CORRELATION OF PREDICTED BREEDING VALUES ACROSS ENVIRONMENTS IN THE PRESENCE OF SELECTION FOR DIRECT AND MATERNAL BREEDING VALUES
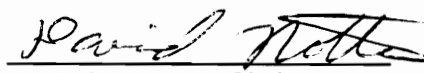
by

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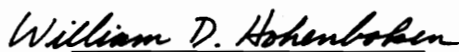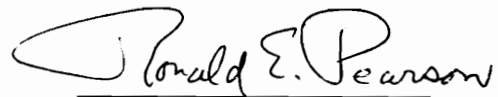
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Abstract

A simulation approach was used to determine the effects of multitrait selection on the correlations of sire direct and maternal predicted breeding values across environments. True and predicted direct and maternal breeding values (BV) of sires were simulated for sires evaluated independently in two different environments. Prediction error variances and covariances among direct and maternal BV within environments were required for the simulation. To obtain the necessary input parameters, a variety of MME coefficient matrices were created and inverted to inspect relationship among accuracies and correlations of prediction errors in sire evaluation models. An empirical prediction equation to predict the necessary prediction error covariances was obtained. Divergent, directional and random multitrait selection was then practiced using direct and maternal predicted BV as selection criteria. Samples of 40 sires were randomly obtained from each selected population. Observed correlations between direct and maternal predicted BV across environments were compared to expectations derived from univariate distribution theory. Selection definitely affected the expectations. However, the adjustment developed from univariate theory appeared to accommodate the effect of selection in these expectations.

An experimental approach was taken in order to determine existence of genotype by production system (G x P) in the maternal component of weaning weight. A sample of 43 Polled Hereford sires was chosen from the American Polled Hereford Association (APHA) sire summary by practicing divergent selection on yearling weight (YW) and total maternal expected progeny differences (EPD). Those Polled Hereford sires were mated to Angus cows to yield first generation calves. Females were kept and used to study the maternal performance. A positive association of Polled Hereford sires' net maternal (MILK) and WW EPD with the maternal performance of their daughters and growth of their grandprogeny was observed. Additional sire residuals were also detected after fitting EPD in the model. Polled Hereford sire EPDs were calculated using only experimental data with a model that included effect of genetic groups and sires. Expected values of correlations between APHA and experimental EPDs seemed to be affected by covariance generated during the estimation of predicted BV under the genetic groups model. Selection did not have any impact on the variances among predicted BV relative to those expected in an unselected population, therefore no adjustment of expected correlations were performed. G x P did not appear to affect weaning weight but may have an impact on the net maternal trait.

One hundred sixteen daughters of the selected sires were milked with milking machines. A positive relationship between sire MILK EPD and daughters' actual milk production was found. Correlation between milk production and sires MILK EPD was .26, correlation between calf weaning weight and dam milk production was .64 and correlation between calf weaning weights and sire MILK EPD was .20.

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Thanks are due to the members of my committee , Drs. Eller, Hohenboken and Pearson for their always cooperative attitude. I particularly want to thank Dr. Ina Hoeschele for being always opened whenever I went to ask.

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My stay in this country has brought me the opportunity of meeting a huge diversity of people. I know now that this has greatly enriched me as a human being. I must truly thank

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INTRODUCTION

Expansion of beef cattle populations over a wide range of environments has created the need to consider the effect of environmental conditions on the expression of production characters of economic interest. The genetic basis of animal performance may vary from environment to environment (Falconer, 1952), and genetic improvement programs involving a wide diversity of environments ought to consider the effectiveness of selection when animals are evaluated under one set of environmental conditions, but when the future performance of those animals or their progeny will be measured in a different environment. The existence and magnitude of possible genotype by environment (G x E) interactions must first be established before designing programs to accommodate G x E interactions.

The movement of animals from environment to environment usually also involves to accommodate selection. Increasingly, such selection is based on predicted breeding values, and normally involves a number of traits of economic interest. Thus, the study of G x E interaction must recognize the selected nature of the animals providing data.

To assess the existence of G x E interaction, both experimental and field data may be and have been used (e.g. Tilsh et al., 1989; Mahrt et al., 1990; Notter and Cundiff, 1991; Bertrand et al., 1987; Notter et al., 1992). The correlations of predicted breeding values for the same animal evaluated in pairs of environments have been utilized to assess the genetic correlations involving animal performances across environments (Tilsh et al., 1989; Mahrt et al., 1990; Swan, 1992). Proper interpretation of results from such studies requires knowledge of the expectations of these correlations (Calo et at., 1973; Blanchard

et al., 1983; Notter and Diaz, 1992) and/or of the applicability of the assumptions required to use the methodology (Taylor, 1983; Notter and Diaz, 1992). Proper experimental designs can allow accommodation of the experimental conditions to the assumptions. Notter and Diaz (1992) determined the effect of different selection strategies on the expectations of correlations of predicted breeding values across environments. The selection was assumed to be imposed on a single trait and the sires evaluations were assumed to come from single trait analyses. However, more realistic situations would encompass multitrait model evaluations and selection for multiple traits.

Weaning weight is a trait of particular economic interest. It is the expression of two characters, the direct effect of genes for growth of the calf and the effect of genes for maternal ability of the dam. Most National Cattle Evaluations (NCE) in beef cattle include evaluation of sires for both characters, growth and maternal ability. The predictions of BV for direct and maternal effect generally are predicted simultaneously (Benyshek et al., 1988).

Populations of domestic animals usually present a hierarchical structure (Vu Thien Kang, 1983) with three basic layers: nucleus, multiplier and commercial. In most of the domestic populations, the genetic situation will depend upon a number of herds (nucleus breeders) from which the flow of genes is established. While diversity of environments is observed among nucleus herds, a wider variety is recognized when animals move between nucleus and commercial herds. Mahrt et al. (1990), in a one-generation experiment, evaluated the correspondence between predicted sire breeding values in purebred beef herds and progeny performance under commercial crossbreeding. Sires were divergently selected using predicted breeding values derived from industry data.

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Crossbred females are also widely used under commercial conditions. Selection of sires for maternal characters is based on predicted breeding values estimated by separation of direct and maternal components affecting weaning weights. Thus, the objectives of this thesis were threefold. The first was to evaluate, by computer simulation, the effect of various types of selection on the expected value of the correlation of predicted BV across environments when selection is practiced simultaneously on two traits and based on breeding value predictions. Direct and maternal traits were taken as a working case. The second objective was to assess the efficacy of sires' milk transmitting abilities (net maternal or MILK EPD) in predicting crossbred daughters' performances in a commercial environment using divergent selection for growth and maternal ability. Finally, the third goal was to assess the relationship of sires' MILK EPDs to their daughters' actual milk production.

CHAPTER 1

LITERATURE REVIEW

Genotype by environment interactions

The simplest model to explain the phenotype of an individual assumes that the phenotype is the result of an additive genotypic value plus an environmental deviation (Falconer, 1989). One of the assumptions of this model is that genotype and environment do not interact with each other to affect the phenotype. If this assumption is correct, then differences in phenotype due to differences in genotype should not be expected to depend upon the environment. Individuals that are genetically superior would be able to express such superiority independently of the environment in which performance is measured.

Genotype by environment (G x E) interaction can be quantified as the genetic correlation of the same trait measured in two different environments (Falconer, 1952). Two different types of genotype by environment interaction might occur. In the first, changes exist in ranking of animals across environments and the genetic correlation between performances in two environments may differ substantially from one. This situation indicates that selection within each environment for genes that act specifically in that environment will allow greater genetic progress, given the same variances. The second situation arises if variances are heterogeneous across environments but genetic correlation is close to one. The absolute magnitude of genetic differences will be smaller in the less variable environment. However, reranking of animals across environments would not be expected. Success of selection in another environment will depend on the value for the genetic correlation as well as the genetic variances (Dempfle and Gründl, 1988).

Procedures for estimation of the genetic correlation between performances in different environments, r_G, were developed by Dickerson (1962) and Yamada (1962), such that:

$$r_G = \frac{\sigma_s^2}{\sigma_s^2 + \sigma_{se}^2}$$

where σ_s^2 and σ_{se}^2 are the sire and sire by environment variance components, respectively. If σ_{se}^2 is equal to 0, the genetic correlation will be one and the trait will have the same genetic basis in different environments. However, the genetic correlation can be underestimated if genetic variances are not equal across environments. A correction factor to account for heterogeneity of sire variances is normally applied (Robertson, 1959; Dickerson, 1962 ; Yamada, 1962) to correct bias. A further censure of this procedure was made by Fernando et al. (1984) who pointed out a possible bias in the estimates of r_G for unbalanced data if genetic and residual variances are not the same in each environment. Obviously then, the question of heterogeneity of variances among environments is inherent to the study of G x E interactions.

The first attempt to classify genotype by environment interactions was done by Haldane (1946). He classified them into four groups by combining, intra- and inter-population interactions with micro- and macro-environments. In domestic livestock, macro-environmental differences, such as diversity of climate and management practice are of major concern within and among populations. To approach the problem, a clear definition of environmental differences and genotypes is necessary. In various studies, the genotypes of interest have been considered to be breeds, lines, or individual sires. The different environments have been defined broadly as well. Factors such as different diets or nutritional levels (e.g., Hohenboken et al., 1988); geographical location or locations with

dissimilar climate or management conditions (e.g., Burns et al., 1979; Pahnish et al., 1983); test stations vs. field conditions (e.g., Smith et al., 1979; Baker et al., 1984; Oldenbroek and Meijering, 1986); countries (e.g., Carabaño et al., 1990; Rozzi et al., 1991), regions (e.g., Nunn et al., 1978; Bertrand et al., 1985;1987; Wiggans and VanRaden, 1991), time (Wiggans and VanRaden, 1991) or herds (e.g., Danell, 1982; Notter et al., 1992) have been considered.

There are two approaches to the study of genotype by environment interaction. The biological approach emphasizes adaptation, sensitivity and resistance to environmental stress of different breeds or crosses and the understanding of the biological mechanisms involved (e.g., Frisch, 1987; Hohenboken et al., 1988). On the other hand, the biometrical approach is more concerned with the quantification of G x E interactions, as well as statistical problems in proper identification of G x E interaction as it affects the accuracy of selection appropriate to the environment or conditions the individuals will experience (Robertson, 1959; Yamada, 1962; Dickerson, 1962; Fernando et al., 1984; Meyer; 1987).

The existence of genotype by environment interactions can have several implications in the development of animal breeding programs. Currently, sires often produce progeny in a wide diversity of environments. Thus, the existence of true interactions has to be seriously considered and could require a decision to either optimize performance over the range of environments or develop separate breeding programs for each environment.

Populations of domestic animals usually present a hierarchical structure (Vu Thien Kang, 1983) in which a number of elite breeders maintain stud animals under rather different conditions from those under which commercial animals are maintained. Sire evaluations

are often used by the elite breeders, with the information for those evaluations coming only from within their herds. Thus, Expected Progeny Differences (EPD) are normally available for them in order to make selection decisions. An EPD is defined as an estimate of the average additive value of the gametes produced by a parent and attempts to predict the transmitting ability of that parent. But what happens to the receptor, the commercial producer? Environmental and managerial differences between stud and commercial breeders are widely recognized. In this context, managerial conditions refer basically to the use of crossbreeding for genetic improvement. Thus, the question to address is whether the genetic basis for performance is the same across environmental and managerial conditions. The effectiveness of selection in the elite herds for improving commercial performance depends on the adequacy of purebred EPDs as a predictor of commercial performance. If the genetic basis is not the same in the two environments, selection based on commercial performance is required to maximize genetic improvement (Falconer, 1952; McBride, 1958). In this context the concept of interaction is used in a very broad sense and relates to the fact that under commercial conditions more poor environmental conditions as well as crossbreeding are currently seen.

Evidence of genotype by environment interactions in different populations

Evidence of genotype by environment interactions in domestic livestock have been described in the literature however, the pattern is different depending upon the species and trait. G x E interaction within the same countries has been studied by different authors (Robertson and Mason, 1956; Danell, 1982; Hill et al., 1983; Carabaño et al., 1990; Ibáñez et al., 1991), but evidence of true genotype by environment interaction has not been found. Attention also has been paid to this subject in the context of international

dairy sire evaluations (Peterson, 1988; Carabaño et al., 1989; Rozzi et al., 1991; Stanton et al., 1991). The range of reported genetic correlations between environments for milk yield is from .78 to .98 (Danell, 1982; Carabaño et al., 1989, 1990; Rozzi et al., 1991; Stanton et al., 1991) with one exception where in a comparison between 40 Canadian and New Zealand dairy sires, the estimated genetic correlation between performance of Canadian bulls at home and in New Zealand was .22 (Peterson, 1988). However, heterogeneity of residual and genetic variances has been reported in dairy populations across herds grouped by level of production and country (e.g. Danell, 1982; Hill et. al., 1983; Carabaño et al., 1989; Ibáñez et al., 1991; Stanton et al., 1991). Heritabilities tend to be higher at higher levels of production (Hill, 1984). Danell (1982) reported heritabilities for total milk production of .21, .25 and .28 when estimated in herds of low, medium and high levels of production, respectively. Stanton et al. (1991) compared genetic and residual variances between USA and Latin America (Mexico and Colombia) for mature-equivalent milk. Latin-American data were divided into high and low within-herd standard deviation groups. In the low group, sire and residual variances were as much as 42 and 40% of the USA values; however, in the high group the proportion increased to 79% and 96%, respectively. Heritabilities were similar, nevertheless the heritability in the low group was higher than that in the high group, basically due to a substantial reduction in residual variances in the low group. Stanton et al. (1991) stated that the consequence of heterogeneous variances was smaller correlated response to selection. Rozzi et al. (1991) did not find evidence of heterogeneity of variances between Italy and Spain.

In swine, genotype by environment interactions have been reported in traits such as daily gain (from birth), backfat thickness (adjusted by weight) and an index containing both

(Standal, 1977; Merks, 1988). Standal (1977) compared breeding values of sires including 124 AI sires evaluated on the basis of on-the-farm tested sons' performance or station-tested daughters. The pairwise estimated genetic correlations between performances significantly deviated from unity (.45, .65, and .63, respectively). However, this result might be in part attributed to genotype by sex interactions since different sexes were represented in each location. Merks (1988) also reported sire by farm interactions for the same traits. He detected a sire by farm interaction component of the same magnitude as the sire component however, as indicated by the author, 30 to 90 % of that interaction was due to heterogeneity of genetic variances. The range of genetic correlations before and after adjustment was from .29 to .73 and .37 to .92, respectively.

Two different approaches have been taken in studies of genotype by environment interactions in beef cattle populations. The first is based on field data provided by breed associations (Buchanan and Nielsen, 1979; Nunn et al., 1978; Burfening et al., 1982; Bertrand et al., 1985, 1987). The second is based on designed experiments where several lines and/or sire within breeds produce progeny in a number of experimental locations (Butts et al., 1971; Burns et al., 1979; Tess et al., 1984; Pahnish et al., 1983; Mahrt et al., 1990).

Butts et al. (1971) and Burns et al. (1979) investigated the effect of G x E interaction in two lines of Hereford cattle maintained in two distinct areas of the USA, Florida and Montana. The differences between the locations were both climatic and managerial. Traits such as birth weight, gain to weaning, weaning weight and final weight were studied. Interaction of location by herd of origin were important for birth weight, weaning weight and gain to weaning. Animals performing in their original locations tended to be heavier

than the 'immigrants'. Implications of such experimental results are that selection response is partially due to adaptation to specific environmental circumstances which might compromise seedstock exchange across dissimilar areas. Postweaning traits of heifers and bulls were investigated in the same locations by Pahnish et al. (1983, 1985); conclusions were the same. Conversely, when data from designed progeny tests of Hereford and Angus sires used in cooperator herds were studied by Wilson et al. (1972), sire by herd interactions were not detected for birth weight, weaning weight and yearling weight. Aken et al. (1976) compared two breeds of sires (Fleckvieh and Gelbvieh) at two locations (Western Germany and Central Texas) and found interaction at the breed level; however, sire within breed by location interactions were not significant. Tess et al. (1984) did not find any evidence of sire x location interaction in a study involving Hereford sires in three different locations in North Carolina. Birth and weaning weights and preweaning daily gain as well as a number of postweaning traits (average daily gain, carcass traits and percentage fat in the rib area) were studied to evaluate sire by location and sire by diet interactions. Estimates of the genetic correlation varied from .50 to 1.25; however when estimates of sire variances within each environment were used to correct bias due to scaling, the resulting genetic correlations were greater than .90.

Table 1.1 summarizes results found in beef cattle field studies of G x E interaction. Field data analyses of G x E interaction in beef have basically evaluated sire by herd, sire by region, sire by contemporary group, sire by sex and sire by season interactions. Significant genotype by environment interaction have been found for birth weight (Bertrand et al., 1985, 1987), weaning weight direct (Nunn et al., 1978; Buchanan and Nielsen, 1979; Bertrand et al., 1985, 1987; Notter et al., 1992) and maternal effects (Hanford et al., 1988). Buchanan and Nielsen (1979) studied G x E interaction effects on birth and

weaning weights of Simmental and Maine-Anjou sires. The interactions studied were sire by region, sire by herd within region, sire by sex and sire by season. While sire by sex and season interactions were of moderate importance, sire by region effects were found for both traits while sire by herd within region was shown to be important only for weaning weight in both breeds. However, herd effects also included year and location effect. Similar results were found by Nunn et al. (1978) using Simmental data. Sire by region interactions were detected for weaning weight but not for birth weight. Sire by region interaction might have been inflated by a breed of dam effect and breed of dam by sire interactions. In both cases, regions were quite large; therefore regional interactions might involve a wide range of environmental differences. No investigation of heterogeneity of variances was performed by Buchanan and Nielsen (1979); however Nunn et al. (1978) noticed that variances among sires progeny means were significantly heterogeneous. No further comment was made. Bertrand et al. (1985, 1987) found significant sire by region, sire x herd within region and sire by contemporary group (herd-weaning date-sex-management code combination) within herd and region interactions for weaning weight. Causes of those interactions were associated with different factors. While the interaction of sire by contemporary groups was related to sire by year, sire by season, sire by sex and sire by management (creep or noncreep) interactions, the sire by herd interaction was associated with sire by location and management condition effects.

Some degree of inconsistency between experimental and field results appears to exist, but several reasons for this result are possible. Failure of models to account correctly for interactions, unbalanced data with sires represented in a limited number of environments and arbitrary definition of 'different environments' may result in bias in the detection of genotype by environment interactions based on field data. In addition, possible differential

non random mating between environments and preferential treatment might have an impact. Furthermore, weaning weights appear to be more sensitive to the effect of interactions. If sires were to some extent crossclassified with different environments, dams are usually still unique to specific environments (nested within environments). Consequently, some sort of sire genotype by dam maternal interaction could be important. Bertrand et al. (1987) reported a reduction in the magnitude of sire by contemporary group interaction when including dams most probable producing ability (MPPA) as a covariate. Average weighted genetic correlation for weaning weights across regions changed from .55 to .64 to .69 before and after accounted for dams and sire by contemporary group effects, respectively. Notter et al. (1992) observed that adjustment for dams' total maternal breeding value yielded a reduction of approximately 15% in the sire by herd interaction variance component. Adjusting for total maternal breeding value should have accounted for non random mating practices that could have enhanced correlations among progeny of sires in some herds and the effect of a possible sire by dam maternal interaction. Presence of common environmental effects within half sib families could also be an important part of the G x E component (Meyer, 1987; Notter et al., 1992). Also, beef cattle populations are subject to a large diversity of environments that can not be accurately reproduced by experimental conditions.

References to the existence of G x E interaction for maternal characters are almost non existent. Hanford et al. (1988) studied the interaction of maternal grandsire by region and by herd within region for birth weight, weaning weight and calving ease. While the interaction with region was not important, there was an important effect of maternal grandsire by herd within region interaction. Adjustment was done for the direct effect of the maternal grandsire, but sire of calf was not included in the model. This G x E

component could involve a number of management factors such as use or not of creep feeding or year effects. From the magnitude of the estimated genetic correlations that was reported (.05 to .34) for weaning weight, some additional effects enhancing the sire x herd within region interaction must have existed. They might be related to either some sort of assortative mating (where the daughters of the best maternal grandsires were bred to the best sires) or possible herd-specific covariances among maternal and temporary environmental effects. A number of studies using combinations of field and test station data have also indicated a poor correspondence between performance of sires in stations and later performance of their progeny in field conditions (Baker et al., 1984; Oldenbroek and Meijering, 1986).

We can thus conclude that reasonable evidences for G x E interactions exist, at least for some populations, and that they may introduce an important source of bias in prediction of BV when interactions are not accounted for in statistical models. The reranking of sires across environments might be important also, and could be more important when the different environments involves breeding and commercial herds where a G x E interaction would be expected to be more substantial.

Evidence of genotype by genotype interactions

Crossbreeding plays a major role in improvement of economically important traits. The use of systematic crosses provides for utilization of heterosis and differences among breeds to optimize the average genetic merit for performances traits in various climates and nutritional environments (Dickerson, 1973). Therefore, the commercial breeder is able to use hybrid vigor and the unique characteristics of different breeds to satisfy the needs of

specific production and marketing situations. An underlying question is the extent to which a producer can be certain that sires evaluated in purebreeding will be appropriate to satisfy his production needs in crossbreeding. The genotype of the sire by genotype of the mate effect can be viewed as a case of genotype x environment interaction, where the breed or cross of the dams can be regarded as representing different environments.

The relationship between performance of sires in purebreeding and crossbreeding should depend upon the proportion of the observed genetic variance that is due to additive gene effects (Falconer, 1989). The relationship will be perfect only in the absence of more complex non-additive gene actions. If specific combining ability is an important source of variation , ranking of individuals may differ in different types of mating. Wei et al. (1991) concluded from simulation of a multi-locus character that the genetic correlation between straightbred and purebred performance may be less than unity in the presence of dominance and if gene frequencies differ greatly in the parental populations.

Genetic correlations have been estimated using paternal half sib models that include information from purebred and crossbred progeny in order to assess the existence of genotype by genotype interactions. Estimates of the genetic correlations found in the literature are reported in Table 1.2. Similarly to the case of G x E interaction, differences across species and traits can be observed in addition to differences among breed crosses.

The ratio of direct response (DR) to selection based on merit of crossbred progeny to the correlated response (CR) per unit of time from within-breed selection has been used to evaluate reciprocal recurrent selection versus within-breed selection (Standal, 1968; McLaren et al., 1985). The prediction equation used was:

$$\frac{DR_c}{CR_p} = \frac{i_c h_c L_p}{i_p h_p L_c r_{G_{p,c}}}$$

where i represents the standardized selection differential, h the square root of heritability, $r_{Gp,c}$ represents the genetic correlation between purebred and crossbred performance, L is the generation interval and the subscripts p and c refer to purebred and crossbred data sources. For values of the ratio that are greater than 1, the comparison is in favor of selection for specific combining ability. The reciprocal of this coefficient (without considering generation interval) has also been reported, with the opposite interpretation (Dim, 1974; Salah et al., 1969). Dim (1974) compared expected breeding values for fat-corrected milk derived in crossbreeding for sires of three different breeds to Swedish straightbred proofs for the same sires. A genetic correlation that was close to one was obtained; however, the ratio of correlated response to direct response (.9) favored direct selection on crossbred performance. However, Salah et al. (1969) in sheep reported that response to selection based on purebred information was 12% higher than that achieved using data from crossbred progeny.

Vinson et al. (1969) reported estimates of additive genetic variances and heritabilities based on paternal half-sibs in purebred and crossbred population of mice. Estimates of high genetic correlation between sires' progeny performance in both situations indicated a large additive component in the genetic variation. However, the ratio of sire variance for purebreds to that of crossbreds was greater than one, which the authors suggested may have been indicative of partial dominance.

No clear advantage of selection for specific combining ability has been found in mice, beef, sheep or swine (Vinson et al. 1969; Salah et al., 1969; Dunn et al., 1970; Koger et al.

1975; McLaren et al., 1985) however it is expected that reciprocal recurrent selection (Comstock et al., 1949) would be advantageous for lowly heritable traits (Vinson et al. 1969; McLaren et al., 1985; Wei and Steen, 1991) and might be appropriate for adverse environments (Wei and Steen, 1991). Miquel and Cartwright (1963) and Dunn et al. (1970) in beef cattle found similar sire variance components and heritabilities for birth weight and weaning weights when comparing estimates obtained from purebred and crossbred progeny. Salah et al. (1969) found that heritability estimates for purebred performances for weaning weight in sheep were higher than those in crossbreds . They also found that the genetic correlation between sire purebred and crossbred progeny performance was .82. Nevertheless, the same authors were critical of the estimate of heritability in the crossbred situation due to failure to recognize differences among dam breeds and consequently inflation of mean square errors in crossbreeding.

Product moment correlations of predicted breeding values for different mating types also have been used to asses the correlation between sire's purebred and crossbred performance (Table 1.3). Results in Table 1.3 must be interpreted carefully since proper expectations of the correlations are needed. This subject will be discussed in the following section. Tilsch et al. (1989) reported systematic departures from expectations when performance of beef sires was compared in purebreeding versus dairy crossing, but the sampling effects were too large to permit any conclusion. Garrick et al. (1989) reported consistency between observed and expected correlation values across sexes and dam types for birth weight and weaning weight (direct and maternal) but not for postweaning gain. However, when comparing observed versus expected correlations by level of accuracy, a possible lack of random sampling of sires after weaning (selection at weaning) could have explained this departure for postweaning gain (Garrick et al., 1989). Contrarily, Swan

(1992) reported strong evidence of possible departures of observed correlations from expectations however, as properly mentioned by the author, the accuracies of breeding value predictions were overestimated, since the complete inverse of the mixed model coefficient matrix was not obtained. The fact that a multitrait analysis was used might have had an additional effect since such an analysis is expected to improve accuracy of evaluation over single trait analysis (Thompson and Meyer, 1986). Theoretical development of the expectation of a breeding value correlation was based on a single-trait analysis (Taylor, 1983). An additional confounding effect of sire by year and sire by herd interaction could be responsible for the observed results (Swan, 1992).

It is very difficult to draw conclusions from the studies reviewed here. Analysis of variance approaches did not show evidence of an important effect of sire specific combining abilities to support the use of reciprocal recurrent selection or any type of selection based on crossbred data to improve sire performance in crossbreeding.

Through the previous two sections, an effort has been made to separate the problem of G x E from genotype x genotypes interaction, however they are often inseparable since in most species commercial crossbreeding leads to both expression of nonadditive genetic effects and 'different' environmental circumstances. Thus, in reality a more general term is needed. We will be referring to genotype by production system (G x P) interaction to include both potential sources of interaction. In order to design breeding programs, they often must be considered together. In conclusion then, establishment of the impact of genotype by environment and/or genotype by genotype interactions using experimental or field data is still needed.

The regression of actual progeny performances on sires transmitting abilities

A practical method of detecting G x P interactions has been used by several authors (Ruvuna and McDaniel, 1983; Mahrt et al., 1990; Persaud et al., 1990; Notter and Cundiff, 1991; Wright and Pollak, 1991). This method compared actual progeny performance in a secondary environment to sires' breeding value estimates in the environment where selection decisions are made using regression analysis. If the observed regression coefficient (regression coefficient of progeny performance in a second environment on sire EPD obtain in the first environment) is not significantly different from that expected (1 kg per kg of EPD for growth traits), then it is possible to conclude that interactions are unimportant. Ruvuna and McDaniel (1983) regressed milk yields of crossbred daughters on PD for milk of Holstein and Brown Swiss sires. Regression coefficients were 1.42 and .77 kg of milk per kg on PD for Holstein and Brown Swiss, respectively; however the magnitude of the sampling errors did not indicate significant departures from expectation. Regression of F_1 calf weaning weights on sire weaning weight EPD have been lower than expected (Mahrt et al., 1990; Notter and Cundiff, 1991; Notter and Mahrt, 1991); however when Notter and Cundiff (1991) regressed weaning weights of progeny of F_1 females on maternal grandsires' direct and maternal weaning weight EPD, neither regression coefficient differed from expectation (.5 and 1; respectively). However, since direct EPD's were those of the maternal grandsires, the power of the test of the effects of direct weaning weight EPD was reduced. Nevertheless, maternal weaning weight EPDs did seem to be predictive of actual calf weights in crossbreeding.

Expectation of the correlation of predicted breeding values across environments

In the previous section, the use of the correlation of predicted breeding values to estimate the genetic correlation between expressions of the same character under different environmental conditions has been discussed. Different authors have correlated EPD of sires under different 'environmental' conditions in an attempt to identified possible reranking of sires among environments and management conditions (Table 1.3). The same methodology was initially used to obtain an estimate of genetic correlation between two different traits, such as milk and beef production of Holstein-Friesian bulls (Calo et al., 1973) and milk and fat yield as well as a number of type traits (Blanchard et al., 1983). In either case, interpretation of results must depend on the expected value of the observed product moment correlation between predicted breeding values (Calo et al., 1973; Blanchard et al., 1983; Taylor 1983; Garrick et al., 1989; Notter and Diaz, 1992).

