

MEXICAN SIMMENTAL-BRAHMAN GENETIC CHARACTERIZATION, GENETIC
PARAMETERS AND GENETIC TRENDS

By

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Javier Rosales-Alday

To God.

To Serafín and Micaela, my parents.

To Javy and Enry, my family.

To Eduardo, Silvia, Jorge, Raúl, Ignacio, Joel, Gabriel, Horacio and Olga Lidia, my
brothers.

And to M. A. Elzo, the researcher.

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Covariance components for birth weight direct (BWT_D), birth weight maternal (BWT_M), weaning weight direct (WW_{205D}) and weaning weight maternal (WW_{205M}) were estimated in a Mexican Simmental-Simbrah population. In the first study, data from three disconnected herds where the cattle were reared under subtropical conditions were used to estimate genetic additive and nonadditive parameters. Estimates of regression genetic group effects for BWT and WW_{205D} showed an important effect of nonadditive factors on each of these traits in all three herds. Thus, these nonadditive effects should be considered in any genetic improvement program. The genetic parameters that were estimated indicated more genetic variability for weaning weight than for birth weight in these herds. A second study using purebred Simmental data from the Mexican Simmental-Simbrah Association was conducted. Estimate of heritability for birth weight additive direct was 0.40 while it was 0.12 for additive maternal. The genetic correlation between additive direct and additive maternal effects was -0.63 for birth

weight. Weaning weight heritabilities were 0.33 for additive direct and 0.19 for additive maternal. The additive direct-maternal correlation for weaning weight was -0.67 . The only across-trait nonzero genetic correlation was between birth weight direct and weaning weight direct (0.73). Genetic parameters found in this study were almost identical to those found in the American Simmental population, suggesting that the Mexican Simmental population is a subset of the American Simmental population. A third study was conducted using data from a purebred and crossbred Simmental-Simbrah population to determine the effect of cytoplasmic line. Only small cytoplasmic effects were found for BWT and WW205D ranging from 2 to 3%. The genetic correlations between direct and maternal effects, between direct and cytoplasmic effects and between maternal and cytoplasmic effects were 0.12, 0.29 and 0.98, respectively. Even though the cytoplasmic effect was small, it may be useful in the selection of maternal lines to use in specific genetic improvement programs such as cloning and embryo transfer within the Mexican Simmental-Simbrah population.

CHAPTER 1 INTRODUCTION

Performance of livestock in tropical regions of the world is known to be inferior to that of livestock in temperate zones. Attempts to improve cattle production in the tropics have met with only limited success. Technological advances developed in industrialized countries and applied to tropical animal production have not generally worked well. In general breeds imported from temperate zones have not adapted well to the extreme conditions encountered in many of the tropical climates (Pearson de Vaccaro, 1973; Olson et al., 1990; Rios-Utrera et al., 1996; Vega-Murillo et al., 1996; Rosales-Alday et al., 2002a).

Large amounts of bovine semen and live animals have been exported from the United States to Mexico. Semen has been used to improve Mexican beef production, but no evaluation has been made to quantify the genetic impact of introduction of new genes to the Mexican beef population. The commercial relationship between the United States and Mexico is important and Mexico has been introducing large quantities of germplasm from the USA. The imported breeds with the largest numbers in the tropical regions of Mexico are purebred Simmental and Simbrah. Cattlemen are using live sires and dams and frozen semen from these breeds on the Zebu based population of the region. However, crossbreeding between Simmental and Zebu has been done without a clear strategy and performance of these animals under tropical and subtropical conditions is unknown.

Mexican tropical beef producers are trying to increase productivity by introducing new breeds such as Angus, Charolais, Limousin, Simmental, Holstein and Brown Swiss to the Zebu-based population (Rios-Utrera et al., 1996; Vega-Murillo et al., 1996). The objective of Mexican cattlemen is to increase production while maintaining some Zebu influence for adaptation. Beef production can be improved using appropriate sources of germplasm and properly designed mating systems. Information is needed on expected performance of available breeds and their crosses for economically important characteristics, under varying levels of management, in different climatic conditions and in different geographic areas (Falconer, 1989; Weigel, 2002). The breeding value of imported animals is usually unknown. Perhaps some of the imported animals may have a genetic evaluation in their country of origin, but these breeding values may be different under different environment and production systems.

Another alternative for increasing production in the tropics is the genetic improvement and wider distribution of the native breeds which are naturally adapted to their surroundings (Alves Santiago, 1976). Unfortunately, little documented information is available on the productive traits and behavior of these indigenous breeds. Reproductive efficiency has been reported as poor (Randel, 1984; Galina and Russell, 1987; Galina and Arthur, 1989, 1991). Mexican cattle breeders have recognized the necessity of having genetic evaluations of their livestock. Several factors, however, limit their ability to do so at this time. One of these limiting factors is a lack of qualified personnel; another is the absence of a proven genetic program. To solve these problems, a genetic program was proposed with the participation of Mexican National Institutes of Research, universities and cattlemen's associations (SAGAR, 1998).

In Mexico the bovine population has a truncated pyramidal structure with commercial producers forming the base. The middle is formed by breeders who import sires from other countries. The top part of this pyramid is missing because specific breeding plans to include selection within the entire Mexican beef cattle population are lacking (De los Santos et al., 2003). In order to solve this situation, the Mexican government has implemented a breeding plan in which genetic evaluations are included. This plan includes the participation of Mexican beef breeder associations, universities and the National Institutes of Research in Forestry, Agriculture and Livestock Production (INIFAP) (SAGAR, 1998).

Zebu breeds are widely used in the Mexican tropics for beef production. However, declining values of feeder calves with Zebu characteristics have convinced cattlemen to use alternative crossbreeding systems using *Bos taurus* sires (Angus, Charolais, Limousin, Simmental, Holstein and Brown Swiss) on Zebu dams. Several breed comparisons have been conducted involving crosses of *Bos taurus* sires and *Bos indicus* cows under tropical Mexican conditions (Rios-Utrera et al., 1996; Vega-Murillo et al., 1996; Quiroz-Valiente et al., 1994). These authors concluded that *Bos taurus* × *Bos indicus* crossbred F₁ animals were younger at first calving and had a higher weaning rate. However, no genetic evaluation has been conducted in this region. Precise estimates of genetic parameters are required to define genetic strategies to increase animal production under Mexican conditions.

Another factor to consider is that the genetic evaluations to date have been made using a one breed approach, considering only additive genetics effects. However, when sires are intended to be used on cows of a different breed, another approach is needed.

This approach is called a multibreed analysis (Elzo and Bradford, 1985; Elzo and Famula, 1985). Using this procedure, it is possible to evaluate not only additive genetic values, but also non-additive effects as well. This approach allows one to determine which sire has the best performance with a particular breed group of dams (Elzo, 1999).

Genetic improvement in the USA has been based on selection for economically important traits such as birth weight, weaning weight, yearling weight and others (ASA, 2003). The Mexican database includes only birth weight and weaning weight.

Consequently, the series of studies in this dissertation are expected to achieve the following objectives:

- 1) to estimate genetic parameters for birth weight (BWT) and 205 d-adjusted weaning weight (WW205) for three disconnected herds under Mexican subtropical conditions (Chapter 3),

- 2) to estimate additive direct and maternal genetic variances and covariances, heritabilities, genetic correlations and genetic trends for birth weight and weaning weight in the Mexican Simmental population (Chapter 4) and

- 3) to determine the contribution of cytoplasmic line effect on birth weight and weaning weight (Chapter 5).

CHAPTER 2 LITERATURE REVIEW

Some countries are importers and others exporters of animal products with distance not being an issue anymore. For this reason the product that cattlemen are selling or buying should be of the best quality possible. Genetic improvement of cattle has become a global venture. Producers routinely use semen from foreign sires and breeding companies acquire genetics from a variety of countries. The international exchange of cattle, semen and embryos necessitates a methodology to compare animals that differ in housing conditions, feeding programs and genetic composition. Years ago, genetic differences between strains of cattle in different countries were large and to identify which breed, line or animal was superior, a simple comparison of phenotypic records was sufficient. Over time countries that were once importers of genetic material became competitors, with export aspirations of their own. Genetic differences between strains within various countries are now smaller and advanced statistical procedures are needed to compare animals fairly and accurately (Weigel, 2002). Currently efforts exist to analyze information generated from beef and dairy cattle (Canavesi et al., 2002; Emmerlin et al., 2002; Lidauer et al., 2002) from several countries simultaneously.

Linear Models in Animal Breeding

Prediction of breeding values constitutes an integral part of most breeding programs for genetic improvement. Crucial to the accurate prediction of breeding values is the availability of records. In a population, data available at the initial stages are usually from individual animals which may or may not be related. Data collected later

may include information on offspring and other relatives. Initially the prediction of breeding values may be based on records of individuals and a few relatives. To analyze production records and get a genetic evaluation, it is necessary to model the data.

Modeling is based upon the assumption that every phenotypic observation of an animal is determined by environmental and genetic factors and may be defined by the following model:

Phenotypic observation = environmental effects + genetic effects + residual effects

or

$$y_{ij} = \mu_i + g_i + e_{ij}$$

where

y_{ij} is the record j of the animal i th,

μ_i includes the identifiable non-random (fixed) environmental effects such as herd management, year of birth, sex of the i th animal,

g_i is the sum of the additive (g_a), dominance (g_d) and epistatic (g_e) genetic values of the genotype of the i th animal and

e_{ij} is the sum of random environmental effects affecting animal i .

The additive genetic value in the g term above represents the average additive effects of genes an individual receives from both parents and is termed the breeding value. Each parent contributes a sample half of its genes to its progeny. The average effect of the sample half of genes which a parent passes to its progeny is termed the transmitting ability of the parent and corresponds to one-half of its additive genetic value ($\frac{1}{2}g_a$). The breeding value of the progeny, therefore, is the sum of the transmitting abilities of both parents. Since the additive genetic value is a function of the genes

transmitted from parents to progeny, it is the only component that can be selected for and therefore is the main component of interest. In most cases, dominance and epistasis, which represent intralocus and interlocus interactions respectively, are assumed to be of little significance (Falconer, 1989; Mrode, 1996) and are included in the e_{ij} term of the model as

$$y_{ij} = \mu_i + g_{ai} + e_{ij}^*$$

with e_{ij}^* including the sum of the random environmental effects, dominance and epistatic genetic values. This equation constitutes the linear model usually employed in most problems of breeding value prediction in animal breeding (Henderson, 1975b; Fries, 1998). Usually it is assumed that y_{ij} follows a multivariate normal distribution (MVN) (Searle, 1971), implying that traits are determined by an infinite number of additive genes each with infinitesimal effects at unlinked loci; the so-called infinitesimal model (Falconer, 1989; Weigel, 2002). Also it is assumed that $\text{var}(g_{ai})$ and $\text{var}(e_{ij}^*)$ are known, or at least, their proportionality is known and that there is no correlation between g_{ai} and e_{ij}^* ($\text{cov}(g_{ai}, e_{ij}^*) = 0$) and no correlation among mates ($\text{cov}(e_{ij}^*, e_{ik}^*) = 0$). Also μ represents the mean performance of animals in the same management group (contemporary group). The mean of animals reared under the same management system and of the same age and sex is assumed to be known. This reduces the problem of predicting breeding values to adjusting phenotypic observations for identifiable non-random environmental effects and appropriately weighting the records of animals and their available relatives.

From the previous model one should define a_i as the breeding value of animal i , then

$$a_i = g_{ai} = \frac{1}{2}a_s + \frac{1}{2}a_d + m_i$$

where a_s and a_d are the breeding values of the sire and dam respectively and m_i is the deviation of the breeding value of animal i from average breeding value for both parents, that is, Mendelian sampling (Mrode, 1996). The sampling nature of inheritance implies that each parent passes only a sample half of its genes to its progeny. Therefore, genetic variation exists between offspring of the same parents since all offspring do not receive exactly the same genes. Mendelian sampling could be regarded as the deviation of average effects of additive genes an individual receives from both parents from the average effects of genes common to all offspring of the same parents (Elzo, 1996).

Accurate prediction of breeding value constitutes an important component of any breeding program since genetic improvement through selection depends on correctly identifying individuals with the highest true breeding values. The method employed for the prediction of breeding value depends on the type and amount of information available on candidates for selection.

Mixed Model Equations

Henderson (1953) developed a methodology called best linear unbiased prediction (BLUP) by which fixed effects and breeding values can be simultaneously estimated.

The BLUP acronym stands for:

Best – means it maximizes the correlation between true (a) and predicted breeding value

(\hat{a}) or minimizes prediction error variance (PEV), ($\text{var}(a - \hat{a})$)

Linear – predictors are linear functions of observations

Unbiased – estimation of realized values for a random variable such as animal breeding

values and of estimable function of fixed effects are unbiased $E[\hat{w}] = E[w]$ and

Prediction – involves prediction of true breeding values.

BLUP has found widespread usage in genetic evaluations of domestic animals because of its desirable statistical properties. Its usage has been enhanced by the steady increase in computing power and has evolved in terms of its application from simple models such as the sire model in its early years to more complex models such as the animal, maternal and multivariate models in recent years.

Matrix algebra can be used to describe the power of Henderson's mixed model equations. These equations have been and will be used extensively by animal breeders and will continue in the future to be the basis for linear mixed model analyses. Let y be a vector of observations of order n . The general linear model for the observations can be written as

$$y = X\beta + \varepsilon$$

where

β is a vector of fixed effects,

X is the matrix that associates the fixed effects with the observation in y and

ε is a vector of random effects.

$$E[y] = X\beta$$

$$V(y) = V(\varepsilon) = V \text{ of order } n \times n.$$

The generalized least squares solution for β is obtained from the generalized least squares equations:

$$(X'V^{-1}X)\beta = X'V^{-1}y$$

The problem is that V^{-1} must be calculated. Computational time to obtain inverses of matrices such as V^{-1} is proportional to n^3 . Thus, with the number of observations to

analyze, which currently are of the order of thousands and some countries have millions of records, obtaining the inverse is impossible. If $X'V^{-1}X$ can be calculated, iterative methods can be used to obtain solutions to the equations, but obtaining V^{-1} for all except trivial problems may still be impossible. The generalized least squares equations do define solutions for the fixed effects β . Such solutions denoted as $\hat{\beta}$ yield $X\hat{\beta}$ are best linear unbiased estimators (BLUE) of $X\beta$. But what animal breeders need are predictors of random effects such as breeding values. These are included in ε as in the mixed linear model:

$$\varepsilon = Zu + e$$

where

u is the vector of random effects to be predicted (e.g., breeding values),

Z is the matrix associating effects in u with the animal record (y) and

e is the vector of random effects uncorrelated with u .

Predictors of elements of u which have the properties of BLUP, best linear unbiased predictors, can be obtained as $E[u|y]$ with the restriction that $E[\hat{u}] = E[u]$. One way to obtain \hat{u} is

$$\hat{u} = GZ'V^{-1}(y - X\hat{\beta})$$

where $GZ' = \text{cov}(u, y')$. The corresponding selection index predictor (also called linear predictor) is

$$u = GZ'V^{-1}(y - X\beta)$$

where β is the solution of fixed effects, is assumed to be known exactly instead of using $\hat{\beta}$ the BLUE of β . To adjust for fixed effects to obtain BLUP, not only must V^{-1} be calculated, but also $\hat{\beta}$ must be obtained from solving the generalized least squares equations.

The problem is to obtain $\hat{\beta}$ and \hat{u} without inverting V . Even with the assumption that good estimates of variance components represented in V are available, the problem is how to obtain V^{-1} . Henderson (1953) gave a solution; it was intuitive and did not involve calculation of V^{-1} . He very likely tried to find efficient ways to do that, but was unsuccessful. What he did do was this: if elements of u are assumed to be fixed effects, then for the linear model

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

the weighted least squares equations to solve when assuming both β and u are fixed are

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where $R = V(e)$, which usually has a simple structure: diagonal and homogeneous for single trait or block diagonal for multiple traits, so that R^{-1} is easily obtained.

Henderson's first formulation involved single trait equations multiplied through by σ^2 , the homogeneous variance of $R = I\sigma^2$. In that case, the equations are called ordinary least squares equations

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

In the general formulation, Henderson added G^{-1} where $G = V(u)$ to the $Z'R^{-1}Z$ block of the least squares equations:

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

Henderson proved several years later that the solutions to these “modified” least squares equations were, in fact, BLUE for β and BLUP for u . Because R^{-1} is usually easily obtained and in many cases the structure of G is such that G^{-1} is also easily obtained, then simple iteration can be used to obtain $\hat{\beta}$ and \hat{u} from the mixed model equations, known to most animal breeders and statisticians as Henderson’s mixed model equations. The proofs that solutions from mixed model equations are the BLUE of β and BLUP of u are in Henderson et al. (1959).

Relationship Matrix

Another contribution of Henderson to animal breeding is a method to obtain G^{-1} . Wright (1922) worked out a measure of this genetic relationship between pairs of animals called the numerator relationship. A numerator relationship matrix contains the relationships among any number of animals. Having a fraction of genes in common is like a fractional replication of genetic effects for related animals. Animal breeders typically want to make use of this partial genetic replication through $A\sigma^2$ to obtain more accurate predictions of breeding values or to predict breeding values for animals without records. In models typically used in animal breeding the number of animals may range

from thousands to millions. However, to apply Henderson's mixed model equations, G^{-1} rather than G is needed. Thus, for $G = A\sigma_g^2$ what is needed is $A^{-1}G^{-1} = A^{-1}\sigma_g^2$. To solve this problem Henderson (1975a) published a simple set of rules to obtain elements of A^{-1} without having to calculate A . With those rules a list of animals with each animal's sire and dam (pedigree file) is needed. The A^{-1} matrix computed by Henderson's rules is of the order of the number of unique animals, including sires and dams, some of which may not have records. Thus, equations need to be included for all animals having records. Usually the least squares equations will involve only the model for the available records. In 1976 Henderson published a procedure to include animals without records in the genetic evaluation, augmenting equations to the mixed model (Henderson, 1976a, b, c). These equations are tied to the equations for animals with records with the $G^{-1} = A^{-1}\sigma_g^2$ part of the mixed model equations. Solutions for animals without records are basically selection index predictions using relationships to relatives with records and their predicted breeding values. This method is particularly valuable for multiple trait models and for models with both direct and maternal effects when all animals do not have measurements for all traits, or not all cows become mothers of progeny with records (Henderson, 1975b, 1976d).

The sum of Henderson's discoveries of 1) the modification of least squares equations to form mixed model equations with solutions that have BLUE and BLUP properties, 2) the easy calculation of A^{-1} and 3) the augmentation of the mixed model equations to include equations for animals without records (for all or some traits) has provided animal breeders worldwide with the best possible tools for genetic selection (Van Vleck, 1991).

