D}$	0.30	0.59	0.06 ± 0.07	0.03 ± 0.01
$\mathrm{YW_D}$	1.46	1.53	0.21 ± 0.07	0.14 ± 0.03
$\mathrm{YW_M}$	0.01	1.53	0.00 ± 0.11	0.14 ± 0.03
$\mathrm{SC_D}$	-0.03	0.00	-0.06 ± 0.09	0.00 ± 0.00
$\mathrm{REA_D}$	0.37	0.00	0.21 ± 0.21	0.00 ± 0.00
$\mathrm{BF_D}$	-5.54	0.00	-0.08 ± 0.23	0.00 ± 0.00
$\mathrm{MARB_D}$	-0.17	0.00	-0.08 ± 0.19	0.00 ± 0.00
$\mathrm{HCW_D}$	-0.16	0.00	-0.03 ± 0.25	0.00 ± 0.00
$\mathrm{UREA_D}$	0.27	0.16	0.16 ± 0.08	0.03 ± 0.01
$\mathrm{UBF_D}$	0.05	0.17	0.14 ± 0.08	0.01 ± 0.01
$\mathrm{UIMF_D}$	0.01	0.01	0.06 ± 0.08	0.02 ± 0.01

[1] $\mathrm{BW_D}$ = birth weight direct (kg); $\mathrm{Pre\text{-}WG_D}$ = Pre weaning gain direct (kg); $\mathrm{Pre\text{-}WG_M}$ = Pre weaning gain maternal (kg); $\mathrm{WW_D}$ = weaning weight direct (kg); $\mathrm{WW_M}$ = weaning weight maternal (kg); $\mathrm{WW_{PE}}$ = weaning weight permanent environment (kg); $\mathrm{Post\text{-}WG_D}$ = post weaning gain direct (kg); $\mathrm{YW_D}$ = yearling weight direct (kg); $\mathrm{YW_M}$ = yearling weight maternal (kg); $\mathrm{SC_D}$= scrotal circumference direct (cm); $\mathrm{REA_D}$ = rib eye area direct (cm^2); $\mathrm{BF_D}$ = backfat direct (mm); $\mathrm{MARB_D}$ = marbling score direct; $\mathrm{HCW_D}$ = hot carcass weight direct (kg); $\mathrm{UREA_D}$ = ultrasound rib eye area direct (cm^2); $\mathrm{UBF_D}$ = ultrasound backfat direct (mm); $\mathrm{UIMF_D}$ = ultrasound intramuscular fat direct (%).

Table 3.5 Summary of Beef Improvement Federation accuracy values estimated from single trait model for heifer pregnancy (HPG) and multiple trait model with HPG and Pre-weaning gain.

	All Animals				Parents[1]	Non-parents[2]
Model	Mean	Min	Max	SD	Mean	Mean
Univariate	0.057	0.000	0.660	0.044	0.081	0.054
Multiple trait model	0.064	0.000	0.660	0.046	0.083	0.061

[1] Animals that were parents of a female with a heifer pregnancy observation

[2] Animals that were not parents of a female with a heifer pregnancy observation

LITERATURE CITED

Beef Improvement Federation 2011. Guidelines for uniform beef improvement programs. http://www. beefimprovement. org/library/06 guidelines. Pdf. (Accessed August 1, 2016).

Brinks, J.S., M.J. McInerney, and P.J. Chenoweth. 1978. Relationship of age at puberty in heifers to reproductive traits in young bulls. Proc. West. Sect. Am. Soc. Anim. Sci. 29:28-30.

Brown, C.J., Z.B. Johnson, and D.W. Wright. 1990. Pre- and postnatal direct and maternal addaitive genetic influences on preweaning growth traits of beef cattle. Proc. 4th World Congr. Appl. Livest. Prod., Edinburg, Vol. XV: 267-270.

Cammack, K.M., M.G. Thomas, and R.M. Enns. 2009. Review: reproductive traits and their heritabilities in beef cattle. Prof. Anim. Sci. 25: 517-528.

Crews, D.H., and R.M. Enns. 2008a. Models for Genetic Evaluation of Scrotal Circumference in Red Angus. Prof. Anim. Sci. 24: 128-135.

Crews, D.H., and R.A. Kemp. 2001. Genetic parameters for ultrasound and carcass measures of yield and quality among replacement and slaughter beef cattle. J. Anim. Sci. 79: 3008-3020.

Crews, D.H., E.J. Pollak, R.L. Weaber, R.L. Quaas, and R.J. Lipsey. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. J. Anim. Sci. 81: 1427-1433.

Crews, D. H., and R. M. Enns. 2008b. Genetic Improvement of Heifer Pregnancy and Performance in Beef Cattle. http://beefrepro.unl.edu/proceedings/2008ftcollins/12_csu_genetics_crews.pdf. (Accessed August 1, 2016).

Cushman, R.A., M.F. Allan, L.A. Kuehn, W.M. Snelling, A.S. Cupp, and H.C. Freetly. 2009. Evaluation of antral follicle count and ovarian morphology in crossbred beef cows: Investigation of influence of stage of the estrous cycle, age, and birth weight. J. Anim. Sci. 87:1971-1980.

Evans, J.L., B.L. Golden, R.M. Bourdon, and K.L. Long. 1999. Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. J. Anim. Sci. 77: 2621-2628.

Fortes, M. R., W.M. Snelling, A. Reverter, S.H. Nagaraj, S.A. Lehnert, R.J. Hawken, K.L. DeAtley, S.O. Peters, G.A. Silver, G. Rincon, J.F. Medrano, A. Islas-Trejo, and M.G. Thomas. 2012. Gene network analyses of first service conception in Brangus heifers: use of genome and trait associations, hypothalamic-transcriptome information, and transcription factors. J. Anim. Sci. 90: 2894-2906.

Gilmour, A. R., B. Gogel, B. Cullis, R. Thompson, and D. Butler. 2009. ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK.

Golden, B.L., D.J. Garrick, S. Newman, and R.M. Enns. 2000. Economically relevant traits: A framework for the next generation of EPDs. Proc. Beef Improv. Fed. 32nd Ann. Res. Symp. Annu. Meet. 32: 2-13.

