

## SELECTION BIAS ON ANIMAL MODEL EVALUATION

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### SUMMARY

A short overview of the selection problem and its latent effects on animal genetic evaluation, as well potential ways of accounting for selection with their possible limitations were presented. Clearly there is not a general statistical solution for the selection problem even though the understanding about genetic and statistical effects of selection has increased.

**Keywords:** Selection, bias, overview, genetic evaluation

### INTRODUCTION

There are many types of selection forces that influence the data collected from commercial livestock operations. Some examples are non-random selection and mating of breeding animals (parental selection), sequential selection, culling of animals before records are official, preferential treatment, selective reporting, and misclassification or manipulation of contemporary groups. Parental selection is the primary process by which genetic improvement can be made in livestock populations, and consequently it is invariably present in animal breeding work.

Selection of any type may cause problems for estimating genetic parameters and breeding values and may require specific statistical treatment. Data commonly available to animal breeders from the field are invariably provided by herds in which artificial selection has been practised for a long time. Consequently, the usual assumption of random sampling invoked for estimation and prediction is no longer valid (Henderson 1984). Inferences based on such data may be misleading (Fernando and Gianola 1990). A basic challenge still lies in questioning the supremacy of current methods such as Best Linear Unbiased Prediction (BLUP) via Mixed Model Equations (HMME) (Henderson 1963) and Restricted Maximum Likelihood (REML) (Patterson and Thompson 1971) when selection is known to have occurred (Foulley 1990). Bayesian analysis of selected data (e.g. Sorensen *et al.* 1994; Van Tassell *et al.* 1995) and Bayesian inferences seem to be able to handle different types of selection. The Gibbs sampler, as a tool for numerical integration, allows broad application of Bayesian analyses in animal breeding (Wang *et al.* 1994a; Wang *et al.* 1994b; Rodriguez *et al.* 1996). Non least squares methods have also been suggested as an alternative to handle selected data (e.g. Gianola 1990; Simianer 1991).

The objectives of this paper were to review selection problems and their possible effects on genetic evaluation, and tackle potential ways to appropriately account for selection under a statistical point of view, assuming an infinitesimal additive genetic model.

## SELECTION PROBLEMS

Henderson (1984) gave an overview of the possible statistical consequences of genetic selection of animals. An assumption with HMME is that the expected value of every element of  $a$  (vector of breeding values) is 0. If animals result from a long-term selection program, then the expected value of breeding values in later generations should be different from 0. Further, for the records of selected individuals, all variances are reduced and non-zero covariances are generated between previously uncorrelated effects, such as between  $a$  and  $e$  (residual effects).

An important consequence of culling before an animal leaves an observation or of selective reporting is the change of the null expectation of the Mendelian sampling effects which is a basic assumption for the nice properties of individual animal models. The effect of preferential treatment, selective reporting, and data manipulation have been discussed (e.g. Mallinckrodt *et al.* 1993; Tierney and Schaeffer, 1994; Weigel *et al.* 1994) and shown to be important for data from livestock populations.

## PREDICTION OF BREEDING VALUES UNDER SELECTION

In 1975 Henderson proposed methods based on the results of Pearson (1903) assuming multivariate normality. Henderson (1975) used the matrix  $L$  to describe the selection process, and assumed under repeated sampling that this matrix is fixed, and that only samples that can use this  $L$  would be kept. The real nature of selection processes, however, would suggest that  $L$  is random (Thompson 1979; Gianola *et al.* 1989).

Using Pearson's selection model, assuming known dispersion parameters and giving conditions for ignoring selection, Gianola *et al.* (1988) concluded that selection can be ignored when the distribution of the culling variate  $w$  and the conditional distribution of  $w$  given  $a$  and  $y$  (observation vector) do not depend on unknowns being estimated or predicted. When selection is based on linear or nonlinear functions of the data, a sufficient condition for "ignorability" of selection is that  $L'X=0$  or equivalently that the culling variate does not depend on  $\beta$  or is within levels of fixed effects. Gianola *et al.* (1988) also showed that when selection is based on functions of  $a$  and  $e$  the selection process can sometimes be ignored and to yield more genetic progress even though the predictors obtained are biased.