Thus, an estimate of the genetic correlation may be obtained by comparing the observed product moment correlation of predictions to its expectation. From selection index theory the expected correlation can be expressed as

$$r_o = acc_1 r_G acc_2$$

where r_O is the product moment correlation between separate estimates of sires' BV in different environments or for different traits; acc_1 and acc_2 are correlations between true and predicted breeding value in environment 1 and 2, respectively; and r_G is the underlying genetic correlation. Assuming a genetic correlation of 1, the expectation becomes equal to the product of accuracies, $acc_1 acc_2$. This formulation of the expectation requires

accuracy of prediction of sire BV to be equal for all sires within each environment. An expectation of 1 would demand accuracies of estimates equal to unity in both environments. However, such homogeneity of accuracies is not very realistic, even under the best experimental conditions, such a balanced situation would be difficult to achieve. Calo et al. (1973) and Blanchard et al. (1983) derived the expectation of r_o accounting for unequal information for each sire and, therefore different accuracies. The derived expectation was then :

$$Corr(\hat{u}_1, \hat{u}_2) = \frac{r_G \sum_{i=1}^{m} acc_{1i}^2 \sum_{i=1}^{m} acc_{2i}^2}{\sqrt{\sum_{i=1}^{m} acc_{1i}^2 \sum_{i=1}^{m} acc_{2i}^2}}$$

where acc_{1i} and acc_{2i} are the accuracies associated with the prediction of BV of the *ith* sire in each environment (1 and 2) and m is the number of sires.

This expectation has produced estimates of r_G that were out of the parameter space (Taylor, 1983). Taylor (1983) established the theoretical framework under which this expectation will achieve proper estimation of r_G. The derivation of those conditions is based on single trait evaluations in each environment. Those conditions are: (1) no relationships among parents of measured animals, (2) no environmental correlations between performance of animals across environment, (3) no other covariances among predicted BV values within either environment. An implicit assumption (4) is that sires are chosen at random. If those assumptions do not apply, an inappropriate estimate of the genetic correlation will be obtained due to use of an improper expectation. The propriety of these assumptions will vary depending upon the source of information, either

experimental or field data. Under either condition, environmental covariances should not be a problem since different animals are usually measured in different environments; however the remaining assumptions are more critical. As pointed out by Notter and Diaz (1992), assumptions 1 and 4 might be overcome through the sampling of sires when an experimental approach is taken, but under field conditions are out of the experimenter's control and will often not be met (Taylor, 1983). Assumption 3 will likely never be completely met since it is almost always violated as a result of the prediction process. The process of estimation using Mixed Model Methodology generates covariances among predictions arising from the estimation of fixed effects even in the absence of relationships among sires. Existing prediction error covariances, which are elements of the inverse of the mixed model coefficient matrix corresponding to the random part of the model (C_{22}), may be of importance depending upon the data structure. In very unbalanced designs, predictions and contemporary groups estimates tend to be confounded unless the number of sires contemporary to the connecting sires are numerous. When the elements of C_{22} involve sires with progeny equally distributed across contemporary groups, the off diagonals of C_{22} become negligible if reasonable numbers of sires are involved; however, if data are unbalanced and only a few sires are represented across contemporary groups, ignoring covariances among predicted BVs in the expectation of r_o might bias the estimate of genetic correlation (Notter and Diaz, 1992).

Taylor (1983) recognized the likely existence of these covariances but still assumed that they were null. In practical terms, such an assumption is usually necessary when dealing with field data, since MME solutions are found by iteration and therefore the complete inverse of the coefficient matrix is not likely to be obtained. Notter and Diaz (1992) quantified the impact of ignoring prediction error covariances under simulated

experimental conditions. For situations with balanced designs under which sires have progeny equally distributed over a number of contemporary groups, the bias, defined as the difference between the expectation of the correlation (considering the prediction error covariances) and the product of accuracies, was practically null with 24 sires (12 in each contemporary group). However, when less ideal situations were considered, larger numbers of sires per contemporary group were required to attain negligible bias.

An additional assumption that was implicitly made in Taylor's (1983) derivation was the absence of selection. However, use of field data will usually invalidate that assumption, since movement of animals from one environment to another basically occurs as the result of a selection decision. Under this circumstance, correlation of predicted breeding values of sires across environments is biased by selection (Notter and Diaz, 1992); however regression is not biased so long as selection is practiced only on the independent variable (predicted breeding value in the first environment). Notter and Diaz (1992) derived the expected value of the correlation under various types of selection, the resulting expression is:

$$Corr(\hat{u}_1, \hat{u}_2) = r_G acc_{12} \sqrt{\frac{1-s}{1-r_G acc_{12} s}}$$

where $r_G acc_{12}$ is equal to the expectation developed by Calo et al. (1973) and s is an empirical definition of the selection practiced (Robertson, 1966), such that

$$s = 1 - \frac{Var(\hat{u}_1)}{\sigma_{\hat{u}_1}^2}$$

where $Var(\hat{u}_1)$ is the variance of $\hat{u}_1$ in the selected sample and $\sigma^2_{\hat{u}_1}$ is the variance of $\hat{u}_1$ in the population of sires prior to selection. Notice that in the case of directional truncation selection, $s = i(i - x)$ and for divergent selection $s = -ix$ where i is the standardized selection differential and x is the truncation point on an standard normal curve.

The use of this methodology implies several assumptions related to the adequacy of the accuracy estimates. Accuracies are assumed to come from the full inverse of the MME and to be adjusted for current selection, and not only to reflect the amount of data available. However, in current sire evaluations computational limitations invalidate the first assumption; furthermore, adjustment for selection is not reflected in the published accuracies since changes in the variances-covariance structures under selection are not accounted for (Dekkers, 1992).

Prediction of breeding values: *maternal effects, grouping and accuracy of evaluation.*

Best Linear Unbiased Prediction (BLUP) (Henderson, 1963; Henderson, 1973) is commonly used to predict breeding value in current National Sire Evaluation (NSE) programs (Henderson, 1988). The BLUP of w is:

$$\hat{w} = P\hat{\beta} + C'V^{-1}(y - X\hat{\beta})$$

where $\hat{\beta}$ is the BLUE of β or $\hat{\beta} = (XV^{-1}X)^{-1}X'V^{-1}y$ and

$V = var(y)$

$C = cov(y, w')$ and

$$E(w) = P\beta$$

The computation of BLUP of w is based on mixed model equations (MME)(Henderson, 1984; Quaas, 1984). Solution of MME provides simultaneous solutions for β and w without the need of computing V^{-1} (Quaas, 1984). MME were first reported in 1949 (Henderson, 1949) and, as emphasized by Henderson (1990), they attempted to combine Generalized Least Squares (GLS) to estimate fixed effects with the desirable characteristics of Selection Index .

MME were initially used in 1970 for AI dairy sire evaluation (Henderson, 1990); a few years later this methodology was implemented in beef NSE programs (Berger, 1983; Benyshek, 1987). The first model used in NSE was referred to as the 'contemporary group-sire model':

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

where y is the vector of observations, β is the vector of the fixed effect of the contemporary group associated with the observations by the incidence matrix X, u is the vector of sires effects associated with the observations by the incidence matrix Z and e is the vector of random errors.

$$E\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix} \quad \text{and} \quad var\begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} Z'GZ+R & GZ' & R \\ Z'G & Z'GZ & 0 \\ R & 0 & R \end{bmatrix}$$

The model required several assumptions to result in unbiased predictors of BV: sires were considered to be randomly mated to cows, cows were assumed to have only one progeny in the data set, no genetic trend was assumed to exist and progeny of sires were assumed

to be similarly treated within contemporary groups (i.e., no preferential treatment). These assumptions might have been met in the early 1970's but certainly are not applicable to current beef cattle data bases (Benyshek, 1987; Benyshek et al., 1988).

New events took place in the implementation of Mixed Model methodology that were later incorporated in NSE. Henderson (1976) derived the direct computation of the inverse of Wright's numerator relationship matrix, A. The incorporation of the A matrix allowed greater use of information on relatives, accommodation of inbreeding and accounting for genetic trend (Kennedy et al., 1988). The relationship matrix was first incorporated in NSE in 1983.

Henderson and Quaas (1976) initially described the model which combined own records of individuals with records of relatives to obtain BLUP of breeding values when a number of traits were simultaneously evaluated. This model was later baptized as the 'Animal Model' by Quaas and Pollak (1980). The animal model or, more properly said, the animal models, have a number of desirable properties that were extensively reviewed by Kennedy et al. (1988). In particular, they produce an adjustment for the merit of mates, therefore taking account of the effects of nonrandom mating (Quaas and Pollak, 1980; Kennedy et al., 1988).

Current sire evaluation programs use multitrait models that incorporate a number of characters simultaneously (Benyshek et al., 1988). Multiple trait evaluations account for effects of selection on the same and on correlated traits (Quaas, 1984; Thompson and Meyer; 1986) and increase accuracy of prediction (Henderson and Quaas, 1976; Quaas, 1984; Thompson and Meyer; 1986). However, the implementation of those models has

required development of improved computational strategies (e.g. Schaeffer and Kennedy, 1986; Misztal and Gianola, 1987; Tier and Smith, 1989; Groeneveld and Kovac, 1990; Tier and Graser, 1991) .

Approximately fifteen beef breed associations in The United States have some sort of NSE. Genetic predictions involve a number of characters , including growth (birth weight, weaning weight and mature weight), milk, calving ease, scrotal circumference and yearling and mature hip heights.

Model for prediction of maternal traits

Maternal effects have been of interest to animal breeders since the early years of animal breeding as a discipline. Dickerson (1947) discussed different biometrical aspects of maternal effects. Subsequently, Kempthorne (1955), Willham (1963, 1972) and Falconer (1965) proposed linear models to explained actions of maternal effects. More recently, extensive effort has been made toward the estimation (Thompson, 1976; Hohenboken and Brinks, 1971; Koch, 1972; Foulley and Leffort, 1978; Cantet et al., 1988; Cantet, 1990; Meyer, 1992) and prediction (Van Vleck, 1970; Quaas and Pollak, 1980; Quaas, 1984; Henderson, 1988; Benyshek et al., 1988; Van Vleck, 1990) of maternal effects. As a result, most NCE programs provide information on sires' growth and maternal breeding values for weaning weight. Most beef cattle genetic evaluation reports provide two traits related to maternal performance at weaning. The first one is maternal milk, which refers to differences in weaning weight of sires' daughters calves due exclusively to net maternal ability, mostly milk production (APHA, 1992; AAA, 1991; ASA, 1991). The second is usually referred to as maternal weaning weight (MAT) or total maternal effect. This measure includes genetic differences in maternal ability and genetic differences in growth potential transmitted from sire to grandprogeny via their dams.

Many traits expressed early in life are environmentally influenced by the dam, especially in species where progeny are suckled by the dam. Weaning weight is thus a joint expression of at least two genetic values, a direct value for growth of the calf and a maternal genetic value for the dams (Willham, 1963). Dams pass a sample half of their genes to their offspring and additionally express their own maternal genetic value in the weight of their progeny. Therefore, traits that are maternally influenced such as weaning weight are a joint expression of two phenotypes: the phenotype of the calf for growth and the phenotype of the dam for maternal characteristics (i.e., milk production). Although the calf producing the record carries genes for maternal ability from both sire and dam, these genes will only be expressed if the calf is female and later produces progeny. Thus, the maternal component is genetic with respect to the mother but environmental with respect to offspring (Willham, 1963;1972; Falconer, 1989). Direct and maternal characters may be correlated (Hohenboken and Brinks, 1971; Koch, 1972; Bertrand and Benyshek, 1987; Cantet et al., 1988; Cantet, 1990). However, the magnitude and direction of that correlation appears to vary from breed to breed (Meyer et al., 1992; Johnson et al., 1992).

Although maternal traits normally constitute a part of more comprehensive multitrait models, we will focus on direct-maternal effect models where only weaning weight records are considered. The multitrait approach is an extension of this model where genetic and environmental correlations among a number of traits are considered (Quaas and Pollak, 1980; Benyshek et al., 1988). The first formal description of a model including direct and maternal breeding values was done by Quaas and Pollak (1980). Subsequently, references to this model have been made by Henderson (1984) and Quaas (1984). The

model usually described for prediction of direct and maternal breeding values is an animal model or 'maternal animal model' (Henderson, 1984).

The model for evaluation is a genotypic model where the additive genotype of calf and dam are included as :

$$y_{ijk} = fx_i + u_{dj} + u_{mk} + u_{pk} + e_{ijk}$$

where y_{ijk} is the weaning weight of the *jth* calf and fx_i represents all fixed effects affecting y, u_{dj} represents the direct breeding value of the jth individual, u_{mk} is the maternal breeding value of the *kth* dam, u_{pk} is the maternal permanent environmental effect of the *kth* dam and e_{ijk} is a environmental deviation. In matrix notation:

$$y = X\beta + Z_d u_d + Z_m u_m + Z_p u_p + e$$

where,

y is a vector of weaning weights records;

X is a incidence matrix that relates fixed effect in β to the vector of records y;

Z_d is a incidence matrix that associates the elements of the vector of additive direct u_d to the records in y;

Z_m is a incidence matrix that associates elements of the vector of u_m to the records

in y;

Z_p is an incidence matrix that relates the vector e_p to the records in y;

e is a vector of random residuals associated with y;

u_d, u_m are vectors of additive direct and additive maternal random breeding values, respectively;

u_p is vector of permanent maternal environmental effects on weaning weights which are common to all progeny of a dam;

The assumptions regarding first and second moments of the random effects are that means are null and that the u vectors are uncorrelated with e. The variance- covariances matrix of $u=(u_d', u_m')$ is equal to $G_o \otimes A$, where A is the numerator relationship matrix among all animals (dams, calves, ancestors) and G_o is a 2x2 matrix of additive genetic variances and covariances (g) of the direct (d) and maternal (m) effects:

$$G = G_o \otimes A = \begin{bmatrix} g_{dd} & g_{dm} \\ g_{md} & g_{mm} \end{bmatrix} \otimes A = \begin{bmatrix} g_{dd}A & g_{dm}A \\ g_{md}A & g_{mm}A \end{bmatrix}$$

Variances-covariances matrices of the other random effects, uncorrelated with u are:

$var(u_p) = I\sigma_p^2$ where σ_p^2 is the variance of permanent environmental effects;

$var(e) = I\sigma_e^2$ where σ_e^2 is the variance of residuals;

The model represented in this way implies that each animal is represented in both direct and maternal vectors, so simplified inversion of the A matrix can be applied. Vector u_p is assumed to be uncorrelated with the other u vectors. Finally, uncorrelated environmental effects are assumed as well. The incidence matrices relate records to the individual making the record (calves for direct and dam for maternal) and then A allows prediction of BV for animals without records for direct or maternal performances (Henderson, 1977). From this maternal animal model, estimates for direct and net maternal (milk) breeding values are obtained for all animals. There are some alternative equivalent models (Henderson, 1973; Quaas and Pollak, 1980; Henderson, 1985) which are computationally more appealing, since the basic difficulty of the previous one is the number of equations to be solved. Two models are said to be linearly equivalents if the first and the second moments

of y are the same (Henderson, 1985). A sire-maternal grandsire model can be formulated in this way (Quaas and Pollak, 1980):

$$y_{ijk} = fx_i + .5\, s_{dj} + .25\, mgs_{dk} + .5\, mgs_{mk} + e_{ijkl}$$

where fx_i are fixed effects included in the model, s_{dj} is the additive direct effect of the *jth* sire and mgs_{dk} and mgs_{mk} are the additive direct and maternal effects, respectively, of the *kth* maternal grandsire.

This model is equivalent to an animal model under certain conditions: maternal grandsires are mating at random with maternal grandams and from each mating, only one progeny is produced; grandams are unrelated; dams do not have more than one progeny and no information other than maternal grandsire merit is used to select mates for dams. When dams' have their own information as calves, the gametic model is not completely equivalent because it treats dams and calves as full sibs (Quaas and Pollak, 1980). There are two reparameterized models which result in quite different computational requirements (Garrick et al., 1989):

$$y = X\beta + (Z_s + .5 Z_{mgs}) u_d + Z_{mgs} u_m + e \qquad [1]$$

or

$$y = X\beta + Z_s u_d + Z_{mgs}(.5 u_d + u_m) + e \qquad [2]$$

The first formulation contains a vector of direct and a vector of maternal effects, however there are two incidence matrices related to the direct effect, one for sires and one for maternal grandsires. The second reparametization considered the contribution of the maternal grandsire as a whole (direct and maternal) which greatly simplifies solution of the

equations since a lot of zero elements in the Mixed Model coefficient matrix that are generated in 1 are avoided in 2. The first expression leads to separate predictors for direct and net maternal transmitting abilities whereas the second one produces estimates of sires' direct and maternal grandsires' total maternal transmitting abilities.

In this section different models for evaluation of maternal effects have been summarized. However, the final decision on which model to choose will depend upon the assumptions that can be made concerning the population as well as the computational facilities that are available.

Grouping

In the derivation of BLUP, a frequent assumption is that $E(u)=0$ which implies that all animals in the analysis descended from the same unselected base population and that information used in the selection process is included in the analysis (Henderson, 1984; Quaas, 1984; Quaas and Pollak; 1987).

The main objective of assigning animals to different genetic groups is to avoid bias in breeding value estimation due to genetic trend, the existence of genetically distinct subpopulations and/or selection patterns (Henderson, 1973; Henderson, 1984; Quaas, 1984; Westell et al., 1988). However, when relationships are considered genetic grouping theoretically would not be indispensable (Quaas and Pollak, 1983) if complete pedigree information is available linking animals to an unselected base population. In current populations, pedigrees are necessarily finite and in many cases not complete (Quaas, 1988). Animal grouping is often a subjective activity (Quaas, 1988), and in many cases grouping results in arbitrary decisions since no single criterion to define group effects is

generally accepted (Robinson, 1986). However, any criterion that allows one subpopulation to be distinguished from another may be valid (Quaas, 1984).

There are two general approaches to the definition of genetic groups:

1 - Genetic groups model (Henderson, 1969; 1973; Tong et al., 1980; Quaas, 1984): in this model sires are assigned to groups generally defined as stud-region-year of birth combinations. However, this strategy has two inherent problems in that it does not account for the inheritance of the group value (Thompson, 1979) and might produce full sib sires in different genetic groups (Robinson, 1986).

2 - Accumulated groups model : this model was first mentioned by Thompson (1979) in the case of a sire model who expressed the sire effect as a 'accumulation of independent terms from its ancestors and itself'. A further development of this grouping strategy was undertaken by different authors to extend it to animal models (Robinson, 1986; Westell et al., 1984, 1988). Westell et al. (1988) formalized inclusion of the relationship matrix A together with the group definitions. Genetic groups are formed by assigning unknown parents (base individual) of known individuals in the pedigree (Westell et al., 1988; Quaas 1988) to groups. In this context, each group effect is assumed to be the average of the corresponding base population. To generate genetic groups from the data in this way seems to be more objective, especially because relationship are used (Thompson, 1979) and only unknown parents are assigned to groups (Quaas, 1988). Several criteria have been used to define group effects such as time period and selection path (Robinson, 1986; Westell et al., 1984;1988) and different breeds (Swan, 1992; Van Vleck et al., 1992). The inclusion of accumulated genetic groups only introduces a small change to the MME where A^{-1} is replaced by W^{-1} which can be formed by a small modification of Henderson's rules to construct A^{-1} because groups are treated as fixed rather that random (Westell et al. 1984,1988).

Van Vleck extended genetic grouping theory to accommodate maternal effects. When maternal effects are present in the model, new considerations in the construction of W must be addressed, since one more ancestor generation is required to accommodate the maternal effect of the most recent female ancestor without records (Van Vleck, 1990). Van Vleck (1990) recommended assigning every unknown parent to the same group for direct and for maternal effects. Nevertheless, different genetic trends for both characters (direct and maternal) on weaning weight have been reported by Benyshek et al. (1988) and Cantet (1990). If so, a differential grouping would be justifiable (Cantet 1990; Cantet et al., 1992).

A remark concerning the treatment of group effects in the models needs to be made. Group effects are traditionally treated as fixed effects and therefore are not estimable; instead only differences among them typically are estimable. Therefore, in a model containing genetic groups, the breeding value of an animal is not predictable but differences among animals' breeding values are (Quaas, 1984; Quaas, 1988). However, the validity of the assumption made about the nature of group effects must be carefully considered (Quaas and Pollak, 1983) and needs further investigation.

Consequences of ignoring genetic groups in sire evaluation have been studied by Tong et al. (1980) and Kennedy (1981). Under the true model (model including genetic groups), the mean square error (MSE) is equal to prediction error variances (PEV); however this is not true if the operational model (model applied in the evaluation) does not contain genetic groups when it should. In the latter case, $MSE = PEV + bias^2$. Kennedy (1981) found that the effect of ignoring genetic groups in the model depends on the magnitude of

the differences among genetic groups. The MSE appeared to be smaller when genetic groups were ignored since the reduction of PEV was big enough to compensate for the bias. From this result, one might conclude that use of genetic groups may not always be indicated unless group differences are really important.

Accuracy of predictions

A measure of accuracy is necessary to express the degree of confidence to be placed on an EPD. The lack of uniformity in the terminology used in current NCE programs across industries (beef and dairy) presents a rather confusing situation. From selection index theory (Van Vleck, 1988; Falconer, 1989), accuracy (*acc*) is defined as the correlation between the predictor and the predictand, or in other words, the correlation between the estimated and true breeding value. In beef cattle NCE following BIF (1986), accuracy of EPDs (*Bacc*) corresponds to :

$$Bacc = 1 - \sqrt{\frac{PEV}{\sigma_s^2}}$$

where σ_s^2 refers to the sire variances. If the PEV is for a predicted breeding value, the sire variance is replaced by additive genetic variance. The relationship between *Bacc* and *acc* is:

$$acc = \sqrt{1 - (1 - Bacc)^2}$$

The term reliability is currently used in the dairy industry and corresponds to the square of *acc* (Van Raden and Wiggans, 1991).

Most measures of accuracy are based on functions of the prediction errors variances (PEV). From Mixed Model theory, the PEV corresponds to the appropriate diagonal

element of the inverse of the coefficient matrix (C) of the mixed model equations (MME)(Henderson, 1973). C can be partitioned as:

$$\begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}$$

where C_{11} contains the sampling (co)variances of estimates of fixed effects, C_{12} contains covariances among estimates of fixed effects and the prediction errors of random effects and C_{22} corresponds to the (co)variances of prediction errors of random effects. The structure and magnitude of the elements of C depends on the model and the data structure (Tosh and Wilton, 1991).

Nowadays, computation of accuracies is a problem related to the dimension of the coefficient matrix, which often prevents obtaining a full inverse. Several iterative procedures have been developed to solve mixed model equations to yield estimates of fixed effects and predictions of random effects. The inability to invert the mixed model coefficient matrix prevents the exact determination of the elements of the diagonal of the submatrix C_{22}. Several procedures have been developed to approximate diagonals of C_{22}. Most of these underestimate PEV and therefore overestimate accuracies (Ufford et al., 1979a; Wilmink and Dommerholt, 1986; VanRaden and Freeman, 1985; Greenhalgh, et al., 1986; Quaas, 1987; Robinson and Jones, 1987; Meyer, 1989; VanRaden and Wiggans, 1991; Boichard and Lee, 1992).

Additional problems in deriving accuracies come from the model specifications. For unbiased situations (correct model specification), BLUP procedures are designed to minimizes PEV When genetic groups are included in the model, the concept of sire evaluation vs. sire prediction or $\hat{w}_j = \hat{g}_i + \hat{s}_{ij}$ vs. $\hat{u}_j$ is involved (Ufford et al., 1979a, b;

Kennedy, 1981) such that the sire evaluation or total additive genetic merit of a sire is equal to the mean of his group plus a deviation from that mean. The sampling error of estimates of group effects will have an impact on the prediction error of evaluation ($\hat{w}_j$) (Ufford et al., 1979a; Greenhalgh et al., 1986; Foulley et al., 1990; Van Vleck et al., 1992). However, if a lot of information is available for each sire and a number of sires are represented in each group, then PEV of the sires' evaluations will tend to be dominated by the sires predictions error variances (Ufford et al., 1979a). In this context, Ufford defined 'reliability or repeatability' as:

$$r_{\hat{w},w} = 1 - \frac{Var\,(\hat{g}+\hat{s}-s)}{V(s)}$$

where $Var\,(\hat{g}+\hat{s}-s)$ correspond to the PEV of evaluations.

Further effects on PEV and accuracies are introduced by assumptions about each component of the model. Henderson (1975) showed that including an effect as fixed when it should be random does not bias the predictions of the other random effects in the model but does increase the PEV of random effects.

CONCLUSIONS

Reasonable doubts about the existence of G x E interaction as well as genotype by genotype interactions exist, since there is not a conclusive result that allows their importance to be affirmed. Maternal traits have scarcely been study in this context.

Different methodological approaches have been taken to evaluate the magnitude of genotype by production system (G x P) interaction in a broad sense. With the use of BLUP in current NCE, the use of correlations between predicted breeding values to

assess the value of genetic correlations appears to be an interesting tool however, several considerations are required for proper interpretations of results. The use of this methodology assumes proper estimation of accuracies; however, several limitations related to computational restrictions, model misspecifications and lack of adjustment for undergoing selection should be taken into consideration in assessing the likely correctness of published accuracies. The effect of single-trait selection as a factor biasing the correlation has been exposed; however consideration of the fact that selection is often practiced on more that one trait should be established.

TABLE 1.1 LITERATURE ESTIMATES OF CORRELATION OF SIRES PROGENY PERFORMANCES IN DIFFERENT ENVIRONMENTS IN BEEF CATTLE (FIELD DATA)

Author	Trait	Genetic correlation	Study description
Nunn et al., (1978)	Birth weight	.86 - 1.0	Simmental sires in 8 regions of USA. ANOVA type
	Weaning weight	.72 - .78	Adjusted by age of dam
		.65	
Buchanan and Nielsen (1979)	Birth weight Simmental	.63[a] .98[b] 1.22[c] .35[a] .56[b]	Simmental and Maine-Anjou. ANOVA type [a] sire x region two data sets
	Weaning weight Simmental Maine -Anjou	-.12[a] -.18[b] .47[c] .32[a] .68[b] .77[a] .98[b] .30[c] .71[d]	[b] sire x sex [c]sire x herd/region [d] sire x season (Adjusted by age of dam)
Tess et al., (1979)	Weaning weight	.42 - .90 (1.7-.2)[a] .09 - .36 (9.0-2.7)[b]	Simmental sires in three regions of USA. ANOVA type [a] sire x region;pairwise corr (range of s.e.) [b] sire x herd/region;pairwise corr (range of s.e.)
Burfening et al., (1982)	Calving score Birth weight	1.13[a] .34[b] 1.0[a] .50[b]	Simmental four regions. ANOVA type [a]sire x region [b]sire x herd/region (2 yr old dams)
Bertrand et al., (1985)	Weaning weight	.59[a] 37[b] .64[c] .64 (.39-1.0)[d]	Polled Hereford nine regions. ANOVA type [a]sire x herd/region [b]sire x contem. group/herd [c]sire x region [d]r (EPD_1,EPD_2) pooled of pairs betw. regions(range) (Adjusted by age of dam)

(Continued)

Oldenbroek and Meijering (1986)	Gestation length Daily gain on test Feed conversion Carcass fleshiness	.40* -.08 -.03 .24	Correlation between sire's test performance and sires's progeny performance. No expec. given .* diff. than zero.
Bertrand et al., (1987)	Birth weight Weaning weight	.71[a] .78[b] .81[c] .55[a] .66[b] .69[c]	Limousine in nine regions. ANOVA type [a]sire x region [ba] + dams [cb] + sire x contem.group/region (Adjusted by age of dam)
Hanford et al., 1988	Birth weight (maternal) Weaning weight (maternal) Calving ease (maternal)	.20 - .74[a] .05 - .34 .55 - .90	Simmental in four regions ANOVA type [a]Range of pairwise regions comparisons. Maternal grandsire x herd/region 2 yr old dams
Garrick et al., 1989	Birth weight Weaning weight (direct) Weaning weight (maternal) Post-wean. gain	.61 (.57) [a] .83 (.92)[b] .50 (.54)[a] .81(.93)[b] .47 (.45) [a] .81 (.93)[b] .54(.39)[a] .76(.91)[b].	Simmental GxE sire x sex r (EPD$_1$,EPD$_2$) [a]Acc $\geq$ .1, Acc $\geq$ .9
Notter et al., (1992)	Weaning weight	.52 - .61	Australian Angus REML

TABLE 1.2 LITERATURE ESTIMATES OF CORRELATION OF SIRES' PUREBRED AND CROSSBRED PROGENY PERFORMANCES IN DIFFERENT SPECIES

Author	Trait	Genetic correlation			Study description
		BEEF CATTLE			
Dunn et al., (1970)	Birth weight Weaning weight Adj. final weight	**a** 1.21 1.52 .83	**b** vs .47 vs .35 vs .18		Crosses among Hereford, Angus and Shorthorn ANOVA type [a]steer [b]heifers
Koger et al. (1975)	Weaning weight Condition score 20 mo. wt ratio	**a** 1.04 1.01 .74	**b** 1.24 1.16 -	**c** .98 .90 -	ANOVA type [a]Angus sires [b]Brahman [c]Hereford
Massey and Benyshek (1981)	Birth weight Pre-we gain Weaning weight Post weaning weight Yearling weight	.81 .76 .78 .85 .57			Limousin sires mated to Angus and Hereford dams. ANOVA type
Cunninghan and Magee (1986)	Birth weight Pre-we gain Weaning weight	.95 .17 .02			Simmental sires mated to two crossbred dam types. ANOVA type
		SHEEP			
Salah et al., (1969)	Weaning weight	.82			Sire's breed Hampshire, Shropshire, Southdown, Merino Birth year confounded with sire effects.