Harville, D.A., and R.W. Mee. 1984. A mixed-model procedure for analyzing ordered categorical data. Biometrics: 393-408.

Hetzel, D.J.S., R.L. Quass, G.W. Seifert, K.G. Bean, H.M. Burrow, and W.J. Aspden. 1990. Genetic parameters for growth of tropical beef cattle. Proc. 8th Conf. Australian Association for Animal Breeding and Genetics, Hamilton, NZ, pp. 517-520.

Koots, K.R., J.P. Gibson, C. Smith, and J.W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Beed. Abstr. 62: 309-338.

MacNeil, N.D. and T.B. Mott. 2006. Genetic analysis of gain from birth to weaning, milk production, and udder conformation in Line 1 Hereford cattle. J. Anim. Sci. 84:1639-1645.

Martin, L.C., J.S. Brinks, R.M. Bourdon, and L.V. Cundiff. 1992. Genetic effects on beef heifer pubery and subsequent reproduction. J. Anim. Sci. 70:4006-4017.

Martinez-Velazquez, G., K.E. Gregory, G.L. Bennett, and L.D. Van Vleck. 2003. Genetic relationships between scrotal circumference and female reproductive traits. J. Anim. Sci. 81: 395-401.

McAllister, C.M., S.E. Speidel, D.H. Crews, Jr., and R.M. Enns. 2011. Genetic parameters for intramuscular fat percentage, marbling score, scrotal circumference, and heifer pregnancy in Red Angus cattle. J Anim Sci. 89: 2068-2072.

Melton, B. 1995. Conception to consumption: The economics of genetic improvement. roc. Beef Improv. Fed. 27nd Ann. Res. Symp. Annu. Meet. 27: 40-47.

Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31: 179-204.

Nephawe, K.A., L.V. Cundiff, M.E. Dikeman, J.D. Crouse, and L.D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. J. Anim. Sci. 82: 647-653.

Patterson, D.J., R.C. Perry, G.H. Kiracofe, R.A. Bellows, R.B. Staigmiller, and L.R. Corah. 1992. Management considerations in heifer development and puberty. J. Anim. Sci. 70: 4018-4035.

Perry, R.C., L.R. Corah, R.C. Cochran, J.R. Brethour, K.C. Olson, and J.J. Higgins 1991. Effects of hay quality, breed, and ovarian development on onset of puberty and reproductive performance of beef heifers. J. Prod. Agric. 4:13-18.

Peters, S.O. K. Kizilkaya, D.J. Garrick, R.L. Fernando, E.J. Pollak, R.M. Enns. 2014. Use of robust multivariate linear mixed models for estimation of genetic parameters for carcass traits in beef cattle. J. Anim. Breed. Genet. 131: 504-512.

Peters, S.O., K. Kizikaya, D.J. Garrick, R.L. Fernando, J.M. Reecy, R.L. Weaber, G.A. Silver, and M.G. Thomas. 2013. Heritability and Bayesian genome-wide association study of first service conception and pregnancy in Brangus heifers. J. Anim. Sci. 91: 605-612.

Roberts, A.J., T.W. Geary, E.E. Grings, R.C. Waterman, and M.D. MacNeil. 2009. Reproductive performance of heifers offered ad libitum or restricted access to feed for a one hundred forty-day period after weaning. J. Anim. Sci. 87: 3043-3052.

Speidel, S.E., R.M. Enns, and D.J. Garrick. 2007. Weaning weight inheritance in environments classified by maternal body weight change. J. Anim. Sci. 85:610-617.

Su, H., D.J. Garrick, B.L. Golden, and L. Hyde. 2016. Estimation of Genetic Parameters for Carcass Traits and Their Corresponding Ultrasound Measurements in Crossbred Beef Cattle. Anim. Ind. Rep. http://lib.dr.iastate.edu/ans_air/vol662/iss1/18.

Swierstra, E.E., G.W. Rahnfeld, R.L. Clipief, and J.H. Strain. 1977. Age and weight of puberty of crossbred heifers sired by Charolais, Limousin, and Simmental bulls. Can. J. Anim. Sci. 57: 697-403.

Wiltbank, J.N., C.W. Kasson, and J.E. Ingalls. 1969. Puberty in crossbred and straightbred beef heifers on two levels of feed. J. Anim.Sci. 29: 602-605.

Wiltbank, J.N., K.E. Gregory, L.A. Swiger, J.E. Ingalls, J.A. Rothlisberger, and R.M. Koch. 1966. Effects of herterosis on age and weight at puberty in beef heifers. J. Anim. Sci. 25: 744-751.

Winder, J.A., J.S. Brinks, R.M. Bourdon, and B.L. Golden. 1990. Genetic analysis of absolute growth measurements, relative growth rate and restricted selection indices in red Angus cattle. J. Anim. Sci. 68: 330-336.

CHAPTER IV

GENETIC PARAMETERS FOR PRODUCTION TRAITS AND STAYABILITY IN RED ANGUS CATTLE.