Several researchers have considered the theoretical effects of selection on prediction of breeding values or estimation of variance components under a likelihood or Bayesian point of view (e.g. Gianola and Fernando 1986; Goffinet 1987; Gianola *et al.* 1989; Fernando and Gianola 1990; Im *et al.* 1989; Sorensen 1996). In the likelihood approach, if the history of the selection process is contained in the data, then the likelihood function has the same mathematical form with or without selection and inferences could be made ignoring selection. This is true for any distribution, any likelihood based method of inference, for linear or nonlinear estimators and for non translation invariant (regarding to fixed effects) selection criteria.

HMME could be derived by maximization of the joint posterior distribution of  $\beta$  and  $a$  (taking a flat prior for  $\beta$ ) with respect to  $\beta$  and  $a$  (Henderson *et al.* 1959). The modifications needed to

the HMME for obtaining BLUP when selection is not based on translation invariant functions, even when all data that led to the current population are available (Henderson 1975), seem to contradict the likelihood principle (Goddard 1990). However Goffinet (1983) and Fernando and Gianola (1990) argued that BLUP of  $a$  ( $\hat{a} = C'V^{-1}(y - X\beta)$ ) under normality is identical to  $E(a | w, X, Z, A, R, \sigma_e^2)$ , where  $w$  is any set of  $n-r$  linearly independent translation invariant functions of  $y$  and  $n$  and  $r$  are the order and rank of  $y$  and  $X$  respectively. If selection decisions are based on any function of a subset of  $w$ , then the information used to calculate the posterior conditional mean contains the whole history of the selection process, and BLUP ignoring selection will be unbiased. One can express  $y$  as  $y = X\beta + w$ . If selection decisions are based on a subset of  $y$ , the posterior density constructed using only  $w$  will not in general be the same as when selection takes place, and selection has to be described when the likelihood function is defined. With the Bayesian approach,  $E(a | y, X, Z, A, R, \sigma_e^2)$  can be calculated even when  $\beta$  is unknown. The uncertainty about  $\beta$  is expressed in the form of a prior density. If selection is based on  $y$  or on a subset of  $y$ , then  $E(a | y, X, Z, A, R, \sigma_e^2)$  is calculated ignoring selection. When the prior density of  $\beta$  is taken to be constant,  $E(a | y, X, Z, A, R, \sigma_e^2) = E(a | w, X, Z, A, R, \sigma_e^2)$  and the previous discussion holds.

## ACCOUNTING FOR SELECTION IN GENETIC EVALUATIONS

**Parental selection.** To account for parental selection the following ideal conditions should be available: a) complete pedigrees back to a base population of non selected, non related, and non inbred animals (Sorensen and Kennedy 1984; Kennedy and Sorensen 1990); and b) data on all candidates for selection (Henderson 1975; Goffinet 1983); or c) knowledge of the selection process and distribution of selection criteria (Henderson 1975; Im *et al.* 1989; Fernando and Gianola 1990). The first two conditions guarantee that likelihood based inferences not accounting for selection are the same as those obtained considering selection regardless of translation invariance of the selection criterion or its form (linear or nonlinear) (Gianola and Fernando 1986; Im *et al.* 1989 and Fernando and Gianola 1990). Even if the first and second conditions are met, in general, an additional condition of translation invariance of selection criteria must be verified for HMME to yield BLUE and BLUP, otherwise unbiasedness does not hold. The third condition is generally needed when data are missing. Im *et al.* (1989) showed that if data are missing at random, inferences could be made using the likelihood function without accounting for the missing data process. Otherwise, the missing data process has to be described and included in the likelihood function.