Animal Model

The objective of the animal model is to predict the breeding value (BV) of animals based on their own records and (or) records of their relatives. The animal model has the following assumptions:

- 1) animals belong to a single population,
- 2) animals may have one or more records and covariances among records that are due only to genetic factors,
- 3) there is either no selection in the population or,
- 4) if selection occurred based on records, the selection was within fixed effects and
- 5) if selection occurred based on the BV of animals, the relationship matrix was complete.

The animal model in matrix notation is

$$y = Xb + Zu + e$$

where

$$E[y] = Xb$$

And because of assumptions (i) and (ii), we can say that

$$\begin{aligned} \text{var} \begin{bmatrix} u \\ e \end{bmatrix} &= \begin{bmatrix} G & 0 \\ 0 & I\sigma_e^2 \end{bmatrix} \\ &= \begin{bmatrix} A\sigma_A^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix} \end{aligned}$$

$$\text{Var}(y) = ZGZ' + R$$

$$= ZAZ' \sigma_A^2 + I\sigma_e^2$$

where

y = vector of animal records,

b = vector of unknown fixed effects,

u = vector of unknown random BVs belonging to the animals making records,

e = vector of unknown random residual effects,

X = known incidence matrix relating records to fixed effects in vector b ,

Z = known incidence matrix relating records to BVs in vector u .

Let

$$\alpha = \sigma_A^2 / \sigma_e^2$$

Then the mixed model equations (MME) for the animal model, after multiplying both sides by σ_e^2 are

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha^{-1} \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}$$

where A^{-1} is the inverse of the matrix of additive relationships among the animals with records.

The matrix A is the relationship matrix and it indicates the additive genetic relationship among individuals. This matrix is symmetric and its diagonal element for animal i (a_{ii}) is equal to $1 + F_i$, where F_i is the inbreeding coefficient of animal i (Falconer, 1989). The off-diagonal element, a_{ij} , equals the numerator of the coefficient of relationship between animal i and j . When multiplied by the additive genetic variance (σ_u^2), $A\sigma_u^2$ is the covariance among breeding values. Thus, if u_i is the breeding value for animal i ,

$$\text{Var}(u_i) = a_{ii} \sigma_u^2 = (1 + F_i) \sigma_u^2$$

The matrix **A** can be computed using path coefficients, but when there is a large amount of animals it is time consuming to do so. Henderson (1976a) proposed a recursive method that is suitable for computation and is the method currently used.

Maternal Trait Models

The phenotypic expression of some traits in progeny, such a weaning weight in beef cattle, is influenced by the performance of the dam. Thus, the dam contributes to the performance of the progeny through genes that she passes to her progeny and also through her ability to provide a suitable environment (for example milk production). Traits such as birth and weaning weights in beef cattle fall into this category and are termed maternally influenced traits. The ability of the dam to provide a suitable environment for expression of such traits in her progeny is partly genetic and partly environmental. Like the genetic component of an individual, the maternal genetic component can be partitioned into additive, dominance and epistatic effects (Willham, 1972). The environmental component may be portioned into permanent and temporary effects. It is the maternal additive genetic component of the dam that is passed on to her offspring, but it is expressed only when the female offspring have progeny of their own.

In the usual mixed linear model for maternally influenced traits, the phenotype is partitioned into the following:

1. Additive genetic effects from the sire and the dam, usually termed direct genetic effects.
2. Additive genetic ability of the dam to provide a suitable environment, usually termed indirect or maternal genetic effects.

3. Permanent environmental effects, which include permanent environmental influences on the dam's mothering ability and maternal non-additive genetic effects of the dam and

4. Other random environmental effects, termed residual effects.

The model for maternally influenced traits, in matrix notation, is

$$y = Xb + Zu + Wm + Spe + e$$

where

y = vector of observations

b = vector of fixed effects

u = vector of random animal effects

m = vector of random maternal (indirect) genetic effects

pe = vector of permanent environment effects

e = vector of random residual effects

X , Z , W and S are incidence matrices relating records to fixed animal, maternal genetic and permanent environmental effects respectively.

It is assumed that

$$\text{var} \begin{bmatrix} u \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} g_{11}A & g_{12}A & 0 & 0 \\ g_{21}A & g_{22}A & 0 & 0 \\ 0 & 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where

g_{11} is the additive genetic variance for direct effects

g_{22} is the additive genetic variance for maternal effects

g_{12} is the additive genetic covariance between direct and maternal effects

σ_{pe}^2 is the variance due to permanent environmental effects

σ_e^2 is the residual error variance

The variance of y is

$$\text{var}(y) = \begin{bmatrix} Z & W \end{bmatrix} \begin{bmatrix} g_{11}A & g_{12}A \\ g_{21}A & g_{22}A \end{bmatrix} \begin{bmatrix} Z' \\ W' \end{bmatrix} S I \sigma_{pe}^2 S' + \sigma_e^2$$

The best linear unbiased estimator (BLUE) of estimable functions of b and the BLUP of u, m and pe are obtained by solving the following mixed-model equations (MME):

$$\begin{bmatrix} X'X & X'Z & X'W & X'S \\ Z'X & Z'Z + A^{-1}\alpha_1 & Z'W + A^{-1}\alpha_2 & Z'S \\ W'X & W'Z + A^{-1}\alpha_2 & W'W + A^{-1}\alpha_3 & W'S \\ S'X & S'Z & S'W & S'S + I\alpha_4 \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \\ \hat{m} \\ \hat{pe} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ W'y \\ S'y \end{bmatrix}$$

Sire Model

Application of a sire model implies that only sires are evaluated, using progeny records. Most early applications of BLUP for the prediction of breeding values, especially in dairy cattle, were based on this model. The main advantage with the sire model is the number of equations is reduced compared with an animal model since only sires are evaluated. However, with a sire model, the genetic merit of the mate (dam of progeny) is not accounted for. It is assumed all mates are of similar genetic merit and this can result in biases in predicted breeding values if there is preferential mating (Elzo, 1996; Mrode, 1996).

The model in matrix notation is:

$$y = Xb + Zs + e$$

All terms were defined earlier and s is the vector of random sire effects and Z relates records to sires and

$$\text{Var}(s) = A \sigma_s^2$$

$$\text{Var}(y) = ZAZ' \sigma_s^2 + R$$

Where A is the numerator relationship matrix for sires,

$$\sigma_s^2 = \frac{1}{4} \sigma_A^2$$

and

$$R = I \sigma_e^2 .$$

The MME are exactly the same as animal model except that

$$\alpha = \sigma_e^2 / \sigma_s^2 = (4-h^2)/h^2.$$

Sire-Maternal Grand Sire Model (SMGSM)

An approach to estimation of maternal effects avoiding the bias given by the non-maternal genetic effects is the use of the Sire-Maternal Grand Sire Model. The model rests on simplifying assumptions made with respect to the data. The objectives can be to reduce computations or to generate a better behaved set of mixed model equations. The assumptions for this model are:

- 1) Parents have no records and
- 2) Dams are related only through their sires.

These simplifying assumptions reduce an animal model to a sire-maternal grand sire model (Elzo, 1996).

Connectedness

Connectedness can be defined as a measure of the relationships between herds or contemporary groups as they affect the accuracy of comparing the genetic values of

animals from one herd or group to another. When there is higher connectedness, there are more accurate comparisons of expected breeding values (EBVs) across groups or herds. Therefore, it is important to measure the degree of connectedness and, if necessary, bring it to a level that allows comparison of EBVs with reasonable accuracy (Mathur et al., 1998).

Genetic evaluations are used to compare individuals based on their relatives' breeding values. When comparing individuals from different countries, or other definable sub-populations, predicted differences between individuals include predictions of average genetic differences between the sub-populations. There may also be environmental differences affecting performance in each sub-population and the evaluation model must therefore partition the observed differences in performance into average environmental and genetic effects for each sub-population.

Genetic connections between sub-populations are required in order to separate genetic and environmental portions of performance differences between the sub-populations. The term connectedness refers to the number and quality of these genetic connections. Kennedy and Trus (1993) reviewed the concepts of connectedness and implications for genetic evaluation, describing situations where sub-population genetic differences would not be estimable or would have high variance of prediction error (PEV). The authors gave special attention to models with genetic groups, since connectedness is particularly important with these models. Hanocq et al. (1996) also found important effects of connectedness on PEV of genetic differences between sub-populations. Connectedness varies among countries and populations (e.g., Banos et al.,

1991) and may be of practical concern for PEV of genetic differences between countries in international evaluations.

Connectedness could also affect the accuracy of covariance component estimates. Schaeffer (1975) suggested only well-connected data subsets should be used to estimate genetic variances. Eccleston (1978) rebutted with a proof that all data should always be used. Banos and Sigurdsson (1996), however, showed that with international data undergoing selection within and across countries, the use of all data resulted in biased estimates of genetic correlations between countries. Use of a well-connected data subset gave unbiased estimates. The importance of connectedness clearly depends on the evaluation model being used and characteristics of data being evaluated. Connectedness is most important when genetic and environmental factors in the model are confounded, unless there are genetic connections between the sub-populations and when data are undergoing selection forces that may not be fully accounted for by the model.

When animals are reared under different environmental conditions, the accuracy of sire comparison depends upon the degree of connectedness among those groups. Kennedy and Trus (1993) argued that the most appropriate measure of connectedness is the average PEV of differences in EBV between animals in different management units. However, computing this statistic is extremely time consuming and not feasible for routine application (Roso et al., 2002). Thus, Kennedy and Trus (1993) proposed the use of variance of estimated differences between management unit effects, which were highly correlated with the PEV of the differences between EBV in their simulation study. Mathur et al. (1998) argued that the PEV of difference between herd effects can be used to measure the degree of connectedness between two herds. They proposed the

connectedness rating (CR), defined as the correlation between estimated effects of two management units. This CR is less dependent on size and structure of management units. Fries (1998) proposed the use of a number of direct genetic links (GLt) between different management units due to common sires and dams as a method for measuring degree of connectedness among contemporary groups. Roso et al. (2002) described the comparison between connecting rating and genetic links for measuring the degree of connectedness among contemporary groups of station-tested bulls. They concluded CR is more dependent on the size of the CG than GLt and the use of CR as a connectedness measure will cause larger contemporary groups (CG) to be favored. GLt, unlike CR, allows differentiation between completely disconnected CG from connected ones. GLt is computationally much less demanding than CR and can be routinely used with the aim of increasing the level of connectedness, obtaining more accurate comparisons of EBVs between CG.

Genetic Computational Software

The complexity of models used or considered for use in genetic evaluation is increasing. Examples of new models are test-day models in dairy cattle (Meyer and Hill, 1997; Gengler et al., 1999; Meyer, 2002), growth models in beef cattle or random regression models (Schaeffer, 2004) and models with dominance and/or quantitative trait loci (QTL) effects (Broman, 2002; Szyda et al., 2002). These models are usually linear but analyses of some traits may require nonlinear models which are usually more complicated to write and test. More complicated models may require larger data sets. In the future one may expect new types of models that will be used to analyze even larger data sets (Misztal, 1999).

Efforts have been made to make software more efficient. Lidauer and Strandén, (1999) compared two procedures, MiX99 and DMUIOD and it is clear there is genetic software that is more efficient than others. Time required to finish an analysis depends on the number of records and complexity of the model (Table 2-1). Other new alternatives for data analyses include use of parallel computers and scalability to increase memory and reduce computational time (Larsen and Madsen, 1999; Madsen and Larsen, 1999).

Table 2-1. Wall clock time (in minutes) to solve three mixed model equations of different size (M1, M2, M3) and number of iterations until convergence, by different computing software.

Computing software	MiX99			DMUIOD		
	M1	M2	M3	M1	M2	M3
Time to prepare data for solver	2	36	62	2	66	189
Time for solving until convergence	7	161	490	55	1,116	10,152
Number of iterations	212	149	167	438	305	380

M1: 240,000 records and 38,256 animals, single trait.

M2: 6.7 million records and 1,343,337 animals, single trait.

M3: 8.4 million records and 1,343,337 animals, three traits.

Lidauer and Strandén, 1999.

To analyze genetic information there are several computational packages that will be described.

ASREML

This is a general mixed models analysis program with emphasis on the estimation of variance components under a range of variance structures. It was first written in 1996 and is under continuing enhancement with particular attention to agricultural experiments. The two central ideas incorporated in the ASREML program are use of the Average Information (AI) algorithm for obtaining the Restricted Maximum Likelihood (REML) update to the variance parameters and use of sparse matrix methods (Gilmour et

al., 1995). The Average Information algorithm is a quadratic convergence method similar to Fisher Scoring except that it uses an information matrix which is approximately the average of the observed and expected information matrices. These both contain a trace term which takes considerable time to calculate. But when the average is formed, the trace term is canceled. The average information matrix is calculated avoiding the calculation of the trace term. The average information algorithm is supplemented by Expectation-Maximization (EM) steps when the matrix estimated by AI is non-positive definite. The second idea is based upon the assumption that not all elements of the inverse of the coefficient matrix are required. The equations are solved in an order that retains a high level of sparsity (Gilmour et al., 2002).

DFREML and MTDFREML

Derivative Free Restricted Maximum Likelihood and Multitrait Derivative Free Restricted Maximum Likelihood softwares have been written with the analysis of data from animal breeding in mind. They deal with the estimation of covariance components and the resulting genetic parameters, e.g. heritabilities and genetic correlations. In calculating the likelihood it is assumed that data have a multivariate normal distribution. The model of analysis fitted throughout is the Animal Model and these programs allow one or two additional random effects to be fitted. A total of 10 different models of analysis are accommodated, depending on the variances and covariances to be estimated and the assumptions in the model.

Maximum Likelihood Estimation: (ML) is conceptually straightforward. For a given model of analyses, one set of parameters to be estimated with an assumed distribution of the data, we can write the likelihood function L . The ML estimates for a specific data set are the numerical values of the parameter for which L attains its

maximum. The likelihood function is commonly assumed to be proportional to the probability density function of the distribution invoked i.e., the likelihood concept is related to probability calculations. After the parameters are estimated, data prediction is made to make inferences about the parameters which have given rise to observed data. In practice, the log of the likelihood function, often referred to as the support function is maximized (Meyer, 1997).

The scope of ML estimation for estimation of variance components has been reviewed by Elzo (1996). While ML estimators have ‘built-in’ optimal statistical properties such as consistency, efficiency and asymptotic normality and, under certain conditions, can account for non-random sampling of data, there are two major conceptual drawbacks. The first is the distribution of the data, usually a multivariate normal distribution in the estimation of variance components, is assumed to be known. There are some suggestions that the ML estimator assuming normality may be appropriate even if this does not hold. Secondly, ML estimators are biased by the fixed effects and the fixed effects in the model are treated as if they were known. This bias can be removed by considering only the part of the likelihood function which is independent of the fixed effects (Meyer, 1997). This procedure is generally referred to as Restricted Maximum Likelihood (Searle, 1971).

In animal breeding, interest in (RE)ML estimation of (co)variance components has been stimulated because it yields estimates less affected by selection bias than analysis of variance type methods (Henderson, 1975b). More recently, attention has focused on its desirable statistical properties as well as its flexibility. This allows for non-standard designs in estimating genetic parameters, i.e., the combination of information from

different types of relatives (Henderson, 1976b). Developments in the application of REML to analyze animal breeding data have followed closely those in the genetic evaluation of animals by Best Linear Unbiased Prediction (BLUP) (Henderson, 1976a). In particular, the introduction and increasingly widespread use of the animal model has furthered interest in and use of REML. Except for simple and balanced designs, REML estimation of variance components requires the numerical solution of a constrained, non-linear optimization problem. Iterative procedures to locate the minimum or maximum of a function are generally classified according to the amount of information from derivatives of the function which is utilized (Meyer, 1997).

Early applications of REML under a sire model generally used algorithms requiring first or second derivatives (or their expected values) of the log likelihood function, i.e., the EM (Expectation-Maximization) algorithm and Fisher Scoring Method. Though relatively fast to converge, these were computationally demanding. EM is known to be slow to converge. They require the inverse of a matrix of size equal to the number of random effects times the number of traits analyzed in each round of iteration. This was true unless some special features of the data structure could be exploited. Alternatively, the optimum of a function can be located without knowledge of its derivatives. Methods range from direct search procedures, which rely on mere comparison of function values, to procedures approximating first or even second derivatives using numerical techniques. Use of a derivative-free (DF)REML algorithm was first considered by Graser et al. (1987) for univariate analyses under an animal model. While they considered a model fitting animals' additive genetic effects as the only random effect, the approach is suitable for models including additional random effects and multivariate analyses (Meyer, 1989).

Crossbreeding and Multibreeding Mixed Models

Livestock in the tropical regions are known to be generally less productive than those in more temperate zones (Galina and Russell, 1987). With approximately one-third of the world's cattle population situated in the tropics (FAO, 2003), this source of animal protein must be fully exploited to meet the needs of the rapidly growing human population. Attempts to improve cattle production in the tropics have met with limited success. Technological advances developed in industrialized countries and applied to tropical animal production generally have not worked well under local conditions. Breeds imported from temperate zones have not adapted well to the extreme conditions encountered in many tropical climates (Pearson de Vaccaro, 1973). Therefore, much research effort has concentrated on development of crosses between local *Bos indicus* cattle and *Bos taurus* breeds that have shown better adaptability to the tropics (Galina and Russell, 1987; Galina and Arthur, 1989, 1991). Another effort has been to identify *Bos taurus* breeds that have been adapted to the tropics. The objective is to use these breeds in developing countries (Hammond et al., 1996; Elzo et al., 1998a, 2001; Peña, 1998).

Elzo (1999) defined a multibreed population as one composed of straightbred and crossbred animals that interbreed. Multibreed populations can be classified as either complete or incomplete. Complete multibreed populations are those whose mating patterns follow a diallel design. Incomplete multibreed populations are those having different numbers and/or kinds of mating groups of sire and dams. Several approaches have utilized in evaluation of multibreed populations.

The Multibreed Evaluation Procedure developed by Elzo and Famula (1985) allows purebred and crossbred animals to be evaluated simultaneously. This approach allows purebred and crossbred sires to be evaluated for additive, nonadditive and total genetic

effects. The total genetic value of an animal (TEPD) is defined as the sum of an additive expected progeny difference (EPD), plus a non-additive EPD. The Additive EPD is that portion of a multibreed evaluation equivalent to a within-breed EPD. The non-additive EPD measures the combining ability of a sire when mated to dams of a particular breed composition (Manrique, 1992; Elzo, 1999). This approach has been used to analyze several crossbred populations: the Angus-Brahman herd of the University of Florida for preweaning growth traits (Elzo and Wakeman, 1998) and carcass traits (Elzo et al., 1998b); the Romosinuano-Brahman herd of Turipana, Colombia for pre and postweaning growth traits (Elzo et al., 1998a) and the Sanmartinero-Brahman herd of La Libertad, Colombia for pre and postweaning growth traits (Elzo et al., 2001). In the multibreed population of dairy cows of Thailand, this approach has been used to estimate multibreed genetic parameters and genetic values for first lactation 305-d milk, fat yield and fat percentage. It has also been utilized in the estimation of lactation curves and prediction of daily and accumulated milk yield (Koonawootrittriron et al., 2001, 2002a, b).