SUMMARY: Stayability (STAY) EPD is a prediction of the probability of a female to remain productive in the breeding herd until she has produced five consecutive calves by age 6. However, this age of measurement introduces an extended period before phenotypic observations are available. One possible solution to overcome the late age of measurement is to examine the relationship between STAY and traits that can be recorded earlier in life. Therefore, the objective of the study was to investigate the genetic relationships between STAY and other typically recorded production traits. The traits that were examined included: birth weight (BW), 205-d pre-weaning again (direct and maternal, Pre-WG_D, Pre-WG_M), 205-d weaning weight (direct and maternal, WW_D, WW_M), 160-d post weaning gain (Post-WG), 365-d yearling weight (direct and maternal, YW_D, YW_M), scrotal circumference (SC), rib eye area (REA), backfat (BF), marbling score (MARB), hot carcass weight (HCW), ultrasound rib eye area (UREA), ultrasound backfat (UBF), ultrasound percent intramuscular fat (UIMF), mature weight (MW), teat score (TS), udder suspension score (US), and BCS. Data included records on 153,376 animals from the Red Angus Association of America. Genetic relationships were determined from (co)variance parameters, estimated using a series of two trait animal models with a REML procedure. In all analyses, the appropriate contemporary groups were formed and included as a fixed effect, as well as, the direct genetic effects as a random variable. Additional fixed effects included: sex for all weight, carcass and ultrasound traits, age of dam for all weight traits, and age of measurement for UREA, UBF, UIMF, REA, BF, MARB, HCW, BCS, TS, US, and MW. Additionally, maternal genetic effects for Pre-WG, WW and YW were also modeled. Permanent environmental effects of the dam were modeled for the traits Pre-WG, and WW. Permanent environment of the individual for traits with repeated records such as MW, BCS, TS, and US were also included. Heritability estimates were 0.56 ± 0.01, 0.23 ± 0.01, 0.10 ± 0.01, 0.27 ± 0.01, 0.10 ± 0.01, 0.24 ± 0.01, 0.33 ± 0.01, 0.06 ± 0.01, 0.49 ± 0.03, 0.26 ± 0.08, 0.24 ± 0.07, 0.30 ± 0.08, 0.26 ± 0.07, 0.38 ± 0.02, 0.40 ± 0.02, 0.39 ± 0.02, 0.71 ± 0.02, 0.70 ± 0.02, 0.57 ± 0.02, 0.27 ± 0.02, and 0.10 for BW, Pre-WG_{D}, Pre-WG_{M}, WW_{D}, WW_{M}, Post-WG, YW_{D}, YW_{M}, SC, REA, BF, MARB, HCW, UREA, UBF, UIMF, TS, US, MW, BCS, and STAY, respectively. Genetic correlations were highest between STAY and WW_{M} (0.54 ± 0.05), YW_{M} (0.36 ± 0.07), BF (0.53 ± 0.20), MARB (0.40 ± 0.20), UREA (0.19 ± 0.07), UBF (0.37 ± 0.07), TS (0.30 ± 0.11), and US (0.23 ± 0.11). Whereas, relationships between STAY and other production traits were minimal.

Key Words: beef cattle, genetic correlation, stayability

INTRODUCTION

Improving the overall female reproductive performance has the ability to greatly improve the economic viability of a cow calf enterprise. Two of the greatest costs in beef cattle production are associated with the feeding of the cow herd, and development of replacement heifers entering the breeding herd. These costs are offset by the ability of females within the herd to produce viable calves each year. The importance can be illustrated using economic models that estimate the economic value of reproductive traits to be 3.24 times more important than that of weight and carcass traits at the cow calf level (Melton, 1995).

Stayability (**STAY**) EPD is a prediction that was developed to indicate the probability of beef females to remain in the herd for a predetermined number of years. Traditionally, STAY EPD was defined as the ability to remain in the herd to a traditional break even age of 6 years, given that she has had a calf at 2 years of age (Snelling et al., 1995). Currently, the Red Angus Association of America (**RAAA**) defines STAY as the ability of a female to have 5 consecutive calves that are born within the same season each year, starting as a two year old . The current RAAA definition is more strict and allows the ability to select for females that better recover and rebreed in successive years (Martinez et al., 2005).

One of the biggest issues faced when making genetic predictions for a trait like STAY is extended period before an observation is available. The age of measurement for STAY is 6 years of age and sires therefore do not start receiving observations on daughters until 8 years of age, greatly expanding the time required before an accurate prediction of stayability can be made. To alleviate these issues, Brigham et al. (2007) investigated using STAY records at younger ages as correlated traits to 6 year old STAY. While this reduced the time required for an observation for a female to 3 years of age, sires are still 5 years of age before progeny receive observations.

Currently there are two main strategies for making genetic predictions on animals prior to phenotypes being recorded. One method is to use genomic predictions. A second solution is to use correlated traits that can help predict future performance for STAY. However, information on the correlations of early-life measures and stayability is limited. Therefore, the objective of this research was to estimate genetic associations between STAY and various production traits.

MATERIALS AND METHODS

Data used in the analysis was obtained from an existing database of the RAAA, so approval by animal care and use committee was not obtained.

Data files for the analyses were formed beginning with animals that were included in the 2014 winter STAY national cattle evaluation. To avoid computational issues associated with estimating heritability from very large data sets, the base group of animals that served as the foundation of the analysis was limited to females with a STAY observation and that were members of a STAY contemporary group of 60 or more animals. To gather phenotypes for other traits the RAAA defined birth work group was used because it groups animals that are from the same ranch or herd. This approach yielded a list of 152,376 animals which all records were used for the analyses.

Production traits used in the analysis included: birth weight (**BW**), 205-d pre-weaning gain **(direct and maternal, Pre-WG$_{D}$, Pre-WG$_{M}$)**, 205-d weaning weight (direct and maternal, **WW$_{D}$, WW$_{M}$**), 160-d post weaning gain (**Post-WG**), 365-d yearling weight (**direct and maternal, YW$_{D}$, YW$_{M}$**), scrotal circumference (**SC**), rib eye area (**REA**), backfat (**BF**), marbling score (**MARB**), hot carcass weight (**HCW**), ultrasound rib eye area (**UREA**), ultrasound backfat (**UBF**), ultrasound percent intramuscular fat (**UIMF**), teat score (**TS**), udder suspension score (**US**), mature weight (**MW**), and body condition score (**BCS**) in Red Angus cattle.

Binary observations for STAY were formed from calving outcomes. In order for a female to receive a successful observation (1), she must have produced calves in 5 successive years with all progeny must be born in the same season (± 3 months of previous years calving month). If a female failed to meet these requirements, then she was given an unsuccessful observation of 0. For the traits Pre-WG, WW, Post-WG, YW, and SC, observations were adjusted to an age constant end point of 205 d, 205 d, 160 d, 365 d, and 365 d, respectively. Observations for MW were adjusted to a constant BCS of 5 based on factors reported by Tennant et al. (2002). Phenotypic records for all traits were removed from the analysis if either the animal’s age at measurement was greater than 5 SD from overall mean, or the phenotypic observation was 5 SD greater than the overall mean.