(Continued)

PIGS			
Robison et al., (1964)	Weight Backfat Litter size born Litter size raised Weight Backfat	.22 .21 - .74 -1.0 .72 >1.0	Duroc boars Yorkshire boars ANOVA type
Standal (1968)	Birth weight 21 d. weight ADG (20-90kg) Backfat Type score	.70 .83 1.33 .41 1.02	Landrace x Yorkshire boars ANOVA type
Wong et al. (1971)	Post wean. ADG Backfat Feed effic. Index Post wean. ADG Feed Effic. Index	$.55 \pm .13$ > 1 $.09 \pm .36$ $.47 \pm .58$ $.38 \pm .23$ > 1 $.39 \pm .16$	Purebred and F_1 ANOVA type Purebred and 3-breed crosses
McLaren et al., (1985)	Birth weight 21 d. weight 42 d. weight Post wean. ADG Backfat	.0 .0 .03 .34 .47	Duroc, Hampshire, Landrace Spotted and Yorkshire boars

TABLE 1.3 LITERATURE ESTIMATES OF CORRELATION OF SIRES EVALUATIONS FOR DIFFERENT CHARACTERS IN BEEF CATTLE.

Author	Trait	Corr of EBV vs (Exp. Corr)	Study description
Benyshek (1979)	Weaning weight	.49[a] .46[b]	[a]50% and 75% Limousin calves. [b]Limousin sires mated to Angus and Hereford. Expect. no reported.
Bertrand et al., (1985)	Weaning weight	.64 (.39-1.0)	Polled Hereford nine regions. sire x herd/region $r (EPD_1, EPD_2)$ pooled of pairs betw. regions.(range) Expec. no reported
Cunningham and Magee (1986)	Birth weight Prew. gain Weaning weight	.99 .72 .65	Simmental sires mated to two crossbred dams. Expec. no reported
Oldenbroek and Meijering (1986)	Gestation length Daily gain on test Feed conversion Carcass fleshiness	.40* -.08 -.03 .24	Correlation between sire's test performance and sires's progeny performance. No expec. given .* diff. than zero.
DeNise and Ray (1987)	Weights in range vs Initial weight in station 12 mo 20 mo 24 mo	 .38 .42 .34	Hereford Station data vs Range conditions Sex counfounded with environmental situation. Expec. no reported
Garrick et al., (1989)	Birth weight Weaning weight Post-wean. gain	.a b 59 (.61) .69(.92) .50 (.55) .61(.92) .52(.42) .71(.93)	Corr bet. 50% vs 75% Simmental calves by sex of calves [a]Acc $\geq .1$ [b]Acc$\geq .9$
Tilsh et al. (1989)	Liveweight Carcass weight Daily gain on test Daily carcass weight Energy conversion Withers height	-.007(.65) .03 (.63) .13 (.66) .16 (.61) .22 (.68) .46 (.64)	Sires Simmental, Charolais and their crosses vs Black-Pied dairy breed. None of observed corr were significantly > 0 except last one.

(Continued)

Mahrt et al., 1990	Birth weight	.53 (.68)		Polled Hereford Sires x
	Weaning weight	.37 (.61)		Angus dams
	Yearling weight	.54 (.58)		
		a	b	* Significant diff. from
Swan, 1992	Birth weight	$-.08^*$(.30)	.17 (.33)	expec.
	Weaning weight (direct)	$.04^*$(.42)	$.14^*$ (.42)	100% vs ^{a}50% and ^{b}75
	Weaning weight (maternal)	-	$.15^*$ (.42)	%Simmental calves.
	Yearling weight	$.04^*$(.42)	$.02^*$ (.42)	
	Gestation length	.22 (.38)	.34 (.41)	

CHAPTER 2

USE OF CORRELATIONS OF PREDICTED BREEDING VALUES TO ASSESS GENETIC CORRELATIONS IN PERFORMANCES ACROSS ENVIRONMENTS: EFFECT OF MULTITRAIT SELECTION

Introduction

A fundamental question in genetic improvement programs involving diverse environmental conditions is whether the genetic improvement in traits of interest will be larger when selection is practiced under the specific conditions under which the improved animals will have to perform. Falconer (1952) recognized that the genetic basis for performance in one environment does not have to be the same as that for animal performance for the same trait in a different environment. Thus, reliable knowledge of relationships between animals' performance across environments and/or managerial conditions is needed to systematically realize genetic improvement across all environments. To that end, a number of experiments have been conducted with the objective of validating the predicted breeding values (BV) of sires in an environment different from the environment in which the information for the evaluation process was obtained (Ruvuna and McDaniel, 1983; Oldenbroek and Meijering, 1986; Tilsh et al., 1989; Mahrt et al., 1990).

In general, the study of genotype by environment interaction (G x E) has focused in two directions. The first focus is on estimation of the G x E interaction variance component (Robertson, 1959; Dickerson, 1962; Yamada, 1962) which can then be used to estimate the correlation among expressions of the same trait in different environments. The

second approach focuses on estimation of the product moment correlation between sires' predicted BV for the same traits in different environments or production systems (Oldenbroek and Meijering, 1986; Tilsch et al., 1989; Mahrt et al., 1990; Swan, 1992). The interpretation of the latter procedure requires knowledge of the accuracy of the BV prediction and of the method of prediction. Furthermore, the proper interpretation of the observed correlation must consider its expected value, as noted by Calo et al. (1973), Blanchard et al. (1983) and Notter and Diaz (1992) and requires that certain conditions be met (Taylor 1983). These include (1) no relationships among parents of measured animals, (2) no environmental correlations between performance of animals across environments and (3) no other covariances among predicted BV within either environment (Taylor, 1983), as well as the assumption of random sampling of sires (Notter and Diaz, 1992). Regression of sire predicted BV in one environment on the predicted BV of the same sire in a different environment might be also used to assess the existence of G x E interaction (Notter and Diaz, 1992). Regression analysis is particular useful tool in this assessment if selection has been practiced in one of the environments since the regression coefficient is not biased by selection of sires so long as no selection has been practiced on progeny in the second environment.

The special case of divergent selection of sires, which involves excluding sires that are near the mean, can be used to diminish the sampling variances of the regression coefficient and to increase the expected value of the correlation coefficient (Hill, 1972, Hill and Thompson, 1977; Hill, 1990). When divergent selection is to be practiced for two traits, an option is to first allocate sires into two divergent groups based on one trait, and to then select divergently for the other trait (Hill, 1990). As pointed out by Hill (1990), as the number of traits increases the complexity of applying divergent selection also increases.

Notter and Diaz (1992) studied the effect of various types of single trait selection on the correlation of sires' predicted BV across environments and on the regression of sires' predicted BV in the second environment on sires' predicted breeding value in the first environment. Selection was necessarily assumed to be practiced after evaluation in the first environment but before evaluation in the second environment. All evaluations of sires were assumed to come from single-traits analyses. Correlations were biased by selection but the regression appeared unbiased. Formulas were derived to accommodate effects of selection on the expectation of the correlation coefficient.

Genetic evaluation of sires is becoming widespread the industry. Hence, many animals have been evaluated within different environments or managerial conditions. Most beef sire evaluation programs make use of multitrait evaluations (Benyshek et al., 1988), and in the beef cattle industry, the choice of bulls is usually based upon a number of traits. However, the traits are not usually combined in a systematic or optimal way to construct formal selection indices. Thus, the movement of sires from one environment to another involves a selection process which might involve a number of correlated traits. When using correlations of predicted BV across environments in order to detect G x E interaction, the specific selection history of the sires should be taken into consideration in order to properly interpret the results.

Maternal performance has not been extensively studied with regard to G x E interaction (Hanford et al., 1988). The maternal effect on weaning weight is genetically correlated to the direct effect (e.g., Cantet, 1990; Meyer et al., 1992), and both are normally evaluated simultaneously. The direct and maternal components of weaning weight are particularly

interesting from a methodological viewpoint to evaluate the effect of different types of selection on two correlated traits on expected correlations of predicted BV.

The objective of this study was to determine by computer simulation the expected correlation of direct and maternal predicted breeding values across environments as affected by selection based on estimates of breeding values for more than one trait. Effects of accuracies of BV predictions on expected correlations will be also considered.

Materials and Methods

True and predicted direct and maternal breeding values of sires were simulated for populations of sires evaluated independently in two different environments. Selected subsamples of sires were then chosen from the populations based on various selection criteria. Selection was based on predicted BV for both direct and maternal traits in the first environment. Observed correlations across environments for direct and maternal predicted BV were then calculated for the selected subpopulations and compared to both unselected values and to theoretical expected values derived from single trait selection theory (Notter and Diaz, 1992).

Simulation Procedures

True breeding values (BV) and prediction errors of sires for direct and maternal effects in two different environments were simulated for a hypothetical population of sires and used to derive predicted BV for each animal in each environment. Thus, for each animal a random vector of size eight was simulated containing direct and maternal BVs and prediction errors in each environment. Genetic covariances among BV were assumed to

exist within and across environments. Prediction error covariances were assumed between traits within environments, but prediction error covariances across environments were assumed to be null. Given these assumptions, the simulation was performed in a stepwise manner in order to control the process according to the established assumptions.

Simulation of true and predicted breeding values in the first environment.

FORTRAN programs were written to perform the simulations. Direct and maternal breeding values and prediction errors for each trait within the first environment were assumed to have a joint normal distribution N (0, V) with $V = var$ (BV_d, BV_m, PE_d, PE_m).

$$
V = \begin{bmatrix}
\sigma_{d_1}^2 & \sigma_{d_1,m_1} & (1-acc_{d_1}^2)\sigma_{d_1}^2 & r_{pe_{d_1,m_1}}\sigma_{d_1}\sigma_{m_1}\sqrt{(1-acc_{d_1}^2)(1-acc_{m_1}^2)} \\
 & \sigma_{m_1}^2 & r_{pe_{d_1,m_1}}\sigma_{d_1}\sigma_{m_1}\sqrt{(1-acc_{d_1}^2)(1-acc_{m_1}^2)} & (1-acc_{m_1}^2)\sigma_{m_1}^2 \\
 & sym & (1-acc_{d_1}^2)\sigma_{d_1}^2 & r_{pe_{d_1,m_1}}\sigma_{d_1}\sigma_{m_1}\sqrt{(1-acc_{d_1}^2)(1-acc_{m_1}^2)} \\
 & & & (1-acc_{m_1}^2)\sigma_{m_1}^2
\end{bmatrix}
$$

where for environment 1,

$\sigma_{d_1}^2$ = variance of the direct breeding value;

$\sigma_{m_1}^2$ = variance of the maternal breeding value;

σ_{d_1,m_1} = covariance between direct and maternal breeding value;

acc_{d_1} = accuracy of direct predicted breeding value;

acc_{m_1} = accuracy of maternal predicted breeding value;

r_{pe_1} = correlation of direct and maternal prediction errors.

Values for additive genetic variances and covariances are given in Table 2.1. The value for the correlation of prediction errors depends upon the structure of the data and was

empirically obtained as described in a later section. Accuracies were assigned in two different manners which will likewise be described later.

To simulate BV and prediction errors within an environment, a Cholesky factorization of $\mathbf{V}$ into $\mathbf{T'T}$ was performed where $\mathbf{T}$ is an unique upper triangular matrix, such that $\mathbf{T'T} = \mathbf{V}$ (Graybill , 1976; IMSL, 1987). A row vector containing four independent normal deviates from $\mathbf{N}(0,1)$ distributions was then generated for each animal, and the matrix containing all row vectors of deviates was postmultiplied by $\mathbf{T}$. The final expression of true direct BV was then:

$$BV_{d_1} = Rn_{d_1}\,\sigma_{d_1}$$

where:

$\quad Rn_{d_1} = \mathbf{N}\,(0,1)$ random deviate for direct breeding value.

The maternal breeding value then was formulated as:

$$BV_{m_1} = Rn_{d_1}r_{G_{d,m}}\sigma_{m_1} + Rn_{m_1}\,[\sqrt{(1-r_G^2)}\,\sigma_{m_1}]$$

where :

$\quad Rn_{m_1} \quad = \mathbf{N}\,(0,\,1)$ random deviate for residual maternal breeding value; and

$\quad r_G \quad =$ genetic correlation between direct and maternal breeding values.

Estimated breeding values then were defined as:

$$EBV_{d_1} = BV_{d_1} - PE_{d_1}$$
$$EBV_{m_1} = BV_{m_1} - PE_{m_1}$$

where PE stands for prediction error and is defined as the difference between true and predicted breeding value (BV-EBV).

Simulation of true and predicted breeding values in the second environment.

Prediction error covariances across environments were assumed to come only from the genetic correlation among traits across environments. Given this assumption, simulation of true and predicted breeding values in the second environment was accomplished in three steps:

Simulation of true breeding values in the second environment:

True breeding values across environments were assumed to have a joint normal distribution N $(0, G)$, where G is the (co)variance matrix of direct and maternal effects within and across environments.

$$
G = \begin{pmatrix}
\sigma_{d_1}^2 & r_{G_{d_1,m_1}} \sigma_{d_1}\sigma_{m_1} & r_{G_{d_1,d_2}} \sigma_{d_1}\sigma_{d_2} & r_{G_{d_1,m_2}} \sigma_{d_1}\sigma_{m_2} \\
r_{G_{m_1,d_1}} \sigma_{m_1}\sigma_{d_1} & \sigma_{m_1}^2 & r_{G_{m_1,d_2}} \sigma_{m_1}\sigma_{d_2} & r_{G_{m_1,m_2}} \sigma_{m_1}\sigma_{m_2} \\
r_{G_{d_2,d_1}} \sigma_{d_2}\sigma_{d_1} & r_{G_{d_2,m_1}} \sigma_{d_2}\sigma_{m_1} & \sigma_{d_2}^2 & r_{G_{d_2,m_2}} \sigma_{d_2}\sigma_{m_2} \\
r_{G_{m_2,d_1}} \sigma_{m_2}\sigma_{d_1} & r_{G_{m_2,m_1}} \sigma_{m_2}\sigma_{m_1} & r_{G_{m_2,d_2}} \sigma_{m_2}\sigma_{d_2} & \sigma_{m_2}^2
\end{pmatrix}
$$

where:

$r_{G_{d_1,d_2}}$, $r_{G_{m_1,m_2}}$ = genetic correlations between breeding values for the same trait across environments;

$r_{G_{m_i,d_j}}$ = genetic correlation between breeding values for different traits across environments, $i \neq j$; and

$r_{G_{m_i,d_i}}$ = genetic correlation between breeding values for different traits in the same environment;

Assumptions about genetic correlations involved in this (co)variance matrix will be described in a later section.

True breeding values in the second environment were defined as :

$$BV_{d_2} = \beta_1 BV_{d_1} + \beta_2\, BV_{m_1} + R_{d2}$$
$$BV_{m_2} = \beta_3 BV_{d_1} + \beta_4\, BV_{m_1} + R_{m2}$$

or, in matrix notation as :

$$\begin{bmatrix} BV_{d_2} & BV_{m_2} \end{bmatrix} = \begin{bmatrix} BV_{d_1} & BV_{m_1} \end{bmatrix} G_{21} G_{11}^{-1} + \begin{bmatrix} R_{d_2} & R_{m_2} \end{bmatrix}$$

where the partial regression coefficients of BV in environment 2 on BV in environment 1 were obtained as,

$$\begin{bmatrix} \beta_1 & \beta_2 \\ \beta_3 & \beta_4 \end{bmatrix} = G_{21} G_{11}^{-1}$$

and R_{d2} and R_{m2} are two vectors coming from a bivariate $N(0,R)$ distribution where $R =$ var $(BV_{d_2}, BV_{m_2} | BV_{d_1}, BV_{m_1})$ that was obtained by partition of the G matrix (Graybill, 1976) into

$$G = \begin{pmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{pmatrix}$$

such that

$$R = G_{22 \cdot 1} = G_{22} - G_{21}\, G_{11}^{-1}\, G_{12}$$

A Cholesky factorization (IMSL ,1987) of the 2x2 R matrix was performed. Two independent normal deviates (Rn_{d_2}, Rn_{m_2}) were generated and the matrix containing the vectors was postmultiplied by the T matrix. The $E(BV_{d_2}, BV_{m_2} | BV_{d_1}, BV_{m_1})$ and the

resulting random vectors were summed to yield the final simulated values for BV_{d_2} and BV_{m_2}.

Simulation of prediction errors in the second environment:

True breeding values and prediction errors in the second environment were assumed to have a joint normal distribution $N(0,C)$, where C has a similar structure to V, which has been shown already.

Prediction Errors in the second environment were defined as:

$$PE_{d_2} = \beta_1 BV_{d_2} + \beta_2 BV_{m_2} + S_{d2}$$

$$PE_{m_2} = \beta_3 BV_{d_2} + \beta_4 BV_{m_2} + S_{m_2}$$

or, in matrix notation as :

$$\begin{bmatrix} PE_{d_2} & PE_{m_2} \end{bmatrix} = \begin{bmatrix} BV_{d_2} & BV_{m_2} \end{bmatrix} C_{21} C_{11}^{-1} + \begin{bmatrix} S_{d_2} & S_{m_2} \end{bmatrix}$$

where, the partial regression coefficients of prediction errors on BV were obtained as above, and S_{d2}, S_{m2} have a bivariate $N(0,S)$ distribution where $S = $ var $(PE_{d_2}, PE_{m_2} | BV_{d_2}, BV_{m_2})$ was obtained by partition of the C matrix as described earlier for the G matrix. Similarly, $E(PE_{d_2}, PE_{m_2} | BV_{d_2}, BV_{m_2})$ was obtained and added to the S vectors to obtain PE_{d_2} and PE_{m_2} as defined in the previous section.

Simulation of predicted breeding values in the second environment:

Once true breeding values and prediction errors were obtained, predicted BV in environment 2 were simulated as:

$$EBV_{d_2} = BV_{d_2} - PE_{d_2}$$

$$EBV_{m_2} = BV_{m_2} - PE_{m_2}$$

Correlations of prediction errors within environments.

Prediction error covariances (PEC) within V and C were derived from correlations of prediction errors direct and maternal predicted breeding value prediction errors within an environment. The correlations were estimated as a function of the accuracies of direct and maternal predicted breeding values by means of a semistochastic simulation. A variety of design matrices were created in order to inspect relationships among accuracies of prediction, prediction error variances (PEV) and PEC. PEV and PEC associated with predicted BV can be obtained from the section of the inverse of mixed model equations associated with the random effects (Henderson, 1973).

Predicted direct and maternal BV can be conveniently obtained from a 'direct-maternal' model where a direct effect for sire and maternal grandsire as well as a maternal effect for the maternal grandsire are fit. Several assumptions must be made for this model to be valid. Random mating was assumed; maternal grandams and dams were assumed unrelated and did not have more than one progeny and grandprogeny, respectively; and sires and maternal grandsires were also assumed to be unrelated. Fitting this model implies a two-generation approach in which coefficient matrices of the mixed model equations (Henderson, 1973) were created using separate models for each generation. An additional assumption was then made, first generation calves were assumed to have unknown maternal grandsires and second generation calves were assumed to have unknown sires. Thus, the model for first generation records were fit into the following model:

$$Y_{ijk} = cg_i + sd_j + e_{ijk}$$

where

Y_{ijk} is the weaning weight of the *kth* progeny of the *jth* sire in the *ith*

                contemporary group;

cg_i is the fixed effect of the *ith* contemporary group;

sd_j is the random additive genetic direct effect of the *jth* sire;

e_{ijk} is a residual effect associated with the *ijkth* record.

For records from the second generation, the model was:

$$Y_{ijk} = cg_i + \tfrac{1}{2} sd_j + sm_j + e_{ijk}$$

where

½ sd_j is one-half of the random additive effect of the *jth* maternal grandsire;

sm_j is the random additive genetic maternal effect of the *jth* maternal grandsire.

Use of different models in the two generations led to different error terms. In addition to random direct and maternal environmental effects, the residual variance in the first generation contains three fourths of the additive direct variance plus the total additive maternal variance. The residual variance in the second generation contains fifteen sixteenths of the additive direct variance, plus three fourths of the additive maternal variances as well as the direct and maternal environmental variance. Residuals were assumed to be uncorrelated. Variance of sires direct effect $\sigma^2_{sd} = 67$; variance of the maternal sire effect was; $\sigma^2_{sm} = 89$ and the covariance direct-maternal sire effects was $\sigma_{d,m} = -21$. Genetic correlation between direct and maternal effects was assumed to be -.27 (APHA, 1990).

A FORTRAN program was written to build coefficient matrices for these models. Firstly, a total number of records was assumed to be available for evaluation of all sires (from 512 to 16384 in a geometric progression of order 2). Secondly, for each data set , a number of

sires (from 2 to 256 also in a geometric progression of order 2) was assumed to be in evaluation. Each sire in a given design was assumed to have the same number of progeny, but progeny were distributed differently over a maximum number of contemporary groups (4 to 16 in geometric progression of order 2).

To generate each coefficient matrix, a random number from a uniform distribution ranging from 1 to the maximum number of contemporary groups was first obtained for each sire in the design. This number determined the number of contemporary groups in which a sire would have progeny. If the number of contemporary groups to which a sire was assigned was larger than the number of progeny of that sire, the procedure was repeated. Progeny of the sires were then randomly assigned to specific contemporary groups so that the appearance of progeny in a contemporary group was a complete random process. For each hypothetical data set available, up to 24 design matrices were constructed, each corresponding to a number of sires by number of contemporary groups combination. For the smaller progeny numbers all combinations of sires and contemporary group numbers could not be accommodated.

All sires were also assumed to produce records as maternal grandsires. However, maternal grandsires were assumed to have only half as many records as they had as sires. This assumption seem to be a reasonable if we consider a sire to have 50% female progeny and evaluations of maternal BV to be based primarily on first lactation. Maternal grandsires were assumed to have progeny distributed in a number of contemporary groups and the contemporary groups for sire progeny were assumed distinct from those for grandprogeny (i.e., contemporary groups were nested within generations). The maximum number of contemporary groups (4 to 16 in geometric progression of order 2) in which

each maternal grandsire was allowed to have grandprogeny was assumed to be the same as the maximum number of contemporary groups in which he was allowed to have progeny as a sire. However, at this point, two extreme situations were considered. In the first, bulls were assumed to have a similar distribution of records over contemporary groups as sires and as maternal grandsires. Therefore, sires with contemporary progeny also had exactly corresponding contemporary grandprogeny. This situation represents a common beef cattle situation where daughters of sires born as contemporaries are kept in the respective herds and perform as contemporaries to females born at the same time. The second approach was taken in order to depict a situation where daughters of different sires which were contemporaries as calves did not have to remain in the same contemporary groups as dams. In this situation, sires sharing information in a number of contemporary groups did not necessarily share information in the same contemporary groups as maternal grandsires. To create this second situation, a second randomization process similar to, but independent of, the one described previously to create the sire progeny distribution was accomplished to create grandprogeny distributions.

The coefficient matrix that would have been required to solved for p unknown direct and maternal effects as well as q unknown fixed effects was created and inverted. The corresponding PEV and PEC for each direct and maternal effect were output to a file for each run of the program. An example of a given design is one in which 512 records were assumed to be available for eight sires with 64 records per sire.   Those eight sires were also assumed to perform as maternal grandsires with 32 records each. Each sire was given the possibility of being allocated to a maximum of four contemporary groups, and therefore a maximum of 4 contemporary groups was also assumed for the maternal grandsires. The randomization process was performed once. Then, the coefficient matrix

that would have been required to solve sixteen unknown direct and maternal sire effects of each bull and eight unknown for fixed effects was constructed and inverted. Then, the PEV for direct and maternal effect and the PEC were written into a file and the procedure continued.

Each designed combination was run twice, once for each of the two option in assigning sires and maternal grandsires to contemporary groups. RAN1 will henceforth denote the situation in which the randomization process was done once and RAN2 will refer to independent randomization of sire and maternal grandsire progeny records to contemporary groups.

Accuracies for direct and maternal predicted breeding values and the correlation of prediction errors (r_{pe}) between direct and maternal sire effects were computed. Accuracies were calculated as :

$$acc_d = \sqrt{1 - \frac{PEV_d}{\sigma_{sd}^2}} \quad \text{and} \quad acc_m = \sqrt{1 - \frac{PEV_m}{\sigma_{sm}^2}}$$

where σ_{sd}^2 is the variance of sire direct effect, and σ_{sm}^2 is the variance of the maternal sire effect. Correlations of prediction errors were calculated as :

$$r_{pe} = \frac{PEC}{\sqrt{PEV_d PEV_m}}$$

Regression equations to predict r_{pe} from acc_d and acc_m were derived using the SAS (1990) General Linear Models procedure. The dependent variable was the correlation of

prediction errors, and accuracies for direct and maternal effects were fitted as linear and quadratic regressors. The regression equations to predict r_{pe} were fitted separately for each randomization scenario (RAN1 and RAN2) and then used to construct the elements of the matrices V and C involving PEC as a function of the values of acc_d and acc_m used in the simulation.

Correlation between direct and maternal breeding values across environments

We return now to the simulation of actual and predicted BVs in two environments. To simulate BV across environments one must recognize that the genotype of an individual encompasses the entire set of genes that individual possesses. Particular sets of genes influence particular traits, and genes with pleiotropic effects influence the expression of more than one character (Falconer, 1989). The genetic correlation between two traits expresses the extent to which two characters are determined by the same set of genes, if the correlation is due to pleiotropic effects and not linkage caused by selection. In the presence of G x E interaction, a particular set of genes affecting one trait under one environmental circumstance may not be the same as the set controlling that particular trait in a different environment. This idea was first stated by Falconer (1952) who postulated that a trait under different environmental conditions could be viewed as two different traits if G x E is present. Furthermore, genes coding for a given character in one environment might also be involved in the expression of a different character in a different environment. With this situation in mind, the correlations between an individual's genotype for direct and maternal effects in two different environments were represented in the form of a path diagram (Figure 2.1). The average genotypes across environments for direct and maternal traits are represented by G_D and G_M, respectively. A deviation from the average genotype for either the maternal or direct character was assumed to exist

under particular environmental conditions, such that G_{D_i} and G_{M_i} represent deviation from the mean genotype for both traits in the ith specific environment. The deviations, G_{D_i} and G_{M_i}, were assumed to be independent of G_D and G_M, respectively. Finally u_{D_i} and u_{M_i} correspond to the individual's breeding values for direct and maternal traits in each specific environment, such that :

$$u_{D_i} = G_D + G_{D_i} \text{ and}$$
$$u_{M_i} = G_M + G_{M_i}$$

The variables included in a path diagram are represented by arrows as either completely determined by other variables (dependent variables) or as causal factors (independent variables)(Wright, 1968). Each pair of causal factors can be connected by a double-headed arrow indicating possible correlations. The correlation between any two variables can be obtained by cumulating the products along all paths connecting the variables. Thus, the primary relationships between direct and maternal breeding values within and across environments are represented by solid arrows in Figure 2.1; dashed lines represent hypothetical correlation paths that may exist when modeling possible relationships between direct and maternal characters as affected by G x E, but which will be assumed to be null in the present situation.

The path coefficients measure, in term of standard deviations, the direct influence of the various factors in causing changes in the dependent variable. Thus, the fraction of the variation among genotypic values for direct and maternal traits attributable to the genotypic deviation specific to an environment, or to the genotype by environment

component for each specific environment, are represented by d_{11}^2, m_{11}^2, d_{22}^2, and m_{22}^2. Thus,

$$d_{ii} = \frac{\sigma_{G_{d_i}}}{\sigma_{u_{d_i}}} = \frac{\sigma_{GxE_d}}{\sqrt{\sigma_{G_d}^2 + \sigma_{GxE_d}^2}}$$

$$m_{ii} = \frac{\sigma_{G_{m_i}}}{\sigma_{u_{m_i}}} = \frac{\sigma_{GxE_m}}{\sqrt{\sigma_{G_m}^2 + \sigma_{GxE_m}^2}}$$

where σ_{GxE_d} and σ_{GxE_m} represent the proportion of variation observed in either direct and maternal breeding values attributable to a genotype by environment component.