The current approach used to compare bulls across breeds consists of adding a correction factor to the difference between the intrabreed EPDs of two bulls. These correction factors are based on differences in performance of progeny of bulls of various breeds when mated to Angus and Hereford females. These correction factors have been computed at the U. S. Meat Animal Research Center (USMARC) in Clay Center, Nebraska (Barkhouse et al., 1995; Gosey, 1997; Van Vleck and Cundiff, 2004). This type of comparison may not be appropriate because it ignores differences between environments and assumes that all animals in the analysis are of uniform genetic composition (Nuñez-Dominguez et al., 1995).

Cytoplasmic Effects

In eukaryotic cells there are two kinds of DNA; nuclear DNA and mitochondrial DNA. The inventory of nuclear and mitochondrial-coded proteins required to assemble a functional mitochondrion shows clearly that nuclear and mitochondrial genomes interact in at least two ways. First, both contribute to mitochondrial protein function. Secondly, affect the synthesis and assembly of mitochondrial proteins. The first type of interaction is important for the regulation of oxidative energy production. Isoforms of the nuclear-coded subunits of cytochrome c oxidase affect the catalytic functions of its mitochondrially-coded subunits. These isoforms are differentially regulated by environmental and developmental signals and allow tissues to adjust their energy production to different energy demands. The second type of interaction, biosynthesis of mitochondrial proteins, requires the bidirectional flow of information between the nucleus and the mitochondrion. Communication from the nucleus to the mitochondrion makes use of proteins that are translated in the cytosol and imported by the mitochondrion. Communication from the mitochondrion to the nucleus involves metabolic signals and one or more signal transduction pathways that function across the inner mitochondrial membrane. Just as the nuclear genome affects the expression of mitochondrial genes, the mitochondrial genome can affect the expression of nuclear genes for mitochondrial and other proteins (Poyton and McEwen, 1996).

Cattle breeders have long believed in special attributes of certain maternal lineages, often referred to as cow families. For example, when they are buying a bull or dam, they request not only for the genetic evaluation, but also for the maternal lineage and they prefer animals that come from outstanding females. A possible cause could be correlated environmental effects within lineages; perhaps cows born into outstanding lineages

receive preferential treatment in proportion to the perceived quality of the family (Gibson et al., 1997).

There are three genetic explanations for maternal effects: maternal additive inheritance, cytoplasmic inheritance and maternally-biased parental imprinting. Parental imprinting occurs at some loci, some genes function properly only when they are donated by the father, while others function properly only when they are contributed by the mother (Surani et al., 1984; Hoffman, 1991).

The mitochondria (mt) provide a possible mechanism of cytoplasmic inheritance, being inherited exclusively through the maternal lineage (Hutchison et al., 1974). Arguments in favor of mitochondrial contributions to variation include: 1) the mitochondria are central to cellular function, particularly energy metabolism; 2) there are probably several thousand copies of mtDNA in an average cell and only two copies of nuclear DNA; 3) mtDNA may code for up to 10% of gene products expressed in mitochondria, though it may be much less given the lack of knowledge about the number of enzymes and structural products involved in mitochondrial function; and 4) mtDNA has about 10 fold higher mutation rate than nuclear DNA (Gibson et al., 1997).

Environmental effects for some economically important traits in beef cattle include the maternal environment provided by the dam. A maternal effect is any influence, other than the contribution resulting from nuclear genes that the dam has on the phenotype of her progeny (Rohrer et al., 1994). Since mitochondria play an important role in intracellular protein and energy metabolism, the assumption that cytoplasmic effects could be involved in productive traits is reasonable (Bell, 1985).

Differences among maternal cytoplasmic lines in dairy cattle accounted for 2% of the total variation for milk yield and 3.5% of total variation for fat percentage. They were a significant source of variation for open days (Tess et al., 1987). Huizinga et al. (1986) found cytoplasmic variation for milk yield was 5.6%, fat percentage was 4.8%, protein percentage was 6.2%, kilograms of fat plus protein was 10.1% and milk return was 2.5% of the total variation.

Cytoplasmic effects in beef cattle accounted for 2% for birth weight, 5% for average daily gain and 5% for weaning weight adjusted to 205 days in Hereford calves (Tess et al., 1987). On the other hand, Brown et al. (1988) reported that variability in mitochondrial respiratory activity had little association with weaning weight and yearling growth in beef cattle. Cytoplasmic effects were not detected for birth weight, weaning weight and post weaning average daily gain in Brangus cattle (Rohrer et al., 1994). In sheep, no cytoplasmic effects were found for birth weight, weaning weight, fleece weight and number of lambs born (Hanford et al., 2003; Van Vleck et al., 2003).

Under tropical conditions, *Bos indicus* x *Bos taurus* crosses have been used to increase production traits (Elzo et al., 2001; Olson et al., 1990; Rosales-Alday et al., 2004b). Roberson et al. (1986) found differences between reciprocal crosses for birth traits. A difference of more than 7 kg for birth weight has been observed between reciprocal cross embryos regardless of breed type of surrogate dam (Baker et al., 1990; Thallman et al., 1992). Cytoplasmic inheritance could be responsible for some of these differences.

Effects of mitochondrial DNA have been reviewed and recently estimated by embryo transfer or by statistical procedures (Bell et al., 1985; Huizinga et al., 1986; Tess

et al., 1987). Bell et al. (1985) reported that cytoplasmic effects accounted for 2, 1.8, 1.8 and 3.5 % of the total variance for milk yield, milk fat, fat corrected milk and fat percentage, respectively. Cytoplasmic effects were significant even after adjustment for sire, maternal grandsire and dam's production. Northcutt et al. (1991) analyzed birth and weaning weight for 847 and 427 synthetic beef cattle, using Jersey, Angus and Simmental sires on crossbred cows, in three lines (small, medium and large size) divided between two herds, representing up to 69 lineages and tracing back to foundation cows in 1977. Use of the animal model with lineage as a random effect gave estimates of lineage contribution to total variance in different lines and herds from zero to 5%, with 8 of 12 estimates being zero. The authors concluded that there was no evidence for cytoplasmic inheritance in those herds.

Important cytoplasmic genetic effects of beef cattle could have large effects on breeding programs. Identification of superior cytoplasmic lines would increase the value of some cows for use in embryo transfer. Similarly, breeds with superior cytoplasm would become more valuable as maternal lines in crossbreeding systems or as foundation females for composite breeds. Large cytoplasmic genetic effects would increase the value of maternal relatives' performance (Tess et al., 1987).

When mitochondrial effects are ignored, the estimation of heritability and permanent environmental variances and additive genetic variance were overestimated (Boettcher et al., 1996). Southwood et al. (1989) obtained similar results and noted the additional confounding of additive direct and cytoplasmic variance with the additive maternal variance.

CHAPTER 3
GENETIC PARAMETERS IN SIMMENTAL-BRAHMAN HERDS UNDER
MEXICAN SUBTROPICAL CONDITIONS

Introduction

Tamaulipas is a Mexican border state, located south of Texas. The commercial relationship between these two states is important for Mexico and the USA and includes livestock products such as live animals from Tamaulipas to Texas and bovine germplasm from Texas to Tamaulipas. This germplasm has been used according to specific Mexican cattlemen criteria. These criteria have not included predicted genetic values that could increase the productivity of Mexican herds for economically important traits and would increase quality of cattle sent from Mexico to the USA (De los Santos et al., 2003).

The imported breeds with the largest numbers in Tamaulipas are Simmental (S) and Simbrah (SB). Males and females of these imported breeds have been crossed with Mexican Brahman (B) cattle. Crossbreeding has been done without a clear strategy and genetic ability of the resulting crossbred animals under Mexican subtropical conditions is unknown. However, several phenotypic studies comparing *Bos taurus* and *Bos indicus* crosses under tropical Mexican conditions concluded that F₁ heifers calved at younger age than purebred *Bos indicus* and F₁ animals had higher weaning rates than *Bos indicus* (Rios-Utrera et al., 1996; Vega-Murillo et al., 1996). These studies dealt with phenotypic mean values of groups of animals.

Genetic evaluations of purebred and crossbred animals for economically important traits (e.g., growth) are needed to genetically improve the cattle population in the

Tamaulipas region. Only recently genetic evaluations in Angus, Charolais and Simmental breeds have been conducted in Mexico, but included only purebred animals (Martinez et al., 2002; Rosales-Alday, et al., 2002b; Vega et al., 2002). Conversely, Mexican commercial producers practice both straight breeding and crossbreeding. Thus, it becomes necessary to obtain estimates of genetic parameters for these types of herds under their environmental conditions. Unfortunately, because individual commercial producers make decisions independently of one another when choosing germplasm, herds are disconnected and genetic parameters cannot be estimated for the entire population. The only current alternative is to estimate genetic parameters within herds and to carry out intra-herd genetic evaluations.

To obtain genetic parameters for growth traits, three independent beef herds under Mexican subtropical conditions with available growth information agreed to participate in this study. Herd 1 included purebred Simmental and Simbrah sires mated to S, $\frac{3}{4}$ S $\frac{1}{4}$ B, Simbrah, $\frac{1}{2}$ S $\frac{1}{2}$ B, $\frac{5}{16}$ S $\frac{11}{16}$ B, $\frac{1}{4}$ S $\frac{3}{4}$ B and Brahman cows. Herd 2 contained Simmental and Brahman sires mated to $\frac{5}{16}$ S $\frac{11}{16}$ B and Brahman cows. Herd 3 used Simmental and Brahman sires to mate Brahman cows. Thus, the objectives of this study were to estimate genetic parameters for birth weight (BWT) and 205 d-adjusted weaning weight (WW205) for three disconnected herds under Mexican subtropical conditions.

Material and Methods

Data and Herd Management

Data were field records from Simmental, Brahman and crossbred between Simmental and Brahman calves from three commercial herds in the NE region of Mexico (Tamaulipas). This region has dry subtropical conditions, with a yearly average temperature of 23°C and 812 mm of rainfall. Animals were kept on pastures composed

of star grass (*Cynodon nlemfuensis*) and native grasses throughout the year. Vitamins and mineral supplements were provided throughout the year. Heifers were bred to calve at approximately three years of age. Herds 1 and 2 used natural service during the year. Herd 3 used artificial insemination with Simmental semen and if cows were not pregnant after three inseminations, they were mated to Brahman bulls. Cows without pregnancies in two consecutive years were culled. Calving occurred throughout the year for the three herds. Calving seasons were classified according to the climatic conditions as follows: Winter (January to March), Spring (April to June), Summer (July to September) and Fall (October to December). Records for birth weight and weaning weight, were obtained for all three herds.

Herd 1 had 2,134 BWT and 1,729 WW205 records from 2,134 calves born in five years (1994 to 1998). These calves were produced by the mating of 32 Simmental and 32 Simbrah sires to 555 Brahman, 22 $\frac{1}{4}$ S $\frac{3}{4}$ B, 43 $\frac{5}{16}$ S $\frac{11}{16}$ B, 288 $\frac{1}{2}$ S $\frac{1}{2}$ B, 44 Simbrah, 122 $\frac{3}{4}$ S $\frac{1}{4}$ B and 47 Simmental dams. Herd 2 had 1,270 BWT and 373 WW205 records from 1,270 calves born in two years (1995 to 1996). These calves were produced by the mating of 3 Simmental and 53 Brahman sires to 980 Brahman and 79 $\frac{5}{16}$ S $\frac{11}{16}$ B cows. This herd had four calf groups: purebred Brahman and three crosses between Simmental and Brahman breeds. Herd 3 had 582 BWT and 443 WW205 records from 582 calves born in four years (1993 to 1996). These calves were produced by the mating of 11 Simmental and 11 Brahman sires to 386 Brahman cows. Number of sires, dams and calves by sire-breed-group \times dam-breed-group combination by herd are shown in Table 3-1.

Table 3-1. Number of sires, dams and calves by herd and breed-group-of-sire  breed-group-of-dam combination

	Breed group of Dam	Breed group of sire				
		Simmental	Simbrah (5/8S 3/8B)	Brahman		
		Breed group of calf		Breed group of calf		
Herd 1	Simmental	9 ^a				
		47 ^b				
		70 ^c	S			
	3/4S 1/4B		10		27	
			19		117	
			23	7/8S 1/8B	218	11/16S 5/16B
	Simbrah (5/8S 3/8B)			18		
				44		
				81	5/8S 3/8B	
	1/2S 1/2B			30		
				288		
				521	9/16S 7/16B	
	5/16S 11/16B		2		10	
			3		40	
			4	21/32S 11/32B	43	15/32S 17/32B
1/4S 3/4B		8		7		
		19		10		
		25	5/8S 3/8B	16	7/16S 9/16B	
Brahman		30		29		
		410		249		
		756	1/2S 1/2B	377	11/16S 5/16B	
Herd 2	5/16S 11/16B	3			53	
		9			79	
		9	21/32S 11/32B		79	5/32S 27/32B
	Brahman	3			53	
		62			918	
	63	1/2S 1/2B		1119	B	
Herd 3	Brahman	11			11	
		289			159	
		376	1/2S 1/2B		207	B

^a Number of sires within breed group of sire × breed group of dam interaction.

^b Number of dams within breed group of sire × breed group of dam interaction.

^c Number of calves within breed group of sire × breed group of dam interaction.

Calf records without birth date and of unknown parents (sire and dam) were deleted. Because 205 days was the standard age at weaning in Tamaulipas, weaning weights were adjusted to 205 days using the Beef Improvement Federation adjustment procedure (BIF, 1996). Age of dam (AOD) in days was divided into eight year categories (BIF, 1996). Contemporary groups (CG) were defined as groups of calves born in the same year, season and had the same sex. Calves of all breed group combinations were allowed in a CG (Elzo, 1983; Elzo and Famula, 1985; Klei et al., 1998). At least two sires were required per CG. Because no connection across herds was present, analyses were made within herds. All pedigree information available was included in the analyses to reduce bias due to selection and to increase accuracy of estimation through ties among related animals (Henderson, 1974).

Estimation of Variance Components and Heritabilities

Estimates of variance components were obtained by maximizing the REML log-likelihood function using the Average Information algorithm (Gilmour et al., 1995), implemented in the ASREML program (Gilmour et al., 2000). Convergence was assumed to have been achieved when the log-likelihood changed less than 0.002 in two consecutive iterations.

A single trait sire-dam model was used to estimate variances. Traits were assumed to have direct and maternal genetic effects. Because herds had different breed composition, environmental fixed effects and genetic group effects in the model varied across herds. Random effects were the same for all traits in the three herds.

Model for Herd 1. Fixed effects for BWT and WW205 were contemporary group and calf-sex \times age-of-dam \times breed-group-of-dam interaction. Age of dam was treated as

a continuous variable and expressed in years. Breed group of dam was modeled as a regression on the Simmental fraction of the dam and were included depending on the presence or not of the genetic group effect in the crossbred sire, dam or calf. The fixed regression genetic group effects were: 1) sire intrabreed additive direct, (as a function of the expected fraction of Simmental alleles in all sires, (pS^{SIRE})), 2) dam intrabreed additive direct plus maternal (as a function of the expected fraction of Simmental alleles in all dams (pS^{DAM})), 3) sire interbreed nonadditive direct, as a function of the probability of Simmental and Brahman alleles at one locus of the progeny of all sires (pS/B^{calf}) and 4) dam interbreed nonadditive maternal as a function of the probability of Simmental and Brahman alleles at one locus of the dam (pS/B^{DAM}) (Appendix A) (Elzo and Wakeman, 1998). Random genetic effects were sire additive direct, dam additive direct plus maternal and residual (Table 3-2). In this model, sire random effects contained $\frac{1}{2}$ of the additive direct genetic effects, whereas dam maternal effect included $\frac{1}{2}$ of the additive direct genetic effects plus all maternal genetic effects.

The mixed model was:

$$y = X_c c + X_g g + Z_s s + Z_d d + e$$

where

y = vector of observations (BWT or WW205).

c = vector of contemporary groups and calf-sex \times age-of-dam \times breed-group-of-dam interaction,

g = vector of regression group genetic effects (sire intrabreed additive direct, dam intrabreed additive direct plus maternal, sire interbreed nonadditive direct and dam interbreed nonadditive maternal),

s = vector random additive direct sire genetic effects,

d = vector of random additive direct and maternal dam genetic effects,

e = vector of residuals,

X_c = matrix of 1s and 0s that relates calf records to elements of c ,

X_g = matrix of expected fraction of Simmental alleles that relates calf records to elements of g ,

Z_s = matrix of 1s and 0s that relates calf records to elements of s and

Z_d = matrix of 1s and 0s that relates calf records to elements of d .

It was assumed that

$$\begin{bmatrix} y \\ s \\ d \\ e \end{bmatrix} \sim MVN \left(\begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} ZGZ' + R & Z_s \sigma_s^2 * A_{ss} & Z_d \sigma_d^2 * A_{dd} & I \sigma_e^2 \\ \sigma_s^2 * A_{ss} Z_s' & \sigma_s^2 * A_{ss} & 0 & 0 \\ \sigma_d^2 * A_{dd} Z_d' & 0 & \sigma_d^2 * A_{dd} & 0 \\ I \sigma_e^2 & 0 & 0 & I \sigma_e^2 \end{bmatrix} \right)$$

where

$$b = [c \ g]',$$

$$X = [X_c \ X_g],$$

$$Z = [Z_s \ Z_d],$$

$$G = \begin{bmatrix} \sigma_s^2 * A_{ss} & 0 \\ 0 & \sigma_d^2 * A_{dd} \end{bmatrix},$$

σ_{sa}^2 is the sire direct genetic variance,

σ_d^2 is the dam direct plus maternal additive genetic variance,

* denotes direct matrix product.

The covariance between sire additive direct and dam direct plus maternal genetic effects was assumed to be zero.

Table 3-2. Fixed environmental effects, fixed genetic group effects, random genetic effects presented in the model, by herd and trait

Effect ^a	Herd 1		Herd 2		Herd 3	
	BW T	WW205	BWT	WW205	BWT	WW205
Fixed						
CG	*	*	*	*	*	*
SEX × AOD × BGD ^b	*	*	*			
SEX × AOD				*	*	*
IAD	*	*	*	*	*	*
IAM	*	*	*			
INTERBNAD	*	*	*			
INTERBNAM	*	*				
Random						
SIRE	*	*	*	*	*	*
DAM	*	*	*	*	*	*

^aCG = Contemporary group (year × season × sex);

^bSEX × AOD × BGD = calf sex × age of dam × breed group of dam interaction.