Contemporary groups **(CG)** for each trait were formed in a similar manner to those used in the national cattle evaluation. Breed codes (**BC**) was defined as an animal that were 87.5 percent Red Angus or greater, or animals that were between 50 and 87.4 percent Red Angus. Animals that contained any Brahman influence were separated into separate BC subcategories as described previously. Formal definitions of all contemporary groups used in the analysis are presented in Table 4.1. For udder traits and BCS, contemporary group was defined as the calf's birth contemporary group when the measurement was taken. Mature weight contemporary group was defined as the calf's weaning contemporary group when the cow weight was taken. If an animal was a member of a CG that exhibited no variation, the CG was converted to unknown. The total number of CG for STAY, BW, Pre-WG, WW, Post-WG, YW, SC, REA, BF, MARB, HCW, UREA, UBF, UIMF, TS, US, MW, and BCS were 462; 3,569; 4,779; 4,776; 4,678; 4,474; 832; 46; 47; 39; 47; 2,105; 2,099; 2,104; 148; 160; 1,597; and 1,264, respectively. Average CG size were 94, 44, 30, 30, 19, 20, 17, 36, 36, 37, 37, 13, 13, 13, 7, 7, 19, and 22 for the traits STAY, BW, Pre-WG, WW, Post-WG, YW, SC, REA, BF, MARB, HCW, UREA, UBF, UIMF, TS, US, MW, and BCS.

Fixed and random effects included in the model for each trait are summarized in Table 4.2. All analyses were performed as a series of two trait animal models using the ASREML 3.0 software package (Gilmour et al., 2009). Due to the binary nature of STAY, observations were converted to an underlying normal distribution using a probit link function which restricts residual variance to 1 (Gianola and Fouley, 1983; Harville and Mee, 1984), alternatively, all other traits were analyzed as continuous outcomes. Across all analyses, the fixed effects of CG and the direct genetic random effects were included in the model. Sex of individual at measurement was fit for all weight, carcass, and ultrasound traits. Sex classifications for birth weight were defined as bull and heifer, whereas, all other traits sex was defined as bull, heifer, and steer. Age of dam **(AOD)** was included as a categorical, fixed effect in all weight traits (BW, Pre-WG, WW, Post-WG, and YW) to model age-related differences in maternal environments provided by dams (Rumph and Van Vleck, 2004). Classes for AOD were defined in accordance with BIF guidelines of 2, 3, 4, 5-9, 10, and 11+ years of age (BIF, 2011). The linear effect of age of measurement was included for REA, BF, MARB, HCW, UREA, UBF, UIMF, TS, US, MW, and BCS. Maternal genetic effects were modeled for Pre-WG, WW, and YW. The permanent environmental effects of the dam were included for WW and Pre-WG, whereas, the permanent environmental effects of the individual were included for TS, US, MW, and BCS as these traits are repeatedly recorded on the same individual.

A three generation pedigree was formed for each two trait analysis using animals with observations for STAY and the production traits. Pedigree information for all analyses are summarized in Table 4.3. Within each analyses a total of 100,769 animals were included in every analysis because they were sires/dams or grand sires/grand dams of animals with a STAY observation that was used in every analyses. Deviations from this number represents the amount of animals added to the evaluation for the other production traits.

Since carcass traits and SC phenotypes could not be recorded on the same individual with a STAY observation, the residual covariance of these traits with STAY were restricted to zero. Due to limited number of animals with both phenotypes recorded, the residual covariance for STAY with udder traits and BCS were also constrained to be zero.

RESULTS AND DISCUSSION

Table 4.4 presents summary statistics for all traits. The overall success rate for STAY was 0.28, indicating that only a small portion females entering production were able to remain in the herd and produce five consecutive calves. This estimate of success (0.28) was consistent with the range of estimates, for various breeds, published in literature (Martinez et al., 2005; Van Melis et al., 2010). In beef cattle, the desire to maintain a calving interval of 365 d is common, and is achieved by rebreeding females within 80 days following parturition (Short et al., 1990). This restricted time may cause the low success rate of females that might be able to produce five successive calves.

Heritability estimates from the current study are presented in Table 4.5. The heritability estimate for STAY was 0.10 ± 0.01 (reported with the largest standard error) and was calculated by averaging variance estimates across all two trait analyses. Historically, heritability estimates for STAY varied from population to population, but additional variability in heritability estimate result from the differences in the definition of the trait. In Hereford cattle, Martinez et al. (2005) achieved a heritability estimate of 0.30 ± 0.14, for the ability of a female to remain in the herd until six years of age, and a heritability estimate of 0.35 ± 0.13 for the ability of a female to have 5 consecutive calves. Comparing these parameters to the heritability estimates by Snelling et al. (1995) that ranged from 0.11 to 0.23 for the ability of a female to have 5 consecutive calves on two farms using several analysis techniques, the variability of estimates is evident. The current estimate was lower than the results presented in previous research. However, the low heritability estimate for STAY from this study were not insensible given the generally low estimates commonly associated with reproductive traits (Cammack et al., 2009).

For the production traits in the analysis, heritability estimates were moderate to high in magnitude. Estimates for BW (0.56 ± 0.01), SC (0.49 ± 0.03), TS (0.71 ± 0.02), US (0.70 ± 0.02), and MW (0.57 ± 0.02), were high in magnitude. The current estimate for BW was higher than the weighted average estimate of 0.31 ± 0.003 reported by Koots et al. (1994a), however, the estimate was similar to the heritability (0.47) used in the current RAAA National Cattle Evaluation (BIF, 2011). Heritability estimates in the current analysis for udder traits were higher than those reported by Bradford et al. (2015). This might be a result of the limited amount of records used in the analysis. Out of the 2,432 records used in this study, only 28 percent of females had multiple observations, and 79 percent of the data was within 1 S.D. of the mean. This may explain why the permanent environmental effects for these traits were 0.00 ± 0.00 and why heritability is high. Heritability estimate for MW was within the range of 0.44 to 0.66 of previously published estimates (Nephawe et al., 2004; Williams et al., 2009). Permanent environment effects for MW accounted for 0.16 ± 0.02 of the total variance and the repeatability was estimated at 0.73 ± 0.01 in the current analysis. This estimate was consistent with previous estimates of 0.15 and 0.72 for permanent environment and repeatability (Nephawe et al., 2004).