Schenkel and Schaeffer (1997) used simulation to generate a phenotypically selected population with 7.5% and 15% randomly missing pedigree information. Strongly biased estimates of additive genetic and residual variances were obtained with both Bayesian and REML procedures when fixed effects other than an overall mean were present. Also the predicted breeding values by HMME using the REML estimates of variance components, and by Bayesian procedure showed increased mean square error and reduced accuracy as selection accumulated. Assuming a proper informative prior for the fixed effects in the Bayesian procedure reduced the bias of the variance component estimates but they were still different from the values of the base population. The importance of the relationship matrix, when it is complete and correct, in accounting for

selection effects and assortative mating in genetic evaluations has been shown theoretically and through simulation (Pollak and Quaas 1981a; Sorensen and Kennedy 1984; Kennedy *et al.* 1988). Kennedy and Sorensen (1990) showed that the relationship matrix accounts for decline in variance due to genetic drift and circumvents (if records of all animals are available (van der Werf and de Boer 1990) ) further reduction in variance due to gametic disequilibrium. They also showed that after repeated cycles of selection and mating, the equality  $VAR(a) = A\sigma_a^2$ , where  $\sigma_a^2$  the additive genetic variance before selection, still holds, assuming multivariate normality.

Woolliams and Thompson (1994) showed that if all genetic relationships to an unselected, unrelated base population are available, then breeding values of all animals can be expressed as the sum of their own Mendelian sampling (MS) effect plus the MS effects of their ancestors going back to the base animals, whose expected breeding values are equal to MS effects. Therefore under an infinitesimal model the change in expected value of  $a$  is accommodated through a complete and correct  $A$  matrix. However with field data  $A$  is barely complete or fully correct. Long *et al.* (1990) showed that with 20% random errors in the pedigree file the advantage of individual animal model (BLUP) over phenotypic selection was halved to 3.8 and 14.6% for  $h^2=0.53$  and 0.13, respectively, even though the swine population analyzed was randomly selected. Mallinckrodt *et al.* (1993) studied the impact of data falsification and selective reporting on estimation of genetic parameters in beef cattle using REML and concluded that reliability of estimates could be improved by analyzing representative data subsets known to be completely and accurately reported.

Genetic groups (GG) have been used to account for missing pedigree information in genetic evaluation (Westell 1988). Quaas (1988) noted that complex definitions of GG could be confounded with other fixed effects in the model. Pieramati and Van Vleck (1993) through simulation have shown that the use of GG to account for prior selection leads to underestimates of additive genetic variance compared to an unselected base population, and raised the question of which variance to use on genetic evaluation when GG are included. In practice, the use of fixed GG implies non translation invariant selection.

The best method for evaluation of selected animals depends not only on the selection process but also on the information available, and on criterion for judging alternative methods. Generally two kinds of information are available: a) the records of animals and their relatives (a posteriori information), and b) knowledge about the specific population from which an animal comes (a priori information). Assume an animal model represented by  $y = X\beta + Za + e$  (1), where  $y$  is a vector of phenotypic values on individuals,  $X$  and  $Z$  are incidence matrices,  $\beta$  is a vector of fixed effects,  $a$  is a vector of additive genetic effects multivariate normally distributed ( $s, A\sigma_a^2$ ) and  $e$  is a vector of residual effects multivariate normally distributed ( $0, R\sigma_e^2$ ). In absence of selection,  $E(y) = X\beta$  ( $s$  is a null vector) and  $var(y) = V = ZAZ'\sigma_a^2 + R\sigma_e^2$ , assuming  $a$  and  $e$  independent.  $R\sigma_e^2$  is a known variance-covariance matrix of residual effects, and  $\sigma_a^2$  is the known genetic variance in the base population. Now assume that due to genetic selection  $s$  is not null while the other assumptions still hold. If one derives BLUE/ BLUP under these conditions maximizing the function  $F = m'Am + L'VL - m'AZ'L - L'ZAm + (L'X - K')\theta_1 + (L'Z - m')\theta_2$  to