Model for Herd 2. The model for BWT included the fixed environmental effects of contemporary group and sex × age-of-dam × breed-group-of-dam interaction. Fixed genetic group effects were sire intrabreed additive direct, dam intrabreed additive direct plus maternal and sire interbreed nonadditive direct. Random genetic effects were sire additive direct, dam additive direct plus maternal and residual (Table 3-2). The model for WWT included the fixed environmental effects of contemporary group and sex × age-of-dam interaction. Breed-group-of-dam interaction was not included because this herd had no calf records from crossbred dams. The only fixed genetic group effect was sire intrabreed additive direct. Fixed genetic group of dam was omitted after preliminary runs failed because of confounding (93% of dams in this herd were Brahman). Random genetic effects were sire additive direct, dam additive direct plus maternal and residual. age of dam × breed-group-of-dam interaction; SEX × AOD = calf sex × age of dam interaction; IAD = sire intrabreed additive direct; IAM = dam intrabreed additive direct

plus maternal; INTERBNAD = sire interbreed nonadditive direct; INTERBNAM = dam interbreed nonadditive maternal (Appendix A).

Model for Herd 3. The model for BWT included the fixed environmental effects of contemporary group and sex \times age-of-dam interaction. Fixed dam genetic group effect was excluded because all dams were purebred Brahman. Random genetic effects were sire additive direct, dam additive direct plus maternal and residual (Table 3-2).

Heritabilities for additive direct genetic effects were computed as four times the sire additive direct genetic variance divided by the phenotypic variance. Heritabilities for maternal genetic effects were computed as the difference between dam direct plus maternal genetic variance and the sire additive direct genetic variance divided by the phenotypic variance. Thus, maternal heritabilities will contain any nonzero covariance between additive direct and additive maternal genetic effects.

Results and Discussion

Group Genetic Effects

Herd 1. Estimates of regression genetic groups effects for BWT were 1.34 ± 0.93 kg for sire intrabreed additive direct, -2.65 ± 1.02 kg for dam intrabreed additive direct plus maternal, -1.59 ± 0.88 kg for sire interbreed nonadditive direct and 1.19 ± 0.63 kg for dam interbreed nonadditive maternal. The positive sire intrabreed additive direct indicates that progeny of Simmental sires had larger BWT than progeny of Brahman sires, whereas the negative dam intrabreed additive direct plus maternal shows the opposite, i.e., that dams with more Simmental genes proportion produced smaller calves at birth than Brahman dams (Table 3-3). Thus, straight bred Simmental dams were apparently less adapted than Brahman dams to the local environmental conditions of herd 1. Negative sire interbreed nonadditive direct effects indicates that crossbred Simmental-

Brahman calves were smaller than the average of straight bred Simmental and Brahman calves. Thus, it appears that the local environment prevented the full manifestation of heterosis for BWT. Contrarily, positive dam interbreed nonadditive maternal effects suggests that calves of Simmental-Brahman crossbred dams were larger than the average of straight bred Simmental and Brahman cows (Table 3-3). Thus, Simmental-Brahman crossbred dams were able to withstand local environmental conditions and allow a fuller expression of intrauterine growth of crossbred calves than either purebred Simmental or Brahman cows.

Table 3-3. Least square means (\pm S.E.) for birth weight and weaning weight by breed group of dam in herd 1

Breed group of Dam	n	Birth Weight (Kg)	n	Weaning Weight (Kg)
Brahman (B)	427	34.60 \pm 0.17	349	222.7 \pm 1.7
8/32S 24/32B	40	34.88 \pm 0.55	31	223.7 \pm 5.8
10/32S 22/32B	46	34.59 \pm 0.52	29	193.0 \pm 6.0
16/32S 16/32B	521	34.32 \pm 0.16	424	203.6 \pm 1.6
20/32S 12/32B	81	34.47 \pm 0.39	74	208.8 \pm 3.8
24/32S 8/32B	241	33.93 \pm 0.23	205	211.3 \pm 2.3
Simmental (S)	41	34.08 \pm 0.55	38	180.2 \pm 5.3

For WW205 the estimates of regression genetic group effects for BWT were -28.96 \pm 8.8 kg for sire intrabreed additive direct, -12.84 \pm 8.8 kg for dam intrabreed additive direct plus maternal, 36.18 \pm 7.7 kg for sire interbreed nonadditive direct and 5.77 \pm 5.27 kg for dam interbreed nonadditive maternal. Negative sire intrabreed additive direct and dam intrabreed additive direct plus maternal suggest that Brahman dams were substantially better mothers than Simmental mothers, probably related to low milk production by Simmental cows under tropical conditions. Positive sire and dam nonadditive genetic effects suggest that crossbred calves grew faster and heavier than straightbred calves, particularly progeny from crossbred dams (Table 3-3). Thus,

adaptability of Simmental-Brahman crossbred calves and dams seemed to be appropriate to the local climatic, management and nutritional conditions of herd 1.

Herd 2. In this herd, the three genetic group's effects were present for the BWT, sire intrabreed additive direct, dam intrabreed additive direct plus maternal, sire interbreed nonadditive direct and just only sire intrabreed additive direct for WW205. Estimates of regression genetic group's effects for BWT were -0.25 ± 1.72 kg for sire intrabreed additive direct, -0.52 ± 1.64 kg for dam intrabreed additive direct plus maternal and 2.34 ± 1.65 kg for sire interbreed nonadditive direct. Negative values for sire intrabreed additive direct and dam intrabreed additive direct plus maternal indicates that Simmental sires used in this herd produced smaller calves than Brahman sires and the Simmental genes in the dam induce to produce smaller calves, this could be due to the small number of Simmental sires and Simmental-Brahman crossbred dams. Conversely, positive values for sire interbreed nonadditive direct indicate a better performance for crossbred calves. For WW205 sire intrabreed additive direct regression coefficient was 80.74 ± 76.3 kg, indicating that Simmental sires produce heavier calves at weaning.

Herd 3. In this herd, due to the no presence of crossbred cows, only sire intrabreed additive direct regression was estimated. For BWT was 1 ± 0.27 kg and for WWT was 19.11 ± 5.22 kg that suggest a superiority of Simmental sires over Brahman sires, due to use of artificial insemination in this herd, even though the principal criteria to buy semen was the price, not the genetic value of the sire.

Variance Components and Heritabilities

Herd 1. Estimates of variance components and heritabilities for BWT and WW205 are shown in Table 3-4. The genetic variance for BWTD was half as large as that for BWTM, indicating that maternal genetic effects were more important than direct genetic

effects in Herd 1. Heritability estimates for both traits were low probably in part due to the practice of utilizing imported Simmental and Simbrah sires of low predicted genetic values for BWT and partly due to the impact of the tough environmental conditions on animals in herd 1. Thermal stress, ticks and low forage quality appear to have prevented both purebred and crossbred animals from expressing their genetic potential for BWT. The small genetic variability expressed for BWT direct and maternal suggests that, under the current environmental conditions of herd 1, response to selection for BWT will be small.

Genetic variances and heritabilities for WW205D direct were larger than for WW205M. Calves' direct ability to grow was more important than the maternal environment between birth and weaning. Thus, selection for WW205D is likely to yield larger responses than selection for WW205M in this herd.

The heritability for WW205D was within the range reported by Mohiuddin (1993) for Simmental in the USA, the UK and Australia. It was close to the unweighted and weighted values given by Koots et al. (1994). The heritability of WW205M in herd 1 was in the upper limit of the values reported by Mohiuddin (1993) for Simmental in the USA, the UK and Australia. It was larger than estimates for Brahman in the USA and Australia (Mohiuddin, 1993).

Herd 2. Estimates of variance components and genetic parameters for BWT and WW205 in herd 2 are shown in Table 3-4. The extreme unbalancedness of this dataset may have caused problems of confounding and multicollinearity. Therefore estimates of variance components and genetic parameters from this herd should be viewed with extreme caution. The sire additive direct genetic variance was larger than the dam

additive direct plus maternal genetic variance. This resulted in a negative variance for additive maternal genetic effects. The extreme unbalancedness of the dataset from herd 2 (Table 3-1) may have contributed to these poor estimates of additive genetic variances for BWT. The additive maternal genetic variance and the maternal heritability were set to zero (Table 3-4).

Table 3-4. Estimates of genetic variances and heritability (\pm S.E.) for birth weight (BWT) and weaning weight (WW205) in all herds

	Trait ^a	Genetic variances	Heritability
Herd 1	BWTD	0.70 \pm 0.45	0.05 \pm 0.03
	BWTM	1.33 \pm 0.05	0.09 \pm 0.03
	BWTP	14.63 \pm 0.46	
	WW205D	191.50 \pm 69.80	0.23 \pm 0.08
	WW205M	96.36 \pm 9.46	0.11 \pm 0.04
	WW205P	847.30 \pm 4.53	
Herd 2	BWTD	6.00 \pm 1.53	0.84 \pm 0.17
	BWTM	0 ^b	0 ^b
	BWTP	7.16 \pm 0.44	
	WW205D	525.40 \pm 229.00	0.63 \pm 0.28
	WW205M	270.20 \pm 179.90	0.33 \pm 0.22
	WW205P	825.90 \pm 41.74	
Herd 3	BWTD	0.16 \pm 0.42	0.03 \pm 0.07
	BWTM	0.93 \pm 0.44	0.15 \pm 0.07
	BWTP	6.19 \pm 0.38	
	WW205D	250.10 \pm 180	0.22 \pm 0.15
	WW205M	206.70 \pm 119.90	0.17 \pm 0.10
	WW205P	1161.83 \pm 86.79	

^a D = direct, M = maternal, P = phenotypic

^b Negative maternal variance set to zero. Heritability set to zero.

Genetic variances and heritabilities for WWT traits were very large (but within the parameter space), indicating again a possible problem of confounding in this dataset. The heritability for WW205D was twice as large as the heritability for WW205M, which indicates that additive direct genetic effects were more important than maternal genetic

effects in herd 2. This result is in agreement with the results for these traits in herd 1. The heritabilities for WW205D traits were not within the range reported by Mohiuddin (1993) for Simmental in the USA and the UK. Conversely, the heritability for BWTD was similar to the value reported by the same author for Brahman in Australia.

Herd 3. Table 3-4 shows the estimates of variance components and genetic parameters for BWT and WW205 for herd 3. The heritability for BWTD was very small (0.03) and five times smaller than the heritability for BWTM (0.15). This suggests a strong maternal effect over birth weight that could be due to all dams in herd 3 were Brahman. Again, the extremely low BWTD heritability may have been partly due to using semen from sires with low predicted genetic values for this trait (as in herd 1) and partly because of difficult environmental conditions.

As with herds 1 and 2, the heritability for WW205D was much greater (almost twice) than the heritability for WW205M, again indicating that additive direct genetic effects were more important than additive maternal genetic effects for WWT under the subtropical conditions of the Tamaulipas region. Similarly, these heritabilities for WWT traits suggest a positive response to selection for weaning weight in this herd, both direct and maternal.

Heritabilities for BWT in herds 1 and 3 were substantially smaller than those obtained in the Romosinuano-Zebu (Turipaná, Colombia, Elzo et al., 1998a), Sanmartinero-Zebu (La Libertad, Colombia, Elzo et al., 2001) and Angus-Brahman (Florida, USA, Elzo and Wakeman, 1998) multibreed herds under subtropical conditions both for direct (.16 to .30) and for maternal genetic effects (.14 to .29). This suggests that environmental conditions of these three herds were less severe than those encountered in

herds 1 and 3 in Mexico. Therefore animals managed to express more fully their genetic abilities. Heritabilities for WWTD and WWTM in herds 1 and 3 were larger than those estimated for Romosinuano-Zebu (.09 to .13) and Sanmartinero-Zebu (.08 to .10) in Colombia and comparable to those for Angus-Brahman (.16 to .25) in the USA. This may be a consequence of the practice of choosing imported sires with low predicted genetic values for BWT, this limits the genetic variability among these sires for BWT, but not for WWT, as evidenced in heritability estimates for WWTD in both herds. Heritabilities for BWT and WWT traits for herd 2 were vastly different from those obtained in these three *Bos taurus* – *Bos indicus* multibreed herds. However, herd 2 was extremely unbalanced and may have had problems of confounding and multicollinearity as indicated above.

Genetic parameter estimation using data from commercial herds is not easy because there are factors that may not be feasible to include in a statistical model, such as owner criteria to define management conditions. The three herds included here were subjected to different environmental and management conditions, even though they had the same breeding objective; to recreate the Simbrah breed. Genetic parameter estimates were different across herds. Only variances and genetic parameter estimates from herds 1 and 3 were relatively similar. Better estimates of variance components and genetic parameters could have been obtained had these three herds been connected by using common sires. This would have permitted estimation of genetic parameters based on records from all three herds, thus increasing the total number of animals and observations and reducing standard errors of variances and genetic parameters.

Weaning weight is an economically important trait because the objective of Mexican subtropical cattle production systems is to produce weaning calves for export to the USA or for sale to regional feeders. Thus, additive direct and maternal genetic effects for weaning weight are important to measure and to use for sire evaluation in this region. The results obtained here for the three herds indicate that weaning weight (direct and maternal) showed enough genetic variation to be used to implement intra-herd selection programs. Additional genetic progress could be achieved if herds were genetically linked through use of common sires. It would be advantageous for commercial producers to consider the use of common sires as part of their genetic management. Other traits, such as yearling weight, carcass and survival traits, all of which are economically important, should also be included in future genetic evaluations and improvement programs.

Implications

Variance estimates and heritabilities for pre-weaning weight traits in three commercial herds in Tamaulipas showed that sufficient genetic variation existed to justify the implementation of within-herd genetic improvement programs, particularly for weaning weight traits. To have an even better chance of success for genetic improvement, herds need to be linked through the use of common sires. This would improve accuracy for both genetic prediction of genetic values and estimation of genetic parameters. Therefore increased genetic progress for weight traits should be expected. It would also be important to implement regional and(or) national genetic improvement programs that can use information from purebred and crossbred animals.

Summary

Purebred and crossbred Simmental and Brahman records from three unconnected herds were used to estimate within-herd variance components for additive direct and

maternal genetic effects for birth weight and 205 d-adjusted weaning weight. Herds were located in the subtropical region of Tamaulipas, Mexico. Variances were estimated by restricted maximum likelihood procedures using a sire-dam mixed model. Fixed effects were contemporary group, age of dam \times sex of calf \times breed group of dam interactions. Genetic group effects were sire intrabreed additive direct, dam intrabreed additive maternal, sire interbreed Simmental-Brahman nonadditive direct and dam interbreed Simmental-Brahman nonadditive maternal. Random genetic effects were sire additive genetic direct, dam additive genetic direct plus maternal and residual. Effects in the model varied according to trait and breed composition of the herd. Within-herd heritability estimates were 1) 0.05 ± 0.03 for BWTD, 0.09 ± 0.03 for BWTM, 0.23 ± 0.08 for WW205D, 0.11 ± 0.04 for WW205M in herd 1, 2) 0.84 ± 0.17 for BWTD, 0.63 ± 0.28 for WW205D and 0.33 ± 0.22 for WW205M, in herd 2 and 3) 0.03 ± 0.07 for BWTD, 0.15 ± 0.07 for BWTM, 0.22 ± 0.15 for WW205D and 0.17 ± 0.10 for WW205M. These intra-herd heritabilities showed more genetic variability was expressed for weaning weight than for birth weight traits. Thus, more genetic progress could be achieved for weaning weight direct and maternal than for birth weight traits in these herds. As more data is collected in these three herds, more precise estimates of genetic parameters and more precise selection for weight traits will be achieved.

CHAPTER 4
GENETIC PARAMETERS AND TRENDS FOR PREWEANING GROWTH TRAITS
IN THE MEXICAN SIMMENTAL POPULATION

Introduction

The Simmental breed has spread throughout the world and its total numbers now approach 41 million animals (BSCSL, 2003). The breed was introduced in Mexico in 1973 with importation of 10 bulls from Germany and Switzerland. In the 1980's large numbers of animals were imported from the USA and Canada and distributed to all regions of Mexico; from arid to tropical. Purebred and crossbred Simmental animals are well accepted by Mexican producers because their offspring are well accepted by both local and international markets and have good adaptability to a wide range of environmental conditions. For Mexican cattlemen to consistently produce beef that meet national and international market demands, it is important to implement national genetic improvement programs that can identify those animals that most closely meet these demands. The Office of the Secretary of Agriculture, Livestock and Rural Development in Mexico recognized the need for a national genetic improvement program in 1998 and published a document containing steps to be taken to achieve this objective (SAGAR, 1998). This document was written with participation of representatives from breed associations, national research institutes and universities. One of the steps was the genetic evaluation of purebred and crossbred beef animals using field data. This work required estimation of genetic parameters for the traits of interest in the populations to be evaluated. In addition, to evaluate the impact of selection decisions on the population,

genetic trends would be needed. Thus, the objectives of this paper were the estimation of additive direct and maternal genetic variances and covariances, heritabilities, genetic correlations and genetic trends for birth weight and weaning weight in the Mexican Simmental population.

Material and Methods

Data and Pedigree Files

Birth weights (BW) and weaning weights (WW) from Simmental calves were provided by 434 herds belonging to the Mexican Simmental-Simbrah Association. Herds were located in all regions of Mexico from arid to tropical (Fig. 4-1). Data were collected from 1982 to 1999.



Figure 4-1. Distribution of Simmental herds in Mexico by state.

Data editing was done according to the Beef Improvement Federation recommendations (BIF, 1996). Records outside three standard deviations were discarded as outliers. Calves with unknown parents and calves without BW and WW records were deleted. Four calving seasons were defined: winter (January-March), spring (April-June), summer (July-September) and fall (October-December). Contemporary groups were defined as animals born in the same herd, year and season. Sex was not included as part of the contemporary group definition because of insufficient data. However, sex was included as part of the mixed model. Contemporary groups with less than 10 calves and(or) less than two sires were eliminated. Alphanumeric animal identifications were renumbered with a FORTRAN program (Misztal, 1993). Contemporary group connectedness through common sires was verified with a FORTRAN program (Elzo, 2002). Ten percent of the original data were not connected and were eliminated. The connected dataset contained 18,383 BW and 9,023 WW from 18,460 calves. These calves were the progeny of 2,152 sires and 11,334 dams. A pedigree file was constructed that included calf, sire and dam. Only calves with purebred parents or with more than 31/32 Simmental were included in the pedigree file. The pedigree file included 26,539 animals. A fixed effects analyzes was made for both variables, BW and WW, including sex, season, age of dam in years and year of calf's birth.

