CORRELATIONS BETWEEN PUREBRED AND CROSSBRED BODY WEIGHTS IN MULTI-BREED LIMOUSIN WITH ANGUS POPULATIONS

by

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(Under the direction of J. Keith Bertrand)

ABSTRACT

Selection and combination of different breeds of animals is a commonly practiced method of improving breeding efficiency. The majority of animals produced in the commercial sector of the beef industry are crossbred animals. However, selection in the beef industry typically uses genetic values predicted from purebred populations or from multi-breed populations using models that assume genetic correlations between purebred and crossbred animals to be 1.0. If correlations between crossbred and purebred animals are less than 1.0, selection may not be as efficient as expected. Correlations between purebred and their F_1 crosses can be calculated using a multiple trait model. If these correlations are found to be below the expected 1.0, other methods of evaluation should be considered. Joint evaluation of crossbred and purebred beef cattle using the crossbred model may aid in improving genetic selection.

INDEX WORDS: Beef cattle, correlations, heritabilities, weight traits, Limousin, Angus, Crossbred models

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DEDICATION

To: My Family.

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CHAPTER 1

INTRODUCTION

Crossbreeding beef cattle is a common method used by producers to increase efficiency of selection. Selection is based on three methods: 1. selection based on performance of purebred cattle; called pure line selection (PLS), 2. selection based on performance of crossbred cattle only; referred to as crossbred selection (CS), and 3. selection based on combined crossbred and purebred information; referred to as combined crossbred and purebred selection (CCPS). The first two methods are based on the assumption that the correlation between purebred and crossbred animals (r_{pc}) is unity or zero.

Previous studies have shown that r_{pc} for swine and poultry is not 1.0 for several traits. If r_{pc} for beef cattle is below 1.0, may be a more efficient method of selection when compared to PLS and CS. Current multi-breed evaluations treat purebred and crossbred performance as a single trait, under the assumption of r_{pc}=1.0. If correlations are below 1.0, purebred and crossbred performance should be considered two separate traits for evaluation.

The purpose of this study was to use the multiple trait (purebred and crossbred weights are different traits) approach to estimate genetic parameters for purebred and crossbred performance in beef cattle to verify efficiency of current models used in multi-breed selection.

CHAPTER 2

LITERATURE REVIEW

Introduction

In animal breeding programs, it is important to maximize the rate of genetic improvement for economically important traits. Animals are selected based on the progeny they produce and performance of those progeny and their relatives. Animals with the highest expected genetic merit are kept as parents for later generations and those who have lower performance are not kept for mating. This genetic merit is not observed but is inferred from available data. The merit may be linear or nonlinear combinations of genetic values for economically important traits (Gianola, 2000). Statistical methods are often used in animal breeding to provide selection methods for mating in order to reach optimum genetic potential. Issues to consider in statistical approaches are: 1. Assessing if the traits of interest have genetic basis, 2. Developing and using methods which are accurate to infer merit from data, and 3. Designing appropriate mating plans. Animal breeders use data to formulate and validate mathematical models with an aim to develop methods of selection and mating of individuals to optimize overall performance.

Traditional Animal Breeding

In animal breeding programs, the main goal is to improve the efficiency of selecting and mating economically productive and efficient livestock. Improvements in livestock production due to management and selection practices have greatly influenced animal breeding. These improvements are largely due to an increased understanding of quantitative genetics in the animal breeding field. Several methods are utilized by individual breeders and larger companies to improve efficiency of selection and new, more efficient methods for improvement are continuously being sought in the industry. Continued improvement in quantitative genetic models and techniques are important for to provide tools that will increase the accuracy of selection, leading to increases in production at decreased cost.

In the livestock industry, genetic improvement programs can be used to maximize the rate of increase of economically important traits which are controlled by an animal's genetic composition (Gianola, 2000). Most economically important traits, such as meat quality, growth rate, and milk production are polygenic traits. Polygenic traits are those which are influenced by several genes, and polygenic genes are normally expressed in a quantitative manner where phenotypes show continuous numerical expression. Since the market typically requires breeders to select for multiple polygenic traits, simultaneous selection for these traits is necessary and can be complex (Bourdon, 2000).

The basic model for quantitative traits is as follows:

$$P=\mu + G + E.$$

With P being the phenotypic value or performance of an individual animal for a trait; μ is the population mean or average phenotypic value for all animals in a population for a trait; E is environmental effect on the individual's performance for a trait, and G is the genotypic value of the individual for the trait. The genotypic value is the overall effect of an individual's genes on a trait.

In making selections, breeders consider an animal's breeding value (BV) for the trait in question. The breeding value represents that part of the genotypic value that a parent can pass to its offspring through its gametes, thus the breeding value is the value of an individual as a genetic parent (Bourdon, 2000). A breeding value is the sum of additive effects and epistasis for a particular trait (Falconer, 1996). Breeding values for an animal are easily calculated through phenotypic expression (Bourdon, 2000).

Sires and dams pass half their genes to their offspring. On average, a parent passes half its breeding value to its offspring. The expectation of what is inherited from the parent is termed a transmitting ability, so a transmitting ability is half of the parent's breeding value. The differences between progeny performance can be predicted from the data, and this predicted value is called an expected progeny difference (EPD). EPD are predictions of transmitting abilities and are often used to make genetic comparisons among animals (Bourdon, 2000). EPD can be useful in selecting bulls for breeding. In order to select bulls for traits included in crossbreeding systems, EPD should be considered on a within and across-breed basis for effective bull selection. This will minimize large fluctuations in performance and production across generations (Greiner, 2009).

Crossbreeding in Beef Cattle

In beef production, two methods of selection for mating are used to increase genetic gain and improve efficiency: selection within breeds and selection among and the combination of breeds (Long, 1980). The second method, selection among and the combination of breeds, also known as crossbreeding, is a commonly used and widely accepted method among producers for improvement of efficiency of selection (Brandt, 2010).