obtain the set of equations to predict  $k'\beta + m'a$  by  $L'y$ , where  $\theta_i$  are LaGrange multipliers, the final equations are Generalized Least Squares (GLS) with  $a$  considered as fixed. GLS in this case gives solutions equivalent to Weighted Least Squares (WLS) because  $Z$  is included in  $V$ . Therefore, no use is made of a priori information about genetic variances. However, if the criterion for choosing the best estimator/predictor is minimum mean square error, then a non least square estimator/predictor could be preferred, such as ridge type estimators. Under a Bayesian setting, the use of prior information implies solutions with smaller risk under a quadratic loss function and inadmissibility of the previous estimators/predictors (Gianola and Fernando 1986). Gianola and Fernando (1986) stated that the statistical property relevant to genetic improvement is the correlation between predictor and predictand, but under selection is often difficult to calculate it using analytical means. For this situation, simulation studies have been used.

Fries and Schenkel (1993) proposed a modification of HMME to account that  $E(a)$  is no longer null without relying on a complete  $A$  matrix to obtain unbiased estimates of fixed effects. The new equations were called Lush's Mixed Model Equations (LMME) and for an individual animal

$$\text{model are: } \begin{bmatrix} X'R^{-1}X & X'R^{-1}I(I'R^{-1}I)^{-1}(I'R^{-1}I+A^{-1}) \\ I'R^{-1}X & (I'R^{-1}I+A^{-1}) \end{bmatrix} \begin{bmatrix} \beta^L \\ a^L \end{bmatrix} = \begin{bmatrix} X'R^{-1}Y \\ I'R^{-1}Y \end{bmatrix}. \text{ They showed that LMME}$$

yields unbiased estimators of fixed effects and consistent predictors of random effects regardless if  $A$  is complete or not, even when  $E(a)$  is different from  $0$ . Brito (1992) argued that an increase of 5% in selection response in beef cattle could be achieved by LMME over HMME. Meanwhile computational difficulties arise because LMME are not symmetric and have rank deficiencies equal to GLS.

Torres Jr. and Braccini Neto (1995) used a sire model to compare LMME to Regressed Least Square (RLS), HMME without genetic groups (MMw), and HMME with genetic groups (MMg). Offspring of related sires were simulated and distributed into two different environments by two different methods. The first was random distribution of progeny, and the second was by association of sire genetic values with environmental values. Relationships among sires were used or not used. Genetic groups were formed on the basis of the association of sires with the environment. For all methods the estimators of environmental effects were empirically unbiased except for MMw when sires were associated with one environment. In this case the estimators were biased regardless of the use of relationships among sires. When sires were not associated with environments, the correlation between the true and predicted genetic values of the sires using MMw and LMME were not different, but were better than the other methods. When an association was present, then MMg was better than LMME which was better than the other methods. With field data LMME will probably be better because a perfect definition of genetic groups may not be possible in that situation.

Non least squares estimators may be an alternative to least squares estimators under selection. Let the class of estimators include biased estimators, and consider the mean squared errors (MSE)