Other production traits used in this analysis had moderate heritability estimates. Heritability estimates for the growth traits in the current study were lower than those reported by Winder et al. (1990), however, they were more consistent with the recent estimates of 0.26 ± 0.03, 0.14 ± 0.02, and 0.19 ± 0.01, for WW_D, WW_M, and WW permanent environment in Red Angus cattle (Speidel et al., 2007). Maternal heritability for Pre-WG and WW in the current analysis was 0.10 ± 0.01 and permanent environmental effects were 0.13 ± 0.00. Furthermore, the estimated genetic correlation between direct and maternal effects of Pre-WG were -0.32 ± 0.03 and -0.30 ± 0.03 for WW. Heritability estimate for Post-WG was similar to the current estimate (0.22) used in the Red Angus genetic evaluation (BIF, 2011). Direct and maternal heritability for YW are consistent with the weighted average of direct heritability (0.33 ± 0.004) and the unweighted average of 0.11 ± 0.06 for maternal heritability (Koots et al., 1994a). Heritability estimates for carcass and ultrasound traits were lower than those reported by Crews et al. (2003) and Su et al. (2016), using Simmental cattle. Carcass traits heritability were also lower than published estimates by Nephawe et al. (2004). In the current analysis, heritability estimates for BCS were higher than those reported by Arango et al. (2002) and Nephawe et al. (2004) whose estimates were consistent at 0.16 ± 0.02 .

Table 4.6 presents genetic and residual covariance and correlation estimates between STAY and the other production traits. Maternal genetic components of Pre-WG, WW and YW were strongly correlated with STAY. Culbertson (2014) examined the relationship between milk production and STAY in Red Angus cattle, and determined the relationship was non-linear. Conversely, Rogers et al. (2004) found that as milk EPD increased, the risk ratio of a cow being culled also increased. This might be due to the environment the cows in that study produced in where they may over produce given environmental resources because of inadequate accumulation of fat reserves. However, in dairy cattle, as milk production increases the relative culling rate decreased (Vukasinovic et al., 2001). This can be attributed to that the highest producing cows are the most beneficial in a dairy herd and nutrition is generally not a problem within these herds. Maternal traits again offer little advantage to more traditional methods of measuring STAY. This is due to the fact that in order for a sire to gain added accuracy for maternal traits his daughters must produce calves to model genetic differences for maternal effects.

Carcass and ultrasound traits showed varying degrees of genetic relationships with STAY. The traits REA, HCW, and UIMF all had S.E. that encompassed 0. The genetic correlation between STAY and MARB was moderate and positive, whereas, the correlation with UIMF was near 0. This may be due to the limited marbling score phenotypes used in the analysis or to the imperfect genetic relationship between MARB and UIMF. Generally, correlations between MARB and UIMF are high (> 0.7) so the conflicting results were unexpected (Crews et al., 2003; McAllister et al., 2011). Correlations between STAY and both BF and UBF were positive and moderate to high in magnitude. These results suggest that cattle with a genetic predisposition to deposit a higher amount of subcutaneous fat also have a higher chance to rebreed and produce 5 consecutive calves. Subcutaneous fat phenotypes offer an advantage as an indicator trait for STAY because they can be collected at younger ages on both males and females, especially via ultrasound backfat measures. These are generally collected at one year of age and before a female enters the breeding herd.

Genetic relationships were negligible between STAY and BW, Pre-WG_D, WW_D, Post-WG, YW_D, SC, REA, HCW, UIMF, MW, and BCS. The additive genetic correlations of weight traits (BW, Pre-WG, WW, Post-WG, and YW) with STAY were negative and weak in magnitude, whereas the genetic correlation with STAY and MW was positive. In Chanchim beef cattle, Buzanskas et al. (2010) reported weak genetic correlation between 420-d weight and STAY. Conversely, Eler et al. (2014) estimated a moderate positive genetic correlation between Post-WG and STAY. Alternatively, in the current analysis, a weak negative genetic association between STAY and Post-WG was estimated. The different results may be attributed to the fact that, in previous research, results were drawn on *Bos Indicus* females that generally experience puberty at later age. Rogers et al. (2004), using a survival regression analysis of *Bos Taurus* composite cattle, showed that BW and 365 d BW did not significantly ($P > 0.1$) affect the length of the productive life in a cross bred population.

In the current study, mature cow traits were not strongly correlated with STAY. Beckman et al. (2006) also estimated genetic correlations between STAY and BCS at ages 2, 3, and 4 years and reported they were not different from 0 in Red Angus cattle. Even though BCS is commonly promoted as a tool to diagnose the nutritional status of cattle in order to prepare them for breeding, the discrete nature and distribution of both BCS and STAY present challenges for determining the genetic relationship between the traits. Additionally, taking BCS are used to adjust feeding strategies so that all animals are in adequate condition at the beginning of the breeding season, and if this goal is accomplished may explain why there is no relationship between the traits.

Moderate positive correlations were estimated between udder traits (TS and US) and STAY. The highest achievable score of 9 would be considered very tight for suspension and very small for teats (BIF, 2011) and this would be considered to be an ideal score (Bradford et al., 2015). A positive correlation between the traits would signify that cows with less pendulous udders are more likely to remain in the herd, because females with larger and more pendulous udders can have a higher chance of issues with calves being able to nurse (Ventorp and Michanek, 1992). However, in terms of decreasing the age of measurement, udder traits offer little advantage over using calving data at younger ages, because observations are taken at the birth of a calf (BIF, 2011).