Crossbreeding is frequently used among beef producers for commercial production to improve production efficiency (Lamb[1]and Tess, 1989). The majority of the beef in the United States is produced from crossbred cattle. A crossbred animal is a result of breeding a sire and dam that are different biological breeds. The sire and dam may be different pure breeds or they may be crossbreds as well (Elzo and Wakman, 1998). Most commercial beef cattle are comprised of a number of breeds which are often unknown (Toosi, 2009). Crossbreeding is widely used because of its advantages and potential for improving production, with the goal being to combine the advantages of crossbreeding to produce the most profitable calf (Greiner, 2009).

One advantage of crossbreeding is the improvement of traits that are difficult to measure (Daley, 2007), such as, feed efficiency and meat tenderness (Donoghue, 2009). There has been a significant increase in the number of traits included in the breeding objective (Gilmour, 2009). Many breeders crossbreed in order to benefit from breed complementarity. Breed complementarity is the overall improvement in the performance of offspring that are crossbred from breeds with different, but complementary genetic makeup and biological types (Bourdon, 2000). Crossbreeding can be done between breeds which meet some, but not all, market requirements, enabling the producer to combine favorable attributes of breeds that are genetically different but have complementary qualities (Zotto, 2009). This allows desired traits from different breeds to be combined to meet market requirements (Brandt, 2010). Each breed in the cross may contribute one or more desired traits that will be realized in the offspring; for example, one breed may be superior in growth traits while another excels in carcass traits; if these breeds are crossed, offspring are expected to excel in both growth traits and carcass traits (Brandt, 2010). For this reason when combining breeds, it is important to recognize the differences and strengths and weaknesses between breeds. Recognizing these differences will allow the breeder to evaluate which breeds are suitable for crossbreeding as combinations, and to assess which of the breeds should be used as paternal and maternal breeds (Brandt, 2010). Since it is impossible to find one breed which is superior in all traits, crossbreeding is often used to create composite offspring which are superior to their parents (Greiner, 2009).

Another benefit to crossbreeding is the influence of heterosis on the performance of crossbred animals (Klei and Quaas, 1995). Heterosis is a difference in crossbred performance from the parental average due to genetic effects occurring in crosses (Bourdon, 2000) and is observed as the deviation of the performance of crossbred progeny from the weighted average of the parental breeds (Klei and Quaas, 1995). Heterosis is caused by the presence of particular allele combinations (Bourdon, 2000). Heterosis will have an effect on the direct performance of crossbred progeny and also the maternal performance of crossbred dams. The interactions of alleles inherited from different breeds cause heterosis. These interactions include dominance, interaction of individual alleles within a locus, or epistasis, interactions between alleles at different loci (Klei and Quaas, 1995), though it has been proven that heterosis is primarily due to dominance (Gregory and Cundiff, 1991). Crossbreeding systems are used to provide and maintain heterosis (Gregory, 1992). Heterosis may occur in different degrees for different traits (Bourdon, 2000) and influences the direct performance of a crossbred animal and the maternal performance of crossbred dams (Klei and Quaas, 1995). The amount of heterosis observed for a certain trait is negatively correlated to the heritability of the trait (Greiner, 2009). When heterosis is capitalized, traits that are lowly heritable, and thus hard to improve genetically, can be more easily and directly improved upon (Gregory, 1992). This allows for improvement in traits, such as fertility, which are lowly heritable. Traits that are moderately heritable, such as growth rate, also have moderate heterosis (Greiner, 2009). The more genetically different the parent breeds are, the more heterosis is expected. A successful crossbreeding program should optimize, but not necessarily maximize heterosis in the calf crop and cow herd (Greiner, 2009), while increasing the proportion of favorable allele combinations in a population (Bourdon, 2000).

Structured crossbreeding programs allow the use of additive and non-additive allelic effects simultaneously to advantage (Seigel, 1988). Additive allele effects are independent allele effects that are expressed additively. Non-additive allele effects are allele combination effects due to factors such as dominance and epistasis (Bourdon, 2000). In a self-contained herd, introducing a terminal sire of a different breed can increase additive genetic merit for traits such as growth rate. Breed differences in additive genetic merit can be used to synchronize performance characteristics more effectively (Gregory, 1992). In a multiple breed population, both additive and non-additive effects should be included in the genetic model, so, combine-ability should be calculated for breed groups (Elzo, 1998).

When implementing a crossbreeding system, it is desirable to see an optimization of genetic merit and heterosis of performance traits under various (Brandt, 2010). Some factors that may affect the success of a crossbreeding program include number of cows in a herd, number of pastures available for breeding, amount and quality of feed available, production and marketing system, and availability of adequate quality bulls of various breeds (Greiner, 2009). In order to capitalize on improving efficiency it is necessary to have consistent goals and managerial practices (Lamb[2] and Tess, 1989). When crossbreeding is correctly implemented, tremendous improvement in number of calves weaned has been demonstrated ,which makes crossbreeding a useful tool in improving overall profitability (Daley, 2007). Effective crossbreeding can lead to: increased accuracy of prediction for purebreds, reciprocal recurrent selection for the improvement of crossbreds, combined purebred and crossbred selection, and the use of data recorded only in crossbreds for the evaluation of purebreds (Lutaaya et al. 2002).

Methods of Crossbreeding

Crossbred animals may be comprised of several different breeds, or come from purebred parents. Producers also practice varying systematic methods of crossbreeding or they may crossbreed at random with no systematic methods. Several commonly practiced methods of crossbreeding have proven to be efficient in improving production (Toosi, 2009). All methods of crossbreeding contribute at least some heterosis, though the amount of heterosis may vary (Fitzhugh, 1975).

Rotational crossbreeding is a popular form of crossbreeding. While there are several methods of practicing this type of crossbreeding system, in the more traditional form of rotational crossbreeding, two purebred animals are mated and the resulting female offspring are kept and mated back to one of the parent breeds. In following generations, females are mated to the breed opposite from their sire (Greiner, 2009). In this system, both breeds being used must be efficient as both paternal and maternal breeds, or efficient in both production and reproduction traits. In this type of crossbreeding system over several generations, 67% of maximum F_1 heterosis is realized. In adding a third breed to this system, over several generations, 87% of maximum heterosis would be realized, although it is difficult to find three compatible breeds (Greiner, 2009).