of estimating the parameter  $\theta$ :  $MSE = E[(\hat{\theta} - \theta)'(\hat{\theta} - \theta)] = \text{Var}(\hat{\theta}) + [\text{bias}(\hat{\theta})]^2$ , this is a different criterion function than the one that leads to the least squares estimator. Let  $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_p$  be the ordered eigenvalues of  $W'W$  ( $W = [X \ Z]$ ). Hoerl and Kennard (1970) have noticed that, for  $\hat{\theta}$  = least square estimate,  $MSE = E[(\hat{\theta} - \theta)'(\hat{\theta} - \theta)] = \sigma_e^2 \text{trace}(W'W)^{-1} = \sigma_e^2 \sum_{i=1}^p \lambda_i^{-1}$ . But  $E[(\hat{\theta} - \theta)'(\hat{\theta} - \theta)] = E(\hat{\theta}'\hat{\theta}) - \theta'\theta$ , so,  $E(\hat{\theta}'\hat{\theta}) = \theta'\theta + \sigma_e^2 \sum_{i=1}^p \lambda_i^{-1} \geq \theta'\theta + \sigma_e^2 \lambda_p^{-1}$ . Thus even though  $\hat{\theta}$  is unbiased for  $\theta$ ,  $\hat{\theta}'\hat{\theta}$  is not unbiased for  $\theta'\theta$  and if the smallest eigenvalue  $\lambda_p$  is near zero, then on average  $\hat{\theta}'\hat{\theta}$  will be much too great. When  $\lambda_p$  is small and MSE is of interest, substantial gain over least squares is possible. These alternative estimators have the common characteristic that they will give an estimate that is more shrunk than least squares, so these techniques shrink the least squares estimates normally toward zero (e.g. Ridge and James-Stein estimators). Gianola (1990) presented theoretical arguments and empirical evidence that nonlinear, biased estimators and predictors of the James-Stein form can yield a considerable improvement over BLUE and BLUP in terms of MSE and absolute error in a sire model with fixed GG effects.

Weigel *et al.* (1991) simulated a balanced sire model with fixed GG and compared different biased estimators of GG effects to ML estimator (BLUE under normality) and found great improvement with modified minimum MSE (STM) that shrinks ML estimator to its average value and with estimated STM (ESTM) in terms of MSE. However, a function of these estimates (linear regression on GG number) was very poor in terms of MSE. Simianer (1991) presented empirical evidence that a nonlinear, biased estimator of fixed GG (obtained by estimated minimum MSE under a situation of low heritability, unbalanced data, and medium selection intensity) was almost twice as superior as BLUE/BLUP in terms of effective selection differential.

The superiority of non least square procedures appears especially in situations which are less favourable from an estimation point of view, such as low heritability, unbalancedness, low connectedness, and lack of independence of genetic and environmental structure (Gianola 1990; Simianer 1991) which are often found in livestock populations such as beef and dairy cattle.

**Sequential selection.** Sequential selection has been discussed in genetic evaluation of beef cattle (Eriksson *et al.* 1981; Pollak and Quaas 1981b), in dairy cattle (Henderson 1973 ; Pollak *et al.* 1984) and in pigs (Long *et al.* 1991 ; Appel *et al.* 1994). Multivariate evaluations have been used to overcome this kind of selection problem. However, in cases without any records on the culled animals, i.e. the history of selection processes is not known, the situation becomes more complicated and the magnitude of the bias will depend on the culling intensity and (co)variances of the traits (Pollak *et al.* 1984; Appel *et al.* 1994). The problems associated with parental selection still may remain for the traits under selection despite multivariate analysis. Henderson (1990) called attention that multivariate analysis are much more sensitive to errors in (co)variance parameters that are more likely to happen with selected data.

**Preferential treatment and data manipulation.** Removal of preferential treatment (Tierney and Schaeffer 1994), selective reporting (Garrick *et al.* 1989), and data manipulation effects by statistical methods seems to be less promising than attempts to control these selection problems by other means such as contract herds for progeny testing of bulls under conditions free of

preferential treatment or selective reporting, or use of representative data subsets known to be completely accurately reported (Mallinckrodt *et al.* 1993). To alert for the consequences of this sort of selection in the genetic evaluations is an important task of animal breeders.

## CONCLUSIONS

Despite all of the investigations on selection effects on estimation of genetic parameters and breeding values, no general solution was found. However parental selection should be studied and kept in mind since it is always present in animal breeding work. Other types of selection such as preferential treatment, selective reporting, and data manipulation should be minimized through clarification about how harmful they could be for the whole genetic evaluation system. Still the better way to handle this sort of selections is to avoid them as much as possible.

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