Estimation of Genetic Parameters

Genetic variances and covariances were estimated by Restricted Maximum Likelihood using a derivative-free algorithm (Graser et al., 1987). Computations were performed using the MTDFREML package (Boldman et al., 1995). A two-trait (BW, WW) animal model with additive direct and maternal genetic effects was used to estimate covariance components and to predict genetic values. Because dams had repeated

records, permanent environment effect of the dam was included. Fixed effects were contemporary group (BW, WW), sex (BW, WW), age of dam (in days) at calving linear, quadratic and cubic (BW, WW) and age of calf (in days) at weaning linear, quadratic and cubic (WW only). Random effects for BW and WW were animal additive direct, dam additive maternal, dam permanent environment maternal and residual. In matrix notation, the two-trait mixed linear model can be represented as follows:

$$y = Xb + Z_i u_i + Z_d u_d + Z_{pe} d_{pe} + e$$

$$E[y] = Xb$$

$$\text{var} \begin{bmatrix} u_i \\ u_d \\ d_{pe} \\ e \end{bmatrix} = \begin{bmatrix} G_{0ii} * A & G_{0id} * A & 0 & 0 \\ G_{0di} * A & G_{0dd} * A & 0 & 0 \\ 0 & 0 & R_{0pe} * I & 0 \\ 0 & 0 & 0 & R_{0e} * I \end{bmatrix}$$

where

y = vector of BW and WW records,

b = vector of contemporary groups (herd-year-season), sexes and age of dam covariates (linear, quadratic and cubic) for BW and WW and calf age at weaning covariates for WW only (linear, quadratic and cubic) fixed effects,

u_i = vector of random calf additive direct genetic effects ($\frac{1}{2}$ sire additive direct plus Mendelian sampling from the sire and the dam of the calf),

u_d = vector of random dam additive maternal genetic effects ($\frac{1}{2}$ dam additive direct plus maternal),

d_{pe} = vector of random dam permanent environment maternal effects,

e = vector of residuals,

X = matrix of 1s, 0s and linear, quadratic and cubic factors that relates calf records to elements of b ,

Z_i = matrix of 1s and 0s that relates calf records to elements of u_i ,

Z_d = matrix of 1s and 0s that relates calf records to elements of u_d and

Z_{pe} = matrix of 1s and 0s that relates animal records to elements of d_{pe} .

For the definitions of covariance matrices, * = direct product, A = additive relationship matrix and the subscripts i = calf, d = dam, 1 = BW and 2 = WW. Thus,

$$G_{0ii} = \begin{bmatrix} \sigma_{i1,i1} & \sigma_{i1,i2} \\ \sigma_{i2,i1} & \sigma_{i2,i2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between calf additive direct}$$

genetic effects for trait j and calf additive direct genetic effects for trait j' ($j, j' = 1, 2$),

$$G_{0id} = \begin{bmatrix} \sigma_{i1,d1} & \sigma_{i1,d2} \\ \sigma_{i2,d1} & \sigma_{i2,d2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between calf additive direct}$$

genetic effects for trait j and dam additive maternal genetic effects for trait j' ($j, j' = 1, 2$),

$$G_{0di} = \begin{bmatrix} \sigma_{d1,i1} & \sigma_{d1,i2} \\ \sigma_{d2,i1} & \sigma_{d2,i2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between dam additive maternal}$$

genetic effects for trait j and calf additive direct genetic effects for trait j' ($j, j' = 1, 2$),

$$G_{0dd} = \begin{bmatrix} \sigma_{d1,d1} & \sigma_{d1,d2} \\ \sigma_{d2,d1} & \sigma_{d2,d2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between dam additive maternal}$$

genetic effects for trait j and dam additive maternal genetic effects for trait j' ($j, j' = 1, 2$),

$$R_{0pe} = \begin{bmatrix} \sigma_{pe1,pe1} & 0 \\ 0 & \sigma_{pe2,pe2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between dam permanent}$$

environment maternal effects for trait j and dam permanent environment maternal effects for trait j' ($j, j' = 1, 2$),

$$R_{0e} = \begin{bmatrix} \sigma_{e1,e1} & 0 \\ 0 & \sigma_{e2,e2} \end{bmatrix} = 2 \times 2 \text{ matrix of covariances between temporary}$$

environmental effects for trait j and temporary environmental effects for trait j' ($j, j' = 1, 2$).

Genetic Trends

Calf additive direct and dam additive maternal genetic values were predicted using the same direct-maternal animal model and MTDFREML software (Boldman et al., 1995) used to estimate covariance components and genetic parameters. Yearly means of predicted calf and dam genetic values were subsequently computed for BW and WW. Calf and dam genetic trends were generated by plotting BW and WW over time (Smith, 1962).

Results and Discussion

Phenotypic results

All effects included in the model were statistically significant ($P < 0.01$). Model explained 4% of the variance for birth weight and 5% for weaning weight. Means for birth weight and weaning weight by calf sex, season and age of dam are presented in the Table 4-1. Birth weight and weaning weight general means were 38.7 ± 5.6 kg and 244.9 ± 45.8 kg, respectively. Birth weight mean is similar to that reported by Cundiff et al. (1998), where several breeds were evaluated including Gelbvieh, which have a similar performance as Simmental. In this study BWT mean is similar with that reported for the Simmental breed by the BIF (1996). For Mexican Simmental females in this study, there is a superiority of 2.4 kg with respect to the BIF (1996) report. Means for calving season do not show a clear difference because the data came from different Mexican regions, including tropical and subtropical conditions where seasonality is not present. The higher

mean value for birth weight was for ten years old dams and the smallest was for three years old dams. There is a discrepancy with the BIF (1996) report, where the mature age is between 5 and 9 years.

Table 4-1. Least square means (\pm S.E.) for birth weight and weaning weight by calf sex, season and age of dam for Mexican Simmental breed

Effect	N	Birth Weight (Kg)	n	WW205-d (Kg)
Total	19,367	38.82 \pm 0.04	8,800	235.22 \pm 0.50
Sex				
Males	9,720	40.34 \pm 0.13	5,460	244.31 \pm 1.22
Females	9,647	38.68 \pm 0.12	3,340	235.63 \pm 1.19
Season				
Jan-Mar	5,802	39.86 \pm 0.13	2,298	243.30 \pm 1.41
Apr-Jun	5,645	39.82 \pm 0.13	2,708	245.54 \pm 1.33
Jul-Sep	4,322	39.39 \pm 0.14	2,091	234.48 \pm 1.39
Oct-Dec	3,598	39.95 \pm 0.14	1,703	236.55 \pm 1.46
Age of dam (years)				
2	2,592	39.44 \pm 0.12	1,087	241.01 \pm 1.56
3	2,684	38.69 \pm 0.15	1,270	235.64 \pm 1.51
4	2,960	39.20 \pm 0.14	1,343	238.24 \pm 1.48
5	2,578	39.43 \pm 0.15	1,264	235.75 \pm 1.53
6	2,318	39.68 \pm 0.15	1,206	240.85 \pm 1.56
7	1,927	39.62 \pm 0.16	1,006	238.99 \pm 1.66
8	1,371	39.74 \pm 0.18	701	243.17 \pm 1.96
9	1,063	39.81 \pm 0.20	529	240.47 \pm 2.20
10	369	39.85 \pm 0.30	162	243.68 \pm 3.80
11	240	39.70 \pm 0.37	109	235.19 \pm 4.61
12	265	39.40 \pm 0.35	123	246.66 \pm 4.35

The weaning weight mean of 235.20 kg is higher than the range of 167-182 kg, for several crossbred groups under Mexican tropical conditions (Rios-Utrera et al., 1996).

Unfortunately they did not use the Simmental breed. Comparing with the USA Simmental breed, the mean found in this study was smaller than the 265.9 kg mean reported by Lee et al. (1997) and is similar to the reported by Szabó et al. (2002) in Europe.

Phenotypic trend for birth weight is -129 grams per year and is highly significant ($P < 0.001$) (Figure 4-2). It looks like Mexican producers intuitively have been selected

sires and dams to reduce the birth weight in their herds, to avoid calving problems.

Phenotypic trend for weaning weight is -2 kg per year and is highly significant ($P < 0.001$) (Figure 4-3).

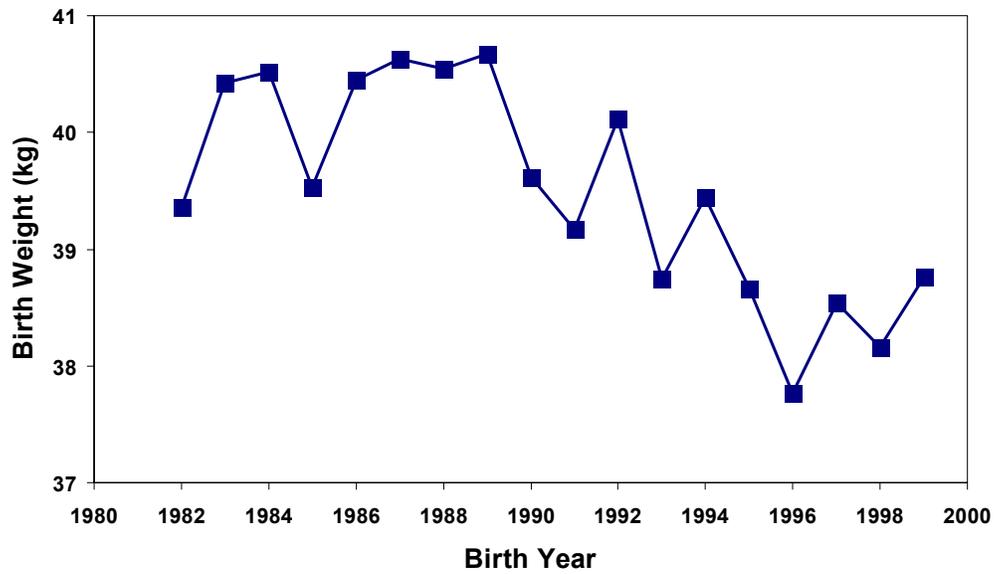


Figure 4-2. Birth weight by birth year of Mexican Simmental breed.

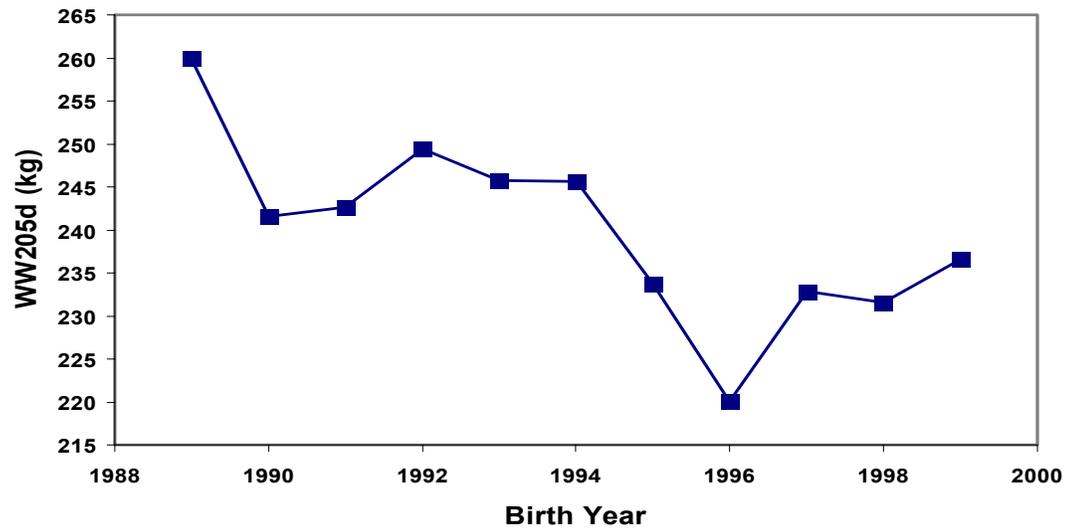


Figure 4-3. Weaning weight by birth year of Mexican Simmental breed.

Estimation of Genetic Parameters

Parameters estimates of covariance components and genetic parameters for BW and WW direct and maternal are shown in Table 4-2. The additive genetic variance for BW direct was three times larger than for BW maternal, yielding heritability estimates of 0.40 for BW direct and 0.12 for BW maternal. Similarly, the additive genetic variance for WW direct was twice the size of WW maternal, producing estimates of heritability of 0.33 for WW direct and 0.19 for WW maternal. These heritabilities were almost identical to those used in the 2003 Simmental Sire Summary for the US Simmental population (0.39 for BW direct, 0.28 for WW direct, 0.16 for WW maternal; ASA, 2003). Phenotypic variances were 19.94 kg² for BW, 690.17 kg² for WW. The similarity of the Mexican and US heritability estimates suggests that Mexican producers imported a representative sample of the American Simmental population during the period covered in this study (1982 to 1999).

Table 4-2. Covariance components and genetic parameters for birth weight and weaning weight in the Mexican Simmental population^a

Trait ^b	BWD	BWM	WWD	WWM
BWD	0.40 (7.91)	-0.63	0.73	0.00
BWM	-2.72	0.12 (2.40)	-0.02	0.00
WWD	31.09	-0.45	0.33 (228.63)	-0.39
WWM	0.00	0.00	-66.06	0.19 (128.05)

^aHeritabilities (genetic variances in kg² in parenthesis) on the diagonal, genetic correlations above the diagonal and genetic covariances (in kg²) below the diagonal.

^bBWD = birth weight direct; BWM = birth weight maternal; WWD = weaning weight direct; WWM = weaning weight maternal.

The negative correlations between additive direct and maternal genetic effects found for BW (-0.63) and WW (-0.39) in the Mexican Simmental population were also comparable to US Simmental values (ASA, 2003; Elzo et al., 1986; Garrick et al., 1989;

Lee et al., 1997). Across-trait additive genetic correlations were all zero or near zero except for the correlation between BW direct and WW direct (0.73); again similar to their corresponding estimates in the US Simmental population. The phenotypic covariance between BW and WW (30.87 kg^2) and the phenotypic correlation (0.26), were both comparable to values obtained in US Simmental (Elzo et al., 1986; Garrick et al., 1989).

Permanent environmental maternal effects were not important for BW (permanent environmental variance = 0.81 kg^2 and ratio of permanent environmental variance to phenotypic variance = 0.04). Permanent environmental effects were more important for WW (permanent environmental variance = 6.86 kg^2 and ratio of permanent environmental variance to phenotypic variance = 0.10). This permanent environment ratio of 0.10 for WW was analogous to the estimates in the US for bulls (0.12) and for heifers (0.09) as reported by Lee et al. (1997). As in the US Simmental population, permanent environmental maternal effects in Mexican Simmental population were substantially less important than either additive direct or maternal genetic effects.

Heritabilities and genetic correlations estimated for preweaning traits in Mexican Simmental population suggest that selection for additive direct genetic effects for BW and WW in the appropriate direction (e.g., smaller BW and larger WW) should be successful. Selection for WW maternal also appears feasible. However, the selection program should monitor genetic predictions for direct and maternal effects and take steps to lessen the impact of the negative correlations between additive direct and maternal genetic effects for BW and WW. One such measure could be to select sires in two steps. First, define a minimum value of sire expected progeny difference for WW maternal. Second, within the set of sires that meets this criterion, choose sires whose expected

progeny difference for direct growth is appropriate to the environmental conditions where their progeny will grow.

Genetic Trends

Trends for predicted calf additive direct and dam additive maternal genetic values are shown in Figure 4-3 for BW and in Figure 4-4 for WW. Trends for calf additive direct genetic values were flat between 1981 and 1988 and tended to increase from 1989 to 1999 for BW (0.25 kg) and WW (1.40 kg). These upward trends for calf BW and WW direct suggest that, since 1988, Mexican cattlemen paid more attention to expected progeny differences (probably for WW direct) when purchasing semen or sires from the US Simmental population. In contrast, the US Simmental population increased their WW direct by approximately 10 kg while maintaining their BW direct constant (ASA, 2003).

Trends for dam additive maternal genetic values tended to decrease from 1981 to 1999 for both BW (-0.07 kg) and WW (-0.02 kg). These small negative trends may be a consequence of Mexican cattlemen choosing US sires primarily for their own ability to grow (i.e., for their additive direct genetic predictions), particularly for WW, regardless of their prediction for maternal genetic effects. If sires chosen during this period had negative predicted values for maternal genetic effects or maternal “milk” (ASA, 2003), negative BW and WW genetic trends for dam maternal genetic effects could occur because of negative correlations between direct and maternal genetic effects. During the same period, the US Simmental population increased their dam additive maternal genetic values by approximately 6 kg (ASA, 2003).

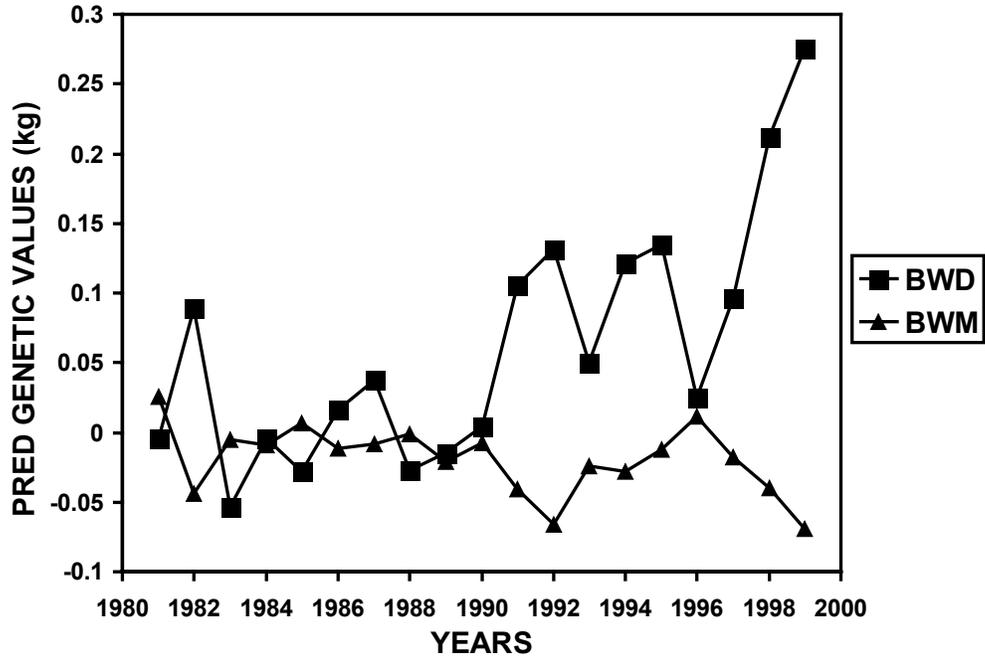


Figure 4-4. Trends for birth weight calf additive direct (BWD) and dam additive maternal (BWM) predicted genetic values in the Mexican Simmental population.