Although several advantages to rotational crossbreeding are apparent, there are some notable disadvantages to this system when compared with other crossbreeding systems. The first disadvantage is, since both breeds have to be sufficient as sire or dam, breed complementarity cannot be capitalized on. Also, breed composition changes with each generation, so variability of the product is greater. The last disadvantage is that less than one hundred percent heterosis is achieved (Kuhlers, 1994).

In another type of crossbreeding system, terminal sire systems, a terminal sire added as a third breed in a two breed rotational cross system may enhance the system. In this type of system, half of the cow herd is mated to the terminal breed while the other half is kept in a two-breed rotational system. In this system, the terminal sire breed should be selected for growth rate, carcass merit and calving ease. This system is expected to increase weight at weaning by about 20% and maximum heterosis is achieved by those calves sired by the terminal breed (Greiner, 2009). Rotating the breed of sire every three to four years is useful in small, single-sire herds. In this system, two breeds are used by replacing the breed of the sire every three to four years. In this system, the weaning weight should increase by 10-15%.

While crossbreeding can be a useful tool in efficiently breeding for improvement in economically important traits, having a complete understanding of the system being used and selecting the most useful parents is key in creating successful offspring.

Growth Traits

Commercial producers are faced with the difficulty of optimizing economically important traits while reducing costs of production in order to remain competitive. These economically important traits influence productivity and profitability and include reproduction, growth, maternal ability and production merit (Greiner, 2009).

Economically important traits in beef cattle, such as growth traits and carcass traits have been shown to increase when crossbreeding is implemented (Williams, 2010). Growth traits are a main focus in beef genetic improvement programs (Donoghue, 2009). The overall objective for commercial beef cattle crossbreeding programs is to maximize the sum of additive genetic values and heterosis for the three major traits: weaning rate, maternal, and growth potential (Koger, 1980). One of the most important traits in evaluating beef cattle performance is preweaning growth. There are several methods by which this trait can be measured including: birth weight, preweaning average daily gain, and weaning weight (Dillard, 1980). Weaning weight of a calf can be increased by up to 20 percent by heterosis through continuous crossbreeding (Gregory, 1992).

Breed differences in performance characteristics can be used as important genetic resources for improving efficiency of beef production (Lunstra et al., 2003). In most beef cattle production systems, genetic improvement programs focus on live animal growth (Marshall, 1994). When breeding for weight traits, it is important to take into account possible breed differences (Laborde et al., 2001).

In a study performed by Lunstra et al. (2003), researchers found that when comparing breeds of sires, sire breed and year had greater significant effects on birth weight, but dam breed and interactions had no significant effects (Lunstra et al., 2003). According to this study when crossbreeding beef cattle, the breed of the sire may have greater effect and should be considered as having a greater effect on weight traits than the breed of the dam. This would be understandable especially in cases where the dam is crossbred and has been selected for maternal abilities rather than growth potential, and where the sire has been selected based on growth potential.

Crossbreeding Models

There are several potential methods that can be used to provide estimations of breeding values in livestock populations One of the most popular methods is best linear unbiased prediction, BLUP. BLUP is a statistical procedure used to estimate fixed effects and breeding values simultaneously (Falconer, 1996). BLUP can be especially useful when data is from genetically diverse contemporary groups (Bourdon, 2000). BLUP can also be used to accommodate non-random mating and bias during selection, factors which cause complications, provided that these are included in the analysis (Falconer, 1996). BLUP was developed by C. R. Henderson in 1973 (Mrode, 2005). BLUP is often used in evaluations due to its many desirable properties (Lo et al. 1997). BLUP maximizes the correlation between true and predicted breeding values while minimizing the prediction error so that effects can be estimated. The following simple animal model can be used to describe effects in livestock populations;

$$y=Xb+Za+e.$$

Where b, is a vector of fixed effects, a, is a vector of random effects, and X and Z are incidence matrices. BLUP is typically used to derive a mixed linear model for phenotypic values (Lo et al., 1997). This model, known as Henderson’s mixed model equations (MME) is as follows:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}X \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix},$$

where R and G are (co)variance matrices with $var(e)=I\sigma_e{}^2=R$ and $var(a)=A\sigma_a{}^2=G$ (Mrode, 2005). The a effects are predictions of breeding values of the animals in the population. This algorithm is used in animal breeding for genomic evaluation of livestock using models where the components of A have genetic meaning (Gianola, 2000). The numerator relationship matrix, A, provides the expected additive genetic relationships among individuals (Mrode, 2005). BLUP assumes that phenotypic and genetic variances are known; however, if they are not, programs such as restricted maximum likelihood, REML, may be used to estimate the parameters from the data (Falconer, 1996). There are several statistical models involved with BLUP, including sire models, sire-maternal grandsire models, direct maternal models, and animal models. The animal model is often used to evaluate animal breeding data. This model accounts for all genetic relationships among individuals and calculates breeding values for those individuals (Falconer, 1996). Other statistical methods, such as Markov chain Monte Carlo methods are often used in animal breeding. The Bayesian approach can be used to solve a large number of animal breeding programs, and often in cases in which REML is unfeasible, Gibbs, a Markov chain Monte Carlo method, can be used (Gianola, 2000).

Improvements in statistic methods and models used in animal breeding have increased the levels of accuracy for prediction. Accuracy of prediction greatly influences the outcome of selection. As the accuracy of genetic prediction increases, the predictability of the offspring increases and the selection risk decreases (Bourdon, 2000). In evaluating and implementing crossbreeding systems, several criteria should be considered. Criteria include merit of component breeds, heterosis, breed complementarity, consistency of performance, replacement considerations, simplicity, and accuracy of genetic prediction. While most of these considerations are easily measured, accuracy of genetic prediction is not (Bourdon, 2000).