Similarly, d_{10}^2, m_{10}^2, d_{20}^2 and m_{20}^2 represent the fraction of the variation among breeding values in each specific environment due to common genes, where:

$$d_{i0} = \frac{\sigma_{G_d}}{\sigma_{u_{d_i}}} = \frac{\sigma_{G_d}}{\sqrt{\sigma_{G_d}^2 + \sigma_{GxE_d}^2}}$$

$$m_{i0} = \frac{\sigma_{G_m}}{\sigma_{u_{m_i}}} = \frac{\sigma_{G_m}}{\sqrt{\sigma_{G_m}^2 + \sigma_{GxE_m}^2}}$$

Notice that d_{i0} and m_{i0} correspond to the square root of the genetic correlation between expression of the same trait in different environments. The genetic correlations required to build the G matrix were then obtained using the path diagram in Figure 2.1. The correlation between direct breeding values across environments was:

$$r_{u_{d_1},u_{d_2}} = d_{10}d_{20} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GxE}^2} = r_{G_{d_1,d_2}}$$

The corresponding correlation among maternal breeding values may be expressed in a similar way,

$$r_{u_{m_1},u_{m_2}} = m_{10}m_{20} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GxE}^2} = r_{G_{m_1,m_2}}$$

Values for $r_{G_{d_1,d_2}}$ and $r_{G_{m_1,m_2}}$ were assumed to be 1 or .5, reflecting the absence or presence of G x E affecting both characters. For simplification purposes, the relationships between both maternal and direct breeding values across environments were assumed to be the same (i.e., both 1 or both .5). The accuracy of this assumption is difficult to establish, since no reference simultaneously treating both characters in the same population are known.

While the correlation among direct and maternal breeding values within environments was assumed to be the same and equal to -.268 for both environments (Table 2.1), a possible effect of G x E in the correlation between direct breeding value in one environment and the maternal breeding value in the other one was recognized. These correlations can be expressed as a function of the G x E variance component affecting each individual component, direct-direct and maternal-maternal across environments (Figure 2.1) such that:

$$r_{u_{d_1},u_{m_2}} = d_{10} \, r_{G_{d,m}} m_{20} =$$

$$\frac{\sigma_{G_d}}{\sigma_{G_{d_1}}} r_{G_{d,m}} \frac{\sigma_{G_m}}{\sigma_{G_{m_2}}} =$$

$$\frac{\sigma_{G_d}}{\sqrt{\sigma_{G_d}^2 + \sigma_{GxE_d}^2}} r_{G_{d,m}} \frac{\sigma_{G_m}}{\sqrt{\sigma_{G_m}^2 + \sigma_{GxE_m}^2}} =$$

$$\sqrt{r_{G_{d_1,d_2}}} \; r_{G_{d,m}} \sqrt{r_{G_{m_1,m_2}}} = r_{G_{d_1,m_2}}$$

Therefore, the values of $r_{G_{d_1,m_2}}$ used to construct the G matrix were either -.268 for $r_{G_{d_1,d_2}}$ and $r_{G_{m_1,m_2}}$ equal to 1 or -.134 for $r_{G_{d_1,d_2}}$ and $r_{G_{m_1,m_2}}$ equal to .5. Note that the hypothetical correlation paths in Figure 2.1 could modify these expectations if they are not truly null.

Accuracies of predictions in each environment

Two sets of accuracies associated with simulation of direct and maternal predictions in each environment were assumed . These were:

1 - An ideal situation in which accuracies of predictions were assumed to be constant in each environment for both traits. Accuracies of both direct and maternal predictions were assumed to be .9 and .6 in the first and the second environments, respectively.

2 - Accuracies of predictions were assumed to reflect a more realistic situation and to vary for both direct and maternal BV predictions. Accuracies for direct breeding value prediction were assumed to follow a uniform distribution with upper and lower bounds of .40 and .95, respectively. Direct and maternal accuracies are not independent. acc_m generally increases as acc_d increase, but with a lag representing the additional generation required to produce maternal evaluations and with some variation in acc_m at fixed acc_d . Thus, once accuracy for direct predicted BV was obtained, the corresponding accuracy of the maternal predicted BV was obtained as a function of accuracy associated with the prediction of direct BV plus a random component as:

$$acc_m = \beta_0 + \beta_1 acc_d - |R_n| \sigma_{acc_m/acc_d}$$

where R_n is a $N\,(0,1)$ random deviate and

$$\sigma_{acc_m/acc_d} = \sqrt{(1 - r^2_{acc_d,acc_m})}\,\sigma_{acc_m}$$

The absolute value of Rn was used to ensure that acc_m is smaller than acc_m. This equation occasionally yielded negative values of acc_m but only the positive numbers were kept. Correlations of accuracies of direct and maternal BV predictions were obtained from the simulations used to predict PEC. The actual values of the elements of the equation will be given in the section of results.

Selection scenarios

To investigate effects of selection on the observed correlation between BV predictions from different environments, four sets of populations, with each population consisting of 3000 bulls, were simulated. Each set of base populations represented a combination of accuracy assumptions (accuracies of direct and maternal BV predictions constant or variable within environments) and genetic correlation between traits across environments ($r_{G_{d_1,d_2}}$ and $r_{G_{m_1,m_2}}$ equal to 1 or .5). Each set of base populations, contained ten replicated populations of 3000 sires. Thus, a total of 40 sire base populations were generated. Selection was practiced in each sire population based on predicted direct and maternal BV in environment 1. Within each population, three selection strategies were applied to the same base population: directional selection for animals with high (H) direct and H maternal predicted BV; divergent selection of animals from the upper and lower tails of

both distributions; and random selection. Independent culling levels were used in selection. Specifically:

Directional selection: 800 sires representing the upper 27 % of the distribution of predicted direct BV and 800 sires representing the upper 27% of the distribution of predicted maternal BV were initially identified such that $| x | = .613$ where $x =$ is the truncation point on a standard normal curve (Snedecor and Cochran, 1967) and $i = 1.225$ is the standardized selection differential (Becker, 1984). Animals that were in both selected groups were then kept. As a result of this selection strategy an average of 134 sires were selected over the ten replicates. From each selected population of sires, a random sample of 40 bulls was retained.

Divergent selection: 800 sires representing upper and lower 13% of the distributions of direct and maternal BV predictions were initially chosen. Four groups of divergently selected sires were then identified as those that were high, high; high, low; low, high; and low, low for direct and maternal predicted BV. Both distributions of predicted breeding values were truncated for $|x| = 1.126$ and $i = 1.627$. Then, sires either in the upper or lower extremes of the selected population of sires for both direct and maternal BV predictions, were kept. The resulting selected population consisted of an average of 231 individuals over the ten replicas, although the distribution of selected sires over the four groups was not symmetrical (HH = 23; HL = 94; LH = 95; LL = 23) because of the negative genetic correlation between direct and maternal BV. A sample of ten bulls was randomly chosen from each subgroup to yield a final sample of 40 sires.

Random Selection: Random samples of 40 sires (1.3%) of the population were obtained.

For the cases in which accuracy of direct and predicted BV were assumed to have variable accuracy, predictions were standardized by $acc_i\sigma$ where, acc is direct or maternal accuracies for each ith sire, and σ corresponds to the additive direct or maternal standard deviation, respectively.

Correlation and regression coefficients of predicted breeding values across environments for the samples from each selected population of sires were obtained and compared to expectations. Expectations of correlations under single trait selection were obtained following Notter and Diaz (1992) as.

$$Corr(\hat{u}_1\hat{u}_2) = acc_1 r_G acc_2 \sqrt{\frac{1-w}{1-acc_1^2 r_G^2 acc_2^2 w}}$$

where r_G is the genetic correlation between BV across environments; acc_1 and acc_2 are accuracies of predicted BV in environments 1 and 2, respectively; w is an empirical definition of the selection practiced, such that

$$w = 1 - \frac{Var(\hat{u})}{\sigma_{\hat{u}}^2}$$

where $Var(\hat{u})$ is the variances among predicted BV values in environment 1 in the selected sample, and $\sigma_{\hat{u}}^2$ is the variance among predicted BV in the unselected population. Notice that $acc_1 r_G acc_2$ corresponds to the expectation of the correlation under random selection. Likewise, for situations in which variable accuracies were assumed, the expectation becomes (Notter and Diaz, 1992):

$$Corr(\hat{u}_1\hat{u}_2) = r_G acc_{12} \sqrt{\frac{1-w}{1-r_G^2 acc_{12}^2 w}}$$

where acc_{12} corresponds to the expectation of the correlation under random selection as derived by Calo et al., (1973):

$$Corr(\hat{u}_1, \hat{u}_2) = r_G \frac{\sum_{i=1}^{m} acc_{1i}^2 \sum_{i=1}^{m} acc_{2i}^2}{\sqrt{\sum_{i=1}^{m} acc_{1i}^2 \sum_{i=1}^{m} acc_{2i}^2}}$$

where acc_{1i} and acc_{2i} are the accuracies associated with the predicted BVs of the *ith* sire in each environment (1 and 2). This formula does not consider adjustments for previous effects of in environment 1; published accuracies are not normally adjusted for to account for traits under selection (Dekkers, 1992).

The expectation of regression coefficients (Notter and Diaz, 1992) were also obtained as:

$$Reg(\hat{u}_2, \hat{u}_1) = r_G \frac{\sum_{i=1}^{m} acc_{1i}^2 \sum_{i=1}^{m} acc_{2i}^2}{\sqrt{\sum_{i=1}^{m} acc_{1i}^2}}$$

Paired t-test were used to compare the observed mean value of the correlation and regression coefficients derived from simulated data to the mean of their expected values.

Results and Discussion

Accuracies of predictions and correlation of prediction errors

Accuracies associated with the prediction of direct and maternal BV, over the range of design matrices considered, were strongly correlated: .99 for RAN1 and .98 for RAN2. The relationship between accuracies of prediction for direct and maternal BV are presented in Figure 2.2 for both cases RAN1 (a) and RAN2 (b). While a wide range of accuracies was generated for both traits in both cases, the range of maternal accuracies for a given level of direct accuracy was minimal for RAN1 (Figure 2.2a). For RAN2, the relationship between direct and maternal accuracies was also strong, but some degree of variation in maternal accuracy was observed (Figure 2.2b). The degree of relationship between direct and maternal accuracies directly reflects the assumptions made relative to data structure and amount of available information in the simulation. Observation of APHA sire accuracies (1992) revealed a similar pattern of relationship, which led us to conclude that this type of relationship among accuracies of prediction for both traits is fairly common in current NSE. In terms of the true data structure in current populations, mature sires are often expected to have enough daughters in production to produce high levels of accuracy for maternal BV, however young bulls with reasonably large number of daughters in production are rare to find.

A graphic representation of relationships of direct and maternal accuracies to correlations of prediction errors and PEC is presented in Figures 2.3, 2.4, 2.5 and 2.6. Changes in PECs showed the same pattern for both RAN1 and RAN2. As expected, an increase inaccuracy of prediction for either direct or maternal breeding value resulted in a decrease in the absolute value of the prediction error covariance. At the limit (accuracies equal to 1) PEC approaches to zero (Figure, 2.3a, 2.4a, 2.5a, 2.6a). Values ranged from the value of the genetic covariance (-21) to zero.

Correlations between direct and maternal PE were predicted for both RAN1 and RAN2. The prediction equation for RAN1 was:

$$r_{pe} = -.27 + .02acc_d - .07acc_d^2$$

As shown in Figure 2.2a, the relationship between accuracies of prediction for direct and maternal breeding values was so strong (r = .99) that the correlation of prediction errors could be predicted from either trait without having to include both in the model. In the process of model selection, the range of values for the coefficients of determination ranged from .95 for the simplest model (including only the accuracies of prediction for either direct or maternal) to .97 for the most complete model (including both accuracy of prediction as linear and quadratic effects as well as the linear interaction). The reduction in error mean squares was around 60 %. The coefficient of determination associated with the equation shown above was .96. The relationships were different for RAN2. A wide range in R^2 (.18 to .80) was observed for different models, and a reduction of more than 80 % in error means square was observed when going from the simplest model to the most complete model. The prediction equation that was finally used to predict r_{pe} for RAN2 was:

$$r_{pe} = -.15 - .42acc_d - .08acc_m + .78acc_d acc_m + .38acc_d^2 - .83acc_m^2$$

This was also the equation that was chosen to predict r_{pe} in the simulation of predicted breeding values across environments to build V and C matrices.

The ranges in observed correlations of prediction errors were relatively small for both RAN1 and RAN2 (Figure 2.3b, 2.4b, 2.5b, 2.6b), although a general trend was observed. For low levels of accuracy for both direct and maternal BV predictions, the correlations of prediction errors tended to cluster near the value of the genetic correlation. With an increase in accuracy, the correlation of prediction errors tended to increase in absolute value. At this point RAN1 and RAN2 behaved differently. For RAN1 (Figure 2.3b and 2.4b) the range in the prediction error correlation changed little with accuracy and never exceeded -.32. However, for RAN2 (Figure 2.5b and 2.6b) values of correlation tended to disperse as accuracy increased in an interval of approximately -.25 to -.39. No matter what the trend, as accuracies approached to 1, the correlations become unpredictable as values of PEC and PEV in the correlation equation approached zero.

Effect of selection on the correlation of predicted breeding values across environments
Turning now to results of the two-environment simulation, selection had an impact on the variances of direct and maternal predicted BV in both environments (Table 2.2 and Table 2.3). As expected, directional selection produced a decrease in variances of predicted BV, while divergent selection had the opposite effect. The observed variances of direct and maternal predicted BV in populations subject to directional selection were reduced by approximately 80% when compared to values of the variances in the population prior to selection. This proportion is indicated by the observed value of w (Tables 2.2 and 2.3). Thus, the larger the magnitude of w, the greater the reduction in variances of predicted BV is expected. However, for divergent selection, variances for direct and maternal predicted BV averaged 2.7 times larger in the selected population than in the population prior to selection (Table 2.2 and Table 2.3), again denoted by w. In this specific case, the

greater the magnitude of w in absolute value, the greater the increase in variance in the selected population.

Tables 2.2 and Table 2.3 also show expected values of variances of direct and maternal breeding values based on univariate selection theory. In case of divergent selection based on truncation of a univariate distribution, w is equivalent to $-ix$ where i corresponds to the standardized selection differential (Becker, 1984) and x is the truncation point on a standard normal distribution. For directional univariate truncation selection, w is equal to $i(i-x)$. Since selection was imposed using independent culling levels, standardized selection differentials and truncation points for the univariate distributions of direct and maternal predicted breeding values following the first stage of selection were compared to the final observed value of w which empirically account for both stages of selection. Predicted values of w were -1.832 for the case of univariate divergent selection and .750 for directional selection. Observed values of w tended to be larger in the case of directional selection, and somewhat smaller in the case of divergent selection, than those expected from univariate truncation selection.

These deviations are probably due to the second stage of selection. When direct and maternal genetic effects are negatively correlated, the second stage of selection would remove extremes direct BV individuals from the tail of the distribution at a disproportionate rate, leading to an accentuation of the reduction in variance for directional selection and a moderation in the increase in variances for divergent selection. A treatment of theoretical effects of bivariate selection on resulting variances is still required.

When constant accuracies were considered for each sire within each environment, correlations between direct or maternal predicted BV across environments were affected by the selection practiced in the first environment (Table 2.4 and Table 2.5). Directional selection yielded a decrease in the magnitude of the correlation coefficient, whereas divergent selection increased the correlation. Adjustment of the expectations of the correlation coefficients for selection following univariate procedures developed by Notter and Diaz (1992) generally accounted for the effect of selection. Tables 2.4 and 2.5 show observed and expected correlations values of the correlations in the presence (r_G = .5) and absence (r_G = 1.0) of G x E interaction. None of the observed differences between observed and expected were statistically significant. However, when the values of the observed correlations were compared to the expectation under random selection, differences ($P < .05$) were found in the selected population.

Adjustment of the expected value of the correlations using values of w of -ix and i(i-x) from univariate sampling theory instead of observed values of w as used by Notter and Diaz (1992) yielded similar conclusions. Thus, directional and divergent selection on two traits simultaneously did not seem to introduce a major departure of the observed correlation from its expectation under univariate selection at the levels of intensity for independent culling levels and genetic correlation between direct and maternal traits.

Tables 2.6 and 2.7 show observed and expected correlations of predicted BV for the case of variable accuracies of BV predictions. As in the previous case, the effects of selection on observed and expected correlation are apparent. As expected, directional selection yielded a decrease in the magnitude of the correlation coefficient whereas divergent selection had the opposite effect relative to values for a random sample from the

population. Under selection, no significant departures were found for either trait (Table 2.6 and 2.7) when comparing observed correlations between predicted BV with their expectations adjusted for selection (Notter and Diaz, 1992). However, for $r_G = 1$ significant differences existed when observed values were compared to expectations under random selection (Calo et al., 1973). Still, when $r_G = .5$, neither expectations of Calo et al. (1973) nor expectations of Notter and Diaz (1992) differed significantly from the observed correlation for the maternal BV predictions. The validity of this result is questionable since the observed values of w indicate that selection was effective in environment 1. However, in this particular case where the values of expectations were lowered, larger sample sizes may have been required to detect significant departures from expectations (Notter and Diaz, 1992).

Random selection yielded significant departures from expectation when examining correlation of predicted maternal BV for variable accuracies. However, confidence intervals of the mean of the departures overlapped 0, which may indicate that in cases of variable accuracies sampling effects were not avoided with the total number of samples obtained.

Regression coefficients of predicted BV in the second environment on predicted BV in the first environment for both direct and maternal trait did not appear to be systematically biased by selection. However, in three situations (involving variable accuracies under directional selection and random selection) (Table 2.6 and 2.7), departures from expectations were significant. This result suggests that sample sizes were not adequate to avoid important sampling effects.

Conclusions

In the presence of small sample sizes (n=40), high accuracies and possibly divergent selection are needed to detect departures of observed values from expectations (Table 2.2 and Table 2.3). The used of divergent selection consistently led to a agreement between observed and expected correlations. Selection based on predicted breeding values affects the expectations of the correlations between BV predictions across environments. However, adjustments developed for a univariate case seemed to yield corrections that were approximately correct, at least for the modestly negative genetic correlation between direct and maternal effects used in these simulations. Nevertheless, the validity of the univariate adjustments for a bivariate case might be restricted to cases where genetic correlation are low or moderate and the selection strategies are similar to the ones followed here. A more extensive theoretical study is needed to determine the generality of the conclusions drawn here as well as simulations including different values of genetic correlations and different selection procedures.

TABLE 2.1 VALUES OF GENETIC PARAMETERS USED IN THE
SIMULATION OF TRUE AND PREDICTED BREEDING VALUES [a,b]

Additive direct variance (σ_d^2)	268
Additive maternal variance (σ_m^2)	359
Covariance direct - maternal ($\sigma_{d,m}$)	-83
Correlation direct - maternal ($r_{G_{d,m}}$)	-.268

[a] Genetic parameters were assumed to be the same for both environments.

[b] Variance components yield an estimate of $h_d^2 = .23$ and $h_m^2 = .30$ used by APHA.

TABLE 2.2 SIMULATED VALUES OF VARIANCES OF PREDICTED DIRECT BV IN THE BASE POPULATION ($\sigma^2_{\hat{u}_i}$) AND OBSERVED AND EXPECTED VARIANCES OF PREDICTED VARIANCES OF PREDICTED BV AFTER SELECTION ($V(\hat{u})$) FOR $r_G = 1$ AND $.5$ AND WITH CONSTANT ACCURACIES [a,b]

Type of selection	$r_G = 1$				$r_G = .5$			
	1st Env. $\sigma^2_{\hat{u}_1} = 215.6$		2nd Env. $\sigma^2_{\hat{u}_2} = 97.0$		1st Env. $\sigma^2_{\hat{u}_1} = 218.3$		2nd Env. $\sigma^2_{\hat{u}_2} = 96.0$	
	$V(\hat{u}_1)$	w^c	$V(\hat{u}_2)$	$E(V(\hat{u}_2))^d$	$V(\hat{u}_1)$	w^c	$V(\hat{u}_2)$	$E(V(\hat{u}_2))^d$
Directional	46.1 (53.9)	.787 (.750)	71.4	74.1	41.9 (54.6)	.809 (.750)	71.3	89.1
Divergent	614.5 (610.6)	-1.852 (-1.832)	149.2	148.1	603.3 (618.2)	-1.762 (-1.832)	105.9	106.9
Random	210.8	.022	96.5		181.3	.169	86.7	

[a] Tables entries are the average of 10 replicates.
[b] Values in parentheses are those predicted from univariate selection theory, i.e., for $w = i(i-x)$ for directional and $w = -ix$ for divergent selection.

[c] $w = 1 - \dfrac{V(\hat{u})}{\sigma^2_{\hat{u}}}$

[d] Expected values of $V(\hat{u}_2)$ from Notter and Diaz (1992).

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TABLE 2.3 SIMULATED VALUES OF VARIANCES OF PREDICTED MATERNAL BV IN THE BASE POPULATION ($\sigma^2_{\hat{u}_i}$) AND OBSERVED AND EXPECTED VARIANCES OF PREDICTED BV AFTER SELECTION (V(û)) FOR EACH FOR $r_G = 1$ AND .5 AND WITH CONSTANT ACCURACIES[a,b]

| Base Population | $r_G=1$ | | | | $r_G=.5$ | | | |
| | 1st Env. $\sigma^2_{\hat{u}_1}=288.1$ | | 2nd Env. $\sigma^2_{\hat{u}_2}=129.6$ | | 1st Env. $\sigma^2_{\hat{u}_1}=292.3$ | | 2nd Env. $\sigma^2_{\hat{u}_2}=131.1$ | |
	$V(\hat{u}_1)$	w^c	$V(\hat{u}_2)$	$E(V(\hat{u}_2))^d$	$V(\hat{u}_1)$	w^c	$V(\hat{u}_2)$	$E(V(\hat{u}_2))^d$
Directional:	54.4 (72.0)	.811 (.750)	100.6	97.7	60.3 (73.1)	.794 (.750)	123.9	121.8
Divergent	777.4 (815.9)	-1.698 (-1.832)	204.5	191.6	779.5 (827.0)	-1.668 (-1.832)	145.0	142.4
Random	269.1	.065	120.5		326.3	-.116	129.2	

[a] Tables entries are the average of 10 replicates.

[b] Values in parentheses are those predicted from univariate selection theory, i.e., for $w = i(i-x)$ for directional and $w = -ix$ for divergent selection.

[c] $w = 1 - \dfrac{V(\hat{u})}{\sigma^2_{\hat{u}}}$

[d] Expected values of $V(\hat{u}_2)$ from Notter and Diaz (1992).

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TABLE 2.4 OBSERVED AND PREDICTED CORRELATION AND REGRESSION COEFFICIENTS FOR DIRECT PREDICTED BREEDING VALUES WITH CONSTANT ACCURACY IN EACH ENVIRONMENT.[a]

Selection		$r_G = 1.0$					$r_G = .5$			
		Correlation		Regression			Correlation		Regression	
	w[b]	Obs.	Exp.[c]	Obs.	Exp.[d]	w[b]	Obs.	Exp.[c]	Obs.	Exp.[d]
Directional	.787	.330	.281	.406	.360	.809	.059	.120	.073	.180
Divergent	-1.852	.724	.734	.357	.360	-1.762	.388	.422	.162	.180
Random	-	.561	.540[e]	.341	.360	-	.229	.270[e]	.159	.180

[a] Tabular entries average 10 replicates.
[b] $w = 1$ - the ratio of variance in predicted BV in the selected samples in environment 1 to that in the population prior to selection.
[c] Adjusted for selection following Notter and Diaz (1992). See text.
[d] Obtained following Notter and Diaz (1992). See text.
[e] Expected value under random selection. See text.
* P < .05 for the differences between observed and expected values.

TABLE 2.5 OBSERVED AND PREDICTED CORRELATION AND REGRESSION COEFFICIENTS FOR MATERNAL PREDICTED BREEDING VALUES WITH CONSTANT ACCURACY IN EACH ENVIRONMENT[a].

| | $r_G = 1.0$ | | | | | $r_G = .5$ | | | | |
| | | Correlation | | Regression | | | Correlation | | Regression | |
Selection	w^b	Obs.	Exp.[c]	Obs.	Exp.[d]	w^b	Obs.	Exp.[c]	Obs.	Exp.[d]
Directional	.811	.265	.266	.357	.360	.794	.104	.126	.142	.180
Divergent	-1.698	.739	.695	.379	.360	-1.668	.455	.416	.199	.180
Random	-	.491	.540[e]	.300	.360	-	.316	.270[e]	.197	.180

[a]Tabular entries average 10 replicates.
[b]w = 1 - the ratio of variance in predicted BV in the selected samples in environment 1 to that in the population prior to selection.
[c] Adjusted for selection following Notter and Diaz (1992). See text.
[d] Obtained following Notter and Diaz (1992). See text.
[e] Expected value under random selection. See text.
* P < .05 for the differences between observed and expected values.

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TABLE 2.6 OBSERVED AND PREDICTED CORRELATION AND REGRESSION COEFFICIENTS FOR DIRECT PREDICTED BREEDING VALUES WITH VARIABLE ACCURACY IN EACH ENVIRONMENT[a].

| | | $r_G = 1.0$ | | | | | $r_G = .5$ | | | |
| | | Correlation | | Regression | | | Correlation | | Regression | |
Selection	w[b]	Obs.	Exp.[c]	Obs.	Exp.[d]	w[b]	Obs.	Exp.[c]	Obs.	Exp.[d]
Directional	.750	.282	.239c (.446)*	.418	.348	.768	.207	.105 (.214)	.382*	.170
Divergent	-1.741	.626	.624c (.437)*	.359	.347	-1.807	.334	.351 (.219)	.174	.176
Random	-	.411	.435	.316	.346	-	.296	.217	.247*	.172

[a] Tabular entries average 10 replicates.
[b] $w = 1$ - the ratio of variance in predicted BV in the selected samples in environment 1 to that in the population prior to selection.
[c] Adjusted for selection following Notter and Diaz (1992). See text. Values in parenthesis and those for random selection are derived following Calo et al., (1973) for unselected populations.
[d] Obtained following Notter and Diaz (1992).
* P < .05 for the differences between observed and expected values.

TABLE 2.7   OBSERVED AND EXPECTED CORRELATION AND REGRESSION COEFFICIENT FOR MATERNAL PREDICTED BREEDING VALUES WITH VARIABLE ACCURACY IN EACH ENVIRONMENT[a].

Selection	$r_G = 1.0$					$r_G = .5$				
	w^b	Correlation		Regression		w^b	Correlation		Regression	
		Obs.	Exp.[c]	Obs.	Exp.[d]		Obs.	Exp.[c]	Obs.	Exp.[d]
Directional	.699	.207	.186 (.328)*	.279	.244	.646	.148	.094 (.158)	.176	.117
Divergent	-1.688	.507	.485 (.321)*	.259	.240	-1.875	.224	.269 (.162)	.103	.123
Random	-	.195*	.321	.135*	.239	-	.260*	.160	.195*	.119

[a] Tabular entries average 10 replicates.

[b] $w = 1$ - the ratio of variance in predicted BV in the selected samples in environment 1 to that in the population prior to selection.

[c] Adjusted for selection following Notter and Diaz (1992). See text. Values in parenthesis and those for random selection are derived following Calo et al., (1973) for unselected populations.

[d] Obtained following Notter and Diaz (1992).