Residual correlations between the production traits and STAY were low in magnitude. Residual correlations between STAY and growth traits trended slightly negative but were close to 0. Additionally, residual correlations between STAY and ultrasound traits could not be identified as different from 0. Mature weight had a positive correlation with STAY. This correlation would indicate that an environment that promotes a higher MW would also increase the probability of a successful STAY observation. Given in this analysis that all MW observations were pre-adjusted to a consistent BCS of 5, the environmental correlation signifies that cows with a larger weight have a higher probability of STAY success. All other traits in the analyses had residual correlations that were fixed at 0 due to either the inability for an animal to express both phenotypes or due to a lack of data and convergence when the parameter was not 0.

Average BIF accuracy values for STAY in both a single trait and multiple trait model that included UBF are summarized in Table 4.7. For all groups of animals accuracy values increased for the multiple trait model when compared to the single trait model. For all animals, average accuracy increased 31%, for parents of an animal with a STAY observation average accuracy increased 27%, and non-parents average accuracy increased 34%.

Overall, genetic relationships between STAY and other production traits were low to moderate in magnitude. The trait that offers the best opportunity as an indicator trait for STAY is UBF. The inclusion of this trait into STAY genetic evaluation will add information from both males and females at approximately a year of age. This is a full 2 years before observations are taken for even multiple trait STAY (Brigham et al., 2007). This will allow increasing STAY accuracy of prediction for young sires by using both phenotypes to make STAY genetic predictions.

Table 4.1 Formal definition of all contemporary groups used for stayability and production trait evaluation in Red Angus cattle.

Contemporary Group	Definition
Stayability	Breeder of the individual, breeder of each calf, year of birth of individual
Birth (BCG)	Birth work group[1], birth management group[2], breed code[3], season[1] and year of birth
Weaning (WCG)	Weaning work group[1], weaning management code[2], breed code[3], birth work group[1], weaning date
Yearling (YCG)	WCG, yearling work group[1], yearling management code[2]
Ultrasound	YCG, ultrasound management code[1], ultrasound date
Carcass	Owner, harvest date

[1] Parameters defined by the Red Angus Association of America

[2] Producer submitted information

[3] Defined as greater than 87.5 percent Red Angus, 50-87.4 percent Red Angus, greater than 87.5 percent Red Angus with Brahman influence, 50-87.4 percent Red Angus with Brahman influence.

Table 4.2 Description of models used for STAY and production traits in Red Angus Cattle.

	Fixed Effects				Random Effects		
Trait[1]	Contemporary Group	Sex	Age	AOD[2]	Additive Genetic Effects	Maternal Genetic Effects	Permanent Environment Effects
STAY	STAY	No	No	No	Yes	No	No
BWT	Birth	Yes[3]	No	Yes	Yes	No	No
Pre-WG	Weaning	Yes[4]	No	Yes	Yes	Yes	Yes
WW	Weaning	Yes[4]	No	Yes	Yes	Yes	Yes
Post-WG	Yearling	Yes[4]	No	Yes	Yes	No	No
YW	Yearling	Yes[4]	No	Yes	Yes	Yes	Yes
SC	Yearling	No	No	No	Yes	No	No
REA	Carcass	Yes[4]	Yes	No	Yes	No	No
BF	Carcass	Yes[4]	Yes	No	Yes	No	No
MARB	Carcass	Yes[4]	Yes	No	Yes	No	No
HCW	Carcass	Yes[4]	Yes	No	Yes	No	No
UREA	Ultrasound	Yes[4]	Yes	No	Yes	No	No
UBF	Ultrasound	Yes[4]	Yes	No	Yes	No	No
UIMF	Ultrasound	Yes[4]	Yes	No	Yes	No	No
TS	Calf Birth	No	Yes	No	Yes	No	Yes
US	Calf Birth	No	Yes	No	Yes	No	Yes
MW	Calf Weaning	No	Yes	No	Yes	No	Yes
BCS	Calf Birth	No	Yes	No	Yes	No	Yes

[1] STAY = stayability; BWT= birth weight; Pre-WG = Pre-Weaning Gain; WW = weaning weight; Post-WG = post weaning gain; YW = yearling weight; SC_D= scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

[2] defined as 2, 3, 4, 5 to 9, 10, and 11+ years of age

[3] defined as bull and heifer

[4] defined as bull, heifer, and steer

Table 4.3 Description of pedigree size for all two trait analyses with stayability in Red Angus cattle.

Trait	Total pedigree size	Number of unique sires	Number of unique dams
Birth weight	251,696	14,741	104,226
Pre-weaning gain	235,885	14,472	99,878
Weaning Weight	235,877	14,472	99,874
Post weaning gain	186,017	13,442	86,313
Yearling Weight	186,017	13,433	86,313
Scrotal circumference	120,611	11,764	65,710
Rib eye area	102,714	11,456	59,350
Backfat	120,760	11,457	59,361
Marbling	102,439	11,455	59,243
Hot carcass weight	102,764	11,457	59,362
Ultrasound rib eye area	126,816	11,861	67,436
Ultrasound backfat	126,855	11,861	67,451
Ultrasound intramuscular fat	126,744	11,861	67,420
Teat score	101,721	11,487	59,172
Udder score	101,721	11,487	59,172
Mature weight	103,934	11,528	60,186
BCS	103,934	11,528	60,186

Table 4.4 Summary statistics for phenotypic measures in Red Angus cattle used for the analysis.

Trait	N	Mean	S.D.	Minimum	Maximum
Stayability (%)	43,328	0.28	0.45	0.00	1.00
Birth weight (kg)	159,204	36.14	5.31	11.34	62.14
Pre-weaning gain (kg)	144,198	219.27	38.90	52.62	448.15
Weaning Weight (kg)	144,198	255.36	41.09	76.66	454.95
Post weaning gain (kg)	92,842	169.06	64.11	0.91	465.84
Yearling Weight (kg)	90,563	430.94	86.39	156.49	746.61
Scrotal circumference (cm)	15,185	34.99	6.67	22.03	47.15
Rib eye area (cm^2)	1,676	82.26	9.42	35.48	119.35
Backfat (mm)	1,717	14.22	4.32	0.51	34.80
Marbling (score)	1,459	5.51	1.09	0.30	9.60
Hot carcass weight (kg)	1,721	371.77	38.15	239.04	498.04
Ultrasound rib eye area(cm^2)	29,406	70.97	12.84	24.52	122.58
Ultrasound backfat (mm)	29,477	5.84	2.29	1.02	16.76
Ultrasound intramuscular fat (%)	29,269	3.64	1.01	0.51	8.69
Teat score	2,483	5.38	2.03	1.00	9.00
Udder score	2,483	4.94	2.02	1.00	9.00
Mature weight (kg)	30,599	537.49	90.21	210.92	893.58
BCS	30,646	5.15	0.99	1.00	9.00

Table 4.5 Estimates of parameter variance, phenotypic variance, heritability (h^2 ± S.E.), and permanent environment effects (c^2 ± S.E.) for production traits and stayability in Red Angus cattle.