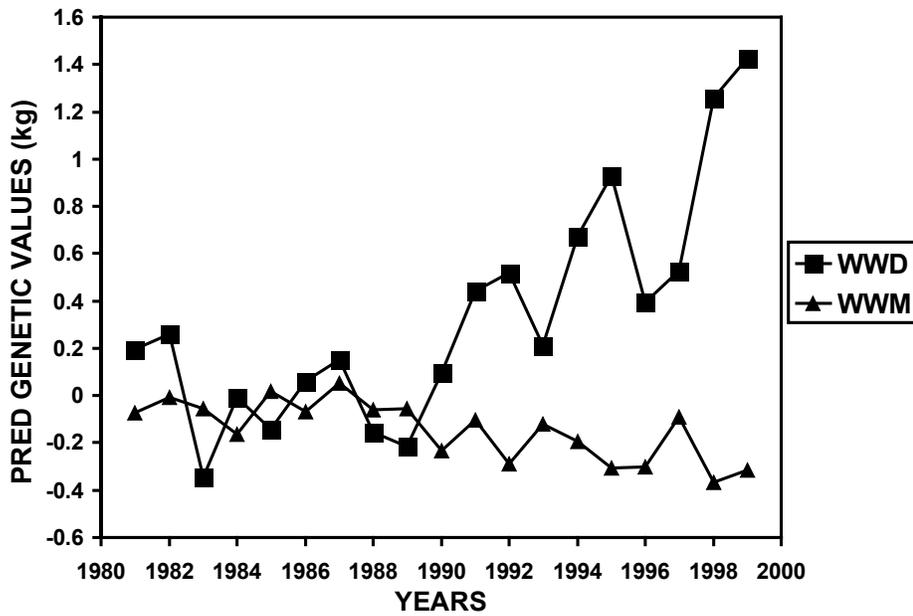


Figure 4-5. Trends for weaning weight calf additive direct (WWD) and dam additive maternal (WWM) predicted genetic values in the Mexican Simmental population.

The amounts of genetic variability found in the Mexican Simmental population suggest that there is ample opportunity for genetic improvement for preweaning direct and maternal growth traits. A national genetic evaluation program followed by judicious use of genetic predictions and sound-mating strategies should yield substantially higher genetic trends than those found between 1982 and 1999.

Implications

The large amounts of genetic variability estimated for birth weight and weaning weight direct and maternal traits suggest that the Mexican Simmental population could quickly respond to selection programs to improve weaning weights. Care should be taken to choose sires with low genetic predictions for birth weight direct to avoid calving difficulties. Further, selected sires should have an appropriate predicted genetic value for weaning maternal genetic effects, otherwise milk yield could decrease substantially because of the negative genetic correlation between direct and maternal effects. Other traits such as yearling weight, carcass traits and reproductive traits should also be considered in future genetic evaluations in order to have a more comprehensive genetic improvement program.

Summary

Birth weight (18,383) and weaning weight (9,023) records from Mexican Simmental beef cattle population were used to estimate genetic additive direct and maternal variances, heritabilities, genetic correlations and genetic trends. Information was collected from 549 herds owned by members of the Mexican Simmental-Simbrah Association between 1982 to 1999. Contemporary groups were defined as herd-year-seasons. A two-trait animal model with additive direct and maternal effects was used to estimate genetic variances and genetic parameters and to predict genetic values.

Heritabilities for birth weight were 0.40 for additive direct and 0.12 for additive maternal and the additive direct-maternal genetic correlation was -0.63. Weaning weight heritabilities were 0.33 for additive direct and 0.19 for additive maternal and the additive direct-maternal correlation was -0.67. The only across-trait nonzero genetic correlation was between birth weight direct and weaning weight direct (0.73). Maternal heritabilities were lower than direct heritabilities and negative correlations between additive direct and maternal effects existed for both traits. Genetic trends in the Mexican Simmental population were positive for additive direct and negative for additive maternal genetic effects. These trends suggest that most of the selection emphasis was likely placed on additive direct genetic effects for weaning weight. Because of the negative correlation existing between additive direct and maternal genetic effects in the Mexican Simmental population, selection programs for preweaning growth will need an appropriate balance between these two types of effects.

CHAPTER 5
MATERNAL LINE EFFECT IN PRODUCTIVE TRAITS IN MEXICAN
SIMMENTAL-SIMBRAH POPULATION

Introduction

Environmental effects for many economically important traits in beef cattle include the maternal environment provided by the dam. A maternal effect is any influence, other than the contribution resulting from nuclear genes, the dam has on the phenotype of her progeny (Rohrer et al., 1994). Since mitochondria play an important role in intracellular protein and energy metabolism, the assumption that cytoplasmic effects could be involved in productive traits is reasonable (Bell et al., 1985). Differences among maternal cytoplasmic lines in dairy cattle account for 2% of the total variation for milk yield and 3.5% of total variation for fat percentage (Bell et al., 1985). Cytoplasmic effect was a significant source of variation for open days (Tess et al., 1987). Huizinga et al. (1986) found that cytoplasmic variation accounted for 5.6, 4.8, 6.2, 10.1 and 2.5 of the total variation in milk yield, fat percentage, protein percentage, kilograms of fat plus protein and milk return in dollars, respectively.

Cytoplasmic effects in beef cattle accounted for 2% of the variation in birth weight, 5% in average daily gain and 5% in weaning weight adjusted to 205 days in Hereford calves (Tess et al., 1987). Brown et al. (1988) found non important correlations between mitochondrial metabolism and weaning weight and yearling growth in beef cattle. Cytoplasmic effects were not detected for birth weight, weaning weight and post weaning average daily gain in Brangus cattle (Rohrer et al., 1994). In sheep no cytoplasmic

effects were found in the Columbia and Targhee breeds for birth weight, weaning weight, fleece weight and number of lambs born (Hanford et al., 2003, Van Vleck et al., 2003).

Cytoplasmic line could be used as an alternative for selection under tropical conditions, where *Bos indicus* x *Bos taurus* crosses have been used to increase production traits (Olson et al., 1990; Elzo et al., 2001; Dominguez et al., 2003) those studies indicate a superiority of the crossbred animal over the purebred animals both *Bos taurus* or *Bos indicus*, for productive traits. Roberson et al. (1986) found differences between reciprocal crosses for birth traits. A difference of more than 7 kg for birth weight has been observed between reciprocal cross embryos regardless of breed type of surrogate dam (Baker et al., 1990; Thallman et al., 1992). Cytoplasmic inheritance could be responsible for some of these differences.

In Mexico producers are concerned about dam selection and because dams usually produce less than 10 calves in their lives, the prediction of breeding values for dams is inaccurate. In some cases enough information for a reliable genetic evaluation of cows becomes available, but too late in the life of the animal to be useful for selection. However, by evaluating dams as a part of a cytoplasmic line group, breeders may have enough information on the lines to detect those that are genetically superior. This information would be included in genetic strategies to improve economically important beef traits. Therefore, the objectives of this study were to determine the effects of cytoplasmic line effect (CY) on birth weight and weaning weight in Mexican Simmental and Simbrah populations.

Material and Methods

Data and pedigree files

The data used in the study were described previously (Rosales-Alday et al., 2004a). All animals were traced to their cytoplasmic origin which was defined as the foundation female in the maternal line of the pedigree. The oldest registered dam in the pedigree was used as the origin of the cytoplasmic line. The Mexican Simmental-Simbrah Association started recording data in 1982 and included some animals born in the early 50's. In some instances maternal lines were traced back for seven generations. A cytoplasmic line was defined as all animals sharing a common cytoplasmic source (Tess et al., 1987). Traits considered were birth weight (BWT) and weaning weight adjusted to 205 days (WW205) according to BIF recommendations (1996).

Three data sets were constructed. The first included the entire data set including both purebred and crossbred animals. This set included 36,292 records for BWT and 11,314 for WW205. The second included only crossbred animals (31,607 records for BWT and 8,936 for WW205), while the third included only purebred Simmental (3,447 records for BWT and 1,492 for WW205). For each data set connectivity for sires throughout contemporary groups was verified and information without any genetic connection was deleted. Only lines with ten or more recorded calves were included in the analysis. A total of 1,680 different maternal lines were used in this in this data set. Another restriction was the contemporary group. Sire groups with less than ten records were deleted.

Estimation of Genetic Parameters

Genetic variances and covariances were estimated by Average Information Restricted Maximum Likelihood (Gilmour et al., 1995, 2002). The computational

package used to calculate (co)variance components was ASREML (Gilmour et al. 2000). A single trait BWT or WW205, sire-maternal grand sire model (SMGS) with additive direct, additive maternal and cytoplasmic line effects was used. Fixed effects were sex, age of dam in days, linear and quadratic, contemporary group and sex \times age of dam interaction. Covariances between direct and residuals, maternal and residual and cytoplasmic and residual effects were assumed to be zero. Random effects were sire additive direct, maternal grand sire additive direct, maternal cytoplasmic line effect and residual. The mixed random model for each trait can be represented as follows:

$$y = Xb + Z_i u_i + Z_m u_m + Z_{cy} u_{cy} + e$$

where

y = vector of observations (BWT or WW205),

b = vector of sex, age of dam in days, linear and quadratic, contemporary group and sex \times age of dam interaction,

u_i = vector of additive direct genetic effects,

u_m = vector of additive maternal genetic effects,

u_{cy} = vector of maternal cytoplasmic line effects,

e = vector of residuals,

X = matrix of 1s and 0s that relates calf records to fixed effects,

Z_i = matrix of 1s and 0s that relates calf records to additive direct genetic effects,

Z_m = matrix of 1s and 0s that relates calf records to additive maternal genetic effects,

Z_{cy} = matrix of 1s and 0s that relates calf records to line of cytoplasmic origin effects.

It was assumed that

$$\begin{bmatrix} y \\ u_i \\ u_m \\ u_{cy} \\ e \end{bmatrix} \sim MVN \left(\begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} XGX' + R & Z_i \sigma_i^2 * A & Z_m \sigma_m^2 * A & Z_{cy} \sigma_{cy}^2 * A & I \sigma_e^2 \\ \sigma_i^2 * A Z_i' & \sigma_i^2 * A & Z_m \sigma_{i,m} Z_i' * A & Z_{cy} \sigma_{i,cy} Z_i' * A & 0 \\ \sigma_m^2 * A Z_m' & Z_i \sigma_{m,i} Z_m' * A & \sigma_m^2 * A & Z_{cy} \sigma_{m,cy} Z_m' * A & 0 \\ \sigma_{cy}^2 * A Z_{cy}' & Z_i \sigma_{cy,i} Z_{cy}' * A & Z_m \sigma_{cy,m} Z_{cy}' * A & \sigma_{cy}^2 * A & 0 \\ I \sigma_e^2 & 0 & 0 & 0 & I \sigma_e^2 \end{bmatrix} \right)$$

where

σ_i^2 = is the sire direct genetic variance,

σ_m^2 = is the maternal grandsire direct genetic variance,

σ_{cy}^2 = is the cytoplasmic variance,

σ_e^2 = residual error variance,

$\sigma_{i,m}$ = covariance between direct and maternal effect,

$\sigma_{i,cy}$ = covariance between direct and cytoplasmic effect,

$\sigma_{m,cy}$ = covariance between maternal and cytoplasmic effect,

A = relationship matrix,

R = $I \sigma_e^2$,

I = identity matrix.

Results and Discussion

Estimation of Genetic Parameters

Purebred and crossbred data. Estimations of covariance components and genetic parameters for BWT direct, maternal and cytoplasmic line for the complete data set, purebred plus crossbred, are shown in Table 5-1. The covariance between BWTD and cytoplasmic line was deleted from the model for BWT because the standard error exceeded the parameter value. While the heritability for BWTD approximated that

reported by Rosales-Alday et al. (2004a), heritability for BWTM was different, 0.04 vs. 0.12, from the previous analysis. Heritability for BWTD is bigger than the parameters reported by Mohiuddin (1993) and the weighted heritability reported by Koots et al. (1994). This difference can be explained by the inclusion of information from crossbred animals and the addition of nonadditive covariance which could bias the estimation of covariances.

The ratio of cytoplasmic line variance ($0.4 \pm 0.01 \text{ kg}^2$) to total phenotypic variance ($22.04 \pm 0.31 \text{ kg}^2$) for BWT was small, 0.02 ± 0.003 . This indicates that only 2% of the total variance was explained by the cytoplasmic line effect. This ratio is within the range reported by others (Bell et al., 1985; Huizinga et al., 1986) who indicated that cytoplasmic effects accounted for 1 to 4% of the total variation in dairy traits. These present results are in agreement with the reports by Rohrer et al. (1994), Tess et al. (1987) and Van Vleck et al. (2003) who found no impact of cytoplasmic effects in beef cattle and sheep. Those differences could be because in this paper cytoplasmic effect was included in a Sire-Maternal Grand Sire model. This model can separate the additive direct genetic effect, the maternal direct effect and the cytoplasmic effect at the same time.

The genetic correlation between BWTD and BWTM was 0.30 ± 0.08 and different from the reported values of ASA (2003), Elzo et al. (1986), Garrick et al. (1989), Lee et al. (1997) and Rosales et al. (2004a) who found negative genetic correlation for those traits. The correlation between BWTM and cytoplasmic line is 0.52 ± 0.43 . This correlation is high because it measures the maternal effect, one from the sire's side and the other through the cytoplasmic effect. Both have their influence through the dam. But

BWTM measures the additive genetic maternal effect and the cytoplasmic effect measures the non-nuclear effects. No correlation was found reported in the literature for those traits.

Table 5-1. Covariance components and genetic parameters and standard error for birth weight in the Mexican Simmental-Zebu purebred and crossbred population

Trait	Genetic Variance (Kg ²)	Heritability
BIRTH WEIGHT DIRECT	8.57 ± 0.65	0.39 ± 0.03
WEIGHT MATERNAL	0.79 ± 0.01	0.04 ± 0.01
GD,BWTM) ^a	0.39 ± 0.01	0.30 ± 0.08 ^b
GM, CYTOPLASMIC LINE) ^a	0.3 ± 0.24	0.52 ± 0.43 ^b
WEIGHT CYTOPLASMIC LINE	0.4 ± 0.01	0.02 ± 0.003 ^c
IG WEIGHT DIRECT	190 ± 31.4	0.27 ± 0.04
IG WEIGHT MATERNAL	34.2 ± 6.4	0.05 ± 0.009
IG WEIGHT CYTOPLASMIC LINE	14.7 ± 4	0.021 ± 0.006 ^c

^aBWTD = birth weight direct; BWTM = birth weight maternal

^bGenetic correlation

^cCytoplasmic variance/Phenotypic variance.

The covariance components, genetic parameters and standard errors for WW205 in the Mexican Simmental-Zebu crossbred population are presented in the Table 5-1. All covariances among those traits were not considered because previous analyses found them not to differ from zero. Heritability for WW205D for the complete Mexican Simmental-Zebu crossbred population was 0.27 ± 0.04. This value is smaller than those previously reported by Rosales-Alday et al. (2004a). But they were close to those parameters reported by Mohiuddin (1993), for American and Canadian Simmental breed.

The ratio of cytoplasmic line variance for WW205 (14.7 ± 4 kg²) to total phenotypic variance (712.1 ± 11.8 kg²) again was small, 0.021 ± 0.006. This indicates

that little of the genetic variation existing for this trait is explained by cytoplasmic line effect on 205d adjusted weaning weight.

Purebred animals. Variance estimates and genetic parameters for purebred animals for BWT and WW205 are shown in table 5-2. Heritability for BWTD was 0.25 ± 0.08 and for BWTM was 0.04 ± 0.02 . These results differ from those reported by Rosales et al. (2004a). And the heritabilities were smaller than those reported by Mohiuddin (1993) and Koots et al. (1994). The main difference is that in the present study Simmental breed was defined as the breed of the maternal grand dam. This causes a reduction of the genetic variance which was detected by the analysis.

Table 5-2. Covariance components, genetic parameters and standard errors for birth weight and weaning weight in purebred Mexican Simmental population

Trait	Genetic Variance (Kg ²)	Heritability
BIRTH WEIGHT DIRECT	5.28 ± 1.71	0.25 ± 0.08
BIRTH WEIGHT MATERNAL	0.88 ± 0.34	0.04 ± 0.02
BIRTH WEIGHT CYTOPLASMIC LINE	0.35 ± 0.19	0.02 ± 0.009^a
WEANING WEIGHT DIRECT	315.8 ± 123.8	0.36 ± 0.13
WEANING WEIGHT MATERNAL	15.11 ± 20.12	0.017 ± 0.023
WEANING WEIGHT CYTOPLASMIC LINE	24.6 ± 17.9	0.03 ± 0.02^a

^aCytoplasmic variance/Phenotypic Variance.

Heritability for WW205D was 0.36 ± 0.13 and it was in agreement with the parameter reported in previous analyses with the same data (Rosales et al., 2004a). The heritability found in this analysis was smaller than the reported by Koots et al. (1994) for WW205D. Heritability for WW205M was 0.017 ± 0.023 . This parameter is not differing from zero. This result is different from other reports whose reported heritabilities bigger than zero (, 1993; Koots et al., 1994; Rosales et al., 2004a). The ratio between

cytoplasmic line and the total phenotypic variance for WW205 was 0.03 ± 0.02 . This ratio is in the range reported for cytoplasmic effects in the literature (Tess et al., 1987; Gibson et al., 1997). No genetic correlations among traits were found for the purebred Simmental analyses. The number of records in this data set was small, only 3,447 records for BWT and 1,492 for WW205 and account for the large standard errors.

Crossbred animals. Covariance estimates and genetic parameters for Simmental-Zebu crossbred population for BWT and WW205 are shown in table 5-3. Heritability for BWTD was 0.44 ± 0.03 . This parameter was bigger compared with those reported by Mohiuddin (1993) and heritability reported by Koots et al. (1994). Heritability for BWTM was 0.03 ± 0.01 and it was smaller than the reported for other authors (Mohiuddin, 1993; Koots et al., 1994; Rosales et al., 2004a). The correlation between BWTD and BWTM was 0.36 ± 0.08 , the value of this parameter was different for those reported by other authors (Elzo et al., 1986; Garrick et al., 1989; Lee et al., 1997; ASA, 2003; Rosales et al., 2004a) who found negative genetic correlation for those traits. The correlation between BWTM and cytoplasmic line is 0.27 ± 0.01 this indicates an important relation between maternal and cytoplasmic effects.