* P < .05 for the differences between observed and expected values.
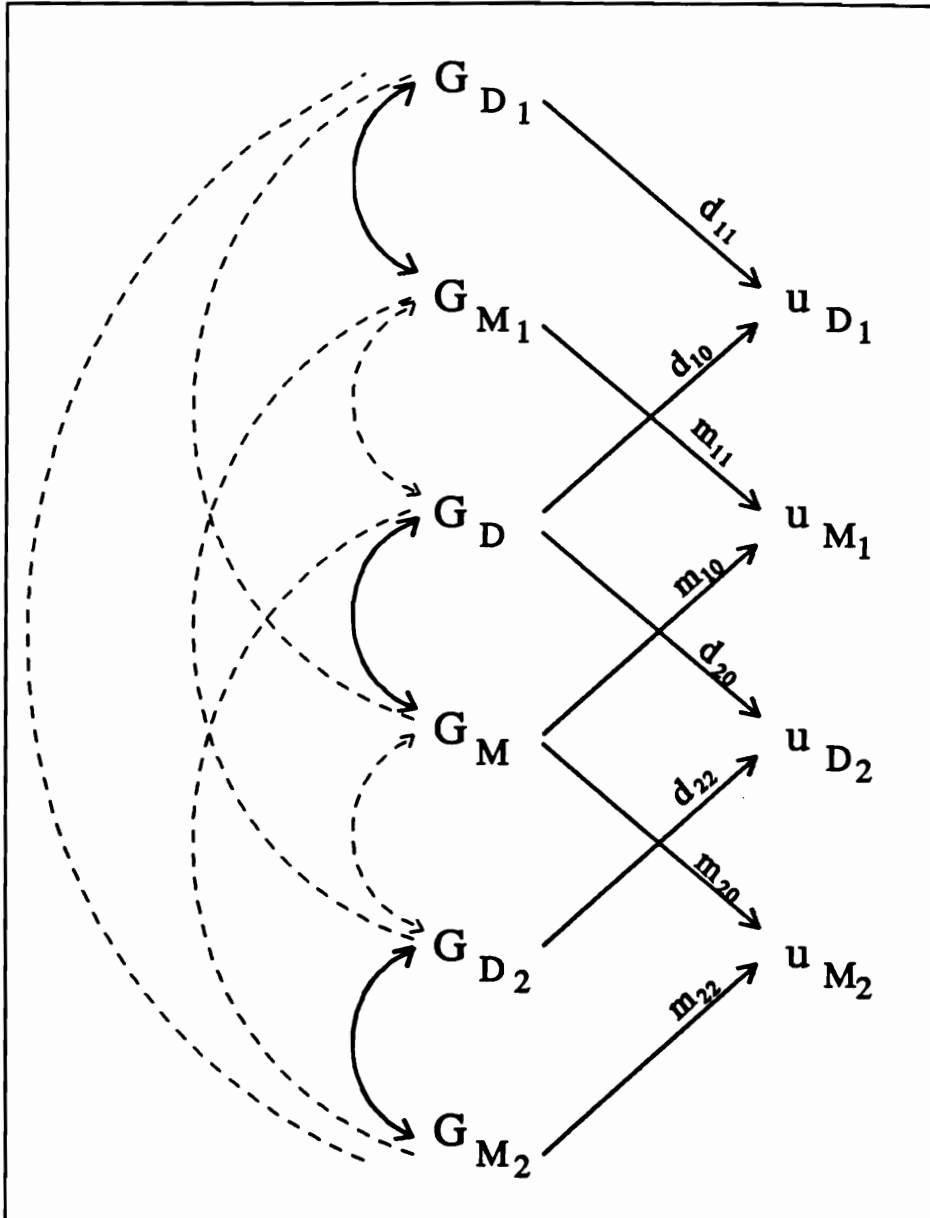
Figure 2.1 Path coefficient diagram modeling relationships between direct and maternal breeding values (u_{d_i}, u_{m_i}) across environments. G_D and G_M represent the average direct and maternal genotype across environments and G_{D_i} and G_{M_i} represent deviations from the mean genotypes in each specific environment.
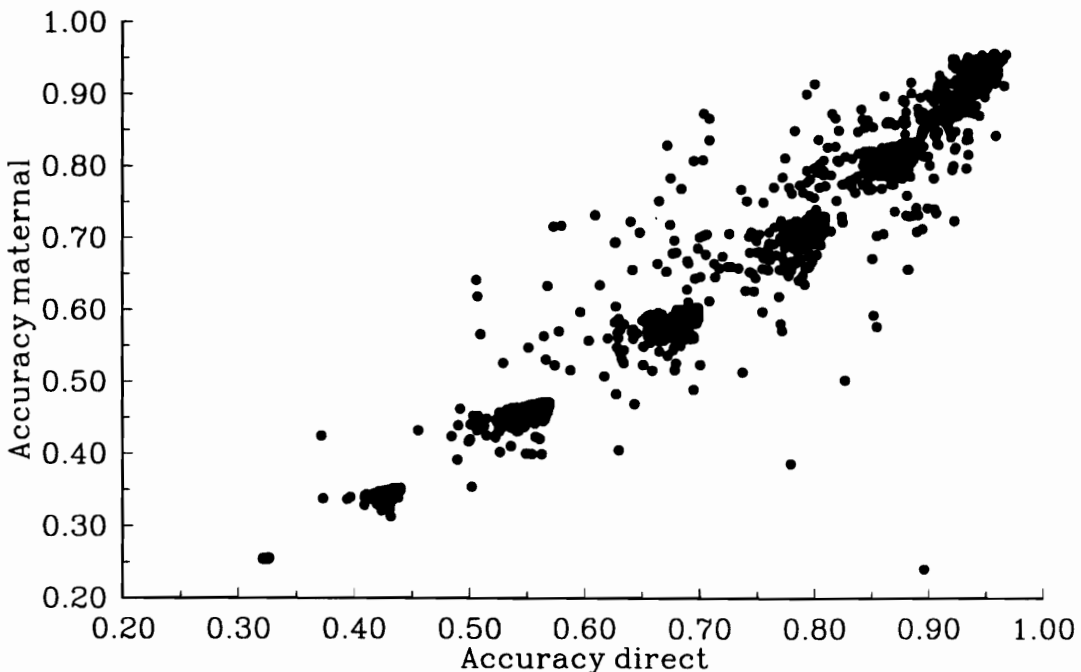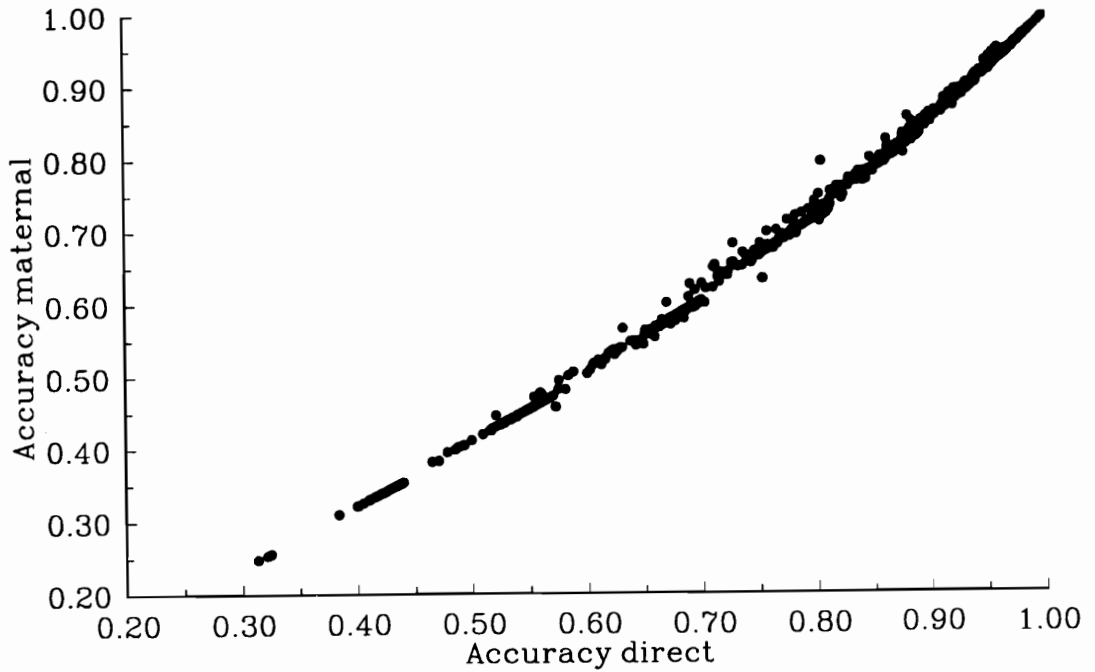
Figure 2.2 Relationship between accuracies of prediction of direct and maternal breeding values for each case of assignment of sires to contemporary groups: RAN1 (a) and RAN2 (b). N = 5864.
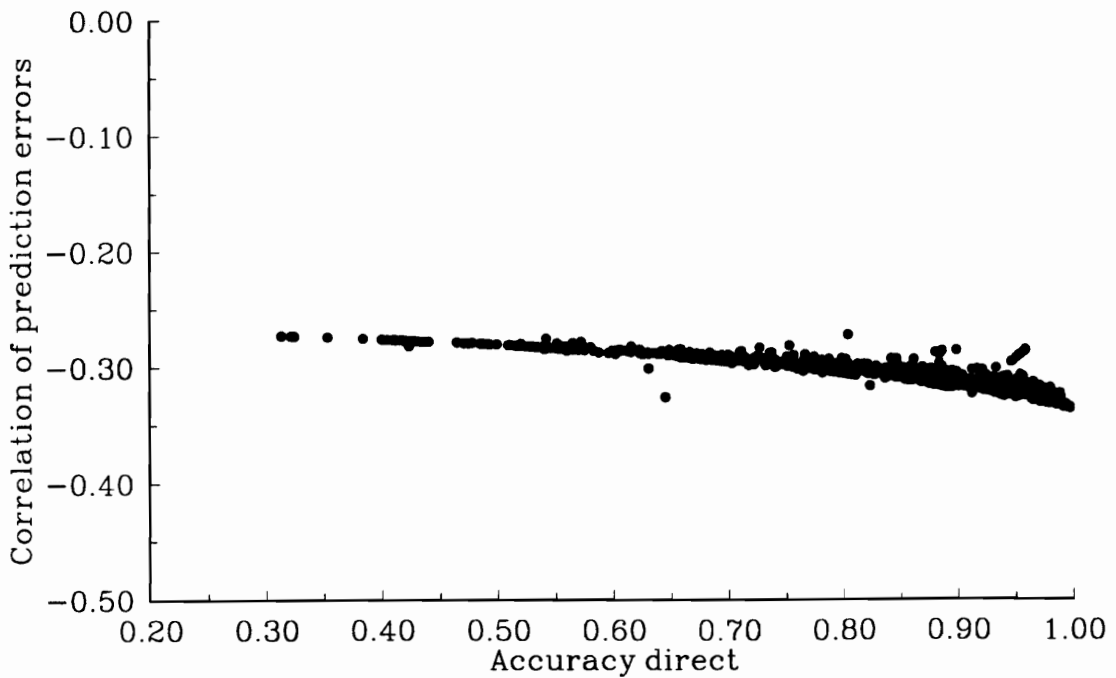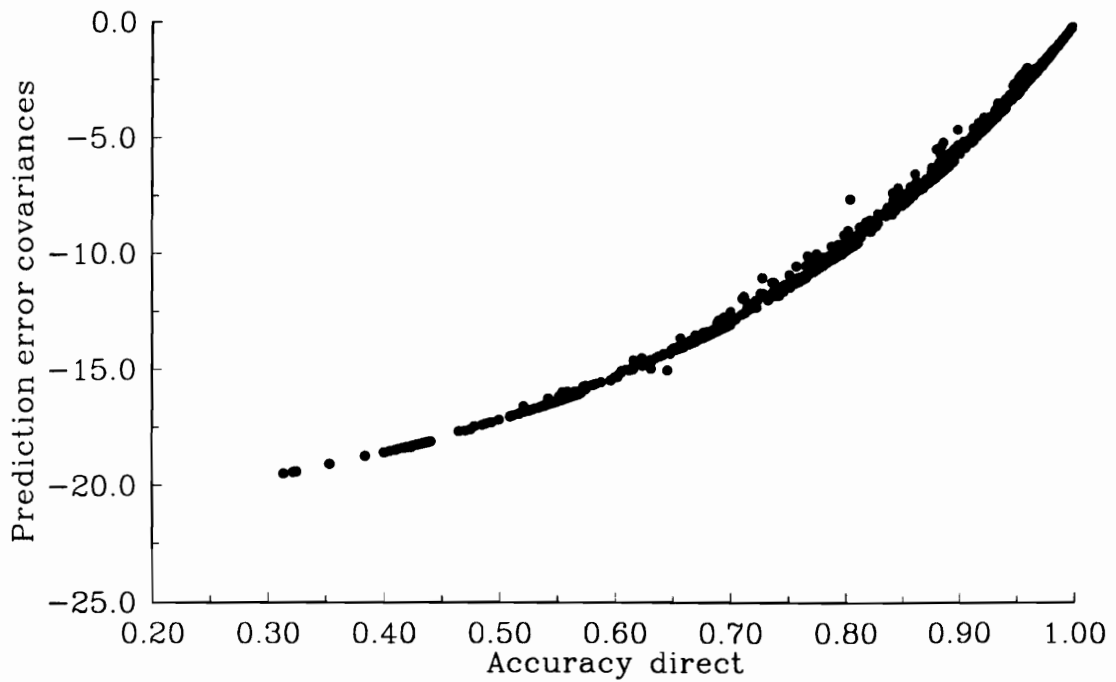
Figure 2.3 Relationship between accuracy associated with the prediction of direct
breeding value and PEC (a) and the correlation of direct and maternal prediction errors
(b). Random assignment of sires to contemporary groups was performed once (RAN1).
N = 5864.
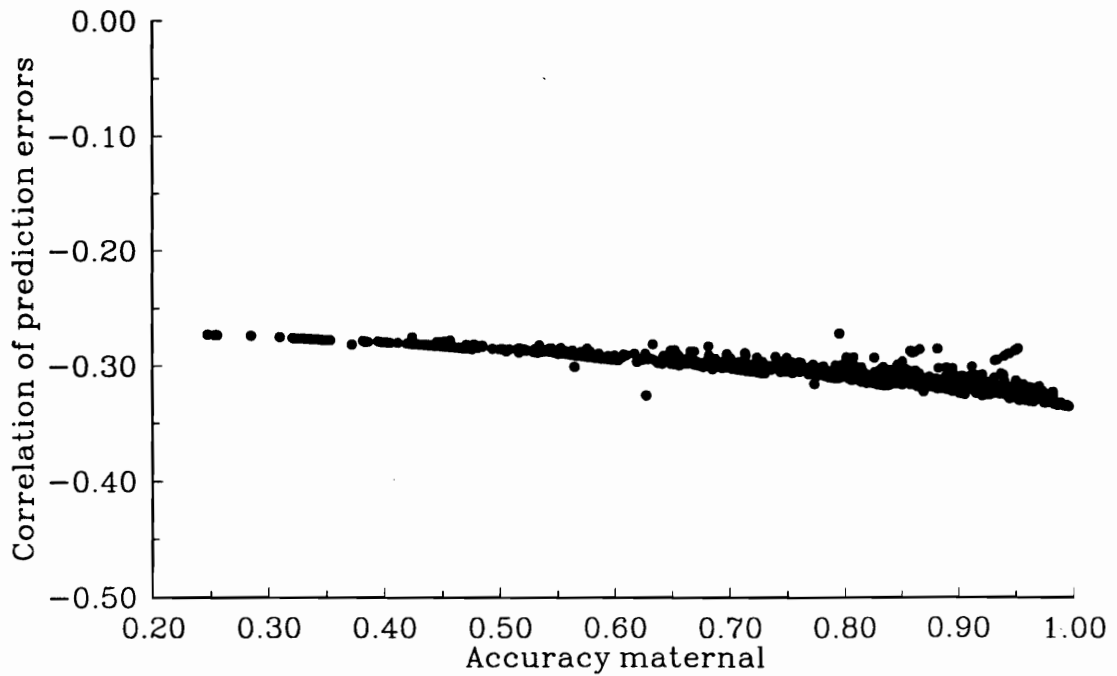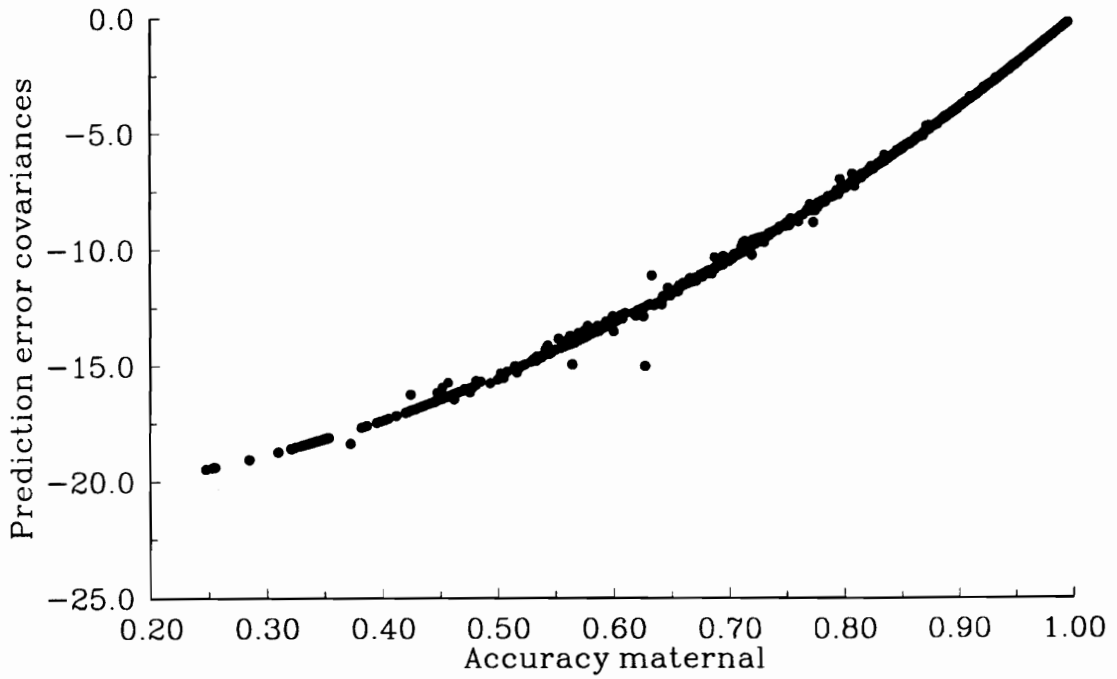
Figure 2.4 Relationship between accuracy associated with the prediction of maternal
breeding values and PEC (a) and the correlation of direct and maternal prediction errors
(b). Random assignment of sires to contemporary groups was performed once (RAN1).
N = 5864.
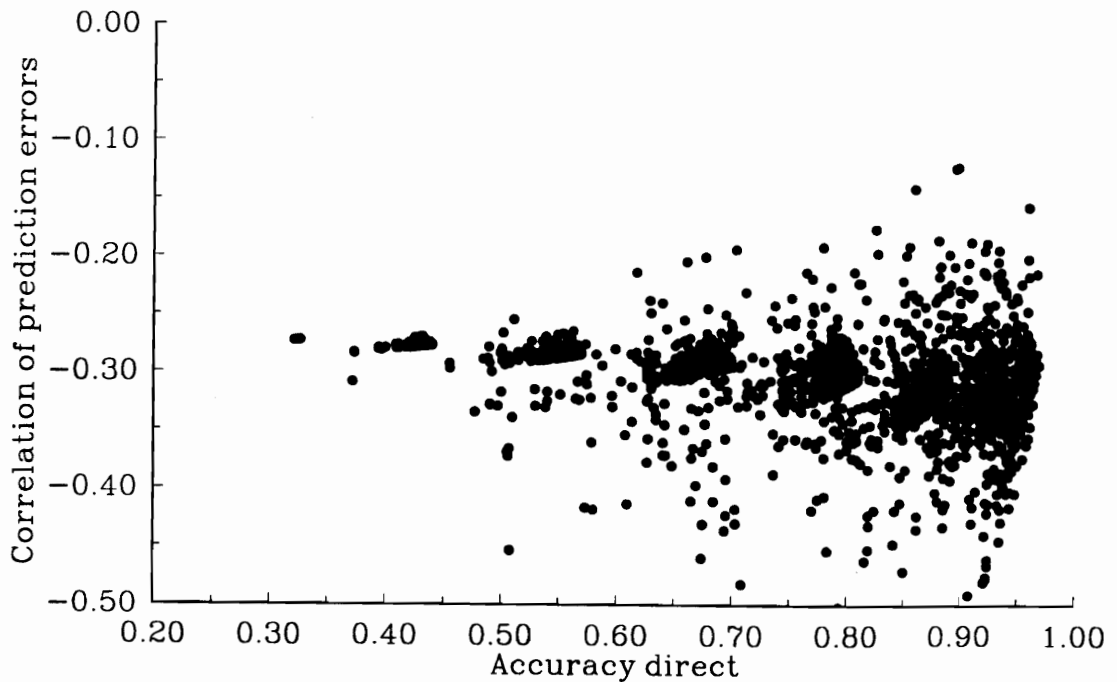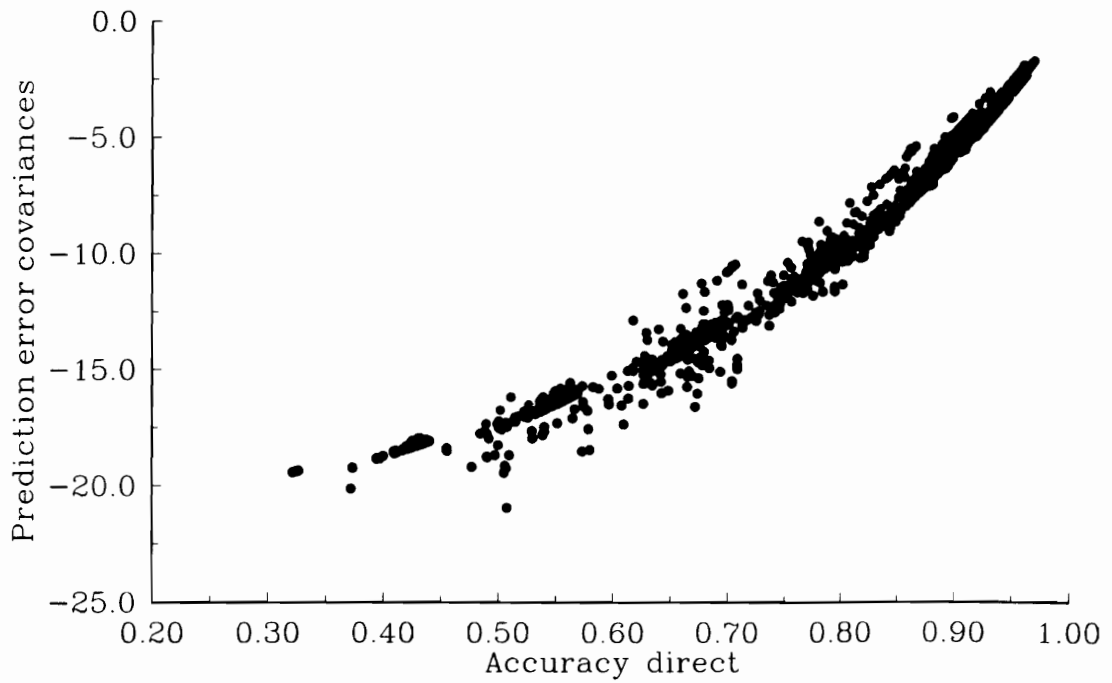
Figure 2.5 Relationship between accuracy associated with the prediction of direct breeding value and PEC (a) and the correlation of direct and maternal prediction errors (b). Random assignment of sires to contemporary groups was performed twice (RAN2). N = 5864.
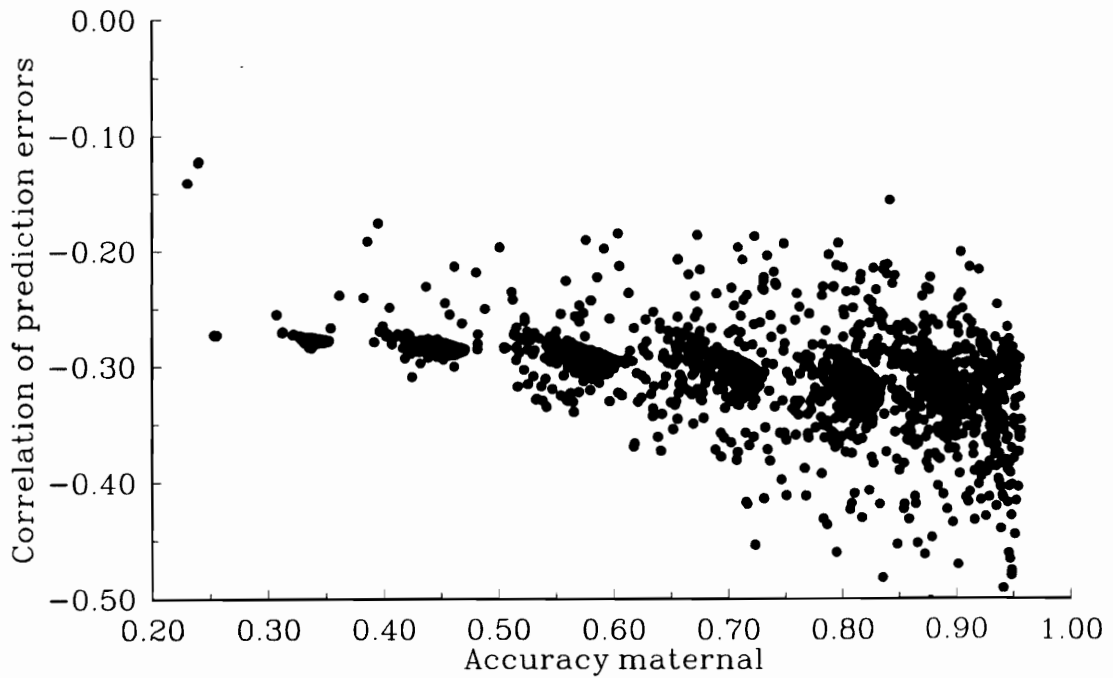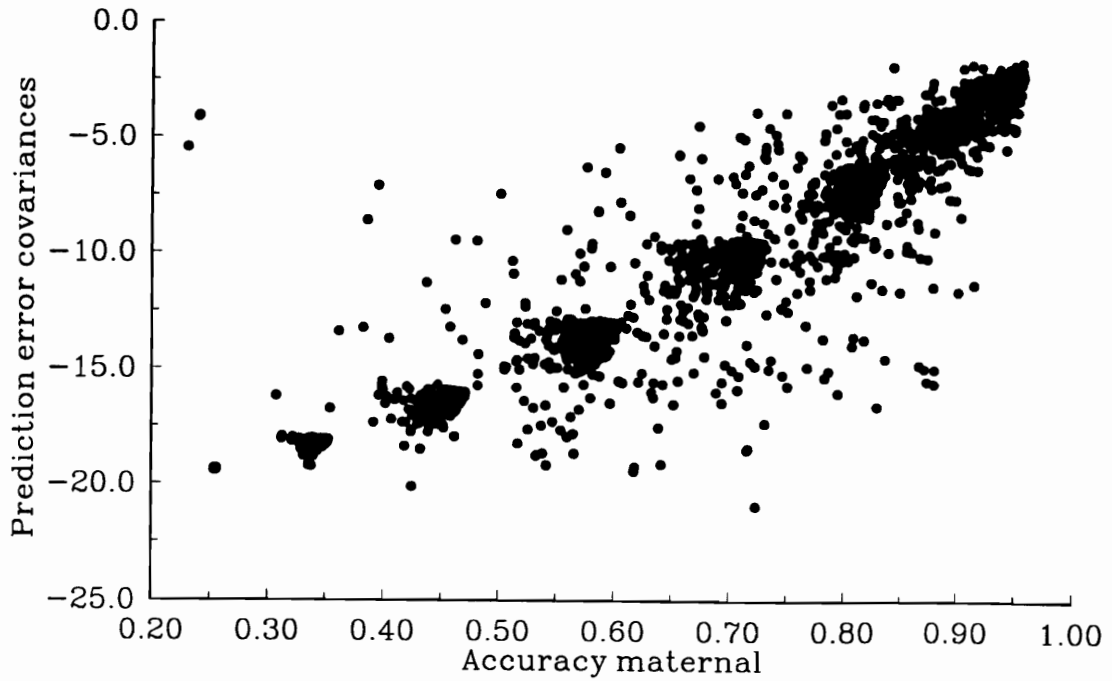
Figure 2.6 Relationship between accuracy associated with the prediction of maternal breeding value and PEC (a) and the correlation of direct and maternal prediction errors (b). Random assignment of sires to contemporary groups was performed twice (RAN2). N = 5864.

CHAPTER 3

NET MATERNAL ABILITY OF CROSSBRED FEMALE PROGENY OF POLLED HEREFORD SIRES DIVERGENTLY SELECTED FOR GROWTH AND MATERNAL ABILITY

Introduction

Weaning weight is a trait of economic importance for most commercial beef producers and is the joint expression of the genotype of the calf for growth and the genotype of the dam for maternal ability. Genes for both growth and maternal ability are passed to the calf from both sire and dam but genes for maternal ability can only be expressed in females and will not be expressed until the females produce progeny of their own. Thus, to evaluate the maternal breeding value (BV) of a sire, progeny of both the sire and the sires' daughters are required. Most beef cattle genetic evaluation reports provide two traits related to maternal performance at weaning. The first is maternal milk (MILK) which refers to differences in weaning weights of sires' daughters' calves that are of maternal origin and which are usually assumed to primarily reflect differences in milk production (Diaz et al., 1992). The second is referred to as maternal weaning weight (MAT) or total maternal effect. This measure includes genetic differences in maternal ability plus genetic differences in growth potential transmitted from sire to grandprogeny via their dams. A number of beef cattle breed associations report sire expected progeny differences (EPDs) for both measures of maternal ability (APHA, 1992; ASA, 1991 ; AAA, 1991).