This increase in accuracy of prediction has allowed for an increase in improvement in economically important traits in all farm species across all the production profiles. These traits include increased milk production, increased weight gain in broiler chickens, and increased egg size and production.

Genetic evaluation of beef cattle using mixed models is an accepted tool for selection by purebred and commercial producers (Arnold, 1992). There is a need for evaluation procedures that include crossbred cattle. Genetic comparisons between breeds would be helpful in developing strong breeding objectives and strategies in multiple breed management systems (Arnold, 1992).

Determining how to select in crossbreeding systems while maximizing genetic response to selection has been questioned (Wei and van der Werf, 1995). This has been difficult to achieve because the breeding goal in crossbreeding systems should be defined at the commercial level which is composed of crossbred animals; however, the selection methods used are optimized to improve animals within lines or breeds. Selection is typically based on either purebred or crossbred information, but not both (Wei and van der Werf, 1995). Although it is common practice for commercial animals to be crossbred, genetic selection is more often made based on purebred performance. Also often assessment of purebred performance is based on the animal that are raised in environments that are different than commercial, crossbred animals. Crossbreds are typically raised in lower quality environments than purebreds, which can have an effect on growth rate (Zumbach et al., 2007). The goal of selection is to improve crossbred performance under field conditions (Ibanez-Escriche et al., 2009). Because correlations may be low between purebred nucleus and commercial crossbred animals, purebred performance may be a poor indicator of crossbred performance. An additional issue in using purebred performance to predict crossbred offspring performance is that survival and disease susceptibility cannot be evaluated (Dekkers, 2007). Since performance of purebred parents may be a poor indicator of performance of their crossbred descendents, an alternative method for prediction is needed (Ibanez-Escriche et al., 2009). In research performed by Lo et al (1995) and Wei and van def Werf (1995), combined purebred selection based on phenotypic data collected on crossbred performance of pigs proved to increase crossbred performance (Dekkers, 2007). Combining purebred and crossbred evaluations is necessary to more accurately evaluate purebreds for crossbred performance (Lutaaya et al., 2001).

Two approaches have been used in selection to improve crossbred performance. The first, pure line selection (PLS) is based on the information from the purebred breeding animal and its relatives within the population. The second methods, recurrent and reciprocal selection, are crossbred selection (CS) methods in which the breeding animals are chosen based on crossbred information (Wei and van der Werf, 1995). The crossbred selection methods have shown to be advantageous in improving traits with low heritability and large non-additive variation. Although CS has its advantages, studies have shown that PLS and CS are not optimal methods for improving crossbred performance (Wei and van der Werf, 1995).

Combining performance of pure and crossbred animals should be considered as a more appropriate method of selection. A simple method for combining performance of purebred and crossbred performance would be to consider crossbred and purebred performance as the expression of two separate traits with a genetic correlation, r_{pc}, between them. Heritabilities of crossbred and purebred populations may also differ. The correlation between the two populations should be 1.0, if no dominance is present or if gene frequencies are equal in the parental populations. The correlation decreases from 1.0 with increasing dominance and increasing gene frequency difference between parental populations (Wei and van der Werf, 1995).

The amount of genetic variation among purebreds for crossbred performance influences crossbred heritability (Wei and van der Werf, 1994). Random drift and selection are causes of differences in gene frequencies in different breeds. Genetic regression of crossbred performance based on purebred performance is influenced by gene frequency and dominance level (Lutaaya et al., 2002).

In order to implement sound breeding programs and to assess the progress of ongoing parameters, genetic parameter estimates are needed. These estimates can be used to improve both purebred and crossbred animals (Demeke et al., 2003). The efficiency of selection for crossbred animals is dependent on the correlation between the crossbred and purebred animals. However, low correlations could be due to genotype X environment interactions (Zumbach et al., 2007). Good estimates and understanding of genetic correlations between crossbred and purebred performance and heritability are important when improving and evaluating a crossbreeding system. Correlations are especially useful when progress in purebreds is achieved by applying a combined purebred and crossbred selection method (Wei and van der Werf, 1994).

A multibreed population is one which consists of crossbred and purebred animals that interbreed. In a multibreed population, additive and non-additive effects should be accounted for in the genetic model (Elzo and Wakeman, 1998). Structured crossbreeding can efficiently capitalize on additive and non additive effects. Accurately modeling variances in crossbred populations can be very complex. Models that account for additive and dominant (co)variances among all crosses of two purebred lines require numerous parameters and are not practical (Lutaaya et al., 2001). Treating each line as separate traits has been considered as the most advanced approximation of correlations and correlations for variances (Lutaaya et al., 2002). Using only F_1 terminal crossbreds in the model can give much more realistic and simplified computations (Lutaaya et al., 2001). In this model, all additive and dominance (co)variances are accounted for (Lutaaya et al., 2002). With using only F_1s in the model, the model contains two additive effects and allows separate variances for each crossbred and purebred lines (Lutaaya et al., 2001)

The multi-breed model Klei and Quaas (1995), developed initially for the Simmental Association, included direct and maternal genetic effects, direct and maternal breed effects, and fractions of direct and maternal heterosis effects under an assumed dominance model. In this multi-breed model is was assumed that not all breed combinations could be used in the model and correlations of breeding values between crossbred and purebred animals were 1.0 (Klei and Quaas, 1995).

It has been proposed to select purebred relatives based on crossbred performance, using combined crossbred and purebred selection (CCPS). This can increase response to selection for crossbred performance (Ibanez-Escriche et al., 2009). In a study performed by Wei and van der

Werf, (1994) comparing PLS, CS and CCPS, they found that selection accuracy is highest in CCPS. In this study, when using CCPS, if r_{pc}=0.7 there was a 4.8 percent increase in crossbred response; if r_{pc}=0.5, there was a 23.8 percent increase in crossbred response compared to PLS. There was also greater crossbred response in CCPS than CS when the correlation was greater than 0 (Wei and van der Werf, 1995). In their study using CCPS, Wei and van der Werf (1994), found that with correlations below 0.8, CCPS has greater response, and as correlations decrease, response in crossbreds increased.