Trait	Parameter Variance	Phenotypic Variance	h^2	c^2
STAY$_D$	0.11	1.11	0.10 ± 0.01[2]	
BWT$_D$	24.62	43.71	0.56 ± 0.01	
Pre-WG$_D$	342.41	1408.54	0.24 ± 0.01	
Pre-WG$_M$	146.39	1408.54	0.10 ± 0.01	
Pre-WG$_{PE}$	189.66	1408.54		0.13 ± 0.00
WW$_D$	422.33	1564.44	0.27 ± 0.01	
WW$_M$	158.06	1564.44	0.10 ± 0.01	
WW$_{PE}$	202.91	1564.44		0.13 ± 0.00
Post-WG$_D$	408.75	4414.32	0.24 ± 0.01	
YW$_D$	1097.07	3234.75	0.34 ± 0.01	
YW$_M$	212.46	3234.75	0.07 ± 0.01	
SC$_D$	2.64	5.45	0.49 ± 0.03	
REA$_D$	2.55	10.00	0.26 ± 0.08	
BF$_D$	0.15	0.64	0.24 ± 0.07	
MARB$_D$	0.24	0.80	0.30 ± 0.08	
HCW$_D$	496.18	1941.06	0.26 ± 0.07	
UREA$_D$	3.02	7.86	0.38 ± 0.02	
UBF$_D$	0.04	0.10	0.40 ± 0.02	
UIMF$_D$	0.22	0.56	0.39 ± 0.02	
TS$_D$	2.07	2.93	0.71 ± 0.02	
TS$_{PE}$	0.00	2.93		0.00 ± 0.00
US$_D$	2.16	3.09	0.70 ± 0.02	
US$_{PE}$	0.00	3.09		0.00 ± 0.00
MW$_D$	3606.96	6375.24	0.57 ± 0.02	
MW$_{PE}$	1017.38	6375.24		0.16 ± 0.02
BCS$_D$	0.14	0.54	0.27 ± 0.02	
BCS$_{PE}$	0.10	0.54		0.18 ± 0.01

[1] STAY = stayability; BWT= birth weight; Pre-WG = pre weaning gain; WW = weaning weight; Post-WG = post weaning gain; YW = yearling weight; SC= scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

[2] Reported as the average of heritability estimates and largest S.E. of all two-trait analyses between Stayability and production traits.

Table 4.6 Estimates of genetic covariance, residual covariance, genetic correlation, and residual correlation between stayability (STAY) and production traits in Red Angus cattle.

Trait	Genetic covariance with STAY	Residual covariance with STAY	Genetic Correlation With STAY	Residual Correlation With STAY
BW$_D$	-0.04	-0.09	-0.03 ± 0.04	-0.03 ± 0.01
Pre-WG$_D$	0.01	-0.33	0.00 ±0.06	-0.02 ± 0.01
Pre-WG$_M$	1.54	-0.33	0.54 ± 0.05	-0.02 ± 0.01
WW$_D$	-0.13	-0.44	-0.03 ± 0.06	-0.02 ± 0.01
WW$_M$	1.64	-0.44	0.55 ± 0.05	-0.02 ± 0.01
Post-WG$_D$	-0.40	-0.19	-0.09 ± 0.05	-0.01 ± 0.01
YW$_D$	-0.55	-0.61	-0.07 ± 0.06	-0.06 ± 0.03
YW$_M$	1.20	-0.61	0.36 ± 0.07	-0.06 ± 0.03
SC$_D$	0.03	-	0.04 ± 0.08	-
REA$_D$	0.01	-	0.01 ± 0.21	-
BF$_D$	0.34	-	0.53 ± 0.20	-
MARB$_D$	0.06	-	0.40 ± 0.20	-
HCW$_D$	0.67	-	0.14 ± 0.21	-
UREA$_D$	0.27	-	0.19 ± 0.07	0.01 ± 0.02
UBF$_D$	0.13	-	0.37 ± 0.07	0.01 ± 0.02
UIMF$_D$	0.00	-	-0.01 ± 0.07	0.01 ± 0.02
TS$_D$	0.14	-	0.30 ± 0.11	-
US$_D$	0.11	-	0.23 ± 0.11	-
MW$_D$	0.17	1.91	0.01 ± 0.06	0.07 ± 0.02
BCS$_D$	0.01	-	0.05 ± 0.07	-

[1] STAY = stayability; BW= birth weight; Pre-WG = pre-weaning gain; WW = weaning weight; Post-WG = post weaning gain; YW = yearling weight; SC= scrotal circumference; REA = rib eye area; BF = backfat; MARB = marbling score; HCW = hot carcass weight; UREA = ultrasound rib eye area; UBF = ultrasound backfat; UIMF = ultrasound intramuscular fat; TS = teat score; US = udder suspension score; MW = mature weight; BCS = body condition score.

Table 4.7 Summary of Beef Improvement Federation accuracy values estimated from single trait model for stayability (STAY) and multiple trait model with STAY and ultrasound backfat.

	All Animals				Parents[1]	Non-parents[2]
Model	Mean	Min	Max	SD	Mean	Mean
Univariate	0.058	0.000	0.620	0.044	0.073	0.053
Multiple trait model	0.076	0.000	0.660	0.053	0.093	0.071

[1] Animals that were parents of a female with a stayability observation

[2] Animals that were not parents of a female with a stayability observation

LITERATURE CITED

Arango, J.A., L.V. Cundiff, and L.D. Van Vleck. 2002. Genetic parameters for weight, weight adjusted for body condition score, height, and body condition score in beef cows. J. Anim. Sci. 80: 3112-3122.