Purebred cattle are the source of much of the genetic material for the beef cattle industry. However, it is generally recognized that differences in environmental and management

conditions often exist between purebred and commercial herds. Mahrt et al. (1990) examined the utility of national sire evaluations BV predictions derived primarily from purebred herds as a tool to predict animal performances in commercial crossbreeding. The progeny of 47 Polled Hereford sires mated to grade Angus cows were used. Mahrt et al. (1990) concluded that sires' expected progeny differences (EPD) for birth weight (BW), weaning weight (WW) and yearling weight (YW) were positively associated with the performances of their crossbred calves.

Crossbred females are extensively used for commercial purposes. Commercial breeders often rely on sire evaluations for maternal ability based on purebred data to make selection decisions. The assumption is that the EPD derived from the performance of daughters in their original environment will be also expressed in commercial herds. The objective of this study was to investigate the use of sire EPDs for maternal ability as a predictor of maternal performance in commercial crossbreeding and to account for selection practiced on the sires in the interpretation of the results.

Material and Methods

Animal Description.

This study was conducted at the Shenandoah Valley Agricultural Experiment Station, Steeles Tavern, VA, between 1982 and 1990. A total of 1,031 calves were born during this period. The first group of calves (n=457) were born between 1983 and 1987 and were produced by mating Polled Hereford sires to grade Angus dams. Performance of these calves has been described by Mahrt et al. (1990). Males calves were sold as yearlings. Females were retained for breeding and produced 574 calves between 1985 and

1990 in matings to Angus, Salers and Simmental sires. This section of the study focused primarily on the progeny of the crossbred females.

Polled Hereford Maternal Grandsires. The 47 Polled Hereford bulls were chosen from the American Polled Hereford Association (APHA) sire summary in 1982 through 1986 based upon their yearling weight (YW) and total maternal (MAT) EPD's. Selection was divergent in order to identify four distinct groups of sires:

> HH = High YW and High MAT
>
> HL = High YW and Low MAT
>
> LH = Low YW and High MAT
>
> LL = Low YW and Low MAT

A minimum level of accuracy (BIF, 1986) of .80 was required and within that constraint the most extreme individuals in each group were identified This level of accuracy corresponds to an expected correlation between actual and predicted BV of .98. Final selection decisions were based on the availability of semen. In each year, a new sample of bulls was identified from the annual sire summary. Sixteen bulls were used in more than one year (Mahrt et al., 1990). Fourty three of the 47 sires contributed at least one daughter to the herd.

Several changes in the APHA evaluation system occurred after 1986. At the time the bulls were selected, MAT EPD was estimated directly from the performance of the first calves of sires' daughters and as such included both genetic differences in maternal ability and in growth potential transmitted from sire to grandprogeny via the dam (Mahrt et al., 1990). Beginning in 1988, MILK EPDs were added to the APHA sire summary to allow partition

of the total maternal effect into components due to maternal ability and transmitted growth.

Current EPDs for sires were obtained from the 1992 APHA Sire Summary (Table 3.1) and used for all analyses. The four groups were less distinct than they were at the time of selection due to accumulation of additional data and changes in methodology in later sire summaries, but results of the divergent selection can still be observed as a shortage of animals that are near average for both traits, resulting in fewer animals at the center of the distribution (Figure 3.1).

Angus Maternal Grandams. One hundred fifty seven straightbred Angus cows formed the foundation cow herd. They included two distinct groups divided according to their birth year. The first group of cows (n=104) were purchased from Virginia feeder calf sales and entered the experiment in the spring of 1982 when all of the cows were 5 yr old. The second group (n= 53) came from a single farm and entered the experiment in 1983 at 1 yr of age. Between 1982 and 1986, these cows were randomly mated by AI using semen from the selected Polled Hereford sires. Relationships among cows were unknown and they will subsequently be considered unrelated.

Crossbred Dams and Sires of Calves. One hundred eighty eight Polled Hereford x Angus crossbred cows were produced. Performance of these cows as calves has been described by Mahrt et al. (1990). Age of crossbred cows at calving ranged between 2 and 7 yr. Females were inseminated for the first time at about 15 mo of age. Sixty seven sires of four different breeds were mated by A.I. to crossbred cows during the second phase of the experiment. Those breeds were North American Angus (n=25), Salers (n=5), Simmental

(n=31) and New Zealand Angus (n=6). Figure 3.2 shows the data distribution among cow ages, years of calving and sire breeds. North American Angus bulls were used in every year except 1987. Salers were used with North American Angus in 1986. Simmental bulls were used from 1987 to 1990 and coexisted with North American Angus in all years except 1987. New Zealand Angus were used during 1988 and 1989. Simmental bulls were randomly mated to 2 and 3 yr old cows because crossbred cows were additionally involved in an experiment to detect factors related to calving difficulty (Nugent and Notter, 1991). Note from Figure 3.2 that age of cow, year of calving and breed of the sire of the calves were partially confounded. Cows were culled only in case of major physical problems that prevented conception or successfully raising a calf to weaning.

Calves. Five hundred seventy four calves were born out of the crossbred dams between late February and late April during 1985 through 1990. Table 3.2 shows the distribution of data across years. Males were castrated shortly after birth. Calves were pastured with their dams and did not receive creep feed before weaning. Four hundred ninety two of the calves born also had a recorded weaning weight. Calves were weaned between late October and mid-November at a average age of 224 d (SD = 18 d). Average weaning weight was 194.8 kg (SD = 26.6 kg). Due to possible sire misidentification based upon recorded breeding and birth dates, sixty six weaning records were subsequently discarded from the data set, leaving 426 weaning weight records for analysis (Table 3.2).

Regression analysis

Second generation calf data were initially analyzed using the General Lineal Model Procedure of SAS (1990). Prior to analysis, weaning weights of calves were adjusted to

205 d of age (BIF, 1986). Twenty seven contemporary groups were defined representing birth year, age of cows and calf sire breed combinations (Figure 3.2).

The four groups of Polled Hereford maternal grandsires were first compared using the model:

$$Y_{ijklmno} = \mu + sx_i + cg_j + mdg_k + sc_l + mgsg_m + mgs_{mn} + e_{ijklmno} \qquad [1]$$

where

$Y_{ijklmno}$ is the adjusted weaning weight of a calf;

μ is a constant common to all observations;

sx_i is the fixed effect of the *ith* sex (i =1,2 for steer or heifer);

cg_j is the fixed effect of the *jth* contemporary group (j = 1,...27);

mdg_k is the fixed effect of the *kth* maternal grandam group (k = 1,2);

sc_l is the random effect of the *lth* sire of calf (l = 1.....67);

$mgsg_m$ is the fixed effect of the *mth* maternal grandsire group (m = 1,...4);

mgs_{mn} is the random effect of the *nth* maternal grandsire nested within the *mth* maternal grandsire group (m = 1,...43);

$e_{ijklmno}$ is a random error associated with Y.

Effects of maternal grandsire groups were tested using the between sire mean square. Individual effects of YW (H vs. L) and maternal groups (H vs. L) as well as their interaction were also tested using orthogonal contrasts.

Adjusted calf weaning weights were also regressed on MAT EPD of the Polled Hereford maternal grandsires according to the following model:

$$Y_{ijklm} = \mu + sx_i + cg_j + mdg_k + sc_l + \beta_1 \left(matepd - \overline{matepd}\right) + e_{ijklm} \qquad [2]$$

where

β_1 is the regression coefficient of calf weaning weight on maternal grandsire MAT EPD; and

$\left(matepd - \overline{matepd}\right)$ is the deviation of the sire MAT EPD from the mean MAT EPD of all sires.

The total maternal contribution of the maternal grandsire was also partitioned into its two components, WW EPD and MILK EPD and regression coefficients of observed calf performance on both EPDs were derived simultaneously. The model was:

$$Y_{ijklm} = \mu + sx_i + cg_j + mdg_k + sc_l + \beta_2 \left(wwepd - \overline{wwepd}\right)$$

$$+ \beta_3 \left(milkepd - \overline{milkepd}\right) + e_{ijklm} \qquad [3]$$

where

β_2 is the partial regression coefficient of calf weaning weight on maternal grandsire WW EPD;

$\left(wwepd - \overline{wwepd}\right)$ is the deviation of the sire WW EPD from the mean WW EPD;

β_3 is the partial regression coefficient of calf weaning weight on maternal grandsire MILK EPD; and

$\left(milkepd - \overline{milkepd}\right)$ is the deviation of the sire MILK EPD from the mean MILK EPD.

Other effects are as defined in the model [2].

Additional maternal grandsire effects that were not accounted for by WW and MILK EPD were tested by the following model :

$$Y_{ijklmn} = \mu + sx_i + cg_j + mdg_k + sc_l + \text{ß}_2 (wwepd - \overline{wwepd})$$
$$+ \text{ß}_3 (milkepd - \overline{milkepd}) + mgs_m + e_{ijklmn} \qquad [4]$$

Prediction of Breeding Values

Data.

A total of 863 adjusted weaning weights were used to predict WW and MILK EPDs. These records represent both Polled Hereford x Angus calves and the subsequent progeny of the crossbred females. Figure 3.3 shows the structure of these data. Instead of defining contemporary groups as in the previous section, data were adjusted for cow age prior to analysis. Additive correction factors applied by the APHA were used for this purpose (K. Bertrand, personal communication). This approach allowed effects of breed of calf sire to be defined as genetic groups and provided for connections between first and second generation calves born in the same year to be considered as contemporaries. Effects of birth year and sex were included in the model. Calves were progeny of 114 sires, including 47 Polled Hereford sires and 67 sires belonging to the four other breeds. Fourty three of the Polled Hereford sires had both progeny and grandprogeny in the data set. Therefore, additive genetic maternal effects were only estimated for 43 of the 47 Polled Hereford sires. The number of Angus dams was 153. One hundred and eight of these Angus dams were both dams and maternal grandams. The only intentional selection present in the data was the original selection practiced to obtain the Polled Hereford sires. Both heifers and steers were represented in the data set.

Genetic grouping.

Genetic grouping can be used to account for systematic differences in the genetic merit or origin (subpopulation) of animals being evaluated (Henderson, 1973; Quaas 1988).

Genetic groupings should represent animals with different genetic means since the average genetic merit of an animal then will be regressed towards the mean of the appropriate group rather than to the mean of all animals. Thus, genetic groups were identified for the parent individuals in the data set to account for selection and the presence of different subpopulations. Eight groups were defined for sires' additive direct effects; four corresponding to the four selected groups of Polled Hereford sires (HH, HL, LH and LL) and four corresponding to the four sire breeds mated to the crossbred cows (North American Angus, Simmental, Salers and New Zealand Angus). Furthermore, since selection practiced on Polled Hereford sires was also based on maternal EPD, four selection groups were also designed for the Polled Hereford maternal grandsires for maternal effect. Finally, Angus cows were assigned to two different genetic groups, identifying the two age-origin groups.

Model of evaluation.

Adjusted 205-d weaning weights of calves sired by Polled Hereford bulls were fitted using the following model:

$$Y_{ijklmno} = sx_i + by_j + gd_k + sd_{kl} + ga_m + a_{mn} + pe_n + e_{ijklmno}$$

where,

$Y_{ijklmno}$ is the adjusted weaning weight of a calf;

sx_i is the fixed effect of the *ith* sex (i =1,2 being steer or female);

by_j is the fixed effect of the *jth* calf's birth year (j = 1,...5);

gd_k is the fixed effect of the *kth* genetic group effect for the direct effect of sire (k = 1,...4) to denote the four Polled Hereford sires groups;

sd_{kl} is the random, additive genetic direct effect of the *lth* sire deviated from the mean of his group ($l = 1,...47$);

ga_m is the fixed effect of the *mth* genetic group for the total genetic Angus cow effect ($m = 1,...2$) including the confounded group effect additive and maternal genetic effects.

a_{mn} is the random total genetic effect of the *nth* Angus cow ($n = 1,...153$) deviated from the mean of her group;

pe_n is the *nth* random permanent effect common to all calves born out of the *nth* Angus cow ($o = 1,...153$);

$e_{ijklmno}$ is a random residual effect.

For calves with Polled Hereford maternal grandsires, the model was:

$$Y_{ijklmnopq} = sx_i + by_j + gd_k + sd_{kl} + \tfrac{1}{2}\,gd_k + \tfrac{1}{2}\,sd_{km} + gm_n + sm_{nm} + \tfrac{1}{2}\,ga_o + \tfrac{1}{2}\,a_{op}$$
$$+\; e_{ijklmnop}$$

where

by_j is the *jth* calf's birth year ($j = 3,...8$);

gd_k is the fixed effect of the *kth* genetic group for the direct effect of sire ($k = 5,...8$) to denote the four calf's sire groups;

sd_{kl} is the random, additive genetic direct effect of the *lth* sire deviated from the mean of his group ($l = 48,...114$);

$\tfrac{1}{2}\,gd_k$ is one half of the fixed effect of the *kth* genetic group effect for the direct effect of maternal grandsires ($k = 1,...4$);

$\tfrac{1}{2}\,sd_{km}$ is one-half of the random additive direct effect of the *mth* maternal grandsire deviated from the mean of his group ($m = 1,...47$);

gm_n is the fixed effect of the *mth* genetic group for the maternal effect of the maternal grandsire ($m = 1,...4$);

sm_{mn} is the random additive genetic maternal effect of the *nth* maternal grandsire deviated from the mean his group ($n = 1,...43$);

½ ga_o is one half the *oth* genetic group for the total genetic Angus cow effect ($o = 1,....2$);

½ a_{op} is one half of the *pth* total genetic effect of the Angus cow within the *oth* group ($p = 1,...108$) deviated from her group;

$e_{ijklmnopq}$ is a residual effect;

The implication of this partition of models for the two generations is related to the error terms, such that each error term contains different elements.

In matrix notation for both models:

$$y = X\beta + Z_d Q_d g_d + Z_d s_d + Z_m Q_m g_m + Z_m s_m + Z_a Q_a g_a + Z_a a_a + Z_p e_p + e$$

where

y is a (863 x 1) vector of records.;

X is a (863 x 10) incidence matrix that relates fixed effects (sex and birth year) in β (10 x 1) to the vector of records y ;

Z_d is a (863 x 114) incidence matrix that associates the vector of sire additive direct deviations s_d(114 x 1) to the records in y;

Q_d is a (114 x 8) incidence matrix that relates s_d to g_d ;

Z_m is a (863 x 43) incidence matrix that associates the vector of sire maternal deviations s_m (43 x 1) to the records in y.;

Q_m is a (43x4) incidence matrix that relates s_m to g_m;

Z_a (863 x 153) incidence matrix that relates Angus total genetic effects a_a (153 x 1) to the records in y;

Q_a is a (153 x 2) incidence matrix that relates a_a to g_a;

Z_p (863 x 153) incidence matrix that relates Angus maternal permanent effects e_{pe} (153 x 1) to the records in y;.

e is a (863 x 1) vector of residuals associated with y;

s_d, s_m,   are vectors of additive direct and additive maternal sire deviations respectively;

g_d, g_m, g_a are vectors of group effects for additive direct, maternal and total cow effect respectively;

a_a, e_p are vectors of total genetic deviations and permanent effects, respectively, of Angus cows;

X and Z_m are incidence matrices containing 0 and 1. Z_m contains 0 for first generation calves and 1 for second generation calves. However notice that in the way the model is parametized, Z_d and Z_a contain 0,1 and .5 for the sire and maternal grandsire direct effects and for dam and maternal grandam Angus cows. Each row of Z_d and Z_a contains 0 and 1 for first generation calf ; but for second generation calves Z_d contains 0, 1 or .5 and Z_a contains just 0 or .5.

The expected values and variances of each random effect in the model were assumed to be as follows:

$$E\begin{bmatrix} y \\ s_d \\ s_m \\ a_a \\ e_p \\ e \end{bmatrix} = \begin{bmatrix} Xb + Z_d Q_d g_d + Z_m Q_m g_m + Z_a Q_a g_a \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

$$Var\begin{bmatrix} y \\ s_d \\ s_m \\ a_a \\ e_p \\ e \end{bmatrix} = \begin{bmatrix} Z_d G_d Z_d' + Z_m G_m Z_m' + Z_a G_a Z_a' + Z_p G_p Z_p' + R & Z_d G_d & Z_m G_m & Z_a G_a & Z_p G_p & R \\ G_d Z_d' & G_d & 0 & 0 & 0 & 0 \\ G_m Z_m' & 0 & G_m & 0 & 0 & 0 \\ G_a Z_a' & 0 & 0 & G_a & 0 & 0 \\ G_p Z_p' & 0 & 0 & 0 & G_p & 0 \\ R & 0 & 0 & 0 & 0 & R \end{bmatrix}$$

The matrices G_d, G_m, G_a, G_p and R are diagonal matrices containing variances for the random sire direct, sire maternal, total Angus cow effect, permanent effect and error, respectively. Some of the Polled Hereford sires were related but relationships were ignored since selection was on EPD with accuracies of almost 1.

Variance components were derived from the data set using REML (Meyer, 1990). Variance of the sires' additive direct effect (σ_{sd}^2) within genetic groups was obtained for Polled Hereford sires and was assumed to be homogeneous across the four selected groups. Likewise, the variance component for sires direct effects in the second generation calves was assumed to be homogeneous across genetic groups (defined as breed of sires) but different from that for Polled Hereford sires. Selection practiced on Polled Hereford

sires might have diminished the within group variance in relation to a random population of sires. The maternal sire component, total genetic effect of Angus cows as well as the permanent environment component for Angus cows were also estimated. As before, the total genetic component of the Angus cows was assumed to be homogeneous across the two cow age groups. Table 3.3 shows values of the variance components obtained. The covariance between sire direct and maternal component was not estimated and was therefore assumed to be zero. Furthermore, R is a diagonal matrix containing two different elements; one for progeny and the other one for grandprogeny of Polled Hereford sires. The residual variance in the first generation calves contains one half of the additive direct variances in addition to the environmental variances. The residual variance in the second generation calves contains ten sixteenths of the additive direct variance plus one half of the additive maternal variance in addition to the environmental variances.

The mixed model equations to be solved

$$
\begin{bmatrix}
X'R^{-1}X & X'R^{-1}Z_dQ_d & X'R^{-1}Z_d & X'R^{-1}Z_mQ_m & X'R^{-1}Z_m & X'R^{-1}Z_cQ_c & X'R^{-1}Z_a & X'R^{-1}Z_p \\
Q_d'Z_d'R^{-1}X & Q_d'Z_d'R^{-1}Z_dQ_d & Q_d'Z_d'R^{-1}Z_d & Q_d'Z_d'R^{-1}Z_mQ_m & Q_d'Z_d'R^{-1}Z_m & Q_d'Z_d'R^{-1}Z_cQ_c & Q_d'Z_d'R^{-1}Z_a & Q_d'Z_d'R^{-1}Z_p \\
Z_d'R^{-1}X & Z_d'R^{-1}Z_dQ_d & Z_d'R^{-1}Z_d+G_d^{-1} & Z_d'R^{-1}Z_mQ_m & Z_d'R^{-1}Z_m & Z_d'R^{-1}Z_cQ_c & Z_d'R^{-1}Z_a & Z_d'R^{-1}Z_p \\
Q_m'Z_m'R^{-1}X & Q_m'Z_m'R^{-1}Z_dQ_d & Q_m'Z_m'R^{-1}Z_d & Q_m'Z_m'R^{-1}Z_mQ_m & Q_m'Z_m'R^{-1}Z_m & Q_m'Z_m'R^{-1}Z_cQ_c & Q_m'Z_m'R^{-1}Z_a & Q_m'Z_m'R^{-1}Z_p \\
Z_m'R^{-1}X & Z_m'R^{-1}Z_dQ_d & Z_m'R^{-1}Z_d & Z_m'R^{-1}Z_mQ_m & Z_m'R^{-1}Z_m+G_m^{-1} & Z_m'R^{-1}Z_cQ_c & Z_m'R^{-1}Z_a & Z_m'R^{-1}Z_p \\
Q_c'Z_c'R^{-1}X & Q_c'Z_c'R^{-1}Z_dQ_d & Q_c'Z_c'R^{-1}Z_d & Q_c'Z_c'R^{-1}Z_mQ_m & Q_c'Z_c'R^{-1}Z_m & Q_c'Z_c'R^{-1}Z_cQ_c & Q_c'Z_c'R^{-1}Z_a & Q_c'Z_c'R^{-1}Z_p \\
Z_a'R^{-1}X & Z_a'R^{-1}Z_dQ_d & Z_a'R^{-1}Z_d & Z_a'R^{-1}Z_mQ_m & Z_a'R^{-1}Z_m & Z_a'R^{-1}Z_cQ_c & Z_a'R^{-1}Z_a+G_a^{-1} & Z_m'R^{-1}Z_p \\
Z_p'R^{-1}X & Z_p'R^{-1}Z_dQ_d & Z_p'R^{-1}Z_d & Z_p'R^{-1}Z_mQ_m & Z_p'R^{-1}Z_m & Z_p'R^{-1}Z_cQ_c & Z_p'R^{-1}Z_a & Z_p'R^{-1}Z_p+G_p^{-1}
\end{bmatrix}
$$

$$
\begin{bmatrix}
\hat{\beta} \\
\hat{g}_d \\
\hat{s}_d \\
\hat{g}_m \\
\hat{s}_m \\
\hat{g}_a \\
\hat{a} \\
\hat{e}_p
\end{bmatrix}
=
\begin{bmatrix}
X'R^{-1}y \\
Q'_d Z'_d R^{-1}y \\
Z'_d R^{-1}y \\
Q'_m Z'_m R^{-1}y \\
Z'_m R^{-1}y \\
Q'_a Z'_a R^{-1}y \\
Z'_a R^{-1}y \\
Z'_p R^{-1}y
\end{bmatrix}
$$

[5]

All the elementsof these matrices have been defined before.

Once solutions were obtained, the total genetic merit of Polled Hereford sires ($\hat{w}_d, \hat{w}_m$) for direct and maternal effects were expressed as the sum of the group solution and the sire deviation for their direct and maternal effect, respectively. Thus,

$$\hat{w}_d = Q_d \hat{g}_d + \hat{s}_d$$

$$\hat{w}_m = Q_m \hat{g}_m + \hat{s}_m$$

Three terms were used from now to the end of this section. From selection index theory, accuracy (*acc*) is normally defined as the correlation between predicted and true breeding value. Following BIF (1986) in current beef sire summaries, the term accuracy (*Bacc*) corresponds to :

$$Bacc = 1 - \sqrt{\frac{PEV}{\sigma_s^2}}$$

where PEV stands for Prediction Error Variances and σ_s^2 refers to the sire variances.

The term reliability is currently used in the dairy industry and corresponds to the square of *acc* (VanRaden and Wiggans, 1991).

Reliability of EPD estimates for maternal and direct effects were calculated. Since groups were included in the model and variances components were then the within-group sire variances for Polled Hereford sires, 'reliability' was defined as the squared correlation between true (w) and predicted transmitting ability $(\hat{w})$ recognizing that variances among sires are also due to variation among groups. Hence, groups were assumed to be random in the true model with a distribution with mean μ_g and variance var(g), but fixed in the operational model. 'Reliability' was then defined as follows:

$$R^2{}_{\hat{w},w} = \frac{\left[cov(\hat{w},w)\right]^2}{var(w)var(\hat{w})} \qquad [6]$$

where

$$w = g + s$$
$$\hat{w} = \hat{g} + \hat{s}$$

thus,

$$cov(\hat{w},w') = cov(\hat{g},g') + cov(\hat{g},s') + cov(\hat{s},g') + cov(\hat{s},s') \qquad [7]$$
$$var(\hat{w}) = var(\hat{g}) + var(\hat{s}) + cov(\hat{g},\hat{s}') + cov(\hat{s},\hat{g}') \qquad [8]$$
$$var(w) = var(g) + var(s) \qquad [9]$$

From properties of the solutions of the MME, we can obtain each of the (co)variance matrices in [7] through [9]. Following the basic model

$$y = Xg + Zs + e$$

the corresponding MME are:

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

where

R is the residual (co)variance matrix;

G is the additive genetic variances $I\sigma_s^2$.

$\hat{g} =$ the vector of estimates of each group effect, and

$\hat{s} =$ the vector of estimates the sire effects within groups.

C is the inverse of the MME coefficient matrix and contains the sampling (co)variances of the estimates of fixed effects and prediction error variances of random effects (Henderson, 1973), such that

$$C = \begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}.$$

Therefore, solutions were found as

$$\begin{bmatrix} \hat{g} \\ \hat{s} \end{bmatrix}=\begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}\begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$
[10]

Since C is the inverse of MME then :

$$\begin{bmatrix} C_{11} & C_{12} \\ C_{21} & C_{22} \end{bmatrix}\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z+G^{-1} \end{bmatrix}=\begin{bmatrix} I & 0 \\ 0 & I \end{bmatrix}$$
[11]

The $Cov(\hat{w},w')$ was obtained by accumulating terms from [10] in [7] and making use of [11] as:

$$cov(\hat{g},g') = cov(\hat{g},g') = \left[\left[C_{11}X'+C_{12}Z'\right]R^{-1}cov(y,g')\right]$$

$$= \left[\left[C_{11}X'+C_{12}Z'\right]R^{-1}Xvar(g)\right]$$

$$= var(g) \text{ because,}$$

from [11] $\left[C_{11}X'R^{-1}X+C_{12}Z'R^{-1}X\right] = I$

$$cov(\hat{g},s') = \left[C_{11}X'+C_{12}Z'\right]R^{-1}Zvar(s)$$

$$= \left[C_{11}X'R^{-1}Z+C_{12}Z'R^{-1}Z\right]var(s)$$

$$= -C_{12}G^{-1}G$$

$$= -C_{12}$$

$$cov(\hat{s},g') =$$

$$= \left[\left[C_{21}X'+C_{22}Z\right]R^{-1}cov(y,g')\right]$$

$$= \left[\left[C_{21}X'+C_{22}Z\right]R^{-1}Xvar(g)\right] = 0$$

$$cov(\hat{s},s') = \left[G-C_{22}\right]$$

Then,

$$cov(\hat{w},w') = \left[var(g)-C_{12}+(G-C_{22})\right] \hspace{2cm} [12]$$

Variances of $\hat{w}$ and w were obtained following the same procedure. Thus, substituting $\hat{g}$ and $\hat{s}$ from [10] into [8] and making use of [11],

$Var(\hat{w}) = Var(\hat{g}+\hat{s})$ where

$$var(\hat{g}) =$$

$$= var\left[\left[C_{11}X'+C_{12}Z'\right]R^{-1}(y)\right]$$

$$= \left[\left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right] var(y) \left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right]' \right]$$

$$= \left[\left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right] \left[X var(g)X' + ZGZ' + R \right] \left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right]' \right]$$

$$= \left[\left[var(g)X' + \left[C_{11}X'R^{-1}Z + C_{12}Z'R^{-1}Z \right] GZ' + C_{11}X' + C_{12}Z' \right] \left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right]' \right]$$

$$= \left[\left[var(g)X' - C_{12}G^{-1}GZ + C_{11}X' + C_{12}Z' \right] \left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right]' \right]$$

$$= \left[\left[var(g) + C_{11} \right] \left[C_{11}X'R^{-1}X + C_{12}Z'R^{-1}X \right]' \right]$$

$$= \left[var(g) + C_{11} \right]$$

Also:

$$var(\hat{s}) = \left[G - C_{22} \right]$$
and:

$$cov(\hat{g}, \hat{s}') =$$

$$= \left[\left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right] var(y) \left[C_{21}X'R^{-1} + C_{22}Z'R^{-1} \right]' \right]$$

$$= \left[\left[C_{11}X'R^{-1} + C_{12}Z'R^{-1} \right] \left[X var(g)X' + ZGZ' + R \right] \left[C_{21}X'R^{-1} + C_{22}Z'R^{-1} \right]' \right]$$

$$= \left[\left[var(g)X' - C_{12}Z' + C_{11}X' + C_{12}Z' \right] \left[C_{21}X'R^{-1} + C_{22}Z'R^{-1} \right]' \right] = 0$$

Finally,

$$var(\hat{w}) = \left[var(g) + C_{11} \right] + \left[G - C_{22} \right] \qquad [13]$$

From 9, then

$$Var(w) = \left[var(g) + G \right] \qquad [14]$$

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Using the expressions obtained in [12], [13] and [14] and letting $c_{i,i}$ be the diagonal element of C_{11}, $c_{i,ij}$ the element of the C_{12} for the *jth* sire in the *ith* group and c_{jj} the diagonal element of the C_{22} for the *jth* sire, the reliability for a given sire as defined in [6] was obtained as follows:

$$R^2_{\hat{w}_j, w_j} = \frac{\left[\mathrm{var}(g) - c_{i,ij} + (\sigma_s^2 - c_{jj}) \right]^2}{\left[\mathrm{var}(g) + c_{i,i} + (\sigma_s^2 - c_{jj}) \right]\left[\mathrm{var}(g) + \sigma_s^2 \right]} \qquad [15]$$

where var(g) is the variance among groups effects and σ_s^2 is the variance among sires within group. Since var(g) cannot be directly obtained, certain assumptions had to be made to postulate that value. Thus, group effects were assumed to be measured without error:

$$\mathrm{var}(g) = \frac{\sum\limits_{j=1}^{m} (\hat{g}_j - \bar{g})^2}{m-1}$$

where, $\quad \bar{g} = \dfrac{\sum\limits_{j=1}^{m} \hat{g}_j}{m}$

$m = $ is the total number of Polled Hereford sires; and

$\hat{g}_j = g_j$ for all j

The observed product moment correlation (r_o) between EPDs as estimated in this study and those reported in APHA (1992) for both effects, direct and maternal, were equated to their expectations. Calo et al. (1973) and Blanchard et al. (1983) derived the expectation of r_o in the case of unequal amounts information available for each sire as reflected in different individual accuracies. The derived expectation was:

$$Corr(\hat{u}_1, \hat{w}_2) = \frac{r_G \sum\limits_{j=1}^{m} acc_{1j}^2 \sum\limits_{j=1}^{m} acc_{2j}^2}{\sqrt{\sum\limits_{j=1}^{m} acc_{1j}^2 \sum\limits_{j=1}^{m} acc_{2j}^2}} \qquad [16]$$

where

$\hat{u}_1, \hat{w}_2$ are the EPDs reported by APHA (1) and the ones obtained in this study

(2). EPDs correspond to either direct or maternal effect;

r_G is the genetic correlation among performances across environments; and

acc_{1j} and acc_{2j} are accuracies associated with the EPD of the jth sire in each

environment (1 and 2).