Obtaining breeding values using BLUP with Henderson's mixed model equations requires the covariance matrices of each random effect to be inverted. A genotypic model is a model in which the genotypic value is included as a random effect. In a genotypic model, the genotypic covariance matrix is inverted. Although finding the inverse of the genotypic covariance matrix can be easily computed under additive inheritance, a method for finding the inverse of the genotypic covariance matrix under dominance inheritance has not been developed for crossbred populations. For this reason, using a genotypic model for BLUP is not appropriate for large crossbred populations (Lo et al., 1997).

Wei and van der Werf, (1995) proposed a genotypic model for genetic evaluation by BLUP for a two-breed terminal crossbreeding system (2BTC). Wei and van der Werf (1995), treated purebred and crossbred performance as two separate traits with a genetic correlation between them. The following linear model was used by Wei and van der Werf (1995) for purebred animals:

$$y_{1ijkl} = \mu_1 + GROUP_{1i} + HW_{ij} + s_{1ik} + e_{1ijkl},$$

where y_{1ijkl} is the observation of the ijklth purebred individual; μ_1 is the general mean; $GROUP_1$ is the ith group effect; HW_{ij} is the ijth hatch week effect within groups; s_{1ik} is the random effect of the ik^{th} sire within group but across hatch weeks and e_{1ijkl} is the residual random effect. Fixed effects are $GROUP_{1i}$ and $HW_{ij.}$ For crossbreds, the model Wei and van der Werf (1995), is as follows:

$$y_{2ijkl} = \mu_2 + GROUP_{2i} + RP_{ij} + s_{2ik} + e_{2ijkl,}$$

where y_{2ijkl} is the mean performance of n_{ijkl} crossbred hens in the $ijkl^{th}$ cage; μ_2 is the general mean; $GROUP_2$ is the i^{th} group effect; RP_{ij} is the ij^{th} trial effect within groups; s_{2ik} is the random effect of the ik^{th} sire within group but across trial effects and e_{1ijkl} is the residual random effect. Fixed effects are $GROUP_{2i}$ and RP_{ij}.

In this research performed by Wei and van der Werf (1995), genetic correlations between purebred and crossbred performance for egg production traits in laying chickens was estimated to be between 0.56 and 0.81. They found crossbred heritabilities to be lower than purebred heteritabilities (Wei and van def Werf, 1995).

In the model used by Wei and van der Werf, (1995), the covariance matrices can be inverted, however only additive covariances can be accounted for. This model is not equivalent to the genotypic model (Lo et al., 1997). Lo et al, (1997) proposed a model that accounts for both additive and dominance covariances. There are three groups an individual can belong to in a two-breed terminal crossbreeding system. These groups include A or B purebred groups and AB terminal crossbred group. By constructing the matrix for genotypic covariances for individuals within and between breed groups A, B, and AB, it is possible to obtain genetic evaluations by BLUP for a two-breed terminal cross (2BTC) (Lo et al., 1997).

Lo et al., (1997), showed that covariances between relatives in 2BTC are functions of additive and dominance relationship coefficients within a breed; this means that ignoring inbreeding, methods for within-breed genetic evaluation by BLUP can be used in a 2BTC. Lo et al., (1997), extended the model by Wei and van der Werf (1994), to account for dominance covariances. The model for phenotypic values for individuals in A, y^A used by Lo et al., (1997) is as follows:

$$y^A=X^A\beta+Z_\alpha{}^A u_\alpha{}^A+Z_\delta{}^A u_\delta{}^A+e^A,$$

where β is the vector of location parameters for breed groups A, B, AB; X^A is a matrix of three columns with ones in column 1 and zeros in columns 2 and 3; $u_\alpha{}^A$ is the random vector of additive effects for individuals in A; $Z_\alpha{}^A$ is a matrix relating $u_\alpha{}^A$ to y^A; $u_\delta{}^A$ is the random vector of dominance effects for individuals in A; $Z_\delta{}^A$ is a matrix relating $u_\delta{}^A$ to y^A; and e^A is the random vector of residuals for individuals in A.

The model for phenotypic values for individuals in B, y^B used by Lo et al. (1997), is as follows:

$$y^B=X^B\beta+Z_\alpha{}^B u_\alpha{}^B+Z_\delta{}^B u_\delta{}^B+e^B,$$

where X^B is a matrix of three columns with ones in column 2 and zeros in columns 1 and 3.

The model for phenotypic values for individuals in AB, y^{AB} used by Lo et al. (1997), is as follows:

$$y^{AB}= X^{AB}\beta+Z_\alpha{}^{A,AB}u_\alpha{}^{A,AB}+ Z_\alpha{}^{B,AB}u_\alpha{}^{B,AB} +Z_F{}^{AB}u_F{}^{AB}+e^{AB},$$

where X^{AB} is a matrix with ones in column 3 and zeros in columns 1 and 2, $u_\alpha{}^{A,AB}$ is the random vector of additive effects for individuals in A on their AB offspring, $Z_\alpha{}^{A,AB}$ is a matrix relating $u_\alpha{}^{A,AB}$ to y^{AB}, $u_\alpha{}^{B,AB}$ is the random vector of additive effects for individuals in B on their AB offspring, $Z_\alpha{}^{B,AB}$ is a matrix relating $u_\alpha{}^{B,AB}$ to y^{AB}, $u_F{}^{AB}$is the random vector of sire-dam subclass effects for individuals in AB, $Z_F{}^{AB}$ is a matrix relating $u_F{}^{AB}$ to y^{AB}, and e^{AB} is the random vector of residuals for individuals in AB.