Beckman, D.W., S.E. Speidel, B.W. Brigham, D.J. Garrick, and R.M. Enns. 2006. Genetic parameters for stayability and body condition score in beef females. Proc. West. Sect. Am. Soc. Anim. Sci. 57:93.

Beef Improvement Federation 2011. Guidelines for uniform beef improvement programs. http://www. beefimprovement. org/library/06 guidelines. Pdf. (Accessed August 1, 2016).

Bradford, H.L., D.W. Moser, J. Minick Bormann, and R.L. Weaber. 2015. Estimation of genetic parameters for udder traits in Hereford cattle. J. Anim. Sci. 93: 2663-2668.

Brigham, B.W., S.E. Speidel, R.M. Enns, and D.J. Garrick. 2007. Stayability to alternate ages. Proc. Am. Soc. Anim. Sci., West. Sect. 58: 27–30.

Buzanskas, M.E., D. A. Grossi, F. Baldi, D. Barrozo, L. O. C. Silva, and R. A. A. Torres. 2010. Genetic associations between stayability and reproductive and growth traits in Canchim beef cattle. Livest. Prod. Sci. 132: 107-112.

Cammack, K.M., M.G. Thomas, and R.M. Enns. 2009. Review: reproductive traits and their heritabilities in beef cattle. Prof. Anim. Sci. 25: 517-528.

Crews, D.H., E.J. Pollak, R.L. Weaber, R.L. Quaas, and R.J. Lipsey. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. J. Anim. Sci. 81: 1427-1433.

Culbertson, M. M. 2014. Effects of beef cow milk production levels on longevity and stayability. MS Thesis. Colorado State University, Fort Collins.

Eler, J.P., A.B. Bignardi, J.B.S. Ferraz, and M.L. Santana. 2014. Genetic relationships among traits related to reproduction and growth of Nelore females. Theriogenology 82: 708-714.

Gianola, D., and J. L. Fouley. 1983. Sire evaluation for ordered categorical data with a threshold model. Genet. Sel. Evol. 15: 201–224.

Gilmour, A.R., B. Gogel, B. Cullis, R. Thompson, and D. Butler. 2009. ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK.

Harville, D.A., and R.W. Mee. 1984. A mixed-model procedure for analyzing ordered categorical data. Biometrics: 393-408.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62: 309-338.

Martinez, G.E., R.M. Koch, L.V. Cundiff, K.E. Gregory, S.D. Kachman, and L.D. Van Vleck. 2005. Genetic parameters for stayability, stayability at calving, and stayability at weaning to specified ages for Hereford cows. J. Anim. Sci. 83: 2033-2042.

McAllister, C.M., S.E. Speidel, D.H. Crews, Jr., and R.M. Enns. 2011. Genetic parameters for intramuscular fat percentage, marbling score, scrotal circumference, and heifer pregnancy in Red Angus cattle. J. Anim. Sci. 89: 2068-2072.

Melton, B. 1995. Conception to consumption: The economics of genetic improvement. Proc. Beef Improvement Federation 27th Research Symposium and Annual Meeting. Sheridan, WY. 27: 40-71

Nephawe, K.A., L.V. Cundiff, M.E. Dikeman, J.D. Crouse, and L.D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. J. Anim. Sci. 82: 647-653.

Rogers, P.L., C.T. Gaskins, K.A. Johnson, and M.D. MacNeil. 2004. Evaluating longevity of composite beef females using survival analysis techniques. J. Anim. Sci. 82: 860-866.

Rumph, J.M., and L.D. Van Vleck. 2004. Age-of-dam adjustment factors for birth and weaning weight records of beef cattle: a review. Genet. Mol. Res. 3: 1.

Short, R.E., R.A. Bellows, R.B. Staigmiller, J.G. Berardinelli, and E.E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68: 799-816.

Snelling, W.M., B.L. Golden, and R.M. Bourdon. 1995. Within-herd genetic analyses of stayability of beef females. J. Anim. Sci. 73: 993-1001.

Speidel, S.E., R.M. Enns, and D.J. Garrick. 2007. Weaning weight inheritance in environments classified by maternal body weight change. J. Anim. Sci. 85: 610-617.

Su, H., D.J. Garrick, B.L. Golden, and L. Hyde. 2016. Estimation of Genetic Parameters for Carcass Traits and Their Corresponding Ultrasound Measurements in Crossbred Beef Cattle. Anim. Indus. Rep. http://lib.dr.iastate.edu/ans_air/vol662/iss1/18.

Tennant, C.J., J.C. Spitzer, W.C. Bridges, and J.H. Hampton. 2002. Weight necessary to change body condition scores in Angus cows. J. Anim. Sci. 80: 2031-2035.

Van Melis, M.H., J.P. Eler, H.N. Oilvira, G.J.M. Rosa, J.A.V. Silva, J.B.S. Ferraz, and E. Pereira. 2010. Additive genetic relationships between scrotal circumference, heifer pregnancy, and stayability in Nellore cattle. J. Anim. Sci. 88: 3809-3813.

Ventorp, M., and P. Michanek. 1992. The importance of udder and teat conformation for teat seeking by the newborn calf. J. Dairy Sci. 75: 262-268.

Vukasinovic, N., J. Moll, and L. Casanova. 2001. Implementation of a routine genetic evaluation for longevity based on survival analysis techniques in dairy cattle populations in Switzerland. J. Dairy Sci. 84: 2073-2080.

Williams, J.L., D.J. Garrick, and S.E. Speidel. 2009. Reducing bias in maintenance energy expected progeny difference by accounting for selection on weaning and yearling weights. J. Anim. Sci. 87: 1628-1637.

Winder, J.A., J.S. Brinks, R.M. Bourdon, and B.L. Golden. 1990. Genetic analysis of absolute growth measurements, relative growth rate and restricted selection indices in red Angus cattle. J. Anim. Sci. 68: 330-336.