Making use of this expression, an estimate of r_G was obtained. Since acc in the first environment are involved in the expectation, the $Baccs$ reported by APHA sire summary (1992) for the Polled Hereford sires EPDs were transformed into acc as:

$$acc = \sqrt{1-(1-Bacc)^2}$$

Taylor (1983) established the conditions under which equation [16] will yield a proper estimate of r_G. Those conditions are (1) no environmental correlations between performance in the two environments, (2) no relationships among parents of the measured animals, (3) no other covariances among predicted BV within either environment. An additional assumption is that sires are chosen at random. If those assumptions do not apply, an improper estimates of the genetic correlation will be obtained. In this study assumptions (1) and (2) do apply, however (3) and (4) do not. Notter and Diaz (1992) developed expressions to account for the selection practiced and for other covariances

among predicted BV within an environment. The latter one requires knowledge of the full C matrix. Therefore a full inversion of MME coefficient matrix in [5] was obtained using Henderson's subroutine for inversion. Following Notter and Diaz (1992), sample variances and covariances were obtained. Denote the (co)variances matrix of $\hat{u}_1$ by Q_1 where $\hat{u}_1$ corresponds to the predicted transmitting abilities (EPDs) reported by APHA (1992) for the Polled Hereford sires. Denote the (co)variances matrix of $\hat{w}_2$ by Q_2, and let Q_{12} be the covariance matrix between $\hat{u}_1$ and $\hat{w}_2$. Since acc associated with $\hat{u}_1$ were very close to unity, Q_1 was assumed to be a diagonal matrix such that $Q_1 = I\sigma_{u_1}^2$ given that $\sigma_{\hat{u}_1}^2$,the additive genetic variances among the selected Polled Hereford sires, tends to $\sigma_{u_1}^2$ as acc tends to 1. If genetic groups had not been present in the model, indicating that the sampled sires corresponded to a random sample from the Polled Hereford population, the elements of Q_2 would have been obtained straightforwardly following Notter and Diaz (1992) as:

$$Q_2 = G_2 - C_{22}$$

However, the fact that the sample of Polled Hereford sires represented a selected sample has to be taken under consideration. The presence of selection was considered in the evaluation model by including genetic groups and using within-sire-groups variance components. The definition of such a model introduce a additional complication. With grouping, the diagonal elements of Q_2 (var($\hat{w}_{jj}$)) approximately are as in [13]:

$$\text{var}(\hat{w}_{jj}) = \text{var}(\hat{g}_i) + \text{var}(\hat{s}_j) = \text{var}(g) + c_{i,i} + (\sigma_s^2 - c_{jj})$$

If sire j is in group i, $c_{i,i}$ is the diagonal element of the C_{11} for the ith genetic group for the jth sire and c_{jj} is the diagonal element of the C_{22} submatrix corresponding to the prediction

error variance associated with the EPD of the *jth* sire. The offdiagonal elements of Q_2 contain the covariances among $\hat{w}$'s of different sires, such that:

$$\text{cov}(\hat{w}_j, \hat{w}_{j'}) = \text{cov}(\hat{g}_i, \hat{g}_{i'}) + \text{cov}(\hat{s}_j, \hat{s}_{j'}) = c_{i,i'} - c_{j,j'}$$

Notice that if sires belong to the same genetic group $c_{i,i'}$ is the diagonal element of the C_{11} submatrix, but if sires are in different genetic groups, that element is the offdiagonal element corresponding to the ith group of the jth sire and the *i'th* group of the *j'th* sire. The elements of Q_{12} were expressed as assuming that $u_1 = \hat{u}_1$:

$$\text{cov}(u_1, \hat{w}_2) = \text{cov}(u_1, \hat{g}) + \text{cov}(u_1, \hat{s}_2)$$

Following Notter and Diaz (1992) for this particular case where sires are proven sires,

$$\text{cov}(u_1, \hat{s}_2) = (G - C_{22})\text{r}_G\sigma_{u_1}/\sigma_{s_2}$$

The $\text{cov}(u_1, \hat{g}) =$ was obtained from the data using observed values of $\hat{u}_1$ and $\hat{g}$.

Finally, once the Q matrices were built, the sample variances ($s_{\hat{w}_i}^2$) and covariances ($s_{u_1, \hat{w}_2}$) were obtained as:

$$s_{\hat{w}_i}^2 = \frac{[m\ tr(Q_i) - sum(Q_i)]}{m(m-1)} \text{ for i=1,2}$$

$$s_{u_1, \hat{w}_2} = \frac{[m\ tr(Q_{12}) - sum(Q_{12})]}{m(m-1)}$$

where *tr* is the trace of the matrix and sum is the sum of all elements (Notter and Diaz, 1992). The sample variance and covariance accounts for different accuracies and covariances among BV predictions within environments ($\hat{w}$).

The effect of selection on the expected value of the correlation coefficient may be accounted for using an empirical measurement of the effect of selection, *sw*, where *sw* is defined as:

$$sw = 1 - \frac{\text{var}(\hat{u}_1)}{\sigma^2_{\hat{u}_1}}$$

where $\text{var}(\hat{u}_1)$ corresponds to the variances in the selected sample of the population, and $\sigma^2_{\hat{u}_1}$ is the variance in a random sample from the population. $\sigma^2_{\hat{u}_1}$ in a random sample of sires with accuracies near 1 becomes the sire additive genetic variance; therefore $\sigma^2_{\hat{u}_1}$ was replaced by $\sigma^2_{u_1}$.

Results and Discussion

Regression Analysis

Differences among the four Polled Hereford genetic groups were not detected. However, the partition of group effects by orthogonal contrasts into H and L YW and H and L MAT bulls effect and interaction showed significant differences in calf weaning weight between the H and L maternal groups (P = .0003) but neither H vs. L YW nor interaction effects were significant. In contrast, Mahrt et al. (1990) found that calves out of H YW EPD bulls averaged 7.5 kg heavier than calves from L YW EPD bulls, but no difference between progeny of H and L MAT were observed. In the current study, the differences in weaning weights between grandprogeny of H and L YW bulls was 2.7 kg. However,

calves out of H MAT dams averaged 6 kg heavier than calves out of L MAT dams. HH calves were clearly heaviest. HL calves tended to be similar to LH calves (Figure 3.4, a and b) which would explain the lack of a significant differences between H and L YW calves. Individual Polled Hereford sire effects within selected groups were also observed ($P<.001$). Thus, the selection on YW and MAT EPD did not homogenize groups enough to avoid residual sires differences.

Figure 3.4 shows average weaning weights versus average MILK EPD (a) and WW EPD(b) by group. Although selection for growth was not based on WW EPD, it appears to be highly correlated ($r=.97$; $P<.001$) with the selection criterion, YW EPD. Therefore selection decisions based on either trait would have been similar. Figure 3.4a indicates that when cows with a high milking potential (HH and LH) nursed calves of high growth potential (HH) those calves were heaviest, whereas if calves had low growth potential (LH) the higher milking ability of their dams did not result in heavier calves. In this context, growth potential of calves acted as a constraint in the expression of maternal ability of the dam. Similarly, when calves from H growth groups (HH and HL) received milk from a H MAT cow (HH), the average weaning weight of calves was higher than the average weaning weight of high growth calves nursed by L MAT cows (HL). In this sense, milk was a constraint for the expression of growth character of calves (Figure 3.4b). Furthermore, HH calves (calves with a high growth potential reared by high milking potential dams) were 11 kg heavier than HL calves, even though no differences were observed in WW EPDs between these two groups. In addition, LH calves (calves with a low growth potential nursed by high milking potential cows) were on average 8 kg lighter than the HH calves, although differences in MILK EPD (6 kg of EPD; $P < .05$) favored the first group. Although the argument, may not be very conclusive since the YW by MAT

group interaction was not significant, the result suggests that it is important to maintain a balance between growth and net maternal ability when making selection decisions to improve growth and milk based on weaning weights.

The regression coefficient of calves weaning weight on MAT EPD as obtained from model [2] was $.89 \pm .17$ kg/kg and did not differ from its expected value of 1. WW EPD and MILK EPD were positively and linearly associated with observed calf weaning weight. The partial regression coefficient of observed calf weaning weight on WW EPD was $.67 \pm .19$ kg/kg and did not differ significantly from the expected value of .5. The partial regression coefficient of weaning weight on MILK EPD was $.80 \pm .18$ kg/kg and, as in the previous case, was not significantly different than its expected value of 1. Thus 80% of the variation in weaning weights predicted by MILK EPDs was realized in these calves. Mahrt et al. (1990) and Notter and Cundiff (1991) reported a significant departure from expectation of the regression coefficient of weaning weights of the F_1 calf on sires' WW EPD. However, when Notter and Cundiff (1991) regressed weaning weights of the progeny of the F_1 females on WW EPD of the maternal grandsires, they failed to detect the same differences. Regressions on MAT and MILK EPD were in agreement with the results obtained in this study.

When fitting individual Polled Hereford sire effects (model 4) in addition to their corresponding direct and maternal EPD, a significant reduction in error sum of squares (P < .001) was obtained. Thus, sires EPDs did not fully explain genetic differences in daughter's calf weights, suggesting a true sire effect independent of his predicted additive value in the purebred environment and under the managerial conditions under which the study was developed. Since *acc* of the selected Polled Hereford sires were close to unity

for both WW EPD and MILK EPD, a reranking of sires might be expected compared to the performance observed in herds contributing data for EPD predictions. As pointed out by Notter and Cundiff (1991), this conclusion can be drawn only with regard to proven bulls. Otherwise, the lack of accuracy of predictions could introduce and additional source of variation. Residual sires effects were also detected when fitting sires in addition to MAT EPDs.

Correlation of EPDs across environments

Table 3.4 shows averages of EPDs and *acc* of prediction obtained using data from this study. The adjustment in the accuracies to include variances among the groups had an impact on the accuracies. However, the effect was not always as expected. Average accuracy within groups for direct EPDs (WW EPDs) was .66 while with the adjustment for variance among groups, the accuracy increased to .76 (Table 3.4). However, the maternal accuracy was negatively affected by the adjustment. Average within-group accuracy for maternal (MILK EPD) was .73 while the adjustment yielded an accuracy of .55 (Table 3.4). The fact that a lot of variation among the groups was observed for direct effect in WW (19.95 kg^2) and that the sampling errors of groups solutions were smaller than the estimated variance of g enhanced the value of the group adjustment for WW EPD. On the other hand, variation among maternal groups (6.67 kg^2) was minimal compared to the within-group sire variances (27.3 kg^2) and sampling errors of group solutions were larger than the estimated variance of g which resulted in a poorer adjustment of accuracy of MILK EPD. Given this result, it is questionable if maternal groups should have been included in the model. The inclusion of groups in models produces a decrease in accuracy of prediction that is only valuable if the differences among groups are important relative to the bias generated by ignoring them (Kennedy, 1981).

The observed values of *sw* as an empirical measurement of the effect of selection were -.074 and .069 for WW EPD (direct) and MILK EPD (maternal), respectively. This result indicates that the effect of selection was to restore the variance present in the original Polled Hereford population, instead of increasing that variance as theoretically one might expect from divergent selection. Apparently, available A.I. sires had already been directionally selected. Since the selection did not appear to affect the observed sample variance of predictions, there was no need to adjust expectation of correlations across environments.

The value of observed product moment correlations between EPDs reported by the APHA sire summary and those obtained in this study are shown in Table 3.5. The observed correlations between WW EPDs and MILK EPDs across environment were .64 and .58, respectively. Table 3.5 also present the expected values of those correlations according to Calo et al. (1973) and to a modification by Notter and Diaz (1992) described in the previous section. Notter and Diaz (1992) considered the effect of covariances in the sample of sires which in the current study arose in part from the existence of genetic groups in the model. However, the effect of this adjustment of the expectations differed between traits. The impact of accounting for the offdiagonal elements of C_{11} greatly reduced the sample variances of $\hat{w}_2$ in the sample for both traits. In this experiment, expectations of the correlation of WW EPDs or MILK EPDs across environments were expected to be larger than or similar to those of Calo et al. (1973) given the divergent selection that was attempted. However, in the definition of Q_{12} the $cov(u_1, \hat{g}_2)$ was smaller than the variance of g for WW EPD and somewhat larger in the case of MILK EPD. Since those values appeared in the estimation of reliability (see [16]), and therefore accuracy, this results offered a mathematical explanation of changes occurring in the

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expectations of the correlation between WW EPD and MILK EPD across environments compared to Calo et al. (1973).

Estimates of the genetic correlation of performances across environments are shown in Table 3.5. Both Calo et al. (1973) and the approximation used in this paper led to the same conclusion. In any case estimates of genetic correlations were reasonable close to 1. Thus, no apparent effect of genotype by production system (G x P) interactions that might compromise animals genetic performances across environments were clearly identified for either the net maternal and direct components of WW. Therefore, the genetic control of net maternal ability as well as weaning weight may not differ from one production system to another. Nevertheless, G x P interaction may be important for net maternal ability since the estimate of the genetic correlation is reasonably close to .80 (which in practical terms is normally considered to be the limit) and significant residual maternal grandsires effects were detected. G x P interaction is referred to because it is not possible to separate a component attributable to pure G x E interaction and the one attributable to genotype by genotype interaction, under either the experimental conditions or commercial crossbreeding. However, this result is in contradiction with Mahrt et al. (1990) who detected G x P affecting direct component of weaning weights in the first generation calves.

Conclusions

Polled Hereford sires MILK EPDs showed a positive relationship with the maternal performance of their crossbred daughters. Polled Hereford sires WW EPDs also showed a positive relationship with the weaning weight of their grandprogeny. Divergent selection restored the variances to a level existing in the original unselected Polled Hereford

population, but did not increase variances beyond that level. Covariances due to estimates of group solutions affected the expectations of correlations of EPD across environments. Although G x P interaction did not seem to affect either the net maternal trait or direct weaning weight, a possible interaction may be expected to occur affecting the net maternal trait.

TABLE 3.1 MEANS OF EXPECTED PROGENY DIFFERENCES (EPD; kg) AND ACCURACIES FOR SELECTED SIRE GROUPS FROM THE 1992 APHA SIRE SUMMARY[a]

Sire group	No of sires	YW EPD	Acc.[b]	MAT EPD	WW EPD	Acc.[b]	MILK EPD	Acc.[b]
H YW and H MAT	11	18.9	.88	7.7	12.2	.92	1.6	.88
H YW and L MAT	13	22.2	.82	2.6	13.1	.89	-3.9	.82
L YW and H MAT	12	5.3	.79	9.5	3.2	.87	7.9	.80
L YW and L MAT	11	5.3	.82	-2.1	2.9	.87	-3.5	.80
Overall mean	47	13.1	.83	4.5	8.0	.89	.48	.83

[a] H = high, L= low , YW= yearling weight, MAT= total maternal, WW= weaning weight and MILK= net maternal.

[b] Calculated following BIF (1986).

TABLE 3.2 DISTRIBUTION OF RECORDED AND USED CALF RECORDS
ACCORDING TO YEAR OF BIRTH OF CALF

Year	Born	Weaned	Records used[a]
1985	10	8	7
1986	58	46	44
1987	102	79	77
1988	125	112	109
1989	140	114	106
1990	139	133	83
Total	574	492	426

[a] After editing the file

TABLE 3.3 VARIANCE COMPONENTS (kg²) USED FOR PREDICTION
OF EPDs FROM EXPERIMENTAL DATA[a]

	σ^2_{sd}	σ^2_{sm}	σ^2_{a}	σ^2_{p}	σ^2_{e}
Among Polled Hereford sires[b]	12.4	27.3	-	-	-
Among Other sires[b]	29.5	-	-	-	-
Among Angus Cows	-	-	121.4	113.0	
Polled Hereford Progeny WW	-	-	-	-	321.0
Polled Hereford Grandprogeny WW	-	-	-	-	407.7

[a] σ^2_{sd} is the sire additive direct variances; σ^2_{sm} is the sire maternal additive variance; σ^2_{a} is the total Angus cow additive genetic variance; σ^2_{e} is the variance of the permanent environmental effects and σ^2_{e} is the error variances.
[b] Within sire groups.

TABLE 3.4 MEANS OF EXPECTED PROGENY DIFFERENCES (EPD; kg) AND ACCURACIES BY SELECTED SIRE GROUPS ESTIMATED FROM THE CURRENT DATA[a]

Sire group	No of sires	WW EPD	Acc.[b]	No of sires	MILK EPD	Acc.[b]
H YW and **H** MAT	11	7.4 ± .51	.73	11	5.9 ±1.1	.52
H YW and **L** MAT	13	0.1 ± .42	.83	11	0.0 ± 1.4	.65
L YW and **H** MAT	12	-3.9 ±.34	.73	11	6.1± .85	.50
L YW and **L** MAT	11	-3.5±.48	.73	10	2.7±1.1	.53
Overall mean	47	-0.1±.68	.76	43	3.7±.67	.55

[a] H = high, L= low , YW= yearling weight, MAT= total maternal, WW= weaning weight and MILK= net maternal.

[b] Correlation between true and predicted BV, as defined in the text.

TABLE 3.5 OBSERVED (r_O) AND EXPECTED VALUES (r_E) OF CORRELATION AMONG EPDs OF POLLED HEREFORD SIRES ACROSS ENVIRONMENTS AND THE CORRESPONDING ESTIMATES OF GENETIC CORRELATION ($\hat{r}_G$)

	r_O	$r_E{}^a$	$\hat{r}_G{}^a$	$r_E{}^b$	$\hat{r}_G{}^b$
MILK[c]	.58	.55	1.05	.71	.82
WW[c]	.64	.75	.85	.69	.93

[a] Following Calo et al. (1973).
[b] Account for covariances as developed in the text.
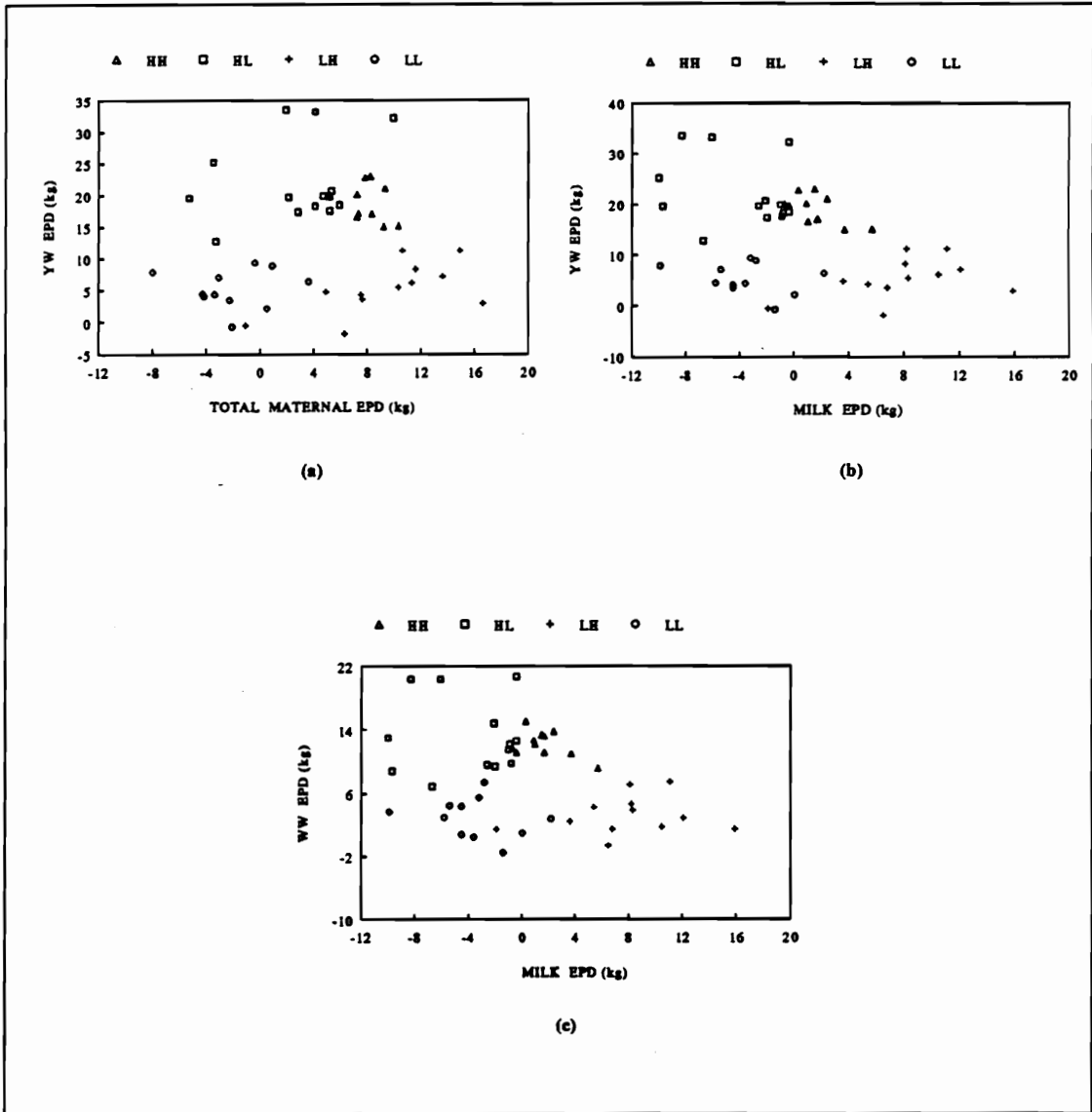[c] MILK= Maternal milk; [b] WW=Weaning weight

Figure 3.1 Total maternal EPD vs. yearling weight EPD (a), milk EPD vs. yearling Weight EPD (b) and milk EPD vs. weaning weight EPD (c) of divergently selected Polled Herefords sires. HH refers to High growth High maternal, HL to High growth Low maternal, LH to Low growth and High maternal and LL to Low growth Low maternal.

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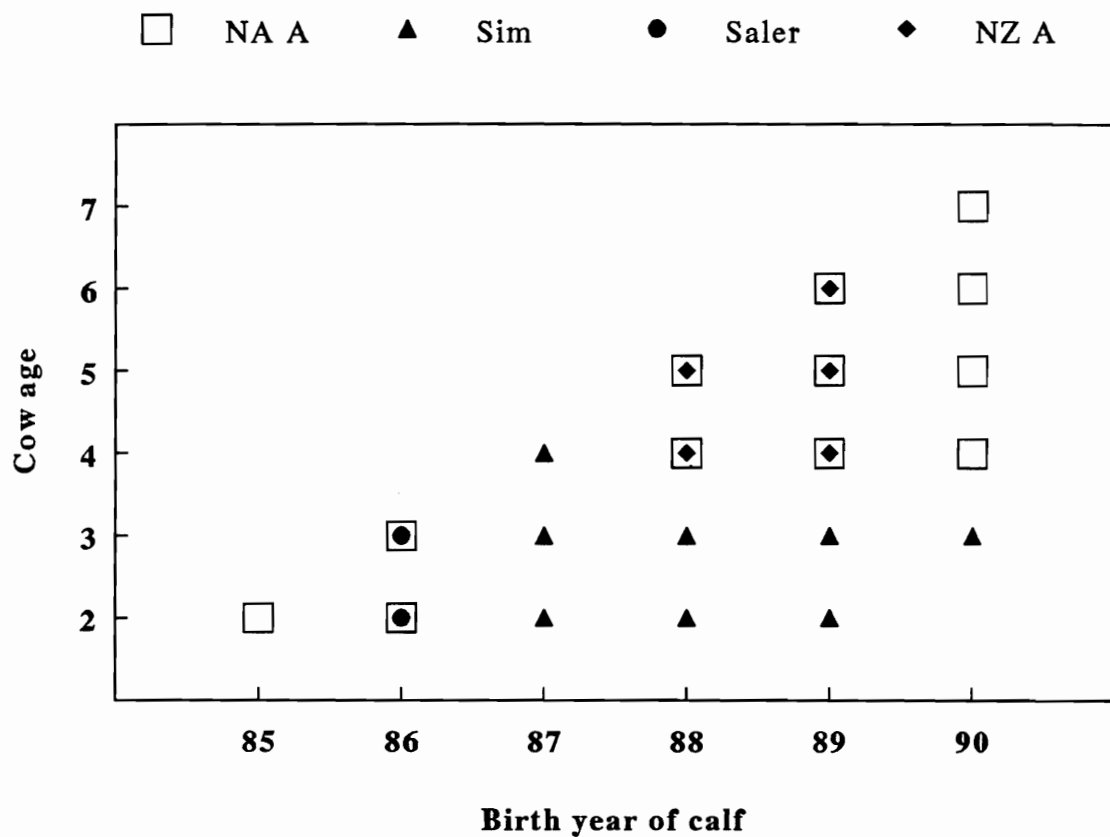
Figure 3.2 Structure of second generation calf data including distributions of birth year of calves, cow age and breed of sires. NA A stands for North American Angus, Sim for Simmental and NZ A for New Zealand Angus.

Figure 3.3 Structure of matings to produce first and second generation calves.