Using this model, Lo et al. (1997), partitioned the genotypic effect into additive and dominance effects allowing for within breed genetic evaluation by BLUP for a two-breed terminal cross (2BTC). Lo et al. (1997), proposed two methods which can be used for selection for crossbreeding. In the first method, possible sires and dams are ranked according to the BLUP of possible crossbred offspring from unrelated randomly selected parents. This method would be useful in genetic improvement of purebreds for crossbred animals in later generations. In the second method, BLUP is used to rank each possible pair of sire and dam of a possible future offspring. Using this method allows selection of parents to produce currently superior crossbred offspring (Lo et al., 1997).

Lutaaya et al. (2001) used the model by Lo et al. (1997) and Gibbs sampling to obtain genetic parameters of a terminal cross for lifetime daily gain and backfat in swine (Lutaaya et al., 2001). Lutaaya et al. (2001) found that additive, residual and phenotypic variances were similar across the purebred lines and the crossbred line. They found that heritabilities found from the within line model and crossbred model were similar. The r_{pc} was found to range from 0.32 to 0.99 using the crossbred model indicating that dominance was a factor. They also suggested the lower correlations in backfat were most likely due to different feeding regimes for purebreds and crossbreds.

In 2002, Lutaaya et al. set out to determine the gains in reliability as a result of jointly evaluating crossbred and purebred evaluations using the crossbred model by Lo et al (1997). In their study, Lutaaya et al. (2002) found that reliability of predicted purebred breeding values showed an increase from 0.01 to 0.03. The reliability of purebred breeding value for crossbreds ranged from 0.05 to 0.21.

Zumbach et al., (2007) estimated the genetic correlations between two purebred groups and their terminal crosses. The purebred and crossbred animals in this study were raised in different environments. Two-trait models, similar to those used by Lo et al., (1997) for each group, were used to estimate heritabilities for each trait and genetic correlations between groups. Genetic correlations between crossbred and purebred animals ranged from 0.53 to 0.89.

These studies indicate, while correlations between crossbred and purebred of two species were originally assumed to be 1, these correlations were actually below 1. This indicates a problem in the selection process for crossbred animals that had previously been used. In fact, these studies indicate that other methods, such as **CCPS**, would be more efficient for selection.

Summary

Crossbreeding of beef cattle is an accepted and common method for improving production efficiency. Typically when selecting animals to be used for crossbreeding, information from purebred animals are used for selection with the assumption that the correlation between crossbred and purebred animals is 1.0. In this type of selection program, success relies on whether purebred performance accurately predicts crossbred performance. The genetic correlation between purebred and crossbred performance provides an indication of the evaluation of the ultimate effectiveness of the breeding program on the crossbred progeny performance when selection is based on the purebred animals (Comstock et al., 1949). The genetic correlation can also be an indicator for the effectiveness of combined purebred and crossbred selection and the use of crossbred information for the evaluation of purebreds (Cecchinato et al., 2010)

In cases where the genetic correlation between crossbred and purebred animals is not 1.0, purebred performance is not likely to predict accurately crossbred performance. In attempting to improve crossbred performance, it is logical to include both crossbred information and purebred information of any crossbreeding system in selection criteria. Combined selection using crossbred and purebred information can be easily used in crossbreeding systems where information of crossbreds is already collected for management purposes (Wei and van der Werf, 1995).

In evaluation of some beef cattle, only progeny of the purebred sire are included in evaluations. This means F_1s from the purebred dam that has been mated to a bull from another breed are not included in evaluations. By using multiple breed evaluations, more animals can be included in the evaluation (Klei and Quaas, 1995).

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CHAPTER 3

CORRELATIONS BETWEEN PUREBRED AND CROSSBRED BODY WEIGHTS IN MULTI-BREED LIMOUSIN WITH ANGUS POPULATIONS[1]

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[1] Davis, R, I. Misztal, S. Tsuruta, and M. Lukaszewicz. To be submitted to the Journal of Animal Science

Abstract

The purpose of this study was to estimate correlations between purebred and crossbred performance to verify efficiency of current models used in multi-breed selection. Records on three weight traits: birth weight (BW), weaning weight (WW) and post-weaning gain (PW) from purebred Limousins (L) and Limousin*Angus progeny (F_1), were used to estimate genetic parameters using a multiple trait (purebred and crossbred weights are different traits) approach. For BW there were 148,647 records for L and 17,981 for F_1, for WW 81,585 for L and 21,778 for F_1, and for PW 37,687 for L and 11,021 for F_1. Fixed effects in models for L and F_1 animals were contemporary group and month. Random effects for L animals were direct genetic, maternal genetic and maternal permanent environment. Random effects for F_1 were sire genetic effect and dam joint genetic and permanent environment effect. The pedigree for Angus dams was unavailable and therefore these dams were assumed unrelated. The direct h^2 estimates for purebred animals were 0.35, 0.25 and 0.31 for BW, WW and PG respectively. For F_1, the same estimates were 0.25, 0.38 and 0.34. Genetic correlations estimates between purebreds and crossbreds were 0.4, 0.6 and 0.3 for BW, WW and PG respectively. The results indicate cthat purebred selection is only partially effective on crossbreds; in particular, sires may be misevaluated for BW and PG. Even though the correlation is lower than unity for WW (0.6), selection in purebred populations may still be very effective in this trait due to a higher heritability in crossbred animals than purebred animals. Estimates in this study may be biased by the ignoring of maternal pedigrees in F_1.

Key words**: **body weight, purebreds, crossbreds, genetic correlation, Angus, Limousin

Introduction

The majority of beef products consumed in the United States comes from crossbred animals which are maintained in multibreed populations – populations composed of purebred and crossbred animals that interbreed (Elzo and Wakeman, 1998). Multibreed evaluation compares animals of different breeds using information from pooled data sets (Klei and Quaas 1995). While genetic evaluation of a multibreed population should account for both additive and non-additive effects, national beef cattle sire evaluations have used comparisons of sires across breeds neglecting non-additive effects in those comparisons (Elzo and Wakeman, 1998). To cope with this problem, efforts were undertaken to account for non-additivity in the direct and maternal genetic effects (e.g. Klei et al., 1996; Elzo and Wakeman, 1998). However since a data structure that allows the estimation of all additive and non-additive effects has proven to be difficult to achieve (Legarra et al., 2007), multibreed evaluations routinely keep regarding performance recorded in purebreds and crossbreds as the same traits.