Heritability for WW205D was 0.31 ± 0.05 , this value was bigger than those found by Mohiuddin (1993) and Koots et al. (1994). Heritability for WW205M was 0.05 ± 0.01 and was smaller than those reported by Mohiuddin (1993) and Koots et al. (1994). The ratio between cytoplasmic line and the total phenotypic variance for BWT was $0.02 \pm .001$ and for WW205 was 0.022 ± 0.007 . The range of percentage of variation explained by cytoplasmic line for birth weight and for 205 days adjusted weaning weight was from

2% to 2.2% respectively and they are within the range reported by Bell et al. (1985), Huizinga et al. (1986) and Tess et al. (1987) in beef cattle and milk yield.

Table 5-3. Covariance components, genetic parameters and SE for birth weight and weaning weight in Mexican Simmental-Zebu crossbred population

Trait	Genetic Variance (Kg ²)	Heritability
BIRTH WEIGHT DIRECT	9.76 ± 0.79	0.44 ± 0.03
BIRTH WEIGHT MATERNAL	0.74 ± 0.01	0.03 ± 0.01
Cov(BWTD, BWTM) ^a	0.48 ± 0.12	0.36 ± 0.08 ^b
Cov(BWTM, CYTOPLASMIC LINE) ^a	0.15 ± 0.11	0.27 ± 0.21 ^b
BIRTH WEIGHT CYTOPLASMIC LINE	0.41 ± 0.06	0.02 ± 0.01 ^c
WEANING WEIGHT DIRECT	212.8 ± 37.45	0.31 ± 0.05
WEANING WEIGHT MATERNAL	34.42 ± 7.11	0.05 ± 0.01
WEANING WEIGHT CYTOPLASMIC LINE	14.62 ± 4.61	0.022 ± 0.007 ^c

^aBWTD = birth weight direct; BWTM = birth weight maternal

^bGenetic correlation

^cCytoplasmic variance/Phenotypic variance.

The results found in this paper means that breeders could have another trait to evaluate the productive performance on cows. With cytoplasmic line effects, breeders can have more control over birth weight and weaning weight. As a result, the producer can select lines according to their specific needs. If they need to maintain the birth weight constant, they can choose maternal lines with cytoplasmic line genetic value for birth weight close to zero. If they want to increase or decrease the birth weight they can select the corresponding extreme cytoplasmic line. The same procedure can be utilized with weaning weight.

Implications

The data seem to suggest that variation due to maternal cytoplasm may exist but has only a small effect on birth weight and weaning weight in the Mexican Simmental-Zebu population. If cytoplasmic line effects had been greater they may have offered an additional tool to improve economically important traits such as birth weight and weaning weight. By combining cytoplasmic line data with EPD's, breeders could possibly obtain more genetic improvement than if they use only the EPD. Further investigation is needed in order to determine if selection response could be improved by including maternal cytoplasmic line in beef cattle selection programs. Even relatively modest contributions to variation imply substantial differences in performance between mitochondrial lineages. This may be valuable information when selecting donor cows for in vitro fertilization, embryo transfer or cloning in the future.

Summary

Purebred Simmental and crossbred Simmental-Zebu records were used to estimate variance components for additive direct, additive maternal and cytoplasmic line genetic effects on birth weight and weaning weight traits. Records were from the Mexican Simmental-Simbrah Association. Three data sets were formed; the first included both purebred Simmental and crossbred animals. The second included only purebred animals. The third included only crossbred animals. Variances were estimated by Restricted Maximum Likelihood procedures using a Sire-Maternal Grand Sire model. Fixed effects were sex, age of dam linear and quadratic contemporary groups and calf-sex×age of dam interaction. Heritabilities for both purebred and crossbred animals were 0.39 ± 0.03 , 0.04 ± 0.01 for BWTD and BWTM, respectively. The genetic correlation between BWTD and BWTM was 0.30 ± 0.08 and for BWTM and cytoplasmic effects was 0.52 ± 0.43 .

Heritabilities for WW205D and WW205M were 0.27 ± 0.04 and 0.05 ± 0.009 , respectively. Heritabilities for Simmental purebred data for BWTD and BWTM were 0.25 ± 0.08 and 0.04 ± 0.02 , respectively. Heritabilities for WW205D and WW205M were 0.36 ± 0.13 and 0.017 ± 0.023 , respectively. Heritabilities for crossbred animals were 0.44 ± 0.03 and 0.03 ± 0.01 for BWTD and BWTM, respectively. The genetic correlation between BWTD and BWTM was 0.36 ± 0.08 and for BWTM and cytoplasmic effects was 0.27 ± 0.21 . Heritabilities for WW205D and WW205M were 0.31 ± 0.05 and 0.05 ± 0.01 , respectively. Cytoplasmic line variance and total phenotypic ratio ranged from 2 to 3% for all traits in all data groups. Modest contributions of the cytoplasmic mitochondrial effect to birth weight and weaning weight variation were found in this study. This could be help to select maternal lineages to select cows to be used as donor for in vitro fertilization, embryo transfer or cloning in the future in Mexican Simmental population.

CHAPTER 6 GENERAL CONCLUSIONS

Three studies were conducted utilizing data from three commercial herds maintained under subtropical conditions in Mexico and also with data from the Mexican Simmental-Simbrah Association to determine genetic parameters for birth weight and weaning weight. The initial study was conducted with purebred and crossbred Simmental and Brahman records from three unconnected herds. A Sire-Dam model was used to estimate within-herd variance components for additive direct and maternal genetic effects for birth weight and 205 d-adjusted weaning weight. Within-herd heritability estimates were 0.05 ± 0.03 for BWTD, 0.09 ± 0.03 for BWTM, 0.23 ± 0.08 for WW205D and 0.11 ± 0.04 for WW205M in herd 1; 0.84 ± 0.17 for BWTD, 0.63 ± 0.28 for WW205D and 0.33 ± 0.22 for WW205M in herd 2 and 0.03 ± 0.07 for BWTD, 0.15 ± 0.07 for BWTM, 0.22 ± 0.15 for WW205D and 0.17 ± 0.10 for WW205M for herd 3. These intra-herd heritabilities showed greater genetic variability was expressed for weaning weight than for birth weight. Thus, more genetic progress could be achieved for weaning weight, direct and maternal, than for birth weight traits in these herds. As more data are collected from these three herds, more precise estimates of genetic parameters and more precise selection for those weight traits can be achieved.

In the second study, birth weight and weaning weight records from the Mexican Simmental beef cattle population were used to estimate genetic additive direct and

maternal variances, heritabilities, genetic correlations and genetic trends with a two-trait animal model with additive direct and maternal effects. Heritabilities for birth weight were 0.40 for additive direct and 0.12 for additive maternal and the additive direct-maternal genetic correlation was -0.63. Heritabilities for weaning weight were 0.33 for additive direct and 0.19 for additive maternal. The additive direct-maternal correlation was -0.67. The only across-trait nonzero genetic correlation was between birth weight direct and weaning weight direct (0.73). Maternal heritabilities were lower than direct heritabilities and negative correlations between additive direct and maternal effects existed for both traits. Genetic trends in the Mexican Simmental population were positive for additive direct and negative for additive maternal genetic effects. These trends suggest that most of the selection emphasis was likely placed on additive direct genetic effects for weaning weight. Because of the negative correlation that exists between additive direct and maternal genetic effects in the Mexican Simmental population, selection programs for preweaning growth will need to strike an appropriate balance between these two types of effects.

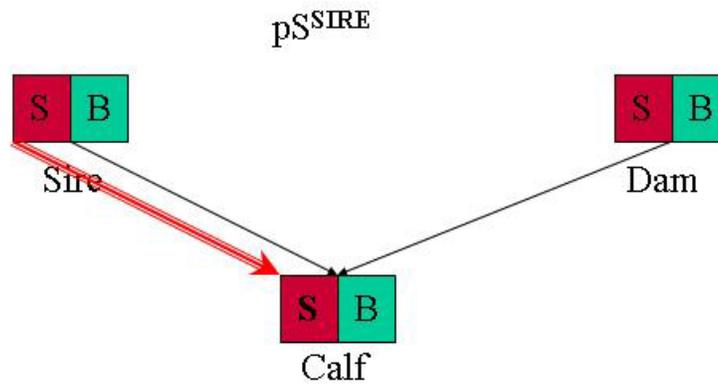
In the third study, purebred and crossbred Simmental and Brahman records were used to estimate variance components for additive direct, additive maternal and cytoplasmic genetic effects for birth weight and weaning weight. Records were from the Mexican Simmental-Simbrah Association. Three data sets were formed. The first included purebred Simmental and crossbred animals. The second included only the purebred animals. The third included only the crossbred animals. Variances were estimated by Restricted Maximum Likelihood procedures using a Sire-Maternal Grand Sire model. Fixed effects were sex, age of dam linear and quadratic contemporary groups

and calf-sex×age of dam interaction. Heritabilities for purebred and crossbred animals were 0.39 ± 0.03 , 0.04 ± 0.01 for BWTD and BWTM, respectively. The genetic correlation between BWTD and BWTM was 0.30 ± 0.08 and for BWTM and cytoplasmic effects was 0.52 ± 0.43 . Heritabilities for WW205D and WW205M were 0.27 ± 0.04 and 0.05 ± 0.009 , respectively. Heritabilities for Simmental purebred data for BWTD and BWTM were 0.25 ± 0.08 and 0.04 ± 0.02 , respectively. Heritabilities for WW205D and WW205M were 0.36 ± 0.13 and 0.017 ± 0.023 , respectively. Heritabilities for crossbred animals were 0.44 ± 0.03 , 0.03 ± 0.01 for BWTD and BWTM, respectively. The genetic correlation between BWTD and BWTM was 0.36 ± 0.08 and for BWTM and cytoplasmic effects was 0.27 ± 0.21 . Heritabilities for WW205D and WW205M were 0.31 ± 0.05 and 0.05 ± 0.01 , respectively. Cytoplasmic line variance and total phenotypic ratio ranged from 2 to 3% for all traits in all data groups. Modest contributions of cytoplasmic mitochondrial effect to birth weight and weaning weight variation were found in this study. This could be helpful in selecting maternal lineages of cows to be used as donors for in vitro fertilization, embryo transfer or cloning in the future in Mexican Simmental population.

This series of studies are the first conducted in Mexico. Further genetic evaluation will be made with the participation of other cattle associations, such as the Angus, Brangus and Charolais. Mexican cattlemen are requesting this type of research to enable them to supply a better and competitive product to the regional, national and international markets. They realize that there are more traits to be evaluated and have agreed to include yearling weight, scrotal circumference and carcass traits among others. Also

international participation is required to evaluate sires and obtain the expected breeding values in a wide range of environments like the subtropical conditions of Mexico and temperate conditions of the USA.

APPENDIX
GRAPHIC REPRESENTATION OF NON-ADDITIVE GENETIC EFFECT ON
CROSSBRED ANIMALS

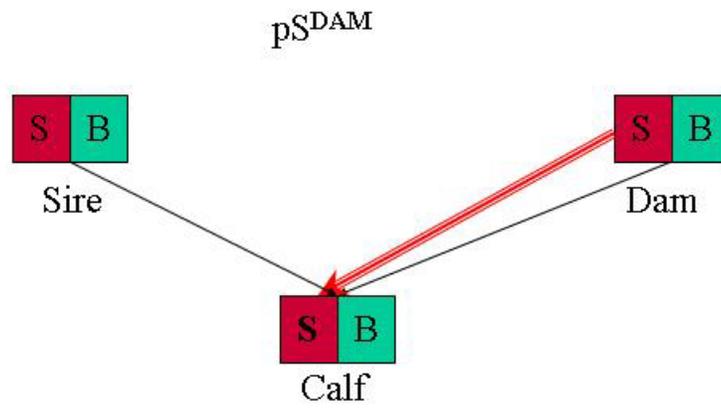


1. Sire Intra-breed
Additive Direct

S=Simmental

B=Brahman

pS^{Sire} =Simmental genes proportion on Sire

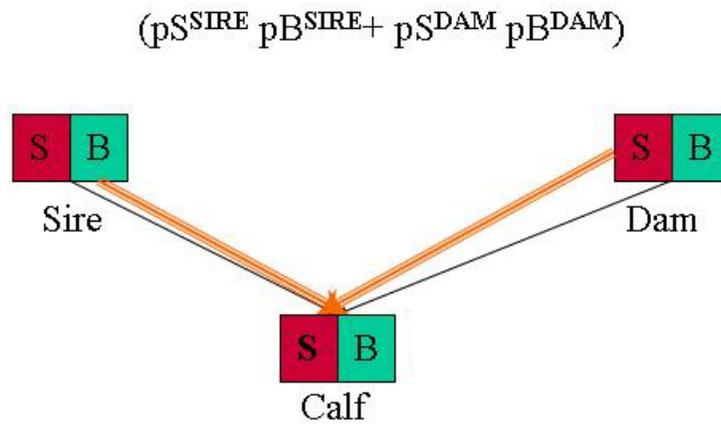


2. Dam Intra-breed Additive
Direct plus Maternal

S=Simmental

B=Brahman

pS^{DAM} =Simmental genes proportion on Dam



3. Sire Interbreed Nonadditive Direct

S=Simmental

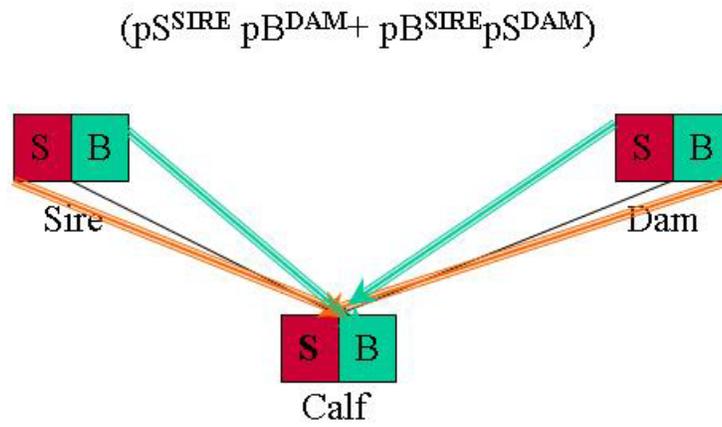
B=Brahman

pS^{SIRE} =Simmental genes proportion on Sire

pB^{SIRE} =Brahman genes proportion on Sire

pS^{DAM} =Simmental genes proportion on Dam

pB^{DAM} =Brahman genes proportion on Dam



4. Dam Interbreed Nonadditive Maternal

S=Simmental

B=Brahman

pS^{SIRE} =Simmental genes proportion on Sire

pB^{DAM} =Brahman genes proportion on Dam

pB^{SIRE} =Brahman genes proportion on Sire

pS^{DAM} =Simmental genes proportion on Dam

LIST OF REFERENCES

- Alves Santiago, A. 1976. El cebú: Ganado bovino para los países tropicales. The zebu: Cattle for tropical countries. UTEHA, México.
- American Simmental Association [ASA]. 2003. Multi-breed international cattle evaluation. Spring 2003 Simmental/Simbrah sire summary. Online. Available: <http://www.simmental.org/asadata/s03ss.pdf>. Accessed August 20, 2003.
- Baker, J. F., C. G. Dorn, and G. A. Rohrer. 1990. Donor, fetal and recipient effects on birth weight and gestation length of calves. *J. Anim. Sci.* 68(Suppl. 1):22(Abstr.).
- Banos, G., L. R. Schaeffer, E. B. Burnside, 1991. Genetic relationships and linear model comparisons between United States and Canada Ayrshire and Jersey bull populations. *J. Dairy Sci.* 74:1060-1068.
- Banos, G., A. Sigurdsson. 1996. Application of contemporary methods for the use of international data in national genetic evaluations. *J. Dairy Sci.* 79:1117-1125.
- Barkhouse, K. L., L. D. Van Vleck, and L. V. Cundiff. 1995. Mixed model methods to estimate breed comparisons for growth and maternal traits adjusted to a 1996 base. In: Proc. Beef Improvement Federation. 27th Research Symposium and Annual Meeting. Sheridan, WY.
- Bell, B. R., B. T. McDaniel, and O. W. Robison. 1985. Effects of cytoplasmic inheritance on production traits of dairy cattle. *J. Dairy Sci.* 68:2038-2051.
- Beef Improvement Federation [BIF]. 1996. Guidelines for uniform beef improvement programs (7th Ed). Kansas State Univ., Kansas.
- Boettcher, P. J., M. T. Kuhn, and A. E. Freeman. 1996. Impacts of cytoplasmic inheritance on genetic evaluations. *J. Dairy Sci.* 79:653-675.
- Boldman, K. G., L. K. Kriese, L. D. Van Vleck, C. P. Van Tassel, and S. D. Kachman. 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances. U. S. Department of Agriculture, Agriculture Research Service.
- Broman, K. W. 2002. A tour of R/qtl. Department of Biostatistics, John Hopkins University. Online. Available: <http://www.biostat.jhsph.edu/~kbroman/qtl/rqtltour.pdf>. Accessed January 30, 2004.

- Brown, D. R., S. K. DeNise, and R. G. McDaniel. 1988. Mitochondrial respiratory metabolism and performance of cattle. *J. Anim. Sci.* 66:1347-1354.
- British Simmental cattle society Ltd. 2003. Simmental: the dual purpose breed for beef and milk, both for pure and crossbreeding. Online. Available: <http://www.britishsimmental.co.uk/breed/index.html>. Accessed August 25, 2003.
- Canavesi, F., D. Boichard, V. Ducrocq, N. Gengler, G. de Jong, and Z. Liu. 2002. An alternative procedure for international evaluations: Production traits European joint evaluation (PROTEJE). Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 17-03.
- Cundiff, L. V., K. E. Gregory, and R. M. Koch. 1998. Germplasm evaluation in beef cattle-cycle IV: Birth and Weaning traits. *J. Anim. Sci.* 76:2528-2535.
- De los Santos V. S. G., R. Guarneros A., J. Rosales A., J. W. Holloway and R. D. Randel. 2001. Evaluación productiva de germoplasma Tuli y Fleckvieh: Comportamiento de las crías al destete. Mem. XXIX Reunión AMPA. Cd. Victoria, Tamaulipas, México 383-387.
- De los Santos V. S. G., J. Rosales A., and M. A. González P. 2003. Diagnóstico de la ganadería de leche y carne en el municipio de Aldama, Tamaulipas. INIFAP-SAGARPA. p 74.
- Domínguez V. J., R. Núñez D., R. Ramírez V. and A. Ruiz Flores. 2003. Environmental effects and repeatability for growth traits in Tropicarne cattle. *Téc. Pecu. Méx.* 41:1-18.
- Eccleston, J. A. 1978. Variance components and disconnected data. *Biometrics* 34:479-481.
- Elzo, M. A. 1983. Multibreed sire evaluation within a country and across countries. Ph. D. dissertation. Univ. of California, Davis.
- Elzo, M. A. 1996. Animal breeding notes. Advanced animal breeding course ANS6386. Spring 1996. Mimeo. University of Florida, Gainesville.
- Elzo, M. A. 1999. Multibreed evaluation theory and application. Seventh Genetic Prediction Workshop, Kansas City, MO, December 3, 1999.
- Elzo, M. A. 2002. Multibreed connectedness program CSET (version 11/21/2001). Animal Breeding Mimeo Series, No. 54, University of Florida, Gainesville. p 11.
- Elzo, M. A., and G. E. Bradford. 1985. Multibreed sire evaluation across countries. *J. Anim. Sci.* 60:953-963.
- Elzo, M. A., and T. R. Famula. 1985. Multibreed sire evaluation procedures within a country. *J. Anim. Sci.* 60:942-952.