Figure 3.4 Average milk EPD (a) and weaning weight EPD (b) vs. actual calf weaning weights according to genetic groups of Polled Hereford sires: High growth High maternal (HH), High growth Low maternal (HL), Low growth and High maternal (LH) and Low growth Low maternal (LL).
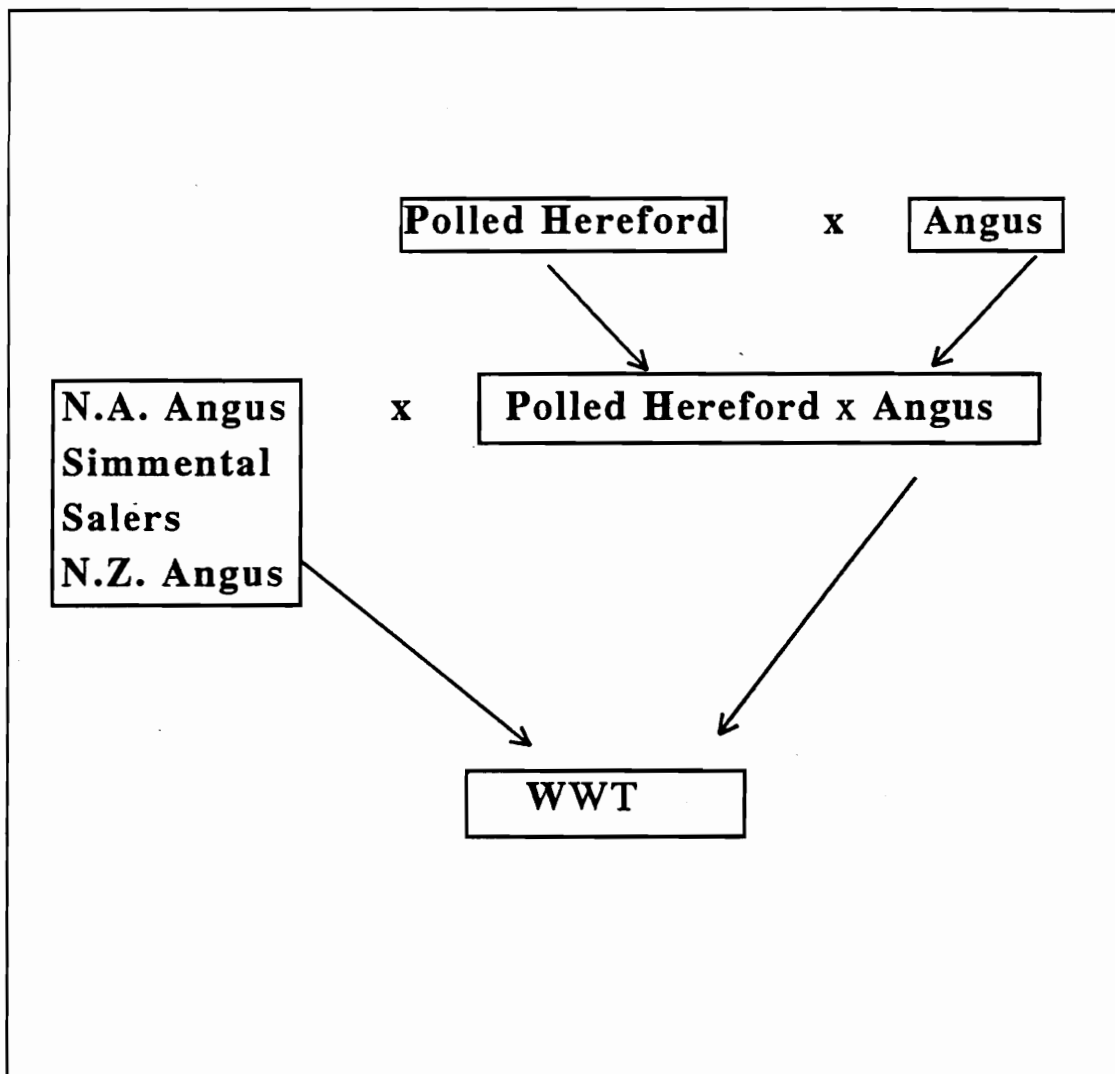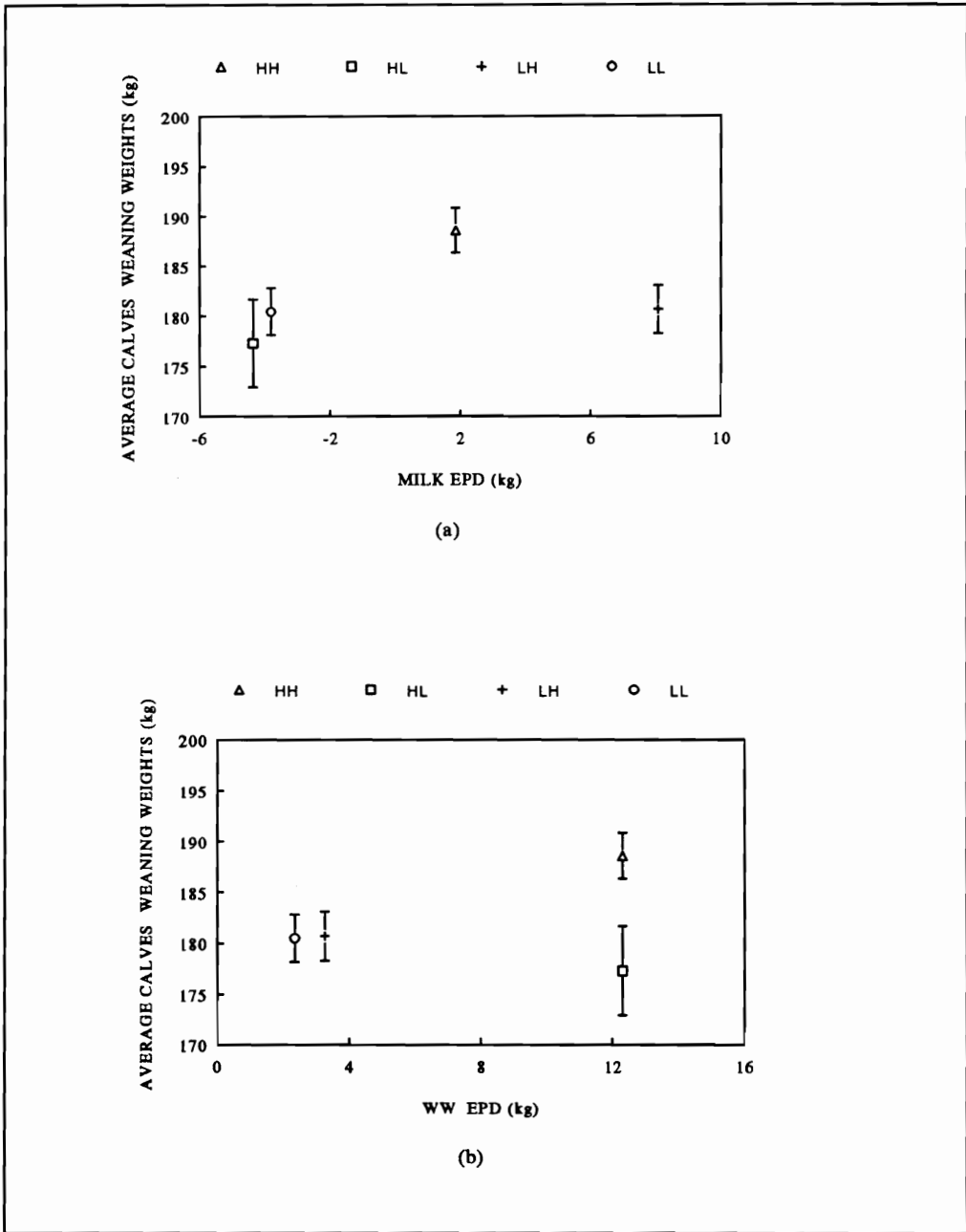
CHAPTER 4

RELATIONSHIP BETWEEN MILK EXPECTED PROGENY DIFFERENCES OF POLLED HEREFORD SIRES AND ACTUAL MILK PRODUCTION OF THEIR CROSSBRED DAUGHTERS

Introduction

Milk production is a potential component of the selection objective in beef cattle improvement. However genetic trends in breeds such as Angus and Polled Hereford (AAA, 1989; APHA, 1990) show that almost no genetic change has been realized for the maternal component of weaning weight in U.S. beef cattle populations. Because direct measures of milk production are not normally available for beef cattle, weaning weights are used as an indicator of the milk production of the dam. Weaning weights are assumed to be a joint expression of genes for growth of the calf and genes for milk production of the dam. Statistical procedures, based on the resemblance among relatives, have been used to separate these effects in beef cattle (Koch, 1972; Cantet et al., 1988).

In contrast, actual milk production of beef cows has been extensively measured under experimental conditions. Techniques to measure milk production have included weigh-suckle-weigh (Rutledge et al., 1971; Totusek et al., 1973; Beal et al., 1990), hand milking (Totusek et al., 1973) and machine milking (Gleddie and Berg, 1968; Beal et al., 1990). The objective of this study was to assess the relationship between the milk EPD of the sire and the actual milk production of crossbred daughters, using sires divergently selected for yearling weight (YW) and total maternal (MAT) EPD. The MAT EPD expresses

differences in weaning weight of bulls' daughters' calves due to the milking ability of bulls' daughters plus the growth potential of their daughters' calves.

Materials and Methods

Experimental Procedures

One hundred sixteen Polled Hereford x Angus cows were milked with milking machines at the Shenandoah Valley Agricultural Experiment Station, Steeles Tavern, VA. Polled Hereford sires of cows had been divergently selected according to their YW and MAT EPD to generate four sire groups. Sire group means for YW EPD, MAT and milk EPD and associated accuracies (BIF, 1986) from the 1990 Polled Hereford Sire Summary (APHA, 1990) are presented in Table 4.1. Forty-one sires were represented, with a range in milk EPD of -10 to 16 kg. Accuracy of milk EPD averaged .80. The pool within group SD in YW EPD, MAT and milk EPD were 4.1, 3.4 and 2.9 respectively, indicating that, significant differences among sires groups in EPD were achieved. Details of sire sampling and general cow-calf management were given by Mahrt et al.(1990). At milking, cows were 2 to 6 yr old and had calved between February 13 and April 24. Cows were an average of 77 d postpartum at milking (range: 44 to 114 d). Heifers began calving 2 wk before cows and thus averaged 19 d more postpartum. Cows that were 2 or 3 yr old nursed calves sired by Simmental bulls; older cows nursed calves sired by Angus bulls.

Time of separation of calves from their dams before milking has been presented as a critical effect in estimation of milk production (Williams et al., 1979). Thus, to minimize differences in separation time, cows were milked in six groups of 18 to 21 cows each. Cows were blocked by age, days postpartum and MAT EPD group and then randomly assigned within blocks to milking groups. During a 3-d period, one group of cows was milked in the morning and a second group was milked in the afternoon to yield a single

milk record for each cow at the end of the 3 d. Before separation, calves in each group were allowed to suckle and then were separated from their dams.

Cows were injected (i.v.) with 20 IU of oxytocin immediately before milking. Machine milking procedures have been described by Beal et al. (1990) and were determined to be most appropriate for comparing differences in milk production among individual cows based on a single estimate of milk production. Beal et al. (1990) estimated that the repeatability of individual milk production measures taken 3 d apart within a lactation by this method was .97 (P <.01). This repeatability suggests that a single milking provides an adequate measure of milk production at a specific point in lactation. Beal et al. (1990) also observed correlations of .84 to .92 between milk production measures taken at 66, 123 and 179 d postcalving within the same lactation. These correlations suggest that a single milking can provide a reasonable characterization of milk production levels throughout lactation.

Milk was weighed immediately after collection and samples were taken for subsequent analyses of milk fat, protein, lactose and total nonfat solids following methods described by Akers and Thompson (1987). Calves were weighed at birth and at weaning at an average age of 223 d. Birth weights were missed in two of the calves, therefore only 114 records were used in the analysis, representing 40 Polled Hereford sires.

Statistical Procedure

Two models were used in the analysis. The first one, as follows, tested differences among the four groups of sires:

$$Y_{ijkl} = \mu + mg_i + a_j + sg_k + \beta_1(d_{ijkl} - \overline{d}_j) + \beta_2 bw_{ijkl} + e_{ijkl} \qquad [1]$$

where

Y_{ijkl} is the observed 12-h milk production;

μ is a constant common to all observations;

mg_i is the fixed effect of the ith milking group (i =1,...3);

a_j is the fixed effect of the jth cow age group (j =1,...4);

sg_k is the fixed effect of the kth sire group (k =1,...4);

β_1 is the partial regression coefficient of Y on calving date (d) as a deviation from mean

   $\overline{d}$. of the jth cow age group (d_j);

β_2 is the partial regression coefficient of Y on calf birth weight (bw);

e_{ijkl} is a residual random error associated with the lth cow;

Calving date was expressed in julian days, and, since milking took place within three days is an indication of day of lactation. Because of confounding of age of cow and calving date due to early breeding of heifers, milk production was adjusted to the mean calving date of the jth age of cow group. Also, because there were only six 6-yr-old cows, these were combined with 5-yr-old cows for analysis. Orthogonal linear contrasts were used to compare high versus low MAT EPD sire groups, high versus low YW EPD sire groups and interaction of YW EPD and MAT EPD sire groups.

Model 2 replaced sire group effects with the regression of actual milk production on sire milk EPD to quantify the relationship between these variables. Model 2 thus, was as follows:

$$Y_{ijl} = \mu + mg_i + a_j + \beta_1(d_{ijl} - \overline{d}_j) + \beta_2 b_{ijl} + \beta_3 \, milk \, epd_{ijl} + e_{ijl} \qquad [2]$$

where,

β_3 is the partial regression coefficient of Y on sire MILK EPD.

Interactions of age of cow with milk EPD and age of cow with calving date and quadratic effects of calving date and milk EPD were also tested but were not significant and were removed from the model (2). Additional sire effects not accounted for by regression on milk EPD were also tested. A sequential F-test was used to test sire effects as the additional reduction of error sum of squares due to addition of a sire of cow effect to Model 2. Furthermore, residual correlations of dams' milk production, calves' weaning weights and milk EPD of the sire of dam were estimated after adjustment for all effects in model [2] except milk EPD. All statistical analysis were performed using the GLM procedure of SAS (1985).

Results and Discussion

Means for 12-h milk production and milk composition are presented in Table 4.2. The average milk production, as well as the average composition, is within the range presented by other authors for different suckler breeds (e.g., Gleddie and Berg, 1968; Rutledge et al., 1971; Totusek et al., 1973). Milk composition was not affected by any design variable, but all effects in Model [2] except milking group were significant for milk production (Table 4.3).

Calving date was positively related to milk production (Table 4.3). Thus, cows that calved later were fewer days postpartum at milking and produced more milk. Significant positive effects of calf's birth weight on milk production were found (Table 4.3). Similar results were also reported by Rutledge et al. (1971), Richardson et al. (1977) and Butson and

Berg (1984). Whether this relationship is due to an increased calf demand for milk that stimulates lactation or to a higher capacity to consume available milk is not clear. Mezzadra et al. (1989) reported differences in calf milk consumption, calf maximum intake, and persistency of consumption among different genotypes. They found that the highest consumption was associated with a higher maintained weight, but it is difficult to clarify causal relationships. In the current study, effects of calf's sire breed and calf's sire within sire's breed did not affect dam's milk production. However, in our study , 2- and 3-yr-old cows were mated to Simmental bulls and older cows had been mated to Angus bulls. Thus, the youngest cows suckled calves with an expected higher growth potential but similar birth weights (due to cow age effect on birth weight). Selection of sires of cows ensured near genetic independence between milk production of cows and birth weight of calves; the correlation between milk EPD and birth weight EPD for sires of cows was only -.12 ($P < .21$). Thus, sires with a higher birth weight EPD were not expected to sire daughters that were genetically capable of producing both heavier calves and more milk. Therefore, the basis for the relationship between calf birth weight and dam milk production seemed to be environmental rather than genetic.

Least-square means for milk production (Table 4.4) differed only between high and low maternal sire groups ($P < .03$); neither growth group ($P < .74$) nor interaction ($P < .17$) effects were significant.

Milk EPDs of sires of cows were positively and linearly related to daughters' actual milk production. Quadratic effects of milk EPD were not significant, indicating that genetic effects on milk production were uniformly expressed over the range of milk levels tested. The magnitude of the linear partial regression coefficient of cow milk on sire milk EPD is

difficult to interpret. First, milk EPDs are estimated based on an indicator trait (adjusted weaning weight), so milk EPD can only predict which bull would be expected to sire daughters that are capable of producing heavier calves because of their maternal ability. These differences are presumed to reflect differences in milking ability. Second, the 12-h milk production measured in this study may not be perfectly representative of the milk production of a complete lactation. However, reported genetic correlations between a single milk sample and total milk production have been found to range from .8 to 1 (Dillard et al., 1978; Danell, 1982). Over the range of sire milk EPD sampled (-10 to 16 kg), the difference in milk production predicted by Model [2] between the daughters of bulls with the highest and the lowest milk EPD was approximately 1 kg of milk, which was equivalent to 27% of the mean of 12-h milk production, or an increase in milk production of about 1% of the mean per kg milk EPD.

Marston et al. (1990) regressed estimated 205-d milk production of Angus and Simmental cows on the cows' milk EPD and obtained regression coefficients of 69.9 and 70.7 kg of 205-d milk/kg of milk EPD, respectively. If secretion of milk and effects of milk EPD are uniform over the lactation, a regression of 205-d milk on milk EPD of 70 kg/kg would correspond to a regression of 12-h milk on cow milk EPD of .170 kg/kg. Also, because the milk EPD of a cow equals one half her milk breeding value the regression coefficient of cow milk production on cow milk breeding value from Marston et al. (1990) would have to be further halved to .085 kg/kg to be comparable to the regression coefficient of .038 in our study. Yet the value reported by Marston et al. (1990) is still more than twice as large as our value. This result might be expected if a lack of uniformity of milk production and of the regression coefficient across lactation were involved.

After fitting milk EPD, no residual sire of cow effects remained (P < .22). Published sire milk EPD are predicted from data on purebred animals. Heterosis effects on milk production in crossbred cows have been reported (Cundiff et al. 1974; Notter et al. 1978). However, the lack of individual sire of cow effects in addition to effects of milk EPD indicates that the purebred sires' milk EPD were adequate to predict the milk production of their crossbred daughters and suggests that effects of specific combining ability of sires were not important in these matings. Alternatively, average environmental differences between the purebred herds in which EPD were derived and the commercial production environment of the study were not associated with residual sire effects beyond those predicted by milk EPD. In dairy cattle, Ruvuna and McDaniel (1983) regressed milk production of crossbred daughters on milk predicted differences of Holstein and Brown Swiss sires. They concluded that regression coefficient were within the expected range of values, with small discrepancies attributable to a sampling effect. Persaud et al. (1990) found that the regression of sire transmitting ability on daughters' milk production was very close to the expected value in high-yielding dairy herds. They pointed out that expression of the transmitting ability of progeny tested dairy bulls may be affected by the level of production of the herds in which those bulls are used. Nevertheless, the regression coefficient was lower for cows than for heifers. In the current study, the regression of actual milk production on sires' milk EPD did not vary with age of cow as indicated by the fact that the interaction of milk EPD and age of cow was not significant, and therefore was removed from Model [2].

The estimated residual correlation between milk production and sire milk EPD was .26 (P < .01). The residual correlation between weaning weight and milk production was .64 (P < .0001) and the corresponding correlation of residual weaning weight and milk EPD was

.20 (P <.05). Interrelationships among the milk EPD of a sire (EPD^M_s), actual 12-h milk production of his daughters (P^M_d) and weaning weight of his daughters' calves (P^W_c) are shown in figure 1. Given this diagram, the observed correlation of .26 between EPD^M_s and P^M_d has expectation $.5a_m h_m$ where a_m is the correlation between EPD^M_s and the true breeding value (BV) of the sire for milk (G^M_s) and h_m is the square root of heritability for milk. Notice that milk EPD measures a net maternal effect and may or may not be exactly the same trait as milk production of the cow (P^M_d). However, in Figure 1, the net maternal milk effect is shown as equivalent to the milk production of the cow (P^M_d). This assumption may be an oversimplification but will be retained during this discussion. Given this assumption, if milk has a genetic correlation of 1 with 12-h milk production, heritability of 12-h production is h^2_m. For sires in this study, a_m was obtained transforming Beef Improvement Federation (BIF) accuracy (Benyshek et al., 1988), reported in the Polled Hereford Sire Summary, into the correlation between the predicted (EPD^M_s) and the true breeding value of the individual (G^M_s) (Mahrt et al., 1990) and averaged .98. The observed correlation of .26 would thus equate to an estimate of h^2_m of .28, which is reasonably consistent with previous reports of heritabilities of milk production in dairy cows (Maijala and Hanna, 1974; Wade and Van Vleck, 1989). Dillard et al. (1978), however, reported a heritability of milk production of .44 in Hereford cows. Our estimate of h^2_m is also fairly similar to (Koch, 1972; Cantet et al., 1988; Trus and Wilton, 1988; APHA, 1990) or higher than (Quaas et al., 1985; Bertrand and Benyshek, 1987; Wright et al., 1987 Garrick et al. 1989) published estimates of heritability of net maternal weaning weight which range from .11 to .30. Our calculated correlations may also not be appropriate to a random sample of sires; divergent selection practiced on sire EPD could have increased observed correlations somewhat relative to those expected for unselected sires.

The observed correlation of .20 between $EPD^M{}_s$ and $P^W{}_c$ has an expectation of $.5a_m h_m m$ which is also equal to the product of the correlations of $EPD^M{}_s$ with $P^M{}_d$ and of $P^M{}_d$ with $P^W{}_c$. This product has a value of .17, which is close to the observed value. The expectation holds as long as there are no any additional environmental or maternal genetic effects involved. Although estimates of correlation between direct and maternal effects on weaning weight are generally reported to be negative (Koch, 1972; Cantet et al., 1988; Garrick et al., 1989; APHA, 1990; Meyer et al., 1991) there are estimates that are positive estimates or very close to 0 (Foulley and Menissier, 1974; Quaas et al., 1985; Wright et al., 1987; Meyer et al. 1991). In this study the observed correlation between milk and weaning weight EPD in selected sire of cows ($r^G{}_s$) was almost 0 (-.07; P < .43).

The 95% confidence limits of the correlation of .20 between $EPD^M{}_s$ and $P^W{}_c$ were estimated by using a Fisher z transformation (Snedecor and Cochran, 1967). The width of the confidence interval (.06 to .44) indicates that the estimate of the correlation is highly variable due to small sample size. Thus, although the effect of sampling is considerable in this study and makes it difficult to draw precise inferences about population parameters, the results provide a reasonably consistent picture of relationship among milk EPD, actual milk production and calf weights. Likewise, it is suggested that actual milk production may be an important component of the net maternal trait and can be improved by selection on milk EPD.

Implications

Milk expected progeny differences of sires do predict differences in actual milk production of their daughters. Thus, milk expected progeny differences can be used as a selection

criterion to change milk production as a breeding objective in improvement program in beef herds. Also, milk expected progeny differences of Polled Hereford sires derived from purebred records seem to be adequately expressed in crossbred daughters.

TABLE 4.1. MEANS OF EXPECTED PROGENY DIFFERENCES (EPD;kg) AND ACCURACIES (ACC) BY SIRE GROUP[a]

Group of sires	No. of sires	No. of cows	YW EPD		MAT EPD	MILK EPD	
			Mean	Acc[b]	Means[c]	Means	Acc[b]
High YW and High MAT	11	27	13.6	.85	8.2	3.1	.86
High YW and Low MAT	11	27	17.2	.81	.1	-5.2	.81
Low YW and High MAT	9	30	2.8	.71	9.4	8.3	.77
Low YW and Low MAT	10	32	.6	.78	-3.8	-3.9	.77
Overall means	41	116	8.1	.79	3.3	.5	.80

[a] YW = yearling weight, MAT = total maternal and MILK = net maternal EPD.
[b] BIF, 1986.
[c] Accuracies were not calculated for MAT EPD (APHA, 1990).

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TABLE 4.2. ARITHMETIC MEANS AND STANDARD DEVIATION (SD) OF
12-h MILK YIELD (kg) AND COMPOSITION[a]

Traits	Means	SD
Milk yield	3.7	1.3
% protein	3.2	.2
% fat	3.3	1.0
% lactose	4.8	.2
% solid, not fat	8.7	.3

[a] 116 observations

TABLE 4.3.   MEAN SQUARES FOR MODEL [1] AND [2]

Source	df	Model 1	df	Model 2
Milking group	5	1.198	5	1.211
Age of cow	3	2.559***	3	23.060***
Calving date	1	8.310***	1	12.444*** $(.023 \pm .016$ kg/kg$)$[a]
Birth weight	1	3.896***	1	4.702*** $(.050 \pm .020$ kg/d$)$[a]
Group of sire	3	1.715	-	_ [b]
Milk EPD	-	_ [b]		5.975** $(.038 \pm .014$ kg/kg$)$[a]
Remainder	100	.790	102	.766

[a] Regression coefficient and standard error.

[b] Effect not included in the model.

* $P < .05$
** $P < .01$
*** $P < .001$

TABLE 4.4   LEAST-SQUARES MEANS AND STANDARD ERRORS FOR MILK PRODUCTION BY SIRE GROUP[a]

Sires Group[b]	N	Means SE
High YW and High MAT	27	$3.72 \pm .18$
High YW and Low MAT	27	$3.11 \pm .17$
Low YW and High MAT	29	$3.42 \pm .18$
Low YW and Low MAT	31	$3.29 \pm .17$

[a] From model 1.

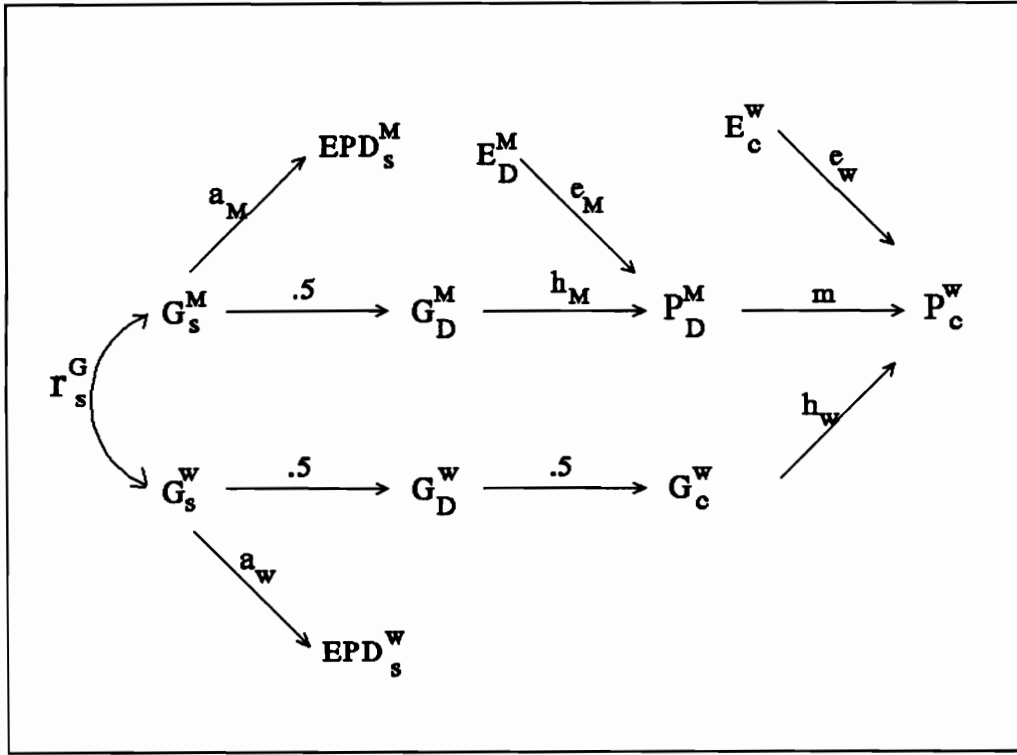[b] YW= yearling weight and MAT = total maternal.

Figure 4.1 Path coefficient diagram showing relationships among EPDs, breeding values (G), environmental effects (E) and phenotypes (P) for milk (M) and weight (W) traits in sire (s) dam (d) and calf.

OVERALL CONCLUSIONS

Correlations of predicted BV across environments have been used to estimate genetic correlations of performance across environments. Selection biases the correlation coefficient but not the regression coefficient so long as selection is not practiced on the dependent variable.

Selection is almost always involved in the movement of animals across environments, and that selection usually involves multiple traits. In this study, direct and maternal predicted breeding values were assumed to be the selection criteria. Directional, divergent, and random selection were considered to establish the effect of the selection imposed on both traits on the correlation between direct and maternal breeding values across environments. Selection proved to affect the expectation of those correlations. However, adjustments based on univariate selection theory seemed to yield corrections that were approximately correct , at least for the case of modest negative genetic correlation between direct and maternal breeding values and selection with independent culling levels. Nevertheless, the validity of this adjustment may be restricted to the cases where genetic correlations are low or moderate and selections strategies are similar to the ones followed in this study. Divergent selection led consistently to an agreement between observed and expected correlations. In terms of experimental designs, if the sample of sires is small use of sires with high accuracies and divergent selection seemed to create the most appropriate design in order to detect departures of observed correlations from expectations.

An experiment involving Polled Hereford sires divergently selected based on growth and total maternal predicted BV was used to evaluate the existence of genotype by production system (G x P) interaction for direct and maternal components of weaning weights.

Considerations of the design which led to a specific model of evaluation were examined. A positive relationship between sires MILK EPD, as an estimate of net maternal ability, with the maternal performance of their crossbred daughters was observed. A positive relationship was also observed between sire WW EPD and their grandprogeny weaning weights. Residual sire effects were detected after fitting WW and MILK EPD (direct and net maternal effects, respectively) in the model, indicating possible effects of G x P interaction.

Polled Hereford sires were reevaluated under the experimental conditions using a model which included genetic group effects and within groups corresponding to the four groups of selected sires, and within-groups sires effects. An approximation was developed to account for the variation among groups in order to estimate accuracies of predictions. While this approximation increased the accuracy of WW EPD (direct effect on weaning weight), it reduced the accuracies of prediction of MILK EPD. Poor estimation of group effects for maternal effect, and very little variation among maternal groups relative to the within-groups sire variance caused the decrease of MILK EPD accuracies. Covariances among predicted BV in the sample of sires had an impact on the expectation of correlations of EPD across environments. Properly interpreted, those correlations led to several conclusions. No apparent effect of G x P interaction existed for the direct component of weaning weight, however a possible interaction affecting the net maternal trait may be expected. Reference has been done to production system since it is not possible to separate environmental conditions from genotype by genotype interactions.

A relationship was observed between sires MILK EPDs and actual MILK production of crossbred daughters. Correlation between milk production and sires MILK EPD was .26,

correlation between calf weaning weight and dam milk production was .64 and correlation between weaning weight and sire MILK EPD was .20. All of them seemed to agree with their theoretical expectations. These results indicate that MILK EPDs are a valid criterion to improve maternal ability.

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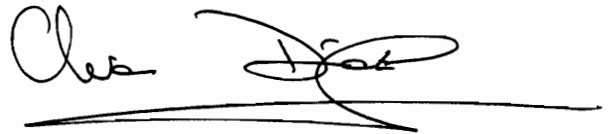
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