Wei and van der Werf (1994) and Lutaaya et al. (2001) used F_1s and purebred swine in a two-breed terminal crossbreeding (2BTC) plan to jointly evaluate crossbred and purebred pigs and to predict correlations between purebred and crossbred performance. Wei and van der Werf (1994) found that when correlations between purebred and crossbred performance were below 0.8, crossbred response increased as correlations decreased, under the 2BTC model. Lutaaya et al. (2001) reported correlations between purebred and crossbred performance were even below 0.4, indicating previous models were less efficient than the 2BTC model.

As the current methods of evaluation of beef cattle assume genetic correlations between crossbred and purebred performances to be 1.0, efficiency of genetic selection using these models may be decreased due to the actual lower correlations. The 2BTC model has not yet been used in beef cattle evaluation and correlations between purebred and crossbred beef cattle performance have not been estimated. The objective of this study is to use the multiple trait (purebred and crossbred weights considered as different traits) approach to estimate genetic parameters for purebred and crossbred performance in beef cattle to verify efficiency of current models used in multibreed selection.

Materials and Methods

Data

Data for this study was obtained from the American Limousin Association. Institutional Animal Care and Use Committee approval was not needed for the study since the performance data was obtained from existing databases. Records were from cattle born from 1970 through 2007. The populations consisted of purebred Limousin and crossbred Limousin*Angus (F_1) cattle in which the F_1 cattle were obtained by crossing purebred Limousin sires with purebred Angus dams. Weight at birth (BW), animal's adjusted weight at weaning (WW), and the amount of weight gained from weaning to yearling (PG) were the three body weight traits analyzed. The numbers of observations across genotypes and traits are represented in Table 1.

Due to the lack of the pedigrees for Angus dams, they were assumed unrelated and the dam variance diagonal component was pooled across its possible sources.

Multiple Trait Crossbred Model

The crossbred model by Lo et al. (1997) was adapted to account for missing Angus dams' pedigree and lack of purebred Angus performance:

$$y_P = X_P b_P + Z_P u_P + Z_{Pm} ma_P + W_P mpe_P + e_P$$

$$y_C = X_C b_C + Z_{PC} u_{PC} + Z_{AC} u_{AC} + e_C.$$

In the above, subscript *P* denotes purebred Limousin, subscript *C* denotes F_1 crosses, and *A* denotes the pooled Angus dams' contribution to the crosses. The fixed effects contained in $\boldsymbol{b_P}$ and $\boldsymbol{b_C}$ include contemporary group and month of weaning or yearling (birth month is an element of the contemporary group for BW and PG). The predictions for random factors include purebred Limousin animal additive effects – $\boldsymbol{u_P}$ [~ N(0, $\boldsymbol{A}\sigma_a^2$)], corresponding additive Limousin sire effects in the crossbred performance – $\boldsymbol{u_{PC}}$ [~ N(0, $\boldsymbol{A_s}\sigma_s^2$)], additive – $\boldsymbol{ma_P}$ [~ N(0, $\boldsymbol{A}\sigma_{ma}^2$)] and permanent environment – $\boldsymbol{mpe_P}$ [~ N(0, $\boldsymbol{I}\sigma_{mpe}^2$)] purebred Limousin maternal effects, corresponding Angus dams' contribution to the crosses – $\boldsymbol{u_{AC}}$ [~ N(0, $\boldsymbol{I}\sigma_d^2$)] in the crossbred performance model, and $\boldsymbol{e_P}$ and $\boldsymbol{e_C}$ are adequate residuals. $\boldsymbol{u_P}$ and $\boldsymbol{ma_P}$ are assumed correlated [cov($\boldsymbol{u_P}$, $\boldsymbol{ma_P}$) = $\boldsymbol{A}\sigma_{a,m}$]. The $\boldsymbol{X}$, $\boldsymbol{Z}$, and $\boldsymbol{W}$ matrices of matching subscripts are incidence matrices. Correlations (r_{pc}) for BW, WW, and PG are between $\boldsymbol{u_P}$ and $\boldsymbol{u_{PC}}$ [cov($\boldsymbol{u_P}$, $\boldsymbol{u_{PC}}$) = $\boldsymbol{A}\sigma_{s,a}$].

Variance components were estimated with the Gibbs2f90 software of Misztal et al. (2002) using the Gibbs sampling procedure. One hundred thousand samples were obtained with 20,000 discarded as burn-in, following visual inspection.

Results and Discussion

Correlations between crossbred and purebred animals in this study are expected to be below 1.0 for two main reasons. First, F_1s have the greatest crossbreeding potential – greatest possible heterozygosity, and hence, full dominance effects add to their performance (Kinghorn, 1983). Second, there are imperfections to the available data – relationships between Angus dams are unaccounted for, pure- and crossbred performance records do not share the same contemporary group effects and only a sample of sires that had purebred progeny records had F_1 progeny records. Additionally, confounding of sire with contemporary group and with dam could further bias the results for the crossbred population.

Variance Component Estimates

Variance component estimates for all three weight traits are presented in Table 2. The relative magnitude of the sire component to the direct additive component from the purebred model increases from BW to PG – from 0.13, through 0.27, to 0.31. The departure from the 0.25 ratio could be considered a measure of differentiation of purebred and crossbred performance, however, the present estimates might have also been affected by only a rough accounting for the maternal component in F_1s, particularly for birth weight. The size of fetus has long been known as related to uterus environment, following the classical experiment in horses (Walton and Hammond, 1938). However, it is widely accepted that maternal effects are very important for weaning weight, and the sire variance estimate in the crossbred data set is close to the 0.25 ratio of the additive variance estimate in the purebred data set.