- Elzo, M. A., E. J. Pollak, and R. L. Quaas. 1986. Genetic parameter estimates for weight and calving ease traits in the Simmental population. Mimeo. Cornell University, Ithaca. p 29.
- Elzo, M. A., C. Manrique, G. Ossa, and O. Acosta. 1998a. Additive and nonadditive genetic variability for growth traits in the Turipaná Romosinuano-Zebu multibreed herd. *J. Anim. Sci.* 76:1539-1549.
- Elzo, M. A., R. L. West, D. D. Johnson, and D. L. Wakeman. 1998b. Genetic variation and prediction of additive and nonadditive genetic effects for six carcass traits in an Angus-Brahman multibreed herd. *J. Anim. Sci.* 76:1810-1823.
- Elzo, M. A., and D. L. Wakeman. 1998. Covariance components and prediction for additive and nonadditive preweaning growth genetic effects in an Angus-Brahman multibreed herd. *J. Anim. Sci.* 76:1290-1302.
- Elzo, M. A., G. Martínez, F. González, and H. Huertas. 2001. Additive, nonadditive, and total genetic variation and genetic predictions for growth traits in the Sanmartinero-Zebu multibreed herd of la Libertad. *J. CORPOICA* 3(2):51-64.
- Emmerlin, R., E. A. Mantysaari and M. Lidauer. 2002. Reduced rank covariance functions for multi-lactation test-day model. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 17-03.
- Falconer, D. S. 1989. Introduction to quantitative genetics. 3rd ed. Longman Press, Essex, UK.
- FAO's Information System on Water and Agriculture. 2003. On line Available: <http://www.fao.org/ag/agl/aglw/aquastat/dbase/index.stm>. Accessed February 29, 2004
- Fries, A.F. 1998. From deviation records to animal models. Proc. 6th World Cong. Genet. Appl. Livest. Prod., Armidale, Australia, 25:617-620.
- Galina, C. S., and G. H. Arthur. 1989. Review of cattle reproduction in the tropics. Part 1. Puberty and age at first calving. *ABA* 57:583-590.
- Galina, C. S., and G. H. Arthur. 1991. Review of cattle reproduction in the tropics. Part 6. The male. *ABA* 59:403-412.
- Galina, C. S., and J. M. Russell. 1987. Research and publishing trends in cattle reproduction in the tropics: Part 1. A global analysis. *ABA* 55:743-749.
- Garrick, D. J., E. J. Pollak, R. L. Quaas, and L. D. Van Vleck. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. *J. Anim. Sci.* 67:2515-2528.

- Gengler, N., A. Tijani, and G. R. Wiggins. 1999. Iterative solution of random regression models by sequential estimation of regression and effects on regression. Online. Available: <http://www.csc.fi/ttn/ccb99/articles/NGengler.pdf>. Accessed February 03, 2004.
- Gibson, J. P., A. E. Freeman, and P. J. Boettcher. 1997. Cytoplasmic and mitochondrial inheritance of economic traits in cattle. *Livest. Prod. Sci.* 47:115-124.
- Gilmour, A. R., B. R. Cullis, S. J. Welham, and R. Thompson. 2000. ASREML Reference manual. Printed by NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange, NSW, 2800 Australia. p 217.
- Gilmour, A. R., R. Thompson, and Cullis B. R. 1995. Average information REML, an efficient algorithm for variance parameter estimation in linear mixed models. *Biometrics* 51:1440-1450.
- Gilmour, A. R., R. Thompson, Cullis B. R., and S. J. Welham. 2002. ASREML estimates variance matrices from multivariate data using the animal model. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 28-05.
- Gosey, J. 1997. Bull genetics: purebreds, composites, fullsibs and half-sibs. Proc. The range beef cow symposium XV. Rapid City, South Dakota.
- Graser, H. U., S. P. Smith, and B. Tier. 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Anim. Sci.* 64:1362-1370.
- Hammond, A. C., T. A. Olson, C. C. Jr. Chase, E. J. Bowers, E. D. Randel, C. N. Murphy, D. W. Vogt, and A. Tewolde. 1996. Heat tolerance in two tropically adapted *Bos taurus* breeds, Senepol and Romosinuano, compared with Brahman, Angus and Hereford cattle in Florida. *J. Anim. Sci.* 74:295-303.
- Hanford, K. J., G. D. Snowden, and L. D. Van Vleck. 2003. Models with nuclear, cytoplasmic, and environmental effects for production traits of Columbia sheep. *J. Anim. Sci.* 81:1926-1932.
- Hanocq, E., Boichard, D., Foulley, J. L. 1996. A simulation study of the effect of connectedness on genetic trend. *Gen. Sel. Evol.* 28:67-82.
- Henderson, C. R. 1953. Estimation of variance and covariance components. *Biometrics.* 9:226-252.
- Henderson, C. R. 1974. General flexibility of linear model techniques for sire evaluation. *J. Dairy Sci.* 57:963-972.
- Henderson, C. R. 1975a. A rapid method for computing the inverse of a relationship matrix. *J. Dairy Sci.* 58:1727-1730.

- Henderson, C. R. 1975b. Best linear unbiased estimation and prediction under a selection model. *Biometrics*. 31:423-447.
- Henderson, C. R. 1976a. Use of relationships among sires to increase accuracy of sire evaluation. *J. Dairy Sci.* 58:1731-1738.
- Henderson, C.R. 1976b. A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics* 32:69-83.
- Henderson, C. R. 1976c. Inverse of a matrix of relationships due to sires and maternal grandsires in an inbred population. *J. Dairy Sci.* 59:1585-1588.
- Henderson, C. R. 1976d. Multiple trait sire evaluation using the relationship matrix. *J. Dairy Sci.* 59:769-774.
- Henderson, C. R., O. Kempthorne, S. R. Searle, and C. M. von Krosigk. 1959. The estimation of environmental and genetic trends from records subject to culling. *Biometrics*. 15:192-218.
- Hoffman, M. 1991. How parents make their mark on genes. *Science* 252:1250-1251.
- Huizinga, H. A., S. Korver., B. T. McDaniel, and R. D. Politiek. 1986. Maternal effects due to cytoplasmic inheritance in dairy cattle: influence on milk production and reproductive traits. *Livest. Prod. Sci.* 15:11-26.
- Hutchison, C. A., J. E. Newbold, S. S. Potter, and M. H. Edgell, 1974. Maternal inheritance of mammalian mitochondrial DNA. *Nature*, 251:536-538.
- Kennedy, K. W. and D. Trus. 1993. Considerations on genetic connectedness between management units under an animal model. *J. Anim. Sci.* 71:2341-2352.
- Klei, L., R. L. Quaas, E. J. Pollak, and B. E. Cunningham. 1998. Multiple-breed evaluation. Cornell Animal Science/Extension Document Database [on line] Available: <http://www.simmgene.com/multibre.pdf>. Accessed March, 2001.
- Koonawootrittriron, S., M. A. Elzo, S. Tumwasorn, and W. Sintala. 2001. Lactation curves and prediction of daily and accumulated milk yields in a multibreed dairy herd in Thailand using all daily records. *Thai Journal of Agricultural Science* 34:123-139.
- Koonawootrittriron, S., M. A. Elzo, and S. Tumwasorn. 2002a. Multibreed genetic parameters and predicted genetic values for first Lactation 305-d milk yield, fat yield, and fat percentage in a *Bos taurus* × *Bos indicus* multibreed dairy population in Thailand. *Thai Journal of Agricultural Science* 35:339-360

- Koonawootrittriron, S., M. A. Elzo, S. Tumwasorn, and K. Nithichai. 2002b. Estimation of covariance components and prediction of additive genetic effects for first lactation 305-d milk and fat yields in a Thai multibreed dairy population. *Thai Journal of Agricultural Science* 35:245-258.
- 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.
- Larsen, M., and P. Madsen. 1999. The CEBUS project: History and overview. Online. Available: <http://www.csc.fi/ttn/ccb99/articles/MLarsen.pdf>. Accessed February 04, 2004.
- Lidauer, M., R. Emmerling, and E. A. Mäntysaari. 2002. Accounting for heterogeneous variance in a test-day model for joint genetic evaluation of Austrian and German Simmental cattle. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 20-09.
- Lidauer, M., and I. Strandén. 1999. Fast and flexible program for genetic evaluation in dairy cattle. Online. Available: <http://www.csc.fi/ttn/ccb99/articles/MLidauer.pdf>. Accessed Jan. 30, 2004.
- Lee, C., C. P. Van Tassell, and E. J. Pollak. 1997. Estimation of genetic variance and covariance components for weaning weight in Simmental cattle. *J. Anim. Sci.* 75:325-330.
- Manrique, C. 1992. Changes in genetic effects and variance components for preweaning growth traits in an Angus-Brahman herd. PhD. Dissertation, University of Florida, Gainesville.
- Martínez, V. G., V. E. Vega M., M. Montaña B., and J. Rosales A. 2002. Parámetros genéticos para crecimiento hasta los 12 meses de edad en bovinos Charolais. XXXVIII RNIP. Puebla, Mexico.
- Mathur, P. K., B. Sullivan and J. Chesnais. 1998. A new method for assessing connectedness between herds. *Proc. National swine Improv. Fed. Conf. and annual meeting*. On line: <http://www.nsif.com/Conferences/1998/mathur.htm>. Accessed Feb 29, 2004.
- Meyer, K. 1989. Approximate accuracy of genetic evaluation under an animal model. *Livest. Prod. Sci.* 21:87-100.
- Meyer, K. 1997. DFREML version 3.α. Program to estimate variance components by Restricted Maximum Likelihood using derivative-free algorithm. User notes. Animal Genetics and Breeding Unit, University of New England, Armidale NSW (Mimeo).

- Meyer, K. 2002. "RRGIBBS" – A program for simple random regression analyses via Gibbs sampling. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 28-27.
- Meyer, K., and W. G. Hill. 1997. Estimation of genetic and phenotypic (co)variance functions for longitudinal or "repeated" records by restricted maximum likelihood. *Livest. Prod. Sci.* 47:185-200.
- Misztal, I. 1993. RENUM-data preparation program for sire and animal models. University of Illinois, Urbana, IL. p 7.
- Misztal, I. 1999. Complex models, more data: simpler programming? Online. Available: <http://www.csc.fi/ttn/ccb99/articles/IMisztal.pdf>. Accessed Jan. 30, 2004.
- Mohiuddin, G. 1993. Estimates of genetic and phenotypic parameters of some performance traits in beef cattle. *Anim. Breed. Abstr.* 61:495-522.
- Mrode, R. A. 1996. Linear models for the prediction of animal breeding values. CAB International. Biddles Ltd, Guilford. UK.
- Northcutt, S. L., R. L. Willham and D. E. Wilson. 1991. Genetic parameters for nuclear and nonnuclear inheritance in three synthetic lines of beef cattle differing in mature size. *J. Anim. Sci.* 69:4745-4753.
- Núñez-Dominguez R., L. D. Van Vleck, and L. V. Cundiff. 1995. Prediction of genetic values of sires for growth traits of crossbred cattle using a multivariate animal model with heterogeneous variances. *J. Anim. Sci.* 73:2940-2950.
- Olson, T. A., M. A. Elzo, M. Koger, W. T. Butts, Jr., and E. L. Adams. 1990. Direct and maternal genetic effects due to the introduction of *Bos taurus* alleles into Brahman cattle in Florida. I. Reproduction and calf survival. *J. Anim. Sci.* 68:317-323.
- Pearson de Vaccaro, L. 1973. Some aspects of the performance of purebred and crossbred dairy cattle in the tropics. Part 1. Reproductive efficiency in females. *ABA* 41:571-591.
- Peña, R. E. 1998. Genetic characterization of criollo cattle in Bolivia. M Sc. dissertation. Univ. of Florida. Gainesville.
- Poyton, R. O., and J. E. McEwen. 1996. Crosstalk between nuclear and mitochondrial genomes. *Annu. Rev. Biochem.* 65:563-607.
- Quiroz-Valiente, J., V. Vega-Murillo, A. Rios-Utrera, and M. Montaña-Bermúdez. 1994. Milk yield and composition of Brahman and F₁ crossbred Angus, Hereford, Charolais and Brown Swiss x Zebu cows. *Proc. 5th World Congress on Genetics Applied to Livestock Production* 20:379-390.

- Randel, R. D. 1984. Seasonal effects on female reproductive functions in the bovine (Indian breeds). *Theriogenology* 21:170-185.
- Rios-Utrera, A., V. E. Vega-Murillo, M. Montaña-Bermúdez, J. Lagunes-L., and J. V. Rosete-F. 1996. Comportamiento reproductivo de vacas Brahman, Indobrasil y cruzas F₁ Angus, Charolais, Hereford y Suizo Pardo Cebú y peso al destete de sus crías. *Tec. Pec. Méx.* 34:20-28.
- Roberson, R. L., J. O. Sanders, and T. C. Cartwright. 1986. Direct and maternal genetic effects on preweaning characters of Brahman, Hereford and Brahman-Hereford crossbred cattle. *J. Anim. Sci.* 63:438-446.
- Robison O. W. 1981. The influence of maternal effects on the efficiency of selection; a review. *Livest. Prod. Sci.* 8:121-137.
- Rohrer, G. A., J. F. Taylor, J. O. Sanders, and R. M. Thallman. 1994. Evaluation of line and breed of cytoplasm effects on performance of purebred Brangus cattle. *J. Anim. Sci.* 72:2798-2803.
- Rosales-Alday J., M. A. Elzo, M. Montaña B., V. E. Vega M., and A. Reyes V. 2002a. Parámetros genéticos de una población con cruzamientos entre Simmental y Brahman bajo condiciones subtropicales. XXXVIII RNIP. Puebla, México.
- Rosales-Alday J., M. Montaña-Bermúdez, and V. Vega-Murillo. 2002b. Mexican Simmental national genetic evaluation for growth traits. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 02-79.
- Rosales-Alday J., M. A. Elzo, M. Montaña B., and V. E. Vega M. 2004a. Genetic parameters and trends for preweaning growth traits in the Mexican Simmental Population. (In press). *Tec. Pec. Méx.*
- Rosales-Alday J., M. A. Elzo, M. Montaña B., V. E. Vega M., and A. Reyes V. 2004b. Genetic parameters in Simmental-Brahman herds under Mexican subtropical conditions. (In press). *Tec. Pec. Mex.*
- Roso, V. M., F. S. Schenkel and S. P. Miller. 2002. Estimation of the degree of connectedness between test groups of station-tested beef bulls. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication num 02-28.
- Secretaría de Agricultura, Ganadería y Desarrollo Rural [SAGAR]. 1998. Programa Nacional de los Recursos Genéticos Pecuarios. México. 42.
- Schaeffer, L. R. 1975. Disconnectedness and variance component estimation. *Biometrics* 31:969-977.

- Schaeffer, L. R. 2004. Application of random regression models in animal breeding. *Livest. Prod. Sci.* 86:35-45.
- Searle, S. R. 1971. *Linear models*. John Willey and Sons, Inc. New York.
- Smith, C. 1962. Estimation of genetic change in farm livestock using field records. *Anim. Prod.* 4:239-251.
- Southwood, O. I., B. W. Kennedy, K. Meyer, and J. P. Gibson. 1989. Estimation of additive maternal and cytoplasmic genetic variances in animal models. *J. Dairy Sci.* 72:3006-3012.
- Surani, M. A. H., Barton, S. C., and M. L. Norris. 1984. Development of reconstituted mouse eggs suggests imprinting of the genome during gametogenesis. *Nature* 308:548-550.
- Szabó, F., Z. Lengyel, and I. Komlósi. 2002. Some effects on weaning weight of Hungarian Simmental beef calves. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*. CD-ROM communication no 02-81.
- Szyda, J., Z. Liu, R. Maschka, F. Reinhardt, and R. Reents. 2002. Computer system for routine QTL detection and genetic evaluation under mixed inheritance model in dairy cattle. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*. CD-ROM communication no 28-10.
- Tess, M. W., C. Reodecha, and O. W. Robison. 1987. Cytoplasmic genetic effects on preweaning growth and milk yield in Hereford cattle. *J. Anim. Sci.* 65:675-684.
- Thallman, R. M., J. F. Taylor, J. O. Sanders, and R. L. Quaas. 1992. Non-traditional genetic effects in reciprocal cross Brahman Simmental F1 calves produced by embryo transfer. *J. Anim. Sci.* 68(Suppl. 1):22(Abstr).
- Van Vleck, L. D. 1991. C. R. Henderson: Farm boy, athlete, and scientist. *J. Dairy Sci.* 74:4082-4096.
- Van Vleck, L. D., and L. V. Cundiff. 2004. Across-breed EPD tables for the year 2002 adjusted to breed differences for birth year of 2000. Beef Improvement Federation. Online. Available: <http://www.beefimprovement.org/proceedings/vanvleck.html>. Accessed March 01, 2004.
- Van Vleck, L. D., G. D. Snowden, and K. J. Hanford. 2003. Models with cytoplasmic effects for birth weaning, and fleece weights, and litter size at birth for a population of Targhee sheep. *J. Anim. Sci.* 81:61-67.
- Vega-Murillo, V. E., A. Ríos-Utrera, M. Montaña-Bermúdez, J. Lagunes L., and R. Calderón R. 1996. Comportamiento productivo hasta el destete de vacas cebú apareadas con sementales *Bos taurus* y *Bos indicus*. *Tec. Pecu. Méx.* 34:12-19.

- Vega M. V. E., J. Rosales A., G. Martínez V., and M. Montaña B. 2002. Parámetros genéticos para peso al nacimiento y al destete en bovinos de raza Angus. XXXVIII RNIP. Puebla, México.
- Weigel, K. A. 2002. Prediction of international breeding values of dairy sires using individual animal performance records. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production. CD-ROM communication no 01-12.
- Willham, R. L. 1972. The role of maternal effects in animal breeding. III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288-1293.
- Wright, S. 1922. Coefficients of inbreeding and relationship. *American Naturalist.* 56:330-338.

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