The maternal component estimates resulting from the current models were estimated only for BW and WW, as the model for PG fit no maternal effects. For both maternally influenced traits, the pooled maternal component is higher in F_1s than the sum of maternal components in L. For BW, the maternal component in F_1 is almost two-fold as high as the sum of maternal components in L. The ratio dropped down to 1.1-fold for WW. The main differences between the pooled maternal in F_1 and summed maternal in L effects is that the first one also harbors the direct additive differences between the Angus mothers. Also since no relationship was fit between the Angus dams and each dam was used once in the F_1 population, the maternal variance estimates d are confounded with residual effects; therefore, the maternal variance estimates from this data set are probably inflated.

Genetic Correlations

Estimates of the genetic correlations between purebreds and crossbreds are shown in Table 3. They ranged from 0.3 to 0.6 suggesting a re-ranking of Limousin sires across the two populations. This implies that the models suggested by Klei and Quaas, 1995 for multibreed evaluation that are currently used by the several breeds in the beef industry may not provide optimal results. With all r_{pc} being below 0.8, combining purebred and crossbred data using the crossbred model may prove advantageous (Wei and van der Werf, 1994).

Correlations between crossbred and purebred animals in this study were similar to those found in swine for growth traits (Lutaaya et al., 2001). In particular, the correlation for PG, which is a main trait of interest for producers, appeared very low. Nevertheless, even the correlation for WW, though highest, still indicated substantial differences between sire rankings in purebred and crossbred population. Therefore, it would still be less than optimal to select animals for a crossbreeding plan based solely on purebred evaluations without accounting for the correlation between purebred and crossbred performance, which appears to be lower than unity.

Heritability estimates

Heritability estimates are represented in Table 3. Heritabilities in F_1 and purebred animals were between 0.25 and 0.40 indicating moderate heritability for weight traits. These heritabilities are within the previous reported range for weight traits for beef cattle (e.g. Bourdon, 2000). For F_1s, h^2 is highest for the production traits (WW and PG) and lower for BW. Whereas it could be advantageous to have a lower h^2 for BW in crossbreeding animals in cases where a larger breed is used as a sire with a dam of a smaller breed, inadequate correcting for the maternal abilities and possible confounding of sires and dams in the current study, may have resulted in underestimated heritability coefficients.

Conclusions

Due to low correlations, crossbred and purebred performance in beef cattle should not be treated as the same trait. The purebred selection appears to be only partially effective on crossbreds, particularly for BW and PG. The selection is more effective for WW, where the genetic correlation, though lower than unity, is compensated by higher heritability.

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Table 3.1: Trait statistics by genotypes

Trait[*] Genotype	BW N	Mean (SD[+])	WW n	Mean (SD)	PG n	Mean (SD)
Limousin	148,647	39 (5)	81,585	265 (38)	37,687	152 (50)
Limousin*Angus	17,981	33 (4)	21,778	204 (32)	11,021	99 (34)

[*] BW – birth weight (kg), WW – weaning weight (kg), PG – post-weaning gain (kg)

[+] Standard deviation

Table 3.2: Variance component estimates across models

Performance		**Crossbred**	**Purebred**
Model		Sire	Animal
TRAIT[*]	Component[**]		
BW			
	[1]σ_a^2		4.5
	[2]σ_s^2	0.6	
	[3]σ_d^2	4.5	
	[4]σ_{ma}^2		1.8
	[5]σ_{mpe}^2		0.4
	[6]$\sigma_{a,m}$		-1.0
	[8]σ_e^2	4.6	6.2
	[7]$\sigma_{s,a}$	0.7	
WW			
	σ_a^2		144.3
	σ_s^2	38.6	
	σ_d^2	142.8	
	σ_{ma}^2		56.4
	σ_{mpe}^2		71.9
	$\sigma_{a,m}$		-32.8
	$\sigma_{s,a}$	41.9	
	σ_e^2	220.9	359.2
PG			
	σ_a^2		150.9
	σ_s^2	46.7	
	σ_d^2	200.2	
	$\sigma_{s,a}$	23.5	
	σ_e^2	294.9	332.9

[*] BW – birth weight (kg), WW – weaning weight (kg), PG – post-weaning gain (kg),

[**] Variances: [1]animal additive, [2]sire, [3]pooled maternal, [4] maternal additive, [5]maternal permanent environment, [6]covarinace animal additive*maternal effects, [7]covariance sire*animal additive, [8]residual

Table 3.3: Estimates of heritability (h^2) for weight traits and of correlation (r_{pc}) between sire additive in F_1 and animal additive in purebred animals

Performance	**Crossbred**	**Purebred**	
Model	Sire	Animal	
TRAIT			
	h^2		r_{pc}
[1]BW	0.25	0.35	0.4
[2]WW	0.38	0.25	0.6
[3]PG	0.34	0.31	0.3

[1]Birth weight (kg), [2]Weaning weight (kg), [3]Post-weaning gain (kg)

CHAPTER 4

CONCLUSIONS

Genetic correlations in this data for BW, WW, and PG ranged from 0.3 to 0.6, below 1.0. These results indicate that improvement based on current multiple breed evaluations or purebred evaluation alone, may be less optimal than using CCPS with the crossbred model.

In improving crossbred performance, it is logical to include both crossbred and purebred information of any crossbreeding system in selection criteria. Combined crossbred and purebred selection can be easily used in crossbreeding systems where information of crossbreds is already collected for management purposes.

Current multi-breed evaluations treat purebred and crossbred performances as a single trait. Correlations between crossbred and purebred beef cattle for these three weight traits were low, signifying that purebred and crossbred performance should be treated as two separate traits for evaluation.

Correlations between multi-breed and crossbred populations when predicting purebred sires being used for crossbreeding are low, as are correlations between purebred and crossbred populations. Predictions would be more accurate when made within a multi-breed population as compared to when made within a purebred population, though neither would be efficient. Predictions of purebred sires to be used for crossbreeding should be made within a crossbred population, otherwise predictions are inaccurate.

When selection for crossbreeding is being made, crossbreeding effects should be considered. Animals that are ranked as the best among purebreds, may not provide the best crossbred offspring.